

Resource stoichiometry and availability modulate species richness and biomass of tropical litter macro-invertebrates

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Funding information

German Research Foundation (DFG), Grant/Award Number: FZT 118; Ministry of Science and Culture of Lower Saxony, Germany; Ministry of Forestry (PHKA), Indonesia, Grant/Award Number: 2695/IPH.1/KS.02/XI/2012

Handling Editor: Alice Hughes

Abstract

1. High biodiversity and biomass of soil communities are crucial for litter decomposition in terrestrial ecosystems such as tropical forests. However, the leaf litter that these communities consume is of particularly poor quality as indicated by elemental stoichiometry. The impact of resource quantity, quality and other habitat parameters on species richness and biomass of consumer communities is often studied in isolation, although much can be learned from simultaneously studying both community characteristics.
2. Using a dataset of 780 macro-invertebrate consumer species across 32 sites in tropical lowland rain forest and agricultural systems on Sumatra, Indonesia, we investigated the effects of basal resource stoichiometry (C:X ratios of N, P, K, Ca, Mg, Na, S in local leaf litter), litter mass (basal resource quantity and habitat space), plant species richness (surrogate for litter habitat heterogeneity), and soil pH (acidity) on consumer species richness and biomass across different consumer groups (i.e. 3 feeding guilds and 10 selected taxonomic groups).
3. In order to distinguish the most important predictors of consumer species richness and biomass, we applied a standardised model averaging approach investigating the effects of basal resource stoichiometry, litter mass, plant species richness and soil pH on both consumer community characteristics. This standardised approach enabled us to identify differences and similarities in the magnitude and importance of such effects on consumer species richness and biomass.
4. Across consumer groups, we found litter mass to be the most important predictor of both species richness and biomass. Resource stoichiometry had a more pronounced impact on consumer species richness than on their biomass. As expected, taxonomic groups differed in which resource and habitat parameters (basal resource stoichiometry, litter mass, plant species richness and pH) were most important for modulating their community characteristics.
5. The importance of litter mass for both species richness and biomass indicates that these tropical consumers strongly depend on habitat space and resource availability. Our study supports previous theoretical work indicating that consumer species richness is jointly influenced by resource availability and the balanced supply of multiple chemical elements in their resources.

KEYWORDS

consumer biomass, consumer species richness, consumer–resource interaction, ecological stoichiometry, elemental ratios, model averaging

1 | INTRODUCTION

Invertebrates are not only extraordinarily diverse (Wilson, 1987) but they are also critically important for ecosystem functioning (Yang & Gratton, 2014). One example for such an ecosystem function is decomposition of dead organic material in terrestrial and aquatic ecosystems (Gessner et al., 2010; Handa et al., 2014). In terrestrial ecosystems, 90% of primary production is returned to the organic matter pool of the soil ecosystem (Cebrian, 1999), on which highly diverse and trophically complex consumer communities thrive (Digel, Curtsdotter, Riede, Klarner, & Brose, 2014; Hättenschwiler, Tiunov, & Scheu, 2005). In combination with various other biotic and abiotic factors, these consumer communities critically depend on the quantity and quality of this organic matter pool (Cardinale, Hillebrand, Harpole, Gross, & Ptacnik, 2009; Cruz-Rivera & Hay, 2000). More generally, the quantity and quality of local resources jointly modulate the species richness and biomass of consumer communities through a variety of pathways, with these two community characteristics additionally influencing each other (Cardinale et al., 2009).

The framework of ecological stoichiometry allows for investigating impacts of resource elemental quality on consumers (Elser, Fagan et al., 2000; Sterner & Elser, 2002). For heterotroph communities exploiting terrestrial leaf litter, stoichiometric resource quality (hereafter resource stoichiometry) is particularly poor (Elser, Fagan et al., 2000; Ott, Digel, Klarner et al., 2014; Ott, Digel, Rall et al., 2014), especially in tropical ecosystems (McGroddy, Daufresne, & Hedin, 2004). Several hypotheses have been developed to explain effects of differing resource stoichiometry on consumer abundance and biomass. For example, the growth rate hypothesis (Sterner & Elser, 2002) and the secondary productivity hypothesis (Kaspari & Yanoviak, 2009) predict higher abundance of consumers, specifically microbivores, in response to higher phosphorus (P) availability. Similar hypotheses exist for various other chemical elements that appear to influence arthropod consumer biomass and abundance patterns in temperate and tropical litter systems (Kaspari & Yanoviak, 2009; Ott, Digel, Klarner et al., 2014). In addition to these stoichiometric parameters, physical habitat parameters, such as soil acidity, have been shown to affect the abundance of bacteria, fungi and microarthropods in soil ecosystems (Mulder, Van Wijnen, & Van Wezel, 2005). While most studies stress the importance of stoichiometric and other habitat parameters for consumer biomass or abundance, it remains to be investigated whether the same constraints apply to consumer species richness.

