

¹³ **Abstract**

¹⁴ A fundamental pattern in ecology is that smaller organisms are more abundant than larger organ-
¹⁵ isms. This pattern is known as the individual size distribution (ISD), which is the frequency of all
¹⁶ individual sizes in an ecosystem, regardless of taxon. The ISD is described by power law distri-
¹⁷ bution with the form $f(x) = Cx^\lambda$, and a major goal of size spectra analyses is to estimate the
¹⁸ ISD parameter λ . However, while numerous methods have been developed to do this, they have
¹⁹ focused almost exclusively on estimating λ from single samples. Here, we develop an extension
²⁰ of the truncated Pareto distribution within the probabilistic modeling language Stan. We use it
²¹ to estimate multiple ISD parameters simultaneously with a hierarchical modeling approach. The
²² most important result is the ability to examine hypotheses related to size spectra, including the
²³ assessment of fixed and random effects, within a single Bayesian generalized (non)-linear mixed
²⁴ model.

²⁵ Keywords: *Bayesian, body size spectra, hierarchical, Pareto, power law, Stan*

²⁶ **Introduction**

²⁷ In any ecosystem, large individuals are typically more rare than small individuals. This funda-
²⁸ mental feature of ecosystems leads to a remarkably common pattern in which relative abundance
²⁹ declines with individual body size, generating the individual size distribution (ISD), also called the
³⁰ community size spectrum (Sprules et al. 1983, White et al. 2008). Understanding how body sizes
³¹ are distributed has been a focus in ecology for over a century (Peters and Wassenberg 1983), in part
³² because they represent an ataxic approach that reflects fundamental measures of ecosystem struc-
³³ ture and function, such as trophic transfer efficiency. (Kerr and Dickie 2001, White et al. 2007,
³⁴ Perkins et al. 2019). Individual size distributions are also predicted as a result of physiological lim-
³⁵ its associated with body size, thereby emerging from predictions of metabolic theory and energetic
³⁶ equivalence (Brown et al. 2004).

³⁷ More formally, the ISD is a frequency distribution that can be approximated by a bounded power
³⁸ law with a single free parameter λ , corresponding to the following probability density function
³⁹ (Edwards et al. 2020):

$$f(x) = Cx^\lambda, x_{min} \leq x \leq x_{max} \quad (1)$$

⁴⁰ where x is the body size (e.g., mass or volume) of an individual regardless of taxon, x_{min} is the
⁴¹ smallest individual attainable and x_{max} is the largest possible individual (White et al. 2008). C is
⁴² a constant equal to:

$$C = \begin{cases} \frac{\lambda+1}{x_{max}^{\lambda+1}-x_{min}^{\lambda+1}}, & \lambda \neq -1 \\ \frac{1}{\log x_{max}-\log x_{min}}, & \lambda = -1 \end{cases} \quad (2)$$

⁴³ This model is also known as the bounded power law or truncated Pareto distribution. The terms
⁴⁴ “bounded” or “truncated” refer to the limits of x_{min} and x_{max} , which represent the minimum and
⁴⁵ maximum attainable body size values (White et al. 2008). In practice, values of x_{min} and x_{max}

⁴⁶ often come from the minimum and maximum body sizes in a data set or are estimated statistically
⁴⁷ (White et al. 2008, Edwards et al. 2017).

⁴⁸ A compelling feature of size spectra is that λ may vary little across ecosystems as a result of phys-
⁴⁹ iological constraints that lead to size-abundance patterns more broadly. Metabolic scaling theory
⁵⁰ predicts $\lambda + 1 = \frac{\log_{10}\alpha}{\log_{10}\beta} - 3/4$, where α is trophic transfer efficiency in the food web and β is the
⁵¹ mean predator-prey mass ratio (Reuman et al. 2008). The value of $-3/4$ is the predicted scaling
⁵² exponent of log abundance and log mass (Damuth 1981, Peters and Wassenberg 1983). It is the
⁵³ reciprocal of scaling coefficient of metabolic rate and mass (0.75) (Brown et al. 2004) and as a
⁵⁴ result, values of $\lambda + 1$ have been used to estimate metabolic scaling across ecosystems (Reuman
⁵⁵ et al. 2008, Perkins et al. 2018, 2019). Because $\frac{\log_{10}\alpha}{\log_{10}\beta}$ is typically $\ll 0.01$, this implies that a λ val-
⁵⁶ ues of ~ -1.75 represent a reasonable first guess of expected ISD exponents, with values of ranging
⁵⁷ from -1.2 to -2 often appearing in the literature (Andersen and Beyer 2006, Blanchard et al. 2009,
⁵⁸ Pomeranz et al. 2020a).

