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Global patterns of stream detritivore distribution: implications for biodiversity loss in changing climates

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ABSTRACT

Aim We tested the hypothesis that shredder detritivores, a key trophic guild in stream ecosystems, are more diverse at higher latitudes, which has important ecological implications in the face of potential biodiversity losses that are expected as a result of climate change. We also explored the dependence of local shredder diversity on the regional species pool across latitudes, and examined the influence of environmental factors on shredder diversity.

Location World-wide (156 sites from 17 regions located in all inhabited continents at latitudes ranging from 67° N to 41° S).

Methods We used linear regression to examine the latitudinal variation in shredder diversity at different spatial scales: alpha (α), gamma (γ) and beta (β) diversity. We also explored the effect of γ -diversity on α -diversity across latitudes with regression analysis, and the possible influence of local environmental factors on shredder diversity with simple correlations.

Results Alpha diversity increased with latitude, while γ - and β -diversity showed no clear latitudinal pattern. Temperate sites showed a linear relationship between γ - and α -diversity; in contrast, tropical sites showed evidence of local species saturation, which may explain why the latitudinal gradient in α -diversity is not accompanied by a gradient in γ -diversity. Alpha diversity was related to several local habitat characteristics, but γ - and β -diversity were not related to any of the environmental factors measured.

Main conclusions Our results indicate that global patterns of shredder diversity are complex and depend on spatial scale. However, we can draw several conclusions that have important ecological implications. Alpha diversity is limited at tropical sites by local factors, implying a higher risk of loss of key species or the whole shredder guild (the latter implying the loss of trophic diversity). Even if regional species pools are not particularly species poor in the tropics, colonization from adjacent sites may be limited. Moreover, many shredder species belong to cool-adapted taxa that may be close to their thermal maxima in the tropics, which makes them more vulnerable to climate warming. Our results suggest that tropical streams require specific scientific attention and conservation efforts to prevent loss of shredder biodiversity and serious alteration of ecosystem processes.

Keywords

Detritus, diversity, guild, latitudinal gradient, leaf litter, shredders, species richness, stream ecosystems, trophic diversity.

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INTRODUCTION

Ecologists have long been interested in global patterns of biodiversity because they seek to explain the general increase in species richness from the poles to the tropics. Numerous explanations for this gradient have been proposed (e.g. Willig *et al.*, 2003; Mittelbach *et al.*, 2007), and it has been demonstrated that such explanations need to consider the relationship between local and regional diversity. This relationship is not necessarily linear (Caley & Schluter, 1997), as there may be a limit to the number of species that can be supported at a particular site (saturation), but different species assemblages may be found at different sites, thereby leading to higher regional diversity (e.g. Sale, 1977).

Hillebrand (2004) showed that diversity gradients are consistent across most taxa, habitats and spatial scales. However, his meta-analysis was based on species presence-absence data, which are insufficient for investigating ecological processes in which relative abundance of species play a major role (Dangles & Malmqvist, 2004). Also of great ecological significance can be the number of species within particular guilds or trophic levels (Gessner *et al.*, 2010). When species richness within a given trophic level is low, losing one or more species is likely to have particularly severe consequences at the ecosystem level (Duffy, 2009; Dudgeon & Gao, 2010). This is because the chances of different species being functionally redundant (i.e. having similar effects on ecosystem processes) are lower with low diversity, and thus the loss of key species (Mills *et al.*, 1993) is more likely. Moreover, the risk of losing an entire trophic level increases with decreasing species richness, potentially leading to a major reduction in trophic diversity (Hillebrand & Matthiessen, 2009). Reducing the number of trophic levels within an ecosystem strongly affects ecosystem functioning by constraining ecosystem processes (e.g. organic matter decomposition or primary production) and changing the magnitude and efficiency of trophic transfer (Duffy *et al.*, 2007).

