COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Differing nutritional constraints of consumers across ecosystems

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Abstract Stoichiometric mismatches between resources and consumers may drive a number of important ecological interactions, such as predation and herbivory. Such mismatches in nitrogen (N) or phosphorus (P) content between resources and consumers have furthered our understanding of consumer behavior and growth patterns in aquatic systems. However, stoichiometric data for multiple consumers from the same community are lacking in terrestrial systems. Here, we present the results of a study designed to characterize nutritional constraints within a terrestrial arthropod community. In order to place our results in a broader context, we compared our data on resource–consumer stoichiometry to those of stream and lake ecosystems. We found that N and P varied among trophic levels, and that high N:P content of herbivores suggests that herbivores might experience strong N-limitation. However, incredibly low P-content of plant foliage leads to potential P-limitation in herbivores that is nearly as strong as potential N-limitation.

Moreover, arthropod predators may also be strongly P-limited. In fact, potential nutrient limitation of terrestrial herbivores in our study is similar to nutrient limitation from streams and lakes, suggesting that similar nutritional constraints may be operating across all three study systems. Importantly, our data suggest that consumers in lakes experience a trade-off between N- and P-limitation, while terrestrial consumers experience simultaneous strengthening or weakening of N- and P-limitation. We suggest that P may be overlooked as an important limiting nutrient in terrestrial ecosystems.

Introduction

Ecological stoichiometry predicts that mass-specific nutrient concentrations of individual organisms impact many physiological-, population-, and ecosystem-level processes (Sterner and Elser 2002). At the individual level, consumers with high tissue nitrogen (N) concentrations require N-rich diets otherwise they suffer reduced growth (Kinney et al. 1997; Jensen et al. 2006). As a consequence, consumers choose foods that match their stoichiometric requirements, increase consumption of low quality resources in the absence of more nutritious alternatives, or mix diets until the correct proportion of macronutrients is ingested (Raubenheimer and Simpson 2003; Jensen et al. 2006). Stoichiometric mismatch between resources and consumers may explain the prevalence of omnivory among predators (e.g., dietary mixing to obtain necessary nutrients; Denno and Fagan 2003). Resource–consumer stoichiometry also regulates nutrient concentrations that consumers excrete

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and recycle back to the environment thereby impacting ecosystem processes (Alves et al. 2010).

Historically, insect communities have been considered N-limited (Denno and Fagan 2003; Mayntz et al. 2005). Experiments assessing the effects of nutritional quality on insect performance have therefore focused primarily on dietary N concentrations (Williams et al. 1994; Kinney et al. 1997). Insect consumers may, however, experience stronger phosphorus (P) limitation than typically thought (Elser et al. 2000). Indeed, field experiments have demonstrated co-limitation of Orthopteran abundance by N and P that was mediated through changes in plant biomass (Bishop et al. 2010). Physiological studies have reported P-limitation of Lepidopteran larval development (Perkins et al. 2004). Moreover, foliar %N and %P are often positively correlated in plants (Reich and Oleksyn 2004; Han et al. 2005; Niklas et al. 2005), suggesting that patterns of increased insect performance on plants with high N concentrations may therefore be confounding N-limitation with P-limitation or N:P co-limitation.

Despite recent evidence that insects experience P-limitation during development, and that N and P are strongly correlated within plant tissues, potential P-limitation of terrestrial arthropod communities has received surprisingly little attention (e.g., Bishop et al. 2010). Comparisons of resource–consumer stoichiometry across systems provide valuable insights into potential nutrient limitation (Elser and Hassett 1994; Elser et al. 2000). However, we know of no comparison of resource–consumer stoichiometry within an entirely terrestrial community. Few analyses of terrestrial arthropod stoichiometry currently exist, and none to date have simultaneously quantified primary producer stoichiometry (e.g., Woods et al. 2004; Hambäck et al. 2009; González et al. 2011). The paucity of information on stoichiometry of multiple terrestrial consumers contrasts with the numerous studies of consumers in aquatic systems (Elser and Hassett 1994; Dobberfuhl and Elser 2000; Vanni et al. 2002; Cross et al. 2003; Alves et al. 2010). Previous meta-analyses suggest that stoichiometric imbalance between insects and plants may be similar to those experienced by consumers in aquatic systems (Elser et al. 2000). However, these analyses often do not contrast specific resource–consumer pairs within a community but rely on published stoichiometric data from a variety of unrelated sources. Yet, including unrealized interactions (i.e. connections among non-interacting species such as a specialist herbivore and non-host plants) in analyses of stoichiometric imbalance can potentially give spurious results regarding the degree of mismatch between resources and consumers (Fagan and Denno 2004). Assessments of potential N- and P-limitation should therefore focus on patterns within communities of consumers and resources. These analyses are relatively common in aquatic systems (e.g., Elser and Hassett 1994; Cross et al. 2003; Elser et al. 2010), but multi-species studies are rare in terrestrial communities (but see Denno and Fagan 2003 for comparisons of terrestrial predator–prey interactions) and absent for terrestrial plants and herbivores.

