



HAL
open science

Biogeographical Patterns of Species Richness and Abundance Distribution in Stream Diatoms Are Driven by Climate and Water Chemistry

S.I. Passy, C.A. Larson, Aurélien Jamoneau, W. Budnick, J. Heino, Thibault Leboucher, Juliette Tison-Rosebery, J. Soininen

► **To cite this version:**

S.I. Passy, C.A. Larson, Aurélien Jamoneau, W. Budnick, J. Heino, et al.. Biogeographical Patterns of Species Richness and Abundance Distribution in Stream Diatoms Are Driven by Climate and Water Chemistry. *The American Naturalist*, 2018, 192 (5), pp.605-617. 10.1086/699830 . hal-01958855

HAL Id: hal-01958855

<https://hal.science/hal-01958855v1>

Submitted on 18 Dec 2018

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Biogeographical patterns of species richness and abundance**

2

3

4
5 **Distribution in stream diatoms are driven by climate
6 and water chemistry**

6

7

8 **Sophia I. Passy,^{1,*} Chad A. Larson,² Aurélien Jamoneau,³ William Budnick,¹ Jani Heino,⁴**

9 **Thibault Leboucher,³ Juliette Tison-Rosebery,³ and Janne Soininen⁵**

10 **1. Department of Biology, University of Texas, Arlington, Texas 76019**

11 **2. Washington State Department of Ecology, Environmental Assessment Program, Lacey, Washington**

12 **3. Aquatic Ecosystems and Global Changes Research Unit, Institut national de recherche en sciences
13 technologies pour l'environnement et l'agriculture, 50 avenue de Verdun, 33612 Cestas, France**

14 **4. Finnish Environment Institute, Biodiversity Centre, PO Box 413, FI-90014 Oulu, Finland**

15 **5. Department of Geosciences and Geography, University of Helsinki, PO Box 64, FIN-00014 Helsinki,**

16 ***Corresponding author; email: sophia.passy@uta.edu.**

17 **Keywords:** climatic variability and tolerance, latitudinal diversity gradient, metabolic theory, more

18 individuals hypothesis, nutrient enrichment, species-energy

19

20 **Submission type:** Major article

21

22 **Number of words:** 5456

23

24 The manuscript includes 3 tables, 4 figures, and an appendix with 2 tables and 1 figure.

22 **Abstract**

23 This is the first inter-continental comparative assessment of diatom richness and species abundance
24 distribution (SAD) along spatial, climatic, and water chemistry gradients using stream data from the US
25 and Finland. We tested a number of hypotheses about the causes of variability in richness and by
26 extension, the SAD, including the metabolic theory, the species-energy, the more individuals, the climatic
27 variability, and the climatic tolerance hypotheses. We found no support for any of these concepts, given
28 that the relationships of richness with explanatory variables were non-existent, weak or unexpected.
29 Diatom richness and the SAD responded more strongly to climatic variability, climatic extremes, and
30 water chemistry, especially nutrient levels, than to mean temperature. A consequence of the weak energy
31 dependence was a non-linear latitudinal gradient of richness in both countries, and a non-linear latitudinal
32 gradient of the SAD in the US. The SAD was not entirely driven by richness but displayed distinct
33 responses to spatial, climatic, and water chemistry factors, indicating that the environment had
34 complementary effects on richness and the SAD. This emphasizes the utility of the SAD for ecological
35 research—a notion that has been previously debated. Thus, we found sufficient support for the operation
36 of multiple climate and water chemistry mechanisms in structuring diatom communities, which
37 underscores their complex response to the environment and the necessity for novel predictive
38 frameworks.

39 **Introduction**

40 The spatial variability in species richness along latitudinal, longitudinal, and elevational gradients has
41 drawn a continued interest among ecologists for centuries, beginning with the works of Alexander von
42 Humboldt and Carolus Linnaeus (Pianka 1966; Gaston 2000; Willig et al. 2003; Rahbek 2005; Mittelbach
43 et al. 2007). There are numerous hypotheses about the nearly universal poleward decline in species
44 richness with ecological and evolutionary rates, energy, and climatic favorability and stability emerging
45 as important underlying factors. The elevation-richness relationship is more variable, most frequently
46 conforming to a monotonically declining or a hump-shaped form, but there are some commonalities in the
47 driving forces of the latitudinal and elevational gradients (Rahbek 2005). Thus, warmer temperatures in
48 tropical and low elevation regions shorten the generation times and accelerate the metabolic and mutation
49 rates, leading to greater speciation (Rohde 1992; Currie et al. 2004; Allen et al. 2006). These ideas were
50 conceptualized within the framework of the Metabolic Theory of Ecology (MTE), which predicted
51 species richness (S) as a function of temperature (T in Kelvin), according to the equation $\ln(S) = -E_A/kT$
52 $+ I$, where E_A = activation energy with an expected value of about -0.65 , k = Boltzmann constant ($8.62 \times$
53 10^{-5} eV K^{-1}), and I = intercept (Allen et al. 2002; Brown et al. 2004).

54 The species-energy theory proposed that areas with greater total available energy, such as the
55 tropics, have more diverse communities because they can support larger species populations with lower
56 likelihood of extinction (Wright 1983). This theory is also known as the more individuals hypothesis
57 (MIH), because larger species populations result in a greater total number of individuals (Srivastava and
58 Lawton 1998). The MIH predicts that richness scales positively with energy because richness is a function
59 of the number of individuals, which is proportional to the available energy, i.e. communities are energy-
60 limited. Further elaboration of the species-energy theory recognized that temporal variability in energy
61 may directly impact the richness of an area, given that periods of low energy are marked by higher
62 extinction rates, and consequently, by a lower number of individuals. Thus, models that included total
63 energy and energy variability explained the variability in bird and mammal species richness better than
64 either energy variable alone (Carrara and Vazquez 2010).

65 Finally, according to the climatic tolerance hypothesis, the tropics harbor greater richness because
66 their more benign warm and humid conditions fall within the physiological tolerance of many more
67 species compared to the cold and dry extra-tropical regions (Currie et al. 2004). However, the latitudinal
68 species patterns can be complicated by longitudinal effects, such as an east-west heterogeneity in rainfall,
69 which is particularly distinct at mid-latitudes (Terborgh 1973).

70 While the spatial variability of species richness has been extensively studied, we know
71 substantially less about the spatial and environmental dependence of the species abundance distribution
72 (SAD), defined here as the number of individuals across species in a community. In fact, due to a more
73 theoretical and statistical emphasis in the study of the SAD over the past seventy years (May 1975;
74 McGill et al. 2007; Ulrich et al. 2010), the empirical latitudinal, longitudinal, and elevational patterns of
75 the SAD and their underlying mechanisms, including environmental variability, have remained largely
76 unknown.

77 It is possible that the latitudinal gradient of richness is paralleled by a corresponding gradient of
78 the SAD. Brown (2014) suggested that as richness increases toward lower latitudes, the SAD may
79 transition from a less even log linear (a few very abundant and some very rare species) to a more even
80 curvilinear pattern (greater numbers of both intermediate and low abundance species) as a result of
81 intensified enemy effects. There is evidence that the SADs of real forest communities do become less
82 even at high latitudes when compared to neutrally assembled communities due to strong environmental
83 filtering that favors only a few well-adapted species (Qiao et al. 2015). However, there is no broad
84 empirical support for a tendency in the SAD toward greater evenness and lognormality at low latitudes.
85 On the contrary, a recent study of forest trees showed the opposite trend—preponderance of less even log-
86 series SADs at low latitudes but more even lognormal SADs at high latitudes, possibly as a result of
87 overall greater dispersal in the tropics, and subsequent accumulation of rare species (Ulrich et al. 2016a).
88 A global study of dryland plant communities reported an overall prevalence of lognormal compared to
89 log-series SADs, which was linked to environmental variability and stress but not to latitude (Ulrich et al.
90 2016b). There are even fewer and generally terrestrial studies of the SAD along elevational gradients,

91 which either have not reported any distinct patterns (Ulrich et al. 2016a; 2016b) or shown a transition
92 from log-series to lognormal SADs with altitude (Arellano et al. 2017). Therefore, there is clearly a need
93 for further research on the large-scale spatial patterns of the SAD, especially in aquatic ecosystems, which
94 have been largely neglected in this context.

95 Our overall goal was to explore the large scale spatial patterns in diatom species richness and
96 abundance distribution and determine if they are driven by the same environmental factors and whether
97 these factors are climatic, including average temperature, seasonal and diurnal temperature fluctuation,
98 and extreme temperatures, or water chemistry, i.e. nutrient levels, pH, and specific conductance.
99 Anthropogenic eutrophication is changing aquatic ecosystems globally by altering physico-chemistry,
100 increasing primary production, and affecting species richness, composition and abundance with
101 potentially strong ecological and evolutionary consequences (Smith and Schindler 2009; Alexander et al.
102 2017). A comprehensive review of the freshwater literature concluded that water chemistry variables were
103 stronger predictors of diatom community structure than temperature (Soininen 2007). However, climatic
104 factors outperformed water chemistry in predicting the distributions of individual diatom species across
105 northern latitudes, e.g. Finland (Pajunen et al. 2016). Therefore, the roles of climate vs. water chemistry
106 and their interaction with spatial factors in defining diatom community properties are still unresolved and
107 merit further research.

108 Here, we examined the shape of the SAD in freshwater diatom communities by calculating the
109 standard deviation (parameter σ) of a Poisson lognormal distribution model and skewness. Parameter σ
110 indicates how equitably abundances are distributed across abundance classes with lower values
111 suggesting higher equitability. Skewness measures the symmetry of the SAD compared to a lognormal
112 distribution. Negative values (left skew) indicate prevalence of rare species, while positive values (right
113 skew), greater frequency of abundant species.

