

REPORT

Stoichiometry of actual vs. potential predator–prey interactions: insights into nitrogen limitation for arthropod predators

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Abstract

Literature-compiled data sets demonstrate wide interspecific variation in nitrogen content among terrestrial arthropods and raise the possibility of nitrogen (N) limitation for predatory species. It remains unclear, however, whether the same disparities between N supply and demand that appear in literature compilations also exist in particular ecological communities. To address this uncertainty, we compared arthropod predator–prey stoichiometries derived from a compiled database with those from a natural *Spartina* saltmarsh community. Separate assessments of potential N-limitation were made for arthropod predators feeding on herbivores and for intraguild predators feeding on intraguild prey. Relative to the compiled database, saltmarsh consumer–resource interactions exhibited increased disparity between N-content of herbivores and N-demand by predators. The high N content of saltmarsh arachnids relative to predatory insects at large may contribute to the supply–demand disparity. Whether N-limitation of terrestrial arthropod predators is widespread in the marsh, and in nature in general, depends sensitively on the predatory species' gross growth efficiencies for N and carbon. Obtaining hard empirical data for these efficiency parameters should be a research goal.

Keywords

Dietary nitrogen, nitrogen content of grasses, nitrogen content of insects, nitrogen content of spiders, nutrient demand, *Spartina* salt marsh.

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INTRODUCTION

For decades, ecologists have recognized that tremendous variation exists among ecosystems with respect to the nutrient content (e.g. C : N ratio) of plants at the base of terrestrial food webs (e.g. Mattson 1980; White 1993). Only recently have they realized that significant interspecific variation in stoichiometry (C : N : P) also exists among arthropod consumers in the same terrestrial communities (Siemann *et al.* 1996; Fagan *et al.* 2002; Woods *et al.* 2004). For example, differences in body size, phylogenetic affinity, and trophic position all contribute to the two- to threefold variation in mass-specific nitrogen content that is known to occur among terrestrial insects alone (Fagan *et al.* 2002). Understanding the magnitude and sources of this interspecific variation would allow for better characterization of the nutrient demands of the various members forming terrestrial food webs, and thus provide enhanced insights into species interactions and

food web dynamics. For example, a consumer with a low C : N body content should have higher dietary demands for nitrogen than one characterized by a high C : N ratio (Sturner & Elser 2002), and differential demands for resources may translate into altered patterns of behaviour and community impacts (Raubenheimer & Simpson 1993; Simpson *et al.* 2002).

Interspecific differences in N-demand among herbivore species, among predator species, and between herbivores and predators have important implications for the dynamics and complexity of terrestrial food webs and the evolution of dietary specialization and generalization (Denno & Fagan 2003). For example, due to differences in their biochemical construction, some herbivorous insect species feeding on a particular plant may be N-limited even if others are not (Denno *et al.* 2000). Likewise, many predaceous arthropods are sufficiently N-rich relative to commonly available herbivorous prey that these predators would be strongly N-limited if they restricted their feeding to a single

nutrient-poor prey species (Denno & Fagan 2003; Matsumura *et al.* 2004).

These general expectations depend in part on speculation about the functional consequences of interspecific differences in consumer nutrient demand evident in compiled databases of insect stoichiometry (Elser *et al.* 2000; Sterner & Elser 2002; Denno & Fagan 2003). However, the unsystematic nature of literature-compiled databases necessarily leaves open a host of issues concerning the stoichiometry of consumer–resource interactions in specific terrestrial food webs (detailed in Fagan *et al.* 2002). Not the least of these is the need to separate those consumer–resource interactions that actually take place in nature from those that are merely possible based upon data tabulated from multiple sources. Discrepancies between compiled data sets and the real world may arise for many reasons, such as dietary specialization of included species, observer bias toward taxa with unique stoichiometries, or unrecognized constraints on the stoichiometry of interactions in real-world food webs. Consequently, it is important to characterize what differences, if any, exist between hypothetical species interactions and those known to occur in a particular community.

