

MULTIDIMENSIONAL NICHE APPROACH REVEALS CONSTRAINTS OVER
THE ELEMENTAL CONTENT OF ANIMALS

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A thesis submitted to the

Graduate School-Camden

Rutgers, The State University of New Jersey

In partial fulfillment of the requirements

For the degree of Master of Science

Graduate Program in Biology

Written under the direction of

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Camden, New Jersey

May 2019

THESIS ABSTRACT

Multidimensional niche approach reveals constraints over the elemental content of
animals

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The wide spectrum of phenotypic diversity found in life on Earth is a result of both environmental and evolutionary drivers. Functional traits are those elements of organismal phenotypes which have an effect on the organism's performance. Specific trait combinations can reveal ecological strategies that evolved in response to selection pressures. The elemental content of living organisms (carbon (C), nitrogen (N), and phosphorus (P)), represent key functional traits that have a strong influence over organismal form and function. Using a global database of stoichiometric traits of animals from terrestrial, freshwater and marine habitats ($n > 5000$), I applied hypervolume trait approaches to quantify the overall size and shape of the stoichiometric space of animals to determine differences in stoichiometric niche between animals inhabiting different habitats and animals occupying different trophic guilds. I found that the observed multidimensional trait space of animals was significantly smaller than the potential niche

space under null expectations and displayed an elliptical shape due to a significant correlation between C and N contents and independent variation of P content. The stoichiometric trait space of invertebrates and vertebrates occupying different habitats and from trophic guilds varied in their size and shape but displayed significant degrees of overlap suggesting evolutionary constraint over stoichiometric traits. These findings suggest that stoichiometric traits may be evolutionarily conserved in animals because regardless of the habitat in which the animals lived or the trophic guild they occupied, they did not evolve to occupy adjacent space, but overlapped in a large portion of their niche space. We argue that due to these evolutionary constraints, animals converge towards a limited amount of successful stoichiometric trait combinations resulting from trade-offs and covariance.

Keywords: stoichiometric niche, stoichiometric diversity, hypervolume, functional traits, functional diversity.

Introduction

Living organisms display an extraordinary phenotypic diversity both driven and constrained by ecological and evolutionary processes as well as physical laws (Reich et al. 2003, Wiens et al. 2010, Winemiller et al. 2015, Diaz et al. 2016, Pianka et al. 2017). Relevant aspects of organismal phenotypes are those morphological, physiological, biochemical, phenological and behavioral characteristics that influence the response of such organisms to environmental changes and/or underlie their effects on ecosystem processes (hereafter "functional traits") (Lavorel & Garnier 2002, Violle et al. 2007, Violle et al. 2009, Diaz et al. 2012). Trait-based approaches have improved our understanding of the range within and among species functional trait variation and helped to identify positive and negative covariances (i.e., trade-offs) among functional traits (Reich et al. 2003, Diaz et al. 2017, Funk et al. 2017). Specific trait combinations may reveal ecological strategies (e.g., allocation of resources for growth or reproduction), and represent suites of covarying traits that evolved in response to selection pressures imposed by diverse environments (Winemiller et al. 2015). Trait variation provides insights into understanding niche differentiation among species, their responses to environmental conditions, and their effects on ecosystem functions (McGill et al. 2006, Cadotte et al. 2008, Winemiller et al. 2015, Pianka et al. 2017).

The ecological niche is a unifying concept for ecology and evolution (Tilman & Snell-Rood 2014). The niche (*sensu* Hutchinson 1957) describes the set of abiotic and biotic conditions where any given species can persist, traditionally using environmental gradients as the axes of the niche space. Modern approaches have focused on the use of functional traits as fundamental axes of a species niche as surrogates for environmental

conditions (McGill et al. 2006, Violle et al. 2009, Carmona et al. 2016). In fact, the ecological niche depends on functional traits and these can help provide a mechanistic understanding of species responses to environmental variation across taxa and ecosystems (Violle et al. 2009).

Large-scale analyses of functional trait variation and the shape of the niche occupied by living organisms can help to identify general characteristics of organismal form, function, and strategy (Wright et al. 2004, Diaz et al., 2016; Pianka et al., 2017, Walker et al. 2017). Common dimensions of functional trait variation among plants species is the leaf economic spectrum, which represents a trade-off between resource acquisition and resource conservation traits. These trait trade-offs reflect evolutionary constraints, selection for adaptive trait combinations and physical laws acting on plant form and function (Grime JP (1979) Westoby et al. 2002, Banavar et al. 2014, Reich 2014, Diaz et al. 2016, Walker et al. 2017). Global studies on functional trait variation have shown that trade-offs between traits, niche convergence (i.e., the tendency to members of different clades to converge in a niche due to similar adaptive responses to similar environments; Diaz et al. 2016, Pianka et al. 2017), and phylogenetic niche conservatism (i.e, the tendency of lineages to retain their niche-related traits through speciation events; Ackerly, 2003; Ackerly et al. 2009, Cooper et al, 2010) restrict the overall niche space occupied by living organisms to a small proportion of the potential available niche space under null models (Diaz et al. 2016).