⁵⁹ Whether λ represents a fixed or variable value is debated, but it often varies among samples and
⁶⁰ ecosystems (Blanchard et al. 2009, Perkins et al. 2018, Pomeranz et al. 2020a). It is often de-
⁶¹ scribed by its “steepness”, with more negative values (i.e., “steeper”) indicating lower abundance
⁶² of large relative to small individuals, and vice versa. These patterns of size frequency are an emer-
⁶³ gent property of demographic processes (e.g., age-dependent mortality), ecological interactions
⁶⁴ (e.g., size-structured predation, trophic transfer efficiency), and physiological constraints (e.g.,
⁶⁵ size-dependent metabolic rates) (Muller-Landau et al. 2006, Andersen and Beyer 2006, White
⁶⁶ et al. 2008). As a result, variation in λ across ecosystems or across time can indicate fundamen-
⁶⁷ tal shifts in community structure or ecosystem functioning. For example, overfishing in marine
⁶⁸ communities has been detected using size spectra in which λ was steeper than expected, indicating
⁶⁹ fewer large fish than expected (Jennings and Blanchard 2004). Shifts in λ have also been used
⁷⁰ to document responses to acid mine drainage in streams (Pomeranz et al. 2019, 2020b), land use
⁷¹ (Martínez et al. 2016), resource subsidies (Perkins et al. 2018), and temperature (O’Gorman et al.
⁷² 2017, Pomeranz et al. 2022).

73 Given the ecological information it conveys, the data required to estimate size spectra are decep-
74 tively simple; only a single column of data are needed, in which each data point is a single measure
75 of the body size of an individual. As long as the body sizes are collected systematically and without
76 bias towards certain taxa or phenotypes, there is no need to know any more ecological information
77 about the data points (e.g., taxon, trophic position, age, abundance). However, despite the simple
78 data requirement, the statistical models used to estimate λ are diverse. Edwards et al. (2017) doc-
79 umented 8 different analytical methods. Six involved binning, in which the body sizes are grouped
80 into size bins (e.g., 2-49 mg, 50-150 mg, etc.) and then counted, generating values for abundance
81 within each size bin. When both axes are log-transformed, binning allows λ to be estimated using
82 simple linear regression. Unfortunately, the binning process also removes most of the variation in
83 the data, collapsing information about 1000's of individuals into just 6 or so bins. Doing so can
84 lead to the wrong values of λ , sometimes drastically so (Goldstein et al. 2004, White et al. 2008,
85 Pomeranz et al. 2023).

86 An improved alternative to binning and linear regression is to fit the body size data to a power
87 law probability distribution (White et al. 2008, Edwards et al. 2017, 2020). This method uses all
88 raw data observations directly to estimate λ , typically using the maximum likelihood estimation
89 method (Edwards et al. 2017). In addition to estimating size spectra of single samples, ecologists
90 have used this method to examine how λ varies across environmental gradients (Perkins et al.
91 2019, Pomeranz et al. 2022). However, these analyses typically proceed in two steps. First, λ
92 estimates are obtained individually from each collection (e.g., each site or year, etc.). Second,
93 these estimates are used as response variables in a linear model to examine how they relate to
94 corresponding predictor variables (Edwards et al. 2020). A downside to this approach is that it
95 treats body sizes (and subsequent λ 's) as independent samples, even if they come from the same
96 site or time. It also removes information on sample size (number of individuals) used to derive λ .
97 As a result, the approach not only separates the data generation model from the predictor variables,
98 but is also unable to take advantage of partial pooling during model fitting.