Here we analyse the stoichiometric structure of consumer–resource interactions that occur within a well-studied food web, the assemblage of arthropods associated with *Spartina* cordgrasses that dominate the intertidal marshes along the mid-Atlantic coast of North America. We seek to understand at the community level how the C : N stoichiometry of real species interactions within the *Spartina* system, where nitrogen-limitation of herbivores is well-documented (Denno *et al.* 2002), compares with the broad range of potential interactions suggested by previous literature compilations. Moreover, we explore why stoichiometric relationships among arthropods in the marsh food web differ from expectations based on the compiled literature. Such explanations include domination of the *Spartina* food web by nitrogen-depauperate herbivores feeding on nitrogen-poor grasses, by predators with exceptionally high body nitrogen content (e.g. spiders), and by the over-representation of predators that frequently engage in intraguild predation (see Denno & Fagan 2003; Matsumura *et al.* 2004). This comparison is the first step towards understanding how the stoichiometries of unique natural systems compare with composite databases. Continuing a line of inquiry introduced in Fagan *et al.* (2002) and Denno & Fagan (2003), we compare the stoichiometries of arthropods in the marsh system with those from a large compiled data set. Our objectives are to quantify the likelihood that terrestrial arthropod predators may routinely face N-limitation and ascertain whether differences exist between strict and intraguild predators.

METHODS

Literature-compiled data set

For comparison with the *Spartina* saltmarsh system, we used the database of arthropod stoichiometries compiled from the literature by Fagan *et al.* (2002). This database, which includes the C : N body content for 119 herbivorous insect species and 33 predatory arthropod species (31 insects and two spiders) collected from dozens of ecosystems on several continents, is available online at: <http://www.nceas.ucsb.edu/ecostoichiometry>. Given the diverse sources that contributed to this database, we use it here only to define what is possible with regard to the nitrogen dynamics of consumer–resource interactions between pairs of terrestrial arthropod species. We recognize that many of the potential interactions would never occur by virtue of mismatched spatial distributions, feeding styles, body plans, and other factors, and instead manipulate the database only to get a sense of how interspecific variability in nitrogen content among insects might translate into variability in how nitrogen moves across trophic levels via different pairwise interactions. We focus here on the stoichiometry of consumer–resource interactions by calculating a ratio of C : N ratios ($C : N_{\text{resource}} / C : N_{\text{consumer}}$) that provides a gauge of how mismatched potential predators and prey might be with regard to nitrogen demand and supply. We calculate this ratio for all possible combinations of predators and prey (i.e. 33×119 ratios for predators feeding on herbivores and 33^2 ratios for intraguild predation, including cannibalism).

Mid-Atlantic saltmarsh data set

Representatives of eight species of herbivorous insects and 23 species of predatory arthropods (11 insects, 11 spiders, and one pseudoscorpion) were collected from meadows of the saltmarsh cordgrasses *Spartina alterniflora* and *Spartina patens* in Tuckerton, NJ, USA during July 2002 (see Matsumura *et al.* 2004 for details on sampling and C : N determination). These species constitute a so-called ‘source food web’ (Morin 1999) that starts with a suite of herbivores that feed on *Spartina* plants and then includes known predators of those herbivores. Some of these predators are also intraguild predators, defined here as predators that feed on both herbivores and predators. Here we also differentiate such intraguild interactions from ‘strict’ predation in which a predatory species is feeding on an herbivorous species. The predators sampled may feed on other species in the saltmarsh, but those species are not represented here. The stoichiometries of these species are available as Appendix A to Matsumura *et al.* (2004).