Gradients of diversity within guilds or trophic levels are, however, virtually unknown. Here we explore global diversity patterns in stream shredders, a key detritivore guild in forest streams, where terrestrially derived detritus is the major energy and carbon source (Wallace *et al.*, 1997). Shredders are able to assimilate carbon and other nutrients from this dead organic matter and associated microbes, and to convert a portion of it to animal tissue; they increase the rate at which coarse detritus is transformed into fine detritus; promote food availability for collectors and filter feeders; and thus play a fundamental role in organic matter decomposition and nutrient cycling (Cummins *et al.*, 1973; Short & Maslin, 1977; Wallace *et al.*, 1982; Wallace & Webster, 1996; Graça, 2001; Hieber & Gessner, 2002). Although shredders belong to the same trophic level as other detritivores, they occupy a different position in the detritus processing chain, as they specialize in the primary processing of whole leaves rather than depending on processed, fragmented detritus (Heard, 1994).

Various local studies suggest that shredder diversity may be greater in temperate regions (see Boyero *et al.*, 2009). This

would imply that tropical streams might be more vulnerable to the loss of key species, or of the entire shredder guild to which shredders importantly contribute, with important consequences for ecosystem functioning. Furthermore, climate warming might be expected to exacerbate this effect, as most shredders belong to cool-adapted taxa and are possibly at the margin of their upper temperature tolerance in the tropics (Dillon *et al.*, 2010). Studies of shredder diversity over broad spatial scales are, however, lacking, and global studies have shown that different stream taxa can exhibit different diversity patterns at both the local and regional scales (Vinson & Hawkins, 2003; Pearson & Boyero, 2009). Strong relationships between regional and local species richness have been demonstrated in Finland (Heino *et al.*, 2003) and Australia (Marchant *et al.*, 2006), suggesting that assemblages are unsaturated and indicating the importance of large-scale processes, but not denying the possible influence of local factors (e.g. water chemistry) on the regional diversity.

We examined shredder diversity across latitudes at a global scale (156 sites from 17 regions located in all inhabited continents at latitudes ranging from 67° N to 41° S). Given the scale dependence of estimates of diversity (Gaston, 2000; Rahbek, 2005), and bearing in mind that local processes and relationships can be of great importance in determining species richness (Heino, 2009), we examined shredder species richness at both the local and regional scales (α - and γ -diversity, respectively), as well as the change in assemblage composition among sites within regions (β -diversity). We hypothesized that shredder diversity would increase with latitude, on the basis of local studies reporting low numbers of shredder species in tropical streams (Boyero *et al.*, 2009). We also explored the dependence of α -diversity on the regional species pool (i.e. γ -diversity) across latitudes, hypothesizing that the relationship would be positive, although we had no a priori expectation regarding the shape of such a relationship. Finally, given that in a global study of this type local factors might mask any general relationships, we examined the influence of local environmental factors on shredder diversity.

MATERIALS AND METHODS

Field and laboratory work

We sampled shredders and their food resources (leaf litter) at 117 sites from a total of 13 regions, in Africa (one region), Asia (three regions), Australia (one region), Central America (two regions), Europe (two regions) and South America (four regions) (Table 1, Fig. 1), using the same methodology. The surveys were conducted between 2006 and 2007, during periods when leaf litter was present in the stream, and within a short period of time in each region to minimize intra-regional seasonal effects. In each region we sampled nine sites, each located in a different headwater stream with no notable human impact. Stream width was ≤ 10 m and site length was approximately 10 times the stream width (50–100 m).

Table 1 Study regions (including acronyms), range of latitude and altitude of sites, observed and estimated (first-order jackknife estimator; Palmer, 1990) regional diversity (γ), and efficiency of sampling in estimated proportion of species collected.