Resource stoichiometry modulates consumer species richness via the summed availability of resources and the balanced supply of multiple resources (Cardinale et al., 2009). Specifically, species-energy theory (Wright, 1983) suggests that with increasing productivity of a system, population sizes of constituent species increase, which

reduces the probability of rare species to stochastically go extinct and thus facilitates coexistence and local species richness (Cardinale et al., 2009). In contrast, the resource-ratio theory (Tilman, 1982) assumes that when the supply of any particular resource is especially high other resources will become limiting and that no species can simultaneously be the best competitor for all resources (Cardinale et al., 2009). Consequently, species richness is maximised where multiple resources are supplied at an intermediate level; a so-called balance between the relative supply of several resources and consumer demand (Hillebrand & Lehmpfuhl, 2011). In addition to resource quantity and quality, other habitat parameters have been suggested to influence species richness of litter arthropods. As such, higher species richness is expected in ecosystems comprising larger habitat space (Kaspari & Yanoviak, 2009) and higher habitat heterogeneity (Tews et al., 2004) which, in litter systems, can be related to plant diversity via the resulting variety of structural microhabitats in the leaf litter (Hansen & Coleman, 1998).

Given that species richness and biomass are often studied in isolation, as well as many studies being restricted to single taxa or trophic levels, the main objective of this study was to simultaneously investigate the effects of differing resource and habitat conditions on consumer species richness and biomass across multiple consumer taxa and trophic levels and under real-world conditions. To this end, we collected consumer data including 7,217 macro-invertebrate individuals of 780 species across 32 sites in tropical lowland rain forest and agricultural systems in Sumatra, Indonesia (Barnes et al., 2014). We combined these data with measurements of leaf-litter stoichiometry (C:X ratios of N, P, K, Ca, Mg, Na and S), litter mass (basal resource quantity and habitat space), plant species richness (as a surrogate for litter habitat heterogeneity) and soil pH (acidity). While the effects of anthropogenic land use on macro-invertebrate consumers in these systems have already been investigated (Barnes et al., 2014), the effects of gradients in resource stoichiometry and other habitat parameters remain unexplored. In this study, we therefore investigate such effects across a variety of tropical land-use systems to gain a broad perspective on the effects of such gradients across different land-use systems.

Specifically, we set out to find the most important predictors of species richness and biomass across consumer trophic levels and taxonomic groups. We generally expected a strong dependence of consumer biomass on litter mass with different consumer groups depending, additionally, on certain key parameters such as plant species richness or specific stoichiometric traits (e.g. phosphorus). Furthermore, we expected consumer species richness to scale positively with litter mass and additionally depend on multiple resource stoichiometric parameters (species-energy theory and resource-ratio theory). For the biomass and species richness of different consumer groups (i.e. the overall consumer community, 3 different feeding guilds and 10 selected taxonomic groups), we applied a model averaging

approach (Burnham & Anderson, 2002; Grueber, Nakagawa, Laws, & Jamieson, 2011) to simultaneously test for the relative impact of multiple parameters, as tropical arthropod consumers are hypothesised to be constrained by multiple rather than single limiting factors (Kaspari et al., 2008; Sperfeld, Martin-Creuzburg, & Wacker, 2012).

2 | MATERIALS AND METHODS

2.1 | Study site and sampling

Animal and leaf-litter material was sampled in the tropical lowlands of the Jambi Province, Sumatra, Indonesia, between October and November 2012. Across two landscapes (near Bukit Duabelas National Park and Harapan Rainforest), eight 50 × 50 m sites were established in each of four land-use systems, lowland rain forest, jungle rubber, rubber and oil-palm plantations ($n = 32$) (Barnes et al., 2014). Animal communities and leaf-litter material were sampled on each of three 5 × 5 m subplots per site, as described in Barnes et al. (2014) and Jochum, Barnes, Ott et al. (2017). To quantitatively sample the animal communities from the leaf-litter layer, on each subplot, all animals were extracted from 1 m² of leaf litter by sieving it through a 2 cm width mesh and collecting the animals which fall through to a collecting tray. From these siftings, all animals visible to the naked eye were hand-collected and stored in 65% ethanol for further processing.

To measure local leaf-litter stoichiometry, fallen leaves of up to 10 dominant plant species per site were sampled from the ground for stoichiometric analysis ($n = 169$). Additionally, plant species richness, litter mass and pH were assessed on each site to account for habitat parameters other than resource stoichiometry. To quantify local plant species richness as a surrogate measure of habitat heterogeneity, at each site, all trees with a diameter equal to or larger than 10 cm at breast height as well as all vascular plants on five 5 × 5 m subplots were identified. To assess local litter ecosystem size and resource quantity, dry litter mass (g/cm²) was measured on each subplot by Krashevskaya, Klarner, Widyastuti, Maraun, and Scheu (2015) by removing the litter layer on an area of 16 × 16 cm, after which all coarse woody debris and inorganic matter was removed and the litter was dried and weighed. Soil pH analysed on the same sites in a 1:4 soil-to-water ratio by Allen, Corre, Tjoa, and Veldkamp (2015) was used as an additional habitat parameter.

2.2 | Stoichiometric analysis of leaf-litter samples

For each of the 169 leaf samples, total carbon (C) and nitrogen (N) concentration was analysed by an automated CHNSO analyser from 5 mg dry material. Furthermore, phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), sodium (Na) and sulphur (S) concentrations of the same dried material were measured after HNO₃ digestion by ICP-OES analysis (Perkin Elmer Optima 5300 DV). Carbon-to-element ratios for all analysed elements were calculated based on mg per g dry weight of the analysed material. Ratios of single leaf samples were then weighted according to their relative importance in local leaf litter at each site (Jochum, Barnes, Ott et al., 2017). All raw

predictor variables used in our analyses are deposited in the Dryad Digital Repository, <https://doi.org/10.5061/dryad.qn119> (Jochum, Barnes, Weigelt et al., 2017).