114 We tested the following theories, hypotheses, and predictions. First, we tested whether $\ln(S) \sim$
115 $-E_A/kT$ with $-E_A$ between -0.6 and -0.7 , as postulated by the MTE (Brown et al. 2004). We predicted
116 that if this relationship holds, then parameter σ of the SAD would scale positively with E_A/kT ($\sigma \sim$

117 E_A/kT), given that $\sigma \sim -\ln(S)$, as empirically shown for freshwater diatoms (Passy 2016). Second, we
118 tested the predictions of the MIH that richness (S) increases with energy (here temperature, T) because S
119 is a positive function of the number of individuals (N), which in turn, is proportional to the amount of
120 energy (Srivastava and Lawton 1998). However, since the effect of T on S is indirect through N, the
121 expectation is that the correlations between T and N and N and S, would be equal to or greater than the
122 correlation between T and S (Currie et al. 2004; Carrara and Vazquez 2010). Given the above
123 consideration about the parameter σ - $\ln(S)$ relationship, we also predicted that if the MIH operates,
124 parameter σ would scale negatively with T and N, i.e. communities would become more even (lower σ) at
125 higher levels of available energy and higher numbers of individuals. Third, we extended our reasoning to
126 the energy variability and climatic tolerance hypotheses and tested if seasonal (and diurnal) energy
127 fluctuation and climatic harshness, respectively, decrease S, but increase parameter σ . Fourth, considering
128 the strong impact of water chemistry on freshwater ecosystems, we predicted that climatic variables alone
129 would be insufficient to describe the species richness and SAD patterns, but a combination of climatic
130 and water chemistry factors would be required. For our objectives 1-4, we assumed that if the shape of the
131 SAD is purely defined by richness, then parameter σ would respond to the same environmental predictors
132 as richness and in a complementary way, e.g. parameter σ would show positive responses to predictors
133 eliciting a negative response in richness and vice versa. However, if the SAD has unique environmental
134 underpinning, parameter σ may display distinct environmental responses. Finally, we examined the spatial
135 effects on richness and the SAD and how they constrained the community responses to climate and water
136 chemistry to gain a deeper understanding of the causes of large scale community variability.

137

138 **Materials and Methods**

139 **Datasets**

140 **US.** Data on stream water chemistry and diatom composition were collected from 669 distinct stream
141 localities in the US (fig. A1) by the National Water-Quality Assessment (NAWQA) Program
142 (<http://water.usgs.gov/nawqa>). Diatoms were sampled from a defined area of hard substrate or

143 macrophytes. Water chemistry, including total phosphorus, nitrate + nitrite, ammonia, pH, and specific
144 conductance, was measured for the month of algal collection (Table A1). Samples were taken in July and
145 August from 1993 to 2009 along a latitudinal range of 36 degrees, longitudinal range of 83 degrees, and
146 elevational range of 2676 m. Climatic variables, including mean annual temperature (T_{mean}), temperature
147 seasonality (standard deviation, T_{SD}), mean diurnal temperature range (mean difference between monthly
148 maximum and minimum temperatures, T_{diur}), minimum temperature of the coldest month (T_{min}), and
149 maximum temperature of the warmest month (T_{max}), were obtained from the WorldClim database
150 (Hijmans et al. 2005). Diatoms were identified in 590-700 cell counts and the total count was converted to
151 total density ($\text{cells}\cdot\text{cm}^{-2}$).

152

153 **Finland.** Data on climate (the same variables as in the US) and water chemistry, including total
154 phosphorus, pH, and specific conductance, were available for 100 streams in Finland (fig. A1). Diatoms
155 were sampled in July and August from 2001 to 2004 along a latitudinal range of 10 degrees, longitudinal
156 range of 7 degrees, and elevational range of 302 m. Diatoms were identified in counts of about 500 cells.

157

158 **Analysis of the species abundance distribution**

159 Using count data, community SADs were fit with a Poisson lognormal distribution model, which is
160 comparatively insensitive to sampling effort and performs equally well to other commonly used models
161 (Sæther et al. 2013; Baldrige et al. 2016). We estimated the standard deviation, parameter σ , with the
162 `poilog` R-package (Grøtan and Engen 2008). A comparison of the rank of the observed log likelihood with
163 the log likelihood derived from 1000 bootstraps provided a goodness of fit (gof) metric. Values of gof
164 between 0.05 and 0.95 indicate good fit. We also calculated the proportion of the species pool revealed by
165 the sample, which represents the proportion of the total area of the fitted Poisson lognormal distribution.

166 We calculated the skewness (γ) of the \log_2 -transformed counts of individuals and the standard
167 error of skewness (SES) as $(6/n)^{0.5}$. Skewness is considered significant if the absolute value of the ratio
168 γ/SES is greater than 2 (SYSTAT Software, Inc. 2009).

169 **Theory testing**

170 We performed a series of regression analyses to test the outlined theories and hypotheses. The metabolic
171 theory was tested with model 1 (Tables 1, 2) using $\ln(S)$ as a dependent variable. However, since the
172 richness response to $1/kT$ can be curvilinear (Algar et al. 2007), in a second model (model 2, Tables 1, 2),
173 we added a quadratic term. We further explored whether the predictions of the MTE can be extended to
174 the SAD parameter σ , given its dependence on $\ln(S)$, and calculated models 1 and 2 for parameter σ as
175 well (Tables 1, 2).

176 Testing the more individuals hypothesis required several equations, including models 3 and 4
177 from Table 1 (the dependent variable was richness), and equation (1) below, which contained a quadratic
178 term to account for potential nonlinearity in the density (N) response to mean temperature (T_{mean}).

179
$$\ln(N) = \ln(T_{\text{mean}}) + \ln(T_{\text{mean}})^2 \quad (1)$$

180 Our hypothesis that if the MIH operates, parameter σ would scale negatively with T and N, was tested
181 with models 3 and 4 from Table 1. These ideas were tested only with the US dataset because it contained
182 density data.

183 The climatic variability hypothesis, suggesting that variability in temperature would constrain
184 richness, and consequently the SAD, was tested with model 5 from Tables 1 and 2. The climatic tolerance
185 hypothesis, implicating extreme temperatures as driving factors of community properties, was tested with
186 model 6 from Tables 1 and 2 for both richness and the SAD.

187 Additional models from Tables 1 and 2 were calculated in order to test the responses of richness
188 and the SAD to climatic factors (model 7), nutrient (nitrogen and/or phosphorus) enrichment (model 8),
189 overall water chemistry (model 9), climate and nutrient enrichment (model 10), and climate and overall
190 water chemistry (model 11). The remaining models from Tables 1 and 2 determined the latitudinal (model
191 12), longitudinal (model 13), and elevational trends (model 14). Model 15 tested the overall spatial effect.
192 For the SAD, model 16 estimated the effect of richness on parameter σ . For each multiple regression
193 model in Tables 1 and 2, we performed backward selection of significant terms only to reduce
194 redundancy and collinearity (Table A2). All models were compared using the Akaike Information

195 Criterion (AIC). Models with lower AIC provided better fits. Variance partitioning assessed to what
196 extent the community responses to environmental factors were due to covariance of the environment with
197 latitudinal, longitudinal, and elevational gradients. Specifically, we estimated how much of the variance
198 explained by models 1-11 from Tables 1 and 2 was contributed by covariance of the respective predictors
199 in these models with the predictors in model 15. For the SAD, variance partitioning using models 1-15
200 also determined whether the response of parameter σ to the predictors (environmental and spatial) in these
201 models was in fact driven by their covariance with richness (model 16). The response of skewness to
202 climatic and water chemistry predictors was examined with multiple regressions using the backward
203 stepping procedure. Variance partitioning and multiple regressions were performed with SYSTAT 13
204 (SYSTAT Software, Inc. 2009).

205

206 **Results**

207 In both the US and Finnish datasets, the Poisson lognormal model fit the abundance data well ($0.36 \leq \text{gof}$
208 ≤ 0.53). Parameter σ was a comparatively strong and negative function of ln-transformed richness (slope
209 of -0.67 in the US, $n = 669$ and -0.83 in Finland, $n = 100$, $P < 0.00001$, Tables 1, 2), i.e. rich
210 communities had lower parameter σ and were thus more equitable. The relationship of ln-species richness
211 with the Boltzmann temperature factor ($1/kT$) was not significant in the US and convex in Finland,
212 inconsistent with the prediction of the MTE (Tables 1, 2, models 1 and 2). Parameter σ exhibited a
213 quadratic relationship with the Boltzmann temperature factor (more or less concave in both countries).
214 Thus, our expectation for opposing responses of ln-richness and parameter σ to $1/kT$ was not well
215 supported.

216 In testing the species-energy and the MIH, we examined the relationships among richness, mean
217 temperature, and density in the US dataset (Table 1, models 3 and 4). In contrast with the expectations of
218 these hypotheses, richness displayed a U-shaped response to mean temperature (Table 1, fig. 1) and a
219 marginally non-significant decline with density (slope = -0.64 , $R^2 = 0.01$, $p = 0.06$, $n = 669$), while the
220 density-mean temperature relationship was hump-shaped ($\ln N = 12.98 + 0.04T_{\text{mean}} - 0.01T_{\text{mean}}^2$, $R^2 =$

221 0.04, $P < 0.02$, $n = 667$). Thus, richness was related weakly to mean temperature but not to density,
222 indicating that the effect of temperature on richness was not due to a temperature dependence of density.
223 Parameter σ was weakly related to mean temperature (Table 1, fig. 2) and density (parameter $\sigma = 1.86 +$
224 $0.03\ln(N)^2$, $R^2 = 0.03$, $P < 0.00005$, $n = 669$), exhibiting a U-shaped response to both. In Finland, the
225 greatest richness was observed at intermediate temperature and the lowest parameter σ , at the highest
226 temperature (Table 2, figs 3, 4).

227 To test the role of climatic variability in defining community patterns, we examined the response
228 of richness and parameter σ to seasonal and diurnal temperature fluctuation (Tables 1, 2, model 5, figs 1-
229 4). In the US and Finland, temperature variability provided a better fit for both variables than mean
230 temperature, as indicated by their lower AIC. With the exception of parameter σ in Finland, diatom
231 richness and abundance equitability exhibited non-linear responses to diurnal and/or seasonal temperature
232 variability (Table A2).