To date, relatively few studies have assessed how stoichiometry varies with arthropod body mass and trophic level. Studies on freshwater fishes have shown that significant variation in stoichiometry with body mass can have large effects on nutrient recycling rates and other ecosystem processes (Vanni et al. 2002). It is likely that similar mechanisms exist in terrestrial systems, but results of recent studies have been mixed. For example, some studies show that %N either increases, decreases, or shows no relationship with arthropod body mass depending on trophic level (Fagan et al. 2002; Hambäck et al. 2009). Other studies have reported no relationship between %N and body mass, despite large variation among trophic levels (Martinson et al. 2008; González et al. 2011). Likewise, %P either declines with body size (Woods et al. 2004; Hambäck et al. 2009; González et al. 2011) or is body-size invariant (Martinson et al. 2008). The variability of these results suggests that stoichiometric variation among trophic levels and by body mass might be system-specific, but the paucity of studies makes it difficult to identify trends.

The goal of this study was to assess the relative potential of N- and P-limitation of multiple herbivores and predators in a terrestrial arthropod community. First, we asked whether consumer stoichiometry varies with trophic level and body mass in ways consistent with prior studies (Woods et al. 2004; Hambäck et al. 2009; González et al. 2011). We predicted that %N and %P would be highest in predators, and that %P would decline with increasing body mass. Second, we quantified the mismatch in resource: consumer stoichiometry for multiple consumers in our system, providing an estimate of the relative potentials of N- and P-limitation. We predicted that potential P-limitation would be as strong as, if not stronger than, potential N-limitation among consumers. Third, we asked how the stoichiometric patterns in our terrestrial arthropod assemblage compare with data from different ecosystems. Given recent calls for cross-ecosystem comparisons in herbivore behavior and foraging strategies (Burkepile 2013; Rotjan and Idjadi 2013), integrating our data with those from other systems places our results within a broader ecological context that might help identify general patterns in stoichiometric imbalances. In particular, stoichiometry is rarely applied to terrestrial communities (Moe et al. 2005), and comparisons of resource:consumer stoichiometry across terrestrial and aquatic systems are sorely needed (Burkepile 2013). We therefore compared our data to previously published data from lakes (Dobberfuhl and Elser 2000) and streams

(Cross et al. 2003). We predicted that patterns of both N-and P-limitation in our study system would be similar to that described for aquatic systems.

Materials and methods

Arthropod collection and stoichiometric analyses

In April 2012, arthropods were collected by hand or with sweep nets from an open grassland in Miami, Florida. All arthropods were identified to the lowest possible taxonomic level (i.e. genus or species) and assigned to one of four trophic levels (detritivore, herbivore, predator, or omnivore) based on scientific literature, field guides, or first-hand observations (Table A1). However, we excluded omnivores from our analyses due to difficulties in matching omnivores to appropriate food sources and quantifying the percentage of plant and insect food sources comprising omnivore diets. Most species were collected as adults, although two taxa were represented by immature individuals (Table A1). We did not collect both adults and juveniles of any one species. Data describing ontogenetic shifts in body elemental composition are rare. However, there is evidence that body %P declines with age as growth rate slows (Elser et al. 2003; Elser et al. 2006; Back et al. 2008). Thus, our analyses of adult tissues provide a conservative estimate of the severity of P-limitation for insect consumers. Further, stoichiometric mismatches can have negative effects on both juvenile and adult fitness (Jensen et al. 2006).

Food items for herbivores (e.g., grasses, forbs) and detritivores (e.g., leaf litter, detrital material) were gathered during the same sampling period. Potential diet items were identified to the lowest possible taxonomic level. Samples were kept frozen until they were dried to constant mass at 60 °C (~48 h) and weighed to determine an average dry mass for each species. Individuals of each species were pooled and ground for nutrient analyses, yielding one data point for each species. Carbon (C) and N content of arthropod and plant samples were determined using a carbon–nitrogen elemental analyzer (Thermo Scientific) (Tao and Hunter 2012). Phosphorus content was determined using dry oxidation–acid hydrolysis extraction followed by colorimetric analysis (Elser et al. 2003; Woods et al. 2004). All stoichiometric ratios (C:N, C:P, N:P) are reported as molar ratios.

