

RESEARCH ARTICLE

Maximum entropy models reveal spatial variation of metabolic scaling in stream fish communities

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Handling Editor: Henrique Cabral**Abstract**

1. Metabolic scaling provides valuable information about the physiological and ecological functions of organisms, although few studies have quantified the metabolic scaling exponent (b) of communities under natural conditions. Maximum entropy theory of ecology (METE) is a constraint-based unified theory with the potential to empirically assess the spatial variation of the metabolic scaling.
2. Our main goal is to develop a novel method of estimating b within a community by integrating metabolic scaling and METE. We also aim to study the relationships between the estimated b and environmental variables across communities.
3. We developed a new METE framework to estimate b in 118 stream fish communities in the north-eastern Iberian Peninsula. We first extended the original maximum entropy model by parameterizing b in the model prediction of the community-level individual size distributions and compared our results with empirical and theoretical predictions. We then tested the effects of abiotic conditions, species composition and human disturbance on the spatial variation of community-level b .
4. We found that community-level b of the best maximum entropy models showed great spatial variability, ranging from 0.25 to 2.38. The mean exponent ($b = 0.93$) resembled the community-aggregated mean values from three previous metabolic scaling meta-analyses, all of which were greater than the theoretical predictions of 0.67 and 0.75. Furthermore, the generalized additive model showed that b reached maximum at the intermediate mean annual precipitation level and declined significantly as human disturbance intensified.
5. The parameterized METE is proposed here as a novel framework for estimating the metabolic pace of life of stream fish communities. The large spatial variation of b may reflect the combined effects of environmental constraints and species interactions, which likely have important feedback on the structure and function of natural communities. Our newly developed framework can also be applied to study the impact of global environmental pressures on metabolic scaling and energy use in other ecosystems.

Meng Xu and Ignasi Arranz contributed equally to this manuscript.

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KEYWORDS

body size, constraint-based model, information theory, maximum likelihood method, metabolism, model parameterization, Shannon entropy

1 | INTRODUCTION

One of the most fundamental patterns in ecology is the power-function relationship between metabolic rate and body size: metabolic rate = $a(\text{body size})^b$, known as the metabolic scaling relationship, where a is the scaling coefficient and b is the scaling exponent. Understanding this relationship and its mechanisms would help reveal energy uptake and nutrient flow through trophic interactions at various levels of biological organization (Brown et al., 2004; Reuman et al., 2009). Most research has focused on the exponent b , which dictates the pace at which organisms allocate resources to perform life-essential tasks, such as growth and reproduction (West & Brown, 2005). Although debates have been about whether b is equal to 0.67 or 0.75 (Dodds et al., 2001; Heusner, 1991; Kleiber, 1932; Savage et al., 2004), numerous empirical studies have shown evidence against the universality of b and revealed a large variation of b across taxa, lifestyles and environmental conditions (Bokma, 2004; Clarke & Johnston, 1999; Glazier, 2009; Isaac & Carbone, 2010; Killen et al., 2010; Post & Lee, 1996; White & Seymour, 2005).

Previous theoretical models have offered mechanistic explanations for b by optimizing various fitness functions of organisms (e.g. resource transport cost and reproductivity) under physiological and environmental constraints (Glazier, 2005; Maino et al., 2014). Perhaps the most well-known models are surface area models (Sarrus & Rameaux, 1839), which predict $b=0.67$; and resource transport models (including the West-Brown-Enquist model from West et al., 1997), which predict $b=0.75$. On the other hand, the metabolic-level boundaries hypothesis (Glazier, 2005) attempts to predict the variation in b from 0.67 to 1 using two physiological constraints: (1) the surface area controlling the flux processes of resources and (2) the dependence of body size on metabolic activity. However, despite extensive research of theoretical models to explain b , it remains challenging to understand the variation of b in empirical data.

One of the main reasons for the variation of b is the effect of multiple intrinsic and extrinsic factors (Glazier, 2005). For example, Glazier (2009) showed that in several ectothermic species, individuals had greater b during activity than during rest. Killen et al. (2010) showed that b decreased as temperature increased within teleost fish species and suggested that ambient water temperature was a key driver in the metabolic activity of ectothermic species. Gjoni et al. (2020) showed that the effects of temperature on b in amphipod crustaceans can be modulated by the presence of predators. In addition to biotic and abiotic factors that can influence b , the improper use of statistical procedures can lead to miscalculation and misinterpretation of b . It has been argued that the variation of intraspecific b can be a statistical consequence of the small sample size and limited body size range (Brown et al., 1997). Phylogenetic

effects that are used to correct regression models of interspecific b may produce biased estimates (Westoby et al., 1995). Moreover, most empirical studies and theoretical models use specific methods and functions to study metabolic scaling. For example, intraspecific b is often estimated using metabolic rate proxies that are measured for a specific taxon under specific experimental setup and conditions (Chabot et al., 2016; Mori et al., 2010). Most theoretical models of metabolic scaling rely on an internal fitness function that is often system specific. Thus, a general model that is devoid of these limitations is needed to reconcile the discrepancy between the empirical values and the theoretical predictions of b .

We develop new models based on the maximum entropy theory of ecology (henceforth, METE) to predict the metabolic scaling exponent b within local communities. METE uses Shannon's entropy of information science (Jaynes, 1957a, 1957b; Shannon, 1948) and produces explicit predictions of macroecological patterns, such as the species abundance distribution (Harte et al., 2008), the species-area relationship (Harte & Kitzes, 2015; McGlinn et al., 2013), the individual metabolic rate distribution (Newman et al., 2014) and the individual size distribution (henceforth ISD, see Xiao et al., 2015). As a constraint-based theory, the METE relies on two macro-state constraints: (1) the mean number of individuals per species (N/S); and (2) the mean metabolic rate per species within a community (E/S), where N (total number of individuals), S (number of species) and E (total metabolic rate of individuals) are the macro-state variables (Harte, 2011). In a previous test of METE (Xiao et al., 2015), b was assumed as a universal constant borrowed from external theories (e.g. $b=0.75$ from the West-Brown-Enquist model). This assumption makes it difficult to unravel the effects of the intrinsic framework of METE and the external theories on the performance of the model. Our new models differ from the original METE by treating b as a community-level parameter. Such parameterization allows us to estimate the empirically most plausible b from the fitting of the predicted ISD to the observed ISD within a community.