We focus on the stoichiometries of pairwise consumer–resource interactions, and we distinguish pairwise interactions involving a predator feeding on an herbivore from those involving intraguild predation. For each of these two cases, we develop three subsets of pairwise interactions from the *Spartina* arthropod stoichiometry database. First, we consider all possible pairwise interactions without regard to whether they actually occur or not; this approach is equivalent in scope to the assessment of what is numerically possible in the literature-compiled database described above. Second, we extract the subset of pairwise interactions that actually occur within New Jersey *Spartina* marshes. We refer to this subset of interactions as ‘realized interactions’. This ‘who-eats-whom’ breakdown of species interactions in the *Spartina* saltmarsh system has been worked out via extensive observations and experiments over the last three decades by Denno and colleagues (e.g. Döbel & Denno 1994; Denno *et al.* 2000, 2002, 2003; Finke & Denno 2002; Gratton & Denno 2003). Third, we extract the still smaller subset of pairwise interactions known to occur on a regular basis (which we call ‘frequently realized interactions’), excluding those interactions that occur only occasionally, by virtue of differences between consumer and resource species involving issues of prey preference, body size, host plant specificity, phenology, and vertical position with the vegetative strata. Realized and frequently realized interactions are identified in a data matrix available upon request from the authors.

Comparison of realized and potential consumer–resource stoichiometries

We focus our analyses of these databases along two axes. First, we compare the full range of potential interactions within the *Spartina* system with what is numerically possible based on the compiled database. Second, we examine how the subset of real-world interactions that actually occurs in the saltmarsh compares with the two distributions of potential interactions, both in the saltmarsh and from the compiled data set at large.

Separate comparisons are made for the pairwise data sets involving predators feeding on herbivores and those involving intraguild predation. Nonparametric Mann–Whitney *U*-tests are used to test for differences in central tendency whereas Kolmogorov–Smirnov nonparametric statistics are used to test for differences in the shape of the frequency distributions between the data sets. Using these comparisons we hope to gain insight into general patterns of nitrogen limitation. For example, do consumers feed on prey that will provide the best matches to their own body stoichiometry, or are saltmarsh predators saddled with problems of nitrogen limitation more extreme than those predicted by the compiled data set?

The threshold elemental ratio and N-limitation of consumers

Stoichiometric theory permits an estimation of the degree to which a particular pairwise consumer–resource interaction affects consumer growth via N-limitation. As introduced by Urabe and Watanabe (1992) and further discussed by Sterner & Elser (2002), it is possible to estimate the ‘threshold elemental ratio’ (TER) of a predator by knowing its N requirements and its efficiency in retaining carbon (C) and N from ingested food. The TER corresponds to the prey C : N ratio above which a predator should experience a growth penalty by virtue of feeding on prey that is of low nutritional quality relative to the predator’s demands, specifically:

$$\text{TER}_{C:N} = (\text{GGE}_N/\text{GGE}_C)C:N_{\text{predator}} \quad (1)$$

where GGE_N is the maximum gross growth efficiency for N (i.e. the fraction of ingested N that the animal converts into new biomass, taking values from 0 to 1), GGE_C is the maximum gross growth efficiency for C (as for N), and $C:N_{\text{predator}}$ is the C : N ratio of the predator’s biomass. In this framework, N-limited predator growth occurs when:

$$(C:N_{\text{prey}}/C:N_{\text{predator}}) > \text{GGE}_N/\text{GGE}_C \quad (2)$$

Estimates of gross growth efficiencies for N and C for specific terrestrial predatory arthropods appear essentially unknown. In general, thermodynamic considerations have been used to argue that GGE_C in metazoans is limited to no more than 0.35–0.50 (Calow 1977, Schroeder 1981). Empirical estimates of GGE_C for a selection of carnivorous species in aquatic habitats are generally similar but some go higher (c. 0.60; Valiela 1984). For some parasitoids, estimates of GGE_C are around 0.20–0.66 (Vinson & Barbosa 1987). Empirical data for GGE_N appear very scarce as well, though modelling studies have assumed estimates of 0.65–1.0 for GGE_N (or the corresponding efficiency for other key nutrients, such as phosphorus) (Olsen *et al.* 1986, Sterner 1990). Given the scarcity of nitrogen relative to carbon in the tissues of potential prey (e.g. Denno & Fagan 2003), it seems reasonable to assume that predatory arthropods would, at a minimum, be at least as good at utilizing N from their prey as C, such that $\text{GGE}_N/\text{GGE}_C \geq 1$ (see also Andersen and Hessen 1995). In actuality, both GGE_N and GGE_C for a particular predatory arthropod could be functions of resource nutrient content (Sterner & Elser 2002), as is true for some herbivores (Urabe and Watanabe 1992, Elser *et al.* 2000). For terrestrial insects, however, it is empirically unknown whether the functions $\text{GGE}_N(C:N_{\text{prey}})$ and $\text{GGE}_C(C:N_{\text{prey}})$ depend differentially on resource nutrient quality such that the ratio $\text{GGE}_N(C:N_{\text{prey}})/\text{GGE}_C(C:N_{\text{prey}})$ would also depend on

