Decreasing Stoichiometric Resource Quality Drives Compensatory Feeding across Trophic Levels in Tropical Litter Invertebrate Communities

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ABSTRACT: Living organisms are constrained by both resource quantity and quality. Ecological stoichiometry offers important insights into how the elemental composition of resources affects their consumers. If resource quality decreases, consumers can respond by shifting their body stoichiometry, avoiding low-quality resources, or up-regulating feeding rates to maintain the supply of required elements while excreting excess carbon (i.e., compensatory feeding). We analyzed multitrophic consumer body stoichiometry, biomass, and feeding rates along a resource-quality gradient in the litter of tropical forest and rubber and oil-palm plantations. Specifically, we calculated macroinvertebrate feeding rates based on consumer metabolic demand and assimilation efficiency. Using linear mixed effects models, we assessed resource-quality effects on macroinvertebrate detritivore and predator communities. We did not detect shifts in consumer body stoichiometry or decreases in consumer biomass in response to declining resource quality, as indicated by increasing carbon-to-nitrogen ratios. However, across trophic levels, we found a strong indication of decreasing resource quality leading to increased consumer feeding rates through altered assimilation efficiency and community body size structure. Our study reveals the influence of resource quality on multitrophic consumer feeding rates and suggests compensatory feeding to be more common across consumer trophic levels than was formerly known.

Keywords: resource quality depletion, ecological stoichiometry, consumer feeding rates, consumer resource interaction, multitrophic communities.

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Introduction

All living organisms are subject to the persistent struggle of finding and exploiting the resources that they depend on. Traditionally, ecological research has concentrated on available resource quantity in terms of biomass or abundance. Over recent decades, however, the concept of ecological stoichiometry (Elser et al. 2000) has shifted our focus to resource and consumer elemental composition. In this context, we study how animals—from individuals to communities—respond to differing resource quality.

The biomass of living organisms consists of a number of different chemical elements occurring in more or less strict proportions (Redfield 1958; Sterner and Elser 2002; McGroddy et al. 2004). In ecological stoichiometry, special attention has been paid to carbon (C), nitrogen (N), and phosphorus (P) as central elements of animal development, activity, and growth (Fanin et al. 2013), with a focus on carbon-to-element ratios and their impacts on individuals, populations, and communities (Sterner and Elser 2002; Hillebrand et al. 2014; Ott et al. 2014*b*). To fulfil their energetic demands, consumers depend on both resource quantity and quality (i.e., resource stoichiometry; Urabe and Sterner 1996; Sterner 1997; Frost et al. 2005; Persson et al. 2010; Ott et al. 2012). However, depending on the trophic positioning of consumers and their resources, there can be a considerable gap between the stoi-

chiometry of their resources and consumer body tissue (Elser et al. 2000), also referred to as stoichiometric mismatch (Hillebrand et al. 2009). Compared to the imbalance between consumers at higher trophic levels and their heterotrophic prey (Fagan et al. 2002), this mismatch seems to be more pronounced between primary consumers and their autotrophic resources, and even more so for detritivores than herbivores (Elser et al. 2000; McGroddy et al. 2004). Moreover, heterotroph body stoichiometry is more constrained than that of their autotrophic resources (Sterner and Elser 2002; Frost et al. 2005; Hillebrand et al. 2014; but see Persson et al. 2010; McFeeters and Frost 2011). Therefore, heterotrophs—especially those feeding on autotrophic resources—need strategies to deal with differing resource nutritional quality.

Generally, the possibilities are limited for consumers facing differing resource quality. Specifically, we propose that these options comprise three main strategies (fig. 1): consumers may either vary in their degree of homeostasis and possibly shift their mean body stoichiometry (Persson et al. 2010) to account for low-quality resources (H1), avoid habitats with low-quality resources (H2; Sterner and Elser 2002; Hillebrand et al. 2009), or alter their consumption rates (H3; i.e., exhibit compensatory feeding; Cruz-Rivera and Hay 2000; Hillebrand et al. 2009; Ott et al. 2012).

Some species have evolved higher carbon-to-nutrient ratios in their body tissue than others (Fagan et al. 2002), and some organisms can regulate their body stoichiometry to a certain degree (Persson et al. 2010; McFeeters and Frost 2011). Shifted relative abundance toward organisms with higher natural carbon-to-nutrient ratios or toward those capable of shifting their body stoichiometry in response to low-quality resources could enable consumer feeding rates and community biomass to remain constant (fig. 1, H1). However, due to strong stoichiometric constraints for heterotrophs (Sterner