The purpose of this work is to apply the METE models to an individual fish body size dataset collected from 118 stream fish communities in the north-eastern Iberian Peninsula. Specifically, our first aim is to use the METE models to estimate a community-level b by statistically fitting the predicted ISD to the observed ISD in each stream fish community. To assess the reliability of our method, we compare the estimated b of the best-fitting METE model with the previously published b . Our second aim is to analyse the effects of biological and environmental factors on the spatial variation of b across stream fish communities. We use generalized additive models to examine the relationship between the best estimate of b and abiotic (i.e. precipitation, nutrients, temperature, human disturbance) or biotic (i.e. species composition) variables across natural communities.

2 | MATERIALS AND METHODS

2.1 | Individual fish size and stream characteristics

Individual fish were sampled from 118 stream locations, mainly in the Ebro basin of the north-eastern Iberian Peninsula, between 2003 and 2006. The sampling survey was carried out using the one-pass electrofishing method following a standardized protocol (European Committee for Standardization, 2005). The one-pass electrofishing method is a proper sampling survey to effectively represent the community structure and species diversity within local surveys (Edwards et al., 2003; Simonson & Lyons, 1995), and provides a flexible way of sampling multiple communities at large spatial extent (Foley et al., 2015). Furthermore, Sutton and Jones (2020) showed that one-pass electrofishing adequately captures the characteristics of the size structure of stream fish communities. The fish samples were individually identified for each species and measured for fork length in mm and body mass in g before release. In total, 12,288 individual fish of 24 species were collected from the 118 stream locations. Further details on the data structure and sampling method are available in Arranz et al. (2022). We treated fish from each stream location as a community and used the corresponding individual fish body mass data to analyse the community-level ISD and the metabolic scaling relationship.

For each stream location, we also documented environmental information on the contents of water nutrients, climatic conditions and human-induced activities (Arranz et al., 2022). Specifically, each stream location was characterized by its spatial geographical coordinates (longitude and latitude; World Geodetic System 1984), mean annual air temperature ($^{\circ}\text{C}$), mean annual precipitation (mm), mean annual concentration of total nitrogen (mgL^{-1} , hereafter N concentration), mean annual concentration of total phosphorus (mgL^{-1} , hereafter P concentration), elevation (m) and IMPRESS score (pressures and impacts; Arranz et al., 2022). We transformed the air temperature to the water temperature following the formula by Punzet et al. (2012) for temperate habitats. This transformation does not qualitatively influence our results since the values between air and water temperature were almost identical (Pearson's correlation coefficient = 0.99; p -value < 0.001). The IMPRESS score is an overall measure for human-induced activities in the stream ecosystem that combines multiple pressures, including water contaminants, hydro-morphological alterations and land-use modifications (European Commission, 2003). We also included the Global Human Footprint Index (GHFI) since it covers other human-induced pressures, including urbanization, population density and access, and presence of infrastructures (Venter et al., 2016). GHFI was taken from a 1km^2 grid cell raster layer, with larger values indicating greater human influence (ranging from 0 to 50; Venter et al., 2016). We performed a principal component analysis (PCA) to combine IMPRESS and GHFI, and used the PCA axis 1 (61.4%) as a synthetic variable that expresses human-induced pressure: larger positive values would indicate more human-induced pressure on the local fish community.

We also performed a principal coordinate analysis (PCoA) from a stream-by-species abundances community matrix. We excluded the influence of rare species (i.e. occurring <25% in all streams) from PCoA. We transformed the matrix with a Hellinger transformation to reduce the effects of highly abundant species at any given stream location. We used the first eigenvalue (PCoA axis 1) to summarize the variation in species composition among streams: PCoA axis 1 (37% variance explained) ranged from communities mainly composed of upstream parts such as trout (*Salmo trout*) to downstream communities composed of *Luciobarbus gaellsii* and *Parachondostroma mieggi* (Figure S1). A summary of these community-level variables is reported in Figure S2. This study does not require ethical approval.

2.2 | Original METE and parameterized METE models

In this section, we give a brief overview of the original METE model and introduce two parameterized METE models. Readers can refer to Harte (2011) and Harte and Newman (2014) for more details on the original METE model. We address two fundamental issues in the testing and prediction of the original METE and explain how parameterized METE models overcome these issues.

The original METE maximizes the Shannon's entropy of the joint distribution of the number of individuals of a species and the metabolic rate of an individual from a species with that many individuals, subject to two mean constraints: the mean number of individuals per species (N/S) and the mean metabolic rate per species (E/S). Entropy is maximized using the method of Lagrange multipliers, with each Lagrange multiplier (here as λ_1 and λ_2 , Figure 1) associated with one constraint. After the Lagrange multipliers are solved from the constraint equations, the predicted joint distribution is used to derive other macroecological patterns, including the community-level ISD. In the original METE, the metabolic scaling relationship is rescaled so that the minimal metabolic rate and minimal body mass within a community are equal to one (Harte, 2011). This rescaling removes the scaling coefficient from the metabolic scaling relationship without changing the exponent (b , see Table 1). In the rest of the paper, we refer to individual body mass and metabolic rate as their rescaled values.

Two issues are present with respect to the testing and prediction of the original METE. Both issues evolve around the total metabolic rate energy E and are resolved if a direct measurement of E can be obtained. However, in practice, E is calculated by summing individual body mass M raised to a certain metabolic scaling exponent b over all individuals (Table 1). First, the original METE does not estimate b from its own formulation but borrows a value of b from external theories ([1] in Figure 1a) during the testing of its predictions. For example, in a previous test of the original METE's prediction of ISD for forest trees (Xiao et al., 2015), it was assumed that b was a universal constant from the metabolic scaling theory ($b=2$ for branch diameter; see West et al., 1999). This treatment does not reveal whether the lack of fit is an intrinsic issue of the original METE formulation or