2.3 | Calculation of consumer species richness and biomass

The body lengths of all 7,217 animals were measured to the nearest 0.1 mm and individual fresh body mass calculated using length–mass regressions from the literature (Barnes et al., 2014). All individuals were identified to morphospecies and assigned to the functional feeding guilds predator, omnivore and detritivore, based on morphology and literature (Barnes et al., 2014). All analyses were performed on the overall dataset and also on different aggregations of the data. This included 3 functional feeding guilds (detritivores, omnivores and predators) and 10 selected taxonomic groups: ants (Formicidae), cockroaches (Blattodea), centipedes (Chilopoda), beetles (Coleoptera), millipedes (Diplopoda), woodlice (Isopoda), termites (Isoptera), harvestmen (Opiliones), crickets (Orthoptera, with 95% of the individuals being Gryllidae) and spiders (Araneae), summing up to 14 consumer groups. For each consumer group, observed consumer species richness was calculated as the number of morphospecies present in the sampled 3 m² at each of the 32 sites (see Table S1 for the number of observed species and individuals). The 10 selected taxonomic consumer groups represent the majority of the overall dataset (82% of observed species richness and 85% of sampled individuals). Extrapolated species richness was calculated for each consumer group per site, based on the three subplot samples, using the nonparametric “jackknife 2” estimator (Brose, Martinez, & Williams, 2003) (see Table S2 for sample coverage and correlation between observed and extrapolated species richness). All analyses were carried out based on extrapolated species richness, rather than observed species richness, to account for differences in the number of individuals between sites (Gotelli & Colwell, 2001). Henceforth, the term “species richness” refers to extrapolated species richness. Finally, fresh consumer biomass (mg/m²) was calculated for each consumer group by summing up the respective individual body masses per site and dividing this overall biomass by 3 (3 m² sampled per site). Calculated values of observed species richness, extrapolated species richness and biomass per consumer group per site are deposited in the Dryad Digital Repository, <https://doi.org/10.5061/dryad.qn119> (Jochum, Barnes, Weigelt et al., 2017).

2.4 | Statistical analyses

To assess the effect of resource stoichiometry, litter mass, plant species richness and soil pH on consumer species richness and biomass, a model averaging approach was employed, following Burnham and Anderson (2002) and Grueber et al. (2011) using the MuMIn package (Barton, 2015) in R version 3.2.3 (R Core Team, 2015). Based on information theory, this procedure was used to select a set of best candidate models based on AIC_c (Akaike’s information criterion corrected for small sample sizes) and subsequently average over these models, rather than selecting a single “best” model. It should be noted

that this approach does not involve the presentation of p -values or the rejection of hypotheses (Burnham & Anderson, 2002) but rather gives an indication of the set of parameters best explaining a given effect and their relative strength. In order to apply this procedure, we first established a full model including all possible predictor variables. The linear mixed effects models, set up using the NLME package in R (Pinheiro, Bates, DebRoy, & Sarkar, 2014), treated land-use system nested within landscape as random effects to account for the hierarchical structure of the study design and the resulting possible differences among landscapes and land-use systems while focusing on the underlying effects of resource stoichiometry, litter mass, plant species richness and soil pH. Before setting up the models, all predictor variables were tested for collinearity using Pearson correlation coefficients, but no correlation coefficients larger than 0.75 were found (Table S3) and thus all predictors were included in the analysis (Zuur, Ieno, & Smith, 2007). To meet the assumptions of normality, all predictor variables (except pH), as well as the response variables species richness and biomass were \log_{10} -transformed. Subsequently, for comparison of effect sizes among models, all variables were standardised before model runs to zero mean and unit variance by subtracting the mean and dividing by the standard deviation. The full models included litter mass, plant species richness and soil pH, as well as the seven C:X ratios for N, P, K, Ca, Mg, Na and S. Henceforth, when describing an effect of a certain element, we refer to the effect of its C:X ratio. In a second step, all models for all possible predictor variable combinations were computed and ranked by AIC_c . A set of best candidate models was chosen, defined by a maximum ΔAIC_c of 4 compared to the model with the lowest AIC_c (Tables S4 and S5). This cut-off point lies within the commonly recommended range (ΔAIC_c 2–10 (Bolker et al., 2009; Burnham & Anderson, 2002)) and accounts for the study-specific trade-off between including too many models in the averaging process and excluding too many (potentially important) models (Grueber et al., 2011). In a third step, this set of best candidate models was then used to perform model averaging using maximum likelihood and the zero method ("full average"), which is recommended when trying to establish which predictor has the strongest effect on the response variable (Grueber et al., 2011; Nakagawa & Freckleton, 2011). This procedure was repeated for every subset of the data (overall dataset, 3 functional feeding guilds and 10 taxonomic groups), yielding one averaged model for extrapolated species richness and one model for the biomass of each consumer group. In addition to the averaged coefficients, variable importance was calculated as the sum of Akaike weights over all best candidate models including the respective variable (Barton, 2015) (Tables S4 and S5). To obtain a goodness-of-fit measure for the averaged models, pseudo- r^2 values were calculated for each model as the adjusted r^2 -value of a linear model fitting the observed values for consumer biomass and extrapolated species richness against the values predicted by the averaged models. Finally, we calculated 95% confidence intervals to assess the reliability of the averaged coefficients for each of the 10 predictor variables (Figures S1 and S2). All averaged coefficients with their 95% intervals are deposited in the Dryad Digital Repository, <https://doi.org/10.5061/dryad.qn119> (Jochum, Barnes, Weigelt et al., 2017).

