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Passy, Sophia I.

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**Environmental filtering and taxonomic relatedness underlie
the species richness-evenness relationship**

**Sophia I. Passy^{1a}, Marius Bottin², Janne Soininen³ &
Helmut Hillebrand⁴**

¹Department of Biology, University of Texas at Arlington, Box 19498, Arlington,
Texas 76019-0498, USA;

²University of Bordeaux. UMR INRA 1202 BioGeCo, F33400 Talence, France, e-mail:
maris.bottin@u-bordeaux.fr;

³Department of Geosciences and Geography, P.O. Box 64, FIN-00014 University of Helsinki,
Helsinki, Finland, e-mail: janne.soininen@helsinki.fi;

⁴Institute for Chemistry and Biology of the Marine Environment (ICBM), Carl-von-Ossietzky
University Oldenburg, Schleusenstrasse 1, 26382 Wilhelmshaven, Germany, e-mail:
hillebrand@icbm.de

^aCorresponding author: e-mail: sophia.passy@uta.edu

phone: +1 (817)-272-2415, fax: +1 (817)-272-2855

Abstract

We examined the relationship between species richness (S) and evenness (J) within a novel, community assembly framework. We hypothesized that environmental stress leads to filtering (increasing the proportional abundance of tolerant species) and taxonomic dispersion (decreasing the taxonomic relatedness among species within genera and families). Environmental filtering would cause a decline in S by eliminating stress-sensitive species and a reduction of J by allowing only tolerant species to maintain large populations. Taxonomic relatedness would influence both S and J by controlling the nature of interspecific interactions—positive under taxonomic dispersion vs. negative under taxonomic clustering. Therefore, the S-J relationship is a product of environmental filtering and taxonomic relatedness. We tested this framework using continental data on watershed environment and diatom and fish communities in US streams. We confirmed that i) environmental stress, defined by basin forest cover, temperature, and slope, caused filtering (increased tolerant species abundance) and taxonomic dispersion (elevated genus:species and family:species ratios); ii) both S and J declined with filtering but increased with taxonomic clustering; and iii) the role of filtering on J was pronounced only under stressful conditions, while taxonomic clustering remained an important predictor of J across stressful and benign environments.

Key words: community assembly; competition; complementarity; functional groups; limiting similarity; stress gradient hypothesis

Introduction

Two aspects of biodiversity, namely richness (S) or the number of species in a community and evenness or the equitability in species' abundance (J), have drawn considerable interest in ecology because of their correlations with important community properties, such as biomass production and decomposition, susceptibility to invaders, stress resistance, and extinction risks (Wilsey & Potvin, 2000; Kennedy et al., 2002; Dangles & Malmqvist, 2004; Wittebolle et al., 2009; Blois et al., 2010). The relationship of S and J has also been extensively investigated across habitats and organismal groups, including algae, plants, fungi, invertebrates, and vertebrates, and shown to depend on both the environment and the level of species richness, i.e. the shape of the relationship changes at a threshold richness (Stirling & Wilsey, 2001; Bock et al., 2007; Soininen et al., 2012). This implies that both abiotic and biotic forces affect the S-J relationship but their relative importance is not well understood. Here, we explore the relationship between S and Pielou's evenness (J) from the perspective of community assembly theory to address a fundamental ecological question—what is the interplay between environmental stress and biotic forcing in driving the patterns of biodiversity?

Two seemingly opposing theories have been invoked to explain community assembly at local scales—limiting similarity and environmental filtering (Weiher & Keddy, 1995; Mayfield & Levine, 2010; HilleRisLambers et al., 2012). According to the limiting similarity model (MacArthur & Levins, 1967), competition for limiting resources selects for niche differentiation and trait divergence among coexisting species. In contrast, the environmental filtering idea proposes that the environment supports only species with converging traits that confer positive fitness under the local conditions (Keddy, 1992). Both limiting similarity (Stubbs & Wilson, 2004; Montaña et al., 2014) and environmental filtering (Peres-Neto 2004; Mouillot et al., 2007;

Mouchet et al., 2013) have been shown to shape local communities. Here we suggest that these processes may function together in controlling the patterns of biodiversity (Fig. 1).