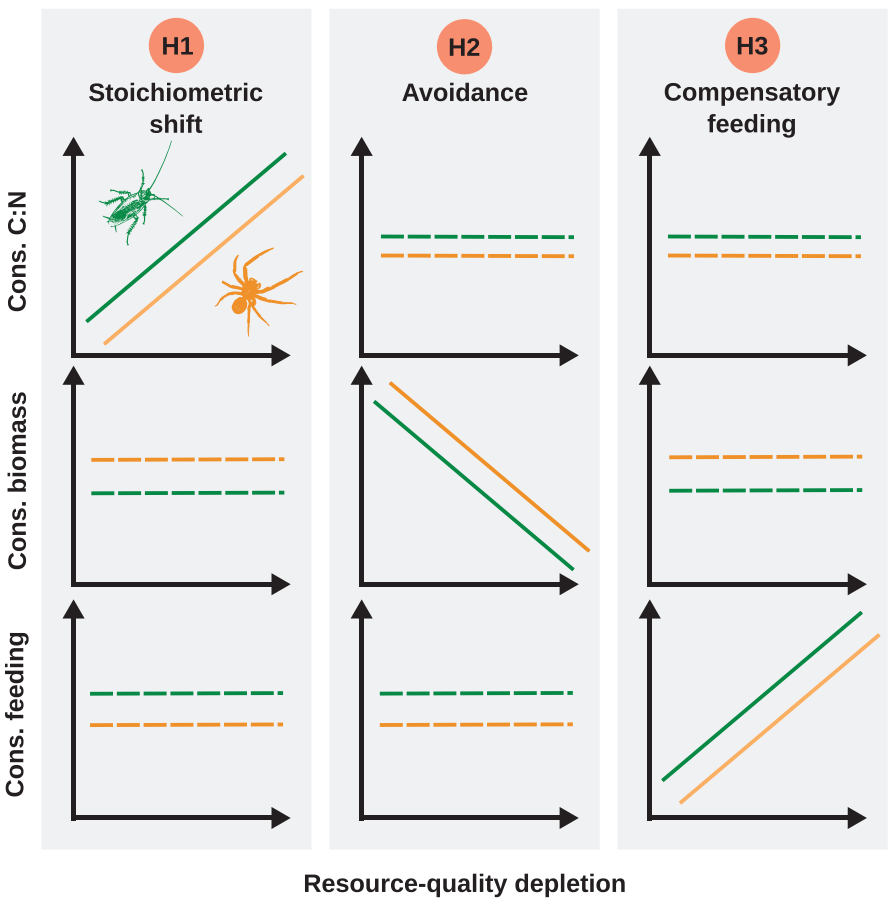

Figure 1: Hypotheses of consumer responses to differing resource quality: In response to resource-quality depletion, heterotrophic consumers (cons.) may shift their own body stoichiometry (e.g., C:N; H1, *left*), show an avoidance reaction (H2, *center*), or exhibit compensatory feeding (H3, *right*). In consequence, consumer body stoichiometry, biomass, and per-unit-biomass feeding rate are expected to show specific patterns as indicated for detritivores (green) and predators (orange) in the three columns. Solid diagonal lines show expected responses to resource-quality depletion and their direction; dashed horizontal lines show expected null responses for the three hypotheses.

and Elser 2002; Hillebrand et al. 2014), only few species are likely to have evolved very high carbon-to-nutrient ratios or sizeable stoichiometric phenotypic plasticity (Persson et al. 2010).

Low nutrient availability or resource quality can also cause reduced feeding rates and invoke an avoidance response by the consumer community (Frost and Elser 2002; Hillebrand et al. 2009; Ott et al. 2012). If not all consumers present can deal with high carbon-to-element ratios, fewer individuals would be able to persist in the given locale, leading to decreased consumer biomass (fig. 1, H2). This would occur as a result of the consumer community shifting toward individuals that can deal with low-quality resources. As such, the number of persisting species would be reduced, subsequently also reducing total community biomass (Borer et al. 2012). However, the remaining consumer community could maintain the same consumption rates because of their adaptations to low-quality resources.

Some species can significantly increase their consumption rate when exposed to a low-quality diet, a mechanism referred to as compensatory feeding (Cruz-Rivera and Hay 2000). They increase uptake of rare elements and, at the same time, release excess elements through a variety of mechanisms (Frost et al. 2005), depending on their ability to process excess elements resulting from increased ingestion (Anderson et al. 2005). If consumers exhibit this behavior (Cruz-Rivera and Hay 2000; Ott et al. 2012), the consumer feeding rate increases substantially with reduced resource quality (fig. 1, H3), resulting in a lowered trophic efficiency (Hillebrand et al. 2009). Given a shift in community composition toward consumers capable of satisfying their energetic demands through compensatory feeding, consumer stoichiometry and biomass would not necessarily respond to resource-quality depletion, but consumer feeding per unit biomass would increase (fig. 1, H3). Interestingly, however, the consequences of a shifting community composition additionally depend on simultaneous changes in community body size structure, which could easily affect consumer community stoichiometry, biomass, and metabolism (Ehnes et al. 2014), with subsequent effects on feeding-rate estimates. It should be noted that the three described response strategies are not mutually exclusive and may act asynchronously at different levels of organization (individual, population, community).

Empirical evidence for population-level, and especially multitrophic community-level consequences of differing resource quality, is scarce because most studies on stoichiometric imbalances between consumers and their resources have focused on the individual level (Moe et al. 2005; but see Fagan and Denno 2004). Moreover, research on terrestrial systems, and especially detritus-based systems, has traditionally been underrepresented (Sterner and Elser 2002), although their resource C∶N ratios tend to deviate strongly from those of their heterotrophic consumers (Elser et al. 2000). In recent years, this gap has been reduced by studies on the structure of soil and litter food webs (Brose and Scheu 2014; Klarner et al. 2014) and the effects of basal resource stoichiometry on consumer biomass densities (Ott et al. 2014*a*). Nevertheless, a broader perspective of resource-quality effects on various consumer community aspects across trophic levels is still lacking.

In this study, we set out to test the three predictions of community-level consequences of differing resource quality along terrestrial resource-quality gradients in tropical litter communities (fig. 1). We combined measurements of C and N concentrations of local leaf litter and the macroinvertebrate community with biomass and calculated feeding rates of multitrophic macroinvertebrate consumer communities facing variable resource quality. Our study undertook a community-level approach to terrestrial resource stoichiometry in real-world ecosystems that presented a gradient of resource quality. This approach investigates consumer responses at the community level, which is a cumulative phenomenon made up of individual-, population-, and community-level processes. In contrast to a laboratory or field experiment, where resource quality can easily be manipulated but the design is heavily constrained by the complexity of the biotic community, we do not describe how communities respond to changing resource quality but how the responses of populations and individuals over multiple generations have brought about differences among communities. As such, this approach enables us to assess differences between consumer communities facing different-quality resources, whereas we do not attempt to assess responses of consumer individuals or populations to changing resource quality over time. Specifically, across trophic levels, we looked for the role of H1 (stoichiometric shift) by calculating and testing shifts in community-level consumer stoichiometry. Subsequently, the importance of H2 (avoidance) was assessed by testing for shifts in community-level consumer biomass. Finally, if these two hypotheses were not supported by the data, we assumed the most likely alternative response would have to be a community-level change in consumer feeding rates (H3, compensatory feeding) to account for the lack of key nutrients in their resources. Thus, we calculated consumer feeding rates per unit biomass based on individual body size, metabolic rate, and resource-dependent assimilation efficiency to assess whether compensatory feeding could be a likely alternative response mechanism of consumer communities facing reduced resource quality. While these feeding rates are a modeled response based on parameters measured directly from these communities, they provide a strong indication of whether such a response is likely across different trophic levels of real-world consumer communities. For the first time, by taking into account community-level processes, we demonstrate that differing resource quality causes consistent responses across trophic groups.