99 Here, we develop a Bayesian model that uses the truncated Pareto distribution to estimate λ in

100 response to both fixed and random predictor variables. The model extends the maximum likelihood approach developed by Edwards et al. (2020) and allows for a flexible hierarchical structure,
 101 including partial pooling, within the modeling language Stan (Stan Development Team 2022).
 102

103 **Methods**

104 **Translating to Stan**

105 We first translated the probability density function described by Edwards et al. (2020) into Stan by
 106 converting it to the log probability density function (lpdf). Stan is a probabilistic modeling language
 107 that is capable of fitting complex models, including those with custom lpdf's. The resulting lpdf is
 108 given as

$$lpdf = \begin{cases} \log \frac{\lambda+1}{x_{max}^{\lambda+1} - x_{min}^{\lambda+1}} + \lambda \log x, & \lambda \neq -1 \\ -\log(\log x_{max} - \log x_{min}) - \log x, & \lambda = -1 \end{cases} \quad (3)$$

109 with all variables as described above. We call this the *paretocustom* distribution, which we can
 110 now use to estimate λ of a given data set. For example, an intercept-only model would look like
 111 this:

$$x_i \sim paretocustom(\lambda, x_{min}, x_{max})$$

$$\lambda = \alpha$$

$$\alpha \sim Normal(\mu, \sigma) \quad (4)$$

112 where x_i is the i th individual body size, λ is the size spectrum parameter (also referred to as the
 113 exponent), x_{min} and x_{max} are as defined above, and α is the intercept with a prior probability

₁₁₄ distribution. In this case, we specified a Normal prior since λ is continuous and can be positive or
₁₁₅ negative, but this can be changed as needed.

₁₁₆ The simple model above can be expanded to a generalized linear mixed model by including fixed
₁₁₇ predictors ($\beta\mathbf{X}$) and/or varying intercepts ($\alpha_{[x]}$):

$$x_{ij} \sim \text{paretocustom}(\lambda_j, x_{min,j}, x_{max,j})$$

$$\lambda = \alpha + \beta\mathbf{X} + \alpha_{[j]} + \alpha_{[x]}$$

$$\alpha \sim \text{Normal}(\mu_\alpha, \sigma_\alpha)$$

$$\beta \sim \text{Normal}(\mu_\beta, \sigma_\beta)$$

$$\alpha_{[j]} \sim \text{Normal}(0, \sigma_{[j]})$$

$$\sigma_{[j]} \sim \text{Exponential}(\phi)$$

$$\alpha_{[x]} \sim \text{Normal}(0, \sigma_{[x]})$$

$$\sigma_{[x]} \sim \text{Exponential}(\phi) \quad (5)$$

₁₁₈ with one or more β regression parameters, represented by the vector β , for one or more fixed
₁₁₉ predictors \mathbf{X} , and one or more varying intercepts α_x . We specify α_j separately because it is needed
₁₂₀ to account for the non-independence of body sizes. In other words, each body size x_i is clustered
₁₂₁ within each site and so they are not independent and identically distributed. The addition of a
₁₂₂ varying intercept for each sample accounts for this non-independence. Prior distributions are given
₁₂₃ as *Normal* for the parameters and varying intercept and *Exponential* for $\sigma[x]$, but these can also
₁₂₄ be changed as needed.

₁₂₅ The model above assumes that each body size x represents a single individual such that the data
₁₂₆ set might have many repeats for individuals of the same size (e.g., $x = \{0.2, 0.2, 0.2, 0.4, 0.4, 0.5,$
₁₂₇ 9.8\}). However, when individual body sizes are repeated in a data set, they are often accompanied