To date, most studies of global trait variation have been limited to a few particular taxa (i.e., mainly plants, but see Winemiller et al. 2015 for freshwater fishes, Pianka et al. 2017 for lizards, and Céréghino et al. 2018 for freshwater macroinvertebrates), restricting

our ability to better understand organismal trait diversity, its evolutionary trajectory and constraints, and its potential responses to environmental conditions. In the same way that functional traits are identified as drivers of variation in function in plants, the elemental content (carbon (C), nitrogen (N), and phosphorus (P)) of living organisms represent key functional traits because of their role in shaping plant and animal form, function, and diversity (Sterner & Elser 2002, Woodward et al. 2005, Elser et al. 2006, González et al. 2011, Vanni & Gephart 2011, González et al. 2017, González et al. 2018). Chemical elements are the building blocks of life and they are found in different proportions in the biomass of living organisms across domains of life (i.e., elemental phenotype) (Elser et al. 2006, Sterner & Elser 2002, Jeyasingh et al. 2014, Leal et al. 2016, González et al. 2017). The elemental phenotype represents the outcome of selective pressures and biophysical constraints acting on the chemical needs of life to build biomass and perform biological functions (Elser et al. 2006, Leal et al. 2016, Turner et al. 2017). Expressing living organisms in terms of their elemental composition helps reduce the number of relevant trait axis required to quantify and compare the niche within and across taxa (González et al. 2017, Peñuelas et al. 2019). Despite the prevalence of quantifications of the multidimensional ecological niche by plant ecologists (Lavorelle 2002, Peñuelas et al. 2008, Violle 2009, Diaz et al. 2016), a trait-based approach based on the chemical composition of organisms as a key aspect of a species niche has only been recently generalized and formalized (González et al. 2017, Peñuelas et al. 2019).

The overall goal of this study is to quantitatively characterize the global stoichiometric trait diversity and the shape of the multidimensional stoichiometric trait space of vertebrate and invertebrate organisms using C, N, and P as fundamental axes of

their niche (see González et al. 2017). Here, we will address three research questions: (i) What is the overall size and shape of the stoichiometric trait space of animals? We hypothesize that if variation in animal stoichiometric traits is highly constrained due to trait correlations and/or clumped distribution of stoichiometric traits along axes, we would expect animals to occupy only a subset of the potential volume of stoichiometric niche space (Díaz et al. 2016; Céréghino et al. 2018). In regard to the stoichiometric niche space shape, we hypothesize that if P is sequestered differently in vertebrates versus invertebrates due to the composition of bone, and C and N are invariant for vertebrates versus invertebrates, we would expect P content to vary independently from C and N, and the niche space will have an elliptical shape (Urist 1962, Woodward et al. 2005); alternatively, if C, N, P have relatively equal contribution to the niche, its shape will be spherical.

The final two questions will then analyze factors which may drive functional formation of the niche contributing to the constraint of the niche space which we hypothesized. (ii) Are there stoichiometric niche differences between animals inhabiting major habitats (aquatic versus terrestrial)? Terrestrial and aquatic plants have shown differential stoichiometry mainly driven by a high investment of C in terrestrial plants (Elser et al. 2000, Sterner & Elser 2002). Regardless of the differences in form and function between plants and animals, the physical constraints associated with the transformation, transfer, and exchange of matter in aquatic versus terrestrial environments, should also impose constraints on animal overall morphology and physiology (Banavar et al. 2014). If the adaptation of animals to life on water or land caused differential structural and functional differences in their stoichiometry (similar to

that found for plants), we would expect that aquatic and terrestrial animals would have evolved to fill adjacent areas in stoichiometric niche space. (iii) Are there stoichiometric niche differences between animals from different trophic guilds? Strong evidence suggests that trophic guilds have differential demands for elemental content. Specifically, higher N content in carnivores than detritivores or herbivores, and higher P content in detritivores than carnivores (Strohmeyer et al. 1998, Fagan et al. 2002; Denno et al. 2003; Woods et al. 2004; González et al. 2011; González et al. 2018; Ludwig et al. 2018). This variation in the elemental composition of animals from different trophic guilds has been suggested to arise from developmental outcomes related to the nutrient acquisition from herbivory versus carnivory (Fagan et al. 2002). Therefore, if there is a general relationship between animal nutrient content and their trophic guild, we would expect trophic guilds to occupy adjacent areas in the stoichiometric niche space.

Methods

Database compilation

We assembled a trait database that comprises >5,000 geo-referenced measurements of individual-level invertebrate and vertebrate functional traits: C, N, and P contents from terrestrial, freshwater and marine habitats worldwide. Data was compiled from both published and unpublished sources, and includes information on 1,941 morphospecies, 508 families, 116 orders, 34 classes, and 8 phyla of invertebrates and vertebrates spanning a large range in body size of 9 orders of magnitude (from 0.04 ug to 191 gr). The database was structured by site, geographic location, mean annual temperature (MAT), study site temperature, habitat (terrestrial, freshwater or marine), taxonomic

class, taxonomic order, taxonomic family, taxonomic genus, taxonomic species, stage (adult or larvae), trophic guild (carnivore, detritivore, omnivore or herbivore), C, N, P contents, and body size (mg dry mass). To complete the database and fill any missing values for elemental content, (in our database NAs were found exclusively in P content), we used P content-body size scaling relationships created at the morphospecies level using ordinary least squares (OLS) regressions using the *lmodel2*-package in R, replacing ~1400 NAs with interpolated values from body mass-P content relationships. Only morphospecies with >6 individuals were used for these scaling relationships.

