

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

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23 **Abstract**

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

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

44 **Introduction**

45 Two aspects of biodiversity, namely richness (S) or the number of species in a community and
46 evenness or the equitability in species' abundance (J), have drawn considerable interest in
47 ecology because of their correlations with important community properties, such as biomass
48 production and decomposition, susceptibility to invaders, stress resistance, and extinction risks
49 (Wilsey & Potvin, 2000; Kennedy et al., 2002; Dangles & Malmqvist, 2004; Wittebolle et al.,
50 2009; Blois et al., 2010). The relationship of S and J has also been extensively investigated
51 across habitats and organismal groups, including algae, plants, fungi, invertebrates, and
52 vertebrates, and shown to depend on both the environment and the level of species richness, i.e.
53 the shape of the relationship changes at a threshold richness (Stirling & Wilsey, 2001; Bock et
54 al., 2007; Soininen et al., 2012). This implies that both abiotic and biotic forces affect the S-J
55 relationship but their relative importance is not well understood. Here, we explore the
56 relationship between S and Pielou's evenness (J) from the perspective of community assembly
57 theory to address a fundamental ecological question—what is the interplay between
58 environmental stress and biotic forcing in driving the patterns of biodiversity?

59 Two seemingly opposing theories have been invoked to explain community assembly at
60 local scales—limiting similarity and environmental filtering (Weiher & Keddy, 1995; Mayfield
61 & Levine, 2010; HilleRisLambers et al., 2012). According to the limiting similarity model
62 (MacArthur & Levins, 1967), competition for limiting resources selects for niche differentiation
63 and trait divergence among coexisting species. In contrast, the environmental filtering idea
64 proposes that the environment supports only species with converging traits that confer positive
65 fitness under the local conditions (Keddy, 1992). Both limiting similarity (Stubbs & Wilson,
66 2004; Montaña et al., 2014) and environmental filtering (Peres-Neto 2004; Mouillot et al., 2007;

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

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

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

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

99 As phylogenetic structure determines the distribution of traits, it is linked to species
100 interactions, e.g. competition and complementarity (Webb et al., 2002; HilleRisLambers et al.,
101 2012), which may impact the relationship between richness and evenness. Evenness can increase
102 at low richness as a result of positive interactions (complementarity or facilitation) among
103 taxonomically distant species (Fig. 1). For example, under stressful nitrogen limiting conditions,
104 nitrogen fixers stimulate biomass production of distantly related non-nitrogen fixers through
105 facilitation (Agawin et al., 2007). Conversely, negative interactions (competition among
106 taxonomically similar species) can elevate evenness at high richness by preventing dominance
107 (Fig. 1). This model can explain the shift in species interactions from negative (competition) to
108 positive (complementarity and facilitation) with the transition of the environment from benign to
109 harsh (Bertness & Callaway, 1994; Bruno et al., 2003; Wang et al., 2013) as a consequence of
110 trait convergence corresponding to increased taxonomic clustering.

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

113 was measured by the ratio (ST) of species sensitive vs. tolerant of environmental stress, e.g.
114 resource limitation and physical or chemical disturbance. Thus, low ST ratios (higher abundance
115 of tolerant species), found in harsh environments, indicated filtering (selection for survival
116 traits), while high ST ratios (numerical dominance of sensitive species) were suggestive of
117 environmental favorability. Evaluating the form of species interactions (positive vs. negative) is
118 intractable but it is expected to correlate with phylogenetic distance with low values
119 (phylogenetic similarity) linked to competition (Violle et al., 2011) and high values
120 (phylogenetic dissimilarity), to facilitation and complementarity (Valiente-Banuet & Verdu,
121 2007; Venail & Vives, 2013). Nevertheless, the relationship between phylogenetic distance and
122 interspecific interactions has been controversial (Venail et al., 2014) and further research is
123 necessary to confirm whether the hypothesized correlations do exist in the organismal groups
124 studied here. We adopted the ratio of higher taxa richness to species richness, which reflects the
125 taxonomic redundancy within terminal groups, as a proxy measure of species interactions. Low
126 ratios (taxonomic similarity) were likely to be associated with competition, whereas high ratios
127 (taxonomic dissimilarity), with complementarity.