resource nutrient content. We assume here that this ratio of growth efficiencies lacks any particular functional dependence on resource nutrient content, recognizing that this may well prove to be an oversimplification of nature. This convenient approximation allows us to exploit the arrangement of eqn 2 to examine potential N-limitation in terms of a single parameter, specifically how much better a consumer is at utilizing N than C from its prey. In particular, we can now ask what proportion of the pairwise interactions in the compiled and saltmarsh databases involve prey and predators whose $C : N_{\text{prey}}/C : N_{\text{predator}}$ exceeds various hypothetical values of GGE_N/GGE_C (all ≥ 1). Understanding how this proportion decays as predators hypothetically improve their ability to extract N from prey relative to C allows us to explore how extensive N-limited predator growth might be in terrestrial ecosystems at large, and in the saltmarsh system in particular.

RESULTS

For predators eating herbivores, the distribution of values of $C : N_{\text{prey}}/C : N_{\text{predator}}$ for *Spartina*-inhabiting species (all possible interactions) is significantly right-shifted relative to the corresponding distribution calculated from the literature-compiled database (Mann–Whitney $U = 246673$, $P < 0.001$; Fig. 1a). Likewise, the distribution of interactions actually occurring in the saltmarsh (all realized interactions) was significantly right-shifted relative to the distribution of potential interactions from the compiled database (Mann–Whitney $U = 90838$, $P < 0.001$). Taken together, these results imply that, as a whole, potential pairwise consumer–resource interactions in the saltmarsh and the subset of those interactions that actually occur both exhibit a greater disparity between N-content of prey species and N-demand by predators than is evident in the data set compiled from the literature. However, within the saltmarsh data set, the $C : N_{\text{prey}}/C : N_{\text{predator}}$ distribution involving only those pairwise interactions known to occur in nature (all realized interactions) did not differ significantly from the distribution of all possible saltmarsh interactions. This was true for both the position (Mann–Whitney U -test) and shape (Kolmogorov–Smirnov test) of the distributions. No differences were observed between the distribution involving all realized interactions and the subset involving only those interactions that occur frequently. Table 1 provides the substantiating statistics for the four distributions discussed.

In contrast, for intraguild predation, the position of the distribution of all possible values of $C : N_{\text{prey}}/C : N_{\text{predator}}$ for saltmarsh species does not differ from the position of the corresponding distribution of potential values calculated from the literature-compiled database (Mann–Whitney U -test; Fig. 1b). However, within the saltmarsh data set,