233 The climatic tolerance hypothesis was tested using minimum (T_{\min}) and maximum temperatures
234 (T_{\max}) as predictors of richness and parameter σ (Tables 1, 2, model 6, figs 1-4). Contrary to the
235 expectation of diminished richness at the low temperature extreme, richness was the highest at both ends
236 of the T_{\min} gradient in the US and at lower T_{\min} in Finland. Maximum temperature had a notable effect
237 (quadratic) on richness only in Finland. In the US, parameter σ exhibited low values (high equitability) at
238 low T_{\min} and high T_{\max} levels. In Finland, parameter σ declined with both T_{\min} and T_{\max} . From all sets of
239 climatic variables, extreme temperatures provided the best fit in Finland, while temperature variability
240 outperformed the other variables in the US, as revealed by a comparison of their respective AIC (Tables
241 1, 2, models 4-6). However, the model including all significant climatic variables (Table 1, model 7)
242 explained substantially greater amount of the variance in both richness and parameter σ , indicating that
243 these community properties were products of multiple climatic influences.

244 In the US, all of the variance in richness and most of the variance in parameter σ explained by
245 water chemistry was contributed by nutrient levels, which generally had a positive effect on richness and
246 a negative effect on parameter σ (Table 1, models 8 and 9, figs 1, 2). Adding specific conductance to the

247 parameter σ model increased R^2 by only 3% (Tables 1, A2, model 9). In Finland, richness showed a
248 unimodal response to total phosphorus, while parameter σ exhibited a marginally non-significant U-
249 shaped response ($R^2 = 0.06$, $p = 0.053$). Predictability of richness improved by 5% after including pH in
250 the model (Table 2, model 9). Notably, the effect of total phosphorus on parameter σ became significant
251 and contributed 8% to the explained variance when the influence of specific conductance was accounted
252 for in the full water chemistry model (Tables 2, A2, model 9). The overall best environmental model
253 included climatic and nutrient variables only in the US but climatic, nutrient, and water chemistry
254 variables in Finland and explained 21-40% and 25-30% of the variance in richness and parameter σ ,
255 respectively (Tables 1, 2, A2, model 11). However, a model with climatic and nutrient variables only
256 provided comparable fits in Finland (Tables 2, A2, model 10).

257 The individual responses of richness and parameter σ to latitude, longitude, and elevation (Table
258 1, models 12-14) were weaker in the US (2-19% explained variance) but stronger in Finland (5-22%
259 explained variance). Although the spatial relationships were nonlinear, the richest communities in the US
260 were found at lower latitudes and elevations, and at westernmost and intermediate longitudes. The most
261 equitable communities (lowest parameter σ) in the US were observed at intermediate latitudes, longitudes,
262 and elevations. In Finland, richness was the greatest at intermediate latitudes, extreme longitudes, and
263 higher elevations, while parameter increased with latitude and responded unimodally to longitude and
264 elevation. Nevertheless, the model including all spatial factors provided the best fit for both richness and
265 parameter σ , capturing respectively 16-26% of the variance in the US and 18-24% in Finland (Tables 1, 2,
266 model 15).

267 We asked next if the behavior of richness and the SAD along climatic and water chemistry
268 gradients (Tables 1, 2, models 1-11) was driven by spatial variability of these gradients. To answer this
269 question, we calculated the covariance of environmental variables (Tables 1, 2, models 1-11) with spatial
270 predictors (Tables 1, 2, model 15) using variance partitioning. The amount of variance in richness and
271 parameter σ explained by individual predictor sets, e.g. mean temperature, temperature fluctuation,
272 extreme temperature, nutrients, and water chemistry, was generally due to covariance of the environment

273 with space (i.e., spatially structured environment). In more complex models, including a combination of
274 predictor sets, e.g. models 7, 10, and 11 (Tables 1, 2), spatially structured environment explained only a
275 portion of the variance. For parameter σ , which had a comparatively strong negative correlation with
276 richness, we also assessed whether environment and space contributed to the explained variance
277 independently of richness. Variance partitioning showed that in general, a substantial portion of the
278 explained variance in parameter σ was captured by the environment and space after the richness effect
279 was controlled for.

280 Skewness was positive in all communities in both the US and in Finland indicating a prevalence
281 of common species. Of the skewness values, 50% were significant ($\gamma/\text{SES} > 2$) in the US and 71% in
282 Finland. Skewness was either negatively (Pearson $r = -0.21$, $P < 0.0001$, the US) or non-significantly
283 (Finland) related to richness. In both countries, skewness was positively correlated with parameter σ
284 (Pearson $r = 0.42-0.46$, $P < 0.0001$), i.e. equitable communities were more symmetric with lower
285 skewness and these communities tended to be rich in the US. Skewness increased at intermediate T_{SD} and
286 low pH in the US and at intermediate specific conductance and T_{diur} but low total phosphorus in Finland
287 (Table 3).

288

289 **Discussion**

290 We examined the behavior of both diatom richness and abundance distribution along environmental and
291 spatial gradients in streams from two continents, testing a number of specific hypotheses. The response of
292 richness to the Boltzmann temperature factor and mean temperature contradicted the MTE and the
293 species-energy hypotheses, respectively, predicting a positive relationship (both hypotheses) with a
294 specific rate of increase (MTE). Deviations from the predictions of the MTE were previously reported for
295 both aquatic and terrestrial macroorganisms, where the richness-temperature relationship was found to be
296 curvilinear, linear with a slope significantly different from predictions, or not significantly different from
297 zero (Algar et al. 2007; Hawkins et al. 2007; Pinel-Alloul et al. 2013). In microbes, including lake
298 phytoplankton and soil bacteria, the richness response to temperature was also variable, following

299 respectively, a segmented (Segura et al. 2015) or linear pattern, flatter than observed in macrobes (Zhou
300 et al. 2016). A systematic analysis of multiple datasets across a broad range of terrestrial macroorganisms,
301 testing the predictions of the MTE, found that the richness-temperature relationship was positive in
302 datasets that included areas with colder winters but non-existent or negative in datasets from tropical,
303 subtropical, and warm temperate regions (Hawkins et al. 2007). A review of the species-energy
304 relationship noted that it is scale-dependent and transitions from unimodal at small scales to
305 monotonically increasing at large scales (Evans et al. 2005). Here, the relationship of richness with the
306 Boltzmann temperature factor and mean temperature was non-significant or weak in the US, but
307 comparatively stronger and unimodal in Finland, even though both datasets covered regional to
308 continental scales and included cold climate streams. The SAD response to the Boltzmann temperature
309 factor and mean temperature was weak and U-shaped in the US, but stronger and monotonic in Finland,
310 where inequality (parameter σ) decreased with temperature.

311 The present results were also inconsistent with the more individuals hypothesis, which so far, has
312 received mixed support (Srivastava and Lawton 1998; Kaspari et al. 2000; Mönkkönen et al. 2006;
313 Šímová et al. 2011). The hump-shaped behavior of density along the temperature gradient in the US
314 dataset indicated that higher temperatures actually decrease the number of individuals, which is in stark
315 contrast with the MIH prediction for a positive relationship. This pattern could be a consequence of
316 intensified grazing at higher temperatures due to accelerated herbivore metabolic and consumption rates
317 (O'Connor and Bruno 2009; West and Post 2016). Finally, the richness-density relationship was non-
318 significant, indicating that the temperature effect on richness was not indirect through density. These
319 findings suggest that i) the effect of temperature on both richness and the SAD is weak and may depend
320 on latitude; ii) richness and the SAD may exhibit different and not necessarily complementary behavior
321 along the temperature gradient; and iii) an overriding influence of factors other than temperature, given
322 the non-linear density response to temperature.

323 Temperature variability and temperature extremes were better descriptors of both richness and
324 parameter σ than mean temperature, but did not cause the responses predicted by the energy variability

325 and the climatic tolerance hypotheses, respectively. High richness was observed at both low and high
326 seasonality in the US and high seasonality Finland in contrast with the energy variability hypothesis,
327 which proposes that energy reduction during the cold seasons will lead to lower richness. This result can
328 be partially explained from the perspective of coexistence theory, which postulates that temporal
329 heterogeneity in resource supply increases biodiversity because it allows coexistence of species that
330 alternate between dominance and persistence at different times (Sommer 1985; Tilman and Pacala 1993).
331 In both the US and Finland, richness was high at the lowest minimum temperature, contrary to the
332 expectation of the climatic tolerance hypothesis. It is possible that diatoms deviate from the expectation of
333 this hypothesis because they inhabit the comparatively milder aquatic environment, less prone to extreme
334 fluctuations. Conversely, in terrestrial habitats, where temperatures reach much greater extremes, the
335 climatic tolerance hypothesis was supported (Šímová et al. 2011). Furthermore, low temperatures may
336 favor diatoms over cyanobacteria (Peterson and Grimm 1992; Van der Grinten et al. 2005) or green algae
337 (Roberts et al. 2003); therefore, lower temperature minima and stronger temperature seasonality may
338 prevent diatom exclusion and promote higher biodiversity of this algal group. High seasonality, low
339 temperature minima, and low temperature maxima were also associated with the highest abundance
340 equality (lowest parameter σ) in the US, which suggests more equitable resource partitioning. These
341 results indicate that a decrease in the temporal variability of temperature and an increase in the
342 temperature minima due to global warming (Xu et al. 2013), can lead to lower biodiversity and abundance
343 equitability in some stream diatoms.

344 Although climate had a stronger influence on both richness and parameter σ in the US and
345 Finland, water chemistry captured a notable amount of variance. Nutrients explained 8-14% of the
346 variance of richness and parameter σ , while specific conductance or pH added $\leq 5\%$, indicating that
347 nutrient availability was a more important source of community variability, especially in the US dataset,
348 which comprised primarily non-acidic streams. Richness was generally higher at intermediate or high
349 nutrient values, while equality in the SAD increased with nutrients. An increase of diatom richness with
350 nutrient supply has been previously documented and explained with the ability of more functional groups

351 (e.g., tolerant and sensitive to nutrient limitation) to coexist at high nutrients (Passy 2008; Soininen et al.
352 2016). Here, we further report that the SAD was also constrained by nutrient supply and in the US, it was
353 even more responsive than richness. A recent study on the SAD of stream diatom communities, sampled
354 across a land use gradient, revealed that their equitability increased (parameter σ decreased) with the
355 transition from forest to agriculture and suggested that nutrient enrichment was responsible for this
356 pattern (Passy 2016). In the present investigation we found support for this hypothesis and show that
357 communities indeed became more even at higher nutrient supply across a broad range of latitudes.
358 Nevertheless, the best model for richness and parameter σ included both climatic and water chemistry
359 variables. These variables explained substantial proportion of the variance in richness and parameter σ
360 independently of space, indicating that the environment was an important determinant of community
361 organization. While a combined effect of nutrients and temperature on microbial biodiversity has been
362 reported before (Soininen et al. 2016; Wang et al. 2016), this study is the first to demonstrate that
363 nutrients and climate co-controlled the variability in the diatom SAD at a continental scale.