Material and Methods

Study Site and Sampling Design

In the tropical lowland of the Jambi province, Sumatra, Indonesia, sampling took place in primary degraded rain forest (Margono et al. 2012), jungle rubber, rubber, and oil-palm systems, replicated four times in each of two landscapes ($n = 32$; Barnes et al. 2014). The four land-use systems differ strongly in tree biomass and productivity (Kotowska et al. 2015) and are dominated by very different vegetation, suggesting that their leaf litter, as the basal resource of the decomposer communities, provides a strong gradient of resource quality.

Animal and Leaf-Litter Sampling

Animal and leaf-litter sampling was conducted between early October and early November 2012, as described in Barnes et al. (2014). On three 5 × 5-m subplots of every 50 × 50-m site, we sieved the leaf-litter layer from 1 m^2. All animals visible to the naked eye were collected and stored in ethanol. We sampled 7,472 macroinvertebrates from the leaf litter of the 32 sites and identified them to morphospecies (see tables A1, A2, for sampled taxa and further information on the identification process; tables A1–A8 available online). Furthermore, we measured individual body length to an accuracy of 0.1 mm and assigned all animals to one of four trophic guilds—predators, omnivores, detritivores, or herbivores—based on morphology and literature (tables A1, A2). Individual body masses were calculated using literature-based length-mass regressions (Barnes et al. 2014). We treated leaf litter as the main resource for detritivores, keeping in mind that certain detritivores will exploit dead animal material or other alternative food sources. To assess local quality of the leaf-litter resources, we sampled leaves of the dominant leaf types per site (table A3) from the subplots where animals were sampled. Additionally, to control for effects of habitat structure and detritivore resource quantity, we measured dry litter mass (g cm^{-2}) on each of these subplots of the 32 sites. On an area of 16 × 16 cm, the litter layer was removed and weighed after drying and removal of inorganic matter and coarse woody debris.

Stoichiometric Analyses of Animal and Leaf-Litter Samples

While P concentration differs markedly between autotrophic and heterotrophic organisms (Fanin et al. 2013), it does not show considerable changes between insect consumers of different trophic levels (Woods et al. 2004; Martinson et al. 2008). In order to assess multitrophic responses to differing resource stoichiometry, we therefore focused on C : N ratios, since N concentration differs both between autotrophs and heterotrophs (Fanin et al. 2013) and between consumers of different trophic levels (Fagan et al. 2002). Especially for the leaf litter, resource-quality traits other than C : N, such as lignin or cellulose content, have been shown to affect decomposition rates (Anderson et al. 2004; Hättenschwiler and Jørgensen 2010). However, to a certain degree, C : N accounts for such structural C compounds (Ott et al. 2014*a*). To describe resource quality across autotrophic and heterotrophic resources, we therefore chose C : N ratios, keeping in mind that there are additional factors that affect resource quality for consumers.

To assess macroinvertebrate body stoichiometry, we chose the largest, the smallest, and at least one intermediately sized animal from each of the four trophic guilds per site and measured C and N concentrations as mass percentage of their dry body tissue (table A4) using an elemental analyzer/mass spectrometer setup (Langel and Dyckmans 2014). From these data, we calculated the average mass C : N ratio of the four feeding guilds per site. As ethanol hydrolyses lipids (Sarakinos et al. 2002), our preservation method may have altered animal body C : N, dependent on the lipid content of the specimens, which varies among arthropod taxonomic groups as well as within groups due to, for example, larval nutrition (Lease and Wolf 2011). However, this effect is rather advantageous for investigating consumer responses to N limitation as it reduces the impact of short-term changes in animal body C : N (e.g., due to starvation), therefore strengthening the focus on C : N ratios of structural body compartments (e.g., the exoskeleton of arthropods) and essential tissue components (e.g., muscles). Furthermore, such variation in lipid content mostly affects C rather than N content, meaning this treatment should be rather unimportant for consumers limited by resource N content. Generally, the dissolving of lipids due to preservation in ethanol would result in reduced variation in animal body C : N (generally lower C : N ratios because lipids contain far more C than N compared to nonlipid animal body tissue; Sterner and Elser 2002), and given the focus on consumer N limitation and N being much less affected by lipid reduction, this should provide reliable estimates of resource C : N effects based on essential body compartments.

Similar to the stoichiometric analysis of the animals, C and N concentrations as mass percentage of dried leaf material were individually measured for each leaf type (table A3), and subsequently the mass C : N ratio was calculated. Stoichiometric ratios for leaf types were weighted according to their relative importance in the local litter (Kotowska et al. 2015; table A5). For the leaf litter, we additionally analyzed P concentration in order to test our hypotheses using C : P ratios. However, we did not have sufficient animal material to analyze P concentration of the animal tissue and therefore only tested a subset of the hypotheses (those on biomass and feeding rate of detritivores) with these data (fig. A1; figs. A1–A3 available online).

Calculation of Community Response Variables

From the animal data set, we used individual body mass (M, in mg) and the local soil temperature (T, in K; table A6) together with phylogeny-specific parameters from a recent study (Ehnes et al. 2011) to calculate metabolic rates (I, in J h^{-1}) for each individual animal as

$$\ln I = \ln i_{0PG} + a_{PG} \ln M - E_{PG}\left(\frac{1}{kT}\right),$$

where i_{0PG}, a_{PG}, and E_{PG} are the phylogenetic-group-specific intercept, allometric exponent, and activation energy, respectively, and k is Boltzmann's constant. Subsequently, we calculated community biomass (mg fresh mass m^{-2}) and metabolism (W m^{-2}) for each trophic guild (predators, omnivores, detritivores, and herbivores) independently, summing up the body masses and metabolic rates of the individual animals from 1 m^2 (Barnes et al. 2014). A summary of the calculated community response variables is deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.n5h64 (Jochum et al. 2017).