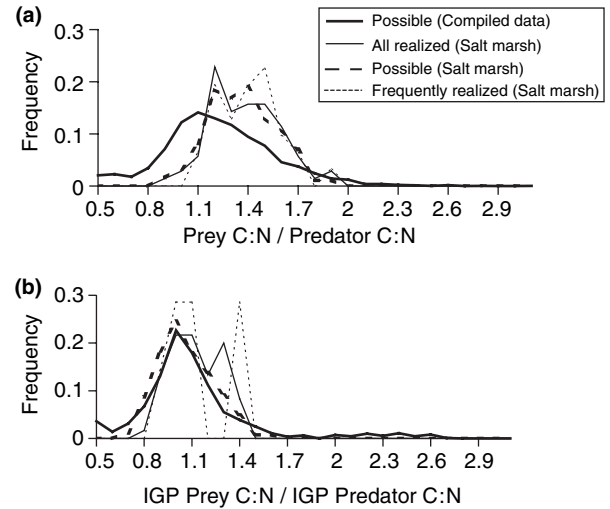


Figure 1 Histograms characterizing disparities in the stoichiometry of consumer–resource interactions for terrestrial arthropod assemblages. On the x -axis, a value of 1.0 indicates matched $C : N$ stoichiometries of prey supply and predator demand. Likewise, x -axis values greater than 1.0 correspond to instances of relatively N-rich predators feeding on relatively N-poor prey. Data for predatory arthropods feeding on herbivorous arthropods (a) and predatory arthropods feeding on other predators (intraguild predation; b) are included from four data sets: (1) a database of all pairwise interactions possible based on a broad-ranging literature compilation of arthropod stoichiometry data, (2) a database of potentially interacting arthropod species from New Jersey *Spartina* marshes, (3) a subset of group 2 involving only those interactions known to occur in the *Spartina* marshes, and (4) a subset of group 3 involving only those interactions that regularly occur.

the distribution of $C : N_{\text{prey}}/C : N_{\text{predator}}$ values involving only those realized pairwise interactions known to occur in nature was slightly, but significantly, right-shifted relative to the distribution of all interactions possible in the saltmarsh (Mann–Whitney $U = 196889$; $P = 0.002$). The distribution of realized saltmarsh interactions was also significantly right-shifted relative to the distribution of potential interactions from the compiled data set (Mann–Whitney $U = 25930$; $P = 0.007$). Taken together, these results imply that the consumer–resource interactions that actually take place in the saltmarsh (realized interactions) exhibit a greater disparity between N-content of prey species and N-demand by predators than is evident in either the array of all possible interactions in the saltmarsh or in the compiled database. No differences were observed between the distribution involving all realized interactions and the subset involving only those interactions that frequently occur. Table 1 provides the basic statistics for the four distributions of values of $C : N_{\text{prey}}/C : N_{\text{predator}}$ from cases involving intraguild predation.

Table 1 Summary statistics for C : N stoichiometry of consumer–resource interactions from a literature-compiled database and from *Spartina*-dominated saltmarshes in New Jersey, USA. Statistics characterize the distributions of pairwise interactions ($C : N_{\text{resource}} / C : N_{\text{consumer}}$)

Interaction type	Metric	Potential (database)	Potential (saltmarsh)	All realized (saltmarsh)	Frequently realized (saltmarsh)
Predators eating herbivores	Mean	1.18	1.32	1.33	1.36
	Median	1.15	1.32	1.33	1.34
	SD	0.33	0.21	0.22	0.20
	<i>n</i>	3927	184	73	31
Intraguild predation	Mean	1.06	1.01	1.08	1.08
	Median	1.00	1.00	1.06	1.01
	SD	0.38	0.17	0.16	0.18
	<i>n</i>	1089	529	61	7

A scatterplot of resource C : N vs. consumer C : N content provides another view of the stoichiometry of realized food web interactions (Fig. 2). For predators feeding on herbivores (Fig. 2a), realized interactions generally fall below the 1 : 1 line; whereas for intraguild predators (Fig. 2b), realized interactions occur closer to and on both sides of the 1 : 1 line, indicating closer matches of predator and prey stoichiometry. In all cases, however, regression lines through the ellipses of points yield slopes not significantly different than zero, suggesting that both strict and IGP predators may not choose their prey strictly on the basis of C : N ratio.

For predators feeding on herbivores, the vast majority of pairwise interactions in each of the four data sets are potentially N-limiting if the consumer species were equally efficient at utilizing N and C from their prey ($GGE_N = GGE_C$; Fig. 3a). Indeed, in the compiled database, fully half of all pairwise interactions are potentially N-limiting for the consumer species even if that consumer is 15% more efficient at utilizing N than C (i.e. $GGE_N = 1.15 \times GGE_C$). For all three variants of the saltmarsh data set (possible, realized, and frequently realized interactions), at least half of all pairwise interactions are potentially N-limiting unless the consumer is at least 32% better at utilizing N than C. At least 10% of the predator–herbivore interactions that actually occur on the saltmarsh would still be N-limiting even if the consumer were 55% more efficient at utilizing N than C.