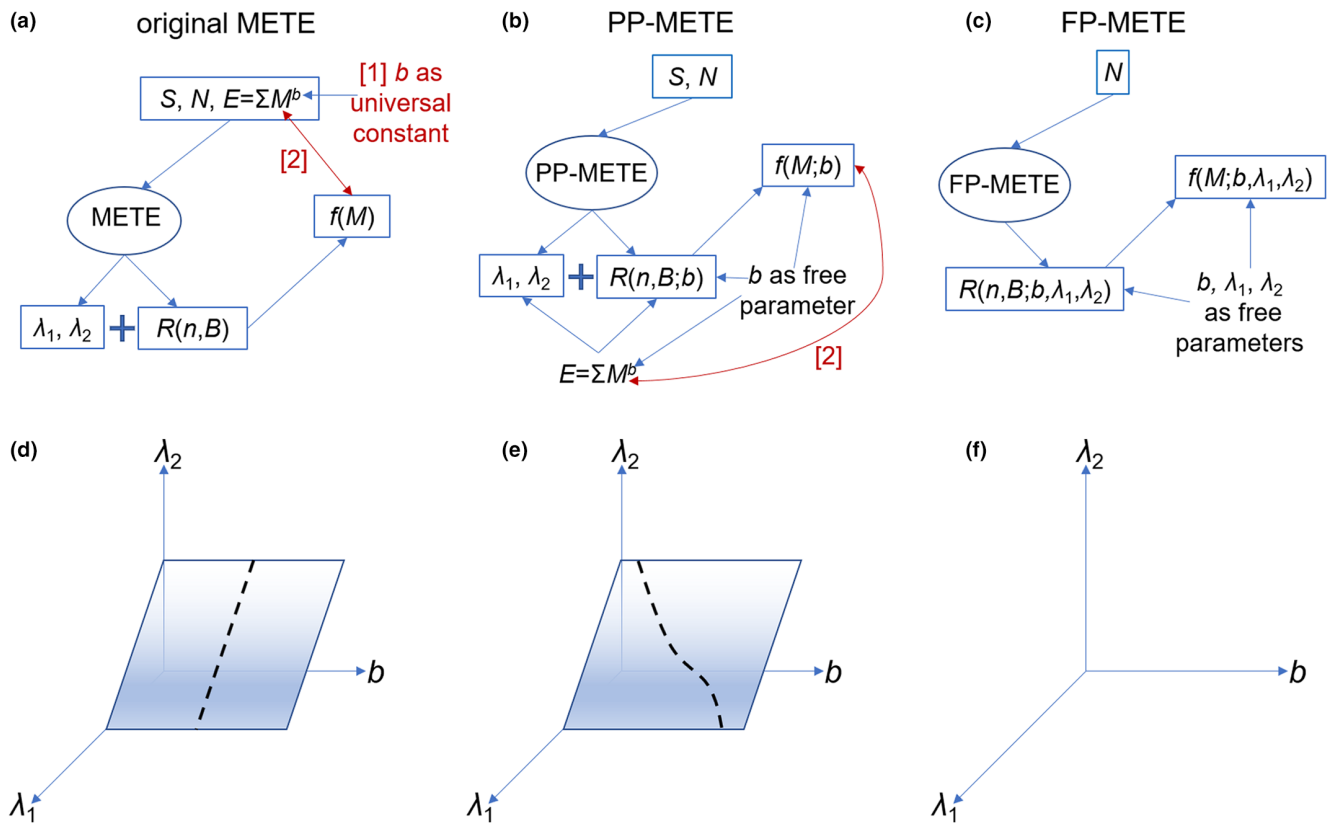


FIGURE 1 Diagram showing the derivation of the predicted individual size distribution (ISD) f from the (a) original maximum entropy theory of ecology (METE), (b) partially parameterized (PP)-METE and (c) fully parameterized (FP)-METE models, and the solution space of each model: (d) for original METE, (e) for PP-METE and (f) for FP-METE. The red text and arrows show the two issues of the original METE: [1] assumption of a universal constant b from external theories and [2] circularity between the input E and the predicted ISD f . The PP-METE model resolves [1] but keeps [2]. The FP-METE model resolves [1] and [2]. The dashed black lines in (d) and (e) represent the paths on which the solutions of b, λ_1 and λ_2 are found for a given community. For the original METE model (d), b is a universal constant and the sum of λ_1 and λ_2 is solved from the constraint equation on N/S as a constant. For the PP-METE model (e), b is a community-specific parameter. The sum of λ_1 and λ_2 is still a constant and solved from the constraint equation on N/S . In addition, λ_2 (solved from the constraint equations as $S/(\Sigma M^b - N)$) is a decreasing function of b . For the FP-METE model (f), b, λ_1 and λ_2 are all free parameters and independent of each other, which means that their values can be any point in the entire three-dimensional space.

is due to the inconsistency of b between external theories and data. Second, the original METE's prediction of ISD is based on a circular argument. This is because E , as a macro-state input variable of the original METE, must first be calculated from individual body mass data, and then the prediction of ISD can be derived ([2] in Figure 1a). Both issues have hindered the testing and application of the original METE in metabolic ecology.

To address the above issues, we develop two parameterized METE models by modifying the parameter estimation procedure of the original METE. Our first parameterized METE model treats b as a community-level free parameter throughout the entire modelling process (Figure 1b). The total metabolic rate E still depends on individual body size data, as in the original METE model (Figure 1a). However, in the new model, E becomes a function of b and remains unknown until b is estimated. The Lagrange multipliers (λ_1 and λ_2) still obey the constraint equations, but they also become functions of b . Consequently, the joint distribution and the predicted ISD contain b as a free parameter. Since this model parameterizes b but preserves the dependence of λ_1 and λ_2 on the constraint equations, we call

it the partially parameterized-METE model (henceforth PP-METE; Figure 1b). Compared to the original METE, which treats b (exponent of the metabolic rate-body mass scaling relationship) as a universal constant regardless of ecosystems, testing of the PP-METE treats b as a parameter that is specific for a given community, thus resolving the first issue of the original METE.

Our second parameterized METE model treats b, λ_1 and λ_2 as free parameters (Figure 1c). Compared to the PP-METE model, λ_1 and λ_2 no longer depend on the constraint equations based on the state variables (N, S and E). In this model, S and E are no longer macro-state inputs, because of the disentanglement between the Lagrange multipliers and the constraints. Consequently, there is no need to calculate E from individual body mass data. The joint distribution and the predicted ISD contain b, λ_1 and λ_2 as independent free parameters. We call this model the fully parameterized-METE model (henceforth FP-METE; Figure 1c). FP-METE removes the assumption of b as a universal constant from the testing and the circularity from the prediction of ISD, resolving both issues of the original METE. We emphasize that the original METE, PP-METE and

TABLE 1 Notations used in the original maximum entropy theory of ecology (METE) and parameterized METE models. In this table and the text hereafter, M and B represent the rescaled body mass and rescaled metabolic rate, respectively, defined by the actual body mass (or actual metabolic rate) divided by the minimal body mass (or minimal metabolic rate) within the studied community. Therefore, M and B are unitless variables.

Notation	Definition
M	Body mass of individual fish (rescaled)
B	Metabolic rate of individual fish (rescaled)
b	Metabolic scaling exponent
S	Number of species
N	Number of individuals
E	Total metabolic rate energy
λ_1	First Lagrange multiplier
λ_2	Second Lagrange multiplier
R	Joint distribution of species abundance and individual metabolic rate
f	Predicted individual size distribution

FP-METE use an identical formula of the predicted ISD (equation 3 in Xu, 2020), but differ in their treatments and estimates of b , λ_1 and λ_2 . The mathematical derivations of the METE models can be found in Harte (2011) and Brummer and Newman (2019), and in the supporting information of Xiao et al. (2015) and Xu (2020).