Statistical analyses

To assess the size and constraints in the overall multidimensional stoichiometric niche space occupied by all individual animals in our dataset, we used the convex-hull approach (following González et al. 2017). To calculate the niche volumes, we used the hypervolume package, which uses a multivariate kernel density estimation technique (see Blonder 2014, 2018 for mathematical details). The units of the stoichiometric niche volumes are expressed as the standard deviations of centered and scaled log-transformed stoichiometric trait values raised to the power of the number of trait dimensions (in this study sd^3 dimensions). We then compared the observed hypervolume to theoretical null models, which are a widely used statistical approach in ecology. These null models represent pattern-generating models based on randomization of ecological data or random sampling from a known or specified distribution. The randomization is designed to produce a pattern that would be expected in the absence of a particular ecological or evolutionary mechanism (sensu Gotelli & Graves 1996). Further, null models are

particularly useful to more reliably identify patterns and infer causal mechanisms when using observational data (Gotelli & Graves 1996). If our observed data distributions differ from a null model, then we can infer that the patterns we observed may be caused by an ecological or evolutionary mechanism. In this study, we hypothesized that the observed hypervolume would be smaller than that of the null models, suggesting ecological and/or evolutionary processes constraining the stoichiometric niche space. We tested our observed data distribution against three theoretical null models proposed by Diaz et al. (2016). Model 1 tests the null hypotheses that traits vary independently and are normally distributed in the niche space, Model 2 assumes that traits vary independently without any a prior distribution expectation, while model 3 assumes that traits are normally distributed and follow the correlative structure of the data.

To determine potential correlations among traits and determine the stoichiometric niche shape, we used a principal component analysis (PCA) on the whole set of animal traits (C, N, and P). To assess which traits or trait combinations drive variations in the shape of niche volumes we used correlation strength between traits and ordination axes (González et al. 2017). The overall shape of the niche could suggest that organisms from particular groups, may have an increased allocation of a particular element or a combination of elements to structural or physiological processes generating an elliptical shaped niche; conversely if the allocation of each element is relatively equivalent, the niche would be spherical.

To answer the questions regarding the differences in the stoichiometric niche of animals inhabiting different habitats and trophic guilds we quantified their similarity by calculating independent hypervolumes (e.g., marine versus terrestrial versus freshwater

organisms), and quantified their overlap via the Sorenson index. This metric ranges from 0 to 1, with values closer to 1 indicating higher niche overlap, while values closer to 0 indicate low niche overlap.

The invertebrate trophic guild analyses included four trophic guilds (omnivore, carnivore, detritivore, and herbivore), but for vertebrates we were only able to analyze and compare stoichiometric niches among omnivores, carnivores and detritivores. Vertebrates, in particular fishes, display a high prevalence of omnivory (Ojwang et al. 2010), which represented the majority of the vertebrate data in our database, and included herbivore species as omnivores. We hypothesized that the observed hypervolumes would fill adjacent spaces in the stoichiometric trait space, suggesting divergent evolution between the groups in response varying structural demands (imposed by habitat type) or dietary demands (imposed by trophic guild), which would result in low degrees of overlap (Sorenson index) between the groups.

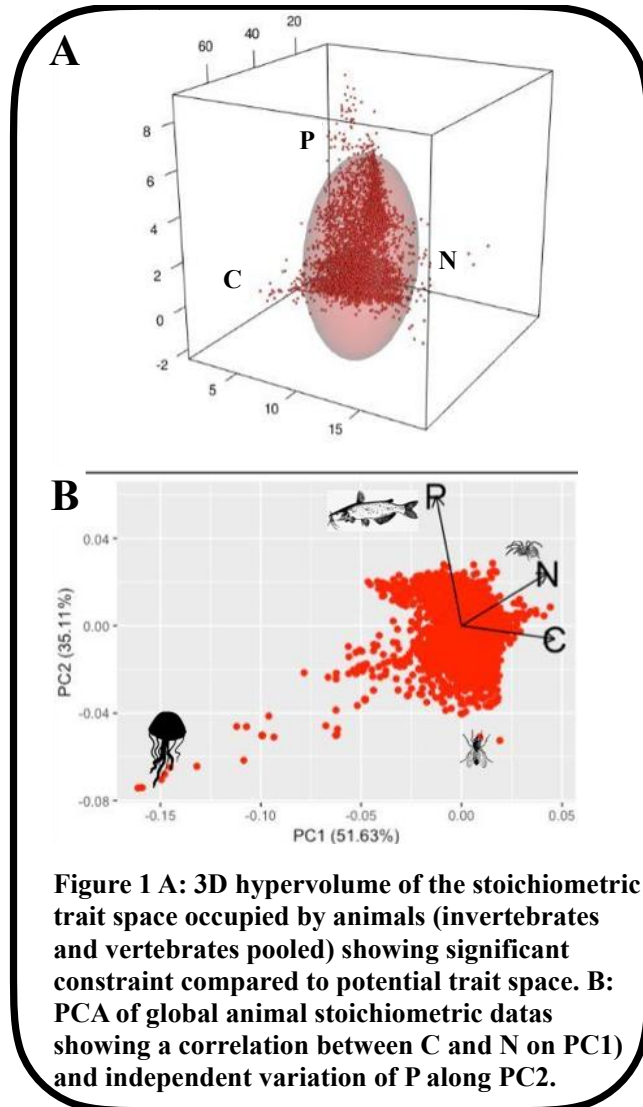
All analyses were performed in R (3.5.1) using packages hypervolume, abind, magic, ggplot, ggfortify, rgl, ade4, geometry, dplyr, alphahull, car, and magrittr. Similarity matrices were plotted in Origin using data generated from hypervolume analyses in R.