Environmental filtering under stressful conditions will reduce richness by allowing growth of only a small subset of the regional pool that exhibits survival traits, e.g. tolerance to resource limitation or disturbance, although some poorly adapted species can also be present due to random dispersal. Filtering will also decrease evenness because it disrupts the balance between growth and immigration of the resident species—tolerant species can reproduce and grow in numbers, while the populations of the less tolerant species will be supported exclusively by immigration and will remain small (Passy, 2016). Consistent with these expectations, both richness and evenness have been reported to decline with environmental stress (Sabater, 2000; Feio et al., 2010; Murphy & Romanuk, 2014; Passy, 2016). However, to share the limited niche space in unfavorable environments, tolerant species must diverge in coexistence traits, ensuring complementary resource acquisition, e.g. microhabitat or diet preferences.

In benign conditions, the environmental filtering weakens and more species from the regional pool, including sensitive forms, can reproduce, contribute significantly to community biomass, and increase both richness and evenness. Favorable habitats have longer and more numerous environmental gradients, i.e. more diverse gradient structure, due to the emergence of complex environment-community interactions. For example, in running waters, the thick benthic mats developing in productive habitats generate longer internal resource gradients than the thin biofilms in unproductive streams (Stevenson & Glover, 1993; Passy, 2008). It has been suggested that a diverse gradient structure is linked to greater niche overlap and phylogenetic similarity among coexisting species, while simplified gradient makeup, to stronger niche differentiation and increased phylogenetic distinction (Passy & Legendre, 2006). The argument

is that variability in resource supply allows coexistence of species with small differences in resource requirements, expressed as divergence at a species level. In contrast, when the gradient structure is simplified and gradients are short or non-existent, species must either utilize different resources or develop different disturbance adaptations to avoid competitive exclusion. Such large physiological and/or morphological differences are associated with greater taxonomic divergence, e.g. at the genus and family categories (Passy & Legendre, 2006). Thus, we expect stressful conditions to restrict biota to a few tolerant (filtering) but taxonomically dissimilar species (limiting similarity), whereas benign conditions to provide for a greater diversity of taxonomically related forms (Fig. 1a).

As phylogenetic structure determines the distribution of traits, it is linked to species interactions, e.g. competition and complementarity (Webb et al., 2002; HilleRisLambers et al., 2012), which may impact the relationship between richness and evenness. Evenness can increase at low richness as a result of positive interactions (complementarity or facilitation) among taxonomically distant species (Fig. 1). For example, under stressful nitrogen limiting conditions, nitrogen fixers stimulate biomass production of distantly related non-nitrogen fixers through facilitation (Agawin et al., 2007). Conversely, negative interactions (competition among taxonomically similar species) can elevate evenness at high richness by preventing dominance (Fig. 1). This model can explain the shift in species interactions from negative (competition) to positive (complementarity and facilitation) with the transition of the environment from benign to harsh (Bertness & Callaway, 1994; Bruno et al., 2003; Wang et al., 2013) as a consequence of trait convergence corresponding to increased taxonomic clustering.

Here, we used continental data on watershed characteristics, and diatom and fish communities in US streams to test our predictions (Fig. 1). The degree of environmental filtering

was measured by the ratio (ST) of species sensitive vs. tolerant of environmental stress, e.g. resource limitation and physical or chemical disturbance. Thus, low ST ratios (higher abundance of tolerant species), found in harsh environments, indicated filtering (selection for survival traits), while high ST ratios (numerical dominance of sensitive species) were suggestive of environmental favorability. Evaluating the form of species interactions (positive vs. negative) is intractable but it is expected to correlate with phylogenetic distance with low values (phylogenetic similarity) linked to competition (Violle et al., 2011) and high values (phylogenetic dissimilarity), to facilitation and complementarity (Valiente-Banuet & Verdu, 2007; Venail & Vives, 2013). Nevertheless, the relationship between phylogenetic distance and interspecific interactions has been controversial (Venail et al., 2014) and further research is necessary to confirm whether the hypothesized correlations do exist in the organismal groups studied here. We adopted the ratio of higher taxa richness to species richness, which reflects the taxonomic redundancy within terminal groups, as a proxy measure of species interactions. Low ratios (taxonomic similarity) were likely to be associated with competition, whereas high ratios (taxonomic dissimilarity), with complementarity.

