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Threshold elemental ratios and the temperature dependence of herbivory in fishes

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Abstract

1. Herbivorous ectothermic vertebrates are more diverse and abundant at lower latitudes. While thermal constraints may drive this pattern, its underlying cause remains unclear. We hypothesized that this constraint stems from an inability to meet the elevated phosphorus demands of bony vertebrates feeding on P-poor plant material at cooler temperatures because low gross growth efficiency at warmer temperatures facilitates higher P ingestion rates. We predicted that dietary carbon:phosphorus (C:P) should exceed the threshold elemental ratio between carbon and P-limited growth ($TER_{C:P}$) for herbivores feeding at cooler temperatures, thereby limiting the range of herbivorous ectothermic vertebrates facing P-limited growth.

2. We tested this hypothesis using the Andean suckermouth catfishes *Astroblepus* and *Chaetostoma*. *Astroblepus* are invertivores that inhabit relatively cool, high-elevation streams while *Chaetostoma* are grazers that inhabit relatively warm, low-elevation streams. We calculated $TER_{C:P}$ for each genus across its elevational range and compared these values to measured values of food quality over an elevational gradient in the Andes. We also broadly summarized measurements of $TER_{C:P}$ across diverse groups of fishes.

3. Supporting our hypothesis, we found that dietary C:P was predicted to exceed the $TER_{C:P}$ for the grazer *Chaetostoma* near the highest elevation where this genus has been recorded. Conversely, the $TER_{C:P}$ for the invertivore *Astroblepus* was consistently higher than that of *Chaetostoma* and thus its dietary C:P never approached the $TER_{C:P}$. We found that, among all fishes, omnivores had higher average $TER_{C:P}$ than invertivores, and $TER_{C:P}$ did not vary with temperature.

4. Our results suggest that, at least for Andean suckermouth catfishes, cool temperatures constrain herbivory at higher elevations. Increased gross growth efficiency at cooler temperatures evidently restricts the ability of P-limited consumers to meet P demand. However, our survey of fish $TER_{C:P}$ estimates suggests that some fishes are able to circumvent this constraint through behavioural and life-history adaptations that reduce P demand or increase P use efficiency.

5. The physiological trade-offs underlying these functional shifts reveal that geographic dietary patterns can be predicted by stoichiometric theory, but variation in food quality and consumer traits that reduce P demand and/or increase P efficiency can create exceptions to these patterns.

1 | INTRODUCTION

The strength of herbivory can shape the structure and function of a wide variety of ecosystems (Carpenter, Kitchell, & Hodgson, 1985; Estes et al., 2011; Hairston, Smith, & Slobodkin, 1960). Moreover, the evolution of herbivory has affected the diversification of multiple animal lineages, as herbivorous clades tend to diversify more rapidly than predatory and omnivorous clades (Davis, Unmack, Vari, & Betancur-R, 2016; Price, Hopkins, Smith, & Roth, 2012; Wiens, Lapoint, & Whiteman, 2015). Whereas herbivory can have strong impacts across multiple scales, its prevalence is often limited by the physiological challenges of processing large amounts of recalcitrant and nutrient-poor material (Karasov, Martínez del Río, & Caviedes-Vidal, 2011). These challenges may have given rise to latitudinal and elevational gradients in herbivore diversity, with members of several animal groups having been shown to consume higher proportions of plant material at warmer temperatures (Behrens & Lafferty, 2007; Boersma et al., 2016; Carreira et al., 2016). For example, herbivorous fishes tend to be more abundant and diverse in warm, tropical ecosystems than in cool, temperate ecosystems (Floeter, Behrens, Ferreira, Paddack, & Horn, 2005; González-Bergonzoni et al., 2012). These observations of increased herbivory at lower latitudes have generated considerable research interest, yet a clear explanation for their cause remains elusive.

Proposed explanations for the increased diversity of herbivorous fishes in the tropics have largely centred around the temperature dependence of metabolism and assimilation efficiency when feeding on plant material (Behrens & Lafferty, 2007; Clements, Raubenheimer, & Choat, 2009). As a result, Clements et al. (2009) advocated for more widespread application of a theory-based nutritional framework in the study of fish herbivory. Ecological stoichiometry, the balance of multiple chemical elements and energy in ecological systems, provides a useful theoretical framework for understanding dietary constraints at the level of individual elements (Sterner & Elser, 2002). Indeed, stoichiometric theory has informed nutrient constraints on fish diets (e.g., Benstead et al., 2014; Hood, Vanni, & Flecker, 2005) and their consequences for ecosystem function (e.g., Moody et al., 2018; Schindler & Eby, 1997; Vanni, Layne, & Arnott, 1997). Integrating stoichiometry with metabolic processes in particular could provide a unified framework for understanding dietary constraints (e.g., Allen & Gillooly, 2009; Doi et al., 2010; Gillooly et al., 2005; Ott et al., 2014). These constraints are characterized by the threshold elemental ratio (TER), which explicitly bridges metabolism and stoichiometry by linking diet quality and assimilation efficiency to organismal growth.