Results

Size and shape of the global stoichiometric trait space

The observed global stoichiometric hypervolume space of invertebrates and vertebrates was significantly smaller than hypervolumes generated by our null models. Our observed distribution was 40% smaller than the null model 1, 30% smaller than null model 2, and

36% smaller than null model 3 (Figure 1A). The PCA of the global stoichiometric trait space revealed two significant axis of variation, with roughly 87% of variation explained by PC1 and PC2. Along PCA axes, we observed a strong trait covariance between C and N contents varying along PC1, which explained about 52% of the variance of the trait space. P content varied independently along PC2, explaining almost 35% of the variance of the trait space (Figure 1B). The role of P as a driver of the shape of the overall stoichiometric niche space was confirmed when

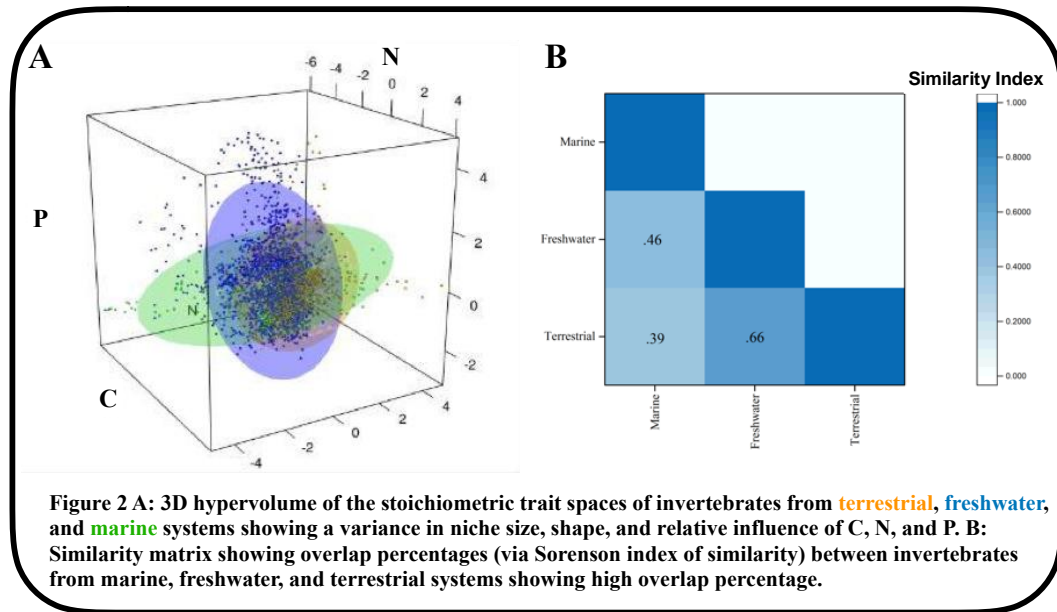


running independent PCAs for invertebrates from vertebrates. The PCA focused on invertebrate stoichiometry showed a C and N covariance on PC1, which accounted for 57% of the variance explained, while P varied independently on PC2 and accounted for about 31% of the variance (Supplementary Figure 1). The PCA based on vertebrate stoichiometry; however, showed C and N covariance on PC1 accounting for about 61% of the variance explained and P varied independently on PC2 accounting for 24% of the

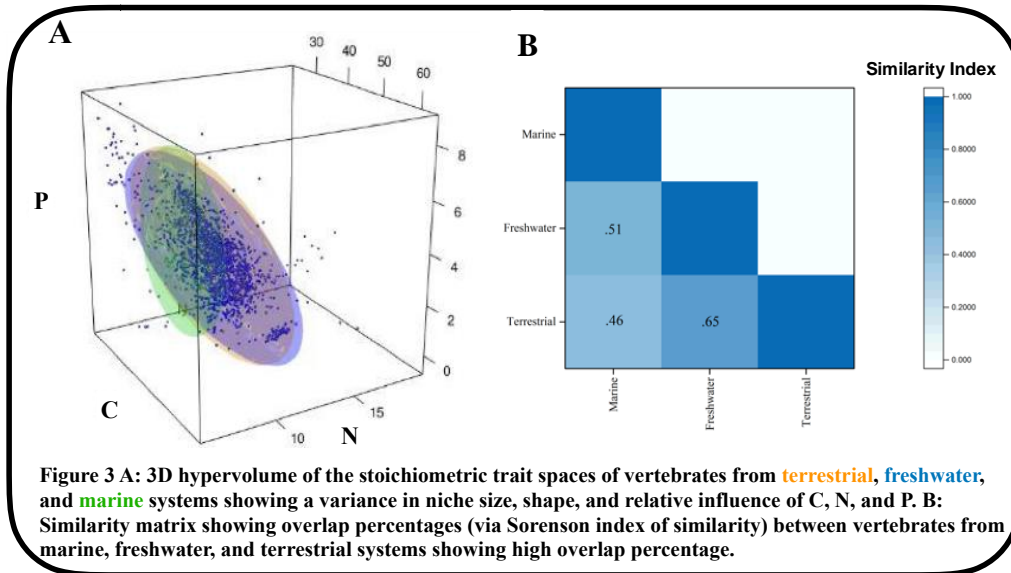
variance (Supplementary Figure 2). The vector patterns for each element in vertebrates were much more evenly spread, evidencing negative correlations among elements, while the invertebrate P vector was much closer to C and N, which clustered together (Supplementary Figures 1 and 2).