To assess the effects of environmental filtering and taxonomic clustering on S, J, and their relationship, we constructed a structural equation model (SEM) (Fig. 1b). We used the family:species (FS) ratio to represent taxonomic clustering (low FS values indicating high taxonomic clustering), but the same results are expected with the genus:species ratio. The sensitive:tolerant (ST) species ratio reflected environmental filtering (low ST values indicating strong filtering). Given their opposing behavior along the environmental favorability gradient (Fig. 1a), the FS ratio and the ST ratio were projected to be negatively correlated (Fig. 1b). The

SEM also predicted similar responses of S and J to the FS and ST ratios, and consequently, a positive S-J relationship.

Materials and methods

We used stream community data from most major watersheds and aquifers in the US, generated by the NAWQA program of the US Geological Survey (see <http://water.usgs.gov/nawqa/>). There were 2822 algal samples from 1435 distinct stream localities, spanning 40 latitudinal and 87 longitudinal degrees. Quantitative samples were collected by the USGS between 1993 and 2009 from the richest-targeted habitats (RTH), comprising riffles or woody snags. A total of 1698 taxa, primarily identified to species, belonged to 117 genera and 46 families. For all constituent taxa, we had data on population density (cells·cm⁻²) and were able to classify 1692 of them into low profile (189 taxa), high profile (604 taxa), and motile guilds (899 taxa), according to Passy (2007) and Rimet & Bouchez (2012). Low profile species are of short habit and tolerant of resource limitation and physical disturbance, while high profile species, having tall stature, and motile species are sensitive to these stressors (Passy, 2007). The 189 tolerant species came from 16 genera and 9 families, while the 1503 sensitive species, from 102 genera and 44 families, resulting in genus to species ratios of 0.08 in the tolerant group and 0.07 in the sensitive group and family to species ratios of 0.05 and 0.03 in the respective groups. A ratio of sensitive to tolerant species (ST), calculated as $\ln(\text{high profile} + \text{motile cell density} + 1) / (\text{low profile cell density} + 1)$, was used as a measure of filtering. Dominance of tolerant species ($\ln \text{ST ratio} < 0$) was considered indicative of environmental stress, while dominance of sensitive species ($\ln \text{ST ratio} \geq 0$), of favorable environmental conditions.

There were 2194 qualitative fish samples with a total abundance between 5 and 9331 individuals. Preliminary research showed that in samples with ≥ 455 counted individuals, species richness was very weakly dependent on abundance and, therefore, reliably measured (Passy, 2016). Consequently, we used only the 761 fish samples with ≥ 455 counted individuals where we observed a total of 460 species from 117 genera and 42 families. These samples were collected between 1993 and 2010 from 399 distinct localities. For the most abundant 216 species, comprising 83% of the total sample abundance, classification into tolerant, moderate, and intolerant of environmental stress was possible, based on data from the Environmental Protection Agency (http://water.epa.gov/scitech/monitoring/rsl/bioassessment/app_c-2.cfm) and NAWQA (<http://water.usgs.gov/nawqa/ecology/data.html>). The 18 tolerant species belonged to 15 genera and 7 families, the 134 moderate species, to 62 genera and 24 families, and the 64 intolerant species, to 26 genera and 11 families. The genus to species ratios were 0.83 in the tolerant group and 0.41 in the intolerant group, while the family to species ratios were 0.39 and 0.17 in the respective groups. An ST ratio was calculated as $\ln(\text{intolerant individuals} + 1) / (\text{tolerant individuals} + 1)$ and used as a metric of filtering. As in diatoms, communities with $\ln \text{ST ratio} < 0$ were viewed as developing under environmental stress and those with $\ln \text{ST ratio} \geq 0$, under environmental favorability.

