



What determines trophic niche breadth? A global analysis of freshwater fishes using isospaces

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Received: 9 July 2025 / Accepted: 18 November 2025

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Abstract Understanding the factors shaping trophic niche breadth is crucial for predicting species interactions, community assembly, and ecological responses to environmental change. Several hypotheses have been proposed to explain global variation in species' trophic niches, but empirical tests are limited. Here,

we used stable isotope analysis ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) to quantify trophic niche breadth of 541 fish populations (358 species, 82 families) from freshwater ecosystems encompassing diverse environmental conditions and six biogeographic regions. Fourteen hypotheses relating niche breadth to environmental factors, traits, and sampling scale were tested. Fish isospaces were broader in regions with warmer temperatures, higher humidity, and precipitation variability, suggesting

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11160-025-10023-2>.

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that more productive, diverse, and seasonal ecosystems are associated with broader trophic niches. Conversely, isospace size declined with increasing basin fish richness, which may reflect the role of competitive interactions. Within-population variation in body size was strongly and positively associated with isospace size, indicating ontogenetic dietary shifts. Fish with truncate-rounded fins had broader isospaces than those with forked-lunate fins, likely reflecting differences in foraging behavior and movement. Primary consumers had larger isospaces than intermediate and top consumers. Predators showed patterns

similar to those across all trophic guilds, but non-predators differed in relation to solar radiation, richness, body size, and fin shape. Isospace size increased with the number of sampled individuals, habitats and years surveyed. Although isospace patterns have well-documented limitations as trophic ecology metrics, our findings nonetheless conform with several longstanding hypotheses for trophic niche variation and stimulate new ideas about environmental and biological drivers of niche breadth.

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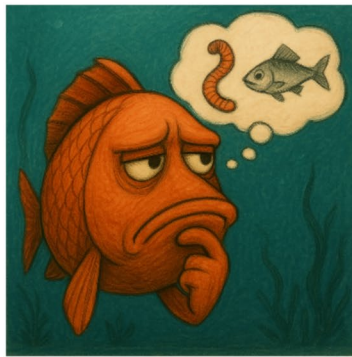
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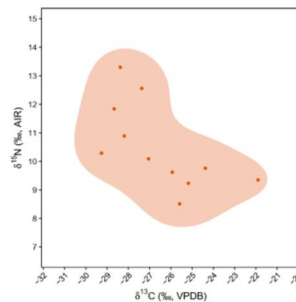
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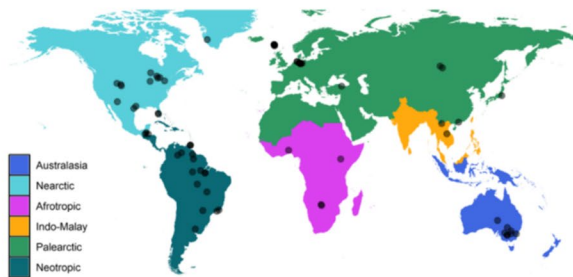
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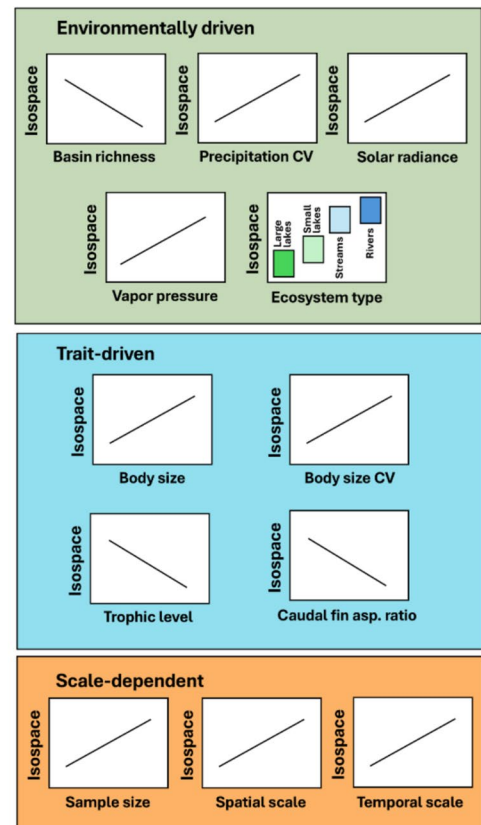
What drives the trophic niche breadth of freshwater fishes?



Global analysis using population isotopic variation as a proxy for trophic niche breadth



What we found?



Keywords Environmental gradients · Isotopic niche · Functional traits · Macroecology · Stable isotope analysis · Sampling scale

Introduction

The niche concept is central to ecology and evolutionary biology (Baker et al. 2022) and underpins many theories in community ecology (e.g., Diamond 1975; Leibold et al. 2004; Vellend 2016). Trophic niche breadth describes the range of food resources used by an organism or population and is one of the most tractable and commonly studied aspects of the ecological niche (Bearhop et al. 2004). Population trophic niche breadth is shaped by both individual diet breadth, as well as dietary differences among individuals that may include trophic specialists and/

or generalists (Bolnick et al. 2003; León et al. 2024). Several hypotheses have been proposed to explain variation in population trophic niches. Broadly, these hypotheses fall into three main categories: (i) environmentally driven, (ii) trait-driven, and (iii) scale-dependent (Table 1, Fig. 1).

Among the environmentally driven hypotheses, those related to latitudinal gradients are particularly relevant due to their implications for biodiversity patterns and climate change responses (De Frenne et al. 2013). Latitudinal gradients in the degree of temporal variation in environmental conditions have long been proposed to influence niche breadth (Dobzhansky 1950). Lower seasonal environmental variability in the tropics is expected to lead to more stable populations with narrower niches (Vázquez and Stevens 2004). Interspecific competition is also expected to be stronger in tropical communities that harbor higher species diversity, which promotes niche partitioning,

Table 1 Description of existing and newly formulated trophic niche hypotheses tested with fish isospaces

Type	Hypothesis	Abbreviation	Rationale
Environmentally driven	Niche Variation (Fig. 1a)	NVH	In less diverse communities, fish populations experience weaker interspecific competition and have less specialized diets and broader trophic niches (Van Valen 1965)
	Environmental Variability (Fig. 1b)	EVH	Intra-annual variation in precipitation causes water level fluctuations that affect food resources and habitat availability (van der Sleen and Rams 2023). Consequently, fish populations in aquatic ecosystems with high water level variability are expected to have broader trophic niches than those able to specialize in more hydrologically stable systems (Levins 1968)
	Ecological Opportunity (Fig. 1a)	EOH	More diverse ecosystems contain more diverse food resources providing fishes with dietary options resulting in broader trophic niches (Sánchez-Hernández 2020)
	Productivity-Diversity (Fig. 1c, d)	PDH	Greater productivity should foster a higher abundance and variety of organisms, increasing opportunities for trophic interactions and resulting in broader trophic niches (Currie 1991)
	Ecosystem type (Fig. 1e)	ETH	Trophic niche breadth varies among aquatic ecosystems due to differences in resource availability and other physical characteristics, like connectivity, surface area, and depth (Pereira et al. 2017). Rivers and streams may have populations with broader trophic niches than lakes due to their higher connectivity with surrounding ecosystems (e.g., riparian zones, floodplains, tributaries, upstream and downstream reaches; Richardson and Sato 2014). Fishes in large lakes have broader trophic niches than small lakes due to greater ecosystem production, which supports more diverse and abundant resources (Pomeranz et al. 2023)
Trait-driven	Body Size-Trophic Expansion (Fig. 1f)	BEH	Trophic niche breadth tends to expand with increasing body size as food consumption by larger fish is less restricted by mouth gape size, gut volume, and mobility (Kempeler and Winemiller 2020a; Mihalitsis and Bellwood 2017)
	Body Size-Trophic Contraction (Fig. 1f)	BCH	Trophic niche breadth may decline—or at most remain constant—as consumers grow and increasingly select less diverse but larger prey to avoid diminishing energetic returns from feeding on abundant, smaller prey (Costa 2009; Werner and Hall 1974)
	Body Size Variation-Trophic Expansion (Fig. 1g)	BVH	Body size variation within a population should promote broader trophic niches due to ontogenetic niche shifts and phenotypic differences among individuals of different sizes (Werner and Gilliam 1984)

Table 1 (continued)

Type	Hypothesis	Abbreviation	Rationale
Scale-dependent	Omnivory-Mediated Trophic Niche (Fig. 1h)	OTH	As omnivorous species feed on diverse food resources, they should have broader trophic niches at intermediate trophic positions than primary consumers (e.g., herbivores, and detritivores) and consumers at the top of the food web (e.g., piscivores) (Woodland et al. 2015)
	Trophic Level–Niche Breadth (Fig. 1h)	TLH	Trophic niche breadth is greater for fishes at higher trophic levels if vertical trophic position is correlated with body size (Jennings et al. 2002; Layman et al. 2005; Scharf et al. 2000)
	Swimming Efficiency-Trophic Breadth (Fig. 1i)	SEH	Fish with a high caudal fin aspect ratio (forked or lunate) can cover larger areas per unit of time, increasing their exposure to diverse food resources and the potential for a broad trophic niche (Pauly 1989)
	Sample size (Fig. 1j)	SSH	With an increase in the number of individuals sampled, the population estimate of trophic niche diversity should increase as a more complete assessment is obtained (Jackson et al. 2011)
	Spatial scale (Fig. 1k)	STH	As the number of sampled habitats increases, the trophic niche expands as more diverse food resources are encountered (Jackson et al. 2011; Ouellet et al. 2024)
	Temporal scale (Fig. 1l)	TSH	As the number of sampling intervals increases, the trophic niche increases as more diverse food resources are encountered (Jackson et al. 2011; Ouellet et al. 2024)

Hypotheses and rationales are provided

specialization, and diversification that in turn facilitates species packing (Niche Variation Hypothesis—NVH; Pellissier et al. 2018; Van Valen 1965) (Fig. 1a). To date, evidence for narrower trophic niches at lower latitudes is limited, weak, and inconclusive (Cirtwill et al. 2015), and the prediction may not apply to some ecosystems. For example, dynamic hydrology may promote broad trophic niches in both temperate and tropical rivers (Environmental Variability Hypothesis—EVH; Levins 1968; van der Sleen and Rams 2023) (Fig. 1b).

The larger geographic area and the greater solar radiation in the tropics enhance productivity, expanding the available trophic niche space. Greater and more stable ecosystem productivity in the tropics might support greater biodiversity without necessarily constraining population trophic niches (Brown 2004; Davies et al. 2007). The Ecological Opportunity

Hypothesis (EOH; Fig. 1a) suggests that when food resources are abundant, greater species diversity can lead to broader trophic niches (Pereira et al. 2017; Sánchez-Hernández et al. 2020). However, not all tropical and subtropical regions are highly productive. Arid regions—such as the African Sahel, Brazilian Caatinga, Northern Australia, and the Arabian Peninsula—have hot, dry conditions that limit ecosystem productivity and diversity (Hawkins et al. 2003), which, in turn, may limit trophic niche breadth (Productivity-Diversity Hypothesis—PDH; Currie 1991) (Fig. 1c and d). Crucially, EOH emphasizes that abundant and diverse prey resources expand trophic niches regardless of ecosystem productivity, whereas PDH specifically predicts that higher productivity enhances food resource availability and, indirectly, trophic niche breadth. Although diversity and productivity are often correlated (Brun et al. 2019; Myers

et al. 2021), some systems, such as the Rio Negro in the Amazon, have impressively high biodiversity despite extremely low productivity (Goulding et al. 1989).

The characteristics of the ecosystems in which populations are embedded likely play a crucial role in defining their trophic niche (Ecosystem Type Hypothesis—ETH) (Fig. 1e). For example, closed or semi-closed systems, such as lakes, limit species' ability to disperse and encounter diverse prey (Pereira et al. 2017). Larger ecosystems, like high-order rivers and great lakes, generally support more extensive and complex food webs due to higher total productivity, diversity and stability (Pomeranz et al. 2023). Conversely, smaller ecosystems, such as headwater streams, wetlands, and ponds, receive large resource subsidies from adjacent terrestrial ecosystems (Richardson and Sato 2014; Vannote et al. 1980), fostering populations with broad trophic niches.

Species traits are increasingly recognized as key determinants of species' trophic niches, and trait-driven hypotheses have become a common framework for explaining niche variation (Keppeler and Winemiller 2020b; McGill et al. 2006). Body size has gained a particular focus owing to its ease of measurement, large natural variation, and strong associations with metabolism, energy demand, longevity, foraging area, food web structure, and other physiological and ecological factors (Arim et al. 2010; Rooney et al. 2008; Woodward et al. 2005). The Body Size-Trophic Expansion Hypothesis (BEH; Fig. 1f) suggests that as fish grow larger, they can consume a wider range of prey sizes, particularly if they are gape-limited predators (Keppeler and Winemiller 2020b; Mihalitsis and Bellwood 2017). Conversely, the Body Size-Trophic Contraction Hypothesis (BCH; Fig. 1f) posits that organisms optimize their diets by becoming more selective as they grow, focusing on larger, more profitable prey while avoiding abundant, smaller prey (Costa 2009; Werner and Hall 1974). Populations composed of individuals with different body sizes are likely to have broader trophic niches (Body Size Variation-Trophic Expansion Hypothesis—BVH) (Fig. 1g) due to ontogenetic niche shifts (Nakazawa 2014; Werner and Gilliam 1984) that increase between-individual variation in size-structured populations (Bolnick et al. 2003).

The relationship between trophic niche breadth and body size may differ among trophic guilds. For

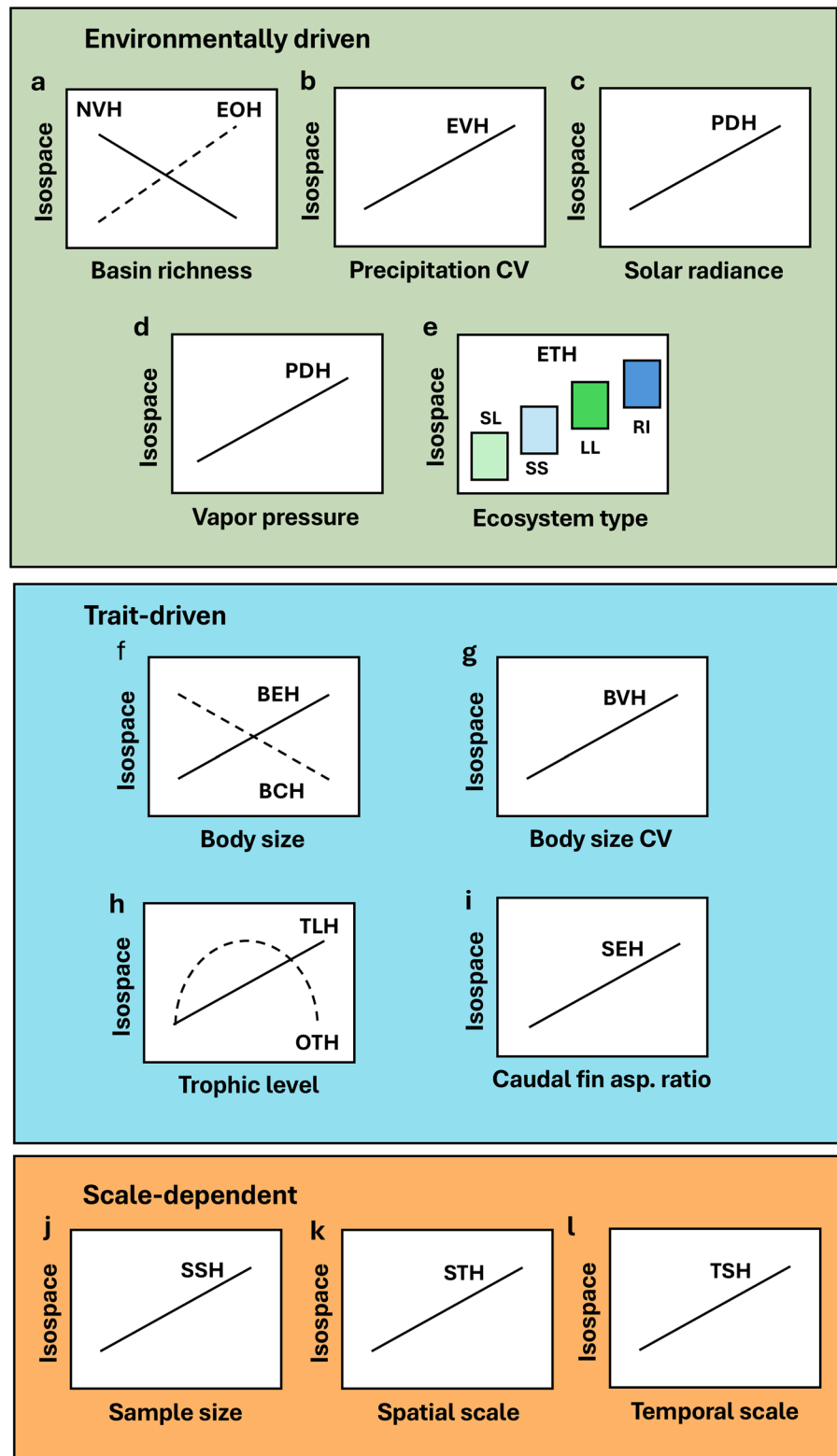
example, the vertical trophic position of predatory fishes tends to increase with body size and the average size of consumed prey, whereas detritivorous fishes show little variation in trophic position, and trophic niche breadth relative to body size (Keppeler et al. 2020; Keppeler and Winemiller 2020b). Trophic niche breadth may increase with trophic position (Trophic Level-Niche Breadth -TLH) as predatory fishes with large mouths are capable of ingesting a relatively broad spectrum of prey compared to fishes at lower trophic levels (Jennings et al. 2002; Layman et al. 2005; Scharf et al. 2000) (Fig. 1h). Conversely, the Omnivory-Mediated Trophic Niche Hypothesis (OTH; Fig. 1h) suggests that trophic niche breadth is greatest for omnivorous species at intermediate levels due to higher proclivity for foraging across multiple trophic levels (Woodland et al. 2015).