2.5 | Identification of important predictors

In order to find the most important predictors of consumer species richness and biomass, we compared effect sizes (subsequently referred to as standardised coefficients β) from the averaged models taking into account the calculated 95% confidence interval. Effects with confidence intervals not overlapping zero were interpreted as important effects. Effects with strong effect sizes that had confidence intervals only slightly overlapping zero were interpreted with caution and are subsequently referred to as marginal effects. Furthermore, the calculated importance of the 10 predictor variables across taxonomic consumer groups (upper barplot in Figures 1 and 2) was used to identify important predictors of species richness and biomass across consumer groups. Interestingly, some of these important predictors did not have any strong effects on specific consumer groups. Their importance arises from their presence in best candidate models with high Akaike weights. As such, although these variables did not show strong effects, they should not be branded unimportant.

3 | RESULTS

Our analyses indicate that tropical litter macro-invertebrate consumer species richness and biomass are modulated by multiple parameters. While all predictor variables from the full model sets remained in all averaged models, a few variables exhibited particularly strong effects (Figures 1 and 2). Across consumer groups, litter mass was the most important driver of species richness and biomass, with strong positive effects on both species richness and biomass of the overall consumer community as well as feeding guilds and a number of taxonomic consumer groups. Additionally, the species richness of consumer feeding guilds was elevated at high nitrogen (detritivores) and phosphorus (predators and omnivores) availability. Apart from these effects on feeding guilds, we found macro-invertebrate consumer taxa to differ in which parameters they were affected by, as well as in the magnitude of these effects. In general, our models provided good fits to our data, explaining much of the variance in the responses of consumer species richness (Figure 1; mean pseudo- r^2 = .56, range = .23–.75) and biomass (Figure 2; mean pseudo- r^2 = .46, range = .20–.69). Despite a correlation between consumer species richness and biomass of the 14 consumer groups (mean r = .62; Table S6), there was still a considerable amount of variation between the two (range = .40–.86), which might be partly explained by differences in their responses to resource and habitat parameters as detailed below. In the following, we compare these effects on consumer species richness and biomass, in order to relate the findings to potential underlying mechanisms.

3.1 | Important predictors of consumer species richness

Litter mass was the dominant predictor of consumer species richness, across consumer groups (Figure 1) having a strong positive effect on overall species richness (standardised coefficient β = 0.91; see

FIGURE 1 Standardised coefficients for the effects of litter mass, plant species richness, soil pH and litter stoichiometry, on extrapolated species richness of selected taxonomic groups, functional feeding guilds and the overall dataset. For simplicity, a negative effect of C:X is shown as a positive effect of the element X. The coefficients are averaged over a set of best candidate models ($\Delta AIC_c \leq 4$, Table S4). Coloured rectangles show positive (blue) and negative (red) standardised coefficients, with stronger colour depicting stronger effects. Asterisks denote effects with confidence intervals not overlapping zero (see Figure S1 for averaged coefficients and confidence intervals). The upper bar graph shows the mean importance (sum over Akaike weights over all best candidate models including the variable, Table S4) for each predictor variable across the taxonomic groups. The right bar graph shows the pseudo- r^2 value for each model as a goodness-of-fit measure. LM = litter mass; prich = plant species richness