We analyzed three stoichiometric response variables: %N, %P, and the N:P ratio. Previous analyses of arthropod stoichiometry suggest that N or P can vary with body size (Woods et al. 2004), trophic level (Fagan et al. 2002), or both (Fagan et al. 2002; Hambäck et al. 2009). For each variable, we used AIC to compare four potential models describing variation in stoichiometry: (1) a null model of

no difference among trophic levels or body mass, (2) a linear relationship between stoichiometry and body mass, (3) differences in stoichiometry among trophic levels, and (4) a full model with additive and interactive effects of body mass and trophic level. The model with the lowest AIC was chosen as the best-fitting model. Models with ΔAIC > 2.0 were considered to provide a substantially worse fit than the best model. If the trophic level model was chosen as the best model, we conducted post hoc pairwise comparisons among trophic levels using Tukey's HSD corrections for multiple comparisons.

Resource:consumer elemental ratios were calculated for plants:herbivores (C:N, C:P, and N:P) and prey:predators (C:N and C:P) following Denno and Fagan (2003). Ratios were only calculated for realized interactions. Realized interactions were determined based on first-hand species knowledge, literature sources, and field guides for herbivores and plants (Table A2) and predators and prey (Table A3). We calculated a single resource:consumer ratio for specialist consumers that target only one food source. For generalists, we calculated resource:consumer ratios for the range of known diet items. For example, two Curculionid weevil species each consume leaves of both *Ficus aurea* and *Coccolobo uvifera* trees, but not grasses or forbs. Thus, we assumed that the stoichiometric ratios of these weevil species to *F. auerea* and *C. uvifera* were important, but the ratios with grasses and forbs were not. Further, the gieger tortoise beetle, *Eurypepla calochroma,* specializes on the gieger tree, *Cordia sebestena*. We therefore calculated only the stoichiometric ratio between *E. calochroma* and *C. sebestena*.

Resource:consumer ratios measure the strength of nutrient limitation for consumers. For example, C:N resource:consumer ratios measure the difference in N-content between consumers and resources ($\frac{C_{res}}{N_{res}}/\frac{C_{cons}}{N_{cons}} = \frac{C_{res}}{N_{res}} \times \frac{N_{cons}}{C_{cons}}$, where C corrects for the minimal differences in carbon content between resources and consumers: $C_{res} \approx C_{cons}$). C:N and C:P resource:consumer ratio values >1 indicate that consumers have higher N or P content than their resources, respectively, and are therefore likely to experience nutrient limitation (see supplementary information Sect. 4 for details). A value of 1 indicates that consumers and resources have identical C:N, C:P, or N:P ratios. Most plant carbon derives from lignins and other indigestible compounds that can reduce nutritional quality of plant material for herbivores. Thus, C:N ratios provide an estimate of nutritional quality whereby plants high in C and low in N have high C:N values and are likely low in quality. Conversely, lower C:N values mean a higher proportion of nitrogen to carbon implying higher nutritional quality. We recognize that such ratios provide only a coarse estimate of consumer nutrient limitation and that they ignore the fact that herbivores do not extract all nutrients from ingested plant material, that the efficiency with which herbivores absorb nutrients can vary

among plant species, and that %C provides a poor estimate of carbohydrate availability for insect herbivores (e.g., Clissold et al. 2013). However, ratios of stoichiometric mismatch similar to those reported here have been successfully used to describe consumer resource limitation in a wide variety of ecosystems (Elser and Hassett 1994; Dobberfuhl and Elser 2000; Elser et al. 2000; Denno and Fagan 2003; Cross et al. 2003; Malzahn et al. 2007). For example, mismatch of elemental ratios can explain survival and growth of terrestrial insects (Huberty and Denno 2006; Jensen et al. 2006).

We used density plots and boxplots to assess the distribution of resource:consumer ratios. A *t* test was used to compare mean C:N and C:P resource:consumer ratios for both prey:predators and plants:herbivores. All data were analyzed for normality and homoscedasticity using plots of residuals and boxplots. When appropriate, we used weighted linear models where weights were the inverse of the variance in each trophic level. This corrected for substantial heteroscedasticity among trophic levels (see Supplementary Information Sects. 1–4). All statistical analyses were conducted in R v.2.15 (R Core Team 2012). All code (statistics and graphics), raw statistical output, and additional figures are provided in the Supplementary Information to enable reproduction of our results (Wolkovich et al. 2012). Raw data from our study system are provided as appendices (Tables A1, A2, A3).

Results

Consumer stoichiometry, trophic level, and body mass

We collected 27 species spanning 13 orders and 21 families. Species encompassed three trophic levels: (1) detritivores ($n = 10$ species), (2) herbivores ($n = 10$ species), and (3) predators ($n = 7$ species) (Table A1). Nitrogen content varied considerably among species [9.84 $\pm$ 2.73 %N (mean $\pm$ 1SD), coefficient of variation = 0.28]. The model allowing for differences among trophic levels was the best model describing variation in %N (Table 1). Post hoc tests determined that detritivores had significantly lower %N than herbivores or predators (Fig. 1a). Predators contained, on average, 1.23 $\pm$ 0.60 (mean $\pm$ 1SE) more %N than herbivores, although this difference was not significant ($p = 0.111$). The model incorporating interactive effects of trophic level and body mass also supported the data well (ΔAIC = 1.5), but following the principle of parsimony, we chose the model with fewer parameters as a better fit to the data.