Region	Acronym of region	Latitude	Altitude (m a.s.l.)	Observed γ	Estimated γ	Efficiency (%)
Main regions						
Argentina (Nahuel Huapi National Park)	ARG	40.46–41.25°S	795–1465	11	12.8	86
Brazil (Minas Gerais)	BRL	18.05–20.50°S	740–1320	3	3.0	100
Colombia (western Andean region)	COL	04.71–04.89°N	950–2560	12	12.0	100
Costa Rica (La Selva Biological Station)	CRA	10.41–10.44°N	30–100	2	2.0	100
Ecuador (montane Andean forest)	ECD	00.09–00.13°S	1167–1380	14	17.6	80
France (Montagne Noire)	FRN	43.39–43.49°N	320–1107	10	10.0	100
Hong Kong	HKN	22.28–22.44°N	70–370	8	8.9	90
India (southern Western Ghats)	IND	08.01–10.50°N	225–450	7	7.9	89
Kenya (various regions)	KEN	00.02–00.37°S	1713–2296	2	2.9	69
Malaysia (various regions)	MLY	00.03–04.42°N	55–1993	22	24.3	91
Panama (Campana and Soberanía National Parks)	PAN	08.68–09.17°N	74–666	2	2.0	100
Portugal (Lousã and Caramulo Mountains)	PTG	40.07–40.60°N	113–814	14	17.6	80
Queensland (Australian wet tropics)	QLD	17.15–19.00°S	40–880	15	17.7	85
Additional regions						
Chile (Bio Bio region)	CHL	36.88–38.00°S	18–878	3	4.6	65
Maryland (Appalachian Plateau)	MLD	39.36–39.71°N	483–842	13	14.6	89
New South Wales (Coffs Harbour Hinterland)	NSW	30.23–30.45°S	33–1560	10	14.2	70
Sweden (Norrländ)	SWD	61.17–66.90°N	25–437	18	24.2	74

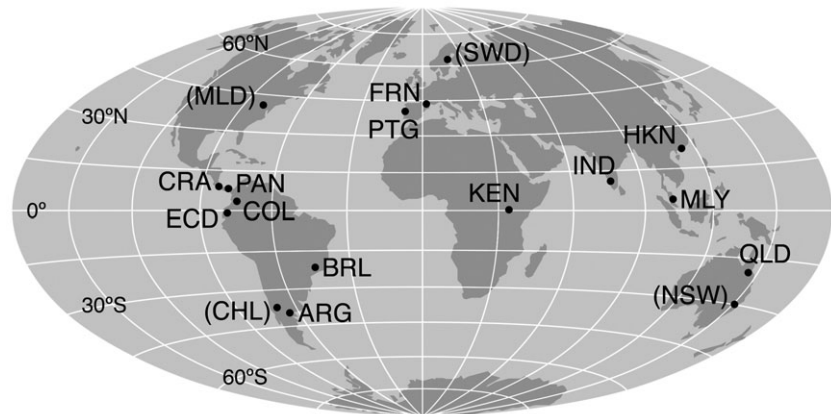


Figure 1 Location of study regions (acronyms in Table 1). Additional temperate regions are indicated in parentheses (see text and Table 1 for details).

At each site, we generally took 10 leaf litter samples, half from pools and half from riffles, from within areas of 20×20 cm in a litter layer of no more than 4 cm, using a net with a 0.5-mm mesh, and transferred them to labelled Ziplock plastic bags. Samples were kept cool and rapidly transported to the laboratory, where they were rinsed and carefully inspected. All macroinvertebrates retained on a 250- μ m screen were removed and preserved in 70% ethanol. The number of plant species in leaf litter samples was estimated by visually distinguishing morphospecies (local botanists were consulted when necessary), and leaf litter was then dried to constant weight (60–80 °C for at least 48 h) and weighed. Invertebrates were separated into morphospecies (identified to species when possible), counted and classified as shredders or non-shredders based on gut content analysis following Cheshire

et al. (2005). We assumed that congeneric species found in different regions belonged to different species.

At each site, we recorded the latitude (degrees from the equator) and altitude (m a.s.l.) with a GPS. When possible, we measured water temperature (°C), conductivity (μ S cm^{-1}), dissolved oxygen saturation (%), pH, alkalinity (mg $\text{CaCO}_3 \text{ l}^{-1}$), total nitrogen (mg l^{-1}), total phosphorus (mg l^{-1}), wetted stream width (mean derived from six cross sections) and water depth (cm; measured every 0.5 m across the cross sections). We also visually estimated the percentage of substrate covered by leaf litter, the percentage of pool habitat, the percentage of canopy cover and the number of riparian tree species. Finally, we used 1:50,000 maps to estimate catchment area (km^2) and the percentage of native forest in the catchments.

Because of the relatively small number of high-latitude sites surveyed, we compiled four additional data sets from temperate regions, to check for consistency with the patterns observed in our survey. Two of these regions conformed to the present global study (sampling methods described above) but were not included in the main data set because of the small number of sites surveyed: Chile (five sites) and New South Wales (Australia; six sites). Data from Maryland (USA) were taken from nine sites randomly selected from 84 described by Swan *et al.* (2009) and data from Sweden were taken from nine sites randomly selected from 23 described by Jonsson *et al.* (2001).