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

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

137

138 **Materials and methods**

139 We used stream community data from most major watersheds and aquifers in the US, generated
140 by the NAWQA program of the US Geological Survey (see <http://water.usgs.gov/nawqa/>). There
141 were 2822 algal samples from 1435 distinct stream localities, spanning 40 latitudinal and 87
142 longitudinal degrees. Quantitative samples were collected by the USGS between 1993 and 2009
143 from the richest-targeted habitats (RTH), comprising riffles or woody snags. A total of 1698
144 taxa, primarily identified to species, belonged to 117 genera and 46 families. For all constituent
145 taxa, we had data on population density (cells·cm⁻²) and were able to classify 1692 of them into
146 low profile (189 taxa), high profile (604 taxa), and motile guilds (899 taxa), according to Passy
147 (2007) and Rimet & Bouchez (2012). Low profile species are of short habit and tolerant of
148 resource limitation and physical disturbance, while high profile species, having tall stature, and
149 motile species are sensitive to these stressors (Passy, 2007). The 189 tolerant species came from
150 16 genera and 9 families, while the 1503 sensitive species, from 102 genera and 44 families,
151 resulting in genus to species ratios of 0.08 in the tolerant group and 0.07 in the sensitive group
152 and family to species ratios of 0.05 and 0.03 in the respective groups. A ratio of sensitive to
153 tolerant species (ST), calculated as $\ln(\text{high profile} + \text{motile cell density} + 1) / (\text{low profile cell}$
154 $\text{density} + 1)$, was used as a measure of filtering. Dominance of tolerant species ($\ln \text{ST ratio} < 0$)
155 was considered indicative of environmental stress, while dominance of sensitive species ($\ln \text{ST}$
156 $\text{ratio} \geq 0$), of favorable environmental conditions.

157 There were 2194 qualitative fish samples with a total abundance between 5 and 9331
158 individuals. Preliminary research showed that in samples with ≥ 455 counted individuals, species
159 richness was very weakly dependent on abundance and, therefore, reliably measured (Passy,
160 2016). Consequently, we used only the 761 fish samples with ≥ 455 counted individuals where
161 we observed a total of 460 species from 117 genera and 42 families. These samples were
162 collected between 1993 and 2010 from 399 distinct localities. For the most abundant 216 species,
163 comprising 83% of the total sample abundance, classification into tolerant, moderate, and
164 intolerant of environmental stress was possible, based on data from the Environmental Protection
165 Agency (http://water.epa.gov/scitech/monitoring/rsl/bioassessment/app_c-2.cfm) and NAWQA
166 (<http://water.usgs.gov/nawqa/ecology/data.html>). The 18 tolerant species belonged to 15 genera
167 and 7 families, the 134 moderate species, to 62 genera and 24 families, and the 64 intolerant
168 species, to 26 genera and 11 families. The genus to species ratios were 0.83 in the tolerant group
169 and 0.41 in the intolerant group, while the family to species ratios were 0.39 and 0.17 in the
170 respective groups. An ST ratio was calculated as $\ln(\text{intolerant individuals} + 1) / (\text{tolerant}$
171 $\text{individuals} + 1)$ and used as a metric of filtering. As in diatoms, communities with \ln ST ratio $<$
172 0 were viewed as developing under environmental stress and those with \ln ST ratio ≥ 0 , under
173 environmental favorability.

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

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

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

196

197 **Results**

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

202 deciduous forest cover (14.6%), air temperature (11.7%), and agriculture (12.4%) in fish (Fig.
203 2a, b). The total explained variance was moderate (39% in fish) to low (17% in diatoms). The
204 first RDA axis in both analyses captured most to nearly all of the explained variance and
205 represented a stress gradient. Small forested streams in watersheds of high slopes provided a
206 stressful environment for diatoms, while cold streams with low deciduous forest cover were
207 stressful to fish, evident in the negative correlation of these factors with the ST ratios. As
208 hypothesized in Fig. 1, the increase in the ST ratio was paralleled by a decrease in the GS and FS
209 ratios.

210 In both diatoms and fish evenness increased with richness but in diatoms, the S-J
211 relationship was comparatively strong ($R^2 = 0.50$, Fig. 3a), while in fish, it was much weaker (R^2
212 = 0.08, Fig. 4a). In both groups, evenness was also constrained by the ST ratio (Figs 3b, 4b) and
213 FS ratio (Figs 3c, 4c). Evenness increased sharply as the dominance of tolerant species
214 decreased, but changed little in low stress communities where sensitive/intolerant forms
215 prevailed, evident in the steepness of the regression slope in these two groups (Figs 3b, 4b). A
216 quadratic function of the ST ratio captured well the saturation of J under sensitive species
217 dominance. In contrast, the relationships of evenness with both richness and FS ratio were
218 comparatively strong in both low stress and high stress communities (Figs 3, 4). This means that
219 while the environmental effect on J was weak in favorable conditions (shallow J-ln ST slope at ln
220 ST ratio ≥ 0), the species interaction effect remained strong across harsh and benign
221 environments. From the two metrics of taxonomic similarity, the genus to species ratio was a
222 weaker predictor of J—after the family to species ratio entered the model, the GS ratio added
223 only 2% to the explained variance in diatoms and 0% in fish. Consequently, we used only the FS
224 ratio in all regression analyses of J and S.