Feeding rates of detritivore and predator communities were calculated using their guild metabolism, X, and assimilation efficiency, e_a. Assimilation efficiency defines the proportion of food uptake that is used for respiration and growth instead of being lost through excretion. This proportion has been shown to increase with the N concentration of the food resource for different consumer taxa (Pandian and Marian 1985, 1986). To obtain more accurate quantitative relationships for our arthropod consumers, we complemented literature data on insects (Pandian and Marian 1986) with further arthropod assimilation efficiency data and food N data based on a broad literature survey (table A7). Using this data set, we analyzed the underlying relationship between food N content and assimilation efficiency (fig. 2; box A1; boxes A1–A4 available online). As assimilation efficiency is bound between 0 and 1, it was logit transformed to obtain a sigmoidal relationship. The resulting regression was then used to calculate site-specific assimilation efficiencies for detritivores and predators in response to the site-specific N concentration of their resources (fig. A2).

Subsequently, we calculated per-unit-biomass consumer feeding, F_C, of detritivores and predators independently as

$$F_C = \frac{X}{e_a \times B_C},$$

where X is the metabolism, e_a is the assimilation efficiency, and B_C is the biomass of the consumer guild, with each of these parameters being site specific. This calculation of consumer feeding does not involve energetic losses to higher trophic levels (Barnes et al. 2014) but specifically aims to as-

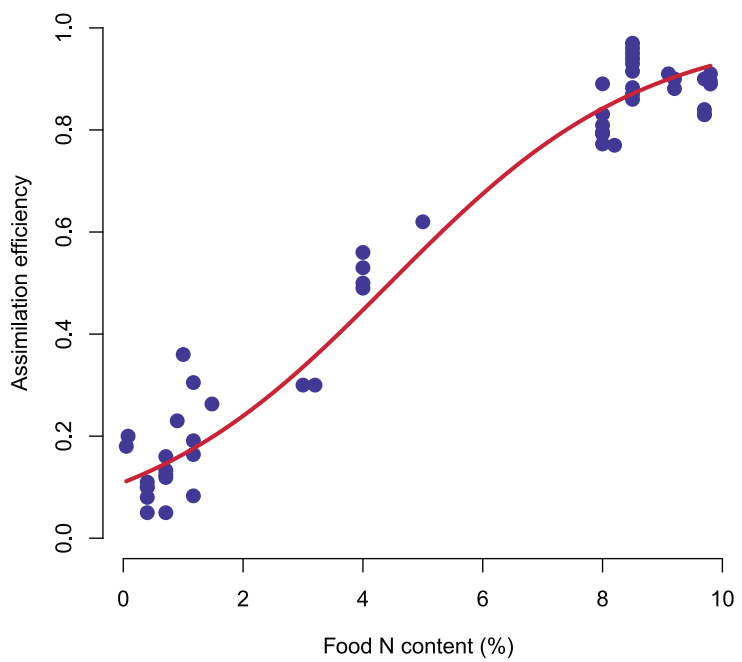

Figure 2: Relationship of food nitrogen (N) content and assimilation efficiency for the literature data (blue circles; see table A7). The red line represents the linear model for logit-transformed assimilation efficiency against food nitrogen content (model formula: logit $e_a = 0.471 \times$ food N $- 2.097$, adjusted $R^2 = 0.903$). Assimilation efficiencies are presented as a proportion between 0 and 1. For detailed regression parameters, see box A1.

sess the per-unit-biomass feeding rate that the consumers would need to fulfil their energetic demands. For the predators, we accounted for the effect of other prey resources by weighting the N concentrations of locally present prey guilds (omnivores, detritivores, and herbivores) by their relative abundance among potential prey organisms per site (table A8) to calculate the assimilation efficiency. Finally, we weighted the resulting predator feeding by the relative abundance of detritivores to present only patterns generated from their feeding on the focal prey guild.

Statistical Analyses

Using R, version 3.2.3 (R Core Team 2015), we applied linear mixed effects models (nlme package; Pinheiro et al. 2014) to test our hypotheses. We tested for an effect of litter C : N on detritivore C : N (H1), biomass (H2), and feeding rate (H3), as well as detritivore C : N on predator C : N (H1), biomass (H2), and feeding rate (H3). In order to test for these effects, we applied a model selection procedure (box A2) additionally controlling for potential effects of habitat structure (litter mass) and resource availability (litter mass for detritivores and detritivore biomass for predators). Biomass, litter mass, and feeding rate were $\log_{10}$ transformed to meet the assumptions of normality. Prior to analysis, all variables were furthermore normalized to $x_n = (x - x_{min})/(x_{max} - x_{min})$, where x_n is the normalized value, x is the untransformed value, and max and min values are the largest and smallest variable values, respectively. Normalization was necessary to achieve model convergence. We used data from a large-scale research project originally designed to investigate land-use effects across four different land-use systems within two different landscapes on Sumatra, Indonesia. Therefore, in order to account for the hierarchical structure of the study design and possible differences between landscapes and land-use systems but investigate the effects of resource quality across these different land-use systems and landscapes, we nested land-use system within landscape as a random effect in each model. Additionally, to test whether there may be any confounding effects of the underlying land-use gradient on resource-quality effects, we repeated the analyses using land-use system as a covariable instead of as a random effect (box A3). These additional analyses showed that if land-use system is included as a covariable, the effects of resource quality remained unchanged compared to the models without land-use system as a main effect, indicating that it is highly unlikely that the land-use gradient might confound our results. To make sure that potential increases in consumer feeding rates with decreasing resource quality are not just an artifact of the literature-based increase of assimilation efficiency with increasing food N concentration (fig. 2), we performed a sensitivity analysis (box A4). This analysis was set up to test if the increase in assimilation efficiency with food N alone is sufficient to drive higher consumer feeding rates when all other consumer community parameters (metabolic rate, biomass, relative abundance, and litter mass) are random.