Phosphorus content also varied considerably among species [0.76 $\pm$ 0.26 %P (mean $\pm$ 1SD), coefficient of variation = 0.34]. The model allowing for differences in %P among trophic levels was chosen as the best model

Table 1 AIC table for % nitrogen

| Model	AIC	*df*	ΔAIC
Trophic level	110.4	4	0.0
Trophic level $\times$ mass	111.5	7	1.5
Mass	123.1	3	13.2
Null	123.2	2	13.3

(Table 2). Predators had, on average, 0.29 $\pm$ 0.09 % (mean $\pm$ 1SE) more P than herbivores ($p = 0.008$; Fig. 1b). All other models had significantly less support (ΔAIC > 3.3). Similar to %N and %P, the trophic level model best explained variation in the N:P ratio of insects in our study system (Table 3). Predators had significantly lower N:P ratios than herbivores [10.32 $\pm$ 3.86 (mean $\pm$ 1SE), $p = 0.033$; Fig. 1c].

Resource:consumer stoichiometric mismatch

Mean prey:predator ratios were significantly >1 for both C:N ($p = 0.004$) and C:P ($p = 0.016$). In fact, mean resource:consumer ratios did not differ between C:N or C:P ($p = 0.542$) (Fig. 2a). This suggests that herbivorous prey contained significantly less N and P than did arthropod predators, potentially causing both N- and P-limitation of predators. In fact, potential P-limitation of predators in our system may be as strong as N-limitation.

Given that herbivores had high %N, low %P, and a high N:P ratio (Fig. 1), we expected the strength of potential nitrogen limitation to be much greater than potential P-limitation. As expected, C:N resource:consumer ratios for plants and herbivores were significantly >1 ($p < 0.001$; Fig. 2b), suggesting N-limitation. However, resource:consumer ratios for C:P were also significantly >1 ($p < 0.001$; Fig. 2b), suggesting strong potential P-limitation in our study system. This was due to the extraordinarily low %P in foliage [0.17 $\pm$ 0.09 (mean $\pm$ 1SD), coefficient of variation = 0.54] compared to herbivores. The mean resource:consumer ratio of C:P was significantly lower than that of C:N ($t = 2.395$, $p = 0.021$). Thus, while phosphorus may be a limiting nutrient, potential N-limitation appears to be, on average, stronger than that of P.

Percent N and P covaried within plant species ($r = 0.69$, $p = 0.058$). Only low sample size ($n = 8$ plant species) kept this correlation from statistical significance. Therefore, plant:herbivore ratios of C:N and C:P are also correlated. Regression of C:P against C:N plant:herbivore ratios revealed a significant, positive relationship (slope = 1.04, 95 % CI = 0.60–1.48, $R^2 = 0.52$, $p < 0.001$; Fig. 3). This suggests that the potential strength of P-limitation increases in direct proportion to potential N-limitation for insect herbivores in our study system.
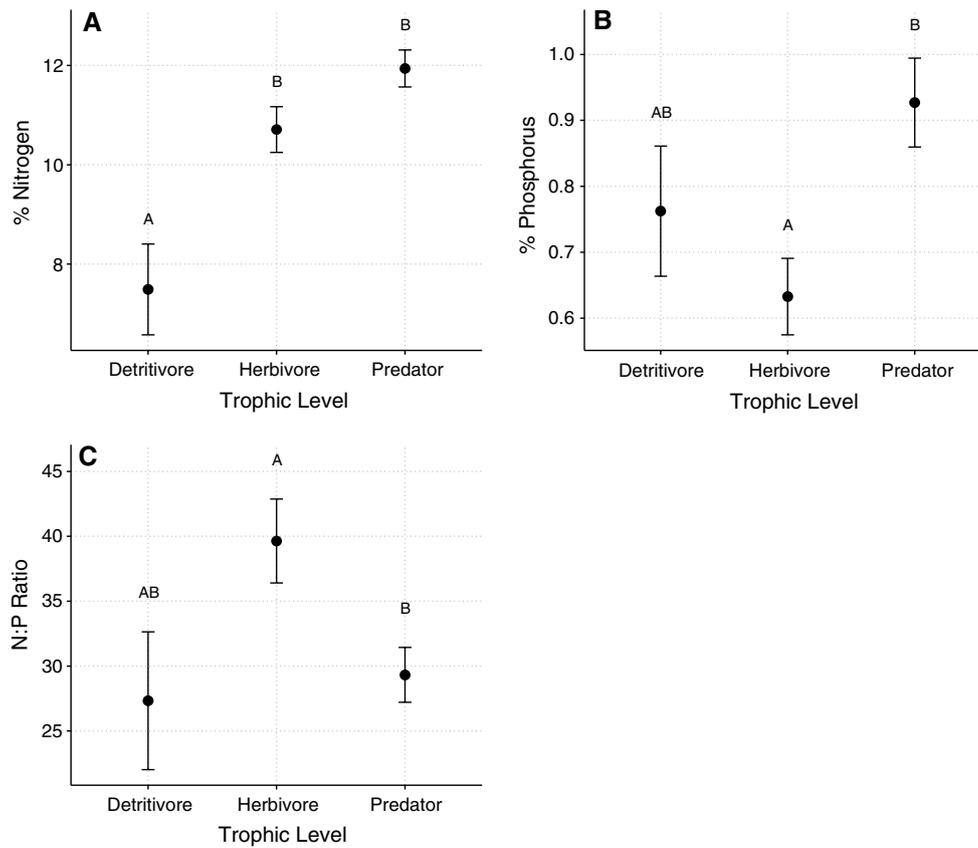
Fig. 1 a Differences in %N among trophic levels. **b** Differences in %P among trophic levels. **c** Variation in N:P ratios among trophic levels. *Points* are mean ± 1SE, *letters* denote significant differences among groups detected by Tukey's HSD post hoc test

