Global biogeography of autotroph chemistry: is insolation a driving force?

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Synthesis

The tissue chemistry of plants can influence ecosystem processes including growth, herbivory, and decomposition. Our comparison of nitrogen and phosphorus in over 1700 autotroph taxa demonstrates that latitudinal trends in tissue chemistry are consistent across non-vascular and vascular species in freshwater, terrestrial, and marine ecosystems. Tissue chemistry varies most within species and taxonomic lineages, yet the nitrogen to phosphorus ratio within individuals is strikingly similar among species in different ecosystems. These results shed new light on existing hypotheses, suggesting that light (e.g. photon flux) and growing season duration are primary drivers of latitudinal gradients in tissue chemistry, but providing little support for temperature, nutrient supply, or soil substrate age.

Photoautotroph nitrogen (N) and phosphorus (P) tissue concentrations can influence ecosystem function via processes including growth, decomposition, and consumption, and may reflect traits maintaining coexistence. Studies in terrestrial systems have led to hypotheses that latitudinal trends in the N and P content of leaves may be driven by soil substrate age, environmental temperature, or season length; however, terrestrial patterns alone cannot differentiate these mechanisms. Here, we demonstrate that broad geographical patterns of N and P in freshwater and marine multicellular photoautotrophs are concordant with those in terrestrial ecosystems. Our >6800 record database reveals that mean tissue N and P increase with latitude in all ecosystems, but P increases more rapidly, causing N:P to decline; mean N:P scaling within individuals also is identical among systems, despite very different evolutionary environments. A partitioning of the variance in these data suggests that species composition and local environmental context likely lead to the variation observed within a latitudinal band. However, the consistency of trends in photosynthetic tissue chemistry across Earth's ecosystems suggests that biogeographical gradients in insolation and growing season length may constrain tissue N and P, whereas global trends in temperature, nutrient supply, and soil substrate age are unlikely to generate the consistent latitudinal trends among ecosystems. Thus, this cross-ecosystem comparison suggests a new hypothesis, global patterns of insolation, while also providing a new perspective on other mechanisms that have been hypothesized to underlie latitudinal trends in photosynthetic tissue chemistry.

The nitrogen (N) and phosphorus (P) contents of photoautotrophs play important roles in a broad array of ecological processes, including herbivore consumption and growth rates, disease severity and transmission, growth and decomposition rates, resource limitation, and the fate of carbon in ecosystems (Cebrian 1999, Smith 2007, Hillebrand et al. 2009). Autotrophs require N for carbon acquisition via photosynthesis and P uptake via cross-membrane

transport and enzymatic activity. Phosphorus is a critical component of RNA and is necessary for growth, photosynthesis, nutrient transport and energy transfer. The ratio of N to P in autotrophs can indicate the nature of autotroph nutrient limitation (Verhoeven et al. 1996) but also may reflect underlying species-level functional traits, serving as a proxy for relative growth rate (Hillebrand and Sommer 1999) or competitive ability (Güsewell 2004).

The photosynthetic tissues of terrestrial and aquatic autotrophs exhibit an extremely broad range of tissue N and P concentrations as well as N:P ratios within and among taxa (Elser et al. 2000). Within major ecosystem types (e.g. freshwater, terrestrial), N and P concentrations in species vary along major environmental gradients (e.g. latitude and mean annual temperature), among growth forms and evolutionary lineages (e.g. conifers vs grasses, phytoplankton vs macroalgae), and as a function of nutrient supply (Klausmeier et al. 2004, Reich and Oleksyn 2004, Han et al. 2005, Kerkhoff et al. 2006, Ordonez et al. 2009). However, the generality of patterns in the concentrations and ratio of N and P in photosynthetic tissue among the world's freshwater, marine, and terrestrial autotrophs, and the mechanisms controlling these patterns, remain unresolved.

Although most studies observe extremely high variation in tissue N:P chemistry among individuals within a location (Atkinson and Shorrocks 1981, McGroddy et al. 2004, Reich and Oleksyn 2004, He et al. 2008), global means and trends in tissue N and P have been used to gain insights into biogeographic drivers of foliar chemistry. Evidence from terrestrial studies has suggested three major hypotheses for global N:P patterns that involve global trends of temperature and edaphic conditions as drivers of global relationships in foliar N, P and N:P (Reich and Oleksyn 2004, Kerkhoff et al. 2005, Lovelock et al. 2007). The *Environmental nutrient supply hypothesis* (Walker and Syers 1976, Chadwick et al. 1999) predicts that P limitation should be stronger than N limitation in equatorial terrestrial environments because weathering has depleted P in older tropical soils, whereas younger glacial soils should be P- and mineral-rich (Walker and Syers 1976, Vitousek and Farrington 1997, Chadwick et al. 1999). Thus, if edaphic conditions control tissue chemistry, we should observe declines in mean tissue N:P ratios with increasing latitude (Reich and Oleksyn 2004).

In contrast, two climate-related hypotheses have been proposed to explain latitudinal trends in terrestrial N and P based on different mechanisms that vary broadly with latitude. First, organisms at high latitudes may grow more rapidly to complete key life stages during an abbreviated growing season (Newman 1977, Roff 1980, Beerling and Osborne 2002). According to this hypothesis, high-latitude species are expected to contain relatively high levels of P because rapid growth rate requires disproportionate investment in P-rich ribosomal RNA, which is necessary for the protein synthesis required to fuel rapid growth and reproduction (*Growing season duration hypothesis*) (Elser et al. 2000, Kerkhoff et al. 2005). Temperature also can alter N and P content independently of growing season length; autotrophs grown at lower temperatures tend to have higher N and P concentrations when compared within and among species, presumably to maintain metabolic functioning in conditions with relatively slow chemical reactions (Woods et al. 2003). Further, P generally increases more rapidly than N in organisms exposed to lower temperatures (Woods et al. 2003), suggesting that mean N:P should generally decline with declining temperatures or increasing latitude, if temperature underlies the observed patterns in terrestrial tissue chemistry (*Temperature-dependent*

physiology hypothesis). Thus, in terrestrial systems, the latitudinal patterns generated by all three of these mechanisms are strongly overlapping, making it difficult to generate predictions that differentiate them.