128 by a count or density, such that the data set above might instead consist of two columns with $x =$
129 $\{0.2, 0.4, 0.5, 9.8\}$ and $counts = \{3, 2, 1, 1\}$. To analyze this more compact data set, Edwards et
130 al. (2020) developed a modification of the log probability density function to include $counts$:

$$lpdf = \begin{cases} counts(\log_{x_{max}^{\lambda+1}-x_{min}^{\lambda+1}}^{\lambda+1} + \lambda \log x), \lambda \neq -1 \\ counts(-\log(\log x_{max} - \log x_{min}) - \log x, \lambda = -1 \end{cases}. \quad (6)$$

131 We refer to this as *paretocounts*, such that the model can be fit by using

$$x_i \sim paretocounts(\lambda, x_{min}, x_{max}, counts)$$

λ = [linear or non-linear model] and

[priors]. (7)

132 Aside from adding *counts*, the model is the same as presented above. These models
133 (*paretocustom* and *paretocounts*) allow us to test how the size distribution parameter,
134 λ , varies in response to continuous or categorical predictors and to include hierarchical structure
135 as needed.

136 Testing the models

137 The *paretocustom* and *paretocounts* lpdfs give the same results, differing only in how the data
138 are aggregated. For simplicity, we demonstrate model performance here for the *paretocounts*
139 distribution, since the empirical data we used (see *Case Study* below) contains counts of individual
140 body sizes. First, we tested for parameter recovery using data simulated from a bounded power law
141 with known values of λ . Second, we fit the model to fisheries trawl data presented in Edwards et
142 al. (2020) to estimate the hypothesis that λ declines over time.

¹⁴³ **Parameter recovery from simulated data**

¹⁴⁴ To ensure that the models could recover known parameter values, we simulated ten data sets from
¹⁴⁵ a bounded power law using the inverse cumulative density function:

$$x_i = (u_i x_{max}^{(\lambda+1)} + (1 - u_i) x_{min}^{(\lambda+1)})^{\frac{1}{(\lambda+1)}} \quad (8)$$

¹⁴⁶ where x_i is the individual body size from the i th simulation, u_i is a unique draw from a
¹⁴⁷ $Uniform(0, 1)$ distribution, and all other variables are the same as defined above. We set x_{min}
¹⁴⁸ = 1, x_{max} = 1000, and simulated $i = 1000$ values from each of 10 λ 's ranging from -2.2 to -1.2.

¹⁴⁹ To generate *counts*, we rounded each simulated value to the nearest 0.001 and then tallied them.

¹⁵⁰ We estimated the ten λ values in two ways. First, we fit a separate intercept-only model to each
¹⁵¹ of the ten data sets. Second, we fit a varying intercept model (Gelman et al. 2014). The structure
¹⁵² of this model is $\lambda = \alpha + \alpha_{[group]}$ where each group represents an offset from the mean value of
¹⁵³ lambda.

¹⁵⁴ Finally, we simulated data for a regression model with a single continuous predictor and a varying
¹⁵⁵ intercept: $\lambda = \alpha + \beta x + \alpha_{[group]}$, where $\alpha = -1.5$, $\beta = -0.1$, and $\sigma_{group} = 0.3$. The predictor
¹⁵⁶ variable x was a continuous predictor. Using these parameters, we simulated 18 λ 's, with each λ
¹⁵⁷ coming from one of three x -values (-2, 0, 2), nested within 3 groups with each replicated twice.

¹⁵⁸ From each λ , we simulated 1000 individuals using the procedure above, with $x_{min} = 1$ and x_{max}
¹⁵⁹ = 1000. Using those 18,000 simulated body sizes (1000 sizes simulated from 18 λ 's), we fit a
¹⁶⁰ *paretocounts* regression model 40 times to measure variation in parameter recovery among model
¹⁶¹ runs.

¹⁶² **Sample Size**

¹⁶³ We examined sensitivity to sample size (number of individual body sizes) across three λ values (-2,
¹⁶⁴ -1.6, -1.2). For each λ , we varied the number of simulated individuals from 2 to 2048, representing

¹⁶⁵ a 2^n sequence with n ranging from 1 to 11. Each of the 11 densities was replicated 10 times
¹⁶⁶ resulting in 110 datasets of individual body sizes. We fit each data set using separate intercept-only
¹⁶⁷ *paretocounts* models and then plotted the resulting λ values as a function of sample size.