Statistical analyses

We evaluated shredder diversity as the number of species at each site (α), the total number of species in each region (γ) and the change in assemblage composition among sites within regions ($\beta = \gamma/\alpha_m$, α_m being the mean α for each region; Baselga, 2010). Gamma diversity was estimated using jackknife resampling procedures [first-order jackknife estimator = $\gamma_o + \alpha_m(n-1)/n$, where γ_o is the observed number of species in each region and n is the number of sites sampled in each region; Palmer, 1990] in the PC-ORD package (McCune & Mefford, 2006), to be used in further analysis and to assess the efficiency of our survey.

Variation in shredder diversity (α -, γ - and β -diversity) with latitude was explored by linear regression. As altitude was variable among regions, we removed its effect by using the residuals of the regression altitude versus latitude in the analyses, rather than latitude itself. We also examined the relationship between γ - and α -diversity by linear regression. The mean α for each region (α_m) was used in this analysis to avoid pseudoreplication (Soininen *et al.*, 2009). We examined the data for curvilinearity or a decreasing slope by including a quadratic term in the regression, as an indication of α_m approaching some limit that would suggest species saturation (see Shurin *et al.*, 2000). Akaike's information criterion (AIC) was used to select the model that best fitted the data; it was calculated using the formula $AIC = n \times \ln(RSS/n) + 2K$, where n is sample size, RSS is the residual sum of squares and K is the number of parameters in the model. We sought differences in species saturation between temperate and tropical zones (defined here as $> 23^\circ$ N or S and $\leq 23^\circ$ N or S, respectively) by exploring this relationship separately for the two zones, including the four additional temperate regions (see Field and laboratory work and Table 1). We used the AIC to assess whether the data better conformed to a linear or a quadratic relationship in each case.

Correlation analysis was used to explore the relationship between environmental factors and shredder diversity, as several gaps in the environmental data set precluded multiple regression analysis. Relationships with α -diversity were explored at the site scale (the range of n was 54 to 112, depending on availability of environmental factors), while relationships with γ - and β -diversity were explored at the region scale (range of n was 6 to 13).

RESULTS

We found a total of 122 shredder morphospecies in the 13 main regions, with 0–10 species per site ($\alpha = 4.61 \pm 0.26$ SE) and 2–22 species per region ($\gamma = 9.38 \pm 1.71$ SE). The four additional temperate regions had 44 morphospecies in total, with 0–9 species per site ($\alpha = 4.66 \pm 0.49$ SE) and 3–18 species per region ($\gamma = 11.00 \pm 3.14$ SE). Jackknife estimates suggested that we recorded on average 90% ($\pm 3\%$ SE) of the species present in each region at the time of sampling, or 86% ($\pm 3\%$ SE) when additional sites were included (Table 1).

Linear regression showed that α -diversity increased with latitude ($\alpha = 4.6 + 0.091 \times \text{latitude}$; $r^2 = 0.22$, $P < 0.0001$; Fig. 2a). When the four additional temperate sites were included in the analysis, the relationship was similar ($\alpha = 4.8 + 0.072 \times \text{latitude}$; $r^2 = 0.22$, $P < 0.0001$). Gamma diversity showed no latitudinal pattern ($\gamma = 9.5 + 0.029 \times \text{latitude}$; $r^2 < 0.01$, $P = 0.83$; Fig. 2b), with a similar outcome when the four additional temperate sites were included ($\gamma = 11.5 + 0.127 \times \text{latitude}$; $r^2 = 0.09$, $P = 0.23$). The relationship between β -diversity and latitude was not significant ($\beta = 2.4 - 0.032 \times \text{latitude}$; $r^2 = 0.16$, $P = 0.17$; Fig. 2c); variability of β -diversity was higher at lower latitudes, but this apparent pattern disappeared when the four additional temperate sites were included in the analysis ($\beta = 2.8 - 0.0005 \times \text{latitude}$; $r^2 < 0.01$, $P = 0.98$).