While the predictions of these hypotheses overlap in terrestrial systems, the significantly different latitudinal patterns of nutrient supply and temperature gradients in the world's freshwater and marine systems generate contrasting predictions when compared to terrestrial ecosystems. For example, mean annual temperature and growing season temperature within a latitudinal band differ among ecosystem types primarily because of water's high heat capacity, with the greatest differences among ecosystems occurring at high latitudes. At mid- to high latitudes, the mean and variation in ocean temperatures are far more moderate than in air, with little annual variation in temperature in polar oceans (Luning 1993, Reynolds and Smith 1995), leading to increasing disparity between air and water temperature in mean values and seasonal amplitude with increasing latitude. In spite of this divergence with increasing latitude, surface temperatures in air, freshwater, and the oceans scale surprisingly tightly within and among seasons (Morrill et al. 2005, Lambert and Chiang 2007). Thus, if photosynthetic tissue N and P increase with declining growing season temperature to sustain metabolic reaction rates (Woods et al. 2003, Kerkhoff et al. 2005), we should expect increasing trends in N and P with latitude in all systems, but slopes of N, P and N:P that differ among ecosystem types primarily because of divergence in temperature among ecosystems with increasing latitude. In particular, the slopes of N and P should increase with latitude more slowly in marine compared to terrestrial autotrophs, with an intermediate slope in freshwater autotrophs.

In contrast, if tissue chemistry is constrained primarily by nutrient supply or ambient nutrient concentrations and ratios, latitudinal trends in tissue N and P should not be concordant among systems. For example, tissue P content should be lower at low latitudes in marine autotrophs because of the predominance of calcareous sediments that sequester P (Smith 1984, Downing et al. 1999) and in terrestrial autotrophs because of low P availability in highly weathered tropical soils (Walker and Syers 1976). In contrast, P content should be lowest in mid- to high-latitude freshwater autotrophs because of slow chemical weathering and supply into aquatic systems (Downing et al. 1999). N supply also differs among systems; for example, N content should be most limited in tropical freshwater systems where dissolved nitrogen is low and denitrification is rapid (Downing et al. 1999), whereas N content should be highest in tropical terrestrial autotrophs because N-mineralization in soils, a surrogate for N supply, declines with increasing latitude (Nadelhoffer et al. 1992). Latitudinal trends in tissue N:P ratios also should vary among systems if nutrient supply underlies autotroph N:P content. While N:P supply ratios in freshwater vary with factors such as oxygen and mineral content, freshwater N:P supply generally increases with latitude (Downing et al. 1999), in contrast to declines in N:P supply with latitude on land (Reich and Oleksyn 2004). N:P supply ratios in the world's oceans do not vary directly with absolute latitude (Fanning 1992) as nutrient availability is largely driven by upwelling

or terrestrial input sources; the ratio of N:P supply in the Atlantic, for example, is higher at low latitudes (3–17°N) and lower at more temperate latitudes (17–41°N) (Kortzinger et al. 2001).

Thus, comparative studies of latitudinal patterns in mean photoautotroph N and P in marine, freshwater, and terrestrial systems provide a new lens with which to examine the proposed mechanisms behind biogeographic gradients observed in terrestrial leaves. Here we use a data set composed of more than 6800 records of multicellular autotroph tissue N and P collected from more than 1700 unique freshwater, marine and terrestrial species to determine whether the latitudinal trends detected in terrestrial ecosystems are mirrored in freshwater and marine systems. We then use this multi-ecosystem comparison to place the latitudinal trends into the broader context of possible drivers including global patterns of phylogeny, traits and growth forms, insolation, and ecosystem type to assess the relative importance of these factors for predicting biogeographic variation in tissue N and P chemistry. This approach represents a contribution to the stoichiometric literature that is generally characterized by studies of whole community chemistry in phytoplankton (Klausmeier et al. 2004, Arrigo 2005) and studies of species-level chemistry in terrestrial plants (McGroddy et al. 2004, Reich and Oleksyn 2004, Kerkhoff et al. 2006). Our cross-system approach comparing multicellular autotrophs allows us to examine the existence, strength, and concordance among global-scale patterns in mean N and P chemistry across latitudes.

Methods

We developed a data set comprising 6808 georeferenced records of photosynthetic tissue N and/or P data in multicellular autotrophs representing 1737 unique taxa across freshwater, marine and terrestrial ecosystems. We did not include unicellular autotrophs in this analysis because they are restricted to marine and freshwater environments, and they experience different nutrient constraints and exhibit greater flexibility in NP chemistry than multicellular autotrophs (Elser et al. 1996, 2010, Sterner and Elser 2002). We searched Web of Science using the Boolean search terms 'N content and P content or N P ratio'. Major secondary data sources included Reich and Oleksyn (n = 1280; 2004), Han et al. (n = 2093; 2005), and Kerkhoff et al. (n = 2206; 2006) for terrestrial and some freshwater species, and Atkinson and Smith (n = 117; 1983) for marine species. Finally, we added data from our own studies (J. E. Smith unpubl. data). We did not include any tissue chemistry data for autotrophs from known fertilized or polluted sites. All records included information on species taxonomic designation, tissue N, tissue P, ecosystem type, and latitude of collection. For species with multiple records, we calculated the mean value for tissue N and P of a species and latitude (to the nearest 0.1 degree), to create a single record per species per location (2789 with N and P, 543 with P only). We use these 3332 unique latitude–species combinations, representing three major ecosystem types, as our data in the current analyses (2969 terrestrial, 197 marine and 166