2.3 | Model evaluation and estimation of b

To test the original METE model (Figure 1a), we assumed $b=0.75$ from the metabolic scaling theory (West et al., 1997) and calculated the total metabolic rate E within each community. We then derived the parameter-free prediction of ISD. To test the two parameterized METE models (Figure 1b,c), we fitted their respective predicted ISD to the observed ISD within each community using the maximum likelihood method. In these cases, b in the PP-METE model and b , λ_1 and λ_2 in the FP-METE model were maximum likelihood estimates. To compare the performance of the models, we calculated the Akaike information criterion corrected for sample size (AICc) for each model within each community, where the 'best' METE model had the lowest AICc (Burnham & Anderson, 2002). The validity of the original METE and PP-METE models relied on two approximate conditions relating λ_1 , λ_2 and E (see Supporting Information). Violation of these two conditions would result in nonsensical AICc and estimates of λ_1 , λ_2 and b . Therefore, if either of the two conditions was not satisfied, we eliminated the corresponding model (original METE or PP-METE) from the model comparison. In each community, the best estimate of the community-level b was chosen from a valid model with the lowest AICc: $b=0.75$ if the original METE model had the lowest AICc

and b was the corresponding maximum likelihood estimate if the PP-METE model or the FP-METE model had the lowest AICc. The b estimated from the PP-METE and FP-METE models showed qualitatively similar distributions (Figure S8). Further comparisons of the three METE models about their Lagrange multipliers and constraints are shown in Figure S9.

We compared the mean of our estimated b with a community-aggregated b from each of the three meta-analyses. Each meta-analysis compiled intraspecific b from regression models fitted to individual metabolic rate and body size data, at various temperatures, ontogenetic stages and trials (67 bs from Glazier, 2005; 89 bs from Killen et al., 2010; and 55 bs from Jerde et al., 2019). Species were included in the comparison only if they were present in our Iberian fish data. In each meta-analysis, the community-aggregated b was a weighted average of intraspecific b . In Killen et al. (2010), each b corresponded to one single species, and the logarithmic body mass ratio of a species was used as weight. In Glazier (2005) and Jerde et al. (2019), multiple bs were estimated for certain species at different ontogenetic stages, temperatures or trials, and the corresponding number of sampled fish was used as weight. This community-aggregated b reflected the species composition within a community and allowed comparison of b at the same level.

In addition, we evaluated the performance of the three METE models and the estimated b in three ways. First, we fitted four probability distribution models (exponential, power-law, Weibull and quasi-Weibull) to the observed ISD in each fish community and compared the AICc between the distribution models and the METE models. These distribution models have been commonly used to describe community-level ISD in ecology (Enquist & Niklas, 2001; Muller-Landau et al., 2006; Pomeranz et al., 2022; White et al., 2007). Second, we evaluated the goodness of fit of the METE models using a pseudo coefficient of determination from Xiao et al. (2015; see equation 7 therein). A higher coefficient of determination would mean that a model's prediction resembles more closely to the observation. Third, we derived the interval estimate of b using bootstrap samples of fish data. In each community, we created 1000 independent bootstrap samples of individual fish mass and refitted the seven ISD models (three METE models and four distribution models) for each bootstrap sample. We used the above model selection procedures to find the best estimate of b . For each community, the lower and upper bounds of the 95% confidence interval of b were, respectively, the 2.5th and 97.5th percentiles of b estimated from all available bootstrap samples.

2.4 | Statistical analyses of the variation in b

We analysed the variation of b using the generalized additive model (GAM) with the restricted maximum likelihood optimization method. These models tested the effects of environmental drivers on the estimated metabolic scaling exponent b in fish communities. GAMs differ from linear regression methods because they do not require the assumption of a linear relationship between the response variable

and the predictors (Wood, 2006; Wood & Augustin, 2002). Each GAM used the best estimate of b (among the three METE models) as the response and the biotic (species composition PCoA axis 1) and abiotic (water temperature, precipitation, N concentration, P concentration, PCA axis 1 of human-induced effects) factors as predictors, with three basis functions in each predictor smoother. Since elevation decreased strongly with water temperature (Pearson's correlation = -0.932 ; p -value < 0.001 ; Figure S2), we did not use elevation as a predictor smoother to reduce multicollinearity.

We compared six models with different smoother and error structures and added an extra penalty to each smoother as the smoothing parameter approached zero. Three basis functions for each predictor were adequate because the resulting residuals were randomly distributed. For each predictor, the concurvity (similar to collinearity in a regression model) was low (< 0.8 ; Wood, 2006). We selected the model with the lowest AICc as the best model, which had Gamma error and residuals that aligned with the normality and homoscedasticity assumptions (Figure S3). We also explored the interaction effects for the most important drivers that govern the variation of the community-level b . Finally, we accounted for the spatial correlation of b by including a two-dimensional smoother of the spatial coordinates of the stream communities.

All statistical analyses were performed in R (R Core Team, 2022). GAMs were fitted in the *mgcv* package in R (Wood, 2006, 2011; Wood & Augustin, 2002).

3 | RESULTS

Among the three METE models, the FP-METE model had the lowest AICc in 90 communities, followed by the PP-METE model (23 communities) and the original METE model (5 communities; Table S1). Community-level b estimated from the best METE model ranged from 0.25 to 2.38, with a mean of 0.93 (Figure 2a,b). We found that the average of our community-level b ($= 0.93$) was close to the community-aggregated b in each meta-analysis (Figure 3), while all were greater than 0.67 or 0.75.

A more stringent model selection using AICc (three METE models and four distribution models) showed similar statistics of b (Table S1; Figures S6 and S7). Among the three METE models, FP-METE had an average R^2 of 0.94 and the highest R^2 in 112 communities (Table S2; Figure 4). The average R^2 was 0.90 for PP-METE and 0.57 for the original METE. PP-METE and the original METE had the highest R^2 in three communities separately. The 95% confidence interval of b within a community was less than 0.67 (or 0.75) in 21 (or 25) communities, contained 0.67 (or 0.75) in 58 (or 62) communities, and was greater than 0.67 (or 0.75) in 39 (or 31) communities (Table S1).