Table 2 AIC table for % phosphorus

Model	AIC	df	ΔAIC
Trophic level	0.1	4	0.0
Trophic level × mass	3.3	7	3.2
Null	6.2	2	6.1
Mass	8.0	3	7.9

Table 3 AIC table for N:P ratio

Model	AIC	df	ΔAIC
Trophic level	208.4	4	0.0
Trophic level × mass	210.5	7	2.1
Null	212.2	2	3.7
Mass	214.2	3	5.7

Stoichiometric mismatch among systems

Mean C:N resource:consumer ratios differed among three different study systems: lakes, streams, and our terrestrial habitat (Fig. 4a; one-way ANOVA, $p < 0.001$). Post hoc tests showed that streams had the highest potential N-limitation, followed by our terrestrial system, and lakes had the lowest potential N-limitation ($p < 0.0001$ for all comparisons). Excluding detritus-based ratios in streams (red highlighted points in Fig. 3) did not substantially change these results, except that our terrestrial system was only marginally different from the stream system (Tukey's HSD, $p = 0.055$).

C:P resource:consumer ratios from our terrestrial system fell within the range of resource:consumer ratios from lake and stream systems, which are traditionally considered P-limited (Fig. 4b). Mean C:P resource:consumer ratios differed among study systems (one-way ANOVA, $p < 0.001$). Post hoc tests revealed that C:P resource:consumer ratios from our terrestrial system did not differ from lakes ($p = 0.743$), but streams had higher C:P resource:consumer ratios than both our system and lakes ($p < 0.001$). These differences remained significant after removing terrestrial detritus-based resources from the stream data (red highlighted points in Fig. 3). Even though streams had higher mean C:P resource:consumer ratios, C:P resource:consumer ratios from our study system fell within the range of C:P resource:consumer ratios present in streams.