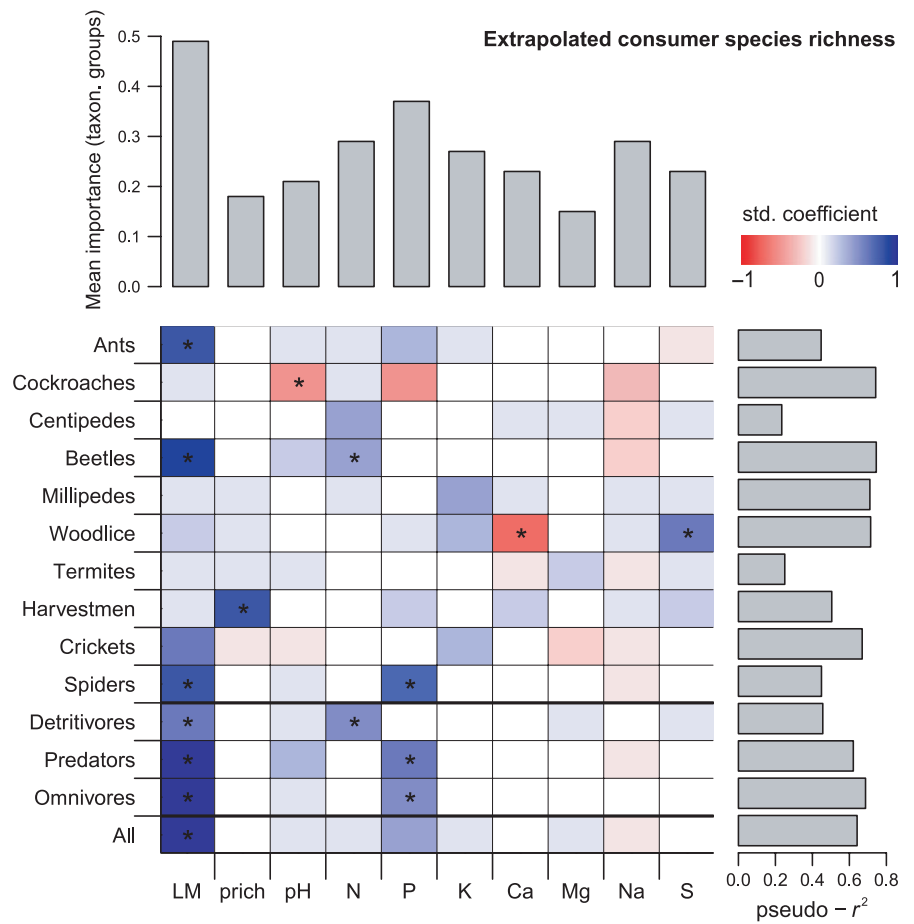


Figure S1 for all coefficients and confidence intervals from species richness models). There was a marginally positive effect of phosphorus on overall species richness ($\beta = -0.37$, 95% CI: -0.83 to 0.10 for the C:P ratio). It should be noted that for all stoichiometric parameters, negative coefficients indicate a positive effect as the models were run on C:element ratios. Furthermore, litter mass had a positive effect on detritivore ($\beta = 0.56$), predator ($\beta = 1.02$) and omnivore species richness ($\beta = 0.92$) confirming its importance across consumer feeding guilds. Additionally, detritivore species richness was higher at high nitrogen availability ($\beta = -0.46$ for the C:N ratio), whereas predator ($\beta = -0.52$ for the C:P ratio) and omnivore ($\beta = -0.47$ for the C:P ratio) species richness scaled positively with phosphorus availability, indicating the importance of these elements for consumer species richness across feeding guilds. Across the taxonomic consumer groups, litter mass had a positive effect on species richness for ants ($\beta = 0.77$), beetles ($\beta = 0.83$) and spiders ($\beta = 0.75$; see Figure 1). Overall, litter mass was the most important predictor of species richness by strongly affecting the richness of specific taxonomic groups as well as showing the highest mean predictor importance across groups (upper barplot in Figure 1).

Across consumer groups, plant species richness had a single positive effect on harvestmen species richness ($\beta = 0.70$; Figure 1) and pH showed a single negative effect on cockroach species richness ($\beta = -0.43$), which was surprising given the expected importance of these habitat parameters for consumer species richness. Beetles showed higher species richness at high nitrogen availability ($\beta = -0.34$

for the C:N ratio) and spiders showed higher species richness at high phosphorus availability ($\beta = -0.64$ for the C:P ratio), again indicating the importance of N and P for various consumer taxa. Across taxonomic groups, phosphorus was the second most important predictor variable (upper barplot in Figure 1), mostly related to higher species richness. Surprisingly, woodlice species richness was strongly reduced at high calcium availability ($\beta = 0.63$ for the C:Ca ratio), magnesium availability did not show any strong effects and cockroach species richness was marginally reduced at high sodium sites ($\beta = 0.25$, 95% CI: -0.07 to 0.56 for the C:Na ratio) although these elements were expected to be crucial for litter invertebrate species richness. Interestingly, the variable importance patterns as calculated from Akaike weights of variable-containing best candidate models (see Methods and Table S4) marked some variables as important across taxonomic groups although they did not show any strong effects on the species richness of specific groups. As such, in line with expectations of the sodium shortage hypothesis (Kaspari, Yanoviak, Dudley, Yuan, & Clay, 2009), sodium was among the most important predictor variables across taxonomic groups (Figure 1), although its strongest effect had a confidence interval overlapping zero. Finally, woodlice species richness was higher at high sulphur availability ($\beta = -0.54$ for the C:S ratio) potentially indicating the importance of high-quality litter for these tropical detritivores.

Taken together, the species richness of most consumer groups only strongly responded to one or two predictor variables with litter