The best GAM showed strong effects of precipitation (p -value = 0.0017) and human-induced pressure (p -value = 0.0026) on b (Table S3; Figure 5c,f). Specifically, the community-level b reached its maximum when the precipitation was around 750mm, and became smaller when the precipitation was lower or higher than the intermediate value. Community-level b decreased significantly as

the level of human-induced pressure increased. In contrast, the temperature of the stream water had a positive but weak effect (p -value = 0.1486; Figure 5b). The interaction model showed significant interaction effects between stream water temperature and precipitation (p -value = 0.0037), and between stream water temperature and human-induced pressures (p -value = 0.0066; Figure S4). However, the interaction model had a higher AIC (117.764) than the best model with only the single effects (AIC = 115.716), suggesting that the single effects were more important in determining the variation in b than including the interaction effects (Table S3). The PCoA axis 1 of species composition, N concentration and P concentration did not show any trend in their effects on b (Figure 5a,d,e). Including spatial coordinates in the best GAM showed that b was the smallest in the northwest part of the sampling region and was greater towards the southeastern part of the region (Figure S5).

4 | DISCUSSION

4.1 | Empirical comparison of b

The mean of our estimated community-level b (0.93) was greater than theoretically predicted b (0.67 or 0.75; Figures 2 and 3). Comparison with previous work gives us confidence in the empirical validity of our estimated b . Specifically, Robinson et al. (1983) used published data to show $b = 0.87$ in foraging fish, which was significantly greater than 0.75. Clarke and Johnston (1999) studied 69 species of teleost fish and obtained a mean b of 0.79, which was significantly greater than 0.75. Their intraspecific estimate of b ranged from 0.4 to 1.2 (see Figure 1b in Clarke & Johnston, 1999). Norin and Gamperl (2018) found that b using various metabolic rates was greater than 0.75 (from 0.82 to 0.96) when fish were grouped within or between trials. In addition, our METE models yielded greater variation of b compared to Glazier (2005) and Killen et al. (2010), which found b mostly between 0.5 and 1 (Figure 3). In our stream fish data, there was no substantial difference in the number of individuals or species between communities with different b . This implies that abundance and species richness alone cannot explain the variation of b between communities.

The large variation of b from our METE models may be attributed to the level of biological organization at which the metabolic scaling relationship is studied. In fact, most previous studies focused on b within or across species, while our best METE models estimated b at the community level regardless of species. In Figure 3, we calculated the community-aggregated b following the 'community-weighted mean' approach that is often used to study trait-environment relationships in ecology (Miller et al., 2019). These community-aggregated b s are summary statistics of individual species and do not consider species interactions. Our community-level b naturally reflects species interactions because it uses an entire community as a study unit. We speculate that species interactions, such as competition and mutualism, can diminish or enhance the metabolic efficiency of the community as

FIGURE 2 Frequency distribution (a) and spatial distribution (b) of the metabolic scaling exponent b estimated from the maximum entropy theory of ecology (METE) models (original METE, partially parameterized-METE and fully parameterized-METE) with the lowest AICc, for each of the 118 fish communities. In (a), the solid line shows the mean ($=0.93$) of the estimated b . In (b), the community-level b of each stream location is mapped in the study region. AICc, Akaike information criterion corrected for sample size.

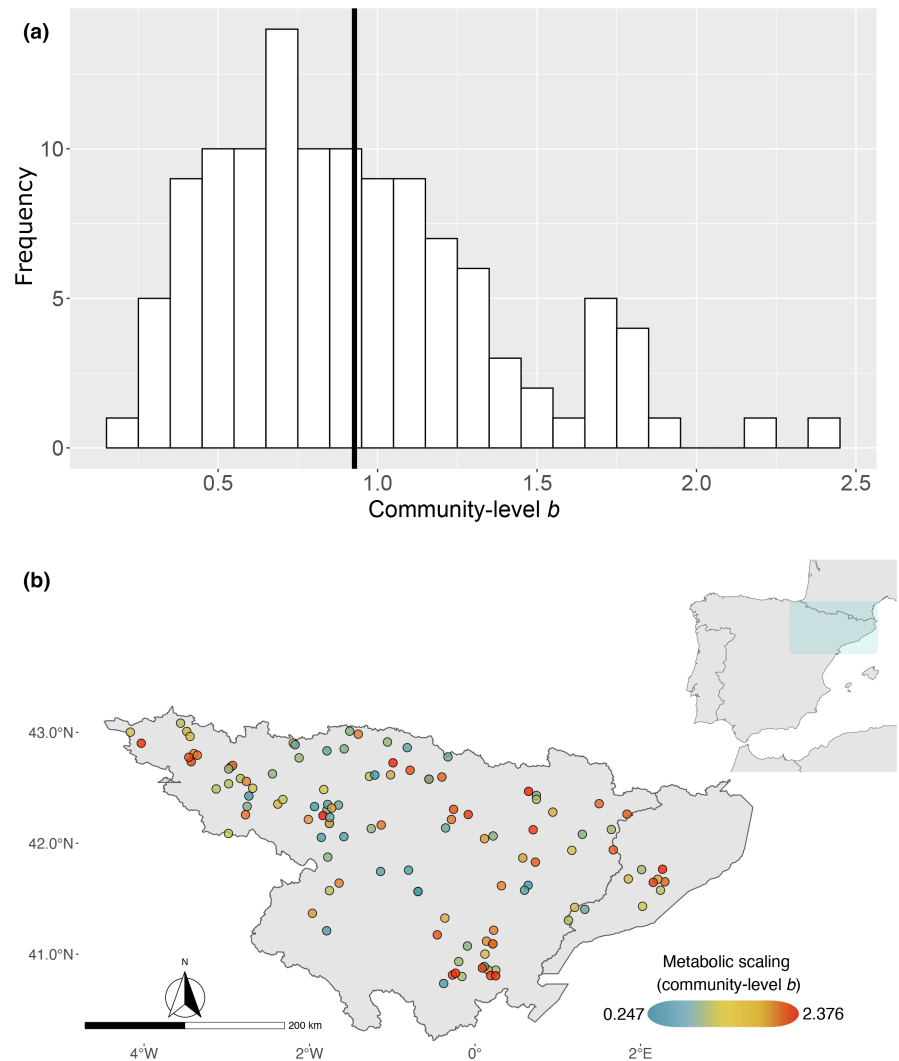
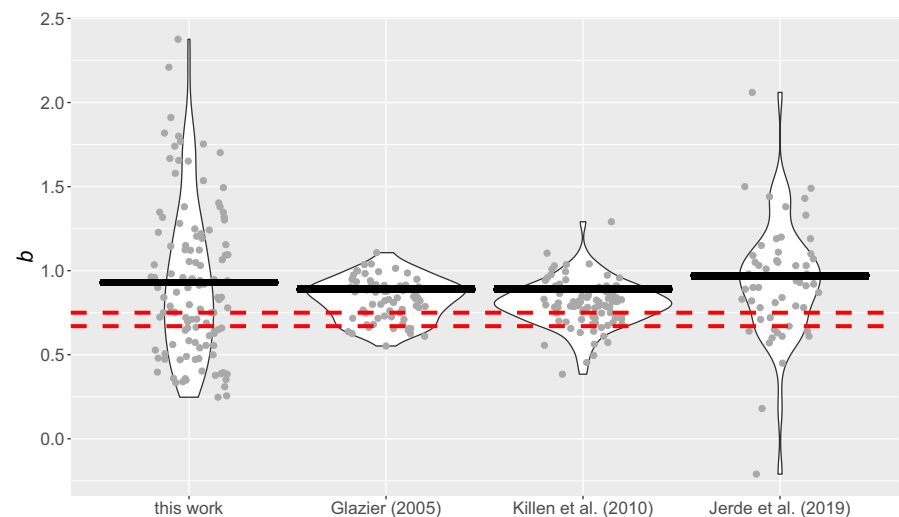