Mobility could influence trophic niche breadth if more vagile organisms can access and exploit a greater variety of habitats and food resources (Pauly 1989). In fish, the shape of the caudal fin is strongly associated with patterns of locomotion and vagility. Species with forked or lunate caudal fins are typically continuous, fast swimmers, whereas those with broad, truncated, or rounded caudal fins tend to be slower swimmers with less endurance but greater lateral maneuverability (Sambily 1990). Fish having a caudal fin with a high aspect ratio (forked, lunate) may cover a larger area per unit of time (Pauly 1989) and thereby exploit more diverse food resources (Rooney et al. 2008), resulting in a positive relationship between fin aspect ratio and trophic niche breadth (Swimming Efficiency-Trophic Breadth Hypothesis—SEH) (Fig. 1i).

Niche breadth estimates based on large numbers of individuals are likely higher than those based on small samples (Sample Size Hypothesis—SSH; Jackson et al. 2011) (Fig. 1j). Estimates of niche breadth are likely to be further inflated if the sample includes individuals from different locations and habitats (Spatial Scale Hypothesis—STH; Fig. 1k) or periods (Temporal Scale Hypothesis—TSH; Fig. 1l) (Ouellet et al. 2024). Failure to account for these factors may bias estimates used in comparative studies of trophic ecology, particularly regarding niche breadth (Jackson et al. 2011).

Of the 14 hypotheses described above, some are mutually exclusive (NVH vs. EOH; BCH vs. BEH; and TLH vs. OTH), whereas other proposed

Fig. 1 Theoretical associations between population isospaces ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) and predictors related to environmental conditions (basin richness, coefficient of variance [CV] of precipitation, solar radiance, vapor pressure, and ecosystem type), species traits (average body size, CV of body size, trophic level, and caudal fin aspect ratio), and scale (sample size, spatial scale, and temporal scale). For graphical simplicity, trophic level is presented instead of the trophic guild. Low trophic positions correspond to primary consumers (herbivores-frugivores and algivorous-detritivores), intermediate trophic positions to omnivores, invertivores, and planktivores, and high trophic positions to carnivores and piscivores. Lines, curves, and boxes portray hypothesized relationships (see Table 1 for the rationales). Hypotheses: *NVH* Niche Variation, *EVH* Environmental Variability, *EOH* Ecological Opportunity, *PDH* Productivity-Diversity, *ETH* Ecosystem Type, *BEH* Body Size-Trophic Expansion, *BCH* Body Size-Trophic Contraction, *BVH* Body Size Variation-Trophic Expansion, *OTH* Omnivory-Mediated Trophic Niche, *TLH* Trophic Level-Niche Breadth, *SEH* Swimming Efficiency-Trophic Breadth, *SSH* Sample Size, *STH* Spatial Scale, *TSH* Temporal Scale. Ecosystem type: *SL* Small lake, *SS* Small stream, *LL* Large lake, *RI* River



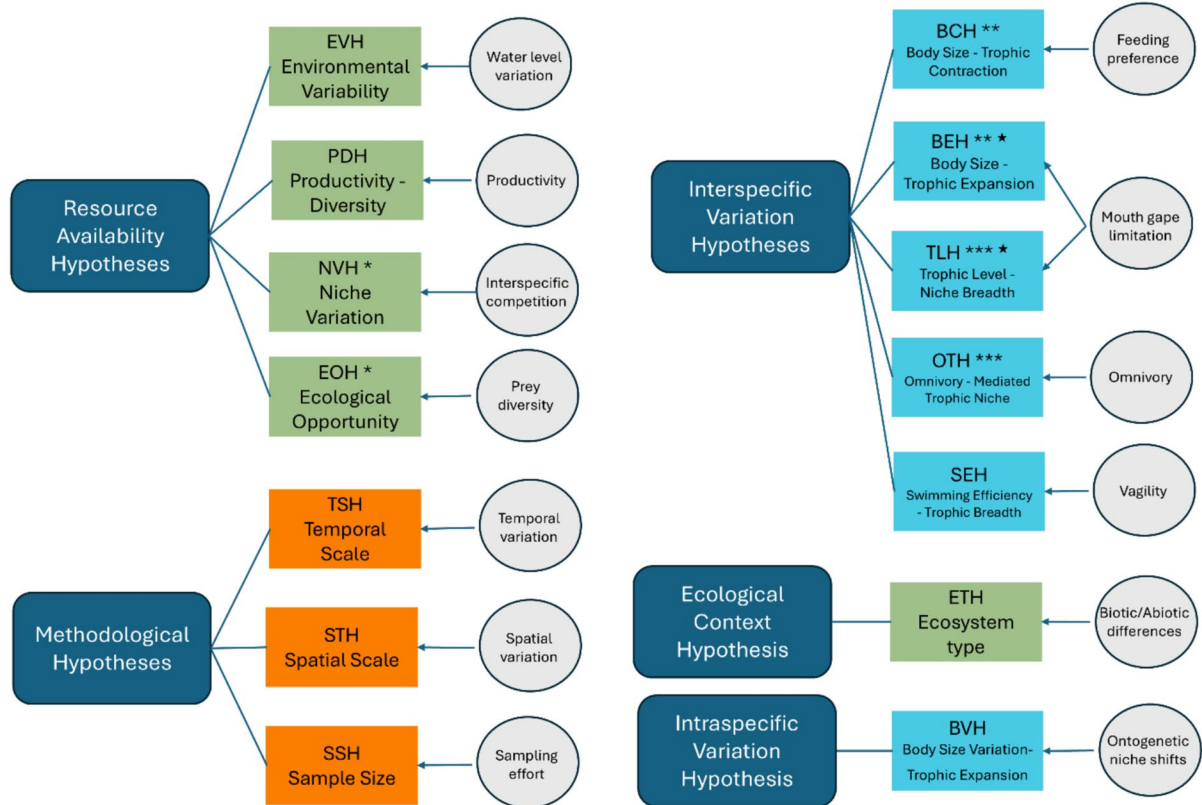


Fig. 2 Schematic map showing the similarities (dark blue polygon) among the studied hypotheses (rectangles) and their underlying ecological mechanisms (grey circles). Rectangle colors denote hypothesis type—environmentally driven, trait

driven, or scale dependent (see Table 1). Equal numbers of asterisks (*) denote mutually exclusive hypotheses, whereas stars (★) indicate mutually dependent hypotheses

mechanisms could occur simultaneously (Fig. 2). TLH is expected to hold only if BEH is also supported. EVH, PDH, NVH, and EOH are all influenced by resource availability, whereas BCH, OTH, TLH, BEH, and SEH are associated with interspecific trait differences, and BVH reflects intraspecific trait variation. ETH is primarily a function of ecological context, and scale-dependent hypotheses arise from aspects of sampling design. Although hypotheses could be organized according to alternative conceptual dimensions, they nonetheless are not redundant, with each addressing a distinct mechanism (Fig. 2).

Given the multiple factors that may influence trophic niche breadth estimates, comparative studies at large spatiotemporal scales are rare (e.g., Franco-Trecu et al. 2022; González et al. 2023; Keppeler et al. 2020a). Most comparative studies of the trophic niche have examined population mean differences

without explicit analysis of intraspecific variation (Bolnick et al. 2003; Des Roches 2017). Another challenge is the lack of standardized methods for quantifying diet breadth among species that may have divergent foraging behaviors and associated morphologies. The general methods used to characterize the diet of animals, such as stomach content analysis and fecal analysis, provide a snapshot of the diet and may not reflect patterns of food consumption over longer periods to provide a more reliable diet estimate. Furthermore, these conventional methods are generally limited in their ability to identify fragmented or partially digested material. They may not necessarily reflect foods assimilated by the individual, since hard food items tend to have a longer retention time in the gut and are digested less efficiently than soft items (Araújo et al. 2007; Keppeler et al. 2020b; Votier et al. 2003).

Stable isotope analysis (SIA) has emerged as a useful tool to examine trophic niches variations in the 1970s (Bearhop et al. 2004; Layman et al. 2012; Turner et al. 2023). Since then, ratios of $^{15}\text{N}/^{14}\text{N}$ ($\delta^{15}\text{N}$) and $^{13}\text{C}/^{12}\text{C}$ ($\delta^{13}\text{C}$) of tissue samples have been increasingly used in food web research (Layman et al. 2012). $\delta^{15}\text{N}$ has a positive correlation with trophic level due to gradual ^{15}N enrichment (usually from 2 to 4‰, termed “trophic fractionation”) during the assimilation of ingested material into consumer tissue (Post 2002). Variation in $\delta^{13}\text{C}$ in plants and other primary producers is associated with, among other factors, differences in the photosynthetic pathways (i.e., C3, C4, CAM). These differences in isotopic ratios of C and other elements provide a basis for inferring animal assimilation of biomass derived from primary producers using mixing models that integrate isotopic signatures of multiple potential sources (Fry 2007; Parnell et al. 2013; Stock et al. 2018). Some advantages of SIA are the ability to obtain data from small tissue amounts (in some cases tissue samples can be obtained by non-lethal methods; e.g., Fredrickson et al. 2021; Maitland and Rahel 2021) and the ability to estimate dietary histories over varying time intervals by analyzing incremental tissues (e.g., otoliths; Newsome et al. 2009), tissues with different turnover rates (Vianna-Gatts et al. 2023) or samples collected during various periods (Ou and Winemiller 2016).

The two-dimensional space defined by $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ is commonly termed the isotopic niche, hereafter referred to as isospace (Yeakel et al. 2016). When primarily driven by diet composition, the isospace can be considered synonymous with the trophic niche as defined by Bearhop et al. (2004), but an isospace can be influenced by a number of environmental factors and biological processes that govern the flow of elements and their isotopes within and among organisms (Araújo et al. 2007; see Caveats in the Discussion). Beyond its role in advancing ecological theory, analysis of population isospaces has been applied in conservation and management, for example in assessing resilience to climate change (Cipriani et al. 2024) and evaluating impacts from biological invasions (Quintana et al. 2023), pollution (De Carvalho et al. 2021), habitat fragmentation (Navarro et al. 2021), and human infrastructure (Guo et al. 2023). Isospace analysis also has advanced understanding of ecosystem restoration (e.g., Keppeler et al. 2024), ecosystem

services (e.g., Resco et al. 2009), and fishery management (e.g., Brownscombe et al. 2022).

We compiled an extensive database of stable isotope signatures ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) of freshwater fishes to perform a global analysis of relationships between population isospace and variables associated with climate, biodiversity, ecosystem type, species traits, and sampling effort. We used solar radiation as a metric of energy availability (Brown et al. 2004), precipitation variation as a proxy of water level fluctuations and seasonality (Oki et al. 2004), and vapor pressure as an indicator of temperature and humidity, which is particularly useful for distinguishing tropical rainforests from drier and/or colder ecosystems (Kottek et al. 2006). In addition, we included (1) basin richness (i.e., number of fish species) as a proxy for potential, either current or past, interspecific competition (Connell 1980); (2) aquatic ecosystem type as a basic descriptor of aquatic habitat conditions (e.g., spatial extent, connectivity) influencing food web structure (Riede et al. 2011); (3) average body size as a trait affecting food consumption (Keppeler and Winemiller 2020a); (4) variation in body size as a metric reflecting the potential for ontogenetic trophic niche shifts (Werner and Gilliam 1984); (5) trophic guild as a description of feeding preferences (Parravicini et al. 2020); and (6) caudal fin aspect ratio as a proxy for potential mobility and spatial extent of foraging activity (Pauly 1989). To account for differences in study design and survey methods, we analyzed three metrics related to sampling scale: the number of samples, the number of years sampled, and the diversity of habitats sampled. Our overarching goal was to test if population isospaces provide support for the aforementioned hypotheses of trophic niche variation (Table 1, Fig. 1).

Material and methods

Stable isotope values and species traits

We compiled a dataset including 33,509 values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ obtained from muscle tissue of 1,422 populations of 880 freshwater fish species from six major ecoregions across the globe (Fig. 3; Online Resource 1). We use ‘population’ as a pragmatic term in this study, referring to fish species sampled from a distinct water body. $\delta^{15}\text{N}$ represents the ratio of ^{15}N

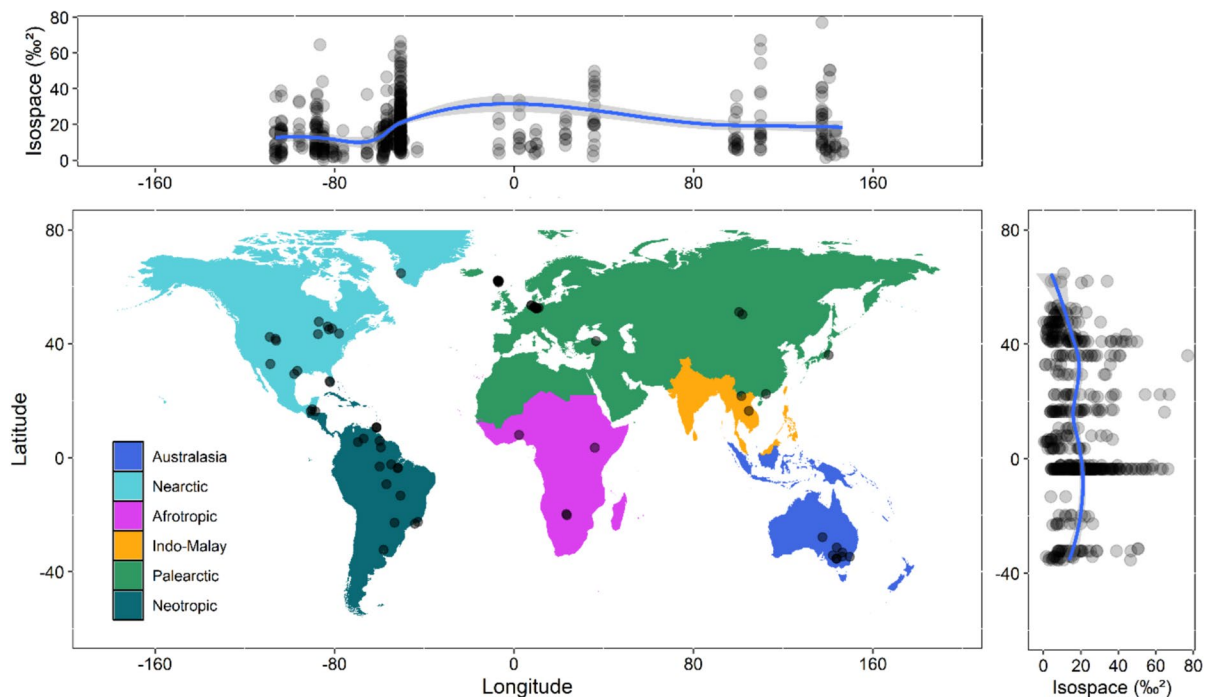


Fig. 3 Spatial variation in isospace size. The upper panel illustrates variation across longitude, and the right panel depicts the relationship across latitude. Trend lines are fitted

using locally estimated scatterplot smoothing (LOESS). Points on the map represent the locations of the studied water bodies

to ^{14}N in a sample relative to atmospheric nitrogen, and $\delta^{13}\text{C}$ represents the ratio of ^{13}C to ^{12}C relative to the Pee Dee Belemnite standard. Both values were expressed in parts per thousand (‰).