freshwater records). For consistency across the database, all data were converted to percent N in dry mass and percent P in dry mass prior to entry into our database; for analyses, the weight:weight N:P ratios were converted into molar ratios. Data from all sources were augmented to produce records with complete and consistent taxonomic designations using Nix (Kemball 2007) for terrestrial and freshwater records and AlgaeBase (Guiry and Guiry 2008) for marine data. In addition, we augmented the database with information for each record about the strata of collection (e.g. aboveground, benthic, emergent), the biotic type (e.g. macrophyte, shrub, foliose alga), and higher-level taxonomic classifications (e.g. kingdom, class, order).

The final database included photosynthetic tissue N and P data for multicellular autotrophs collected between 66.3°S and 81°N, representing two kingdoms (Chromista and Plantae), 9 divisions and 18 taxonomic classes. Terrestrial and freshwater autotroph data were from locations spanning six continents, and marine data spanned four oceans. Although a very wide range of taxa and latitudes were represented in all systems, data were distributed somewhat unevenly across latitudes; the median (absolute) latitudes represented in the marine, terrestrial, and freshwater data were 24.5°, 37° and 42.5°, respectively. Following previous terrestrial studies (Reich and Oleksyn 2004, Kerkhoff et al. 2006), we employ absolute latitude in our analyses.

We developed a variety of models to examine the effects of system (marine, freshwater, or terrestrial) and latitude on percent N, percent P, and the N:P ratio in photosynthetic tissues. Each tissue chemistry measure (N, P and N:P) was analyzed in a separate regression model composed of system, latitude, and the system by latitude interaction. Because the data had an apparent peak at mid-latitudes, we began by fitting quadratic models to the N, P and N:P data. We then fit linear models and compared these using AIC to the quadratic models and to a sigmoidal-shaped angular transformation, cosine ($2l$) where l is absolute latitude expressed in radians. The angular-transformed curvilinear model reflects the overall pattern of energy arrival at Earth's surface, with relatively little change across tropical latitudes, greatest change across temperate latitudes, and reduced rate of change at polar latitudes (Wüst et al. 1954, Smith et al. 1996). All model fits were generated using the lm function in R (R ver. 2.12.1; R Foundation for Statistical Computing) and were compared using Akaike information criterion (AIC, Venables and Ripley 2003).

We used two approaches to assess whether observed latitudinal trends were generated primarily via species turnover or via plasticity within species. First, we used mixed effects models to test whether there was a significant effect of latitude after controlling for taxonomic classification nested within system and biotic type by including these variables as random effects (i.e. species nested within the following hierarchical variable set: system, biotic type, Kingdom, Phylum, Class, Order, Family and Genus) using the lme function in the nlme library in R (ver. 2.12.1) (Pinheiro and Bates 2000). We also calculated the percent of the variance explained by each of the random effects. While explicit phylogenetic distance may be preferable for assessing the role of species relatedness in producing these patterns (Webb et al. 2002), generating such a
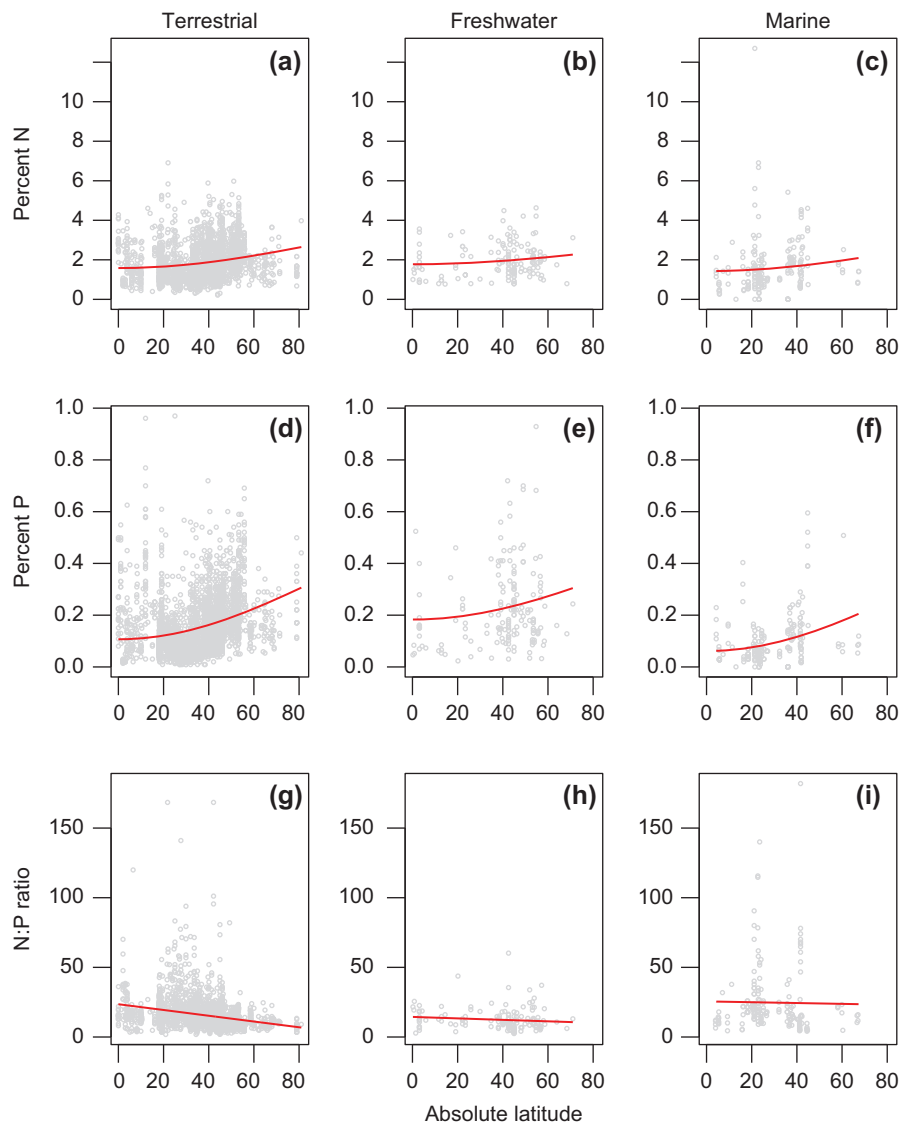
Figure 1. Multicellular photoautotrophs in all three systems display concordant relationships between tissue N, P, N:P and latitude. In all cases, tissue P increased more rapidly than N with increasing latitude. Curvilinear (cosine-transformed) models, produced a better fit for tissue N and P than quadratic or linear models, whereas tissue N:P was best described with a linear model. Best fitting models are displayed on the figure. See Table 1 for details of the regression models.