In contrast, intraguild predation presents fewer opportunities for N-limited growth by the consumer species (Fig. 3). For a given value of GGE_N/GGE_C , smaller fractions of the pairwise interactions are potentially N-limiting for intraguild predators than for predators feeding primarily on herbivores. For example, for each of the two distributions of all possible intraguild interactions extracted from the compiled and marsh data sets, half of the pairs would be N-limiting if the consumer species were equally efficient at utilizing N and C. This is to be expected

because of the symmetry arising from including all possible combinations of intraguild predator and intraguild prey, including cannibalism, when constructing these distributions of potential interactions. However, unlike the saltmarsh data set (all possible interactions), the distribution of all potential interactions from the compiled data set also features a long right tail with over 10% of the pairwise interactions presenting the opportunity for N-limitation even if the predator was 40% more efficient at utilizing N than C. In contrast, for each of the distributions involving actual interactions (realized and frequently realized), the proportion of interactions featuring potential N-limitation decays

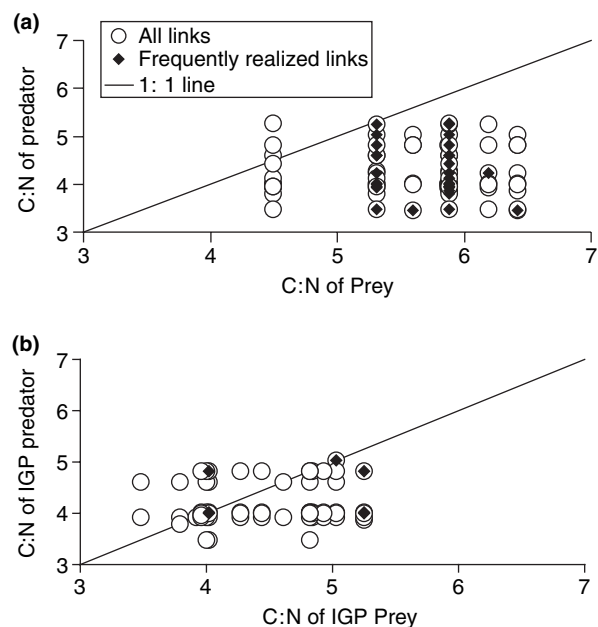
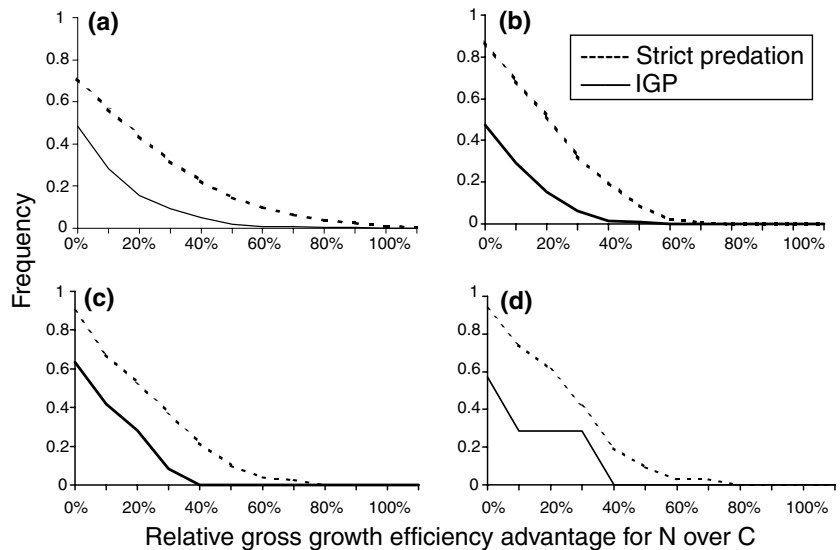


Figure 2 Scatterplots of C : N stoichiometry for realized pairwise consumer–resource interactions from the *Spartina* salt marsh system. (a) For predators feeding on herbivorous arthropods, whereas (b) for intraguild predation.