The TER for two elements, such as carbon (C) and phosphorus (P), is defined as the dietary C:P ratio above which consumer growth switches from C-limitation to P-limitation (Frost et al., 2006). This concept was first developed for crustacean zooplankton (Urabe & Watanabe, 1992), and much subsequent work has retained this taxonomic focus (e.g., Frost, Xenopoulos, & Larson, 2004; Malzahn, Doerfler, & Boersma, 2016; Sterner, 1997). This narrow focus has limited our ability to understand broader patterns in how and why the $TER_{C:P}$ varies among taxa. Because $TER_{C:P}$ depends on maximum gross growth efficiency for C (GGE_C), which itself is proportional to metabolic rate, more detailed studies of TERs could illuminate links between metabolic theory and ecological stoichiometry (Doi et al., 2010; Frost et al., 2006). Variation in the $TER_{C:P}$ may explain geographic patterns in herbivory in ectotherms due to the temperature dependence of metabolic and ingestion rates. As metabolic rate is more sensitive to temperature than ingestion rate, max GGE_C tends to decline with temperature (Doi et al., 2010; Iles, 2014). However, the shallow slope of this relationship may lead to a weak dependence of $TER_{C:P}$ on metabolic rate (Doi et al., 2010). This dependence may be taxon-specific, as the relationship between max GGE_C and temperature is strongest in vertebrates (Doi et al., 2010). Therefore, temperature dependence of the $TER_{C:P}$ should be strongest in ectothermic vertebrates, which are often the dominant consumers in aquatic ecosystems.

If max GGE_C decreases with temperature in ectothermic vertebrates, the $TER_{C:P}$ will increase with temperature when all else is equal. We therefore hypothesize that vertebrate grazers are more abundant in warm, tropical latitudes due to the constraints of P-limited growth at cooler temperatures. If this hypothesis explains the phenomenon of higher grazer diversity in the tropics, then $TER_{C:P}$ should increase with temperature in fishes. Here, we test this hypothesis with a detailed study of closely related invertivorous and grazing suckermouth catfishes in the Andes, *Astroblepus* and *Chaetostoma*, in combination with a broader survey of $TER_{C:P}$ in fishes.

2 | MATERIALS AND METHODS

2.1 | Study system and elevational patterns

Astroblepidae and Loricariidae are sister families of loricarioid catfishes widely distributed throughout tropical South America and into Panamá (Lujan, Armbruster, Lovejoy, & López-Fernández, 2015). Astroblepidae, the naked suckermouth catfishes, contains only the exclusively Andean genus *Astroblepus*, but Loricariidae, the family of armoured suckermouth catfishes, contains over 950 species within 111 genera (Eschmeyer, Fricke, & Laan, 2018). In this study, we focus on *Astroblepus* and the primarily Andean loricariid genus *Chaetostoma* (Lujan, Meza-Vargas, Astudillo-Clavijo, Barriga-Salazar, & López-Fernández,
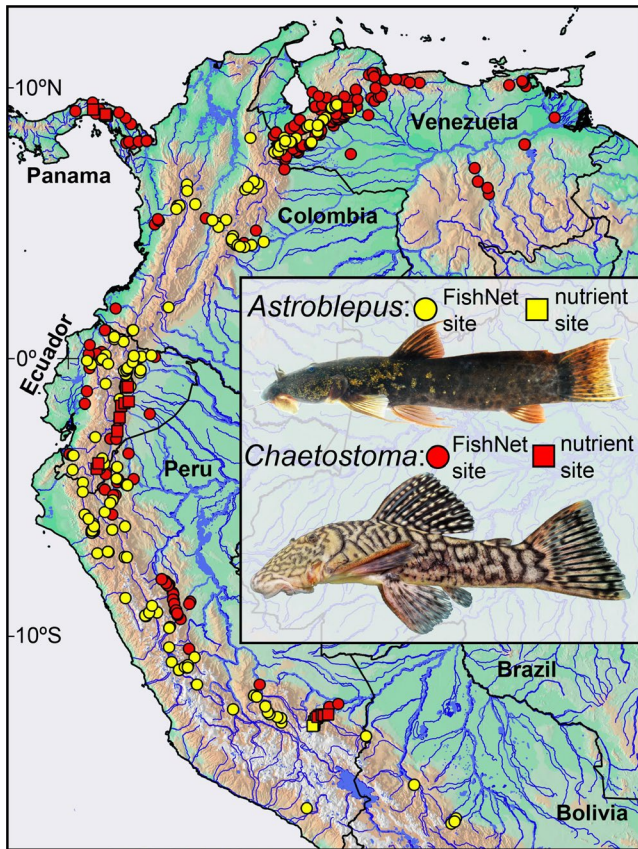
FIGURE 1 Map of museum specimen (circle) and body stoichiometry (square) localities for *Astroblepus* (yellow points) and *Chaetostoma* (red points) across South and Central America. Museum records were compiled from fish specimens indexed in FishNet 2.0

2015; Figure 1). *Chaetostoma* are considered obligate grazers of algae and detritus, whereas *Astroblepus* feed primarily on aquatic invertebrates (Angermeier & Karr, 1983; Lujan, Winemiller, & Armbruster, 2012; Vélez-Espino, 2003). While *Astroblepus* are generally considered to inhabit higher elevation streams than *Chaetostoma* (Carvajal-Quintero et al., 2015; Lujan et al., 2013; Schaefer & Arroyave, 2010), we formally tested this hypothesis by examining museum collection records of both genera in the FishNet 2.0 database. The results spanned the entire distribution of these genera, but the majority of records were from Andean drainages. We filtered these results by those that included GPS coordinates, from which we used a digital elevation model (NASA SRTM3) to calculate elevation. Our final dataset for this analysis included 355 records of *Astroblepus* and 339 records of *Chaetostoma*. We then performed a Mann–Whitney test on these data to test for differences in the elevation occupied by each genus.