phylogeny for the current dataset is well beyond the scope of this work. Latitude was included as a fixed effect in this model, so that our variance estimates account for change in tissue chemistry with latitude. Second, we generated regressions including only species with ranges spanning $> 15°$ latitude and compared the slopes of the within-species change in tissue chemistry to that in the overall dataset.

Results

The regression models, based on more than 6800 records, demonstrate that latitudinal trends of mean N, P and N:P in photosynthetic tissues of multicellular autotrophs are concordant among terrestrial, freshwater, and marine ecosystems (Fig. 1, Table 1). In all three systems, mean N (Fig. 1a–c) and mean P (Fig. 1d–f) increased with latitude, but P increased more rapidly, leading to a decline in mean

N:P with latitude (Fig. 1g–i). Despite the high statistical power associated with the size of our dataset, we found no evidence for differences in slopes among systems for either mean N or mean P content (Table 1). While mean photosynthetic tissue N:P declined with increasing latitude in all ecosystem types, the terrestrial N:P slope declined faster across latitude than the slopes in aquatic systems (Table 1). Overall, the latitudinal trends in photosynthetic tissue nutrients were strikingly similar among diverse autotroph groups in distinct ecosystem types.

Despite these consistent trends, tissue nutrients were quite variable; as in previous studies examining species-level data, latitudinal trends, while highly significant, accounted for only 5–10% of the total variance ($r^2 = 0.05$ for both %N and N:P and 0.09 for %P). These patterns of mean autotrophic tissue N and P content across latitude were robust, however; they remained unchanged with removal of the terrestrial nitrogen-fixing and nitrogen-rich family,

Table 1. Results of regressions of percent N, percent P, and N:P ratio as a function of system and latitude. We compare the intercepts and the slopes across latitude (represented by '× Latitude$_E$') among systems using two planned orthogonal contrasts: 1. Terrestrial (TER) versus Marine (MAR) and Freshwater (FW) and 2. Freshwater (FW) versus Marine (MAR). 'Value' represents the regression estimate of the mean and slope across latitude for the entire dataset and for each contrast; 'SE' represents the error associated with each regression estimate (shown in Fig. 1). The p-values column shows the significance of the estimates and contrasts in each model. The contrasts examining slopes across latitude correspond to Table 1 predictions. Parameters and metrics for best-fit models (determined via AIC) are presented here: N and P models are angular-transformed curvilinear models (Latitude$_E$ ~latitudinal distribution of energy at Earth's surface), and N:P is a linear function of latitude.

Response	Source	Value	SE	t-value	p-value
Nitrogen (N)	intercept	2.6383	0.2003	13.173	<0.001
	TER. vs MAR and FW	0.1281	0.1061	1.207	0.228
	FW vs MAR	0.0049	0.2942	0.017	0.987
	Latitude$_E$	−1.0442	0.2464	−4.238	<0.001
	(TER. vs MAR and FW) × Latitude$_E$	−0.1395	0.1311	−1.064	0.287
	(FW vs MAR) × Latitude$_E$	0.1707	0.3614	0.472	0.637
Phosphorous (P)	intercept	0.3293	0.0227	14.523	<0.001
	TER. vs MAR and FW	<−0.0001	0.0119	−0.001	0.999
	FW vs MAR	0.0340	0.0334	1.020	0.308
	Latitude$_E$	−0.2121	0.0279	−7.613	<0.001
	(TER. vs MAR and FW) × Latitude$_E$	−0.0053	0.0147	−0.360	0.719
	(FW vs MAR) × Latitude$_E$	0.0269	0.0410	0.656	0.512
N:P	intercept	21.1645	1.2144	17.428	<0.001
	TER. vs MAR and FW	1.1557	0.6625	1.744	0.081
	FW vs MAR	−5.5708	1.7629	−3.160	0.002
	Latitude	−0.0945	0.0328	−2.883	0.004
	(TER. vs MAR and FW) × Latitude$_E$	−0.0540	0.0177	−3.054	0.002
	(FW vs MAR) × Latitude	−0.0111	0.0478	−0.231	0.817

Fabaceae, or with analysis of just the submerged freshwater macrophytes with all emergent freshwater taxa reassigned to the terrestrial system.