Figure 3 The proportion of the pairwise consumer–resource interactions in the four databases from Fig. 1 that would represent N-limitation for the consumer species as a function of the relative magnitudes of the consumer species' gross growth efficiencies for nitrogen and carbon (i.e. GGE_N/GGE_C). Each panel contrasts strict predation (predators feeding on herbivorous arthropods) with intraguild predation. (a) For the literature compiled database; (b) from the database of potential interactions within the New Jersey *Spartina* marshes; (c) for the subset of interactions known to occur in the *Spartina* marshes; and (d) for the subset of interactions in (c) that regularly occur.



rapidly as GGE_N/GGE_C increases and extended right tails are not evident. Although over 75% of realized intraguild interactions in the saltmarsh would be N-limiting if the consumer were equally efficient at utilizing N and C, this percentage decays quickly as GGE_N/GGE_C increases. Indeed, if consumers were only 25% better at utilizing N than C, fewer than 10% of real intraguild predation interactions in the saltmarsh would feature potential N-limitation.

DISCUSSION

Pairwise consumer–resource interactions that actually take place in the saltmarsh involve, on average, a greater disparity between N-content of prey species and N-demand by predators than is evident in the compiled database representing a

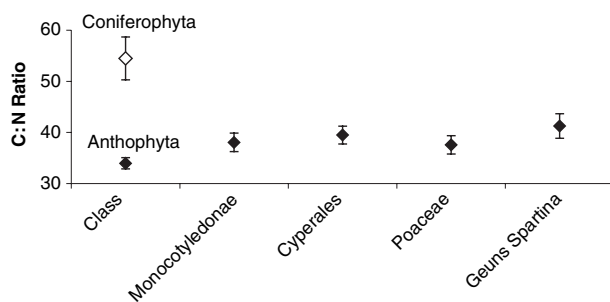


Figure 4 C : N ratios of plant taxa in the classes Coniferophyta and Anthophyta. Within the Anthophyta, ratios for the Monocotyledonae at large as well as for the Cyperales, Poaceae, and the genus *Spartina* are presented. Data were extracted from <http://www.nceas.ucsb.edu/ecostoichiometry> and Matsumura *et al.* 2004.

broad mix of taxa collected from diverse habitat types and biomes. This disparity occurs both for predators feeding on herbivores and for intraguild predators. We believe these differences arise due to taxonomic differences between elements of the *Spartina* food web and the composite food web represented by the literature database.

For example, monocots, including grasses in general and *Spartina* in particular, are relatively N-poor compared with the Anthophyta at large (Fig. 4). Thus, the high C : N ratios of *Spartina* herbivores (Fig. 1a), which are mainly phloem-feeders, may reflect selection for reduced body nitrogen content for consumers specializing on plant resources depauperate in nitrogen. Such stoichiometric effects would mirror selection for a range of adaptations for grass feeding seen in other herbivores (Bernays & Barbehenn 1987). As grass feeders, *Spartina* herbivores are unlikely to be N-rich by virtue of the sequestration of N-rich allelochemicals, which are uncommonly available in phloem tissue, especially in grasses (Raven 1983; Denno & Cook 1994).

The taxonomic composition of higher trophic levels also differs between the *Spartina* system and the literature database. For example, arachnids (primarily spiders) comprise more than half of the predator species in the saltmarsh data set (Döbel & Denno 1994; Matsumura *et al.* 2004), but are poorly represented in the literature-compiled database. This difference is potentially important because spiders in particular appear to have higher body N-content than terrestrial predatory insects. Specifically, combining data from the compiled data set and the marsh collections, spider C : N ratios averaged $4.27 (\pm 0.15)$ vs. $5.12 (\pm 0.11)$ for terrestrial insect predators ($F_{1,52} = 14.63$, $P < 0.001$).