Hypervolume of invertebrates and vertebrates across habitats

The stoichiometric trait spaces of invertebrates across habitats varied in their size and shape but displayed large degrees of overlap. The largest trait space was observed for terrestrial invertebrates, while the trait space of freshwater invertebrates was 25% smaller of that of terrestrial invertebrates. Similarly, the trait space of marine invertebrates was about 70% smaller compared to terrestrial invertebrates. Terrestrial invertebrates displayed the most spherical niche, representing relatively similar contributions of C, N, and P to the variation of the hypervolume (Figure 2A). The niches of marine and freshwater invertebrates displayed an elliptical shape, however the orientation of each hypervolume in relation to elemental content was different; variation in P content drove the niche shape for freshwater invertebrates, while N drove the niche shape of marine invertebrates. Despite these differences, the invertebrates inhabiting each habitat overlapped in a relatively large portion of their stoichiometric trait space (Figure 2B). Terrestrial and freshwater invertebrates were the most similar in their hypervolumes, sharing over half of their stoichiometric space, while freshwater and marine invertebrates shared almost half of their trait space, and terrestrial and marine invertebrates shared roughly 40% of their trait space.

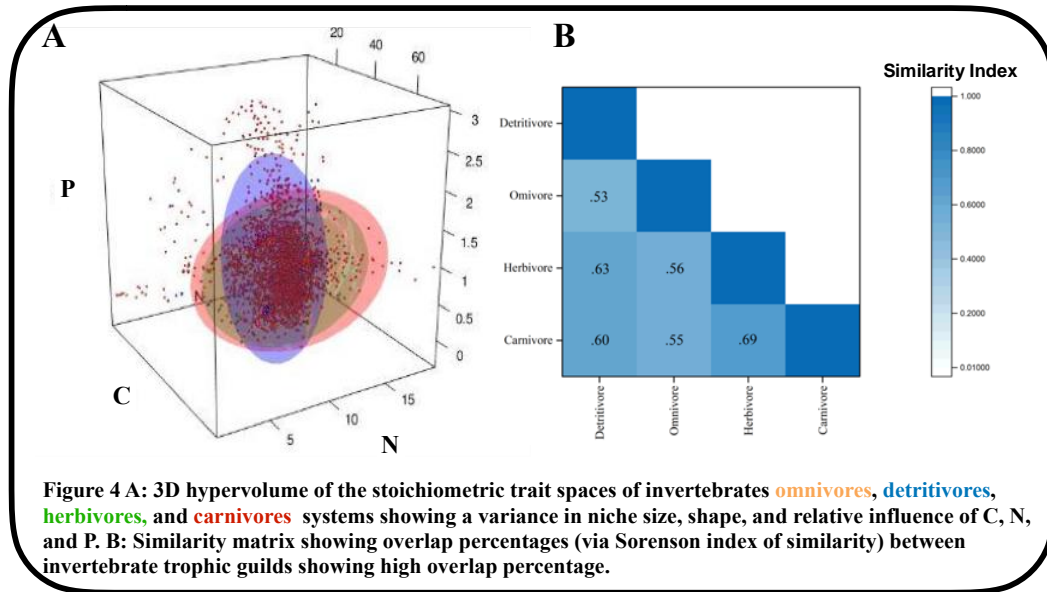


The stoichiometric trait spaces of vertebrates varied in their size but were consistently elliptical in shape. The largest trait space was observed for freshwater vertebrates, but terrestrial vertebrates were only 12% smaller in comparison, while the marine vertebrate trait space was 50% smaller than the stoichiometric niche of freshwater vertebrates (Figure 3A). All three niches showed a strong influence of P content over their shape, however the niche of marine vertebrates was more strongly influenced by N. The vertebrates from varying habitats displayed very similar patterns of overlap to the invertebrates: terrestrial and freshwater vertebrates shared roughly 65% of their stoichiometric trait space, marine and freshwater vertebrates shared 51% of their trait space, and marine and terrestrial vertebrates shared 46% (Figure 3B).