In spite of the apparent hump at mid-latitude in N, P and N:P in all systems (Fig. 1), a model with only a quadratic term for latitude provided a poor fit to the data (i.e. substantially higher AIC), suggesting that the peak was simply an artifact of high data density at temperate latitudes. Models including a trend in mean N and P across latitude produced better descriptions of the data, with curvilinear models (angular transformed latitude) fitting N and P trends better than linear models (Fig. 1). Linear models provided the best fit for mean N:P ratios in all systems.

Mean N:P ratios among individuals also were consistent across ecosystem types (Fig. 2). The means and trends in individual photosynthetic tissue N:P stoichiometry were completely overlapping in all systems, suggesting strong, general physiological underpinnings to this ratio. While the similarity of the slopes and intercepts is striking, the relatively large variance around these trends is also notable in this figure.

A partitioning of all the variation in this dataset demonstrated that variation in tissue N and P for autotrophs in all three systems occurred primarily within and among species; minimal variance in tissue nutrients was explained by differences among systems or among autotroph growth forms (Fig. 3). Tissue N content, in particular, varied phylogenetically; however for tissue N, P and N:P, the variation within species was as large as the variation at any single taxonomic level (Fig. 3). Given this large within-species component of the total dataset variance, we fit regression models using only the subset of species with multiple records across latitude (n = 536). Not all higher taxonomic levels had balanced representation in the data. However, the relative importance of system, biotic type,

taxonomy and residual variance were similar when we included only genus and species in the variance components model (i.e. random effects were system, growth form and morphology ['biotic type'], genus, and species; result not shown). Thus, this subset of species demonstrates that trends within species are similar to those obtained with the full dataset.
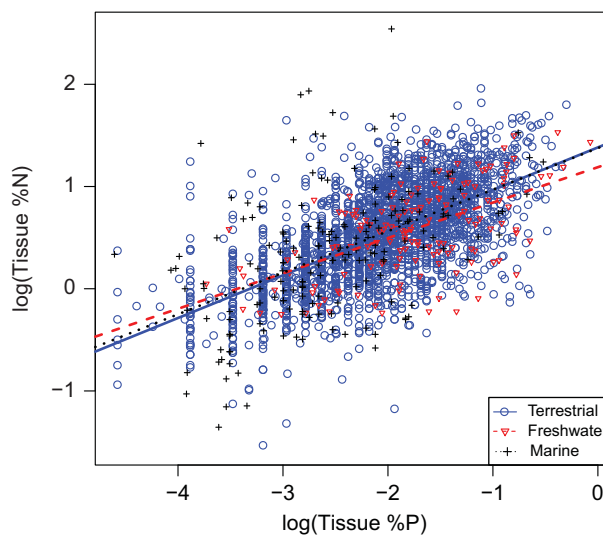

Figure 2. Nitrogen to phosphorous scaling within individuals across three ecosystem types: terrestrial, freshwater, and marine. Regression slopes (± SE) and intercepts were similar for terrestrial (slope = 0.417 ± 0.011; intercept = 1.383 ± 0.023; r^2 = 0.391), freshwater (slope = 0.346 ± 0.043; intercept = 1.189 ± 0.081; r^2 = 0.309), and marine (slope = 0.406 ± 0.054; intercept = 0.406 ± 0.054; r^2 = 0.239) ecosystems. All regression slopes and intercepts were significantly different from zero (p < 0.0001).
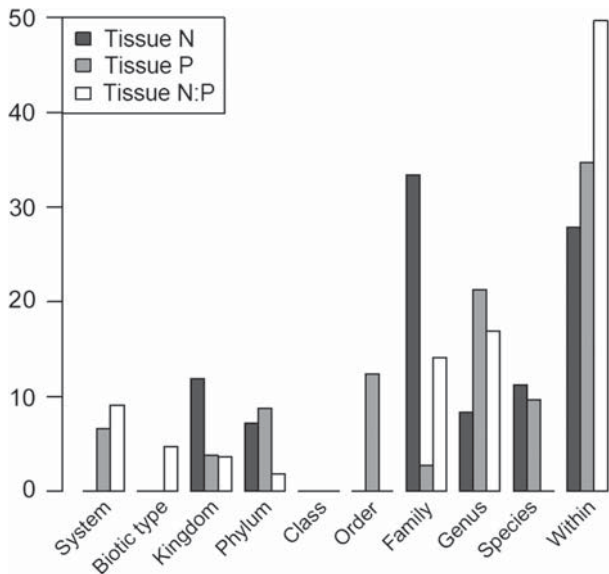
Figure 3. An accounting of all the variance associated with three measures of tissue chemistry across a dataset including marine, freshwater, and terrestrial multicellular photoautotrophs. Models include latitude as a fixed effect. Bars represent the percent of total variance in tissue chemistry explained by each source variable. 'Type' represents categories of autotroph growth form and morphology (e.g. tree, graminoid, filamentous alga, corticated macrophyte). 'Within' represents variation among tissue chemistry measurements for a single species. Note that this analysis was constrained to records for which all nested factors were recorded and there were multiple records per species (536 species and 1367 records). Results were similar for the larger data set that also included species with only a single tissue chemistry measurement in the database (2357 species and 2629 records).