Results

We analyzed C and N concentrations of 250 animals from 185 species of predators (136 individuals, 106 species) and detritivores (114 individuals, 79 species), as well as 169 leaf-litter specimens (see tables A3, A4 for numbers and site-averaged C and N content of stoichiometrically analyzed leaf and animal specimens per site). The C and N measurements of single animal individuals and leaf-litter specimens are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.n5h64 (Jochum et al. 2017). Site-averaged consumer dry mass C : N ratios ranged from 3.7 to 5.8, with an average of 4.1 for predators and 4.8 for detritivores, while litter dry mass C : N ratios ranged from 22.1 to 54.5, with an average of 36.3. Hence, the average leaf litter C : N ratio was 7.6 times as high as the body C : N ratio of the detritivore consumers, whereas the average detritivore C : N was only 1.2 times as high as predator C : N ratios. At the same time, site-averaged leaf litter N concentration ranged from 0.8% to 2.0%, with an average of 1.3%, while consumer N concentration ranged from 5.0% to 13.7%, with an average of 11.8% for predators and 9.4% for detritivores. When relating the variability of animal and litter C : N ratios and N concentration to the respective average values, C : N ratios were more variable in the leaf litter, while differences in N concentration between leaf litter and animal body tissue were not as pronounced. Across trophic groups, increasing litter mass had positive effects on biomass and negative effects on feeding rates (table 1). Increasing detritivore biomass increased predator feeding rates (table 1). Overall, the results suggest that, after accounting for the effects of resource availability and habitat structure, the depletion of resource-quality (increasing C : N ratio) affects both of the consumer guilds' feeding rates but not their stoichiometry and biomass.

The stoichiometric-shift hypothesis (H1) expected consumer C : N to increase with increasing resource C : N, while consumer biomass and feeding rate were not expected to change. However, neither detritivores nor predators significantly altered their body C : N in response to increasing resource C : N (table 1; fig. 3*A*, 3*B*). The data underlying figure 3 are deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.n5h64 (Jochum et al. 2017). Given the lack of significant consumer stoichiometric shifts, our data did not support the stoichiometric-shift hypothesis.

The avoidance hypothesis (H2) assumed a decrease in consumer biomass with increasing resource C : N, while consumer C : N and feeding rate were not expected to change. However, we found that consumer biomass was not altered significantly (table 1; fig. 3*C*, 3*D*) by resource-quality deple-

Table 1: Summary table for the best-selected linear mixed effects models

Response, model, model parameter	Estimate	SE	*t* value/ *z* value	*P*
Detritivore C:N:				
DetCN ~ 1:				
Intercept	.339	.040	8.493	.000
Predator C:N				
PreCN ~ DetCN:				
Intercept:	.417	.092	4.551	.000
DetCN:	−.255	.197	−1.292	.209
Detritivore biomass:				
DetB ~ litterCN + LM:				
Intercept	.386	.089	4.313	.000
LitterCN	−.255	.168	−1.518	.143
LM	.568	.134	4.245	.000
Predator biomass:				
PreB ~ DetCN + LM:				
Intercept	.462	.084	5.521	.000
DetCN	−.180	.121	−1.485	.152
LM	.429	.100	4.309	.000
Detritivore feeding:				
DetF ~ litterCN + LM:				
Intercept	.702	.087	8.057	.000
LitterCN	.384	.163	2.347	**.028**
LM	−.338	.130	−2.597	.016
Predator feeding:				
PreF ~ DetCN + DetB + LM:				
Intercept	.502	.138	3.627	.002
DetCN	.399	.177	2.259	**.035**
DetB	.423	.195	2.176	.041
LM	−.662	.168	−3.945	.001

Note: Best-selected (see "Material and Methods"; box A2) linear mixed effects models testing the effects of litter C:N (litterCN) and litter mass (LM, g cm^{-2}) on detritivore (Det) C:N (CN), fresh biomass (B, mg m^{-2}), and feeding rate (F, W mg^{-1}), as well as detritivore C:N (DetCN), litter mass, and detritivore fresh biomass (DetB) on predator (Pre) C:N, fresh biomass, and feeding rate. Land-use system nested within landscape was used as a random effect for all models to account for the study design. Boldface *P* values indicate significant resource C:N effects plotted in figure 3. Litter mass, biomass, and feeding rate were $\log_{10}$ transformed to meet the assumptions of normality. All variables were normalized prior to analysis. Note that C:N ratios refer to mass percentages rather than molar percentages of C and N in dry tissue of animals and plants, respectively.

tion. Without significant changes in detritivore or predator biomass, our data also did not support the avoidance hypothesis.

Finally, the compensatory-feeding hypothesis (H3) expected consumer feeding rate to increase with increasing resource C:N. Indeed, the calculated per-unit-biomass consumer feeding rates increased significantly with increasing resource C:N ($P = .028$ for detritivores and .035 for predators; table 1; fig. 3*E*, 3*F*). The linear mixed effects models predicted an increase of 55% for the detritivore feeding rate and 80% for the predator feeding rate along their respective resource-quality gradients. Overall, given the significant increase in consumer feeding rates in response to resource-quality depletion, our analyses indicate a high likelihood of compensatory feeding (H3) being the dominant consumer community response across trophic levels. The results of our sensitivity analysis (box A4) confirmed that increasing consumer feeding rates were not simply an artifact of assimilation efficiency increasing with food N content. Instead, the significant increase in consumer feeding rates with decreasing resource quality was jointly driven by assimilation efficiency and the other consumer community parameters (fig. A3).