2.2 | Field sampling

Fish specimens were collected for body stoichiometry analyses using combinations of nets and electricity during expeditions to

southern Peru (2010; ~13°S latitude; Lujan et al., 2013), central Ecuador (2012; ~2°S latitude; Lujan, Meza-Vargas et al., 2015) and eastern Panamá (2013; ~9°N latitude; E. K. Moody, F. Alda, & B. L. Turner, unpublished data). We also included previously published data from the Río Las Marías in Venezuela (Hood et al., 2005; ~9°N latitude) (Figure 1). While *Chaetostoma* were collected in all of these regions, *Astroblepus* were collected only over an elevational gradient in the Inambari watershed of Peru. All fish specimens were euthanized after capture via overdose of clove oil, following approved Royal Ontario Museum and Smithsonian Tropical Research Institute Institutional Animal Care and Use guidelines. Due to the remote sampling locations without access to electricity, whole specimens for nutrient analyses were field preserved in an excess of table salt (NaCl). Additional replicates of all morphotypes used for nutrient analyses were fixed in 10% formalin, then preserved in 70% ethanol and cataloged at the Royal Ontario Museum or the Smithsonian Tropical Research Institute Neotropical Fish Collection for taxonomic confirmation and revision. In addition to fish collections, we also measured water temperature, specific conductance, pH, dissolved oxygen and salinity at each sampling site with a Hydrolab internally monitoring Minisonde (Ott Hydromet, Loveland, CO, USA).

2.3 | Laboratory analyses

Salt-preserved specimens were transported to the United States for laboratory analyses. Specimens were rinsed in NANOpure-filtered water then rehydrated for 3 days to remove any salt or other unrelated soluble material. We then re-dried them at 60°C until they reached constant mass, at which time we individually homogenized each fish using a ball mill. Subsamples of homogenized fishes were then analysed for body elemental contents. We measured body %C and %N using a PerkinElmer 2400 CHN analyser and %P using the acid molybdate method following HCl digestion. We observed the presence of oils in the salt medium, indicating that salt preservation likely led to some losses of lipids relative to standard preservation methods such as freeze drying or immediate drying after collection. Such losses in turn likely reduced %C and elevated %N and %P values. Because the same methods were applied to both genera and our mean C:P value for *Chaetostoma* fell within the range of published values for this genus (Vanni, Flecker, Hood, & Headworth, 2002), we believe any bias resulting from this was minor and should not affect our conclusions.

2.4 | Threshold elemental ratio modelling

To test whether variation in elevational distributions reflects shifts in nutrient limitation, we then used these data to model molar TERs for C:P using Equation (1) as defined by Frost et al. (2006):

$$\text{TER}_{\text{C:P}} = (A_\text{P}/GGE_\text{C}) * (Q_\text{C}/Q_\text{P}) \tag{1}$$

In this equation, A_P represents the assimilation efficiency for P, GGE_C represents the gross growth efficiency for C, Q_C represents

the body C content, and Q_P represents the body P content. While the latter two parameters were directly measured from specimens as described above, the former two were estimated using a variety of sources. We used a fixed value of A_P across temperatures given that there is no clear evidence that A_P is temperature-dependent. Specifically, we used the approximate A_P value calculated by Hood et al. (2005), 0.8, for *Chaetostoma* in an Andean piedmont river. In contrast to A_P, GGE_C typically decreases with temperature (Doi et al., 2010). We thus used the relationship measured by Doi et al. (2010) in vertebrates to model growth rate as a function of temperature over elevational gradients using GGE_C calculated by Hood et al. (2005) at low elevation (225 m a.s.l.). Estimates of variation in body C and P contents with elevation were included in the model based on linear model predictions of body C:P over the range of elevations where each taxon occurred. We then estimated uncertainty in the $TER_{C:P}$ based on intraspecific variation in body C:P by calculating the standard deviation body C:P within each 250 m elevational bin and calculating upper and lower bounds to the $TER_{C:P}$ using these standard deviations. Beyond the known elevational range of each taxon, we conservatively assumed a static C:P predicted at the maximum or minimum range of the distribution. We estimated the relationship between stream water temperature and elevation using data collected during the collection of field samples across an elevational gradient from 50 to 4,300 m a.s.l. Even though multiple factors influence stream temperature, these tropical montane streams tend to be thermally stable, and a logarithmic decay function effectively explained temperature variation with elevation among our sampled streams ($R^2 = 0.86$).

We compared modelled $TER_{C:P}$ values against published C:P data of potential dietary resources over an elevational gradient from 1,260 to 4,045 m a.s.l. in the Ecuadorean Andes (Atkinson et al., 2018). For *Astroblepus*, we used body stoichiometry data from the baetid mayfly genus *Andesiops* as these small mayflies are widespread across the studied elevation gradient and likely an important prey item for fishes that specialize on aquatic invertebrates (Angermeier & Karr, 1983; Pouilly, Barrera, & Rosales, 2006; Vimos, Encalada, Ríos-Touma, Suárez, & Prat, 2015). While *Astroblepus cyclopus* in the Río Quindio, Colombia, fed primarily on aquatic beetle larvae and adults (Román-Valencia, 2001), a widespread stoichiometric dataset for those taxa in the Andes was not available. However, a more limited dataset for larvae of the beetle *Anchytarsus* among six Panamanian streams (E. K. Moody, J. J. Elser, A. T. Rugenski, & B. L. Turner, unpublished data) suggests that body C:P of *Anchytarsus* (mean C:P = 151) is somewhat higher than in *Andesiops* (mean C:P = 113); as this difference would not qualitatively affect our conclusions, we used the more elevationally comprehensive *Andesiops* dataset. For *Chaetostoma*, we used periphyton as the food resource of these algal grazers (Kramer & Bryant, 1995; Lujan et al., 2012). While these dietary stoichiometry data represent only one basin, that is the Napo at approximately 1°S latitude, they are broadly consistent with patterns in other Andean streams that are largely driven by typical alpine trends in

which canopy cover declines and light exposure increases at higher elevations (Atkinson et al., 2018; Kohler et al., 2012; Martyniuk, Modenutti, & Balseiro, 2016). As a result, these data provide necessary context to understand the importance of any observed $TER_{C:P}$ shifts with elevation. Finally, we empirically tested the predictions of the TER models by sampling for the presence of loricarioid catfishes at eight sites in the upper Marañon drainage in Peru with a combination of electrofishing and seining in August 2018.