Although Post et al. (2007) recommended applying mathematical lipid corrections to $\delta^{13}\text{C}$ values when C:N ratios are greater than 3.5, we did not do so for two main reasons. First, C:N ratios were unavailable for some datasets; second, recent studies have shown that lipid corrections are species and tissue specific, with no universally reliable C:N ratio threshold (Cloyed 2019). However, five of our data sources (Georgian Bay, Lake Huron, Lake Kasumigaura, Lake Ontario, and North Channel) involved chemical lipid extraction, representing ~13% of the total. In addition, data from the Gila River and Murray River (~1%) were obtained from museum specimens. Although these were not chemically lipid-extracted, preservation is known to shift carbon values toward lighter signatures in a manner similar to lipid extraction, typically by less than 2‰ and consistently across similarly preserved samples. We conducted exploratory analyses and model selection to evaluate

the effects of lipid extraction and museum preservation on fish population isospaces. In all cases, the effects were negligible (relative importance ~8.5 times lower than the least important retained variable), and the lipid extraction variable was excluded from the models. Therefore, we retained both chemically lipid-extracted samples and those obtained from preserved specimens, assuming no meaningful influence on fish population isospace patterns.

The isotopic data were derived from studies conducted by the authors and based on sample collections representative of the local fish community, including multiple species from different trophic guilds and species with robust sample sizes (Online Resource 1). The data were then filtered to include only populations with complete body size information for all individuals and with at least 10 individuals sampled. The studies also provided information about sampling dates, locations, and habitats.

Individual body sizes were measured either with body length (standard length or total length, mm) or body mass (g) (Online Resource 2). To standardize,

we converted all body lengths to body mass using the allometric formula (Keys 1928):

$$Wi = aLi^b,$$

where Wi is the predicted weight of individual i , Li is its length, and $\log(a)$ and b represent the intercept and slope, respectively, in the logarithmic form of the length–weight relationship for the population of individual i . The parameters a and b for each species were estimated using posterior modes derived from kernel density estimation, following the Bayesian hierarchical approach proposed by Froese et al. (2014), and obtained via the R package *fishflux* (Schiettekatte et al. 2020). Then, the average body size along with their respective coefficients of variation were calculated for each fish population.

The caudal aspect ratio (AR) of each species was obtained from the *FishLife* R package (Thorson 2023) and is calculated as follows (Pauly 1989):

$$AR = \frac{h^2}{s},$$

where h is the height of the caudal fin and s is the surface area of the caudal fin. Low aspect ratios (< 1.5) are associated with truncate and rounded fins; intermediate aspect ratios ($1.5\text{--}3$) are associated with forked and emarginate fins, and high aspect ratios are associated with lunate fins (> 3) (Online Resource 2) (Sambily 1990).

Fishes were classified into eight trophic guilds based on diet studies (Online Resource 2): (1) Algivore/Detritivore, (2) Herbivore/Frugivore, (3) Omnivore (consume primary producers and invertebrates), (4) Planktivore, (5) Invertivore, (6) Carnivore (commonly consume macroinvertebrates, fish, and/or other vertebrates), (7) Piscivore, and (8) Fish Parasite (blood, mucus, and scale feeders). When diet studies were unavailable for a given species, we inferred its trophic guild based on closely related species (i.e., within the same genus, or rarely, family). Given that juvenile and adult size classes often show dietary differences, our classification is based on adult individuals.

Environmental variables

Monthly averages of solar radiation ($\text{kJ m}^{-2} \text{ day}^{-1}$), precipitation (mm), and vapor pressure (kPa) from 1970 to 2000 were obtained at a spatial resolution of

0.5 arcminutes for the entire globe using the WorldClim Version 2 database (Fick and Hijmans 2017) via the *geodata* R package (Hijmans et al. 2024). The WorldClim database captures substantial climatic variability (annual averages ranging from -23 to 29 °C, depending on the region; Mourshed 2016). Recent climate change (~ 1 °C increase in global mean temperature over the past two decades; NASA 2023) introduces a potential source of error; however, this is not expected to bias our analyses and conclusions as the degree of change is minimal in the entire range of temperatures in the data set.

We used these compiled climate databases to calculate average annual solar radiation, annual coefficient of variation of precipitation, and average annual vapor pressure for each data location (Online Resource 3). For basin richness, we estimated the number of fish species in each sub-basin where the stable isotope studies were conducted. These biodiversity estimates (Online Resource 3) were based on values obtained from the literature or regional surveys reported by the studies producing the isotopic data included in our analyses.

We classified the sampled water bodies into four main categories: large lakes ($> 150 \text{ km}^2$), small lakes ($< 150 \text{ km}^2$), streams (river order 1–3), and rivers (river order > 3). As the populations within each ecosystem type could inhabit more than one habitat, for each population we calculated the Shannon diversity of habitat types from which fish individuals were collected (i.e., $H' = -\sum_{i=1}^S p_i \ln(p_i)$, where S is the total number of habitats, p_i is the proportion of individuals in the i th habitat, and $\ln(p_i)$ is the natural logarithm of the proportion) (herein referred as habitat diversity). To do this, we classified sampling habitats into four broad categories to align with the dataset's resolution: main river channel, stream, lake, and other floodplain habitats (e.g., flooded forest, temporary pools). We decided to use the habitat diversity rather than the number of habitats sampled due to the higher predictive performance of the former. Similarly, we recorded the number of years that each population was sampled. In this case, the number of years sampled had better predictive performance than the diversity of years from which fish individuals were collected.

We classified the geographic locations from where tissues were collected into six major ecoregions: (1) Neotropical, (2) Palearctic, (3) Indo-Malay, (4)

Afrotropic, (5) Nearctic, and (6) Australasia (Olson et al. 2001). We also classified the sampling according to four main climate zones: Tropical (0° – 23.5° N/S), Sub-tropical (23.5° – 35° N/S), Temperate (35° – 60° N/S), and Polar (60° – 90° N/S) (Peel et al. 2007). Although ecoregions and climate zones do not directly affect our hypotheses, their inclusion provided additional spatial variables for comparison of fish population isospaces and description of data structure.

Data analysis

We estimated the isospace of each fish population using the kernel utilization density method proposed by Eckrich et al. (2019) (Online Resource 4). We chose the kernel utilization density because, unlike the standard ellipse area approach (Jackson et al. 2011), it does not assume a normal distribution in two-dimensional space and is less sensitive to outliers than the convex hull method (Layman et al. 2007). Kernel utilization density contours can also produce non-continuous (disjointed) polygons, which indicate multimodality and may reflect different dietary strategies, prey types, or habitat use within the same population (Eckrich et al. 2019). Exploratory analyses showed that kernel isotopic space estimates were strongly correlated with standard ellipse areas (SEA and SEAc; Pearson $r > 0.9$), and that both approaches yielded consistent patterns (Online Resource 5). We defined the kernel utilization density isospace at 50%, 75%, and 90% contours for each population. Since these contours were highly autocorrelated (Pearson correlation > 0.97), only the 75% contour was used for isospace modeling (see below).

To ensure a more robust and representative assessment, we estimated isospace only for fish populations with at least 10 individuals. Overall, 541 fish populations from 358 species met the minimum requirements of a sample size of at least 10 with accompanying body size measurements. Sensitivity tests were conducted to evaluate whether increasing this threshold to 15 individuals, as suggested by Eckrich et al. (2019), would alter the results. While the overall patterns remained consistent, increasing the threshold led to the removal of 108 populations, weakening the observed trends. Species classified as fish parasites were removed from analyses due to the small number of populations in the database ($N = 4$).

Three approaches were used to investigate the drivers of fish population isospace variation: multiple regression (MR), phylogenetic generalized least squares (PGLS; Freckleton et al. 2002), and boosted regression trees (BRT; Elith et al. 2008). MR is a comparatively simpler model assuming that population responses to predictors are independent and linear and serving as a baseline for comparison with PGLS and BRT results. PGLS accounts for non-independence of populations due to shared ancestry, providing estimates of relationships between variables within an evolutionary context (Freckleton et al. 2002). Since a complete phylogenetic tree for fishes is not yet available, shared ancestry was estimated using taxonomic information retrieved from the Integrated Taxonomic Information System (ITIS; NMNH 2025) via the *taxize* R package (Chamberlain et al. 2020). The taxonomic signal of population isospace was quantified using Pagel's λ (Pagel 1999) through the *phytools* R package (Revell 2024). A significant λ indicates that population isospace sizes are more similar among closely related taxa than would be expected if isospace sizes were distributed randomly across the phylogeny as defined by taxonomy.

BRT is an ensemble machine-learning algorithm that combines multiple regression trees to enhance predictive accuracy. BRT employs an iterative learning process in which each tree is fitted to the residuals of the previous tree, sequentially reducing errors (Elith et al. 2008). While BRT does not account for non-independence of populations due to shared ancestry, it is a powerful and flexible algorithm capable of handling non-linear relationships, interactions, and multicollinearity (Elith et al. 2008; Pichler and Hartig 2023). BRT models were constructed using learning rates of 0.001, tree complexity of 5, bag fraction of 0.6, and Gaussian family distribution (Elith et al. 2008).

We tested five model structures for all model approaches (i.e., MR, PGLS, and BRT). The scale-dependent model included sample size, habitat diversity, and the number of sampling years as predictors. The trait-driven model incorporated average body size, body size CV, trophic guild, and caudal fin aspect ratio. The environmentally driven model used average solar radiance, precipitation CV, average vapor pressure, ecosystem type, and basin fish richness as predictors. The full model combined all predictors from the previous three models, while the

intercept-only model (i.e., $Y = \beta_0 + \epsilon$, where β_0 is simply the mean value of the response variable across all observations) contained no predictors. To compare model performance, we used three main metrics: (1) the Akaike Information Criterion (AIC) that balance model complexity with goodness-of-fit; (2) explanatory power (R^2 -*explanatory*) to assess in-sample error; and (3) predictive power (R^2 -*predictive*) based on five-fold cross-validation to evaluate out-of-sample error.

We performed backward model selection to simplify the best BRT model following the approach of Elith et al. (2008) that relies on fivefold cross-validation and the change in predictive deviance to identify the best model. We compared the performance of the best BRT model with the best PGLS and MR models using exploratory and predictive power (five-fold cross-validation). To interpret the relationship between predictors and fish isospace estimated for BRT, we used partial dependence plots revealing this relationship after accounting for the average effects of all the other model predictors (Friedman 2001; Friedman and Meulman 2003). Locally Estimated Scatterplot Smoothing (LOESS) was performed for the plots to better visualize the main trends. In addition, LOESS was used to describe latitudinal and longitudinal gradients of fish isospaces.

Given concerns about isospace compression as resource pathways become integrated at higher trophic positions (Hoeinghaus and Zeug 2008), we also conducted BRT models separately for predators (Invertivores, Carnivores, and Piscivores) and non-predators (Algivores/Detritivores, Herbivores/Frugivores, Omnivores, and Planktivores). We opted to analyze these two broad groups rather than individual trophic guilds due to the small sample sizes and limited spatial distributions of some guilds (e.g., herbivores being largely confined to tropical regions), which could bias interpretations of environmental gradients. In addition, previous studies have shown that predators and non-predators may respond differently to environmental gradients and may differ in how traits influence trophic niche and trophic position (Keppeler et al. 2020).

All analyses were carried out in R, version 4.4.1 (R Core Team 2024). BRT was carried out in the *dismo* package (Hijmans et al. 2023), PGLS in the *caper* package (Orme et al. 2023), and MR and LOESS in the *stats* package (R Core Team 2024). The *MuMIn*

package was used for model selection with AIC (Bartoni 2024), and the *caret* package was used for cross-validation (Kuhn 2008).

Results

Dataset composition

The tropics were the most represented region in the dataset, with 328 fish populations, followed by temperate (154), subtropical (62), and polar regions (7). All fish populations from the polar zone were carnivores. In the temperate zone, approximately 64% of fish populations were predators (invertivores, carnivores, or piscivores). This proportion declined to 52% in the subtropics and 45% in the tropics. Omnivores were more prevalent in the subtropics (35%) and tropics (34%) than in the temperate zone (27%). Similarly, algivores/detritivores and herbivores/frugivores were more common in the tropics (19%) and subtropics (11%) compared to the temperate region (4%). Planktivores were more frequent in the temperate zone (~5%) but were less represented in other regions (<2%).

The Neotropics were the most represented ecoregion, with 313 fish populations, followed by the Nearctic (105), Palearctic (66), Australasia (25), and both the Afrotropic and Indo-Malay ecoregions (21 each). The highest proportion of predators was observed in the Afrotropic biome (86%), followed by the Palearctic (66%), Australasia (64%), and Nearctic (63%). Omnivores were most prevalent in the Indo-Malayan (43%) and Neotropics (36%). Algivores/detritivores and herbivores/frugivores were more prominent in the Neotropics (20%), Australasia (12%; exclusively algivores/detritivores), and Indo-Malay (10%). Planktivores were more frequent in the Palearctic (8%), Afrotropic (5%), and Nearctic (4%). Additional details are available in Online Resource 6.

Isospace variation across space and fish families

We observed large variation in population isospace size across geographic regions (Figs. 3 and 4a) and fish families (Fig. 4b). Overall, population isospaces were smaller in the Nearctic and Australasian ecoregions, and largest in the Neotropics, Palearctic, and

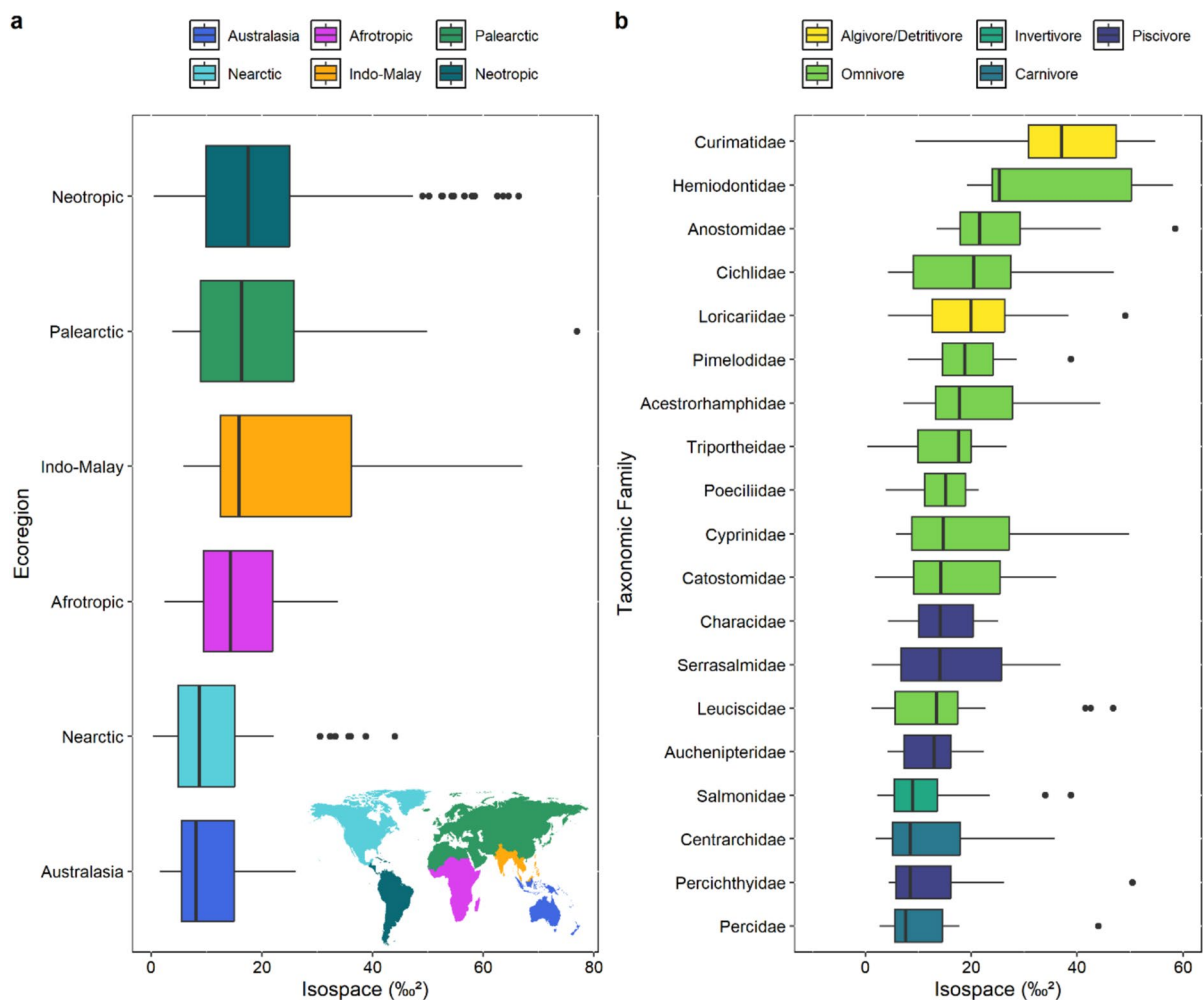


Fig. 4 Isospace size of fish populations across ecoregions (**a**) and taxonomic families (**b**). Only those families with more than 10 populations analyzed are shown. Boxplot showing data

distribution, including median, interquartile range (IQR), and outliers beyond the whiskers

Indo-Malay (Fig. 4a). Furthermore, a consistent latitudinal gradient in isospace size was not observed, although populations at latitudes higher than 40° tended to have smaller isospaces (Fig. 3).