Discussion

Our investigation of multitrophic consumer responses to resource-quality depletion indicates that compensatory feeding might not be restricted to basal consumer groups, such as herbivores or detritivores, but may be generally found across trophic levels. Our analyses suggest that, across trophic levels, consumer communities respond to lower resource quality by increasing their feeding rates, rather than altering their body stoichiometry or avoiding the low-quality resources. Even though autotrophic and heterotrophic resources differ strongly in the constraints that they impose on consumers, we found this pattern to hold across trophic levels. Hence, of the three hypotheses that we tested, our data point to the prominence of the compensatory feeding hypothesis (H3).

Resource-Driven Stoichiometric Shift

We did not find significant changes in consumer body C:N ratios with decreasing resource C:N. These findings suggest that neither detritivores nor predators altered their body stoichiometry in response to resource-quality depletion. Although some heterotrophs can exhibit a somewhat variable body stoichiometry (Persson et al. 2010; McFeeters and Frost 2011) depending on environmental conditions which affect their physiological pathways (Frost et al. 2005), our results are in line with former studies showing that, overall, heterotrophic body stoichiometry is much less flexible than that of autotrophs (Sterner and Elser 2002; Persson et al. 2010; Hillebrand et al. 2014). Within a species, variability of body stoichiometry might overall be relatively low (but see Persson et al. 2010; McFeeters and Frost 2011), but whether heterotrophic consumers or leaf litter show higher variability depends on the way this variability is defined (e.g., N concentration or C:N ratio). Our data show that variation in consumer body tissue N concentration was similar to variation in leaf litter N concentration, while variation in consumer C:N ratios was relatively low compared to variation in leaf litter

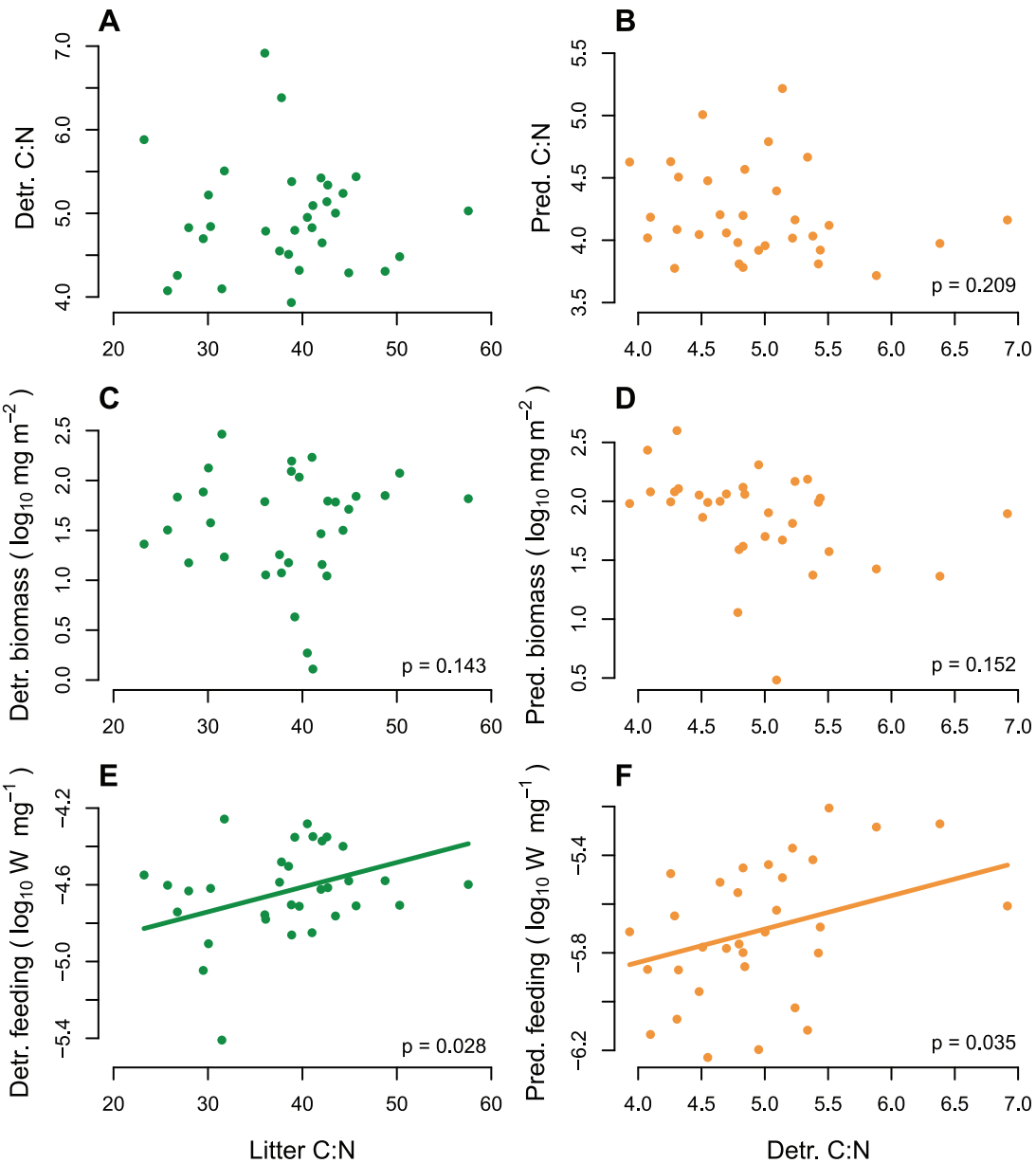

Figure 3: *Left*, linear mixed effects models (green lines and points) for detritivore C:N (*A*), fresh biomass (*C*), and feeding rate (*E*) in response to increasing litter C:N. *Right*, linear mixed effects models (orange lines and points) for predator C:N (*B*), fresh biomass (*D*), and feeding rate (*F*) in response to increasing detritivore C:N. For each site, $n = 32$. Relationships shown and *P* values presented are for just resource C:N (see table 1) from the best-selected models (see "Material and Methods"; box A2). *E*, *F*, Regression fits show the effect of C:N while holding additional parameters constant at their mean. Feeding is per-unit-biomass feeding of the respective feeding guild per site. Solid lines show significant relationships. Note that C:N ratios refer to mass percentages rather than molar percentages of C and N in dry tissue of animals and plants, respectively.