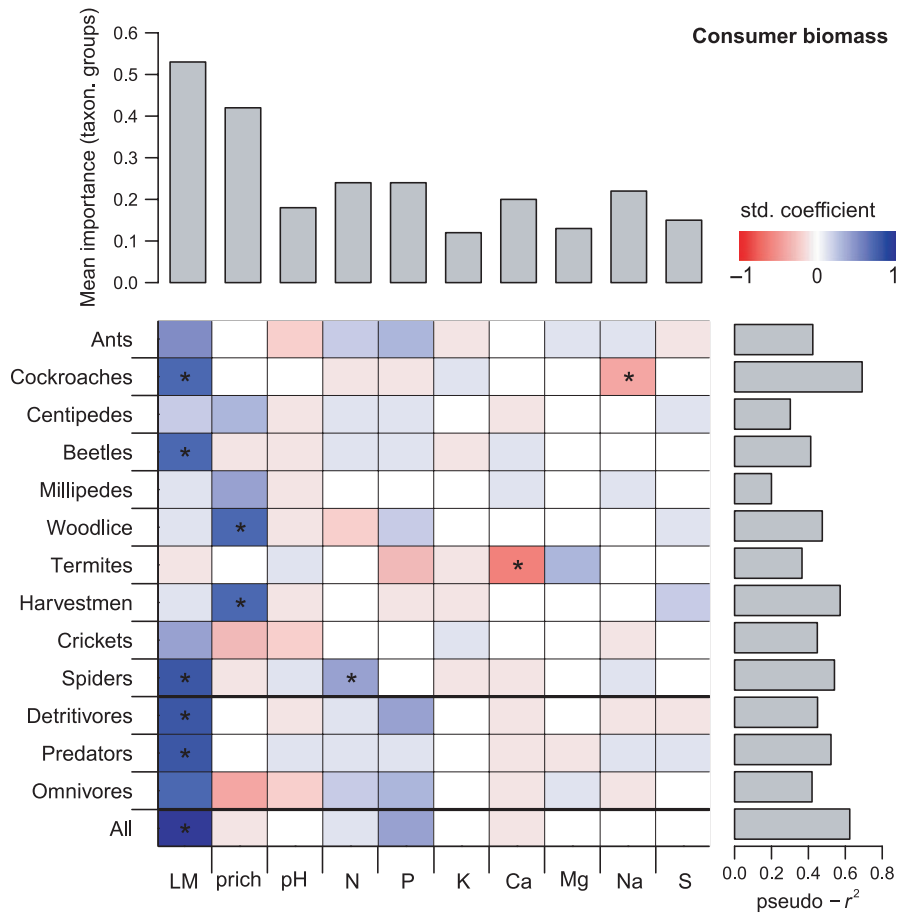


FIGURE 2 Standardised coefficients for the effects of litter mass, plant species richness, soil pH and litter stoichiometry on the biomass of selected taxonomic groups, functional feeding guilds and the overall dataset. For simplicity, a negative effect of C:X is shown as a positive effect of the element X. The coefficients are averaged over a set of best candidate models ($\Delta\text{AIC}_c \leq 4$, Table S5). Coloured rectangles show positive (blue) and negative (red) standardised coefficients, with stronger colour depicting stronger effects. Asterisks denote effects with confidence intervals not overlapping zero (see Figure S2 for averaged coefficients and confidence intervals). The upper bar graph shows the mean importance (sum over Akaike weights over all best candidate models including the variable, Table S5) for each predictor variable across the taxonomic groups. The right bar graph shows the pseudo- r^2 value for each model as a goodness-of-fit measure. LM = litter mass; prich = plant species richness

mass being the only predictor variable affecting more than one taxonomic group (Figure 1). Species richness of feeding guilds was higher at high phosphorus or nitrogen availability. Although there were only few strong effects, all variables were included in all averaged models. Together with the fact that some variables without strong effects showed high across-group importance, these results indicate that the species richness of tropical litter macro-invertebrate consumers is jointly influenced by multiple rather than few predictor variables (i.e. resource and habitat parameters).

3.2 | Important predictors of consumer biomass

Similar to its effects on species richness, litter mass was also the dominant predictor of consumer biomass across consumer groups (Figure 2), with a positive effect of litter mass on overall biomass ($\beta = 0.93$; see Figure S2 for confidence intervals from the biomass models). Litter mass also had a positive effect on detritivore ($\beta = 0.71$) and predator biomass ($\beta = 0.72$) with a similar marginally positive effect on omnivore biomass ($\beta = 0.67$, 95% CI: -0.05 to 1.38). In line with the species richness effects, there was a marginally positive effect of phosphorus availability on overall biomass ($\beta = -0.31$, 95% CI: -0.68 to 0.08 for the C:P ratio). These results confirm the high importance of resource quantity, habitat space and phosphorus for macro-invertebrate consumers across trophic levels.

Of the taxonomic consumer groups, litter mass had a positive effect on the biomass of cockroaches ($\beta = 0.64$), beetles ($\beta = 0.61$) and spiders ($\beta = 0.74$; Figure 2). Consequently, as in the species richness results, litter mass was also the dominant predictor of consumer biomass (upper barplot in Figure 2), with strong effects on three taxonomic consumer groups and the highest across-group importance. In contrast to its minor importance for consumer species richness, plant species richness showed positive effects on woodlice ($\beta = 0.65$) and harvestmen biomass ($\beta = 0.68$), and therefore, had the second-highest across-group variable importance on consumer biomass. Overall, the stoichiometric parameters had fewer effects on consumer biomass than on their species richness. As such, nitrogen availability had a positive effect on spider biomass ($\beta = -0.33$ for the C:N ratio), termite biomass was reduced at high calcium availability ($\beta = 0.53$ for the C:Ca ratio) and cockroach biomass was reduced at high sodium availability ($\beta = 0.31$ for the C:Na ratio), but soil pH, phosphorus, potassium, magnesium and sulphur did not show any strong effects on biomass. As in the species richness results, there were predictor variables showing high across-group importance for consumer biomass although they did not show any strong effects on specific taxonomic consumer groups (e.g. phosphorus, Figure 2).

The biomass of most consumer groups strongly responded to only one predictor variable (Figure 2), the only exception being spider biomass, which was higher at high levels of litter mass and nitrogen availability. In addition, plant species richness was positively related

to the biomass of two taxonomic consumer groups (woodlice and harvestmen) indicating a high importance of litter habitat heterogeneity for consumer biomass. Just as for consumer species richness, their biomass was dominated by few strong effects. However, all variables were again included in all averaged models with some variables showing high across-group importance without exhibiting specific strong effects. These results indicate that consumer biomass is also influenced by multiple rather than single resource and habitat parameters.