Gamma and α -diversity were directly related [linear relationship: $\alpha_m = 1.81 + 0.28 \times \gamma$; quadratic relationship: $\alpha_m = 2.66 + 0.35 \times \gamma - 0.34 \times (\gamma - 10.7)^2$]. Both relationships were significant (linear: $P = 0.007$; quadratic: $P = 0.0001$), but the quadratic model explained more of the total variance (linear: 54%; quadratic: 89%) and had a smaller AIC (linear: 20.9; quadratic: 10.3). When analysed separately, tropical and temperate zones showed distinct tendencies. For temperate regions, the quadratic model explained slightly more of the variance (linear: 58%; quadratic: 69%), but the linear model had a slightly smaller AIC (linear: 12.5; quadratic: 14.6) (Fig. 3a). For tropical regions, the quadratic model explained more variance (linear: 54%; quadratic: 87%) and had a smaller AIC (linear: 15.2; quadratic: 7.9) (Fig. 3b).

Several local habitat variables were correlated with α -diversity: water temperature ($r = -0.53$, $P < 0.0001$), water depth ($r = -0.45$, $P < 0.0001$), stream width ($r = -0.33$, $P = 0.0003$) and percentage of substrate covered by leaf litter ($r = -0.27$, $P = 0.034$). Gamma and β -diversity showed no relationship with any of the environmental variables.

DISCUSSION

Our results suggest that global patterns of shredder diversity are complex and depend on spatial scale, as demonstrated for other organisms (Rahbek, 2005). However, we can draw several conclusions that have important ecological implications. Firstly, we have shown that the number of shredder species present at a given site (α -diversity) increases with latitude, confirming previous suggestions (Boyero *et al.*, 2009). This implies that tropical streams have a higher risk of losing key species or the whole