¹⁶⁸ Case Studies

¹⁶⁹ To examine model performance on empirical data, we re-ran a previously published analysis from
¹⁷⁰ Edwards et al. (2020). In Edwards' study, size spectra parameters were first estimated separately
¹⁷¹ for each sample using maximum likelihood. Then the modeled parameters were used as response
¹⁷² variables in linear regression models. The goal was to test for linear changes in size spectra over
¹⁷³ three decades using bi-yearly size data of marine fishes collected from the International Benthic
¹⁷⁴ Trawl Survey (IBTS). The data set and original model results are available in the `sizeSpectra`
¹⁷⁵ package (Edwards et al. 2017). We tested the same hypothesis as Edwards et al. (2020), but
¹⁷⁶ instead of using a two-step process we fit a single model using the *paretocounts* `lpdf`.

¹⁷⁷ Model Fitting

¹⁷⁸ We fit each of the above models in `rstan` (Stan Development Team 2022) using 2 chains each
¹⁷⁹ with 1000 iterations. All models converged with R_{hat} 's < 1.01. If a known parameter value fell
¹⁸⁰ inside the 95% Credible Intervals, we considered parameter recovery successful. For the replicated
¹⁸¹ regression model, we also tallied the number of times that the known value fell outside of the 95%
¹⁸² CrI. Assessments of prior influence and model checking are available in Appendix S1.

¹⁸³ Data Availability Statement

¹⁸⁴ All data, R code, and Stan code are available at https://github.com/jswesner/stan_isd (to be perma-
¹⁸⁵ nently archived on acceptance).

186 **Results**

187 **Parameter Recovery**

188 For models fit to simulated individual data sets, all 95% credible intervals included the true value of
189 λ and posterior medians were no more than 0.05 units away from the true value (Table 1). Similarly,
190 when the same data set was fit using a varying intercepts model, the posterior median intercept α
191 and group standard deviation σ_{group} were nearly identical to the true values (Table 1). Using the
192 varying intercept model to estimate group specific means yielded similar results as using separate
193 models per group (Figure 1a), demonstrating that a single model can be used to estimate multiple
194 size spectra. The change from “shallow” to “steep” size spectra is also evident in plots of the
195 proportion of values $\geq x$ (i.e., $f(x)$ from Eq. 1) (Figure 1b-d).

196 We also recovered regression parameters (α, β) along with the group-level standard deviation
197 (σ_{group}) (Figure 2). Thirty-seven of the 40 models converged. Of those 37 models the true value
198 fell outside of the 95% CrI once for α and σ_{group} and three times for β (Figure 2). Averaging the
199 deviations (posterior median minus the true value) among the replicates indicated no bias in the
200 modeled estimates (mean bias \pm sd: $\alpha = -0.01 \pm 0.05$, $\beta = 0.001 \pm 0.004$, $\sigma_{group} = 0.02 \pm 0.05$).

201 **Sample Size**

202 Variation in modeled estimates was high for samples containing less than 100 individual (Figure
203 3). For example, when the true λ value was -2, samples with just 8 individuals yielded estimates
204 ranging from -2.7 to -1.7. By contrast, all samples with more than 300 individuals captured the true
205 λ with less than 0.1 unit of error (Figure 3).

206 **Case Study**

207 Using IBTS data (Edwards et al. 2017) with a Bayesian hierarchical regression, we found a negative
208 trend over time. The ISD parameter of IBTS trawl data declined by ~0.001 units per year, but with
209 a 95% CrI ranging from -0.005 to 0.002. These values were nearly identical to those reported by
210 Edwards et al. (2020) using a two-step approach (Table 2). An advantage of fitting the model in
211 a single Bayesian hierarchical framework is that estimates for individual groups are pulled toward
212 the mean via partial pooling. This is apparent in comparing the unpooled MLE estimates (Figure
213 4a) to the partially pooled Bayesian estimates in each year (Figure 4b).