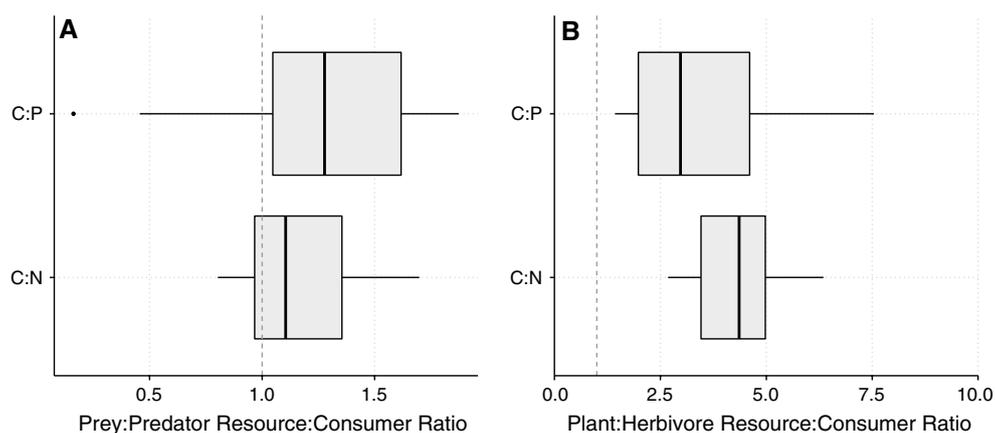
Fig. 2 a Boxplots of predator–prey resource:consumer ratios for C:N and C:P. Ratios were from realized interactions between arthropod predators and prey (Table A3). **b** Boxplots of herbivore–plant resource:consumer ratios for C:N and C:P. Ratios were from realized interactions between insect herbivores and plants (Table A2). The *dotted lines* represent a 1:1 ratio where consumers and resources have identical stoichiometry. *Boxes* denote the inter-quartile range (25–75 percentile) containing the middle 50 % of the data. The *solid line* is the median value. *Whiskers* denote the upper and lower extremes of the data, and *points* represent statistical outliers. Thus, these boxplots show the entire range of the data
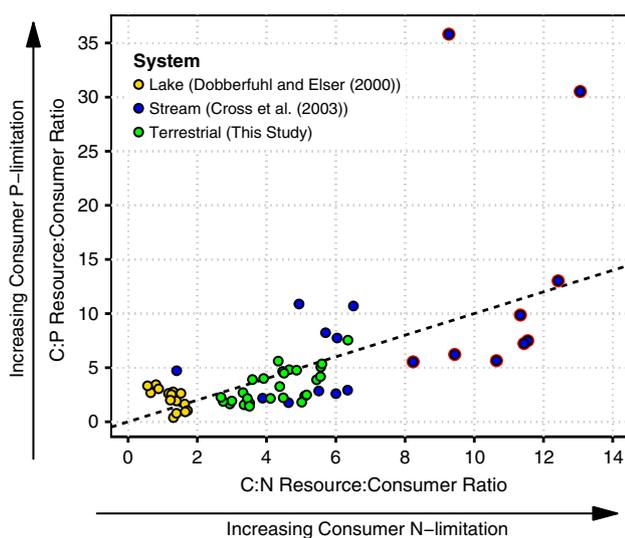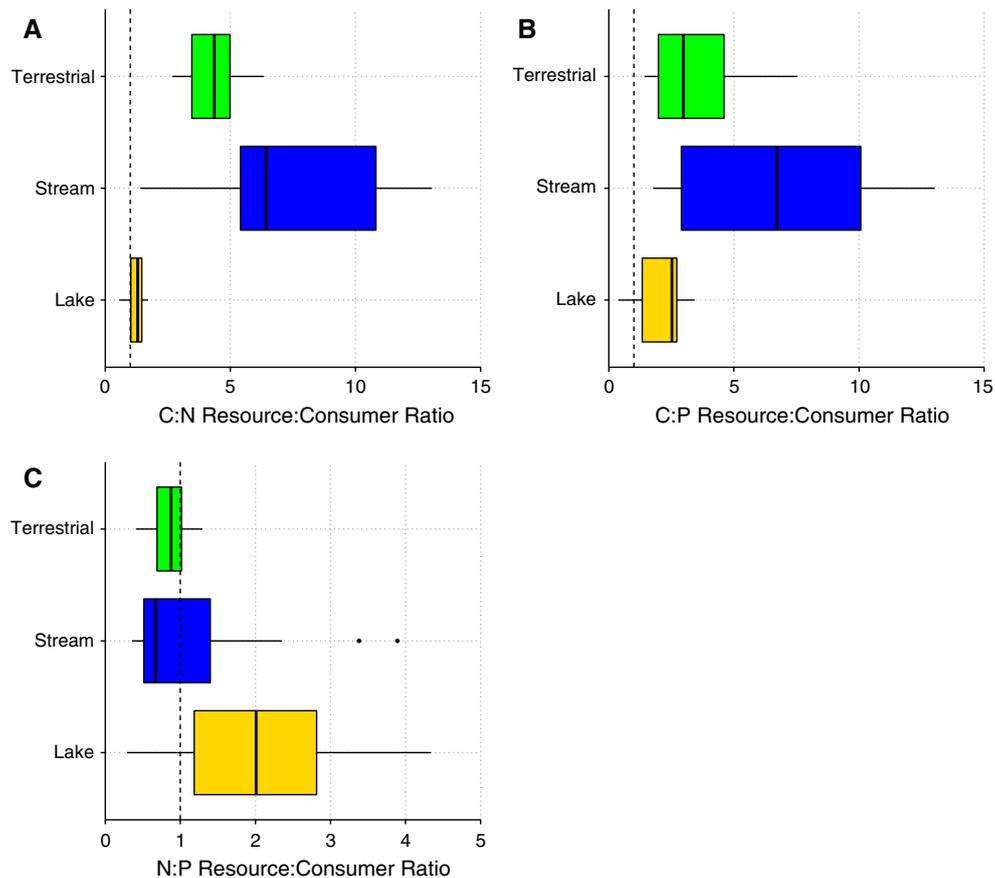

Fig. 3 C:P and C:N resource:consumer ratios for primary producers and consumers. *Dashed line* indicates a 1:1 relationship through the origin. *Red highlighted points* are stream resource:consumer ratios based on leaf detritus and are therefore derived from terrestrial production. Stream data from Cross et al. (2003), lake data from Dubberfuhl and Elser (2000) (color figure online)

Interestingly, C:P and C:N resource:consumer ratios between lake seston and zooplankton were negatively related ($R^2 = 0.50$, $p = 0.003$). C:P and C:N ratios in streams showed a weak, but significant, positive correlation ($R^2 = 0.20$, $p = 0.03$). This suggests that, in contrast to our terrestrial system and the stream system, lake consumers experience trade-offs between N- and P-limitation rather than simultaneous, proportional increases.