In diatoms and fish, the number of all species (i.e., richness), Pielou's evenness (J), and the ratios of genus to species (GS) and family to species richness (FS) were recorded for each sample. A decrease in GS or FS indicates taxonomic clustering, i.e. species tend to come from the same genera or families. Data on basin climate, topography, hydro-modification, and land use, available for 2575 diatom and 732 fish samples, comprised the environmental dataset.

Redundancy analyses with forward selection and 999 Monte Carlo permutations (CANOCO 4.5, 1997-2009 Biometris – Plant Research International, Wageningen, The Netherlands) were performed on diatom and fish correlation matrices to test whether the environment had significant effects on filtering and taxonomic relatedness, as hypothesized in Fig. 1. The environmental dataset consisted of 43 appropriately transformed (ln- or arcsine square root transformed) watershed variables. The dependent dataset included the ST ratio and the ratios of genus to species- (GS) and family to species (FS) richness. The environmental variables with the strongest and significant effects on the dependent set were retained in the final RDA model.

All bivariate relationships, including J, S, ST-, GS-, and FS ratios, were modelled with linear or non-linear equations, selected for their good fit, parsimony, and high R^2 after running a curve-fitting procedure (TableCurve 2D 5.01, SYSTAT Software, Inc., Chicago IL, USA, 2002). The variance in J explained by the predictors individually and interactively, was determined by multiple regressions, followed by variance partitioning using SYSTAT 13.1 (SYSTAT Software, Inc. 2009). Structural equation modelling was performed with SYSTAT 13.1 to test the predictions in Fig. 1b. Goodness of fit was measured by a discrepancy function or root mean square error of approximation (RMSEA).

Results

The variables with the strongest impact on the ratios of sensitive to tolerant species (ST), genus to species (GS), and family to species richness (FS) were the following in the order of their selection by the RDA with percent explained variance given in parentheses ($p = 0.001$ for all variables): forest cover (9.3%), drainage area (4.6%), and slope (2.6%) in diatoms; and

deciduous forest cover (14.6%), air temperature (11.7%), and agriculture (12.4%) in fish (Fig. 2a, b). The total explained variance was moderate (39% in fish) to low (17% in diatoms). The first RDA axis in both analyses captured most to nearly all of the explained variance and represented a stress gradient. Small forested streams in watersheds of high slopes provided a stressful environment for diatoms, while cold streams with low deciduous forest cover were stressful to fish, evident in the negative correlation of these factors with the ST ratios. As hypothesized in Fig. 1, the increase in the ST ratio was paralleled by a decrease in the GS and FS ratios.

In both diatoms and fish evenness increased with richness but in diatoms, the S-J relationship was comparatively strong ($R^2 = 0.50$, Fig. 3a), while in fish, it was much weaker ($R^2 = 0.08$, Fig. 4a). In both groups, evenness was also constrained by the ST ratio (Figs 3b, 4b) and FS ratio (Figs 3c, 4c). Evenness increased sharply as the dominance of tolerant species decreased, but changed little in low stress communities where sensitive/intolerant forms prevailed, evident in the steepness of the regression slope in these two groups (Figs 3b, 4b). A quadratic function of the ST ratio captured well the saturation of J under sensitive species dominance. In contrast, the relationships of evenness with both richness and FS ratio were comparatively strong in both low stress and high stress communities (Figs 3, 4). This means that while the environmental effect on J was weak in favorable conditions (shallow J-ln ST slope at ln ST ratio ≥ 0), the species interaction effect remained strong across harsh and benign environments. From the two metrics of taxonomic similarity, the genus to species ratio was a weaker predictor of J—after the family to species ratio entered the model, the GS ratio added only 2% to the explained variance in diatoms and 0% in fish. Consequently, we used only the FS ratio in all regression analyses of J and S.