214 **Discussion**

215 The most important result of this work is the ability to analyze ISD parameters using fixed and
216 random predictors in a hierarchical model. Our approach allows ecologists to test hypotheses about
217 size spectra while avoiding the pitfalls of binning, which loses information and can lead to biased
218 estimates of λ (White et al. 2008). Maximum likelihood solves this problem by directly estimating
219 the ISD, but testing hypotheses with maximum likelihood is often done with a two-step process in
220 which λ is estimated individually for each sample and the results are then used as response variables
221 in linear or non-linear models (Edwards et al. 2020). Our approach merges these steps, allowing
222 for the incorporation of prior probabilities and hierarchical structure.

223 The ability to incorporate prior information using Bayesian updating has two practical advantages
224 over the two-step process described above. First, adding informative prior distributions can im-
225 prove model fit by limiting the MCMC sampler to reasonable sampling space. In other words it
226 would not be sensible to estimate the probability that λ is -1,234 or -9. Without informative priors,
227 those values (and more extreme values) are considered equally likely and hence waste much of the
228 algorithm's sampling effort on unlikely values (e.g., (Wesner and Pomeranz 2021)).

229 Second, and most importantly, ecologists have much prior information on the values that λ can take.

230 For example, global analysis of phytoplankton reveals values of -1.75, consistent with prediction
231 based on sub-linear scaling of metabolic rate with mass of -3/4 (Perkins et al. 2019). Alternatively,
232 Sheldon's conjecture suggests that λ is -2.05 (Andersen et al. 2006), a value reflecting isometric
233 scaling of metabolic rate and mass, with support in pelagic marine food webs (Andersen and
234 Beyer 2006). However, benthic marine systems typically have shallower exponents (e.g., \sim -1.4;
235 Blanchard et al. (2009)), similar to those in some freshwater stream ecosystems (-Pomeranz et
236 al. 2022). While the causes of these deviations from theoretical predictions are debated, it is clear
237 that values of λ are restricted to a relatively narrow range between about -2.05 and -1.2. But this
238 restriction is not known to the truncated Pareto, which has no natural lower or upper bounds on λ
239 (White et al. 2008). As a result, a prior that places most of its probability mass on these values
240 (e.g., $Normal(-1.75, 0.2)$) seems appropriate. Such a continuous prior does not prevent findings
241 of larger or smaller λ , but instead places properly weighted skepticism on such values.

242 Similar to priors, partial pooling from varying intercepts provides additional benefits, allowing for
243 the incorporation of hierarchical structure and pulling λ estimates towards the global mean (Gelman
244 2005, Qian et al. 2010). In the examples shown here, the amount of pooling is relatively small
245 because the sample sizes are large (>1000 individuals). However, the primary benefit of pooling
246 (both from varying effects and skeptical priors) is in prediction (Gelman 2005, Hobbs and Hooten
247 2015). This becomes especially important when models are used to forecast future ecosystem
248 conditions. Forecasts are becoming more common in ecology (Dietze et al. 2018) and are likely
249 to be easier to test with modern long-term data sets like NEON (National Ecological Observatory
250 Network) in which body size samples will be collected at the continental scale over at least the next
251 20 years (Kuhlman et al. 2016). In addition, because the effects of priors and pooling increase with
252 smaller samples sizes, varying intercepts are likely to be particularly helpful for small samples. In
253 other words, priors and partial pooling contain built-in skepticism of extreme values, ensuring the
254 maxim that "extraordinary claims require extraordinary evidence".

255 One major drawback to the Bayesian modeling framework here is time. Bayesian models of even
256 minimal complexity must be estimated with Markov Chain Monte Carlo techniques. In this study,