4 | DISCUSSION

In our field study on tropical litter macro-invertebrate communities in Southeast Asian forests and agricultural systems, we found consumer species richness and biomass to be modulated by multiple resource and habitat parameters with few strong and many weak effects (all variables included in all models), confirming earlier findings that tropical arthropod consumers are constrained by multiple rather than single limiting factors (Kaspari et al., 2008; Sperfeld et al., 2012). In line with our expectations, our data suggest that both macro-invertebrate species richness and biomass are strongly impacted by local gradients in litter mass and thus habitat space and resource quantity. Interestingly, in line with previous research on tropical systems (Sayer, Sutcliffe, Ross, & Tanner, 2010), there was a tendency towards more pronounced resource stoichiometry effects (i.e. nitrogen and phosphorus availability) on consumer species richness than biomass in our real-world communities. Our data thus also confirm our expectation of consumer species richness being jointly driven by resource availability and the balance of multiple resources (species-energy theory and resource-ratio theory) (Cardinale et al., 2009). Besides these main effects, macro-invertebrate consumer taxa differed in what parameters they were affected by, as well as in the magnitude of these effects. Given the theoretical advances on the regulation of consumer species richness by the balance of multiple resource supply rates, ideally, stoichiometry effects on species richness would have been assessed using an evenness measure of multiple resource supply rates. However, we have refrained from using such an approach here, as we aimed to directly compare species richness and biomass responses. Thus, although for investigating the mechanisms underlying natural species richness patterns it might be ideal to include a measure of resource evenness, our approach does account for the joint importance of multiple resources by allowing for multiple resource availability and stoichiometry effects (weak and strong) in the averaged models.

4.1 | Dominance of litter mass effects across consumer groups

The strong positive relationship between species richness and litter mass supports the ecosystem size hypothesis (Kaspari & Yanoviak, 2009) and the species-energy theory (Wright, 1983) in that larger habitat space and higher resource availability facilitate consumer

species richness. While other studies have shown arthropod density to increase with litter mass and depth (Kaspari & Yanoviak, 2009; Yang, Warren, & Zou, 2007), such effects have rarely been reported for arthropod species richness in tropical litter systems (but see Sayer et al., 2010). Apart from its effects on species richness in our study, litter mass also had strong positive effects on consumer biomass across several consumer groups. Interestingly, a recent study found litter depth to be of minor importance for the biomass of consumer communities in temperate litter systems (Ott, Digel, Klarner et al., 2014). This difference in the importance of litter habitat space and resource mass for consumer biomass might be explained by the much lower litter depth on our research sites compared to these temperate sites. At generally lower litter depth, as found in the tropical ecosystems in our study, small differences in this important resource and habitat space parameter might thus play a more important role.

4.2 | Effects of plant species richness and soil pH

Generally, it is under debate whether and how biodiversity of plants and their litter affect arthropod biodiversity (Brose, 2003; Wardle, Yeates, Barker, & Bonner, 2006). In our tropical litter communities, the species richness of harvestmen was elevated at high plant species richness. Considerable evidence suggests that habitat heterogeneity increases animal species richness (Tews et al., 2004), which has also been validated by positive responses of temperate arachnid species richness to higher habitat complexity; that is, a greater diversity of microhabitats (Uetz, 1975), likely correlated to plant species richness in leaf-litter systems (Hansen & Coleman, 1998). Furthermore, plant species richness had positive effects on woodlice and harvestmen biomass; a result directly comparable to temperate litter communities, where woodlice biomass was strongly affected by litter diversity (Ott, Digel, Klarner et al., 2014). The high across-group importance of plant species richness for consumer biomass, together with its strong positive effects, underlines the importance of high habitat and resource heterogeneity for consumer biomass.

The natural pattern of decreasing fungal and increasing bacterial growth with increasing pH (Rousk, Brookes, & Baath, 2009) could be expected to result in idiosyncratic responses of consumers to differing soil pH depending on which resource pool the consumers more heavily exploit. Additionally, the release of toxic elements at low pH (Rousk et al., 2009) most likely imposes different constraints on consumer taxa. Overall, at pH levels as low as in our study sites (4.1–4.8, mean 4.4), we expected even small differences in soil pH to trigger positive effects on consumer communities. In our study, however, higher pH was only related to strongly reduced cockroach species richness, confirming previously found detrimental effects of higher pH on arthropod species richness from temperate grasslands (Mulder et al., 2005). The overall few effects of soil pH differences on our macro-invertebrate consumers might indicate that these animals are either well adapted to such low pH values or that other resource and habitat parameters, such as litter mass and phosphorus availability, simply play a more important role in these systems.

4.3 | Effects of basal resource stoichiometry

Nitrogen content differs strongly along the food chain, both between autotrophs and heterotrophs (Fanin, Fromin, Buatois, & Hättenschwiler, 2013) as well as between different consumer trophic levels (Martinson et al., 2008), justifying the expectation of consumers showing positive effects of nitrogen availability. Following these expectations, we found beetles and detritivores—consumers of different trophic level—to show higher species richness at high nitrogen availability in our tropical field study. Additionally, spider biomass scaled positively with N availability, which could be explained by their high nitrogen demand due to the nitrogen-rich silk they produce (structural elements hypothesis [Kaspari & Yanoviak, 2009]). Together, in concordance with its previously reported importance for consumer biomass (Ott, Digel, Klarner et al., 2014), N availability seems to also positively impact consumer species richness of various groups.