In both groups richness increased sharply with the ST ratio under stressful conditions, but in benign environments, there was a difference between the two groups. Diatom richness changed little, while fish richness continued to increase (Fig. 5). Additional *t*-tests revealed significantly higher values for S and significantly lower values for FS ratio in low ($\ln \text{ST ratio} \geq 0$) than in high stress ($\ln \text{ST ratio} < 0$) communities ($p < 0.001$, diatoms and fish). These results indicated that species-poor communities in stressed environments comprised taxonomically distant species, while species-rich communities in benign environments, taxonomically related species.

Structural equation models (SEMs) demonstrated that in diatoms and fish the ST ratio and the FS ratio were negatively correlated, as predicted in Fig. 1 (Fig. 6). Both S and J were constrained by the ST ratio, representative of environmental filtering. The linear and quadratic terms of the ST ratio, signifying saturating responses of S and J, were significant in both models except for fish richness, which increased linearly with the ST ratio. The FS ratio was a negative predictor of both S and J, which were the highest when the communities were most taxonomically clustered (lowest FS ratios). The S-J relationship was positive in diatoms, but due to collinearity of S with the FS ratio, it became negative in fish. All other relationships in both SEMs were consistent with the respective bivariate relationships (Figs 3-5). The SEM models further demonstrated that both the FS and the ST ratios had significant direct effects on J. The two SEMs had overall excellent fits—the discrepancy function in the diatom model (0 degrees of freedom, DF) was $7.98e^{-11}$ and the RMSEA in the fish model (1 DF) was <0.001 .

Discussion

Environmental stress, represented by greater forest cover and basin slope in diatoms but lower deciduous forest cover and temperature in fish, generated two gradients of community response—a shift in species tolerance concurrent with a change in taxonomic clustering, as predicted in Fig. 1. Small, forested streams in high elevation watersheds were stressful to algae due to light and nutrient deficiency (Hill et al., 2011). Streams with reduced forest cover were stressful to fish because their lower substrate stability and heterogeneity provide fewer spawning habitats and limited macroinvertebrate prey (Allan, 2004). Lower temperatures were also stressful to fish, evident in the increased abundance of tolerant species. Across both organismal groups, filtering in unfavorable environments resulted in dominance of a small number of tolerant but comparatively taxonomically diverse species. Conversely, numerical abundance of a large number of sensitive but comparatively taxonomically similar forms was characteristic for benign habitats. In fact, taxonomic dispersion of tolerant species and taxonomic clustering of sensitive species were detected not only locally but also in the regional pools. Thus regionally, the genus to species ratios were 1.2 to 2.1 times higher and the family to species ratios, 1.6 to 2.3 times higher in the tolerant than in the sensitive group across diatoms and fish. This suggests that the patterns of local taxonomic similarity emerge as a consequence of environmental selection for functional groups, which differ not only in stress tolerance but also in taxonomic distances. Therefore, taxonomic clustering and overdispersion in local communities are environmentally imposed and may control the form of interspecific interactions. These findings are in agreement with experimental data showing that nutrient stress in stream biofilms causes a reduction in species richness at the expense of sensitive forms but an increase in taxonomic distance among the surviving tolerant species (Larson & Passy, 2013). Although we did not assess traits other than tolerance, our results on taxonomic distances, likely to correlate with trait differences in

general, provide evidence that environmental filtering and limiting similarity may not be opposing processes, as generally considered (Weiher & Keddy, 1995; Mouillot et al., 2007; Mouchet et al., 2013; Montaña et al., 2014), but inherently linked from the local to the regional scale, as suggested in Fig. 1.