364 Skewness was positive in both datasets in contrast with a large body of literature, documenting
365 negative skew as the dominant pattern (Gregory and Gaston 2000; Hubbell 2001; Magurran and
366 Henderson 2003). This discrepancy may be due to both sampling intensity and environmental influences.
367 Thus, when too few individuals are sampled, the left side of the SAD remains veiled and the right side
368 exhibits a positive skew (McGill 2003). Although in both datasets a comparatively large number of
369 individuals was sampled following standard protocols, the proportion of species revealed by the sample
370 had a median of 44-76%, indicating that some species remained veiled. However, skewness had
371 detectable correlations with environmental factors ($R^2 = 0.09-0.20$), pointing to ecological constraints on
372 the SAD symmetry as well. Skewness responded most strongly to temperature variability and pH in the
373 US, while water chemistry and to a lesser extent temperature variability were the underlying factors in
374 Finland. Thus, temperature variability proved to be a key driver of richness and the SAD, including its
375 evenness and symmetry. Determining the mechanisms controlling the distribution of common species, i.e.

376 the SAD symmetry, has important practical implications, given that these species are primarily
377 responsible for delivering ecosystem services (Winfree et al. 2015).

378 In both the US and Finland, diatom richness did not conform to the classical pattern of monotonic
379 latitudinal decrease, consistent with prior diatom studies (Passy 2010; Soininen et al. 2016). These studies
380 attributed the deviation from the classical pattern to the overriding effect of wetlands and their impact on
381 micronutrient availability. Here the non-linear response of richness to latitude was associated with a non-
382 linear response of seasonality, which was one of the major predictors of richness. This suggests that
383 temperature variability, in addition to micronutrient availability, may underlie the latitudinal richness
384 distributions. The expectation for increased evenness in the SAD at low latitudes (Brown 2014) was
385 confirmed only in Finland, while in the US, the most equitable communities were observed at mid
386 latitudes. The elevational response of richness—bimodal in the US but peaking at high elevations in
387 Finland—did not follow the common monotonic decline or hump-shaped patterns. Admittedly, the
388 elevational gradient in Finland was short and not sufficient to reveal the full variability in richness. The
389 SAD was most even at intermediate elevations in the US and at lower elevations in Finland, but this
390 response was weak. Thus, the latitudinal effects on diatom richness and the SAD became more prominent
391 at high latitudes (Finland) compared to lower latitudes (the US). At high latitudes, elevation constrained
392 richness as well, while the SAD remained weakly controlled by elevation across latitudes. These results
393 can be explained with the generally weak correlation of richness and the SAD with mean temperature,
394 which is a major covariate of both latitude and elevation. Notably, longitude had the strongest effect on
395 the SAD in the US, explaining 19% of its variance. This finding may be due in part to the longitudinal
396 dependence of total phosphorus with a peak at mid longitudes, where the SAD was most even (lowest
397 parameter σ). Total phosphorus had virtually no relationships with either latitude or elevation. These
398 findings reveal that richness and the SAD had unique responses to spatial variability, e.g. locations with
399 low richness did not necessarily have low equality (high values of parameter σ). This means that richness
400 and the SAD may have distinct environmental underpinning.

401 Diatom richness and parameter σ were positively correlated, but this correlation did not underlie
402 the responses of parameter σ to environmental and spatial variables, as indicated by variance partitioning.
403 In fact, the covariance of richness with these variables explained generally less than half of the SAD
404 variance, implying that much of the SAD response was independent of richness. Furthermore, in the US,
405 climate, water chemistry, and spatial models explained better the variance of parameter σ , while in
406 Finland, the pattern was reversed and richness was explained better than parameter σ by the respective
407 models. There were also differences in the environmental and spatial predictors that entered the
408 regression models of richness and parameter σ (Table A2) as well as in the shape of the richness and
409 parameter σ responses to common predictors (figs 1-4). For example, parameter σ displayed a monotonic
410 decline with nutrients, while the richness response was non-linear, indicating that eutrophication has a
411 differential effect on richness vs. abundance equality. The form of the SAD is strongly dependent on
412 richness and total abundance (Locey and White 2013) and the usefulness of the SAD for ecological
413 research has been questioned (Yen et al. 2013), in part because of its dependence on richness. The results
414 presented here demonstrate that the abiotic environment has distinct impacts on richness and the SAD,
415 and that the shape of the SAD can be predicted by climatic and water chemistry variables, emphasizing
416 the utility of the SAD in unravelling ecological mechanisms. Although we did not detect scaling
417 relationships between temperature and the SAD, we encourage future research on organisms that are more
418 temperature dependent than diatoms, to explore whether such relationships exist and thus add to the body
419 of knowledge on the temperature effects on community organization.

420

421 **References**

- 422 Alexander, T. J., P. Vonlanthen, and O. Seehausen. 2017. Does eutrophication-driven evolution change
423 aquatic ecosystems? *Philosophical Transactions of the Royal Society B-Biological Sciences*
424 372:20160041.
- 425 Algar, A. C., J. T. Kerr, and D. J. Currie. 2007. A test of Metabolic Theory as the mechanism underlying
426 broad-scale species-richness gradients. *Global Ecology and Biogeography* 16:170-178.

- 427 Allen, A. P., J. H. Brown, and J. F. Gillooly. 2002. Global biodiversity, biochemical kinetics, and the
428 energetic-equivalence rule. *Science* 297:1545-1548.
- 429 Allen, A. P., J. F. Gillooly, V. M. Savage, and J. H. Brown. 2006. Kinetic effects of temperature on rates
430 of genetic divergence and speciation. *Proceedings of the National Academy of Sciences (USA)*
431 103:9130-9135.
- 432 Arellano, G., M. N. Umana, M. J. Macia, M. I. Loza, A. Fuentes, V. Cala, and P. M. Jorgensen. 2017.
433 The role of niche overlap, environmental heterogeneity, landscape roughness and productivity in
434 shaping species abundance distributions along the Amazon-Andes gradient. *Global Ecology and*
435 *Biogeography* 26:191-202.
- 436 Baldrige, E., D. J. Harris, X. Xiao, and E. P. White. 2016. An extensive comparison of species-
437 abundance distribution models. *Peerj* 4: e2823 <https://doi.org/10.7717/peerj.2823>.
- 438 Brown, J. H. 2014. Why are there so many species in the tropics? *Journal of Biogeography* 41:8-22.
- 439 Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory
440 of ecology. *Ecology* 85:1771-1789.
- 441 Carrara, R. and D. P. Vazquez. 2010. The species-energy theory: a role for energy variability. *Ecography*
442 33:942-948.
- 443 Currie, D. J., G. G. Mittelbach, H. V. Cornell, R. Field, J. F. Guegan, B. A. Hawkins, D. M. Kaufman, J.
444 T. Kerr, T. Oberdorff, E. O'Brien, and J. R. G. Turner. 2004. Predictions and tests of climate-
445 based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters* 7:1121-1134.
- 446 Evans, K. L., P. H. Warren, and K. J. Gaston. 2005. Species-energy relationships at the macroecological
447 scale: a review of the mechanisms. *Biological Reviews* 80:1-25.
- 448 Gaston, K. J. 2000. Global patterns in biodiversity. *Nature* 405:220-227.
- 449 Gregory, R. D. and K. J. Gaston. 2000. Explanations of commonness and rarity in British breeding birds:
450 separating resource use and resource availability. *Oikos* 88:515-526.
- 451 Grøtan, V. and S. Engen. 2008. *poilog*: Poisson lognormal and bivariate Poisson lognormal distribution.
452 R package version 0.4. <http://cran.r-project.org/web/packages/poilog>.

- 453 Hawkins, B. A., F. S. Albuquerque, M. B. Araujo, J. Beck, L. M. Bini, F. J. Cabrero-Sanudo, I. Castro-
454 Parga, J. A. F. Diniz, D. Ferrer-Castan, R. Field, J. F. Gomez, J. Hortal, J. T. Kerr, I. J. Kitching,
455 J. L. Leon-Cortes, J. M. Lobo, D. Montoya, J. C. Moreno, M. A. Olalla-Tarraga, J. G. Pausas, H.
456 Qian, C. Rahbek, M. A. Rodriguez, N. J. Sanders, and P. Williams. 2007. A global evaluation of
457 metabolic theory as an explanation for terrestrial species richness gradients. *Ecology* 88:1877-
458 1888.
- 459 Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high resolution
460 interpolated climate surfaces for global land areas. *International Journal of Climatology* 25:1965-
461 1978.
- 462 Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University
463 Press, Princeton, New Jersey.
- 464 Kaspari, M., S. O'Donnell, and J. R. Kercher. 2000. Energy, density, and constraints to species richness:
465 Ant assemblages along a productivity gradient. *American Naturalist* 155:280-293.
- 466 Locey, K. J. and E. P. White. 2013. How species richness and total abundance constrain the distribution
467 of abundance. *Ecology Letters* 16:1177-1185.
- 468 Magurran, A. E. and P. A. Henderson. 2003. Explaining the excess of rare species in natural species
469 abundance distributions. *Nature* 422:714-716.
- 470 May, R. M. 1975. Patterns of species abundance and diversity. Pages 81-120 *in* M. L. Cody and J. M.
471 Diamond, eds. *Ecology and Evolution of Communities*. Harvard University Press, Cambridge,
472 MA.
- 473 McGill, B. J. 2003. Does Mother Nature really prefer rare species or are log-left-skewed SADs a
474 sampling artefact? *Ecology Letters* 6:766-773.
- 475 McGill, B. J., R. S. Etienne, J. S. Gray, D. Alonso, M. J. Anderson, H. K. Benecha, M. Dornelas, B. J.
476 Enquist, J. L. Green, F. L. He, A. H. Hurlbert, A. E. Magurran, P. A. Marquet, B. A. Maurer, A.
477 Ostling, C. U. Soykan, K. I. Ugland, and E. P. White. 2007. Species abundance distributions:

- 478 moving beyond single prediction theories to integration within an ecological framework. *Ecology*
479 *Letters* 10:995-1015.
- 480 Mittelbach, G. G., D. W. Schemske, H. V. Cornell, A. P. Allen, J. M. Brown, M. B. Bush, S. P. Harrison,
481 A. H. Hurlbert, N. Knowlton, H. A. Lessios, C. M. McCain, A. R. McCune, L. A. McDade, M. A.
482 McPeck, T. J. Near, T. D. Price, R. E. Ricklefs, K. Roy, D. F. Sax, D. Schluter, J. M. Sobel, and
483 M. Turelli. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and
484 biogeography. *Ecology Letters* 10:315-331.
- 485 Mönkkönen, M., J. T. Forsman, and F. Bokma. 2006. Energy availability, abundance, energy-use and
486 species richness in forest bird communities: a test of the species-energy theory. *Global Ecology*
487 *and Biogeography* 15:290-302.
- 488 O'Connor, M. I. and J. F. Bruno. 2009. Predator richness has no effect in a diverse marine food web.
489 *Journal of Animal Ecology* 78:732-740.
- 490 Pajunen, V., M. Luoto, and J. Soininen. 2016. Climate is an important driver for stream diatom
491 distributions. *Global Ecology and Biogeography* 25:198-206.
- 492 Passy, S. I. 2008. Continental diatom biodiversity in stream benthos declines as more nutrients become
493 limiting. *Proceedings of the National Academy of Sciences (USA)* 105:9663-9667.
- 494 Passy, S. I. 2010. A distinct latitudinal gradient of diatom diversity is linked to resource supply. *Ecology*
495 91:36-41.
- 496 Passy, S. I. 2016. Abundance inequality in freshwater communities has an ecological origin. *American*
497 *Naturalist* 187:502-516.
- 498 Peterson, C. G. and N. B. Grimm. 1992. Temporal variation in enrichment effects during periphyton
499 succession in a nitrogen-limited desert stream ecosystem. *Journal of the North American*
500 *Benthological Society* 11:20-36.
- 501 Pianka, E. R. 1966. Latitudinal gradients in species diversity: a review of concepts. *American Naturalist*
502 100:33-46.

- 503 Pinel-Alloul, B., A. Andre, P. Legendre, J. A. Cardille, K. Patalas, and A. Salki. 2013. Large-scale
504 geographic patterns of diversity and community structure of pelagic crustacean zooplankton in
505 Canadian lakes. *Global Ecology and Biogeography* 22:784-795.
- 506 Qiao, X. J., F. Jabot, Z. Y. Tang, M. X. Jiang, and J. Y. Fang. 2015. A latitudinal gradient in tree
507 community assembly processes evidenced in Chinese forests. *Global Ecology and Biogeography*
508 24:314-323.
- 509 Rahbek, C. 2005. The role of spatial scale and the perception of large-scale species-richness patterns.
510 *Ecology Letters* 8:224-239.
- 511 Roberts, E., J. Kroker, S. Korner, and A. Nicklisch. 2003. The role of periphyton during the re-
512 colonization of a shallow lake with submerged macrophytes. *Hydrobiologia* 506:525-530.
- 513 Rohde, K. 1992. Latitudinal gradients in species-diversity: the search for the primary cause. *Oikos*
514 65:514-527.
- 515 Sæther, B. E., S. Engen, and V. Grøtan. 2013. Species diversity and community similarity in fluctuating
516 environments: parametric approaches using species abundance distributions. *Journal of Animal*
517 *Ecology* 82:721-738.
- 518 Segura, A. M., D. Calliari, C. Kruk, H. Fort, I. Izaguirre, J. F. Saad, and M. Arim. 2015. Metabolic
519 dependence of phytoplankton species richness. *Global Ecology and Biogeography* 24:472-482.
- 520 Šímová, I., D. Storch, P. Keil, B. Boyle, O. L. Phillips, and B. J. Enquist. 2011. Global species-energy
521 relationship in forest plots: role of abundance, temperature and species climatic tolerances. *Global*
522 *Ecology and Biogeography* 20:842-856.
- 523 Smith, V. H. and D. W. Schindler. 2009. Eutrophication science: where do we go from here? *Trends in*
524 *Ecology & Evolution* 24:201-207.
- 525 Soininen, J. 2007. Environmental and spatial control of freshwater diatoms - A review. *Diatom Research*
526 22:473-490.
- 527 Soininen, J., A. Jamoneau, J. Rosebery, and S. I. Passy. 2016. Global patterns and drivers of species and
528 trait composition in diatoms. *Global Ecology and Biogeography* 25:940-950.

- 529 Sommer, U. 1985. Comparison between steady state and non-steady state competition: experiments with
530 natural phytoplankton. *Limnology and Oceanography* 30:335-346.
- 531 Srivastava, D. S. and J. H. Lawton. 1998. Why more productive sites have more species: An experimental
532 test of theory using tree-hole communities. *American Naturalist* 152:510-529.
- 533 Terborgh, J. 1973. On the notion of favorableness in plant ecology. *American Naturalist* 107:481-501.
- 534 Tilman, D. and S. Pacala. 1993. The Maintenance of Species Richness in Plant Communities. Pages 13-
535 25 in R. E. Ricklefs and D. Schluter, eds. *Species Diversity in Ecological Communities*.
536 University of Chicago Press, Chicago.
- 537 Ulrich, W., B. Kusumoto, T. Shiono, and Y. Kubota. 2016a. Climatic and geographic correlates of global
538 forest tree species-abundance distributions and community evenness. *Journal of Vegetation*
539 *Science* 27:295-305.
- 540 Ulrich, W., M. Ollik, and K. I. Ugland. 2010. A meta-analysis of species-abundance distributions. *Oikos*
541 119:1149-1155.
- 542 Ulrich, W., S. Soliveres, A. D. Thomas, A. J. Dougill, and F. T. Maestre. 2016b. Environmental correlates
543 of species rank abundance distributions in global drylands. *Perspectives in Plant Ecology*
544 *Evolution and Systematics* 20:56-64.
- 545 Van der Grinten, E., A. P. H. M. Janssen, K. de Mutsert, C. Barranguet, and W. Admiraal. 2005.
546 Temperature- and light-dependent performance of the cyanobacterium *Leptolyngbya foveolarum*
547 and the diatom *Nitzschia perminuta* in mixed biofilms. *Hydrobiologia* 548:267-278.
- 548 Wang, J. J., F. Y. Pan, J. Soininen, J. Heino, and J. Shen. 2016. Nutrient enrichment modifies
549 temperature-biodiversity relationships in large-scale field experiments. *Nature Communications*
550 7:13960, doi:10.1038/ncomms13960.
- 551 West, D. C. and D. M. Post. 2016. Impacts of warming revealed by linking resource growth rates with
552 consumer functional responses. *Journal of Animal Ecology* 85:671-680.
- 553 Willig, M. R., D. M. Kaufman, and R. D. Stevens. 2003. Latitudinal gradients of biodiversity: Pattern,
554 process, scale, and synthesis. *Annual Review of Ecology Evolution and Systematics* 34:273-309.

- 555 Winfree, R., J. W. Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015. Abundance of common
556 species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*
557 18:626-635.
- 558 Wright, D. H. 1983. Species-energy theory: an extension of species-area theory. *Oikos* 41:496-506.
- 559 Xu, L., R. B. Myneni, F. S. Chapin, T. V. Callaghan, J. E. Pinzon, C. J. Tucker, Z. Zhu, J. Bi, P. Ciais, H.
560 Tommervik, E. S. Euskirchen, B. C. Forbes, S. L. Piao, B. T. Anderson, S. Ganguly, R. R.
561 Nemani, S. J. Goetz, P. S. A. Beck, A. G. Bunn, C. Cao, and J. C. Stroeve. 2013. Temperature
562 and vegetation seasonality diminishment over northern lands. *Nature Climate Change* 3:581-586.
- 563 Yen, J. D. L., J. R. Thomson, and R. Mac Nally. 2013. Is there an ecological basis for species abundance
564 distributions? *Oecologia* 171:517-525.
- 565 Zhou, J. Z., Y. Deng, L. N. Shen, C. Q. Wen, Q. Y. Yan, D. L. Ning, Y. J. Qin, K. Xue, L. Y. Wu, Z. L.
566 He, J. W. Voordeckers, J. D. Van Nostrand, V. Buzzard, S. T. Michaletz, B. J. Enquist, M. D.
567 Weiser, M. Kaspari, R. Waide, Y. F. Yang, and J. H. Brown. 2016. Temperature mediates
568 continental-scale diversity of microbes in forest soils. *Nature Communications* 7:12083. doi:
569 10.1038/ncomms12083.

570 **Table 1. US diatoms.** Regression models (Eqn) testing the responses of ln-transformed species richness,
571 ln(S) (models 1, 2, and 15), species richness (models 3-15) and parameter σ (models 1-15) to
572 environmental and spatial variables. Covariance of the selected predictors (X) in the respective model
573 with i) the selected spatial variables in model 15 is given by $X \cap \text{Spa}$ and with ii) ln(S), by $X \cap \ln(S)$.
574 Covariance was calculated only for significant X. $n = 669$. AIC = Akaike Information Criterion. The AIC
575 of the best environmental model is boldfaced. T_{mean} = mean annual temperature, T_{SD} = temperature
576 seasonality (standard deviation), T_{diur} = mean diurnal temperature range, T_{min} = minimum temperature of
577 the coldest month, T_{max} = maximum temperature of the warmest month, TP = total phosphorus, Cond =
578 specific conductance, Lat = latitude, Long = longitude, Elev = elevation, and NS = non-significant.