Neotropical algivorous-detritivorous fish in the families Curimatidae and Hemiodontidae exhibited the largest isospaces (Fig. 4b). Conversely, families dominated by invertivorous and piscivorous species (e.g., Centrarchidae, Percidae, Percichthyidae, Salmonidae) from different ecoregions had considerably smaller isospaces. Isospace size had a significant taxonomic signal (Pagel's $\lambda = 0.7$, $p < 0.001$), indicating that closely related populations tend to have similar isospace sizes.

Model comparisons and variable importance

Full models incorporating environmental, trait-dependent, and scale-dependent variables, performed best across MR, PGLS, and BRT models (Table 2). BRT models had superior explanatory ($R^2 = 0.59$) and predictive power ($R^2 = 0.33$) compared to MR (0.25 and 0.20, respectively) and PGLS (0.21 and 0.21, respectively), indicating that relationships between predictors and fish population isospace size were non-linear with relatively minor interactions among predictors. The backward selection applied to the best BRT model (Full) did not eliminate any predictors, suggesting that all variables contribute meaningfully

Table 2 Comparison of results from three modeling approaches: multiple regression (MR), phylogenetic generalized least squares (PGLS), and boosted regressions tree (BRT) used to explain and predict variation in fish population isospace

	Model structure	R ² Pred (Cross-validation)	R ² Expl	AIC	Delta	Weight
Models were ranked according to their predictive capacity (R ² Pred). AIC was not calculated for BRT models due to the inherent limitation on quantifying model complexity	MR					
	Full	0.20 (0.10)	0.25	4200	0	1.00
	Scale	0.14 (0.05)	0.14	4242	43	0.00
	Traits	0.11 (0.06)	0.13	4262	61	0.00
	Environment	0.08 (0.04)	0.09	4281	81	0.00
	Intercept-only	0.00 (0.00)	0	4317	116	0.00
	PGLS					
	Full	0.21 (0.05)	0.21	4119	0.0	1.00
	Environment	0.13 (0.05)	0.12	4171	51.9	0.00
	Scale	0.12 (0.02)	0.13	4143	24.0	0.00
	Traits	0.07 (0.04)	0.06	4193	73.3	0.00
	Intercept-only	0.00 (0.00)	0.00	4210	90.7	0.00
	BRT					
	Full	0.33 (0.00)	0.59	—	—	—
	Environment	0.20 (0.00)	0.27	—	—	—
	Traits	0.16 (0.00)	0.37	—	—	—
	Scale	0.16 (0.00)	0.26	—	—	—
	Intercept-only	0.00 (0.00)	0.00	—	—	—

to predicting population isospace size. Accordingly, we describe the relationships between predictors and population isospace size as estimated by the Full BRT model.

Together, traits accounted for a cumulative relative contribution of 44%, while scale and environmental variables each contributed approximately 28%. Among the analyzed traits, trophic guild was the strongest predictor of isospace size (Relative Contribution [RC]=18%), with body size CV (RC=11%) and caudal fin aspect ratio (RC=10%) also emerging as important predictors. Among the environmental predictors, vapor pressure ranked highest (RC=10%), with solar radiation (RC=6%) and basin richness (RC=6%) also showing high importance. Of the scale-dependent variables, habitat diversity of survey locations was the strongest predictor (RC=11%), followed by number of years sampled (RC=10%) and sample size (RC=7%) (Fig. 5).

Isospace variation—environment

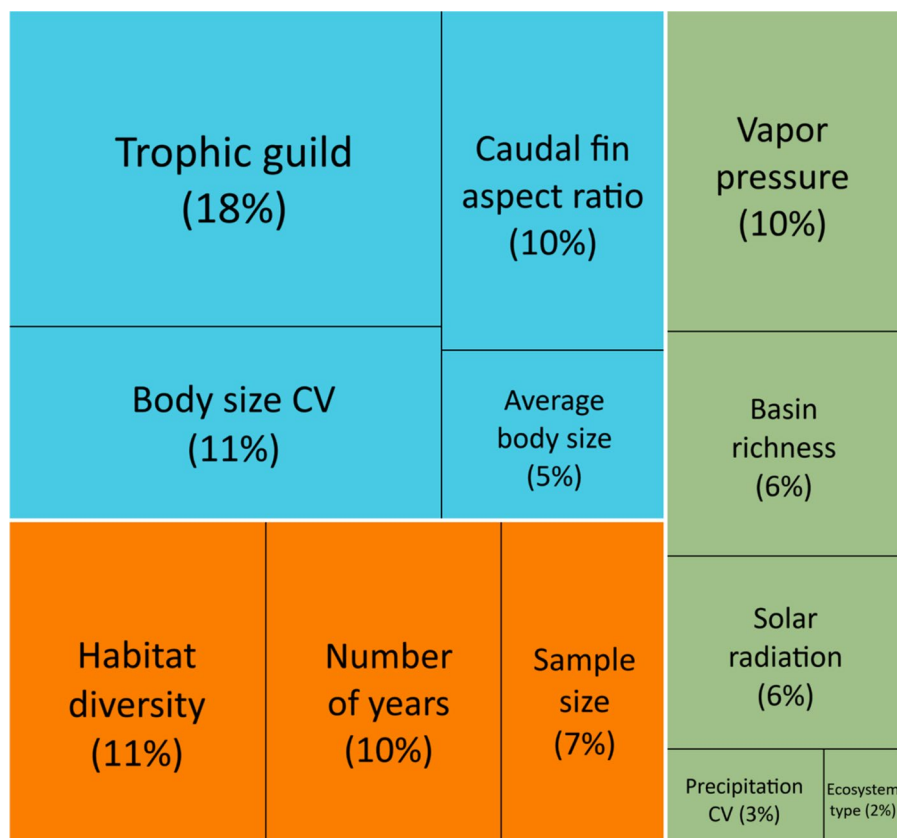
Population isospace size was negatively associated with basin richness, with a sharp decline of ~13% from areas with less than 50 fish species (e.g., Greenland and Trinidad streams) to areas with 100 or more

fish species (e.g., Uruguay River) (Fig. 6a). Precipitation CV was positively associated with isospace size, albeit with a low magnitude of difference (~5%) between regions with low variation in precipitation (e.g., rivers in southeastern Australia) and regions with high variation (e.g., rivers in the Okavango Delta, Botswana) (Fig. 6b). The relationship between solar radiation and isospace size was weak and variable, with two peaks at intermediate and high radiation levels, where the isospaces were approximately ~9–12% larger than those in low-radiation regions at higher latitudes (Fig. 6c). Vapor pressure was positively associated with isospace size, with populations in cold regions, such as Lake Khövsgöl in Mongolia and streams in the northeastern U.S., having ~33% smaller isospaces compared to those in tropical rainforest regions (Fig. 6d). We observed relatively small differences (<4%) in isospace size across ecosystem types (Fig. 6e). Fish populations in rivers had the largest isospaces, and those in large lakes (e.g., Lake Michigan) the smallest.

Isospace variation—traits

The relationship between average body size and isospace size was weakly positive, with increases

Fig. 5 Relative contributions of predictor variables in the Boosted Regression Tree Model (BRT) for fish population isospace size. The blue color indicates trait variables, green indicates environmental variables, and orange indicates scale-dependent variables



of 3% from fishes weighing 1 g to fishes weighing more than 5 kg (Fig. 6f). High within-population variation in body size was also associated with larger isospaces, with an increase of approximately 35% along a gradient from 10 (i.e., the standard deviation is 10% of the mean) to 1000 in coefficient of variation (i.e., the standard deviation is ten times the mean value) (Fig. 6g). Population isospace size differed significantly among trophic guilds, with Algivore/Detritivores and Herbivores/Frugivores having isospaces at least 26% larger compared to those of consumers at higher trophic levels (Fig. 6h). Fishes with caudal fin aspect ratios < 1.0 (truncate and rounded fins) had up to 22% larger isospaces than those with forked or emarginate fins (aspect ratio 1.5–3) and lunate fins (> 3) (Fig. 6i).

Isospace variation—scale

Population isospace size increased relative to spatial and temporal scales and sample size (Fig. 6). Increasing the sample size from 10 to 100 was

associated with an increase of up to 19% in fish population isospace size, whereas further increases from 100 to 600 resulted in little to no additional change (Fig. 6j). An increase in habitat diversity from 0.1 (a single habitat) to 1 (three habitats with high equitability) was related to a ~33% increase in isospace size (Fig. 6k). Additionally, isospace size increased by ~26% when the sampling period was extended from 1 to 9 years (Fig. 6l).

Isospace variation—predators vs non-predators

BRT models performed separately for predators (invertivores, carnivores, and piscivores) and non-predators (algivores/detritivores, herbivores/frugivores, omnivores, and planktivores) revealed important differences. While predators followed trends similar to those observed when all trophic guilds were analyzed together, non-predators displayed distinct responses to four main variables. Among non-predators, isospace declined by ~15% as average solar radiation rose from ~12,000 to ~19,500 $\text{kJ m}^{-2} \text{day}^{-1}$

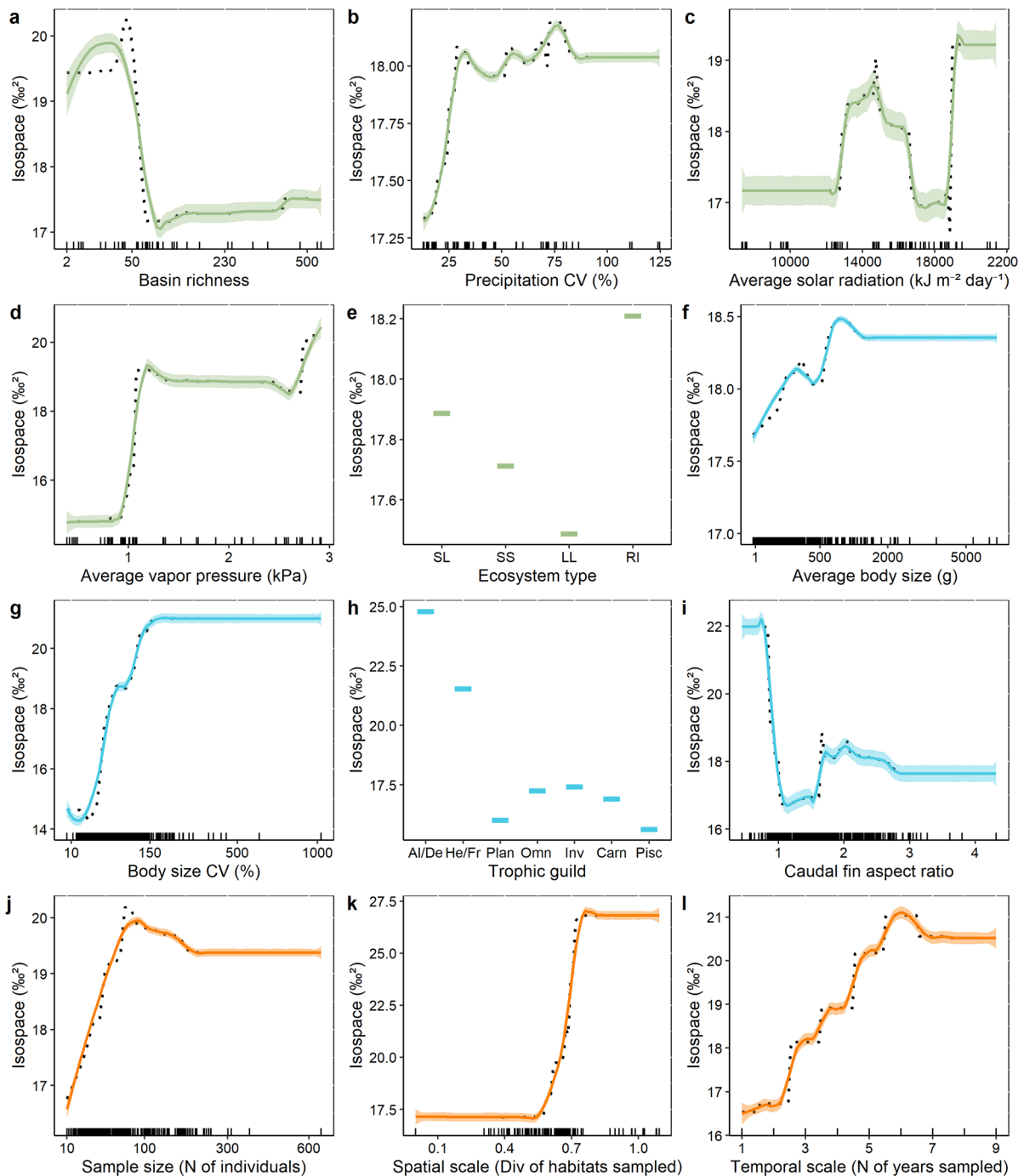
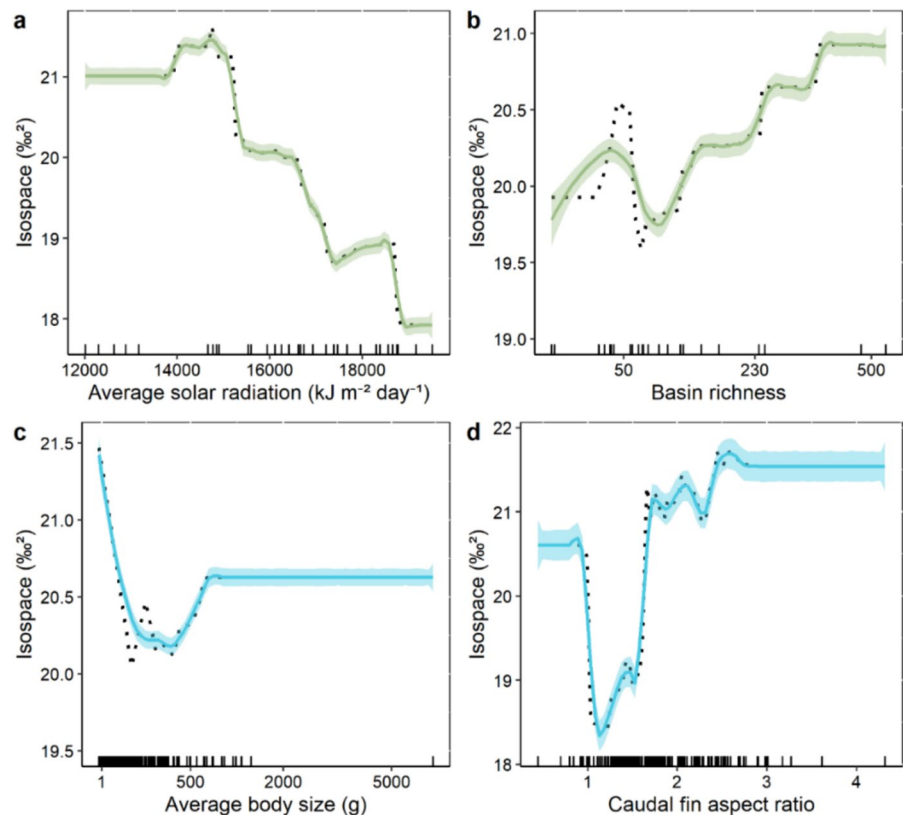