2.5 | Broader TER variation

To place the generality of this case study within the broader context of fishes, we examined the literature for studies of the $TER_{C:P}$. All previously published estimates were found in a single paper (Frost et al., 2006). As a result, we also searched for cases where GGE_C, A_P, and body stoichiometry have been measured in the same genus or species and added an additional 14 studies from which we were able to calculate twenty additional $TER_{C:P}$ estimates, yielding a total of 31 $TER_{C:P}$ estimates. When possible, we calculated individual $TER_{C:P}$ estimates for each temperature for which data were available. In some cases, body stoichiometry data were compiled from a large stoichiometric database (Vanni et al., 2017). If A_P could not be calculated from the study, it was assumed to be 0.8 (Frost et al., 2006). When necessary, we also converted feed conversion ratio, a measure of the wet mass of fish gained relative to the amount of food consumed, to gross growth efficiency, which is based on dry mass, assuming a dry mass to wet mass conversion factor of 0.25 (Doi et al., 2010). We then tested whether $TER_{C:P}$ varied with temperature, dietary strategy or their interaction using ANOVA. Temperature and body mass data were obtained from the source studies, and dietary categories were divided between predators and omnivores/herbivores based on information about trophic ecology reported in the source studies and Vanni et al. (2017). Assumptions of normality and homogeneity of variance of residuals were visually assessed using Q-Q plots and residuals versus fitted values plots, respectively. All statistical analyses were performed in R (R Core Team, 2017).

3 | RESULTS

3.1 | Elevational patterns

Our search of museum records yielded 355 lots of *Astroblepus* and 339 lots of *Chaetostoma* with georeferenced locality information. As predicted, we found that *Astroblepus* inhabited significantly higher elevations than *Chaetostoma* (Mann–Whitney test, $U = 105,860$, $p < 0.001$; Figure 2). In spite of this difference, however, there was a considerable range of overlap in elevations where both genera have been recorded between 100 and 2,000 m a.s.l. (Figure 2). Using the specimens we collected, we then examined whether body stoichiometry of these taxa varied with elevation. For these analyses, we included data from 26 specimens
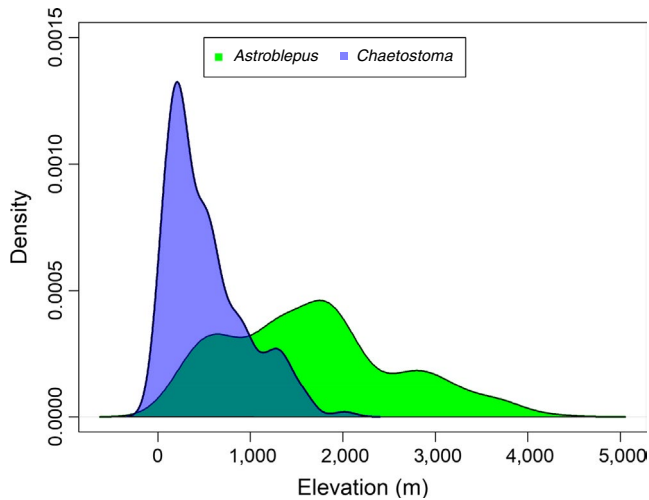
FIGURE 2 Probability density of elevational records of *Astroblepus* and *Chaetostoma* from the Andes in South America. Records compiled from fish specimens indexed in FishNet 2.0

of *Astroblepus* (all from Peru) and 78 specimens of *Chaetostoma* (from Ecuador, Panamá, and Peru). Interestingly, body C:P did not vary with elevation in either genus ($F_{1,100}$ = 0.60, p = 0.440), but was significantly lower in *Chaetostoma* than in *Astroblepus* ($F_{1,100}$ = 144.19, p < 0.001; Figure 3). Body C:P was also considerably more variable in *Astroblepus* than in *Chaetostoma* (Figure 3). We found no interacting effect of elevation and genus on body C:P ($F_{1,100}$ = 2.38, p = 0.126), indicating that differences among genera in body stoichiometry are relatively consistent across the elevations we sampled. However, we did find a non-significant trend of decreasing body C:P with elevation in *Chaetostoma*.
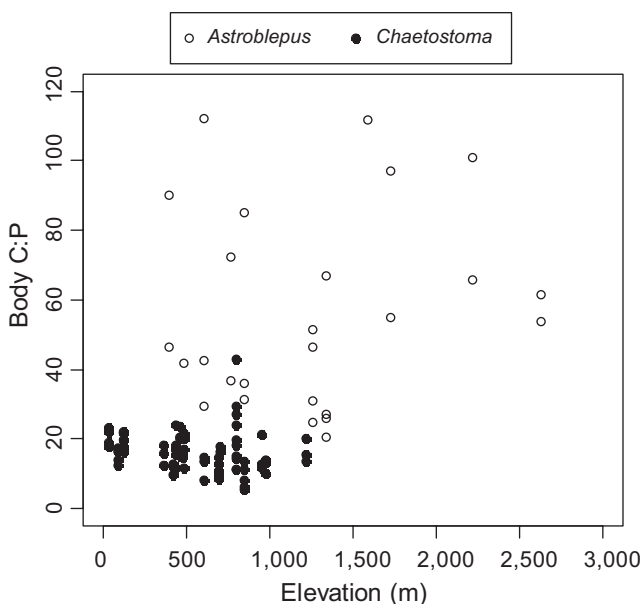
3.2 | TER calculations