As an additional metric of stoichiometric mismatch, we also calculated resource:consumer ratios for N:P stoichiometry in each system. The mean N:P resource:consumer ratio from the lake system was significantly >1 ($p = 0.006$), indicating that, on average, lake consumers had substantially less P per unit N than did lake primary producers and are therefore likely to be more P-limited than N-limited. N:P resource:consumer ratios in streams did not differ from 1 ($p = 0.445$). The mean N:P resource:consumer ratio for our terrestrial system was significantly lower than 1 ($p = 0.002$), indicating that terrestrial herbivores contained, on average, more P per unit N than did plants, indicating that terrestrial herbivores are likely to be more N-limited than P-limited. Accordingly, N:P resource:consumer ratios for terrestrial systems were significantly lower than in lakes ($p = 0.001$) but nearly identical to those found in streams ($p = 0.312$) (Fig. 4c). Removing detritus-based ratios from the stream data did not substantially affect the results.

Discussion

In the past decade, ecologists have devoted considerable attention to understanding macroecological and evolutionary restrictions on consumer stoichiometry in order to determine the causes of nutritional constraints on consumers. However, in order to assess the strength of nutrient limitation, analyses of both consumer and resource stoichiometry for multiple consumers in an ecosystem are necessary. Here, we show systematic variation in stoichiometry among trophic levels in arthropod communities with predators often having the highest levels of N and P. Despite previous

Fig. 4 a C:N, **b** C:P, and **c** N:P resource:consumer ratios for primary producers and consumers from terrestrial (this study), lake (Dobberfuhl and Elser 2000), and stream (Cross et al. 2003) ecosystems. *Vertical dashed line* is at 1, or stoichiometric equivalence between resources and consumers. Values >1 indicate that resources are phosphorus-poor compared to consumers, whereas values <1 indicate that resources are nitrogen-poor compared to consumers. Data presented as in Fig. 2

studies documenting the importance of body mass on consumer stoichiometry, we found little evidence that %N or %P were strongly related to body mass in our study system. Further, we demonstrate strong potential N-limitation of herbivores in our terrestrial study system due to a mismatch between resource and consumer nitrogen content. Importantly, P-limitation, which has historically been assumed to be uncommon in terrestrial systems (Mattson 1980), may also be common in our study system and almost as strong as N-limitation. Further, P-limitation is positively correlated with N-limitation, suggesting likely co-limitation, and is similar in magnitude to potential P-limitation reported in lakes and streams, traditionally considered to be P-limited systems.

Our data indicate substantial variation in nitrogen content among arthropod trophic levels. Detritivores had particularly low %N, an observation at odds with other studies reporting %N of detritivores between herbivores and predators (Martinson et al. 2008; González et al. 2011). Our estimates of %N and %P in herbivores and predators are similar to the values reported from other insect communities (Fagan et al. 2002; Woods et al. 2004; González et al. 2011). However, we found no difference in %N between herbivores and predators, even though similar stoichiometric surveys have reported higher %N in predators (Fagan et al. 2002; González et al. 2011). Despite the lack of a statistically significant difference, %N of predators in our study was 1.23 ± 0.59 (mean $\pm$ 1SE) times higher than that of herbivores, which is similar to effect sizes reported by other studies (Fagan et al. 2002). Detecting significant differences between herbivores and predators often requires contrasts within order or family to minimize phylogenetic variation in stoichiometry (Fagan et al. 2002; González et al. 2011). Unfortunately, we lacked enough replicates of herbivores and predators within each order to make such comparisons, which would increase our statistical power. Additionally, many of the insect species in our study belonged to Coleoptera and Orthoptera, two orders which do not show significant declines in %P with body mass (Woods et al. 2004). Thus, variation in %P with body mass

may be influenced more by phylogeny than by mass per se. In contrast, predatory insects had significantly higher %P than did herbivores. Previous studies have reported no variation in %P among trophic levels (Woods et al. 2004) or higher %P in predators compared to herbivores (González et al. 2011), as reported here. Though terrestrial insects tend to be homeostatic with respect to N, and to a lesser extent P (Persson et al. 2010), diet quality can influence insect nitrogen use and body composition (Karowe and Martin 1989). Differences in %N and %P between our data and other datasets might therefore be related to variation in diet quality among communities.