For species spanning a broad latitudinal range ($\geq 15°$ latitude; 2.4% of the overall N dataset and 1.6% for the P dataset, with approximately 1/3 aquatic and 2/3 terrestrial species), the slope for N (0.006) was lower than for P (0.012), which was consistent with the results obtained with the full data set, although due to the high variability of the restricted data set those slopes were statistically non-significant (Fig. 4). For both tissue P and N, the mean slope of widespread species was not as steep as the full dataset. Within this restricted data set, mean N:P ratios changed with a similar slope across latitude as the overall dataset (Fig. 4). Thus, despite statistical differences entailed by reduced analytical power, the trends obtained with the full data set and with the restricted data set are broadly concordant. In a further analysis, the observed trends across latitude persisted in mixed effects models controlling for system and species means (all p-values remain $<< 0.01$), reinforcing the importance of species turnover in these patterns.

Mean values of N, P, and N:P in photosynthetic tissues overlapped strongly among marine, freshwater, and terrestrial systems (Fig. 1–3); among-system differences accounted for minimal variance in photosynthetic tissue nutrients (Fig. 3). However, we detected slightly higher intercepts for tissue N and P concentration in freshwater autotrophs relative to marine autotrophs after controlling for system-specific differences in data density across latitude

(i.e. intercepts in Table 1). Freshwater and terrestrial autotrophs had similar N:P ratios, with mean ratios of 12:1 and 13:1 (molar), respectively, whereas average P content was somewhat lower in marine autotrophs, elevating the mean N:P of multicellular autotrophs in marine ecosystems to 22:1 (molar).

Discussion

Our analysis of this data-rich and globally extensive dataset reveals concordance in the trends of mean tissue N, P, and N:P among multicellular autotrophs in marine, freshwater and terrestrial systems. Further, the N, P and N:P trends within species with especially broad latitudinal distributions ($\geq 15°$ latitude) are concordant with the full dataset. These results underscore recent work showing consistent patterns of biochemical stoichiometry among all autotrophic organisms (Elser et al. 2000, Ågren 2004), and this cross-ecosystem comparison provides a new perspective from which to examine the potential drivers of biogeographic gradients underlying these trends. The high level of variation observed within any given latitudinal band in our study is a result common to studies where individual species are resolved (Atkinson and Shorrocks 1981, McGroddy et al. 2004, Reich and Oleksyn 2004, He et al. 2008), but contrasts with studies examining community averages, such as those generating estimates of Redfield ratios using aggregate unicellular algal communities (Klausmeier et al. 2004, Arrigo 2005). The mean tissue N, P and N:P estimated in this study for each latitude is analogous to average community-level nutrient ratios calculated across all species and individuals in a location (McGroddy et al. 2004), and the parallel trends we find in these averages suggest shared drivers of autotroph chemistry across Earth's ecosystems.

The concordance in means and trends among systems (i.e. absence of system-level interactions for N or P) and the curvilinear fit of the N and P data suggest that biogeographic trends in photosynthetic chemistry are unlikely to be underlain by growing season temperature or nutrient supply which differ with latitude among terrestrial, freshwater, and marine ecosystems (Fanning 1992, Luning 1993, Reynolds and Smith 1995, Downing et al. 1999, Kortzinger et al. 2001, Reich and Oleksyn 2004, Morrill et al. 2005, Lambert and Chiang 2007). Instead, these means and trends are more consistent with photosynthetic responses to growing season duration or annual patterns of insolation, both of which are responses to energy available to photoautotrophs. Growing season duration, for example, is strongly coupled to annual temperature and light availability particularly for terrestrial and freshwater autotrophs, and growth rates, fueled by P-rich RNA, are predicted to increase along this gradient (Elser et al. 1996, Kerkhoff et al. 2005). Insolation, also related to temperature and growing season duration, is more consistent with latitude among systems. In surface or near-surface habitats, total annual direct insolation follows the same latitudinal trends in all three ecosystem types, albeit with declining relative values with increasing depth in aquatic systems because of light attenuation. Nonetheless, the tim-
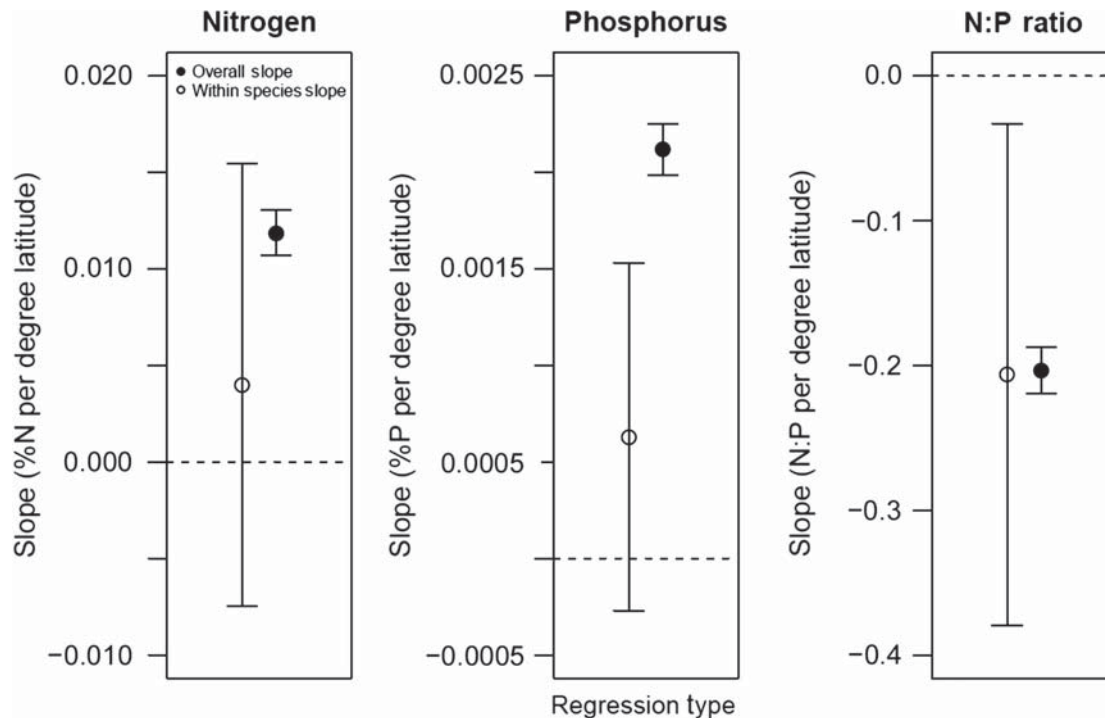
Figure 4. Means (± 1SE) of N (a), P (b), and N:P (c) slope across latitude for species with data across ranges greater than or equal to 15° latitude (open circles) compared to the overall dataset (filled circles). This subset with large latitudinal ranges was about 2/3 terrestrial (30 species for P and 22 for N and N:P) and 1/3 aquatic (9 marine and 5 freshwater species for P, 9 marine and 3 freshwater for N and N:P).