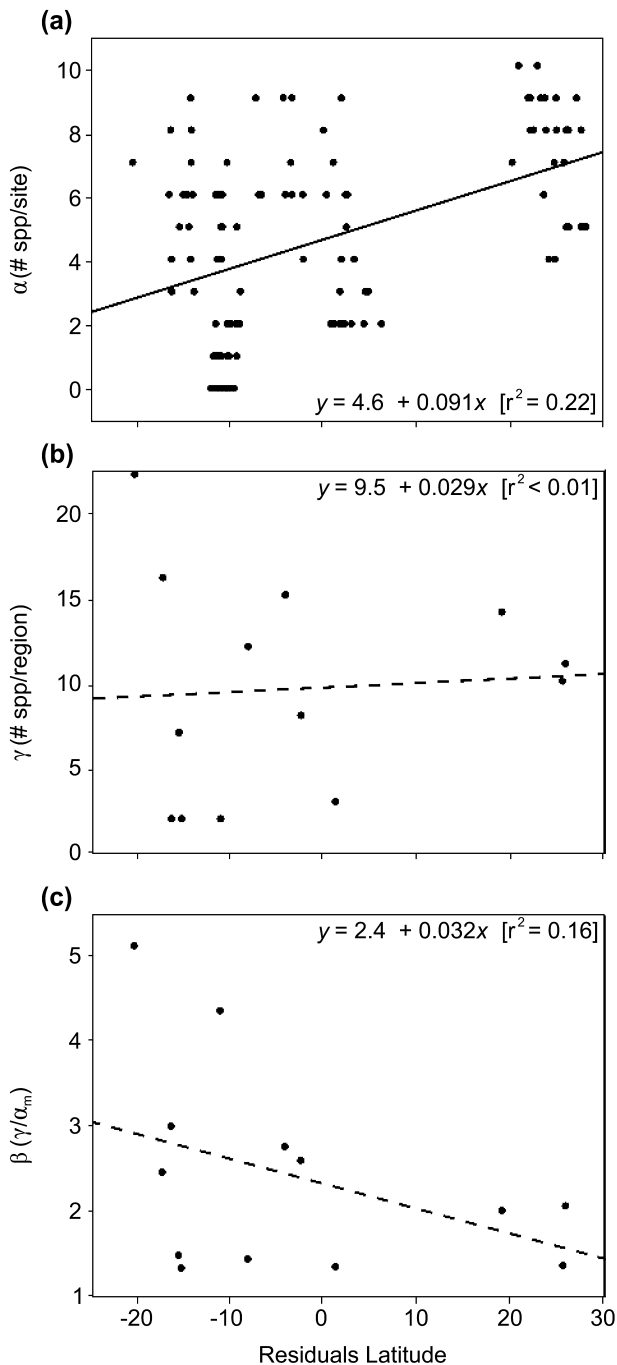


Figure 2 Linear regressions showing latitudinal variation in (a) alpha (b) gamma and (c) beta diversity ($\beta = \gamma/\alpha_m$, α_m being the mean α -diversity for each region) of shredders. To normalize for altitudinal effects, the residuals of the regression altitude versus latitude were used as predictor variable instead of latitude. Dashed regression lines: $P > 0.05$.

shredder guild, which may have serious consequences for stream ecosystem functioning, including slowed leaf litter decomposition (Jonsson & Malmqvist, 2000; Boyero *et al.*, 2007, 2011; Dudgeon & Gao, 2010), poor trophic transfer from the main basal resource (leaf litter) to higher trophic levels (Duffy

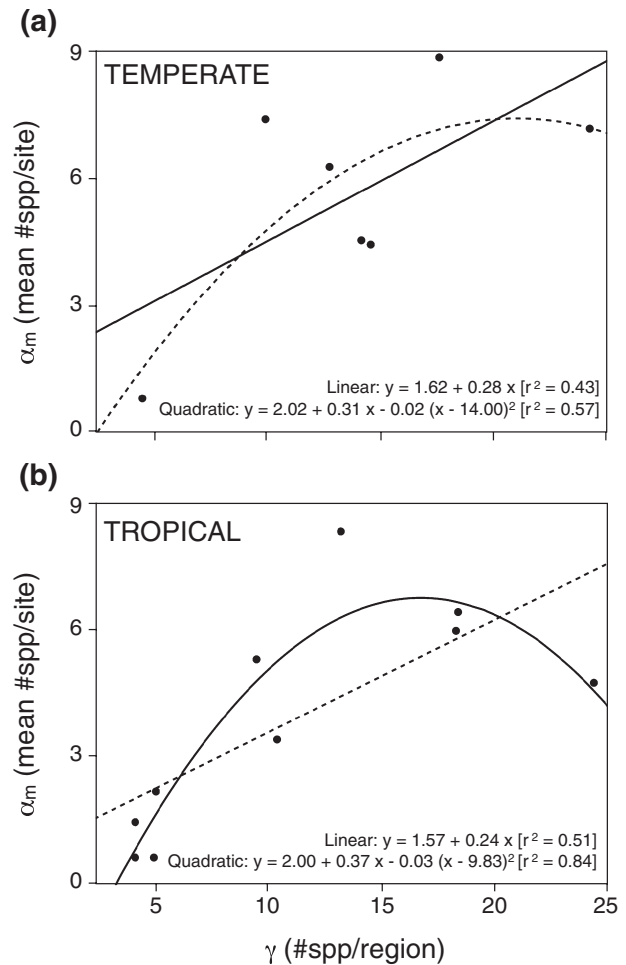


Figure 3 Linear and quadratic models exploring the relationship between regional diversity and the mean alpha diversity for each region in (a) temperate and (b) tropical regions. Because of the lower number of temperate than tropical regions surveyed, four additional temperate regions [Chile, New South Wales (Australia), Maryland (USA) and Sweden] are included in (a) (see text for details). For temperate regions, the quadratic model explained slightly more of the variance, but the linear model had a slightly smaller AIC (linear: 12.5; quadratic: 14.6). For tropical regions, quadratic model explained more variance and had a smaller AIC (linear: 15.2; quadratic: 7.9).

et al., 2007) or disruption of the processing chain (*sensu* Heard, 1994).