Nutrient limitation may be a driving mechanism behind the prevalence of intraguild predation among predatory arthropods (Denno and Fagan 2003; Fagan and Denno 2004). Generally, N has been considered the primary limiting nutrient. Indeed, our estimates of resource:consumer ratios of C:N are nearly identical to those reported by Fagan and Denno (2004), indicating that N-limitation may be prevalent among arthropod predators. Additionally, C:P predator–prey resource:consumer ratios were indistinguishable from C:N ratios, suggesting that P-limitation of arthropod predators may be as strong as N-limitation and could influence many predator foraging decisions. Indeed, large mismatches in %P between predators and herbivores can reduce the growth and fitness of predators (Malzahn et al. 2007). Given that nutrient mismatches can drive foraging decisions of arthropod predators (Mayntz et al. 2005), stoichiometric mismatches may be important determinants of predator diet choice. Thus, P-limitation of predators in terrestrial arthropod assemblages deserves more attention.

Our results support the proposition by Elser et al. (2000) that terrestrial insect herbivores may be as strongly P-limited as aquatic consumers. Indeed, larval insect experience reduced growth and extended development times on P-limited diets (Perkins et al. 2004; Visanuvimol and Bertram 2011). Our data show that the potential strength of P-limitation increases linearly, and strongly, with potential strength of N-limitation for terrestrial herbivores. Experimental fertilization with N and P have reported possible N:P co-limitation of arthropod herbivores (Bishop et al. 2010), and our data suggest that this deserves further consideration in terrestrial systems. Interestingly, the magnitude of mismatch between resource and consumer P-content within communities is similar in terrestrial and aquatic systems (Fig. 4), suggesting similarities in P-limitation across drastically different ecosystems.

We know of no other study examining the strength of consumer nutritional limitation within communities across multiple ecosystems. Co-limitation of primary producers by N and P is surprisingly consistent in both magnitude and prevalence across freshwater, marine, and terrestrial systems (Allgeier et al. 2011; Harpole et al. 2011).

Our data suggest that there may not be such similarities in co-limitation of consumers across ecosystems. For example, resource:consumer C:N ratios suggest that consumers experience much stronger N-limitation in freshwater and terrestrial ecosystems as compared to lake ecosystems (Fig. 3). Furthermore, our data suggest that there is a trade-off between N- and P-limitation of consumers in lake systems, where alleviating N-limitation results in stronger P-limitation (Fig. 3). In contrast, N- and P-limitation of consumers are positively related in terrestrial systems, where alleviating N-limitation should simultaneously alleviate P-limitation (Fig. 3). This pattern matches experimental studies demonstrating that N-enrichment of basal resources induces consumer P-limitation of lake zooplankton (Elser et al. 2010) but not of terrestrial insects (Tao and Hunter 2012). Thus, our data provide support for contrasting experimental outcomes in two different ecosystems.

Our study has a few potential limitations that warrant discussion. First, our data are a coarse examination of trophic interactions in our community. Insects and plants were sampled in a single season, and plant stoichiometry might vary seasonally. Seasonal changes in resource stoichiometry can induce seasonal nutrient limitation of consumers that would not be captured by our study (Schade et al. 2003). However, studies of resource:consumer stoichiometry that ignore seasonality have successfully described patterns of nutrient limitation in a variety of ecosysytems (e.g., Elser and Hassett 1994; Cross et al. 2003; Fagan and Denno 2004). Second, the fact that we sampled organisms from a single site could obscure important spatial differences in stoichiometry. Finally, herbivores of various feeding guilds (e.g., leaf chewers, sap suckers) may have different stoichiometric imbalances resulting from heterogeneity in stoichiometry among plant tissues (i.e. aphids feed on N-depleted phloem) (Tao and Hunter 2012). We were not able to capture such variation, as we did not separate potential diet items on such a fine scale.

Historically, ecologists have focused primarily on N-limitation of terrestrial arthropod communities (Mattson 1980). Ecologists have only recently begun to acknowledge that herbivorous insects may be limited by an array of micro- and macro-nutrients in addition to N (Joern et al. 2012). Interestingly, we found that the strength of N- and P-limitation are linearly related due to strong covariation in foliar %N and %P among plant species, and that this pattern differs considerably from other ecosystems. Given that %N and %P are frequently correlated in plants (Han et al. 2005; Niklas et al. 2005), we suggest that many observations of herbivore feeding preferences that measure only %N may be confounding N-limitation with P-limitation or possible N:P co-limitation. This contrasts with the relationship between N- and P-limitation of consumers in other ecosystems, such as lakes. Thus, stoichiometric patterns

from lake ecosystems may not apply to a broader set of ecological communities. Moreover, predators have consistently higher body N and P content than their herbivorous prey suggesting that nutrient limitation may be present at multiple trophic levels. Thus, phosphorus, like nitrogen, appears to be an important, albeit often overlooked, determinant of arthropod ecology. We suggest that further research on P-limitation in terrestrial communities is especially important for understanding the consequences of resource–consumer stoichiometry and ecosystem function in terrestrial ecosystems.

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