FIGURE 3 Comparison of our community-level b and the community-aggregated b of three meta-analyses: Glazier (2005), Killen et al. (2010) and Jerde et al. (2019). The grey dots show the estimated b from the current and previous work. Solid black lines represent the mean b in the current work (0.93) and the community-aggregated b in each meta-analysis (0.89 for Glazier, 2005; Killen et al., 2010; 0.97 for Jerde et al., 2019). The dashed red lines show b of 0.67 or 0.75.



a whole by altering the metabolic scaling exponent. For example, our result showed that 43 of the 118 communities had a b greater than 1, which meant that in these communities, the mass-specific metabolic rate was greater for large-bodied individuals than for small-bodied individuals. This phenomenon is rarely seen across

the tree of life (Harrison et al., 2022). We speculate that trophically mutualistic interactions within certain stream communities may have benefitted larger individuals in acquiring a greater mass-specific metabolic rate. These communities might reach some optimal metabolic efficiency level that an individual fish or species

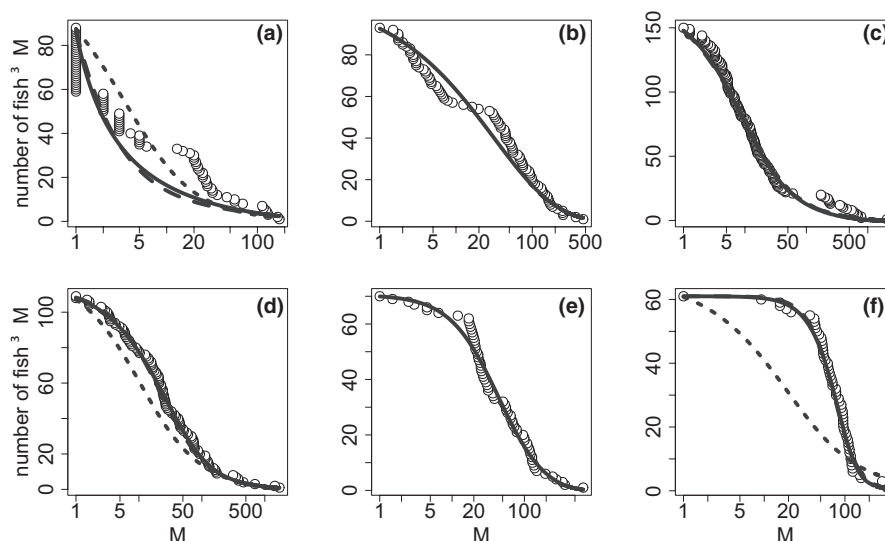


FIGURE 4 Relationship between the number of fish with at least body mass M and M in six communities, which were chosen so that their associated b (in the lower-left corner of each panel) was the minimum (a), the 20th percentile (b), the 40th percentile (c), the 60th percentile (d), the 80th percentile (e) and the maximum (f) of the best b 's from 118 communities. In each community, circles represent the observed data. Solid, dashed and dotted lines represent, respectively, the predictions from fully parameterized-maximum entropy theory of ecology (FP-METE), partially parameterized (PP)-METE and the original METE. In (b) and (e), predictions of the PP-METE and the original METE are not plotted because they violate the approximate conditions (see [Supporting Information](#)). In (c), all three METE models yield similar predictions that result in overlapping curves. The models are plotted in the descending order of their AICc so that the model with the lowest AICc is always plotted on top of the other models. AICc, Akaike information criterion corrected for sample size.

cannot achieve. To further assess the usefulness of our modelling approach, a direct comparison of intraspecific b between the METE models and previous studies is needed.