Secondly, we found that the relation between regional and local diversity differed for temperate and tropical regions. For the tropical assemblages only, we found an upper limit to α -diversity, regardless of γ -diversity. This indicates species saturation, which could explain why the latitudinal gradient in α -diversity that we observed was not accompanied by a gradient in γ -diversity. Shredder α -diversity seems to be limited at tropical sites by local factors such as environmental constraints or competitive species interactions (Caley & Schluter, 1997; Heino, 2009). Alpha diversity correlated with several local habitat variables (water depth, channel width, water temperature) that

relate to position in river networks and reflect the expected distributional pattern, with shredders being most prevalent in small streams (Vannote *et al.*, 1980). High temperatures might limit the presence of certain shredder taxa at tropical lowland sites (Camacho *et al.*, 2009; Yule *et al.*, 2009) because many of them have evolved in cool waters (Fochetti & Tierno de Figueroa, 2008; de Moor & Ivanov, 2008). However, the lack of a clear relationship between shredder diversity and most environmental factors is likely to reflect the importance of multiple factors operating simultaneously at local scales and that are difficult to pinpoint given the broad spatial extent of the present study.

A potential local limiting factor of α -diversity at tropical sites is the existence of strong competitive interactions. This is possible, for example, if resources are limited in terms of the amount, quality and timing of leaf litter inputs. Even though seasonality exists in the tropics, the temporal pattern of leaf fall is much more even than in the temperate zone, lacking the highly pulsed and temporally predictable inputs typical of temperate streams (Cummins, 1974). As a result, leaf litter tends to be more abundant in temperate streams at a particular time of the year, and thus may allow a greater number of shredder species to coexist. Moreover, the leaves of many tropical plants contain high levels of deterrents (Coley & Barone, 1996; Coq *et al.*, 2010; Graça & Cressa, 2010), so palatable leaves are often a scarce resource, notwithstanding that some tropical trees produce high-quality leaves as well (Graça *et al.*, 2001). Thus, tropical streams tend to have less leaf litter of good quality available at any particular time than temperate streams, exacerbating competitive interactions among shredder species (Bastian *et al.*, 2008). Different shredder species show preferences for leaves of the same plant species (Graça *et al.*, 2001; Bastian *et al.*, 2007), and competition is an important mechanism regulating the consumption of leaf litter by shredders (Bastian *et al.*, 2008). Competitively dominant species feed on the preferred leaves, while other species are forced to feed on other, less palatable, leaves, which may affect their growth and reproductive success (Bastian *et al.*, 2008; Gessner *et al.*, 2010). Competition for a scarce resource could then limit the number of shredder species coexisting at tropical sites.

Another potential explanation for the curvilinear relationship between regional and local species richness in the tropics is limitation for dispersal among sites. This could be due to the existence of more effective geographical barriers (which is unlikely) or to a lower dispersal ability of tropical shredders. Most temperate shredders are larvae of insect taxa (e.g. caddisflies, stoneflies) with flying adult stages. Although the dispersal ability of adult caddisflies and stoneflies is often limited (Kovats *et al.*, 1996; Griffith *et al.*, 1998), it is higher than that of other shredder taxa such as crustaceans and molluscs, which lack flying stages altogether. The latter taxa are better represented in the tropics, where they comprised 15% of all shredder species collected in our survey, compared with only 6% in temperate regions. Consequently, although the effect is unlikely to be large, dispersal limitation might have contributed to the greater regional saturation tendency we observed for shredders in the tropics.

Our global-scale study indicates that loss of shredder species might be more critical at tropical sites, where fewer shredder species are present and the loss of key species or the whole shredder guild is therefore more likely. The lack of a latitudinal trend in γ -diversity that we observed suggests that, counter to common perceptions, diversity of regional shredder species pools is similar across latitudes. Local extinctions of shredder taxa, for example in response to climate warming, might therefore be compensated by colonization of other species from regional species pools that were not locally present before. This would be more likely if the colonizers were previously absent because they were competitively inferior to the species that went locally extinct. However, limited dispersal ability of shredders lacking an adult flying stage, including some taxa typical of tropical streams, suggests that colonization from adjacent sites following local extinctions may not be the norm. Furthermore, many shredder taxa belong to mostly cool-adapted taxa, and may be close to their thermal maxima in the tropics, where predicted extinctions from climate warming may have disproportionately greater effects (Dillon *et al.*, 2010). Given their limited local diversity, tropical shredder assemblages would thus merit special scientific attention and conservation effort, to determine or create refugia to prevent species losses and consequent alteration of stream ecosystem functioning.

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