Consistent with our expectations, environmental stress caused filtering of species with convergent survival traits but potentially disparate coexistence traits. As discussed, the prevailing diatoms and fish in stressful conditions were tolerant (low ST ratios). Tolerance is associated with distinct body sizes in both diatoms and fish (Passy, 2012), which in turn determine various aspects of species' physiology and life history with an influence on survival, including growth and metabolic rates, time of reproductive maturity, life span, and pollution tolerance (Peters, 1983; Cattaneo et al., 1998; Brown et al., 2002). However, the most common tolerant diatoms, *Cocconeis placentula* et vars and *Achnantheidium minutissimum*, tend to exhibit microhabitat preference for macrophytes and hard substrates, respectively (Passy et al., 1999; Soininen & Eloranta, 2004). The three most abundant tolerant fish differed in diet and microhabitat, e.g. *Rhinichthys atratulus* is an invertivore, inhabiting rocky substrates and gravel; *Semotilus atromaculatus* is an invertivore and carnivore, with a preference for rocky substrates and sand; and *Pimephales promelas* is a detritivore and invertivore, found in sandy and muddy habitats (<http://water.usgs.gov/nawqa/ecology/data.html>). Therefore, tolerant species across diatoms and fish may diverge in coexistence traits but a more detailed trait analysis is needed to fully support this hypothesis. Previous research showed that environmental filtering and limiting similarity may not be mutually exclusive mechanisms of community assembly if they constrain complementary sets of traits, e.g. those associated with large- vs. small scale components of the niche, respectively (Ackerly & Cornwell, 2007; Ingram & Shurin, 2009). Specifically,

environmental filtering defines the beta niche, or the species' position along broad environmental gradients, while limiting similarity constrains the alpha niche, or traits linked to local habitat utilization (Ackerly & Cornwell, 2007). To what extent tolerance and coexistence traits describe the alpha and beta niche is unclear; nevertheless, it is conceivable that these traits may be under distinct selection pressure and experience differential convergence and divergence along environmental gradients.

Our study further showed that environmental filtering and taxonomic clustering, which varied predictably along the environmental stress gradient (Figs 1a, 2), underlay the relationship of richness and evenness as both S and J responded to these factors in a similar fashion (Fig. 6). In both diatoms and fish, the S-J relationship was positive across stressful and benign conditions. Environmental filtering, i.e. the increase in tolerant species abundance, caused a sharp decline in both richness and evenness. When sensitive species began to dominate and increase in proportion under benign conditions, evenness and diatom richness displayed little change, while fish richness alone showed a positive response. This differential behavior of fish S and J can contribute to their weaker relationship compared to diatoms. In contrast, taxonomic clustering correlated strongly with evenness across stressful and favorable conditions. Communities with the highest richness and evenness, found in benign environments, displayed the lowest FS ratios. These results suggest that environmental filtering has a more restricted influence on community evenness, i.e. only under stress, whereas taxonomic clustering is an important predictor across environmental conditions. Although we do not know to what degree traits are conserved across phylogenetically similar species, we can speculate that in environmentally stressed and impoverished communities the addition of taxonomically distant species that may acquire resources in a complementary fashion increases J. Other positive interspecific interactions, such

as direct facilitation and habitat amelioration, which are important in high stress environments (Bertness & Callaway, 1994; He et al., 2013), can also contribute to the positive S-J relationship. Conversely, diverse communities, developing under benign conditions, have more species per genus and family, which are more likely to compete for the shared resources. Competition among ecologically and competitively similar species can lead to coexistence of a large number of species (Scheffer & van Nes, 2006), and as we see here, high richness is also associated with high abundance equitability. Given the within family taxonomic homogenization occurring with the increase in richness, the S-J relationship may be driven by environmental filtering and positive interactions at low S but negative interactions at high S. However, the SEMs also revealed that taxonomic clustering and environmental filtering had independent effects on J that were not related to richness, adding to earlier findings that richness and evenness have complementary responses to the environment (Hillebrand et al. 2007).

Prior research on fish, implying either environmental (Oberdorff et al., 1998) or biotic control (Montaña et al., 2014) in structuring these communities, has been controversial. This investigation demonstrates that both factors are influential but while environmental filtering weakens under favorable conditions, the role of taxonomic clustering in determining evenness remains unaltered. Although we have not measured directly species interactions, our framework may be used to resolve the contradiction between the stress gradient hypothesis, stating that the prominence of positive interactions increases with environmental stress (Bertness & Callaway, 1994; He et al., 2013), and the dogma in animal ecology that competition intensifies in harsh, unproductive environments (Barrio et al., 2013). In exploring continental gradients of environmental and biotic variability, we showed that stressful environments were inhabited by a significantly more species-poor but less taxonomically clustered fauna (higher FS ratios).