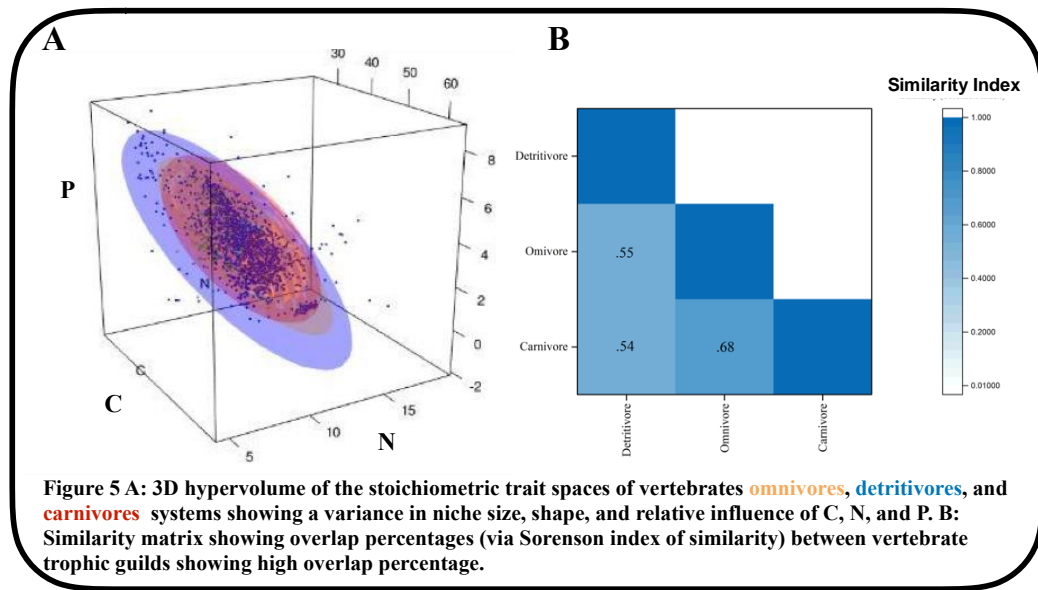


Hypervolumes of invertebrates and vertebrates from different trophic guilds

The stoichiometric trait spaces of invertebrates of different trophic guilds shared similar niche shape but varied in their size and the orientation of their niche. Omnivores occupied the largest niche, the carnivore niche was 38% smaller, the herbivore niche was 43% smaller, and the detritivore niche was the smallest: 55% smaller than the omnivore niche (Figure 4A). Though there was variation in niche parameters, the invertebrates from varying trophic guilds overlapped to a significant extent all >50%. Carnivores and herbivores shared 69% of their niche, followed by herbivores and detritivores whom shared 63%, carnivores and detritivores shared 60%, herbivores and omnivores shared 56%, carnivores and omnivores shared 55%, and omnivores and detritivores shared 53% (Figure 4B).



The stoichiometric trait space of vertebrates varied in their size, but had relatively consistent shapes and orientation towards P. The largest niche was occupied by detritivore vertebrates, the carnivore niche was 46% smaller, and the omnivore niche was 54% smaller than the detritivore niche (the herbivore guild is not represented independently because the herbivorous vertebrates in the dataset are not strictly herbivorous and therefore fall under omnivores) (Figure 5A). All of the niches were elliptical in shape due to the influence of P; however, carnivores were also strongly influenced by N. Vertebrates of varying trophic guilds showed a similar pattern to invertebrates, with the degree of overlap ranging from over a third to over one-half overlap. Carnivores and omnivores overlapped in 68% of their niche, omnivores and detritivores overlapped in 55%, and carnivores and detritivores overlapped in 54% of their niche (Figure 5B).



Discussion

Size and shape of the global stoichiometric trait space

In this study we hypothesized that the size and shape of the stoichiometric niche would be affected by covariance, specifically that animals would occupy a subset of the potential niche space and that the niche would be elliptical due to covariance of C and N, and independent variance of P. Our results support our niche size hypothesis, showing the stoichiometric trait space was highly constrained compared to the hyper volume that would result from random variation of stoichiometric traits. Only 60% of the potential stoichiometric trait space of invertebrates and vertebrates was occupied; this observed functional niche volume is similar to that reported for terrestrial plants worldwide (Díaz et al., 2016) and aquatic macroinvertebrates across Central-South America (Céréghino et al. 2018) using a different suite of traits. These findings suggest that traits do not expand unbounded but are limited by trait correlations that are inherent in the trade-offs necessary for biological structure and function (e.g., physiology). Our niche shape

hypothesis was also supported by our results, which showed that P content varied independently, and C and N contents covaried, giving the niche an elliptical shape. The individual variation along P is most likely explained by the inclusion of vertebrates and invertebrates, and stark contrasts between the way these two groups sequester P.

Vertebrates display a high investment in structural bones and scales, which are P rich (Woodward 2005, Hendrixson et al. 2006, Lall & Lewis-McCrea 2007, McIntyre et al. 2010), while P content in invertebrates is much lower and mainly contained in biomolecules, such as rRNA (~50% of P content of invertebrates is contained in rRNA) and ATP (Sterner & Elser 2002).

Hypervolume of invertebrates and vertebrates across habitats

We hypothesized that if the adaptation of animals to life on water or land caused differential structural and functional differences in animal elemental content (similar to plants), we expected that aquatic and terrestrial animals would have evolved to fill adjacent areas in stoichiometric niche space. Instead, our results show that animals (both invertebrates and vertebrates) inhabiting different habitats showed significant levels of overlap, suggesting strong evolutionary constraints over their chemical make-up, likely due to the internal chemical processes necessary for the formation of living cells. Organic chemistry has demonstrated that internal cells are kinetically controlled and limited by the demands of cellular reduction necessary for the production of essential chemicals as well as by the availability of certain elements and energy in the environment (Williams & DeSilva 2003, Anbar 2008, Schoepp-Cothenet et al. 2013). While organisms do show speciation and adaptation to their environment, they are limited cellularly due to the

nature of organic reactions to happen in equilibria, reducing the variance of the total environmental/biological system and its possible development (Williams & DeSilva 2003, Anbar 2008, Schoepp-Cothenet et al. 2013).