C:N ratios. Thus, despite the substantial variability in animal body N concentration, we did not find evidence that differing resource stoichiometry drives consumer body stoichiometry (C:N ratio). As a result, there were large absolute mismatches between consumers and resources, in particular between detritivores and the leaf litter. However, without evidence for consumers significantly altering their body stoichiometry (i.e., C:N ratio) in response to differing resource quality, the stoichiometric-shift hypothesis (H1) was not supported by our data.

Avoidance of Low-Quality Resources

Under the avoidance hypothesis (H2), we expected consumer biomass to decrease with resource-quality depletion, but detritivore and predator biomass were not significantly altered. If heterotrophs were stoichiometrically homeostatic or maintained their feeding rates in response to decreasing resource quality, the energy reaching the consumer level would be reduced and, consequently, consumer biomass would decline. Generally, experimental N or CNP enrichment increases invertebrate biomass or abundance in soil (Maraun et al. 2001) and grassland ecosystems (Haddad et al. 2000). Here, however we are looking at more subtle differences in resource stoichiometry rather than experimental fertilization of the ecosystem, which confounds changes in resource quantity (primary production) and quality (resource stoichiometry).

Although tests of the avoidance hypothesis are rare, other studies have also shown that resource stoichiometry does not necessarily affect consumer biomass or abundance. In this vein, a recent paper investigating plant effects on decomposer and herbivore communities in grasslands found no effect of plant C : N ratios on decomposer abundance (Ebeling et al. 2014). Nitrogen concentration in plants has also been reported to yield no discernible effects on arthropod communities in a shortgrass prairie (Kirchner 1977), while other studies found strong arthropod responses to fertilizer input (Haddad et al. 2000; Maraun et al. 2001). Our data on detritivore and predator communities in tropical leaf-litter systems did not show significant consumer biomass responses to differing resource C : N ratios. Therefore, in these systems, another mechanism seems to enable maintenance of consumer biomass and stoichiometric homeostasis across a range of resource quality.

Recent work on temperate forests has shown resource stoichiometry to affect biomass densities of litter macroinvertebrates (Ott et al. 2014*b*). Specifically, higher N and P availability (low C : N and C : P ratios) in the local leaf litter resulted in increased population biomass densities. Interestingly, the positive effect of N availability on consumer biomass was especially pronounced for large-bodied species. When comparing the body sizes from our tropical data set with those of Ott et al. (2014*b*), on average, the temperate animals had much larger body masses (mean $\pm$ SE = 18.40 $\pm$ 0.63 mg fresh weight) than the tropical animals (3.16 $\pm$ 0.33 mg fresh weight). Furthermore, the tropical litter C : N ratios (38.32 $\pm$ 1.35) were higher than the temperate ratios (28.67 $\pm$ 0.50). Thus, the absence of a biomass response to differing resource C : N ratio in our tropical data set might be causally related to smaller body masses and higher resource C : N ratios compared to the temperate data set. Despite these differences, previous comparisons of these two data sets have shown that, in both the temperate and tropical ecosystem, whole community energy flux is best predicted by the same two community attributes, namely species richness and total biomass (Barnes et al. 2016). Interestingly, there were stronger effects of environmental variation (e.g., stoichiometric properties of leaf litter) on community composition in the tropical than in the temperate system. Further comparisons of such multitrophic tropical and temperate data sets will help to reveal the underlying mechanisms that describe how structural differences between the tropical and temperate arthropod consumer communities lead to different consumer community responses to resource-quality depletion. However, here we did not find significant resource-quality effects on consumer biomass so that the avoidance hypothesis (H2) was not supported by our data.

Compensatory Feeding to Account for Stoichiometric Resource-Quality Depletion

Both detritivore and predator per-unit-biomass feeding increased substantially with increasing C : N ratios of their resources (55% and 80% increase, respectively). This is in line with prior reports of compensatory feeding in detritivores confronted with poor resources (Ott et al. 2012) and herbivores facing increasing stoichiometric mismatch with their resources (Hillebrand et al. 2009). Our study thus extends these findings to the multitrophic community level of ecosystems. Therefore, the condition supporting the compensatory-feeding hypothesis (H3) was met by our data.

Because of the steeper increase of assimilation efficiency with resource N concentration at lower food N content (observed in the literature-derived scaling relationship; fig. 2), as typical for detritivore diets, an increase in litter C : N—indicating decreasing N concentration and, thus, decreased assimilation efficiency—likely elicits higher per-unit-biomass feeding rates, given that biomass and metabolism are not altered simultaneously. Variability in leaf-litter N concentration (0.8%–2.0%, with an average of 1.3%), combined with the steep increase of assimilation efficiency at such low resource N levels and nonrandom changes in the other community parameters (see sensitivity analysis; box A4; fig. A3), resulted in increased feeding rates. This steep increase indicates the strong limitation of assimilation efficiency that detritivores suffer at low N concentrations in their litter resources. Notably, assimilation efficiency at predator-diet N levels showed a weaker increase in assimilation efficiency with increasing resource N concentration (fig. 2), but predator diets showed a large absolute variability in N concentration (5.0%–15.1%). Ultimately, the combination of resource N variation and the varying slope of the scaling relationship between resource N and assimilation efficiency at detritivore and predator resource N levels facilitated increased per-unit-biomass feeding with decreasing resource quality across trophic levels. Interestingly, our sensitivity analysis strongly sug-

gests that these changes in assimilation efficiency with food quality were not the sole driver of the significant positive response of consumer feeding rates to higher resource C:N. On the contrary, depending on the other community parameters (consumer metabolism, consumer biomass, detritivore relative abundance, and litter mass), feeding rates obtained from our iterative randomization process only very rarely led to significantly higher and sometimes even significantly lower feeding rates in response to lower resource quality (fig. A3). Thus, although we were not able to measure consumer feeding rates in the field, our analysis provides strong indication that decreasing assimilation efficiency, together with nonrandom changes in other consumer community parameters, such as consumer metabolism, causes higher consumer feeding rates in response to lower resource quality.