Therefore, harsh conditions are less conducive to competition but more prone to positive interspecific interactions than benign habitats but confirmation of these ideas requires experimental research on species interactions along environmental gradients. Thus, merging the view of community assembly through environmental filtering and competitive interactions (Weiher & Keddy, 1995) with the stress gradient hypothesis (Bertness & Callaway, 1994) may provide a more complete understanding of the mechanisms of species coexistence.

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Figure legend

Figure 1. (a) Conceptual model identifying the processes underlying the variability in community richness and evenness. Environmental favorability reduces the role of filtering (elimination of sensitive species) but increases the taxonomic clustering of local biota, which has an impact on species interactions. Positive interactions are expected among taxonomically distant species, while negative interactions will predominate among taxonomically similar species. Since richness and evenness exhibit similar behavior along these gradients, their relationship is expected to be positive. Taxonomic clustering is assessed by the family:species (FS) ratio and filtering, the sensitive:tolerant (ST) species ratio. **(b)** Structural equation model predicting the causal relationships among the FS ratio, the ST ratio, S and J. e_1 and e_2 = error terms.

Figure 2. Redundancy analyses of the ratios of sensitive to tolerant species, genus to species, and family to species richness showing the most important environmental predictors in diatoms **(a)** and fish **(b)**. The variance explained by each axis is given in percent. $n = 2575$ samples (a) and 732 samples (b). The environmental variables were measured in percent cover for forest, deciduous forest and agriculture, km^2 for basin drainage area, percent for mean basin slope, and $^{\circ}\text{C}$ for temperature.

Figure 3. Diatoms. Relationships of evenness (J) with richness (S) **(a)**, ratio of sensitive to tolerant species (ST) **(b)**, and ratio of family to species richness (FS) **(c)**. In a-c, the overall fit is given as a solid blue curve, while the fits for stressed communities ($\ln \text{ST} < 0$, in red) and non-stressed communities ($\ln \text{ST} \geq 0$, in black) are given as long- vs. short-dashed blue curves,

respectively (logarithmic in a and linear in b-c). Note in (a) the steeper increase in J with S under stressful conditions. The regression model and statistics for the overall fits are shown in the panels. $n = 2800$ samples.

Figure 4. Fish. Relationships of evenness (J) with richness (S) **(a)**, ratio of intolerant to tolerant species (ST) **(b)**, and ratio of family to species richness (FS) **(c)**. In a-c, the overall fit is given as a solid blue line, while the fits for stressed communities ($\ln ST < 0$, in red) and non-stressed communities ($\ln ST \geq 0$, in black) are given as long- vs. short-dashed blue lines, respectively. Note in (a) the steeper increase in J with S under stressful conditions. The regression model and statistics for the overall fits are shown in the panels. $n = 761$ samples.

Figure 5. Relationships of $\ln$ richness with ratio of sensitive to tolerant species in diatoms ($n = 2803$ samples) **(a)** and fish ($n = 761$ samples) **(b)**. The overall fit (quadratic in a and linear in b) is given as a solid blue curve, while the fits for stressed communities ($\ln ST < 0$, in red) and non-stressed communities ($\ln ST \geq 0$, in black) are given as dashed blue lines. The regression model and statistics for the overall fits are shown in the panels.

Figure 6. Structural equation models (SEMs) for diatoms ($n = 2800$ samples) **(a)** and fish ($n = 761$ samples) **(b)** showing only the significant paths ($p < 0.05$) with the corresponding standardized coefficients. The relationships are causative (one-headed arrows) or correlative (two-headed arrows). e_1 and e_2 = error terms.

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(a)

(b)

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