Eqn	Predictor set	Richness			SAD parameter σ			
		AIC	R ²	X∩Spa	AIC	R ²	X∩Spa	X∩ln(S)
1	1/kT		NS			NS		
2	1/kT + (1/kT) ²		NS		1245	0.02	0.02	-0.01
3	ln(N) + ln(N) ²		NS		1237	0.03	0.06	0.00
4	T _{mean} + T _{mean} ²	5387	0.01	0.01	1245	0.02	0.02	-0.01
5	T _{SD} + T _{SD} ² + T _{diur} + T _{diur} ²	5331	0.09	0.08	1165	0.14	0.11	0.07
6	T _{min} + T _{min} ² + T _{max} + T _{max} ²	5351	0.07	0.05	1194	0.09	0.09	0.04
7	T _{mean} + T _{mean} ² + T _{SD} + T _{SD} ² + T _{diur} + T _{diur} ² + T _{min} + T _{min} ² + T _{max} + T _{max} ²	5299	0.15	0.07	1104	0.22	0.15	0.10
8	TP + TP ² + NO _x + NO _x ² + NH ₄ + NH ₄ ²	5323	0.11	0.07	1172	0.12	0.12	0.07
9	TP + TP ² + NO _x + NO _x ² + NH ₄ + NH ₄ ² + pH + pH ² + Cond + Cond ²	5323	0.11	0.07	1150	0.15	0.12	0.08
10	T _{mean} + T _{mean} ² + T _{SD} + T _{SD} ² + T _{diur} + T _{diur} ² + T _{min} + T _{min} ² + T _{max} + T _{max} ² + TP + TP ² + NO _x + NO _x ² + NH ₄ + NH ₄ ²	5259	0.21	0.10	1080	0.25	0.18	0.12
11	T _{mean} + T _{mean} ² + T _{SD} + T _{SD} ² + T _{diur} + T _{diur} ² + T _{min} + T _{min} ² + T _{max} + T _{max} ² + TP + TP ² + NO _x + NO _x ² + NH ₄ + NH ₄ ² + pH + pH ² + Cond + Cond ²	5259	0.21	0.10	1080	0.25	0.18	0.12

12	Lat + Lat ² + Lat ³	5384	0.02	–	1241	0.02	–	-0.01
13	Long + Long ² + Long ³	5352	0.06	–	1114	0.19	–	0.10
14	Elev + Elev ² + Elev ³	5375	0.03	–	1241	0.02	–	0.00
15	Lat + Lat ² + Lat ³ + Long + Long ² + Long ³ + Elev + Elev ² + Elev ³	5287	0.16	–	1061	0.26	–	0.13
16	ln(S)	–	–	–	1024	0.29	0.13	–

579

580 **Table 2. Finnish diatoms.** Regression models (Eqn) testing the responses of ln-transformed species
581 richness, ln(S) (models 1, 2, and 15), species richness (models 3-15) and parameter σ (models 1-15) to
582 environmental and spatial variables. Covariance of the selected predictors (X) in the respective model
583 with i) the selected spatial variables in model 15 is given by $X \cap \text{Spa}$ and with ii) ln(S), by $X \cap \ln(S)$. $n =$
584 100. The AIC of the best environmental model is boldfaced. Abbreviations as in Table 1.

Eqn	Predictor set	Richness			SAD parameter σ			
		AIC	R ²	X∩Spa	AIC	R ²	X∩Spa	X∩ln(S)
1	1/kT		NS		144	0.07	0.07	-0.03
2	1/kT + (1/kT) ²	68	0.07	0.05	144	0.07	0.07	-0.03
3	ln(N) + ln(N) ²	–	–	–	–	–	–	–
4	T _{mean} + T _{mean} ²	827	0.07	0.06	144	0.07	0.07	-0.03
5	T _{SD} + T _{SD} ² + T _{diur} + T _{diur} ²	814	0.21	0.18	136	0.16	0.13	0.06
6	T _{min} + T _{min} ² + T _{max} + T _{max} ²	812	0.23	0.12	133	0.18	0.17	0.07
7	T _{mean} + T _{mean} ² + T _{SD} + T _{SD} ² + T _{diur} + T _{diur} ² + T _{min} + T _{min} ² + T _{max} + T _{max} ²	801	0.34	0.23	128	0.25	0.17	0.11
8	TP + TP ²	819	0.14	0.13		NS		
9	TP + TP ² + pH + pH ² + Cond + Cond ²	815	0.19	0.13	140	0.13	0.09	0.03
10	T _{mean} + T _{mean} ² + T _{SD} + T _{SD} ² + T _{diur} + T _{diur} ² + T _{min} + T _{min} ² + T _{max} + T _{max} ² + TP + TP ²	797	0.36	0.22	126	0.30	0.18	0.14
11	T _{mean} + T _{mean} ² + T _{SD} + T _{SD} ² + T _{diur} + T _{diur} ² + T _{min} + T _{min} ² + T _{max} + T _{max} ² + TP + TP ² + pH + pH ² + Cond + Cond ²	792	0.40	0.22	125	0.29	0.16	0.09
12	Lat + Lat ² + Lat ³	813	0.20	–	134	0.18	–	0.06

13	$\text{Long} + \text{Long}^2 + \text{Long}^3$	812	0.22	–	145	0.06	–	0.05
14	$\text{Elev} + \text{Elev}^2 + \text{Elev}^3$	813	0.20	–	146	0.05	–	0.00
15	$\text{Lat} + \text{Lat}^2 + \text{Lat}^3 + \text{Long} + \text{Long}^2 + \text{Long}^3 + \text{Elev} + \text{Elev}^2 + \text{Elev}^3$	809	0.24	–	134	0.18	–	0.06
16	$\ln(S)$	–	–	–	128	0.21	0.06	–

585

586 **Table 3.** Regression models of skewness in the US and Finland. Std. = standardized. Abbreviations as in
 587 Table 1.

588

Effect	Std. coefficient	Standard error	<i>t</i>-value	<i>p</i>-value
US, $R^2 = 0.09$, $n = 669$				
Constant	0.00	0.02	43.57	0.000000
T _{SD}	-0.11	0.01	-2.34	0.02
T _{SD} ²	-0.21	0.00	-4.92	0.000001
T _{diur}	-0.13	0.01	-2.93	0.003
T _{diur} ²	0.13	0.00	3.07	0.002
NO _x	-0.10	0.01	-2.65	0.01
pH	-0.15	0.03	-3.71	0.0002
Finland, $R^2 = 0.20$, $n = 100$				
Constant	0.00	0.05	20.88	0.000000
T _{diur} ²	-0.31	0.08	-2.54	0.013
TP ²	0.31	0.04	2.71	0.008
Cond ²	-0.33	0.07	-2.85	0.005

589

590

591 **Figure legend**

592 **Figure 1.** Relationships between richness and climatic (A-E), water chemistry (F-J), and spatial variables
593 (K-M) in the US dataset. The fits were generated by LOWESS with tension of 0.5. All predictors were
594 centered on the mean. $n = 669$. T_{mean} = mean annual temperature, T_{SD} = temperature seasonality (standard
595 deviation), T_{diur} = mean diurnal temperature range, T_{min} = minimum temperature of the coldest month,
596 T_{max} = maximum temperature of the warmest month, TP = total phosphorus.

597

598 **Figure 2.** Relationships between parameter σ and climatic (A-E), water chemistry (F-J), and spatial
599 variables (K-M) in the US dataset. The fits are generated by LOWESS with tension of 0.5. All predictors
600 were centered on the mean. $n = 669$. Abbreviations as in fig. 1.

601

602 **Figure 3.** Relationships between richness and climatic (A-E), water chemistry (F-H), and spatial variables
603 (I-K) in the Finnish dataset. The fits are generated by LOWESS with tension of 0.5. All predictors were
604 centered on the mean. $n = 100$. Abbreviations as in fig. 1.

605

606 **Figure 4.** Relationships between parameter σ and climatic (A-E), water chemistry (F-H), and spatial
607 variables (I-K) in the Finnish dataset. The fits are generated by LOWESS with tension of 0.5. All
608 predictors were centered on the mean. $n = 100$. Abbreviations as in fig. 1.

609 **Appendix**

610 **Table A1.** Basic statistics of climatic, water chemistry and spatial variables included in the regression
 611 analyses (Tables 1, 2). T_{mean} = mean annual temperature, T_{SD} = temperature seasonality (standard
 612 deviation), T_{diur} = mean diurnal temperature range, T_{min} = minimum temperature of the coldest month, and
 613 T_{max} = maximum temperature of the warmest month.

614

Variable	Minimum	Maximum	Median	Mean	SD
US					
Latitude (degrees)	25.40	61.77	41.64	41.58	4.58
Longitude (degrees)	-154.17	-70.74	-92.08	-95.63	16.48
Elevation (m)	57.00	2733.00	303.00	483.85	507.35
Total phosphorus ($\text{mg}\cdot\text{L}^{-1}$)	0.002	3.40	0.07	0.16	0.31
Nitrite + nitrate ($\text{mg}\cdot\text{L}^{-1}$)	0.01	13.95	0.46	1.36	2.22
Ammonia ($\text{mg}\cdot\text{L}^{-1}$)	0.002	5.80	0.03	0.06	0.25
pH	2.95	9.60	7.90	7.83	0.56
Specific conductance ($\mu\text{S}\cdot\text{cm}^{-1}$)	11.00	23595.65	476.00	539.10	966.64
T_{mean} ($^{\circ}\text{C}$)	-0.80	23.70	9.60	9.86	3.59
T_{sd}	3.19	12.58	9.05	8.93	1.70
T_{diur} ($^{\circ}\text{C}$)	7.80	19.60	12.10	12.54	1.86
T_{min} ($^{\circ}\text{C}$)	-22.20	13.40	-9.40	-8.70	5.70
T_{max} ($^{\circ}\text{C}$)	15.20	36.30	29.20	29.35	2.87
Finland					
Latitude (degrees)	60.27	70.06	66.26	65.91	2.81
Longitude (degrees)	23.28	30.44	27.02	27.04	2.09
Elevation (m)	18.00	320.00	180.00	177.49	81.91

Total phosphorus ($\text{mg}\cdot\text{L}^{-1}$)	0.00	0.19	0.02	0.03	0.04
pH	4.50	8.20	7.00	6.80	0.81
Specific conductance ($\mu\text{S}\cdot\text{cm}^{-1}$)	9.40	277.00	44.75	65.37	59.24
T_{mean} ($^{\circ}\text{C}$)	-2.70	5.00	-0.50	0.28	2.03
T_{sd}	6.93	10.19	9.52	9.29	0.80
T_{diur} ($^{\circ}\text{C}$)	6.50	9.20	8.30	8.21	0.67
T_{min} ($^{\circ}\text{C}$)	-21.30	-9.10	-17.15	-16.60	3.29
T_{max} ($^{\circ}\text{C}$)	14.80	21.00	18.75	18.78	1.66

615

616 **Table A2.** Significant variables ($P < 0.05$) included in models 1-15 from Tables 1 (US) and 2 (Finland).