For invertebrates, despite their degree of overlap, the sizes, shapes, and drivers of their niche varied. Nitrogen appeared to be a driver of niche shape for marine invertebrates and P drove freshwater invertebrate niche shape, perhaps due to historical N limitation of marine systems and P limitation of freshwater systems exerted by their influence over the pace of primary production in their respective ecosystems (Howarth 1988, Elser 2000). There may also be more N allocation to muscle necessary for marine invertebrates when compared to freshwater invertebrates due to the differential demands of aquatic locomotion in marine water currents, versus still water found more often in freshwater systems (Vogel 2008). Conversely, the vertebrate niches were all heavily influenced by P confirming the importance of P to vertebrate physiology and there was a slight increase in overlap for vertebrates (compared to invertebrate habitat overlap patterns), which could be due to stronger physiological constraints linked to their large sequestration of phosphorus in their bones, limiting their potential trait combinations (Lall & Lewis-McCrea 2007). The large degree of overlap between animals from different habitats (for both invertebrates and vertebrates) suggests there is conservation of a common niche core representing evolutionary constraints evidenced by the portion of overlap resulting from the chemical limitations of adaptation (Arnold 1992, Williams & DeSilva 2003, Hellmann & Pineda-Krch 2007, Anbar 2008).

Our results were not consistent with those hypothesized that the structural demands of life in water versus land would impose pressures that would drive aquatic and

terrestrial animals to occupy adjacent stoichiometric trait space. Instead, the large degree of overlapping trait space indicates strong evolutionary constraints, which limit the adaptation of organismal elemental content to habitat type in regard to the main chemical elements (C, N, P) which we studied. It could be that organismal environmental adaptation happens in part due to the other, common (e.g., calcium) or rarer elements (e.g., iron, zinc), which are deposited differentially in ecosystems and are also integral to structural support (e.g., shells) and chemical reactions intracellularly (Williams & DeSilva 2003, Russel 2007, Anbar 2008, Schoepp-Cothenet et al. 2013).

Hypervolumes of invertebrates and vertebrates from different trophic guilds

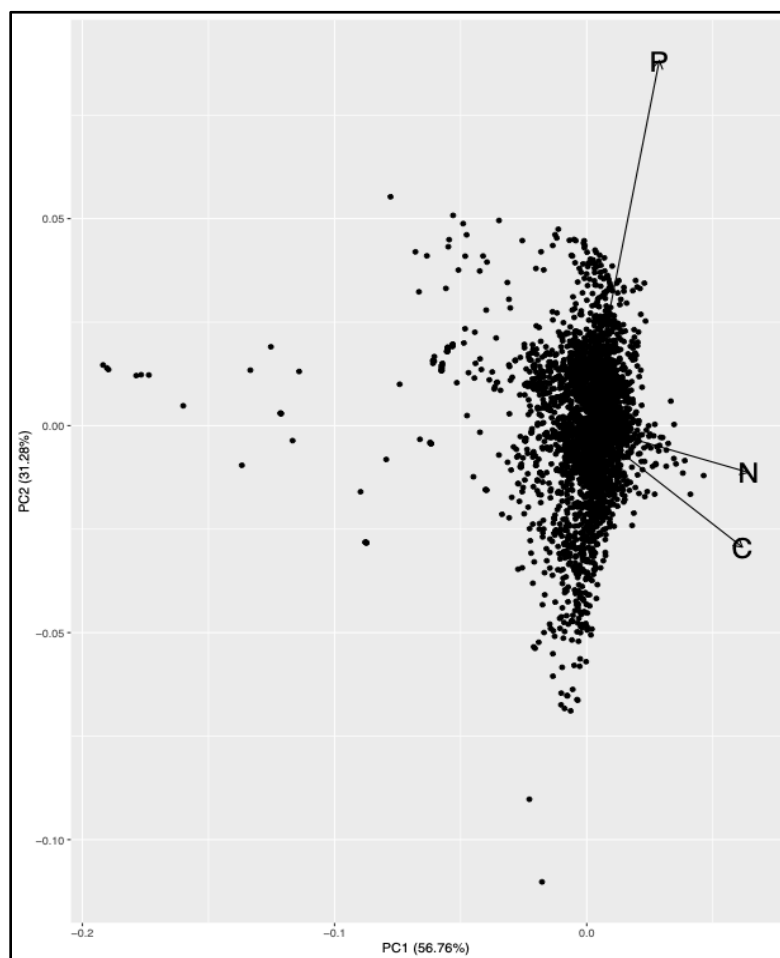
We hypothesized that diet quality (i.e., meat versus plant based) would have an effect on the stoichiometry of animals feeding on carnivore diets versus herbivore or detritivore diet (Fagan et al. 2002, Woods et al. 2004, Woodward et al. 2005, Persson 2010, González et al. 2011, Lemoine et al. 2014, González et al. 2018). Thus, we expected that the trophic guilds would evolve to occupy adjacent areas in the stoichiometric niche space, excluding omnivores whom were expected to have the largest and most overlapping niche, because of their generalist diet (consuming meat and plants). Instead, we found that the niches of animals from different trophic guilds had similar results to that of the habitat analyses, and had high overlap despite their variance. Nitrogen influenced the niche space of carnivores and herbivores. These results support the idea that N allocation (via muscular investment) increases with increasing trophic level, while C content tends to be invariant with trophic position (Schoeninger & DeNiro 1984, Fagan et al. 2002, Moe et al. 2005, González et al. 2011). Detritivores displayed differences

from other trophic guilds mainly in their P content, supporting the idea that P content in detritus is paramount for detritivore structure and function (Danger et al. 2013). Despite this variation, they did not occupy an adjacent space to other trophic guilds, but shared a significantly large portion of their trait space. This suggests strong evolutionary constraints that suppress a clear differentiation in the niche space of distinct trophic guilds. It appears that dietary demands of each trophic guild drive niche differentiation only partially, but their niche seems to be bounded by ancestral elemental content causing large overlap at their core.