Fig. 6 Marginal effects of environmental (a- Basin richness, b- Coefficient of variation [CV] of precipitation, c- Average solar radiation, d- Average vapor pressure, e-Ecosystem type), trait (f- Average body size, g- Body size CV, h- Trophic guild, i- Caudal fin aspect ratio), and scale-related variables (j- Number [N] of individuals, k- Shannon diversity [Div] of habitats sampled, l- N of years sampled) on fish population isospaces. Dots and dashes are predictions based on the Boosted Regres-

sion Tree Model (BRT). Trend lines were fitted using locally estimated scatterplot smoothing (LOESS). SL=small lakes, SS=small streams, LL=large lakes, RI=rivers, Al/De = algivore/detritivores, He/Fr = herbivores/frugivores, Plan = planktivores, Omn = omnivores, Inv = invertivores, Carn = carnivores, Pis = piscivores. The tick marks on the x-axes show the distribution of predictor values in the dataset

Fig. 7 Marginal effects of two environmental variables (**a** Average solar radiation, **b** basin richness) and two traits (**c** average body size, **d** caudal fin aspect ratio) on the isospace of non-predatory fish populations. Black dots are predictions based on the Boosted Regression Tree Model (BRT). Trend lines are fitted using locally estimated scatterplot smoothing (LOESS). The tick marks on the x-axes show the distribution of trait values in the dataset



(Fig. 7a), and expanded by ~6% as basin richness increased from 7 to 540 species (Fig. 7b). Isospace also increased by ~4% as average body size increased from ~1 g to ~6.5 kg (Fig. 7c), and by ~5% in species with truncate or rounded caudal fins (caudal fin aspect ratio < 1.5) compared to those with lunate fins (caudal fin aspect ratio > 3) (Fig. 7d). The relative contribution of predictors also shifted in non-predator models, with habitat diversity explaining the largest portion of variation (19%), followed by body size variation and trophic guild (14% each), sample size (13%), caudal aspect ratio (10%), average body size (8%), number of sampling years (6%), and average solar radiation (5%). All remaining predictors contributed less than 4%. Further details on predator and non-predator analyses are available in Online Resource 7.

Discussion

Our findings revealed considerable variation in fish population isospace size across the globe and taxonomic groups. The BRT model, which incorporated

environmental, trait, and scale-dependent variables, explained up to 32% of the variation in isospace size during testing (i.e., out-of-sample predictions)—a relatively high predictive power for an ecological analysis performed at a global scale. The combined influence of environment, traits, and scale-dependent factors yielded the best predictive model, with environmental and trait-related variables being among the most important predictors.

Our findings supported six of the eleven tested hypotheses linking trophic niche breadth with environmental and trait-associated mechanisms, providing moderate support for the Productivity-Diversity (PDH) and Body Size Variation-Trophic Expansion (BVH) hypotheses, and weak support for the Environmental Variability (EVH), Ecosystem Type (ETH), Niche Variation (NVH), and Body Size-Trophic Expansion (BEH) hypotheses (Table 3). Of the five unsupported hypotheses (Ecological Opportunity [EOH], Omnivory-Mediated Trophic Niche [OTH], Body Size-Trophic Contraction [BCH], Trophic Level-Niche Breadth [TLH], and Swimming Efficiency-Trophic Breadth [SEH]), three were related

Table 3 Summary of results for the 14 hypotheses, including support, relative contribution (strength), and comments

Hypothesis	Evaluating hypothesis support	Strength of the relationships	Comments
Niche Variation (NVH)	Partially supported	Weak	Inverse relationship for non-predators
Environmental Variability (EVH)	Fully supported	Weak	
Ecological Opportunity (EOH)	Partially supported	Weak	Pattern only observed for non-predators
Productivity-Diversity (PDH)	Partially supported	Moderate	Inverse relationship for non-predators
Ecosystem type (ETH)	Fully supported	Weak	Narrow isospace for large lakes and broad for rivers
Body Size-Trophic Expansion (BEH)	Partially supported	Weak	Inverse relationship for non-predators
Body Size-Trophic Contraction (BCH)	Partially supported	Weak	Pattern only observed for non-predators
Body Size Variation-Trophic Expansion (BVH)	Fully supported	Moderate	
Omnivory-Mediated Trophic Niche (OTH)	Not supported	Moderate	Broader isospace for herbivores and frugivores
Trophic Level-Niche Breadth (TLH)	Not supported	Moderate	Broader isospace for herbivores and frugivores
Swimming Efficiency-Trophic Breadth (SEH)	Partially supported	Weak	Pattern observed only for herbivores and detritivores, while the opposite trend was found for predators and when considering all species combined
Sample size (SSH)	Fully supported	Moderate	
Spatial scale (STH)	Fully supported	Moderate	Stronger pattern for non-predators
Temporal scale (TSH)	Fully supported	Moderate	

to caudal fin aspect ratio and trophic guild, both of which showed consistent but opposite patterns to the predictions. Interestingly, the results differed between fish at the base and those at the top of the food web. While predators aligned with the patterns observed in the analysis encompassing all trophic guilds, non-predators showed considerable differences in four key variables—supporting the EOH, SEH and BCH hypotheses but diverging from the predictions of the PDH, NVH, and BEH. Isospace size variation exhibited scale dependence on both predators and non-predators, as suggested by the Sample Size (SSH), Spatial Scale (STH), and Temporal Scale (TSH) hypotheses.

Isospace variation—environment

Population isospaces tended to be larger in warm, humid regions, likely reflecting greater resource diversity and productivity, as proposed by the productivity–diversity hypothesis (PDH; Currie 1991). In these environments, elevated energy availability and climatic stability may promote broader trophic

opportunities and more consistent access to diverse resources. These conditions can support greater individual-level variation in resource use and trophic plasticity, ultimately contributing to population-level niche expansion. The greater availability of aquatic habitats in tropical and subtropical regions—partly driven by higher aquatic plant diversity and abundance—may further facilitate fish populations' isospace expansion. Aquatic plants provide structurally complex habitats that support diverse aquatic communities, including invertebrates that are important prey for many fish species (Thomaz and Da Cunha 2010). In addition, co-occurrence of C3 and C4 plants is expected to be more frequent within hot, humid tropical and subtropical regions, and the wide difference in $\delta^{13}\text{C}$ between these plants at the base of aquatic foods could contribute to isotopic variation among consumers assimilating material derived from these sources (Sage and Monson 1999; Still et al. 2003). This contrasts with cold regions, where low temperatures reduce metabolic rates, ecosystem productivity, and food resource diversity (Brown et al. 2004). Similarly, dry environments often cause

water bodies to shrink or dry completely for intervals that restrict fish movement and foraging opportunities (Williams 2006), degrade water quality (Misaghi et al. 2017), and limit basal resource production (Jaleel et al. 2009).

Supporting the NVH hypothesis, fish isospace size was negatively related to basin richness, but this relationship only emerged after accounting for climate variables associated with humidity and temperature (i.e., after including both in the model), which were positively correlated with isospace size. This suggests that resource availability and diversity are important drivers of global variation in fish trophic niches, with compression of the trophic niche occurring secondarily in more species-rich communities in response to current or past interspecific competition (Connell 1980; MacArthur 1970). Similar results have been observed for Maitland and Rahel (2023) at a smaller scale, where fish isospaces were determined by an interaction between environmental and species diversity. Here, isospace size declined sharply when basin richness exceeded 50 fish species. This may indicate some degree of functional redundancy in highly diverse communities (Loreau 2004; Walker 1992) or suggest that species-poor communities function differently from species-rich ones—being more shaped by stochastic processes, whereas richer communities are more deterministic. Metacommunity dynamics (e.g., mass effects, connectivity) may also influence how competition shapes trophic niche width (Bauer et al. 2021; Quévieux and Loreau 2022). Further studies are needed to disentangle these mechanisms. However, we acknowledge that basin-scale species richness is not equivalent to species diversity at the spatial scale at which species interact, but data for local-scale fish diversity was unavailable for many of our datasets.

Terrestrial food resources subsidize many, if not most, freshwater communities (Lafage et al. 2019; Leal et al. 2023). During river flow pulses, inundated floodplains allow fish to access terrestrial invertebrates, fruits, seeds, leaves, and detritus (van der Sleen and Rams 2023). Thus, fish trophic niches are likely to expand during high-flow pulses, particularly in tropical regions where wet/dry seasonality produces floods of large magnitude and duration annually. We used the CV of precipitation as a proxy for water level fluctuations in aquatic systems. This

variable had a weak, positive association with population isospace size, supporting the EVH hypothesis. Several factors could have contributed to this weak association. First, we did not account for differences in productivity between aquatic and terrestrial ecosystems, which are known to influence the degree of terrestrial subsidies (Marczak et al. 2007). Second, our metric does not account for landscape features that influence hydrology and hydraulics. In some cases, local precipitation may be an inadequate proxy for flow variation, for example, when precipitation or snowmelt in upstream regions is the main driver of hydrology. In addition, hydrological variability differs systematically among ecosystem types: small streams and lakes with high precipitation CV are expected to experience larger fluctuations, whereas large rivers and large lakes tend to be more stable. For example, flow in headwater streams often respond rapidly to local rainfall, whereas large lowland rivers, such as the Amazon, typically undergo more gradual and predictable seasonal fluctuations. These environmental differences are partially captured by our models, and a finer-resolution classification of systems would require compilation of hydrological data that are sometimes unavailable, particularly for rivers in tropical regions. Third, isotopic signatures may not capture seasonal variability in precipitation, as their turnover time is typically limited to a relatively short period—ranging from weeks to a few months (Vander Zanden et al. 2015). Finally, a lack of isotopic differentiation between local aquatic and terrestrial food resources would hinder the ability to detect the effect of terrestrial food-web subsidies on fish isospaces (Winemiller et al. 2022).

Fish population isospace differed among different types of ecosystems, which is consistent with the expectations of the ETH hypothesis. Populations in large lakes had slightly smaller isospaces than those inhabiting small lakes, streams, and rivers. In large lakes, most fishes may be supported by pelagic food chains originating from phytoplankton (Maitland et al. 2024). By contrast, smaller water bodies, including small lakes and streams, have higher shoreline/area ratios, allowing for greater inputs of allochthonous material from surrounding terrestrial ecosystems, which in turn would increase food resource diversity for fishes (Larson et al. 2011). Rivers and streams are heterogeneous and dynamic ecosystems, and their food webs are supported by diverse energy

sources differing in isotopic composition (Potapov et al. 2019; Riede et al. 2011; Roach 2013). However, the relatively small differences in isospace among ecosystem types reflect substantial variability within each ecosystem that was not accounted for in the analysis. Among these, the interaction with marginal floodplain lakes and wetlands where methanogenic carbon assimilation may occur (e.g., Urbano et al. 2025) and changes in resource subsidies from headwaters to mouth (e.g., Soria-Barreto et al. 2020) may represent extreme isotopic variation at the base of food webs reflected to fish consumers.

Isospace variation—traits

Although trophic guild was the strongest predictor of fish isospace size, it did not support the predictions of either the TLH (Jennings et al. 2002; Layman et al. 2005; Scharf et al. 2000) or the OTH (Woodland et al. 2015) hypotheses. Instead, primary consumers tended to have larger isospaces than fishes at intermediate (invertivores, planktivores) and high trophic levels (carnivores and piscivores). Our finding agrees with a recent study of fish food webs in a subtropical river where species at lower trophic levels ($TL < 3$) had larger isospaces than predators (Zhang et al. 2024). The trophic niche of herbivorous and detritivorous/algivorous fishes has historically been underestimated, largely due to the difficulty of identifying minute and often fragmented or amorphous items in gut contents (Martinson et al. 2008). Stable isotope analysis provides an alternative approach to estimate trophic niches, even though considerations that specific diet compositions are unknown. Primary consumers should be selective foragers due to the high variability in the nutritional quality of plant tissues (Clauss et al. 2013; Martinson et al. 2008). However, large herbivorous and detritivorous fishes have high consumption rates, which may hinder the evolution of specialized diets (Arim et al. 2010; Sibly et al. 2012). Some studies have shown that herbivorous and detritivorous fish under certain conditions supplement their diet with invertebrates (e.g., Andrade et al. 2019; Nalley et al. 2021). Furthermore, herbivorous fishes may shift their diet from autochthonous to allochthonous plant material when highly nutritious forms of the latter become available during the flood season (Correa and Winemiller 2013; Ou and Winemiller 2016).

Often a detritivorous or herbivorous fish appears to have a narrow diet when the analysis is based on gut contents, wherein "detritus" or "vegetation" are listed as categories. However, both of these categories can have heterogeneous composition with potential to exhibit a large isospace. Detritus can originate from diverse sources and be subject to different isotopic fractionation processes. For example, detritus decomposed within anoxic environments with methanogenic microbes can have $\delta^{13}C$ values below -35‰ , whereas detritus and algae in oxygenated environments have $\delta^{13}C$ values typically from -30 to -20 and even as high as -15‰ . Stream current velocity can significantly influence $\delta^{13}C$ of benthic algae (Trudeau and Rasmussen 2003), such that algivorous fishes feeding in lentic versus lotic environments could have different values. Therefore, herbivorous or detritivorous fish populations that exploit habitats differing in current velocity or oxygen availability are expected to exhibit broad isospaces. Notably, a species with a diverse diet based on gut contents analysis may exhibit a relatively narrow isospace if food sources have similar isotopic signatures, although this did not appear to be the case for detritivorous and herbivorous fishes in our dataset.

Herbivorous fishes have adaptations for processing carbon-rich, nitrogen-poor foods, including specialized jaws and teeth, long guts, and microbial fermentation (Horn 1989; Keppeler et al. 2020). Because plants vary widely in $\delta^{13}C$ (e.g., C_3 vs. C_4 macrophytes, terrestrial vs aquatic vegetation), herbivores can span a broad $\delta^{13}C$ range depending on which plants and plant parts are exploited. Because herbivores feed at low trophic levels, $\delta^{15}N$ of tissues tends to be uniformly low in relation to animals at higher trophic levels (Woodland et al. 2015). As mentioned previously, detritivorous fishes consume heterogeneous material that include terrestrial and aquatic plant and animal material, fungi, microbes, algae, protozoa and other microfauna (Bowen 1983; Mann 1988). Detritivorous fishes tend to have long guts, gizzards, caeca, and/or microbial symbionts that aid digestion of microbial proteins, which often are the principal nutritional source (Bowen 1983; Mann 1988). Microbial processing tends to increase $\delta^{15}N$ of bulk detritus samples (microbes shift $d^{15}N$ of assimilated material to varying degrees) which could increase within-group variability in $\delta^{15}N$ of detritivores (Steffan and Dharampal 2018).

Greater population isospace variability at the base of the food web may also stem from the progressive loss of isotopic differentiation as material is transferred up the food chain. Consumers integrate the isotopic compositions of their assimilated resources, leading to intermediate $\delta^{13}\text{C}$ values (Fry 2007). Although $\delta^{13}\text{C}$ is skewed toward the most important resource, values tend to average out at higher trophic levels. As a result, when plotted in $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ space, food webs often form a triangular pattern, with high $\delta^{13}\text{C}$ variation at low $\delta^{15}\text{N}$ (a proxy for trophic level) and a narrower range of intermediate $\delta^{13}\text{C}$ values at high $\delta^{15}\text{N}$ (Keppeler et al. 2021; Maitland et al. 2024). This pattern implies that top predators are unlikely to have an extremely depleted or enriched ^{13}C signature. The effect may be particularly pronounced in size-structured food webs, as larger organisms typically have lower tissue turnover rates than smaller ones (Vander Zanden et al. 2015). Slower turnover allows the organism's isotopic signatures to integrate assimilated material over extended periods and across different locations, further driving $\delta^{13}\text{C}$ values toward intermediate levels (Keppeler et al. 2021). The extent to which trophic patterns may be biased by body size and differential rates of organic matter assimilation is unknown, especially since the triangular pattern is not evident in some food webs (e.g., Andrade et al. 2023).