While traditional hypotheses on the importance of phosphorus for consumers focus on consumer growth rate and biomass (Elser, Sterner et al., 2000; Kaspari & Yanoviak, 2009; Sterner & Elser, 2002), we found stronger impacts of phosphorus on consumer species richness than on their biomass under real-world conditions. Similar effects were also found in a study on tropical forest-floor communities where P concentration was found to best predict arthropod diversity as according to Simpson's index (1-D) together with Ca and Na (Sayer et al., 2010). Although phosphorus did not show strong effects on the biomass of any particular taxonomic consumer group, it exhibited relatively high importance across groups and a marginally positive effect on overall biomass. Thus, in our tropical communities, P availability proved important for consumer communities, especially for consumer species richness. Overall, our analyses show that further research is needed to comprehensively disentangle the effects of resource additions and the balanced supply of multiple resources. While such research is relatively common for plant species richness (Harpole et al., 2016), it seems to be largely lacking for animal communities.

Contrary to the results of a previous study on litter nutrient effects on tropical arthropod communities (Sayer et al., 2010) and expectations from the structural elements hypothesis (Kaspari & Yanoviak, 2009), we found calcium availability to have a negative effect on woodlice species richness. Additionally, in contrast to other tropical (Kaspari & Yanoviak, 2009) and temperate (Ott, Digel, Klarner et al., 2014) studies, in our study, woodlice biomass was not elevated at high calcium availability, while termite biomass was strongly reduced at high litter calcium pools. Together, these results might lend support to the resource-ratio theory (Tilman, 1982) as high calcium supply could lead to the strongest competitors for calcium dominating the consumer community, thereby reducing species richness, and constraining or even reducing consumer biomass. In line with previous reports (Sayer et al., 2010), we found sodium to have strong across-group importance for consumer species richness although we did not detect specific effects on any particular consumer group. Furthermore, cockroach biomass was found to be reduced at high

sodium availability. As such, although our results did not confirm positive impacts of sodium availability on consumer biomass (Kaspari et al., 2009; Ott, Digel, Klarner et al., 2014), our data suggest its relatively high importance for consumer species richness in a real-world context. Finally, the strong positive effect of sulphur availability on woodlice species richness and its relatively high across-group importance for species richness might be explained by sulphur being a good indicator of S-rich defence structures and thus nutrient-rich plant material (Bloem, Haneklaus, & Schnug, 2005; Kaspari & Yanoviak, 2009), which is likely of high importance for the detritivores in our tropical litter communities.

4.4 | Few strong and many weak effects

Across our tropical litter communities, most consumer groups exhibited only very few strong effects of our predictor variables on species richness and biomass. None of the consumer groups showed strong effects of more than two predictor variables on either species richness or biomass. However, all averaged models contained the full set of predictor variables from the full models. This indicates that, while there are a few dominating parameters, namely litter mass and phosphorus, our tropical litter communities are jointly influenced by multiple parameters that exhibit a diverse pattern of strong and weak effects. While our results confirm the overarching importance of litter mass, a measure of resource availability and habitat space, and phosphorus for consumer species richness and biomass, they also support recent concepts of co-limitation for consumer–resource interactions (Sperfeld et al., 2012) and decomposition in tropical ecosystems (Kaspari et al., 2008). At a global scale, there are quite pronounced differences of nutrient availability and deposition as well as decomposition rates modulating habitat space in litter systems. Given the importance of such differences in generating patterns of consumer species richness and biomass and their knock-on effects on ecosystem functions such as decomposition, predicted changes in nutrient availability and habitat space due to altered anthropogenic nutrient deposition and land-use patterns will have striking impacts on future biodiversity and ecosystem functioning in ecosystems around the world.

ACKNOWLEDGEMENTS

We thank Megawati, Rizky Nazarreta, Keisha Disa Putirama and Rosario Reza Valentino Lasse for assistance in the field and laboratory. Kara Allen and Bernhard Klarner provided pH and litter mass data, respectively. The Albrecht-von-Haller Institute at Goettingen University conducted elemental analyses. This study was financed by the German Research Foundation (DFG) in the framework of the collaborative German-Indonesian research project EFForTS. We thank the village leaders, local plot owners, PT REKI and Bukit Duabelas National Park for granting us access to and use of their properties. M.J., A.D.B., P.W. and D.O. acknowledge funding in the scope of the BEFmate project by the Ministry of Science and Culture of Lower Saxony, Germany. U.B. gratefully acknowledges the support of the German Centre for

integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig funded by the German Research Foundation (FZT 118). This study was conducted using organisms collected based on Permit 2695/IPH.1/KS.02/XI/2012 recommended by the Indonesian Institute of Sciences (LIPI) and issued by the Indonesian Ministry of Forestry (PHKA).

AUTHORS' CONTRIBUTIONS

M.J., A.D.B. and U.B. designed the study, M.J. and A.D.B. carried out the field and laboratory work, M.J. and A.D.B. prepared the data, and M.J. and P.W. analysed the data. All authors interpreted the results, M.J. wrote a first draft and led the writing, and all authors contributed to writing the manuscript.

DATA ACCESSIBILITY

Data available from the Dryad Digital Repository at <https://doi.org/10.5061/dryad.qn119> (Jochum et al. 2017).

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How to cite this article: Jochum M, Barnes AD, Weigelt P, et al. Resource stoichiometry and availability modulate species richness and biomass of tropical litter macro-invertebrates. *J Anim Ecol*. 2017;00:1–10. <https://doi.org/10.1111/1365-2656.12695>