617 Abbreviations as in Table 1.

618

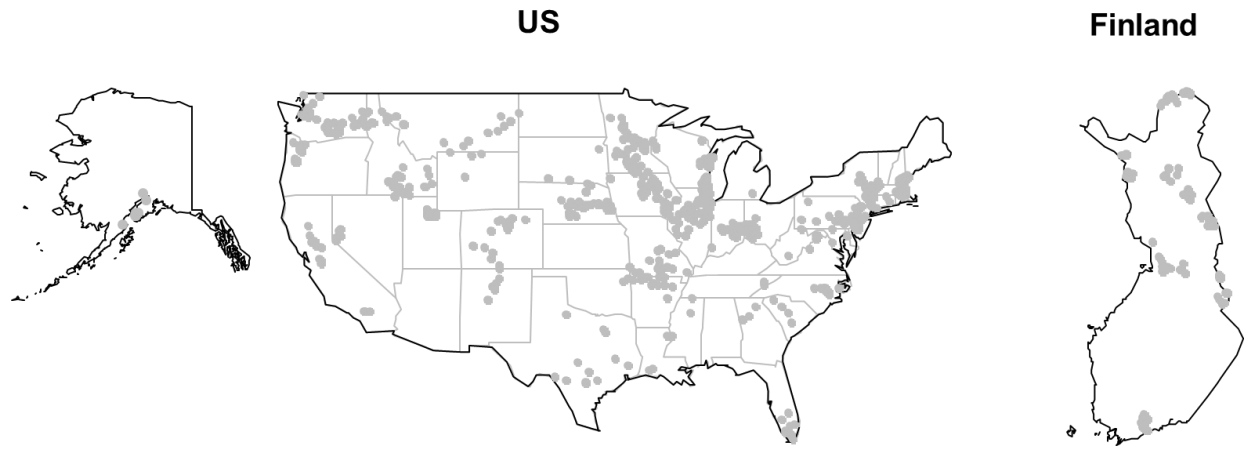
Eqn	US		Finland	
	Richness	Parameter σ	Richness	Parameter σ
1	NS	1/kT	NS	1/kT
2	NS	1/kT + (1/kT) ²	1/kT + (1/kT) ²	(1/kT) ²
3	NS	ln(N) ²	—	—
4	T _{mean} ²	T _{mean} + T _{mean} ²	T _{mean} ²	T _{mean}
5	T _{SD} + T _{SD} ²	T _{SD} + T _{SD} ² + T _{diur} + T _{diur} ²	T _{SD} + T _{diur} + T _{diur} ²	T _{SD} + T _{diur}
6	T _{min} + T _{min} ² + T _{max} + T _{max} ²	T _{min} + T _{min} ² + T _{max} + T _{max} ²	T _{min} + T _{max} + T _{max} ²	T _{min} + T _{max} ²
7	T _{mean} + T _{mean} ² + T _{SD} + T _{SD} ² + T _{diur} + T _{diur} ² + T _{min} + T _{max}	T _{SD} + T _{SD} ² + T _{diur} + T _{min} + T _{min} ² + T _{max}	T _{SD} + T _{diur} ² + T _{min} + T _{max} + T _{max} ²	T _{mean} ² + T _{diur} + T _{min} ² + T _{max} ²
8	TP + TP ² + NO _x	TP + TP ² + NO _x	TP ²	NS
9	TP + TP ² + NO _x	TP + Cond	TP ² + pH ²	TP ² + Cond ²
10	T _{mean} + T _{SD} + T _{SD} ² + T _{diur} + T _{min} + T _{max} + T _{max} ² + TP + NO _x + NH ₄	T _{SD} + T _{SD} ² + T _{diur} + T _{min} + T _{min} ² + T _{max} + TP	T _{mean} + T _{diur} + T _{min} + T _{max} ² + TP ²	T _{mean} + T _{SD} + T _{diur} + T _{min} + T _{max} ² + TP ²
11	T _{mean} + T _{SD} + T _{SD} ² + T _{diur} + T _{min} + T _{max}	T _{SD} + T _{SD} ² + T _{diur} + T _{min} + T _{min} ² + T _{max} + TP	T _{mean} + T _{diur} + T _{min} + T _{max} ² + TP ² + pH ²	T _{SD} + T _{diur} ² + T _{max} ² + TP + Cond

	$+ T_{\max}^2 + TP + NO_x$			
	$+ NH_4$			
12	$Lat + Lat^2 + Lat^3$	Lat^2	$Lat^2 + Lat^3$	$Lat^2 + Lat^3$
13	$Long^2 + Long^3$	$Long^2 + Long^3$	$Long + Long^2$	$Long^2$
14	$Elev + Elev^3$	$Elev^2$	$Elev + Elev^2$	$Elev^2$
	$Lat + Long^2 +$	$Lat^3 + Long + Long^2$		
15	$Long^3 + Elev^2 +$	$+ Long^3 + Elev +$	$Lat^2 + Long^2$	$Lat^2 + Lat^3$
	$Elev^3$	$Elev^2$		

619

620 **Figure A1.** Map of the study streams in the US and Finland.