Our findings support the predictions of the BVH hypothesis, as intrapopulation variation in body size was associated with larger isospaces. Among the tested variables, body size variation emerged as the second strongest predictor. This relationship is attributed to ontogenetic niche shifts, in either feeding, habitat use, or both (Werner and Gilliam 1984). In addition to phenotypic variation associated with ontogeny, the adult fish body sizes have been shown to vary as a function of genetic and environmental factors (Ahti et al. 2020) as well as sexual dimorphism (Parker 1992). Isospace variation could also be influenced by other factors, like territoriality, where larger individuals control spaces with the most profitable resources (Schirmer et al. 2019), resulting in significant between-individual niche variation (Bolnick et al. 2003).

The average body size of fish populations had a positive but weaker relationship with isospace size than variation in body size within populations. The positive trend is consistent with the BEH hypothesis, which suggests that trophic diversification occurs

to meet higher energy demands and is facilitated by mouth-gape release (Arim et al. 2010; Rooney et al. 2008). However, the weak association may indicate that assumptions of the hypothesis do not hold for some species (Keppeler and Winemiller 2020a; Hanson et al. 2024) or that stable isotope analysis is unable to clearly detect the underlying mechanisms for intraspecific variation in trophic niche breadth (Hette-Tronquart 2019).

Contrary to the expectations of the SEH hypothesis, fish populations with truncated or round caudal fins exhibited broader isospaces than those with forked, emarginate, or lunate caudal fins. A possible explanation is that fish with lower vagility (truncated or round caudal fins) forage within smaller areas. If these individuals are more spatially segregated compared to more vagile species that seek preferred food resources over large areas, a broader isospace could result from the isospace structure and/or individuals consuming different locally available resources. By contrast, fish with forked, emarginate, or lunate caudal fins are generally more vagile and may have isotopic signatures that integrate those of resources obtained over broad areas. Additionally, many species with forked caudal fins, such as South American piranhas (*Serrasalmus* spp.) and African tigerfish (*Hydrocynus vittatus*), are carnivorous and tend to have relatively small isospaces compared to fishes at lower trophic levels. Forked caudal fins are also common among schooling fishes (e.g., South American tetras), whose aggregative behavior tends to homogenize prey items among individuals and likely reduce population trophic niche width.

Isospace variation—scale

Although we set a minimum sample size for populations included in our analyses, we still observed moderate increases in isospace size with sample size, consistent with the SSH hypothesis. Additionally, isospace size tended to be larger when more habitats and years were surveyed, in agreement with the STH and TSH hypotheses, respectively. Notably, including additional habitats and years had a considerably greater effect than randomly sampling more individuals, emphasizing the need for standardized sampling protocols when comparing trophic niches of populations. Spatial and temporal variation in isotopic ratios and availability of resources as well as time lags in

the assimilation of elements from ingested food items are factors affecting animal isotopic ratios (Fry 2007; Layman et al. 2012). Our results underscore the importance of factoring out scale-dependent variables, even when adhering to the minimum sample sizes recommended in the literature (Eckrich et al. 2019; Jackson et al. 2011).

Differences between predators and non-predators

Our findings suggest that the factors shaping fish population isospace differ between predatory and non-predatory fish. Scale-dependent factors, for example, were nearly three times more important in explaining isospace variation among non-predators than among predators. Most of this variation was associated with habitat diversity, indicating that spatial differences in the isotopic signature of basal resources have a stronger influence on non-predatory species. This may reflect the greater spatial isolation of non-predators, which tend to be smaller in body size and rely on a narrower range of energy sources (Arim et al. 2010; Rooney et al. 2008). Another possible explanation is the higher variability typically found in the isotopic signatures of basal resources compared to those at higher trophic levels (Hoeinghaus and Zeug 2008).

Non-predators also showed consistently different relationships with solar radiation and basin fish richness compared to predators. Basin richness was positively associated with isospace in non-predators, suggesting that interspecific competition may not be a major constraint on their trophic niche breadth. This may reflect the greater availability of energy at the base of the food web, where less energy is lost through trophic transfers (Thompson and Townsend 2005). However, it is important to note that basin-level fish richness may not be a strong proxy for resource competition in non-predators, as their primary food sources—such as detritus and macrophytes—are also heavily exploited by other aquatic organisms, particularly invertebrates. Further testing of the NVH hypothesis could involve categorizing all species within river basins into trophic guilds, and then examining whether the isotopic spaces of focal species are over- or under-dispersed relative to guild species richness. Because competition is expected to be stronger within than among guilds, comparing average isospace size and intra- versus inter-guild overlap would provide a direct test of this prediction.

We observed lower isospace values in non-predators under high solar radiation. This could result from inhibited basal resource production or shifts in basal community composition under intense solar exposure, especially ultraviolet radiation. Such conditions may favor the proliferation of dominant producers like algal blooms (Paul 2008) and free-floating macrophytes, which can drastically alter water chemistry and light penetration (Häder et al. 2007; Lind et al. 2022). Alternatively, increased productivity associated with solar radiation might lead consumers to concentrate their diets on the most abundant and nutritious resources, thereby narrowing their trophic niche (Peterson et al. 2017).

In contrast to predators, non-predatory fishes exhibited a decline in isospace with increasing body size and an increase with higher caudal fin aspect ratios. The smaller isospace observed in larger species may reflect the inverse relationship between body size and trophic position commonly found in non-predators (Burruss et al. 2016; Keppeler et al. 2020). While smaller non-predatory species tend to incorporate more animal material into their diets—thus expanding their trophic niche—larger non-predatory species are typically more specialized, often possessing long intestines adapted for digesting detritus and/or plant material (Burruss et al. 2016). The relationship between caudal fin aspect ratio and isospace differs between predators and non-predators, though the reasons remain unclear. This pattern may be related both to differences in the isotopic signatures of consumed resources—which are often more heterogeneous for herbivores (Hoeinghaus and Zeug 2008)—and to the functional role of the caudal fin, which is more critical for predators that rely on speed and maneuverability to capture prey (Sambilay et al. 1990).

Latitudinal gradient and ecoregion differences

Although fish isospaces tended to be smaller at higher latitudes, our results did not reveal a consistent latitudinal gradient. Isospaces were smaller in the Nearctic and Australasia. In Australasia, the sampled aquatic ecosystems were notably drier than those on other continents (Online Resource 3), and their fish populations were mostly supported by algae (Beesley et al. 2020; Bunn et al. 2013) and had relatively small isospaces. Most Nearctic fish populations were carnivorous species with relatively small isospaces.

Higher proportions of predatory fishes at higher latitudes are a well-documented macroecological pattern (Moss 2013), and greater incidence of herbivory and omnivory in (sub)tropical fishes (González-Bergonzoni et al. 2012) may explain the broader isospaces observed in the Neotropics and Indo-Malay ecoregions. The larger isospaces in Palearctic fish compared to Nearctic fish may be associated with the lower species richness and potential competition in the former as well as bias due to fewer studies included from that region.

Caveats

Although we found significant relationships supporting several hypotheses and opposing a few others, inherent limitations must be acknowledged when employing population isospace as a metric for trophic niche breadth. For instance, each individual of a population occupies a single point in isospace, whether or not that individual has a narrow or broad diet (Hette-Tronquart 2019). Thus, if a population has low between-individual diet variation, the population isospace would be narrow even though individual diets are broad. In addition, animal isospaces are influenced by isotopic variation among basal sources, and even the isotopic signatures of a source type from different locations or time periods may be influenced by environmental variation (Bearhop et al. 2004). For example, an animal that consumed a wide range of food items having similar isotope signatures would have a smaller isotopic space compared to an animal that feeds on fewer food items with highly divergent signatures. Although this issue could have been a source of bias in our global analysis, the large number of sites and samples for populations at most sites should have facilitated emergence of robust patterns among comparisons.

$\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and other isotopic ratios of organisms can be influenced by factors not directly related to diet (Hette-Tronquart 2019; Hoeinghaus and Zeug 2008), including environmental variables (e.g., temperature, variation in inorganic elemental sources for primary producers), anthropogenic impacts (e.g., sewage effluents, fossil fuel pollution), lipid content, and consumer-associated traits (e.g., metabolism, growth rate) (Davis et al. 2012; Hoffman et al. 2015; Maitland et al. 2021; Vander Zanden et al. 1997; Villamarín et al. 2018). While a comprehensive accounting

for all these variables is infeasible, we recognize their potential influence on global patterns of populations' isospace variation. Future studies may consider using mixing models to refine the contribution of basal sources to the diet of consumers (Hoeinghaus and Zeug 2008); however, these efforts are hindered by limited knowledge about trophic enrichment factors and tissue/elemental turnover rates (Bastos et al. 2017; Vander Zanden et al. 2015). Analysis of fatty acids (Haubert et al. 2011), compound-specific isotopes (Bowes and Thorp 2015), and DNA barcoding (Wolfe et al. 2025) of ingested material could offer greater resolution of diet composition.

Conclusions

Analyzing population isospaces is complicated by various non-trophic factors influencing isotope ratios (Hette-Tronquart 2019; Hoeinghaus and Zeug 2008). Investigation of trophic niches at a global scale presents challenges, including data standardization and statistical approaches to control for potential confounding factors. Despite these limitations and challenges, our global analysis supports several ecological hypotheses, including productivity–diversity (PDH) and Body Size Variation-Trophic Expansion (BVH) hypotheses, and provides insights into new ones, such as Swimming Efficiency-Trophic Breadth hypothesis (SHE). Additionally, even with sample sizes exceeding the minimum recommended in the literature (Eckrich et al. 2019; Jackson et al. 2011), we found significant scale-dependence effects, highlighting the need for future comparative studies to strive for balanced sampling designs. Advancing our understanding of trophic niche breadth is important, not only because niche theory is central to ecology, but also because it informs predictions of species response to environmental variation, including changing conditions of the Anthropocene.

Acknowledgements We thank the National Council for Scientific and Technological Development of Brazil (CNPq) for providing a postdoctoral scholarship (150773/2024-2) to FWK to support this research, as well as many other public (Fundação de Amparo e Desenvolvimento da Pesquisa, US National Science Foundation, US Environmental Protection Agency, Texas Parks and Wildlife Department, Carlos Chagas Filho Foundation for Research Support of the State of Rio de Janeiro, Brazilian Federal Agency for Support and Evaluation of Graduate Education, and The Scientific and Technological

Research Council of Türkiye) and private institutions (Norte Energia, National Geographic Society, and Sabin Center for Environment and Sustainability) that funded field studies and stable isotope analyses. The project was also financed by Norte Energia S.A. under the ANEEL Development and Innovation Program (PD-07427-0325/2025), “Data intelligence for automation of socio-environmental reports and fish monitoring”. We also acknowledge the efforts of numerous volunteers, students, and technicians who collected and processed samples. The views expressed in this manuscript are those of the authors and do not necessarily represent the views or policies of the U.S. Environmental Protection Agency.

Author contributions Conceptualization: FWK, CGM, KOW; Funding acquisition: FWK, TG; Investigation (Data collection and processing): TG, CGM, AA, CCA, EB, TB, RE-S, CER, IG-B, DH, JH, OPJ, EJ, CL, EOL, BM, SSM, JAO, GP, YQ, AG, RKK, AT, PAT, TFT, EZ, KOW; Formal analysis: FWK; Visualization: FWK, TG; Writing—Original Draft: FWK, TG, CGM, KOW; Writing—Review & Editing: All authors.

Funding This study was funded by the National Council for Scientific and Technological Development of Brazil (CNPq) through a postdoctoral scholarship (150773/2024-2) awarded to FWK and also by Norte Energia S.A. under the ANEEL Development and Innovation Program (PD-07427-0325/2025).

Data availability Links to the publicly archived datasets used to estimate fish population isospaces are provided in Online Resource 1. The scripts and data used to run the MR, PGLS, and BRT models are available in the Zenodo archive (<https://doi.org/10.5281/zenodo.17352150>).

Declarations

Conflict of interest The authors declare no competing interests.

References

- Ahti PA, Kuparinen A, Uusi-Heikkilä S (2020) Size does matter — the eco-evolutionary effects of changing body size in fish. *Environ Rev* 28:311–324. <https://doi.org/10.1139/er-2019-0076>
- Andrade MC, Fitzgerald DB, Winemiller KO, Barbosa PS, Giarrizzo T (2019) Trophic niche segregation among herbivorous serrasalmids from rapids of the lower Xingu River, Brazilian Amazon. *Hydrobiologia* 829:265–280. <https://doi.org/10.1007/s10750-018-3838-y>
- Andrade MC, Keppeler FW, Zuluaga-Gómez MA, Conceição JWS, Lisboa OP, Andrades R, Winemiller KO et al (2023) Food web structure in the Xingu River rapids prior to operation of the Amazon’s largest hydropower plant. *Aquat Sci* 85:74. <https://doi.org/10.1007/s00027-023-00971-x>
- Araújo MS, Bolnick DI, Machado G, Giaretta AA, dos Reis SF (2007) Using $\delta^{13}\text{C}$ stable isotopes to quantify individual-level diet variation. *Oecologia* 152:643–654. <https://doi.org/10.1007/s00442-007-0687-1>
- Arim M, Abades SR, Laufer G, Loureiro M, Marquet PA (2010) Food web structure and body size: trophic position and resource acquisition. *Oikos* 119:147–153
- Baker HK, Bruggeman CEF, Shurin JB (2022) Population niche width is driven by within-individual niche expansion and individual specialization in introduced brook trout in mountain lakes. *Oecologia* 200:1–10. <https://doi.org/10.1007/s00442-022-05201-z>
- Bartoń K (2024) MuMin: multi-model inference. R package. <https://CRAN.R-project.org/package=MuMin>
- Bastos RF, Corrêa F, Winemiller KO, Garcia AM (2017) Are you what you eat? Effects of trophic discrimination factors on estimates of food assimilation and trophic position with a new estimation method. *Ecol Indic* 75:234–241. <https://doi.org/10.1016/j.ecolind.2016.12.007>
- Bauer B, Kleyer M, Albach DC, Blasius B, Brose U, Ferreira-Arruda T, Feudel U et al (2021) Functional trait dimensions of trophic metacommunities. *Ecography* 44:1486–1500. <https://doi.org/10.1111/ecog.05869>
- Bearhop S, Adams CE, Waldron S, Fuller RA, Fullert RA, Macleod H (2004) Determining trophic niche width: a novel approach using stable isotope analysis. *J Anim Ecol* 73:1007–1012
- Beesley LS, Pusey BJ, Douglas MM, Gwinn DC, Canham CA, Keogh CS, Pratt OP et al (2020) New insights into the food web of an Australian tropical river to inform water resource management. *Sci Rep* 10:14294. <https://doi.org/10.1038/s41598-020-71331-0>
- Bolnick DI, Svanbäck R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. *Am Nat* 161:1–28. <https://doi.org/10.1086/343878>
- Bowen SH (1983) Detritivory in neotropical fish communities. *Environ Biol Fishes* 9:137–144
- Bowes RE, Thorp JH (2015) Consequences of employing amino acid vs. bulk-tissue, stable isotope analysis: a laboratory trophic position experiment. *Ecosphere* 6:1–12. <https://doi.org/10.1890/es14-00423.1>
- Brown JH (2004) Toward a metabolic theory of ecology. *Ecology* 85:1771–1789. <https://doi.org/10.1890/03-9000>
- Brownscombe JW, Shipley ON, Griffin LP, Morley D, Acosta A, Adams AJ, Boucek R, Danylchuk AJ, Cooke SJ, Power M (2022) Application of telemetry and stable isotope analyses to inform the resource ecology and management of a marine fish. *J Appl Ecol* 59:1110–1121. <https://doi.org/10.1111/1365-2664.14123>
- Brun P, Zimmermann NE, Graham CH, Laverne S, Pellissier L, Münkemüller T, Thuiller W (2019) The productivity-biodiversity relationship varies across diversity dimensions. *Nat Commun* 10:5691. <https://doi.org/10.1038/s41467-019-13678-1>
- Bunn SE, Leigh C, Jardine TD (2013) Diet-tissue fractionation of $\delta^{15}\text{N}$ by consumers from streams and rivers. *Limnol Oceanogr* 58:765–773. <https://doi.org/10.4319/lo.2013.58.3.0765>
- Burruss ED, Holcomb JM, Bonato KO, Armbruster JW (2016) Body size is negatively correlated with trophic position among cyprinids. *R Soc Open Sci* 3:150652. <https://doi.org/10.1098/rsos.150652>