We then used these body stoichiometry data to model the $TER_{C:P}$ for *Astroblepus* and *Chaetostoma* across the elevational ranges of these genera. Because *Astroblepus* are less P-rich than *Chaetostoma* (Figure 2), the $TER_{C:P}$ for *Astroblepus* was approximately twice as high as that for *Chaetostoma* across all elevations (Figure 4). The predicted $TER_{C:P}$ declined steeply with elevation up to around 500 m for *Astroblepus* and up to around 1,200 m for *Chaetostoma*, but then levelled off at higher elevations for both species (Figure 4). The higher elevation at which *Chaetostoma* $TER_{C:P}$ continued to decline was due to the trend of declining body C:P up to 1,200 m in that genus. We also found considerably higher uncertainty in the *Astroblepus* $TER_{C:P}$ due to the higher degree of body stoichiometric variation in that genus. While these results indicate greater potential for P-limited growth in *Chaetostoma*, particularly at higher elevations, the presence of P-limitation can only be inferred relative to dietary C:P. We therefore compared these thresholds to published periphyton and invertebrate C:P ratios over an elevational gradient in the Ecuadorean Andes.

For *Astroblepus*, the C:P of potential invertebrate prey increased slightly with elevation, but was considerably lower than the calculated $TER_{C:P}$ at all elevations (Figure 5). This was true even when considering the high degree of variation in the lower bound of the $TER_{C:P}$. In contrast, variation in *Chaetostoma* dietary C:P led to predicted shifts from C-limited to P-limited growth. As periphyton C:P increased with elevation in the Andes, the dietary C:P was predicted to exceed the $TER_{C:P}$ for *Chaetostoma* at an elevation around 1,900 m (Figure 6). This predicted shift from
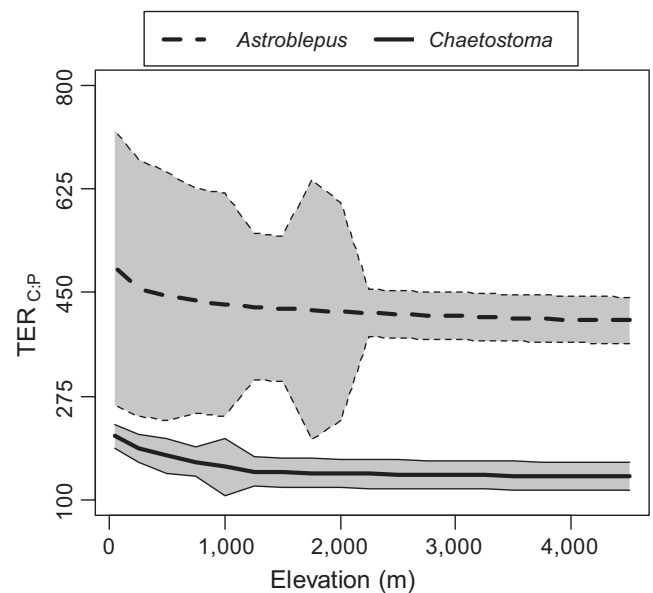

FIGURE 3 Body C:P of *Astroblepus* and *Chaetostoma* across the elevations sampled. Body C:P was consistently lower in *Chaetostoma* than in *Astroblepus* across elevations. Each point represents the body C:P of an individual fish

FIGURE 4 Modelled threshold elemental ratios between C- and P-limited growth ($TER_{C:P}$) for *Astroblepus* (dashed line) and *Chaetostoma* (solid line). Thick lines represent $TER_{C:P}$ modelled based on the model predicted body C:P based on elevation, and shaded grey regions around each model estimate reflect the standard deviation in body C:P within each 250 m elevational bin
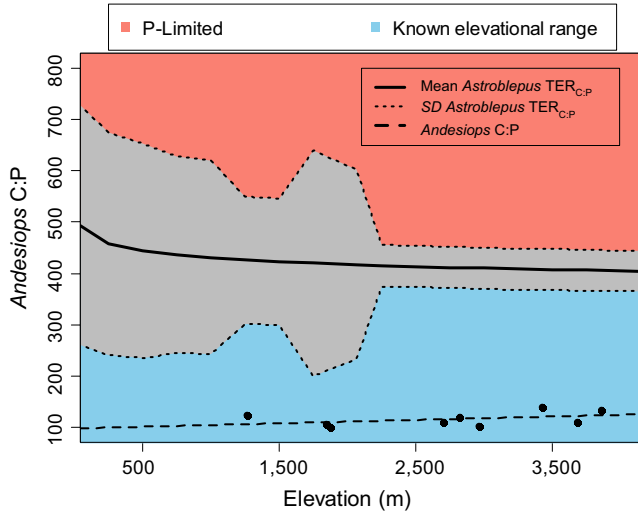
FIGURE 5 TER$_{C:P}$ for *Astroblepus* relative to *Andesiops* C:P (from Atkinson et al., 2018) and the known elevational range of *Astroblepus* in the Andes. The bold line represents the modelled TER$_{C:P}$, while the shaded grey region around it reflects uncertainty due to the standard deviation in *Astroblepus* body C:P. *Astroblepus* are predicted to be C-limited throughout their range when feeding on invertebrates such as *Andesiops*
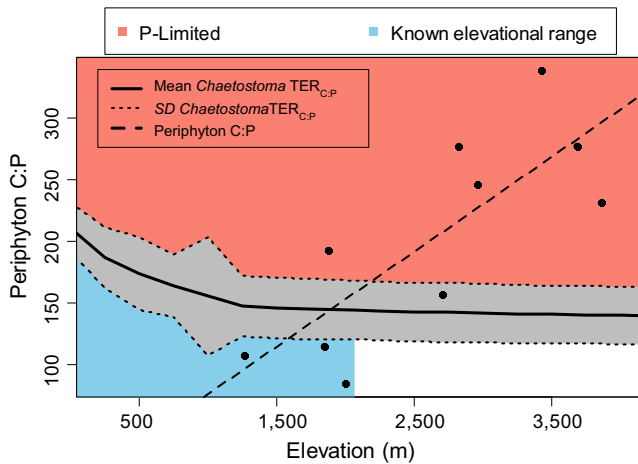