4.2 | Ecological effects on b

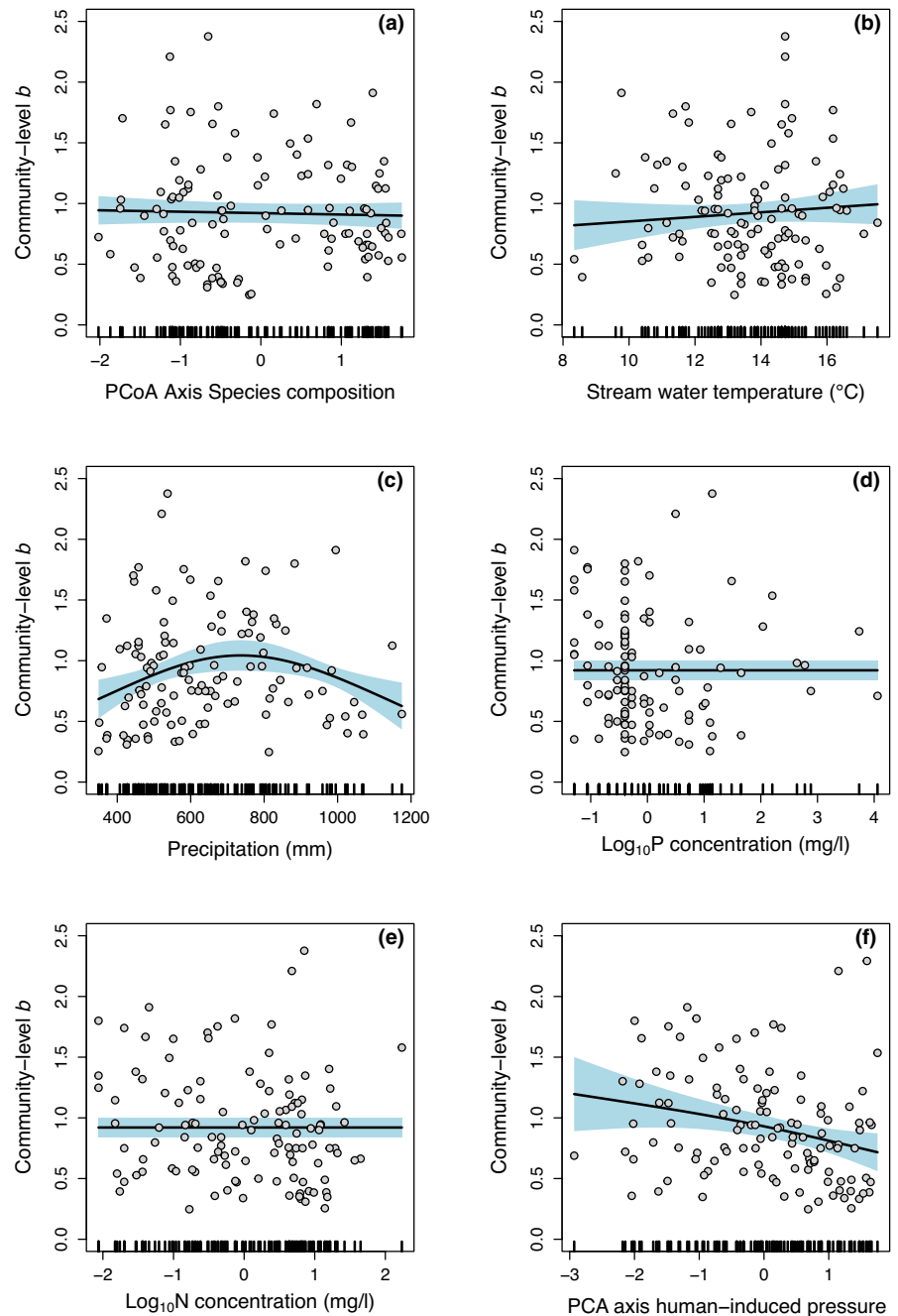
Our best GAM did not reveal a significant effect of temperature on the community-level b ([Figure 5](#)), although the temperature range across stream locations was between 8.34 and 17.53°C (average $13.65 \pm 1.85^\circ\text{C}$). Early experimental evidence showed similar results for individual species (Armitage, 1962; Barlow, 1961; Dehnel, 1960). Additionally, Finn et al. (2002) found that b remained stable as temperature increased for Atlantic cod. Carey et al. (2016) showed that b was not different between low- and high-temperature environments for sea urchins. Tan et al. (2019) did not find any significant relationship between temperature and b for Cephalopod species. On the other hand, some studies have documented the negative effect of temperature on b (Carey & Sigwart, 2014; Gjoni et al., 2020; Killen et al., 2010; Ohlberger et al., 2007; Silva-Garay & Lowe, 2021; Xie & Sun, 1990). The lack of a negative relationship between temperature and b may be because our b was estimated from communities in natural habitats where abiotic and biotic factors were not controlled, in contrast to most studies that analysed metabolic scaling in controlled laboratory environment. To complicate the matter, different ranges of temperature under controlled and natural conditions can also influence its relationship with b . For example, Enders and

Boisclair (2016) used different temperature variation schemes to mimic environmental fluctuations in natural habitat, and found no significant differences in b along the temperature gradient.

Several studies also noted that temperature was not a stand-alone factor, but interacted with other factors to influence b (Gjoni et al., 2020; Glazier et al., 2020; Ohlberger et al., 2012; Rubalcaba et al., 2020). For example, Gjoni et al. (2020) showed that temperature had a negative effect on b when a predator was present, but not when a predator was absent. Glazier et al. (2020) observed the same pattern when a predator was present but also found that temperature positively affected b when a predator was absent. Our interaction model confirmed that precipitation and human-induced pressure influenced the effect of stream water temperature on b ([Figure S4](#)). However, the presence of interaction effects did not improve the performance of the best GAM ([Table S3](#)).

GAM did not reveal a systematic effect of P or N concentration on b ([Figure 5](#)). To our knowledge, there has been no direct evidence of the effect of nutrients on the metabolic scaling of fish communities in natural habitats. This is probably because various physiological, behavioural and ecological factors can influence the process of acquiring and using nutrients (Glazier, 2018). For example, Nicholls et al. (2021) found that dietary composition can affect the metabolic scaling of adult honeybees. Nutrients can also interact with temperature to influence metabolic scaling and other patterns at various levels of biological organization (Cross et al., 2015) and at large spatial scales (Gjoni et al., 2022). The lack of systematic effect in our analysis might reflect the multiple confounding factors that can interact with nutrient.

FIGURE 5 Partial effect plots of the best generalized additive model. Each plot shows a covariate and its partial effect on the metabolic scaling exponent b . The Y-axes represent the best b estimate from the maximum entropy theory of ecology (METE) models, and the X-axes represent predictor values. Black lines show the model fit. The blue shade represents the 95% confidence region of the fitted model. PCA, principal component analysis; PCoA, principal coordinate analysis.



Our results showed that precipitation and human-induced pressure are two important drivers of the spatial variation of community-level b . Since precipitation tends to increase the level of dissolved oxygen by saturating oxygen with water (Danladi Bello et al., 2017; Li et al., 2015), the response of b to precipitation could essentially reflect how oxygen in the environment affects metabolic scaling. Interestingly, a similar nonlinear relationship was observed between environmental oxygen level and b . Using two fish species as the respective model system, Everett and Crawford (2010) and Urbina and Glover (2013) observed that b reached greater values when the partial pressure of oxygen was intermediate and b became smaller when the partial pressure of oxygen was smaller or greater. This similarity suggests the use of

the environmental oxygen level as an experimental variable to explain the variation in b . However, since fish species vary in their hypoxic tolerance and environmental oxygen can affect body size, the detailed biological mechanism of the effect of oxygen level on b needs more research. On the other hand, the negative relationship between human-induced pressure and b showed that human disturbance can slow the metabolic pace of life per unit of mass. Using an optimization model of life-time reproduction, White et al. (2022) showed that in the event of increased mortality caused by human disturbance, lifetime reproduction would drop significantly, leading to diminished b . Thus, our work provided an empirical confirmation of the predicted change in b of fish communities under the influence of environmental changes.