- Chamberlain S, Szoecs E, Foster Z, Arendsee Z, Boettiger C, Ram K, Bartomeus I et al (2020) taxize: taxonomic information from around the web. R package. <https://github.com/ropensci/taxize>
- Cipriani V, Goldenberg SU, Connell SD, Ravasi T, Nagelkerken I (2024) Can niche plasticity mediate species persistence under ocean acidification? *J Anim Ecol* 93:1380–1391. <https://doi.org/10.1111/1365-2656.14163>
- Cirtwill AR, Stouffer DB, Romanuk TN (2015) Latitudinal gradients in biotic niche breadth vary across ecosystem types. *Proc R Soc Lond B Biol Sci* 282:20151589. <https://doi.org/10.1098/rspb.2015.1589>
- Clauss M, Steuer P, Müller DWH, Codron D, Hummel J (2013) Herbivory and body size: allometries of diet quality and gastrointestinal physiology, and implications for herbivore ecology and dinosaur gigantism. *PLoS One* 8:e68714. <https://doi.org/10.1371/journal.pone.0068714>
- Cloyed CS, DaCosta KP, Hodanbosi MR, Carmichael RH (2019) The effects of lipid extraction on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and use of lipid-correction models across tissues, taxa and trophic groups. *Methods Ecol Evol* 11:751–762. <https://doi.org/10.1111/2041-210X.13386>
- Connell JH (1980) Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138. <https://doi.org/10.2307/3544421>
- Correa SB, Winemiller KO (2013) Niche partitioning among frugivorous fishes in response to fluctuating resources in the Amazonian floodplain forest. *Ecology* 95:210–224. <https://doi.org/10.1890/13-0393.1>
- Costa GC (2009) Predator size, prey size, and dietary niche breadth relationships in marine predators. *Ecology* 90:2014–2019
- Currie DJ (1991) Energy and large-scale patterns of animal species and plant species richness. *Am Nat* 137:27–49
- Davies KF, Harrison S, Safford HD, Viers JH (2007) Productivity alters the scale dependence of the diversity–invasibility relationship. *Ecology* 88:1940–1947. <https://doi.org/10.1890/06-1907.1>
- Davis AM, Blanchette ML, Pusey BJ, Jardine TD, Pearson RG (2012) Gut content and stable isotope analyses provide complementary understanding of ontogenetic dietary shifts and trophic relationships among fishes in a tropical river. *Freshw Biol* 57:2156–2172. <https://doi.org/10.1111/j.1365-2427.2012.02858.x>
- De Carvalho DR, Sparks JP, Flecker AS, Alves CBM, Moreira MZ, Pompeu PS (2021) Nitrogen pollution promotes changes in the niche space of fish communities. *Oecologia* 197:485–500. <https://doi.org/10.1007/s00442-021-05029-z>
- De Frenne P, Graae BJ, Rodríguez-Sánchez F, Kolb A, Chabrierie O, Decocq G, De Kort H et al (2013) Latitudinal gradients as natural laboratories to infer species' responses to temperature. *J Ecol* 101:784–795. <https://doi.org/10.1111/1365-2745.12074>
- Des Roches S, Post DM, Turley NE, Bailey JK, Hendry AP, Kinnison MT, Schweitzer JA et al (2017) The ecological importance of intraspecific variation. *Nat Ecol Evol* 2:57–64. <https://doi.org/10.1038/s41559-017-0402-5>
- Diamond JM (1975) Assembly of species communities. In: Cody ML, Diamond JM (eds) *Ecology and evolution of communities*. Harvard University Press, Cambridge, pp 342–444
- Dobzhansky T (1950) Evolution in the tropics. *Am Sci* 38:209–221
- Eckrich CA, Albeke SE, Flaherty EA, Bowyer RT, Ben-David M (2019) rKIN: kernel-based method for estimating isotopic niche size and overlap. *J Anim Ecol* 89:757–771. <https://doi.org/10.1111/1365-2656.13159>
- Elith J, Leathwick JR, Hastie T (2008) A working guide to boosted regression trees. *J Anim Ecol* 77:802–813. <https://doi.org/10.1111/j.1365-2656.2008.01390.x>
- Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int J Climatol* 37:4302–4315. <https://doi.org/10.1002/joc.5086>
- Franco-Trecu V, Botta S, de Lima RC, Negrete J, Naya DE (2022) Testing the niche variation hypothesis in pinnipeds. *Mamm Rev* 52:497–506. <https://doi.org/10.1111/mam.12297>
- Freckleton RP, Harvey PH, Pagel M (2002) Phylogenetic analysis and comparative data: a test and review of evidence. *Am Nat* 160:712–726
- Fredrickson A, Rieucan G, Fontenot Q, Lackmann A, David SR (2021) Nonlethal fin clip model validation for stable isotope analysis of spotted gar and alligator gar. *Trans Am Fish Soc* 151:72–80. <https://doi.org/10.1002/tafs.10331>
- Friedman JH (2001) Greedy function approximation: a gradient boosting machine. *Ann Stat* 29:1189–1232
- Friedman JH, Meulman JJ (2003) Multiple additive regression trees with application in epidemiology. *Stat Med* 22:1365–1381
- Froese R, Thorson JT, Reyes RB (2014) A Bayesian approach for estimating length–weight relationships in fishes. *J Appl Ichthyol* 30:78–85. <https://doi.org/10.1111/jai.12299>
- Fry B (2007) *Stable isotope ecology*. Springer Science & Business Media, Dordrecht
- González IS, Hopper GW, Bucholz JR, Kubala ME, Lozier JD, Atkinson CL (2023) Niche specialization and community niche space increase with species richness in filter-feeder assemblages. *Ecosphere* 14:e4495. <https://doi.org/10.1002/ecs2.4495>
- González-Bergonzoni I, Meerhoff M, Davidson TA, Teixeira-de Mello F, Baattrup-Pedersen A, Jeppesen E (2012) Meta-analysis shows a consistent and strong latitudinal pattern in fish omnivory across ecosystems. *Ecosystems* 15:492–503. <https://doi.org/10.1007/s10021-012-9524-4>
- Goulding M, Carvalho ML, Ferreira EG (1989) *Rio Negro, rich life in poor water*. SPB Academic Publishing, The Hague
- Guo F, Fry B, Yan K, Huang J, Zhao Q, O'Mara K, Li F, Gao W, Kainz MJ, Brett MT, Bunn SE, Zhang Y (2023) Assessment of the impact of dams on aquatic food webs using stable isotopes: current progress and future challenges. *Sci Total Environ* 904:167097. <https://doi.org/10.1016/j.scitotenv.2023.167097>
- Häder DP, Kumar HD, Smith RC, Worrest RC (2007) Effects of solar UV radiation on aquatic ecosystems and interactions with climate change. *Photochem Photobiol Sci* 6:267–285. <https://doi.org/10.1039/b700020k>

- Hanson J, Gordon M, Peterson N, Lepak R, Goldsworthy C, Brady V, Hrabik T et al (2024) Stable isotope analysis of western Lake Superior predatory fishes, part one: trophic niche overlap. *J Great Lakes Res* 51:102441. <https://doi.org/10.1016/j.jglr.2024.102441>
- Haubert D, Pollierer MM, Scheu S (2011) Fatty acid patterns as biomarkers for trophic interactions: changes after dietary switch and starvation. *Soil Biol Biochem* 43:490–494
- Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan JF, Kaufman DM, Kerr JT et al (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117. <https://doi.org/10.1890/03-8006>
- Hette-Tronquart N (2019) Isotopic niche is not equal to trophic niche. *Ecol Lett* 22:1987–1989. <https://doi.org/10.1111/ele.13218>
- Hijmans RJ, Phillips S, Leathwick J, Elith J (2023) Dismo: species distribution modeling. R package version. <https://CRAN.R-project.org/package=dismo>
- Hijmans RJ, Barbosa M, Ghosh A, Mandel A (2024) Geodata: download geographic data. R package. <https://CRAN.R-project.org/package=geodata>
- Hoeinghaus DJ, Zeug SC (2008) Can stable isotope ratios provide for community-wide measures of trophic structure? *Comment. Ecology* 89:2353–2357. <https://doi.org/10.1890/07-1143.1>
- Hoffman JC, Sierszen ME, Cotter AM (2015) Fish tissue lipid:C:N relationships for correcting $\delta^{13}\text{C}$ values and estimating lipid content in aquatic food-web studies. *Rapid Commun Mass Spectrom* 29:2069–2077. <https://doi.org/10.1002/rcm.7367>
- Horn MH (1989) Biology of marine herbivorous fishes. *Oceanogr Mar Biol Annu Rev* 27:167–272
- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER - stable isotope Bayesian ellipses in R. *J Anim Ecol* 80:595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>
- Jaleel CA, Manivannan P, Wahid A, Farooq M, Al-Juburi HJ, Somasundaram R, Panneerselvam R (2009) Drought stress in plants: a review on morphological characteristics and pigments composition. *Int J Agric Biol* 11:100–105
- Jennings S, Warr KJ, Mackinson S (2002) Use of size-based production and stable isotope analyses to predict trophic transfer efficiencies and predator–prey body mass ratios in food webs. *Mar Ecol Prog Ser* 240:11–20
- Keppeler FW, Winemiller KO (2020a) Incorporating indirect pathways in body size–trophic position relationships. *Oecologia* 194:177–191. <https://doi.org/10.1007/s00442-020-04752-3>
- Keppeler FW, Winemiller KO (2020b) Can ancestry and morphology be used as surrogates for species niche relationships? *Ecol Evol* 10:6562–6578. <https://doi.org/10.1002/ece3.6390>
- Keppeler FW, Montaña CG, Winemiller KO (2020) The relationship between trophic level and body size in fishes depends on functional traits. *Ecol Monogr* 90:e01415. <https://doi.org/10.1002/ecm.1415>
- Keppeler FW, Olin JA, López-Duarte PC, Polito MJ, Hooper-Bùi LM, Taylor SS, Rabalais NN et al (2021) Body size, trophic position, and the coupling of different energy pathways across a saltmarsh landscape. *Limnol Oceanogr Lett* 6:360–368. <https://doi.org/10.1002/lol2.10212>
- Keppeler FW, Engel AS, Hooper-Bùi LM, López-Duarte PC, Martin CW, Olin JA, Lamb KJ, Polito MJ, Rabalais NN, Roberts BJ, Swenson EM, Jensen OP (2024) Coastal wetland restoration through the lens of Odum's theory of ecosystem development. *Restor Ecol* 32:e14072. <https://doi.org/10.1111/rec.14072>
- Keys AB (1928) The weight-length relationship in fishes. *Proc Natl Acad Sci U S A* 14:922–925
- Kottek M, Grieser J, Beck C, Rudolf B, Rubel F (2006) World map of the Köppen-Geiger climate classification updated. *Meteorol Z* 15:259–263. <https://doi.org/10.1127/0941-2948/2006/0130>
- Kuhn M (2008) Building predictive models in R using the caret package. *J Stat Softw* 28:1–26. <https://doi.org/10.18637/jss.v028.i05>
- Lafage D, Bergman E, Eckstein RL, Österling EM, Sadler JP, Piccolo JJ (2019) Local and landscape drivers of aquatic-to-terrestrial subsidies in riparian ecosystems: a world-wide meta-analysis. *Ecosphere* 10:e02697. <https://doi.org/10.1002/ecs2.2697>
- Larson ER, Olden JD, Usio N (2011) Shoreline urbanization interrupts allochthonous subsidies to a benthic consumer over a gradient of lake size. *Biol Lett* 7:551–554. <https://doi.org/10.1098/rsbl.2011.0089>
- Layman CA, Winemiller KO, Arrington DA, Jepsen DB (2005) Body size and trophic position in a diverse tropical food web. *Ecology* 86:2530–2535
- Layman CA, Arrington DA, Montaña CG, Post DM (2007) Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology* 88:42–48. [https://doi.org/10.1890/0012-9658\(2007\)88\[42:CSRPFM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[42:CSRPFM]2.0.CO;2)
- Layman CA, Araújo MS, Boucek R, Hammerschlag-Peyer CM, Harrison E, Jud ZR, Matich P et al (2012) Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biol Rev* 87:545–562. <https://doi.org/10.1111/j.1469-185x.2011.00208.x>
- Leal JS, González AL, Soares BE, Nova CC, Marino NAC, Farjalla VF (2023) Global and local drivers of the relative importance of allochthonous and autochthonous energy sources to freshwater food webs. *Ecography* 2023:e06612. <https://doi.org/10.1111/ecog.06612>
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD et al (2004) The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–613. <https://doi.org/10.1111/j.1461-0248.2004.00608.x>
- León FG, Franco-Trecu V, Costa-Pereira R (2024) Keystone niche individuals: some are more unequal than others. *Trends Ecol Evol* 40:14–17. <https://doi.org/10.1016/j.tree.2024.11.006>
- Levins R (1968) Evolution in changing environments: some theoretical explorations. Princeton University Press, Princeton. <https://doi.org/10.1515/9780691209418>
- Lind L, Eckstein RL, Relyea RA (2022) Direct and indirect effects of climate change on distribution and community composition of macrophytes in lentic systems. *Biol Rev* 97:1677–1690. <https://doi.org/10.1111/brv.12858>