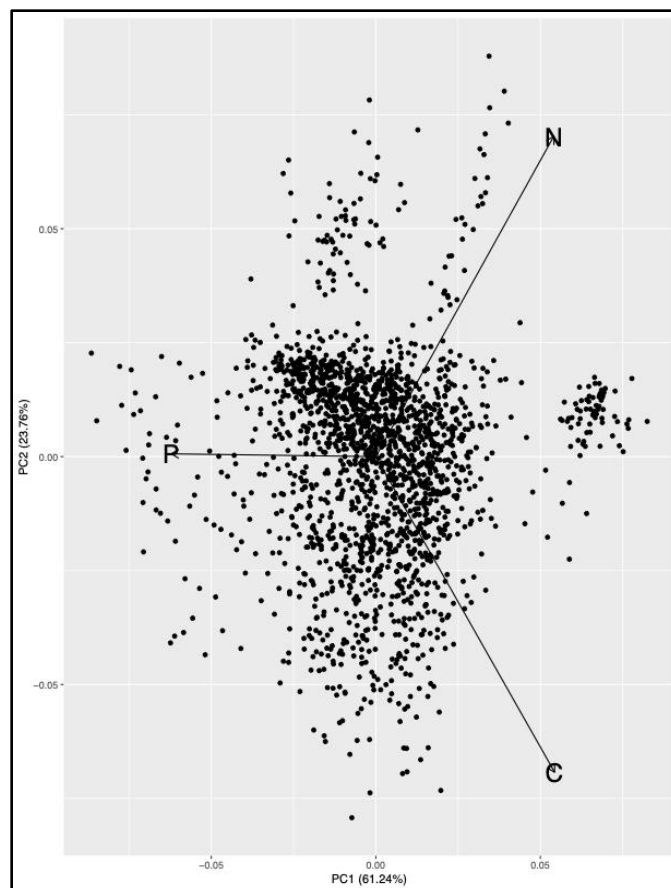
Overall our study showed that viable stoichiometric (C, N, P) trait combinations are limited due to trait correlations and trade-offs. These stoichiometric trait correlations and tradeoffs in animals suggests strong evolutionarily constraints. While the hypotheses of our study were based on the idea of a functional stoichiometric niche driven by adaptation to structural and dietary demands, our results suggest that the stoichiometric niche of invertebrates and vertebrates may be driven by their evolutionary relationships. The high relative degree of overlap for all animals is likely due to the relationships between cellular machinery and genetic constituents of structure and function (e.g., growth), and their evolution under varying nutrient conditions (Jeyasingh et al. 2014). Thus, the unique niche fractions within invertebrates and vertebrates from different habitats and trophic guilds perhaps represent more plastic individuals. Future work must seek to disentangle the forces of niche convergence and conservatism acting on the functional niche of animals to understand the role that evolutionary history plays on shaping the stoichiometric niches. Additionally, given the ongoing and predicted changes in biogeochemical cycles (Elser 2009), studies like this could address how temporal and

spatial changes in the biogeochemistry of the biosphere may drive changes in the stoichiometric trait space of animals or whether animals with particular stoichiometric niches may be more prompt to nutrient limitation effects, and to local extinction.

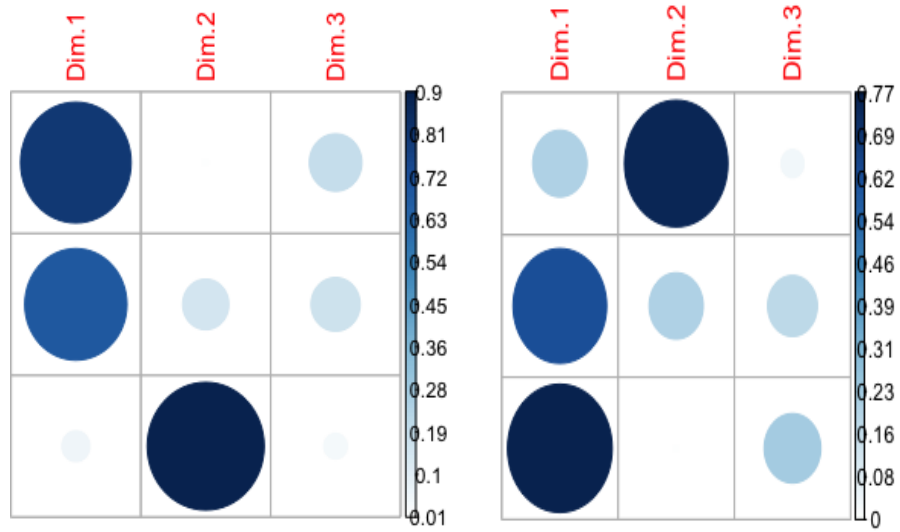
Supplementary Material



Supplementary figure 1: Invertebrate PCA showing comparatively low influence of P over niche shape.



Supplementary figure 2: Vertebrate PCA showing comparatively higher influence of P over niche shape.



Supplementary figure 3: Correlation plots for animals on the left and plants on the right showing dimensional correlations for C, N, and P with increasing intensity of blue representing increasing correlation showing independent variation of P for animals and C for plants, indicating that the organismal structural element varies independently.

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