4.3 | Estimation of b from individual size data

In metabolic scaling research, individual metabolic rate and body mass data are often needed to estimate the metabolic scaling exponent b (mostly through a regression approach). However, measuring individual metabolic rate poses several challenges. First, direct measurement of metabolic rate is rare. Instead, the metabolic rate is often measured by its proxies, such as the photosynthesis and respiration rates of plants and the oxygen consumption rate of animals. Second, organisms are first collected from the field and then kept in controlled environments for a certain period of time before measurement. Consequently, the measured metabolic rate may not reflect the true metabolic rate under field conditions. Lastly, individual metabolic rate data are mostly measured for selected individuals, which may not reflect the realistic individual metabolic rate or body mass distribution in nature.

These shortcomings of traditional metabolic scaling research motivated us to seek an alternative method of estimating b , ideally relevant to the natural habitats where the species live. Our METE models provide a novel method of estimating a community-level b from individual size data. This new method eliminates the need for metabolic rate data and allows us to examine the influence of multiple ecological factors on b across communities. The superior performance of the FP-METE model over the PP-METE and the original METE models may be a consequence of the former relying on the ISD, rather than the mean constraints of macro-state variables. In other words, our result shows that the ISD in natural habitats contains sufficient biological information to infer the metabolic scaling relationship. Therefore, our method opens up new opportunities to estimate b for communities under various conditions, especially those undergoing severe habitat changes or disturbances.

Instead of requiring individual metabolic rate, our method assumes the metabolic scaling relationship and uses individual size as a surrogate for metabolic rate. For researchers who plan to use our models, we give the following recommendations for data collection and analysis. First, efficient sampling protocols are needed to obtain representative samples that reflect the taxonomic composition and body size range of organisms within communities. Second, body size (instead of size class) should be measured for each sampled individual, rather than summary statistics at the species level, such as mean body size. Third, individual weight is the preferred measure of body size. This is because other size measures (e.g. tree diameters or fish total length) would add another layer of uncertainty to the estimated b through the integration of the allometries and metabolic scaling relationship. Lastly, as with any statistical method, sample size should be taken into account when using our method. Based on the model comparison (Table S1), streams with fewer than 50 sampled fish were mostly associated with nonsensible AICc or inferior fit of the METE models. Therefore, we suggest our method to be used for a community with at least 50 individuals so that the estimated b can have statistical support. However, researchers should be aware that this

recommended sample size threshold is not definitive and more research is needed to determine its value.

4.4 | Implications and future directions

Our results could have broad applied and theoretical implications to the functioning of ecosystems and ecological modelling research. The community-level b can be used to scale up ecosystem functions and understand how energy fluxes change and respond to global environmental pressures. For example, in marine ecosystems, deep-sea fish play a vital role in controlling the global carbon cycle between ocean surface and the mesopelagic zone (Trueman et al., 2014). Metabolic scaling of these fish species is crucial for understanding their role in carbon-flow dynamics. Our method can provide a useful alternative to the traditional approach of measuring individual fish metabolic rate using a respirometer, which is infeasible due to the low survival rates of these fish species in laboratory environment (Alewijnse et al., 2021). Our method can be applied similarly to forest ecosystems, where individual tree size data are widely available, but the whole-tree metabolic rate is difficult to measure (Mori et al., 2010). If our method can gain empirical support (as shown in the current work), it would suggest that previous research on energy use that relies on the universal metabolic scaling relationship needs to be revisited (Ernest et al., 2009). Our METE models could leverage the individual size data resources from fish and tree communities and provide empirically relevant metabolic scaling exponent estimates that are important for studying energy flux and carbon cycles.

Our approach presents a new way to integrate mathematical model, ecological scaling and empirical data into a unified theoretical framework. Specifically, the parameterized METE models differ from the original METE by infusing individual size data as information into the corresponding predictions, which enhances the predictive power of the original METE that is based on the Shannon's entropy and the macro-state constraints alone. Scaling relationships have been integrated with dynamical models to remedy the issue of large number of parameters and to improve the model performance (Hudson & Reuman, 2013; Yodzis & Innes, 1992). Our approach is similar to these studies in spirit, but reverses the role of data and scaling relationship in the modelling process. Instead of borrowing established scaling relationships from external theory (i.e. metabolic scaling theory) to predict empirical patterns, we use empirical pattern (i.e. ISD) to estimate the exponent in the metabolic scaling relationship. We believe that our approach has the potential to broaden the scope of theoretical models and improve the understanding of scaling relationships.

Even though our b resembled three community-aggregated b from published work, a more direct comparison of the intraspecific b estimated from species-level METE models and the traditional regression approach is needed to evaluate the applicability of METE in metabolic scaling. Although not discussed here, our METE framework is able to predict intraspecific ISD, which can be fitted to the observed ISD to obtain an intraspecific estimate of b . To do this, we

need size measurements of conspecific individuals from the same community so that spatial variation of environmental factors will not confound the variation in the estimated b .

Finally, several studies have shown that the original METE fails to predict macroecological patterns in disturbed ecosystems (Brush et al., 2022; Franzman et al., 2021; Newman et al., 2020). It will be interesting to test the performance of parameterized METE models in communities under disturbance. If the parameterized METE models generate reasonable predictions, then it suggests that we may use the corresponding estimate of b as a biological indicator to monitor the ecosystem response to natural disturbances or human pressure.

5 | CONCLUSIONS

We analysed a large individual size dataset of stream fish communities to estimate the metabolic scaling exponent under natural conditions. Previous empirical evaluation of metabolic scaling usually relies on taxon-specific proxies, manipulated conditions and selected individuals for experimental studies (Glazier, 2022; Harrison et al., 2022; White & Kearney, 2014). We overcame these challenges by proposing a novel method to estimate the metabolic scaling exponent through the integration of the METE models and ISDs. In contrast to previous studies (Glazier, 2014; Kooijman, 2000; Kozłowski et al., 2003), our parameterized METEs are based on macro-state constraints and ISDs within communities. This allows us to interpret the variation of the community-level b with respect to environmental factors and opens the possibility of understanding changes in the structure and function among natural communities.

AUTHOR CONTRIBUTIONS

Meng Xu conceived the modelling idea. Meng Xu and Ignasi Arranz analysed the data, led the writing of the manuscript and contributed to the manuscript revision.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from Zenodo <https://doi.org/10.5281/zenodo.6327188> (Arranz, 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Approximate conditions of the original METE and PP-METE.

Appendix S2. Comparison of the METE models with other distribution models.

Appendix S3. Supplementary figures.

Appendix S4. Supplementary tables.

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