FIGURE 7 Catch per unit effort (CPUE) of *Astroblepus* (blue points) and *Chaetostoma* (green points) from eight sites over an elevational gradient in the upper Marañon drainage of Peru. All sites were sampled with a combination of electrofishing and seining for 45–90 min. Data are shown against the predicted elevation above which *Chaetostoma* growth is predicted to shift to P-limitation, and above which no *Chaetostoma* were collected

FIGURE 6 TER$_{C:P}$ for *Chaetostoma* relative to periphyton C:P (from Atkinson et al., 2018) and the known elevational range of *Chaetostoma* in the Andes. The bold line represents the modelled TER$_{C:P}$, while the shaded grey region around it reflects uncertainty due to the standard deviation in *Chaetostoma* body C:P. The known range depicted in blue roughly corresponds to the elevation at which periphyton C:P is predicted to exceed the TER$_{C:P}$, indicating that P-limitation may limit the distribution of *Chaetostoma* in the Andes

FIGURE 8 Probability density of TER$_{C:P}$ estimates for invertivorous and omnivorous/grazing fishes from published studies (including this study). TER$_{C:P}$ was higher in omnivores/grazers but did not vary with temperature

per unit effort (CPUE) declined approaching the predicted elevation where growth shifts to P-limitation (Figure 7).

3.3 | Broader TER variation

We compiled or calculated TER$_{C:P}$ values based on data from the published literature to examine whether patterns observed for Andean catfishes are general. Contrary to our hypothesis, we found that TER$_{C:P}$ did not vary with temperature among the 31 TER$_{C:P}$ estimates we compiled ($F_{1,27} = 0.63$, $p = 0.435$). These broader results also contrasted with those from our case study of Andean catfishes. Specifically, we

C-limited growth to P-limited growth corresponded closely with the maximum recorded elevation for *Chaetostoma* in our dataset, a population of *C. microps* at 1,970 m a.s.l. and 6°S latitude in the Río Huancabamba in Peru (Figure 6). Our own validation sampling across an elevational gradient in the Marañon drainage further supported these predictions, as no *Chaetostoma* were recorded above 1,836 m a.s.l. in the Río Huancabamba. Further, *Chaetostoma* catch
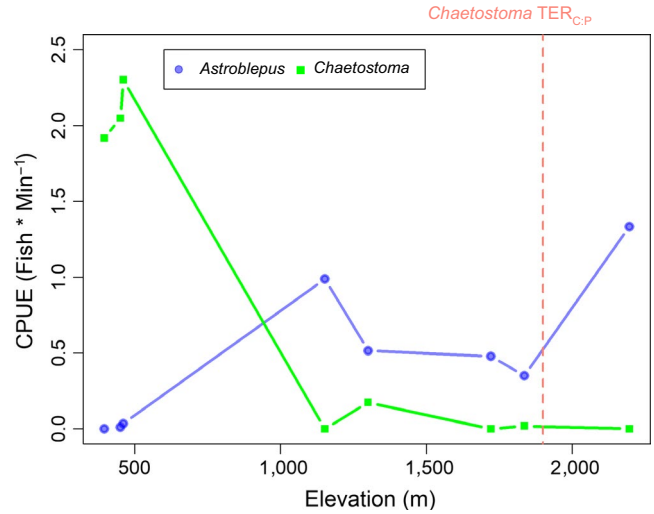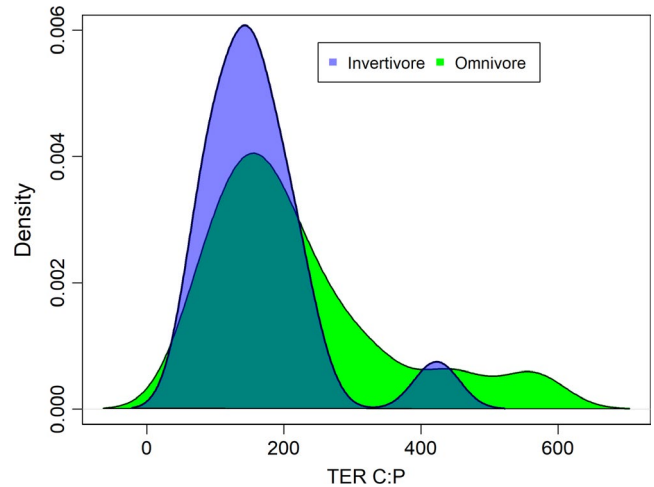
found that omnivorous and grazing fishes had a higher average $TER_{C:P}$ than invertivorous fishes ($F_{1,27} = 5.98$, $p = 0.021$; Figure 8) among all fish $TER_{C:P}$ estimates. There was no significant interaction between temperature and diet ($F_{1,27} = 2.81$, $p = 0.105$). Whereas several omnivores had $TER_{C:P}$ within the same range as invertivores, their higher average $TER_{C:P}$ seems to be driven by a few particular species with high $TER_{C:P}$ (Figure 8). Our highest $TER_{C:P}$ estimates for omnivores were for goldfish (*Carassius auratus*), mullet (*Liza* spp.) and guppies (*Poecilia reticulata*) (Supporting Information Table S1).