Our sensitivity analysis revealed that higher consumer feeding rates at lower resource quality are not simply driven by varying assimilation efficiency across the resource-quality gradient but must at least partly be caused by nonrandom changes in other community parameters. Given that consumer biomass remained constant across the resource-quality gradient (no support for H2), it is likely that differences in consumer community body size structure play an important role here. Changes to community size structure can have significant consequences for trophic interactions and, thus, matter and energy flux through ecological networks (Brose et al. 2017). Interestingly, changing size structure of a single trophic level can affect whole communities through cascading biomass and abundance effects (Jochum et al. 2012). Such changes are, at least partly, mediated by the impact of body size on consumer energy demand due to higher individual metabolic rates but lower mass-specific metabolic rates in larger animals (Brown et al. 2004). Even if total biomass remains constant, shifting community body size structure can therefore strongly impact patterns of feeding rates, energy flux, and thus ecosystem functioning through its impact on the metabolic demand of organisms (Barnes et al. 2014). As such, our results provide an indication of how varying community size structure in response to changes in resource quality might impact feeding rates of invertebrate communities; a pattern that warrants further investigation to better understand mechanisms underlying consumer feeding rates across environmental gradients.

While compensatory feeding has been shown before (Hillebrand et al. 2009; Ott et al. 2012), we expand this knowledge to community responses to resource-quality depletion as we present data from multiple trophic levels. Our analyses show that compensatory feeding is likely a general response to lower resource quality across trophic levels and consumer feeding guilds. Although our results show strong support for community-level compensatory feeding, they still do not provide experimental evidence for increased feeding rates, as it was not possible to measure feeding rates in the field due to the lack of methods for in situ measurement of macroinvertebrate feeding rates. However, despite this limitation, our approach provides a strong theoretical indication of increased feeding rates in response to lower-quality resources when compared alongside the lack of support for the other hypotheses. Our results represent a community-level trend that should not be mistaken for evidence that all consumer populations comprising this community show the same simple response as the community average. On the contrary, these specific populations quite likely respond with a mixture of strategic adaptations (stoichiometric shift, avoidance, compensatory feeding), which—depending on the simultaneous changes in community body size structure—differentially impact consumer community stoichiometry, biomass, and metabolism (Ehnes et al. 2014). However, such fine-scale changes were not strong enough to provide support for a community-level pattern consistent with H1 (stoichiometric shift) and H2 (avoidance), whereas we found patterns that are expected by H3 (compensatory feeding). Even if our results were the product of a type II error that resulted in failure to detect existing stoichiometric shifts (H1) or avoidances (H2), this would not affect the clear support for H3 (compensatory feeding). It is important to note, however, that there could be several mechanisms acting in parallel, as should be expected to occur at the community level. Nevertheless, our analyses suggest that, across trophic levels, compensatory feeding is the most consistently expressed response of consumers to low-quality resources at the community level.

Future Directions

The feeding rate calculations in our study were partially based on the scaling of assimilation efficiencies with resource N concentration. However, rather than only using resource element concentration, focusing on the stoichiometric mismatch between consumer and resource body tissue and its consequences for consumption and energy fluxes within ecosystems is a promising next step. Furthermore, although we focus on resource C:N ratios, terrestrial arthropod communities may also be limited in their biomass density and feeding capacity by resource sodium (Na) and calcium (Ca) concentrations, which are important for maintaining membrane gradients (Kaspari et al. 2009, 2014) and building calcareous exoskeletons (e.g., isopods; Kaspari and Yanoviak 2009), respectively. Additionally, the P concentration of the litter may stimulate microbial biomass production with potential positive bottom-up effects on arthropod biomass (Elser et al. 1996; Kaspari et al. 2008). In this vein, two recent field studies showed that arthropod biomass densities may be driven by N and sulfur (S) concentrations in the litter of American tropical forest stands (Kaspari and Yanoviak 2009) or N, P, and Na in European forests (Ott et al. 2014*a*). While

the consistent importance of N supports the choice of this element for our study, future studies could thus employ our approach to address the interactive role of N, P, and Na in driving arthropod community responses to differing resource conditions (Fagan and Denno 2004).

While soil food webs have a complex structure integrating up to six trophic levels (Scheu and Falca 2000; Digel et al. 2014), we have simplified our community approach to the broad trophic groups of detritivores and predators. However, with better resolved trophic structure of these communities, investigating how relative amounts of N, P, Na, and Ca vary along the food chain (Martinson et al. 2008) and differently alter consumer responses to resource depletion across trophic levels seems promising. Furthermore, investigating the effects of variation in other elements on consumer diversity and feeding rates across trophic levels will be a future challenge to unravel new patterns in community structure. Additionally, our data present consumer-community responses to differing resource quality at a single point in time. Testing our hypotheses repeatedly over time to detect possible differences in the consumer communities' response could therefore lead to further insights on the nature of the resource-quality effect. Moreover, as we took a consumer community approach, our data do not allow investigation of how different lower-level consumer taxa respond to differing resource quality. However, as our hypotheses suggest, this is the level at which strategic adaptations would be expected to occur. While such species-level consumer responses are tough to assess for macroinvertebrates under field conditions, laboratory experiments could adequately answer this question and are needed in order to complement and further analyze our community-level findings.

Conclusions

Our data highlight how reduced resource quality can trigger increased consumption by consumers across trophic levels. Small differences in resource stoichiometry can therefore have far-reaching consequences for their consumers, which need to increase their time and energy expenditure for feeding, thereby decreasing time and energy available for other crucial activities. In addition to providing insights into fundamental processes that structure communities and ecosystems, our study also raises further questions on how global agricultural expansion and intensification as well as climate change might affect ecosystems by altering elemental availability for consumer organisms throughout trophic networks in these systems. Our results present a promising step toward research on ecosystem-wide ecological stoichiometry effects by taking into account the underlying mechanisms that drive consumer-resource interactions at different trophic levels.

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