ing and duration of optimal light for photosynthesis is similarly constrained in all systems (Kain 1989, Roots 1989).

Although our observational data cannot definitively distinguish among these drivers, they do provide somewhat stronger evidence for insolation as a driver of these concordant means and trends in photosynthetic tissue chemistry among ecosystems. In particular, temperature, photon flux, and growing season duration covary far more weakly with latitude for marine macrophytes than for terrestrial or freshwater autotrophs. The marine macrophytes (e.g. red and brown algae) that dominate high latitude marine communities (>60°N or S; e.g. Antarctica and northern Norway) have a long growing season (approx. Nov–May in the Northern Hemisphere), much of which occurs beneath sea ice under low temperature and photon flux conditions (Luning 1993). During the summer months when photon flux is higher in the local environment, these high latitude marine autotrophs have high photosynthetic rates but do not accumulate significant biomass (Dunton 1990, Luning 1993). In general, kelp blade N and P concentrations are highest during the relatively long winter growth season, and they decline with increasing photon flux and water temperature during the summer 'photosynthesis season' (Zimmerman and Kremer 1986, Henley and Dunton 1997). This decoupling of growth and day-length is a strategy shared by a diversity of high-latitude algae in two kingdoms (Chromista and Plantae) (Kain and Bates 1993, Luning 1993). Thus, in marine systems, growing season duration, per se, is not likely to be substantially shorter for high latitude marine macrophytes compared to those at mid-latitudes, and while seasonal change in growth rate is generally quite high at all latitudes (50–100%, Kain 1989), it

increases only weakly with latitude for these organisms. Thus, if growing season duration primarily controlled the observed latitudinal trends in photosynthetic tissue N and P via selection for rapid growth rate (Elser et al. 1996, Ågren 2004, Kerkhoff et al. 2006), marine N and P should show only weak trends with latitude, contrasting with strong trends in terrestrial and freshwater N and P latitudinal trends. While our results do not entirely rule out growing season duration as one component of the observed global trends in photosynthetic tissue chemistry, they do suggest that insolation should be considered separately from temperature.

Concordant responses of autotrophs to latitudinal patterns of photosynthetically active radiation appear to be more consistent with these cross-system results than trends in temperature, nutrient availability, or possibly even growing season duration. Tissue N, with greatest pools in thylakoids (Ghannoum et al. 2005), is generally elevated in photosynthetic cells under low light conditions to maintain photosynthetic rates (Goodchild et al. 1972, Anderson et al. 1973). Similarly, P is bioenergetically important for converting light to chemical energy, and much of the P associated with photosynthesis is found in phospholipids of the thylakoid photosystems and the P-rich molecules that serve as precursors for creation of ribulose-1,5-bisphosphate (Domingues et al. 2010). P is often present in photosynthetic tissues in higher concentrations under unsaturated or low photon flux conditions (Mulligan 1989, Flöder et al. 2006). Autotrophs under low light conditions have substantially different cellular makeup compared to high light autotrophs (e.g. more thylakoid membranes and a relatively high photosystem I:photosystem II ratio, Fuhrmann et al. 2009). Such variation in cellular com-

position could translate into significant shifts in N:P ratios at the whole tissue level; however, the net effect of this variation on whole tissue elemental composition has not been studied. Thus, our interpretation of these concordant N and P trends rests, in part, on the relatively long, but cold and dark growth season for higher latitude marine kelp, a seasonal partitioning not observed in terrestrial plants. Overall, these results suggest a modified interpretation of the growing season hypothesis (Elser et al. 2000, Kerkhoff et al. 2005), suggesting that annual and seasonal light may be an important factor underlying latitudinal trends in tissue chemistry. This novel insight arises from our cross-system approach, and suggests that refining our tests of the temperature-based hypotheses (Kerkhoff et al. 2005) to examine the effects of different aspects of energetic input on global patterns of autotroph physiology is a promising new direction. Future work compiling and examining more direct measures of temperature, insolation, growing season length, and seasonality data for the photoautotrophs in this dataset would further disentangle and clarify the drivers.