4 | DISCUSSION

Interactions between stoichiometric traits and the environment can constrain the distribution of species and even entire functional groups. We found that modelled $TER_{C:P}$ declines as food resource C:P increases with elevation, suggesting that there is a greater risk of P-limitation in cooler, high-elevation streams. The predicted elevation where the $TER_{C:P}$ of *Chaetostoma* exceeds periphyton C:P lies remarkably near the highest elevation where this genus has been recorded, suggesting that this shift to P-limitation could constrain the colonization of grazing loricariids into cooler habitats. Conversely, their insectivorous sister family Astroblepidae dominates at higher elevations where their diet is predicted to fall substantially below the $TER_{C:P}$. While these results support our hypothesis that lower $TER_{C:P}$ in grazing fishes constrains their distribution at cooler temperatures, a broader survey of fish $TER_{C:P}$ estimates found no variation with temperature. In contrast to our results for Andean catfishes, we also found that omnivorous fishes generally have higher $TER_{C:P}$ than predators. These apparent discrepancies merit further consideration to evaluate why our hypotheses were not clearly supported.

We hypothesized that $TER_{C:P}$ should decrease with temperature due to the inverse relationship between GGE_C and temperature. However, we assumed that body C:P was invariant with temperature and with it, metabolic rate. In the case of *Astroblepus* and *Chaetostoma*, we found the expected decline in $TER_{C:P}$ with temperature while body C:P did not vary significantly with temperature in either genus. However, fish body C:P can decrease with metabolic rate due to reduced lipid storage under higher metabolic expenditures (Dalton & Flecker, 2014). Thus, body C:P may also be inversely related to temperature in aquatic vertebrates (e.g., Moody et al., 2018). Therefore, our predictions may only be useful for groups with relatively fixed body stoichiometry. Another possibility, however, is that interspecific variation in the relationship between $TER_{C:P}$ and temperature muddled the relationship among taxa. While GGE_C may decrease with temperature in all or most fishes, the parameters describing this relationship may vary considerably among taxa adapted to different thermal regimes (Moffett, Fryxell, Palkovacs, Kinnison, & Simon, 2018; Munday, Donelson, & Domingos, 2017). Supporting this hypothesis, we found negative relationships between $TER_{C:P}$ and temperature for the three additional taxa for which we were able to calculate $TER_{C:P}$ at multiple temperatures: robust Gambusia (*Gambusia marshi*), mullet (*Liza* spp.) and rainbow trout (*Oncorhynchus*

mykiss) (Supporting Information Table S1). Given these possibilities, we examine our focal study system of *Astroblepus* and *Chaetostoma* in further detail to understand what aspects of these taxa may have led to support for our hypotheses in this system.

Andean suckermouth catfishes provide a highly suitable study system to examine stoichiometric constraints on the trophic niche for many reasons. Loricariidae is among the most diverse fish families in the Neotropics, yet the native geographic range of this family is limited to warmer latitudes and elevations, from approximately 10°N to 35°S and sea-level to approximately 2,000 m a.s.l. While the Central American isthmus historically represented a northern barrier to loricariid expansion (Smith & Bermingham, 2005), loricariids could have easily colonized higher elevation streams in the Andes and streams south of their current southern range limit in central Argentina. In spite of this, upland-dwelling loricariid genera, such as *Chaetostoma* and the phenotypically similar genus *Ancistrus*, typically reach their upper elevational limit between 1,100 and 1,200 m a.s.l. (Carvajal-Quintero et al., 2015; Lujan et al., 2013). While our data suggest that some degree of body stoichiometric variation within these genera can modulate the $TER_{C:P}$ and explain this indistinct upper elevational range limit (Figure 6), there is evidently still a point where temperatures become too cold for any grazing loricariid population to persist. In the Andes, the increase in periphyton C:P with elevation (Atkinson et al., 2018; Martyniuk et al., 2016) in concert with the decreased $TER_{C:P}$ apparently constrains the upper elevation at which these grazers can sustain viable populations. However, other potential contributing factors, such as atmospheric pressure, UV radiation, geology, slope, vegetation and discharge, also vary in relation to elevation. While these factors likely play some role in determining the distribution of the biota across this landscape, we note that introduced populations of loricariids at more northern latitudes typically establish in warm, nutrient-rich systems, such as rivers affected by wastewater treatment discharges and sewage effluent (e.g., Capps, Castillo, Pease, Jarquín-Sánchez, & Rodiles-Hernández, 2017; Nico & Martin, 2001). This observation supports our hypothesis that the interacting effects of food quality and temperature play an important role in delimiting loricariid distributions. In light of this evidence, we must evaluate whether P-limitation alone could truly constrain the distribution of fish populations.