621



622

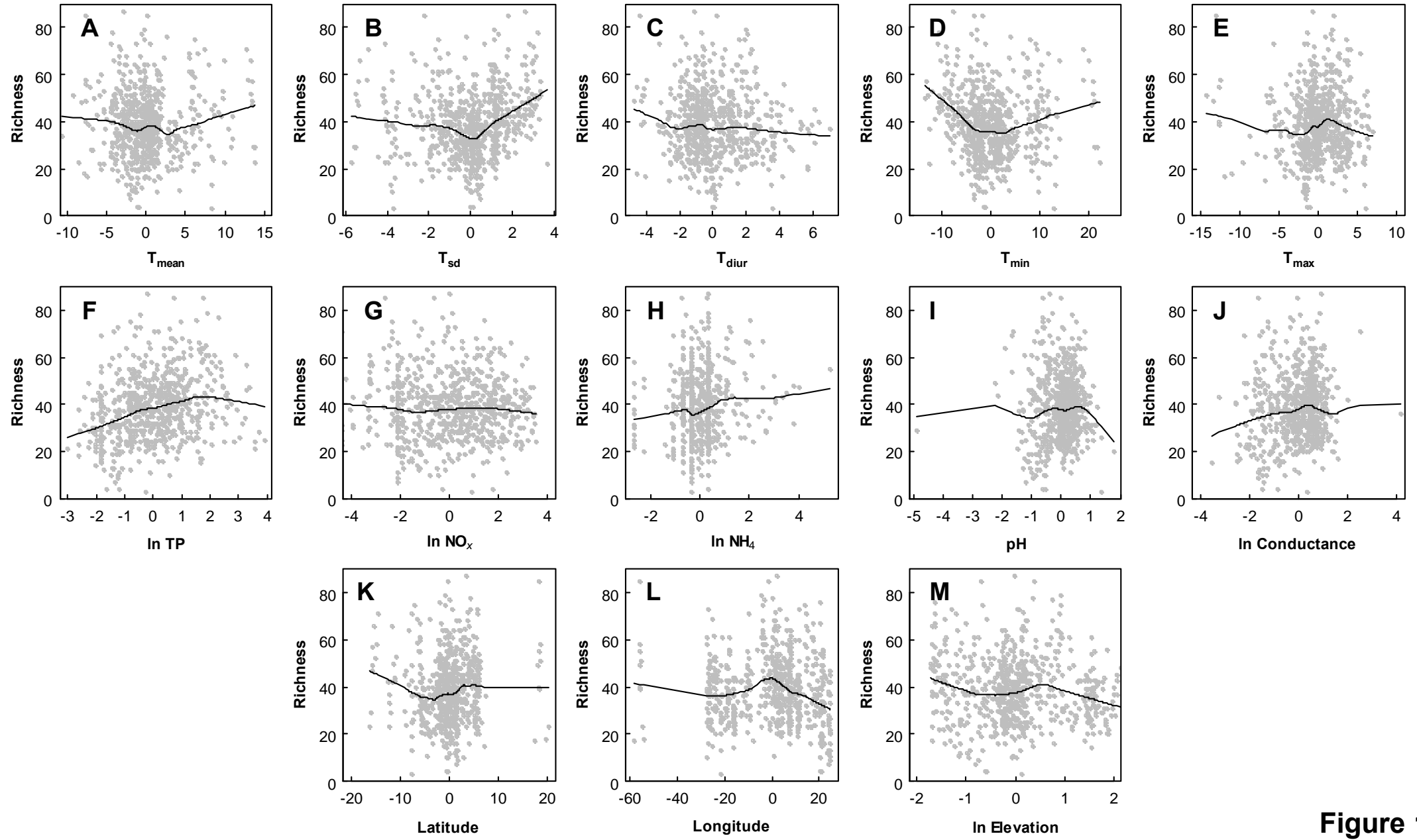


Figure 1

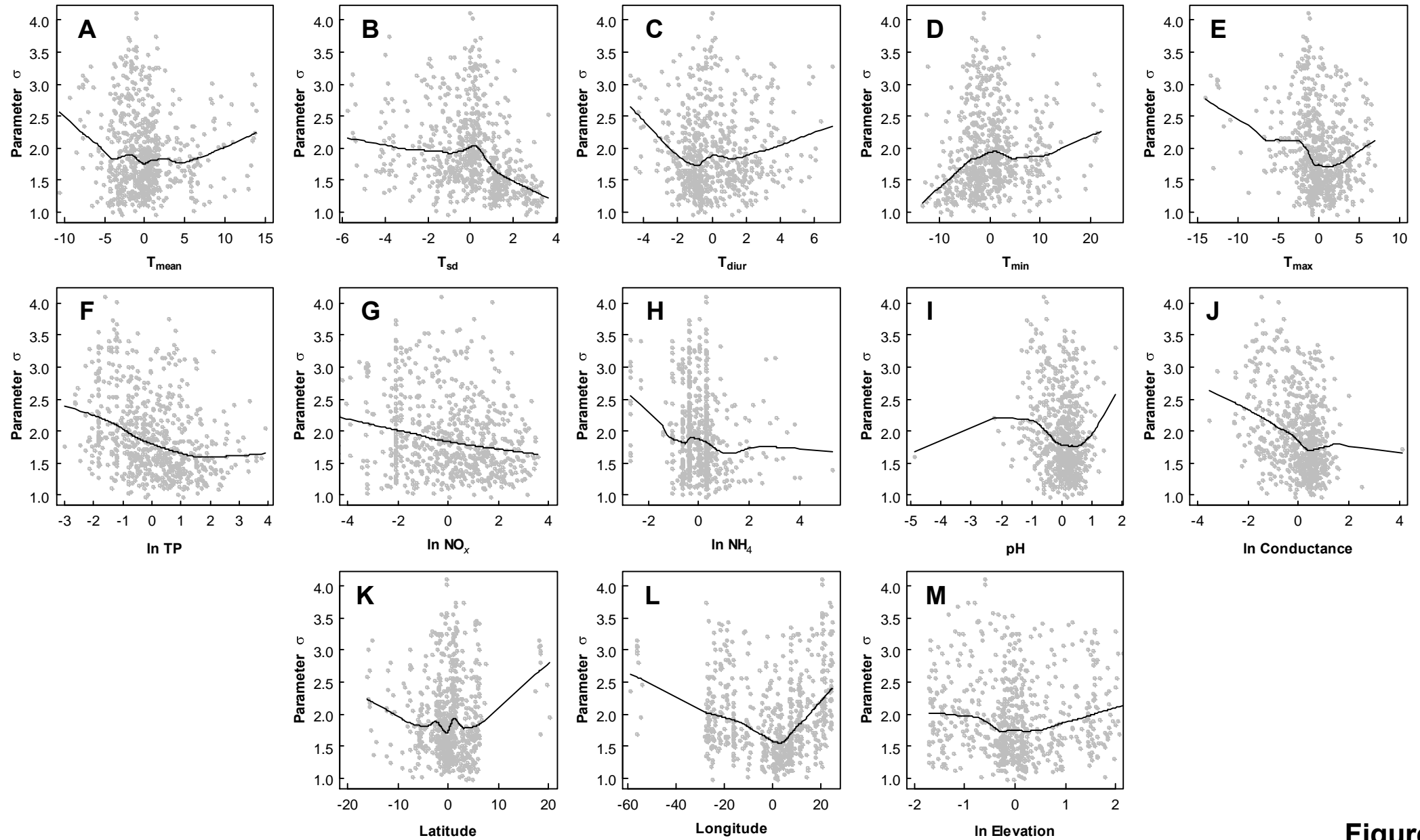


Figure 2

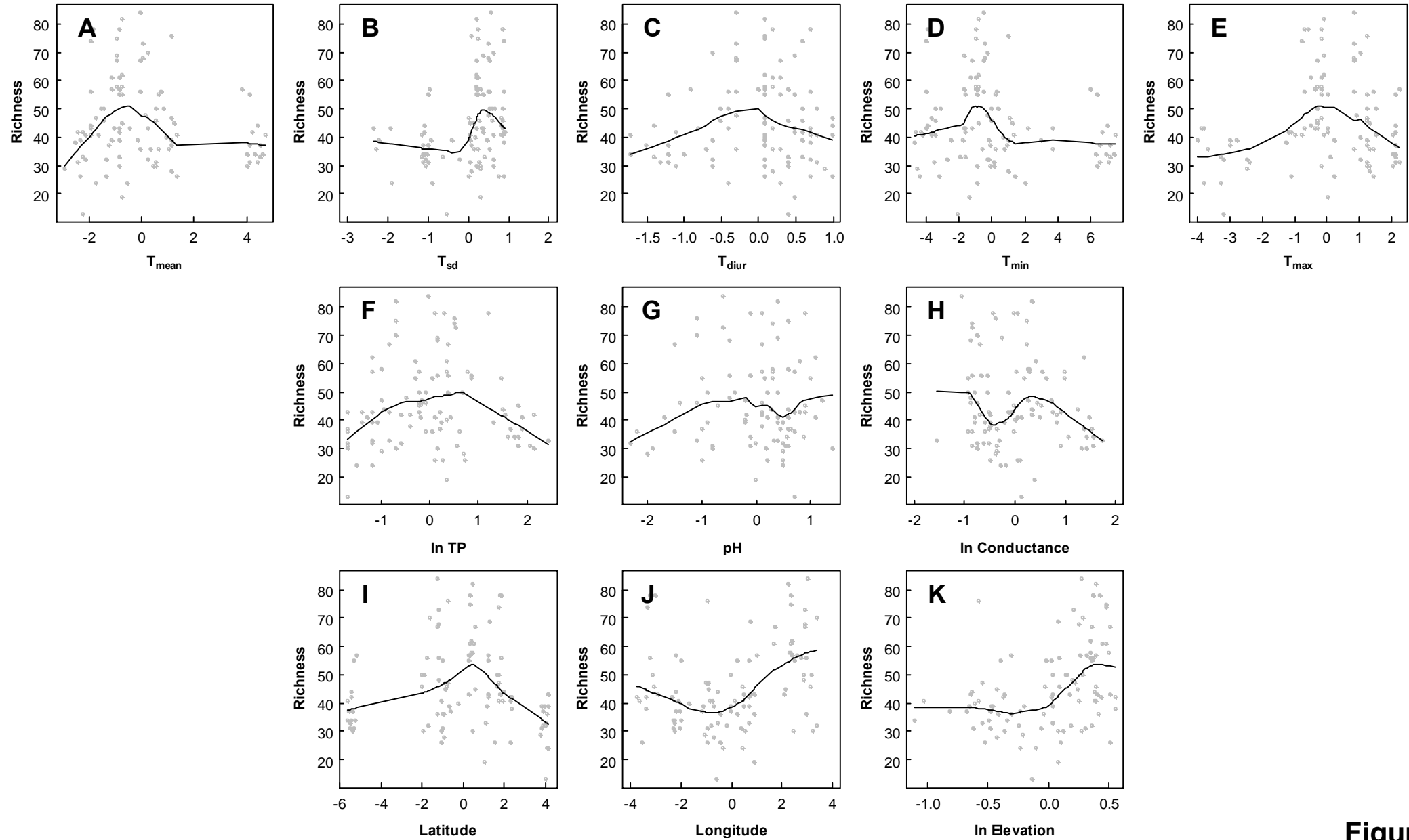


Figure 3

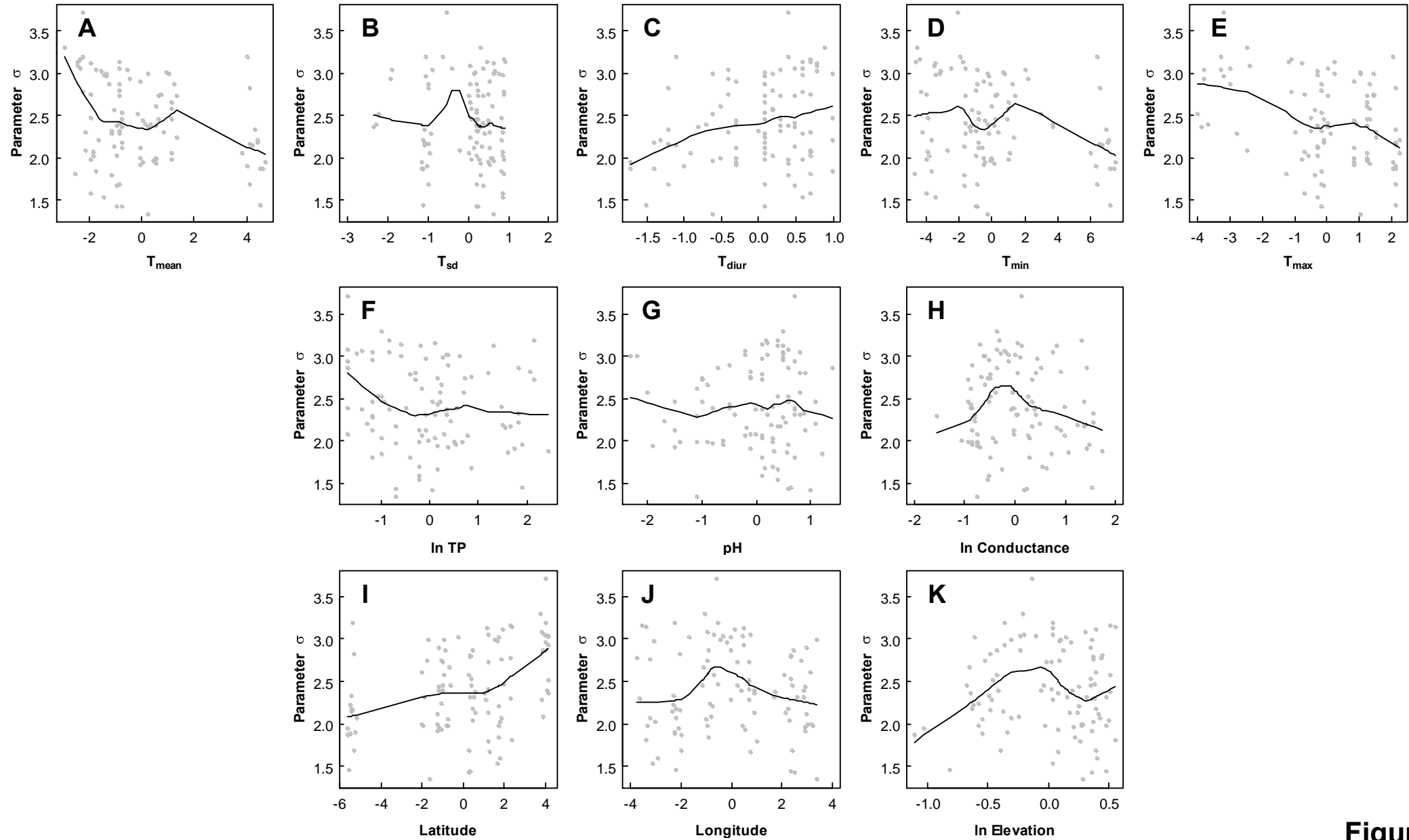


Figure 4