The predominance of N-rich predatory species (i.e. lower C : N_{predator}) and N-poor herbivores (i.e. higher C : N_{prey})

combine to push the distribution of potential values of $C : N_{\text{prey}}/C : N_{\text{predator}}$ for the saltmarsh community rightward (Fig. 1a). Overall, the distribution for predator–herbivore interactions realized in the *Spartina* system appears to be an unbiased subset of the distribution of all interactions possible within that system. This pattern likely results because the *Spartina* community is dominated by nitrogen poor sap-feeders such as planthoppers and leafhoppers that serve as the primary source of prey for many species of nitrogen-rich spiders (Döbel & Denno 1994; Denno *et al.* 2002, 2003). Detailed observational and experimental studies of diet choice for the saltmarsh spider *Pardosa littoralis*, an important and numerically dominant intraguild predator, emphasize that in some cases, prey behaviour that translates into increased risk of attack may be of overriding importance even when stoichiometric mismatches between predators and prey are great (Matsumura *et al.* 2004). Nevertheless, the extensive similarities between the distributions of possible and realized interactions involving intraguild predators on the saltmarsh (Fig. 1b) suggests that it may be possible to make general statements about the potential for extensive N-limited species interactions in a system based solely on stoichiometric analyses alone, even if one lacks the detailed life history information necessary to construct a detailed food web matrix. This expectation should be explored in other habitat types.

Much depends on the extent that predatory arthropods can utilize N from prey tissues more efficiently than they can C (i.e. the magnitude of GGE_N/GGE_C , making the conservative assumption it always is >1). Depending on the magnitude of the predator's relative efficiency for extracting N, anywhere from 70 to 0% of predator–herbivore interactions and from 50 to 0% of interactions involving intraguild predators could be N-limiting for the consumers, based on the compiled data set (Fig. 3). The issue is even more uncertain for the data set based on actual interactions in the saltmarsh community, where between 90 and 0% of predator–herbivore interactions and 75–0% of intraguild predation interactions could be N-limiting. Precious little appears known about values of GGE_N and GGE_C for terrestrial predators. This is unfortunate because these percentages of pairwise interactions that potentially involve N-limitation decay steeply with small increases in GGE_N/GGE_C . Thus, the fraction of potential or real interactions in terrestrial food webs involving N-limitation depends sensitively on an unknown quantity.

Our comparative approach here underscores the importance of elucidating whether particular communities characterized by certain predators and prey with unique $C : N$ stoichiometries might differ from general expectations of nitrogen limitation based on broader data sets. Our finding here that *Spartina* herbivores and predators have particularly high and low $C : N$ ratios, respectively, suggests that

nitrogen limitation may be particularly frequent for predators in the saltmarsh system. To offset this inherent stoichiometric discrepancy, intraguild predation may be unusually frequent, and all evidence suggests that it is (Finke & Denno 2002, 2003; Langellotto 2002; Denno *et al.* 2004). Thus, comparative stoichiometric analyses between targeted systems and compiled data sets may be used to predict the frequency and strength of particular real-world species interactions such as intraguild predation (Fagan *et al.* 2002; Denno & Fagan 2003). Substantially more comparisons than are currently possible today will be needed to test such a prediction.

Topics for future work

Several topics suggest themselves for future analyses. (1) Does the potential for N-limitation of terrestrial arthropod predators change depending on the ecological idiosyncrasies of the particular species involved, and thus a specific food web? For example, it would be important to discern how interspecific variation in growth form, feeding style, diet breadth, and other traits contributes to differences between the realized and potential distributions of interactions in the context of $C : N$ content. (2) What relationships, if any, exist between the stoichiometric properties of species interactions and their interaction strengths (Laska & Wootton 1998) in the context of food web dynamics? For example, it could be that an N-rich predator that specialized on an N-poor prey species would have to consume many individuals of the prey species to satisfy its own dietary demand for N, thereby exerting a large per-capita mortality effect. Quantifying the correlation between the stoichiometric and dynamic traits of species interactions is achievable in a well-studied food web, and achieving such an understanding would be an important step toward integrating ecosystem ecology's focus on nutrient throughput with community ecology's focus on species dynamics and abundance. (3) Finally, future assessments should focus on P in addition to N because of recent discoveries of wide interspecific variation in insect P content (Cross *et al.* 2003, Woods *et al.* 2004) and the potential for P-limitation in terrestrial plant–herbivore interactions (Elser *et al.* 2000).

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