The question of the prevalence and importance of P-limitation to fishes has been a subject of considerable debate (Benstead et al., 2014; Boersma et al., 2008; Hood et al., 2005; Schindler & Eby, 1997). As loricariid catfishes are among the most P-rich of freshwater fishes, they have served as an early model for studying the possibility of P-limited fish growth (Hood et al., 2005). In the Río Las Marías, an Andean piedmont stream at approximately 225 m a.s.l. and 9 °N latitude, Hood et al. (2005) found strong evidence for P-limited growth in both *Chaetostoma* and *Ancistrus*. These fishes maintained robust populations in this river, however, suggesting that they could compensate for P-limited growth by increasing consumption rate. Indeed, this phenomenon has been described in aquaculture studies of fish fed P-poor diets (e.g., Sumagaysay-Chavoso, 2003; Storebakken, Shearer, & Roem, 1998). At cooler temperatures, however, fishes with reduced metabolic rates would be challenged

to increase consumption to meet P demand. As suggested by our validation data from the Marañon drainage, loricariids may persist at lower densities in cooler environments to compensate for reduced food quality (Figure 7). Ultimately, however, they must reach a threshold temperature where population size decreases to the point that the population is no longer viable. This hypothesis lends support to the utility of incorporating stoichiometric traits into species distribution models (Leroux et al., 2017). However, while this may explain why loricariids do not colonize cooler, high-elevation streams, it does not explain why *Astroblepus* do not occur at lower elevations.

Astroblepus occur in streams within the same elevational range as loricariids, but typically inhabit streams at much at higher elevations (Figures 1 and 7). However, they too are absent from the highest elevation streams in the Andes (Carvajal-Quintero et al., 2015; Lujan et al., 2013). These invertivores do not directly compete with loricariids and do not seem to be food-limited at high elevations; thus, some other mechanism must constrain their distribution. One possibility is that *Astroblepus* are susceptible to excess UV radiation in open canopy, high-elevation streams, as suggested by their uniformly dark pigmentation at their upper elevational range limit and their avoidance at these elevations of the main river channel, whereas lower elevation populations can be abundant in the main river channel and more lightly or variably pigmented (N. K. Lujan, personal observations). A second, non-mutually exclusive hypothesis is that these unarmoured catfishes may be adapted to low-predation environments and unable to persist in low-elevation streams with diverse piscivore assemblages. *Astroblepus* populations of high-elevation streams are negatively affected by introduced rainbow trout, *Oncorhynchus mykiss* (Alexiades & Encalada, 2017; Anderson & Maldonado-Ocampo, 2011). Supporting this hypothesis, our FishNet 2.0 search found that *Astroblepus* specimens were collected in the area of La Oroya, Peru (elevation: 3,700 m a.s.l.), in 1918 by Eigenmann, but were not represented in 1974 collections in the same area when rainbow trout was collected. By reducing bone volume and, therefore, P demand, relative to their sister lineage Loricariidae, astroblepids may have expanded their lower thermal limit while trading off their ability to coexist with piscivorous fishes and therefore may be out-competed by other invertivores at lower elevations. Given the high degree of intrageneric variation in *Astroblepus* stoichiometry within a single watershed, however, more work on the taxonomy and functional ecology of these fishes is needed to interpret these geographic patterns. Loricariids, on the other hand, are typically P-rich and co-occur with a wide-range of piscivores in virtually all habitats. Major predators of loricariids include piscivorous birds, such as kingfishers, egrets, herons and cormorants (Power, 1984; K. O. Winemiller personal observations), and fishes, such as *Hoplias malabaricus* (K. O. Winemiller unpublished data), *Arapaima gigas* (Castello, 2008) and pimelodid catfishes (Barbarino Duque & Winemiller, 2003). Potential trade-offs involving ossified structures for defence against predators, P demand, P availability in food resources and temperature provide an excellent basis for future studies of how functional trait variation across environmental gradients can alter ecosystem function and vice-versa.

Broadly, we found that variation in the $TER_{C:P}$ with dietary strategy and temperature appears to depend on the relationship between GGE_C and temperature for a given taxa. Specifically, $TER_{C:P}$ decreased with temperature and with herbivory among two genera of catfishes, but this was not consistent among fishes (Supporting Information Table S1). Similarly, patterns consistent with what we found in *Astroblepus* and *Chaetostoma* have been observed in some aquatic invertebrate taxa (e.g., Malzahn et al., 2016) while contradictory patterns have been observed in other invertebrates (e.g., Persson, Wojewodzic, Hessen, & Andersen, 2011). Among invertebrates, Frost et al. (2006) also found that detritivores had higher average $TER_{C:P}$ than other trophic groups and suggested that this may be due to physiological adjustments needed to process P-poor detritus. Specifically, detritivores may face a trade-off of reducing growth rate (a P-rich investment for invertebrates) in order to exploit detritus. Among fishes, we also found that omnivores had higher average $TER_{C:P}$ than predators (Supporting Information Table S1), suggesting that some fishes may trade-off anti-predator defences such as bony armour and skeletal reinforcement when feeding on P-poor food. This may be especially the case in cooler habitats, where reduced metabolism constrains feeding rate and may lead to a greater risk of P-limitation. Supporting this hypothesis, some of the highest $TER_{C:P}$ values we found for fishes were those with other known anti-predatory defences such as life-history adaptations (*Poecilia reticulata*; Reznick, Bryga, & Endler, 1990), phenotypic plasticity in body shape (*Carassius auratus*; Domenici, Turesson, Brodersen, & Brönmark, 2008) and behavioural defences (*Liza* spp.; Marras & Domenici, 2013) or those that are limited to low-predation environments (*Astroblepus* spp.; Alexiades & Encalada, 2017). While this variation suggests that general patterns in $TER_{C:P}$ are, at best, poor predictors for any given species, it also intriguing potential to serve as a basis for linking evolutionary trade-offs to ecosystem properties. Future work focusing on these trade-offs in the context of food quality and P demand will further illuminate our understanding of how ecological gradients select for traits affecting ecosystem processes such as consumer-driven nutrient recycling.

AUTHORS' CONTRIBUTIONS

E.M., N.L., K.R. and K.W. conceived the ideas, designed the methodology and interpreted results. E.M., N.L. and K.R. collected the data. E.M. analysed the data. E.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

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SUPPORTING INFORMATION

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