- Loreau M (2004) Does functional redundancy exist? *Oikos* 104:606–611
- MacArthur RH (1970) Species packing and competitive equilibrium for many species. *Theor Popul Biol* 1:1–11. [https://doi.org/10.1016/0040-5809\(70\)90039-0](https://doi.org/10.1016/0040-5809(70)90039-0)
- Maitland BM, Rahel FJ (2021) Nonlethal fin sampling of North American freshwater fishes for food web studies using stable isotopes. *N Am J Fish Manag* 41:410–420. <https://doi.org/10.1002/nafm.10539>
- Maitland BM, Rahel FJ (2023) Aquatic food web expansion and trophic redundancy along the Rocky Mountain-Great Plains ecotone. *Ecology* 104:e4103. <https://doi.org/10.1002/ecy.4103>
- Maitland BM, del Rio CM, Rahel FJ (2021) Effect of temperature on ^{13}C and ^{15}N incorporation rates and discrimination factors in two North American fishes. *Can J Fish Aquat Sci* 78:1833–1840
- Maitland BM, Bootsma HA, Bronte CR, Bunnell DB, Feiner ZS, Fenske KH, Fetzer WW et al (2024) Testing food web theory in a large lake: the role of body size in habitat coupling in Lake Michigan. *Ecology* 105:e4413. <https://doi.org/10.1002/ecy.4413>
- Mann KH (1988) Production and use of detritus in various freshwater, estuarine, and coastal marine ecosystems. *Limnol Oceanogr* 33:910–930
- Marczak LB, Thompson RM, Richardson JS (2007) Meta-analysis: trophic level, habitat, productivity shape the food web effects of resource subsidies. *Ecology* 88:140–148. [https://doi.org/10.1890/0012-9658\(2007\)88\[140:MTL-HAP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[140:MTL-HAP]2.0.CO;2)
- Martinson HM, Schneider K, Gilbert J, Hines JE, Hambäck PA, Fagan WF (2008) Detritivory: stoichiometry of a neglected trophic level. *Ecol Res* 23:487–491. <https://doi.org/10.1007/s11284-008-0471-7>
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21:178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- Mihalitsis M, Bellwood DR (2017) A morphological and functional basis for maximum prey size in piscivorous fishes. *PLoS One* 12:e0184679
- Missaghi S, Hondzo M, Herb W (2017) Prediction of lake water temperature, dissolved oxygen, and fish habitat under changing climate. *Clim Change* 141:747–757. <https://doi.org/10.1007/s10584-017-1916-1>
- Moss BR (2013) Ecology of freshwaters: a view for the twenty-first century. Wiley-Blackwell, Hoboken
- Mourshed M (2016) Climatic parameters for building energy applications: a temporal-geospatial assessment of temperature indicators. *Renew Energy* 94:55–71. <https://doi.org/10.1016/j.renene.2016.03.021>
- Myers BJE, Dolloff CA, Webster JR, Nislow KH, Rypel AL (2021) Diversity–production relationships of fish communities in freshwater stream ecosystems. *Divers Distrib* 27:1807–1817. <https://doi.org/10.1111/ddi.13369>
- Nakazawa T (2014) Ontogenetic niche shifts matter in community ecology: a review and future perspectives. *Popul Ecol* 57:347–354. <https://doi.org/10.1007/s10144-014-0448-z>
- Nalley EM, Donahue MJ, Heenan A, Toonen RJ (2021) Quantifying the diet diversity of herbivorous coral reef fishes using systematic review and DNA metabarcoding. *Environ DNA* 4:191–205. <https://doi.org/10.1002/edn3.247>
- NASA [National Aeronautics and Space Administration] (2023) World of change: global temperatures. <https://earthobservatory.nasa.gov/world-of-change/global-temperatures>. Accessed 07 July 2025
- Navarro AB, Magioli M, Bogoni JA, Moreira MZ, Silveira LF, Alexandrino ER, Da Luz DTA, Pizo MA, Silva WR, De Oliveira VC, Donatelli RJ, Christianini AV, Piratelli AJ, Ferraz KMPMB (2021) Human-modified landscapes narrow the isotopic niche of neotropical birds. *Oecologia* 196:171–184. <https://doi.org/10.1007/s00442-021-04908-9>
- Newsome SD, Tinker MT, Monson DH, Oftedal OT, Ralls K, Staedler MM, Fogel ML et al (2009) Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology* 90:961–974. <https://doi.org/10.1890/07-1812.1>
- NMNH [National Museum of Natural History, Smithsonian Institution] (2025) Integrated Taxonomic Information System (ITIS). Checklist Dataset. <https://doi.org/10.5066/f7kh0kbbk>
- Oki T, Entekhabi D, Harrold TI (2004) The global water cycle. In: Sparks RSJ, Hawkesworth CJ (eds) Geophysical monograph. AGU, Washington, pp 225–237. <https://doi.org/10.1029/150gm18>
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GVN, Underwood EC, D'amico JA et al (2001) Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* 51:933. [https://doi.org/10.1641/0006-3568\(2001\)051](https://doi.org/10.1641/0006-3568(2001)051)
- Orme D, Freckleton R, Thomas G, Petzoldt T, Fritz S, Isaac N, Pearse W (2023) caper: comparative analyses of phylogenetics and evolution in R. R package. <https://CRAN.R-project.org/package=caper>
- Ou C, Winemiller KO (2016) Seasonal hydrology shifts production sources supporting fishes in rivers of the Lower Mekong Basin. *Can J Fish Aquat Sci* 73:1342–1362. <https://doi.org/10.1139/cjfas-2015-0214>
- Ouellet V, Fullerton AH, Kaylor M, Naman S, Bellmore R, Rosenfeld J, Rossi G et al (2024) Food for fish: challenges and opportunities for quantifying foodscapes in river networks. *Wires Water*. <https://doi.org/10.1002/wat2.1752>
- Pagel M (1999) Inferring the historical patterns of biological evolution. *Nature* 401:877–884
- Parker GA (1992) The evolution of sexual size dimorphism in fish. *J Fish Biol* 41:1–20. <https://doi.org/10.1111/j.1095-8649.1992.tb03864.x>
- Parnell AC, Phillips DL, Bearhop S, Semmens BX, Ward EJ, Moore JW, Jackson AL et al (2013) Bayesian stable isotope mixing models. *Environmetrics* 24:387–399. <https://doi.org/10.1002/env.2221>
- Parravicini V, Casey JM, Schiettekatte NMD, Brandl SJ, Pozas-Schacre C, Carlot J, Edgar GJ et al (2020) Delineating reef fish trophic guilds with global gut content data synthesis and phylogeny. *PLoS Biol* 18:e3000702. <https://doi.org/10.1371/journal.pbio.3000702>
- Paul VJ (2008) Global warming and cyanobacterial harmful algal blooms. In: Hudnell HK (ed) Cyanobacterial harmful algal blooms: state of the science and research needs.

- Advances in Experimental Medicine and Biology, vol 619. Springer, New York. https://doi.org/10.1007/978-0-387-75865-7_11
- Pauly D (1989) A simple index of metabolic level in fishes. *Fishbyte* 7:22
- Peel MC, Finlayson BL, McMahon TA (2007) Updated world map of the Köppen-Geiger climate classification. *Hydrol Earth Syst Sci* 11:1633–1644. <https://doi.org/10.5194/hess-11-1633-2007>
- Pellissier V, Barnagaud J, Kissling WD, Şekercioğlu Ç, Svenning J (2018) Niche packing and expansion account for species richness–productivity relationships in global bird assemblages. *Glob Ecol Biogeogr* 27:604–615. <https://doi.org/10.1111/geb.12723>
- Pereira LS, Keppeler FW, Agostinho AA, Winemiller KO (2017) Is there a relationship between fish cannibalism and latitude or species richness? *PLoS One* 12:e0169813. <https://doi.org/10.1371/journal.pone.0169813>
- Peterson CC, Keppeler FW, Saenz DE, Bower LM, Winemiller KO (2017) Seasonal variation in fish trophic networks in two clear-water streams in the Central Llanos region, Venezuela. *Neotrop Ichthyol* 15:e160125. <https://doi.org/10.1590/1982-0224-20160125>
- Pichler M, Hartig F (2023) Machine learning and deep learning—a review for ecologists. *Methods Ecol Evol* 14:994–1016. <https://doi.org/10.1111/2041-210x.14061>
- Pomeranz JPF, Finlay JC, Terui A (2023) Ecosystem size and complexity as extrinsic drivers of food chain length in branching ecosystems. *Ecosphere* 14:e4648. <https://doi.org/10.1002/ecs2.4648>
- Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718. [https://doi.org/10.1890/0012-9658\(2002\)083\[0703:USITET\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[0703:USITET]2.0.CO;2)
- Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179–189. <https://doi.org/10.1007/s00442-006-0630-x>
- Potapov AM, Brose U, Scheu S, Tiunov AV (2019) Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. *Am Nat* 194:823–839. <https://doi.org/10.1086/705811>
- Quévreur P, Loreau M (2022) Synchrony and stability in trophic metacommunities: when top predators navigate in a heterogeneous world. *Front Ecol Evol* 10:865398. <https://doi.org/10.3389/fevo.2022.865398>
- Quintana Y, Keppeler FW, Winemiller KO (2023) Does invasion by armored catfish shift trophic ecology of native fishes? Evidence from stable isotope analysis. *Ecology* 104:e4024. <https://doi.org/10.1002/ecy.4024>
- R Core Team (2024) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Resco V, Querejeta JJ, Ogle K, Voltas J, Sebastià M, Serrano-Ortiz P, Linares JC, Moreno-Gutiérrez C, Herrero A, Carreira JA, Torres-Cañabate P, Valladares F (2009) Stable isotope views on ecosystem function: challenging or challenged? *Biol Lett* 6:287–289. <https://doi.org/10.1098/rsbl.2009.0950>
- Revell LJ (2024) Phytools 2.0: an updated R ecosystem for phylogenetic comparative methods (and other things). *PeerJ* 12:e16505
- Richardson J, Sato T (2014) Resource subsidy flows across freshwater-terrestrial boundaries and influence on processes linking adjacent ecosystems. *Ecohydrol* 8:406–415. <https://doi.org/10.1002/eco.1488>
- Riede JO, Brose U, Ebenman B, Jacob U, Thompson R, Townsend CR, Jonsson T (2011) Stepping in Elton's footprints: a general scaling model for body masses and trophic levels across ecosystems. *Ecol Lett* 14:169–178. <https://doi.org/10.1111/j.1461-0248.2010.01568.x>
- Roach KA (2013) Environmental factors affecting incorporation of terrestrial material into large river food webs. *Freshw Sci* 32:283–298. <https://doi.org/10.1899/12-063.1>
- Rooney N, McCann KS, Moore JC (2008) A landscape theory for food web architecture. *Ecol Lett* 11:867–881. <https://doi.org/10.1111/j.1461-0248.2008.01193.x>
- Sage RF, Monson RK (eds) (1999) C4 plant biology. Academic Press, San Diego. <https://doi.org/10.1016/B978-0-12-614440-6.X5000-9>
- Sambily VC Jr (1990) Interrelationships between swimming speed, caudal fin aspect ratio and body length of fishes. *Fishbyte* 8:16–20
- Sánchez-Hernández J, Finstad AG, Arnekleiv JV, Kjørstad G, Amundsen P (2020) Beyond ecological opportunity: prey diversity rather than abundance shapes predator niche variation. *Freshw Biol* 66:44–61. <https://doi.org/10.1111/fwb.13606>
- Scharf FS, Juanes F, Rountree RA (2000) Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Mar Ecol Prog Ser* 208:229–248
- Schiettekatte NM, Barneche DR, Villéger S, Allgeier JE, Burkepile DE, Brandl SJ, Casey JM et al (2020) Nutrient limitation, bioenergetics, and stoichiometry: a new model to predict elemental fluxes mediated by fishes. *Funct Ecol* 34:1–13. <https://doi.org/10.1111/1365-2435.13618>
- Schirmer A, Herde A, Eccard JA, Dammhahn M (2019) Individuals in space: personality-dependent space use, movement and microhabitat use facilitate individual spatial niche specialization. *Oecologia* 189:647–660. <https://doi.org/10.1007/s00442-019-04365-5>
- Sibly RM, Brown JH, Kodric-Brown A (2012) Metabolic ecology: a scaling approach. Wiley Blackwell, Hoboken
- Soria-Barreto M, Montaña CG, Winemiller KO, Castillo MM, Rodiles-Hernández R (2020) Seasonal variation in basal resources supporting fish biomass in longitudinal zones of the Usumacinta River Basin, southern Mexico. *Mar Freshw Res* 72:353. <https://doi.org/10.1071/mf19341>
- Steffan SA, Dharampal PS (2018) Undead food-webs: integrating microbes into the food-chain. *Food Webs* 18:e00111. <https://doi.org/10.1016/j.fooweb.2018.e00111>
- Still CJ, Berry JA, Collatz GJ, DeFries RS (2003) Global distribution of C3 and C4 vegetation: carbon cycle implications. *Glob Biogeochem Cycles* 17:1006. <https://doi.org/10.1029/2001GB001807>
- Stock BC, Jackson AL, Ward EJ, Parnell AC, Phillips DL, Semmens BX (2018) Analyzing mixing systems using a

- new generation of Bayesian tracer mixing models. *PeerJ* 6:e5096. <https://doi.org/10.7717/peerj.5096>
- Thomaz SM, Da Cunha ER (2010) The role of macrophytes in habitat structuring in aquatic ecosystems: methods of measurement, causes and consequences on animal assemblages' composition and biodiversity. *Acta Limnol Bras* 22:218–236. <https://doi.org/10.4322/actalb.02202011>
- Thompson RM, Townsend CR (2005) Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos* 108:137–148
- Thorson J (2023) FishLife: predict life history parameters for any fish. R package. <https://github.com/james-thorson/FishLife>
- Trudeau V, Rasmussen JB (2003) The effect of water velocity on stable carbon and nitrogen isotope signatures of periphyton. *Limnol Oceanogr* 48:2194–2199. <https://doi.org/10.4319/lo.2003.48.6.2194>
- Turner T, Bart H Jr, Besser A, Bowes R, DeArmon E, Dillman C, Driscoll K et al (2023) Long-term ecological research in freshwaters enabled by regional biodiversity collections, stable isotope analysis, and environmental informatics. *Bioscience* 73:479–493. <https://doi.org/10.1093/biosci/biad039>
- Urbano VA, Alves GHZ, Pompeu PS, Contieri BB, Benedito E (2025) Fish acting as sinks of methane-derived carbon in Neotropical floodplains. *Sci Total Environ* 959:178231. <https://doi.org/10.1016/j.scitotenv.2024.178231>
- van der Sleen P, Rams M (2023) Flood pulses and fish species coexistence in tropical rivers – a theoretical food web model. *Environ Biol Fishes* 106:1785–1796. <https://doi.org/10.1007/s10641-023-01458-2>
- Van Valen L (1965) Morphological variation and width of ecological niche. *Am Nat* 99:377–390
- Vander Zanden MJ, Cabana G, Rasmussen JB (1997) Comparing trophic position of freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}\text{N}$) and literature dietary data. *Can J Fish Aquat Sci* 54:1142–1158. <https://doi.org/10.1139/f97-016>
- Vander Zanden MJ, Clayton MK, Moody EK, Solomon CT, Weidel BC (2015) Stable isotope turnover and half-life in animal tissues: a literature synthesis. *PLoS One* 10:e0116182. <https://doi.org/10.1371/journal.pone.0116182>
- Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The river continuum concept. *Can J Fish Aquat Sci* 37:130–137. <https://doi.org/10.1139/f80-017>
- Vázquez D, Stevens R (2004) The latitudinal gradient in niche breadth: concepts and evidence. *Am Nat* 164:E1–E19. <https://doi.org/10.1086/421445>
- Vellend M (2016) The theory of ecological communities (MPB-57). Princeton University Press, Princeton. <https://doi.org/10.1515/9781400883790>
- Vianna-Gatts F, Montanini G, Azevedo AF, Lailson-Brito J, Bisi TL (2023) Feeding ecology based on stable carbon and nitrogen isotopes: a comparative study on different Guiana dolphin tissues. *Mar Environ Res* 192:106234. <https://doi.org/10.1016/j.marenvres.2023.106234>
- Villamarín F, Jardine TD, Bunn SE, Marioni B, Magnusson WE (2018) Body size is more important than diet in determining stable-isotope estimates of trophic position in crocodilians. *Sci Rep* 8:2020. <https://doi.org/10.1038/s41598-018-19918-6>
- Votier SC, Bearhop S, MacCormick A, Furness RW, Ratcliffe N (2003) Assessing the diet of great skuas, *Catharacta skua*, using five different techniques. *Polar Biol* 26:20–26. <https://doi.org/10.1007/s00300-002-0446-z>
- Walker BH (1992) Biodiversity and ecological redundancy. *Conserv Biol* 6:18–23
- Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. *Annu Rev Ecol Syst* 15:393–425
- Werner EE, Hall DJ (1974) Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042–1052
- Williams DD (2006) The biology of temporary waters. Oxford University Press, Oxford
- Winemiller KO, Andrade MC, Arantes CC, Bokhutlo T, Bower LM, Cunha ER, Keppeler FW et al (2022) Can spatial food web subsidies associated with river hydrology and lateral connectivity be detected using stable isotopes? *Food Webs* 34:e00264. <https://doi.org/10.1016/j.fooweb.2022.e00264>
- Wolfe K, Desbiens AA, Patel F, Kwong S, Fisher E, Mumby PJ, Uthicke S (2025) eDNA confirms lower trophic interactions help to modulate population outbreaks of the notorious crown-of-thorns sea star. *Proc Natl Acad Sci USA* 122:e2424560122
- Woodland RJ, Warry FY, Evrard V, Clarke RH, Reich P, Cook PLM (2015) Niche-dependent trophic position distributions among primary, secondary and tertiary consumers. *Oikos* 125:556–565. <https://doi.org/10.1111/oik.02486>
- Woodward G, Ebenman B, Emmerson M, Montoya J, Olesen J, Valido A, Warren P (2005) Body size in ecological networks. *Trends Ecol Evol* 20:402–409. <https://doi.org/10.1016/j.tree.2005.04.005>
- Yeakel JD, Bhat U, Smith EaE, Newsome SD (2016) Exploring the isotopic niche: isotopic variance, physiological incorporation, and the temporal dynamics of foraging. *Front Ecol Evol* 4:1. <https://doi.org/10.3389/fevo.2016.00001>
- Zhang Y, Li J, Li Y, Tarkan AS, Liu C, Britton JR (2024) Trophic niche diversity and redundancy across trophic positions in a subtropical river fish assemblage. *Hydrobiologia* 851:2417–2428. <https://doi.org/10.1007/s10750-023-05467-1>

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