257 we used the No U-Turn sampling (NUTS) algorithm via `rstan` (Stan Development Team 2022).
258 Stan can be substantially faster than other commonly used programs such as JAGS and WinBUGS,
259 which rely on Gibbs sampling. For example, Stan is 10 to 1000 times more efficient than JAGS
260 or WinBUGS, with the differences becoming greater as model complexity increases (Monnahan
261 et al. 2017). In the current study, intercept-only models for individual samples with ~ 300 to
262 1500 individuals could be fit quickly (<2 seconds total run time (warm-up + sampling on a Lenovo
263 T490 with 16GB RAM)) with as little as 1000 iterations and two chains. However, the IBTS
264 regression models took >2 hours to run with the same iterations and chains. These times include the
265 fact that our models used several optimization techniques, such as informative priors, standardized
266 predictors, and non-centered parameterization, each of which are known to improve convergence
267 and reduce sampling time (McElreath 2016). But if Bayesian inference is desired, these run-times
268 may be worth the wait. In addition, they are certain to become faster with the refinement of existing
269 algorithms and the introduction of newer ones like Microcanonical HMC (Robnik et al. 2022).

270 Body size distributions in ecosystems have been studied for decades, yet comprehensive analytical
271 approaches to testing these hypotheses are lacking. We present a single analytical approach that
272 takes advantage of the underlying data structures of individual body sizes (Pareto distributions)
273 while placing them in a generalized (Non)-linear hierarchical modeling framework. We hope that
274 ecologists will adopt and improve on the models here to critically examine hypotheses of size
275 spectra or other power-law distributed data.

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Tables

Table 1: Table 1. Parameter recovery of the same data using two approaches. First, ten separate models individually recapture known lambda values. Second, the same ten data sets are estimated in a single hierarchical model. The true values are compared to the posterior median and 95% Credible Intervals.

Model	Parameter	True Value	q2.5	q50	q97.5
Separate Models	λ	-2.20	-2.23	-2.15	-2.08
Separate Models	λ	-2.09	-2.15	-2.09	-2.02
Separate Models	λ	-1.98	-2.08	-2.02	-1.96
Separate Models	λ	-1.87	-1.93	-1.87	-1.81
Separate Models	λ	-1.76	-1.75	-1.70	-1.65
Separate Models	λ	-1.64	-1.65	-1.60	-1.56
Separate Models	λ	-1.53	-1.54	-1.50	-1.46
Separate Models	λ	-1.42	-1.45	-1.42	-1.38
Separate Models	λ	-1.31	-1.34	-1.30	-1.26
Separate Models	λ	-1.20	-1.23	-1.20	-1.16
Single Model with Varying Intercepts	α	-1.70	-1.96	-1.71	-1.50
Single Model with Varying Intercepts	$\sigma_{\text{[group]}}$	0.34	0.23	0.36	0.58

Table 2: Slope values from a regression testing the relationship between the ISD exponent and year for IBTS trawl data (Edwards et al. 2020). The values are derived using the Bayesian hierarchical model presented here or from the maximum likelihood approach described in Edwards et al. (2020).

Model	Mean	q2.5	q97.5
Bayesian - one step	-0.001	-0.005	0.002
MLE - two steps	-0.001	-0.005	0.003

343 **Figure Captions**

- 344 Figure 1. a) Modeled estimates (median +/- 95% Credible Intervals) of λ using either 10 separate
345 models or a single model with ten varying intercepts. c-d) Fit of ISD relationships at 3 values of
346 λ . Dots are raw data, lines are posterior medians, and shading is the 95% credible interval. Fits are
347 from separate models.
- 348 Figure 2. Posterior distributions of $n = 40$ modeled estimates of alpha, beta, and sigma_group for a
349 linear regression estimating the size spectrum exponent as a function of a continuous predictor. All
350 data were simulated. Gray densities indicate that the 95% CrI contains the true value, while black
351 densities indicate the true values fall outside of the CrI. The vertical lines indicate true values.
- 352 Figure 3. Estimates of λB across 11 different sample sizes (ranging from 2 to 2048 individuals)
353 and three different true λ 's (-2, -1.6, -1.2). Ten separate models were fit for each of the 11 sample
354 sizes. The horizontal lines show the true value of λ .
- 355 Figure 4. Regression results from a) Edwards et al. (2020) using maximum likelihood and linear
356 regression (two steps) and b) the Bayesian model with varying intercepts. In a) the points represent
357 maximum likelihood estimates calculated separately for each year. In b) they represent hierarchical
358 varying intercepts calculated from the model.