Our examination of the variation in this data-rich dataset suggests that variation within species as a function of the many factors that act to determine the stoichiometry of autotrophs at regional and local scales is a stronger predictor of individual N and P chemistry than global variation in insolation or season length. However, the magnitude of this dataset provides high statistical power to discern differences among systems (i.e. extremely small standard error), leading to high confidence in the estimated latitudinal trends and lack of significant system-level interactions in these data. These concordant among-system trends can be resolved despite substantial variation around the system means, reflecting local variation in abiotic factors (e.g. altitude, aspect, depth, groundwater supply, rainfall, upwelling, local nutrient supply) or biotic factors (e.g. phenology, ontogeny, size, photosynthetic pathway, tissue longevity) (Wright et al. 2004, Lovelock et al. 2007, Mantlana et al. 2008, Ordonez et al. 2009, Elser et al. 2010). Many plant traits vary with somewhat different relationships to latitude in the northern and southern hemispheres (Moles et al. 2011), thus the variation observed here also may include differing rates of change in tissue N and P with latitude between the hemispheres. The variation within a latitudinal band underscores the importance of species- and site-specific information for predicting individual or local autotroph chemistry (McGroddy et al. 2004, He et al. 2008). These results reflect a growing awareness that local variation in plant traits is often as great or greater than global-scale trends (e.g. plant height, specific leaf area or seed mass, Moles et al. 2007, 2009, 2011, Poorter et al. 2012). However, the cross-system results presented here indicate that the biotic and abiotic factors that vary among ecosystems and locations likely act in addition to underlying global trends shared across the world's ecosystems.

Compositional turnover appears to underlie latitudinal trends in photoautotroph tissue chemistry, and, further, the similarity in trends among systems suggests that these trends are primarily driven by parallel or ancestrally shared evolutionary adaptations to environmental conditions common to all three ecosystem types. For those species with records spanning broad latitudinal extents, the trends of tissue N, P, and N:P are relatively weak, but the slope direction of each of these tissue nutrient measures is concordant with those in the full dataset. In contrast, the trends in the whole dataset emerge even after controlling for taxonomic affiliation, suggesting that species replacement (adaptation) may explain the observed latitudinal trends in tissue N and P chemistry. The weak, but concordant, within-species plastic responses (acclimation) may also play a role in the shared latitudinal trends in all ecosystem types. Such compositional turnover in response to large-scale variation in conditions appears to underlie other global-scale trends, such as the Redfield ratio observed in oceanic phytoplankton communities (Klausmeier et al. 2004, Arrigo 2005). As in the current study, species turnover in response to local conditions, rather than intraspecific plasticity in nutrient uptake, determines the phytoplankton community-level C:N:P signature.

The partitioning of variance extends this interpretation, clarifying that N, P and N:P are highly variable among individuals within a species, but photosynthetic tissue chemistry does not vary strongly among ecosystem types or growth forms. Although foliar chemistry has been treated as a species-level functional trait that is expected to vary more among species than within (McGill et al. 2006), the substantial variation of N and P within species suggests that these 'traits' may be context-dependent, varying within species and along broad environmental gradients in all systems. This concurs with recent analyses of functional trait diversity finding high variation among individuals within a species compared to variation among species (Cianciaruso et al. 2009), and suggests caution in treating species-level estimates for tissue nutrient concentrations as a functional trait (e.g. useful for local, but not global comparisons). Further, the predictable variation of tissue N across higher taxonomic levels (e.g. phylum, order) in all systems suggests that photosynthetic tissue N involves strong evolutionary constraints in multicellular autotrophs, whereas variation in tissue P and N:P may be less strongly associated with phylogeny (Ordonez et al. 2009).

Although taxonomy provides little explanation of the N:P variation across these data, the mean N:P ratio in this study follows consistent scaling within individuals, regardless of ecosystem. N:P scaling among individuals is a topic that has received substantial attention in terrestrial plants (Niklas 2006, Reich et al. 2010) and unicellular algae (Klausmeier et al. 2004), and our results for terrestrial N:P scaling reflect patterns found in previous studies. Our results extend previous work on autotroph stoichiometric scaling (Ågren 2004) by demonstrating the generality of the mean stoichiometric N:P coupling across multicellular autotrophs spanning extremely diverse physical environments.

Our comparison spans a highly diverse set of photoautotrophs evolutionarily adapted to very different abiotic and biotic conditions in marine, terrestrial and freshwater ecosystems and includes algae, mosses, ferns, gymnosperms and flowering plants. The similarity in mean N:P scaling we observed among ecosystem types clarifies that, while the N:P ratio declines faster in terrestrial autotrophs across latitude compared to aquatic autotrophs in this dataset, the underlying constraints on this ratio at the individual level are most likely associated with fundamental metabolic constraints common across all multicellular autotrophs. Thus,

if N:P stoichiometry indicates species-level nutrient limitation (Güsewell and Koerselman 2002, Tessier and Raynal 2003, Loladze and Elser 2011), our result is concordant with recent findings that autotroph nutrient limitation varies similarly across terrestrial and freshwater systems (Elser et al. 2007).

A variety of global processes are rapidly altering nutrient supply, temperature, growing season length, and insolation, including increasing rates of N deposition, increasing mean global temperature, longer high-latitude terrestrial and freshwater growing seasons due to elevated temperature (Roots 1989), warmer polar oceans (Hansen et al. 2006), and increased cloud cover and altered radiative-forcing at high latitudes (Eugster et al. 2000, Swann et al. 2010). Identifying and understanding the trends in factors that control autotroph tissue chemistry will improve biosphere model projections of NPP, decomposition, and global carbon cycles (Raddatz et al. 2007, Cornwell et al. 2008). The consistent trends of the means in photosynthetic tissue chemistry across Earth's ecosystems suggests that latitudinal variation in insolation, while a minor driver of local tissue chemistry, may underlie these global-scale trends.

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