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

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

245

246 **Discussion**

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

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

274 Consistent with our expectations, environmental stress caused filtering of species with
275 convergent survival traits but potentially disparate coexistence traits. As discussed, the prevailing
276 diatoms and fish in stressful conditions were tolerant (low ST ratios). Tolerance is associated
277 with distinct body sizes in both diatoms and fish (Passy, 2012), which in turn determine various
278 aspects of species' physiology and life history with an influence on survival, including growth
279 and metabolic rates, time of reproductive maturity, life span, and pollution tolerance (Peters,
280 1983; Cattaneo et al., 1998; Brown et al., 2002). However, the most common tolerant diatoms,
281 *Cocconeis placentula et vars* and *Achnantheidium minutissimum*, tend to exhibit microhabitat
282 preference for macrophytes and hard substrates, respectively (Passy et al., 1999; Soininen &
283 Eloranta, 2004). The three most abundant tolerant fish differed in diet and microhabitat, e.g.
284 *Rhinichthys atratulus* is an invertivore, inhabiting rocky substrates and gravel; *Semotilus*
285 *atromaculatus* is an invertivore and carnivore, with a preference for rocky substrates and sand;
286 and *Pimephales promelas* is a detritivore and invertivore, found in sandy and muddy habitats
287 (<http://water.usgs.gov/nawqa/ecology/data.html>). Therefore, tolerant species across diatoms and
288 fish may diverge in coexistence traits but a more detailed trait analysis is needed to fully support
289 this hypothesis. Previous research showed that environmental filtering and limiting similarity
290 may not be mutually exclusive mechanisms of community assembly if they constrain
291 complementary sets of traits, e.g. those associated with large- vs. small scale components of the
292 niche, respectively (Ackerly & Cornwell, 2007; Ingram & Shurin, 2009). Specifically,

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

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

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

328 Prior research on fish, implying either environmental (Oberdorff et al., 1998) or biotic
329 control (Montaña et al., 2014) in structuring these communities, has been controversial. This
330 investigation demonstrates that both factors are influential but while environmental filtering
331 weakens under favorable conditions, the role of taxonomic clustering in determining evenness
332 remains unaltered. Although we have not measured directly species interactions, our framework
333 may be used to resolve the contradiction between the stress gradient hypothesis, stating that the
334 prominence of positive interactions increases with environmental stress (Bertness & Callaway,
335 1994; He et al., 2013), and the dogma in animal ecology that competition intensifies in harsh,
336 unproductive environments (Barrio et al., 2013). In exploring continental gradients of
337 environmental and biotic variability, we showed that stressful environments were inhabited by a
338 significantly more species-poor but less taxonomically clustered fauna (higher FS ratios).

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

345

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465 **Figure legend**

466

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

476

477 **Figure 2.** Redundancy analyses of the ratios of sensitive to tolerant species, genus to species, and
478 family to species richness showing the most important environmental predictors in diatoms **(a)**
479 and fish **(b)**. The variance explained by each axis is given in percent. $n = 2575$ samples (a) and
480 732 samples (b). The environmental variables were measured in percent cover for forest,
481 deciduous forest and agriculture, km^2 for basin drainage area, percent for mean basin slope, and
482 $^{\circ}\text{C}$ for temperature.

483

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

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

491

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

498

499 **Figure 5.** Relationships of \ln richness with ratio of sensitive to tolerant species in diatoms ($n =$
500 2803 samples) **(a)** and fish ($n = 761$ samples) **(b)**. The overall fit (quadratic in a and linear in b) is
501 given as a solid blue curve, while the fits for stressed communities ($\ln ST < 0$, in red) and non-
502 stressed communities ($\ln ST \geq 0$, in black) are given as dashed blue lines. The regression model
503 and statistics for the overall fits are shown in the panels.

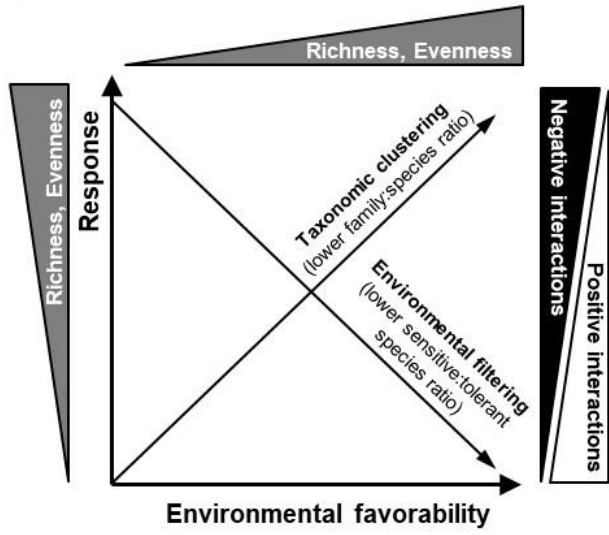
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505 **Figure 6.** Structural equation models (SEMs) for diatoms ($n = 2800$ samples) **(a)** and fish ($n =$
506 761 samples) **(b)** showing only the significant paths ($p < 0.05$) with the corresponding
507 standardized coefficients. The relationships are causative (one-headed arrows) or correlative
508 (two-headed arrows). e_1 and $e_2 =$ error terms.

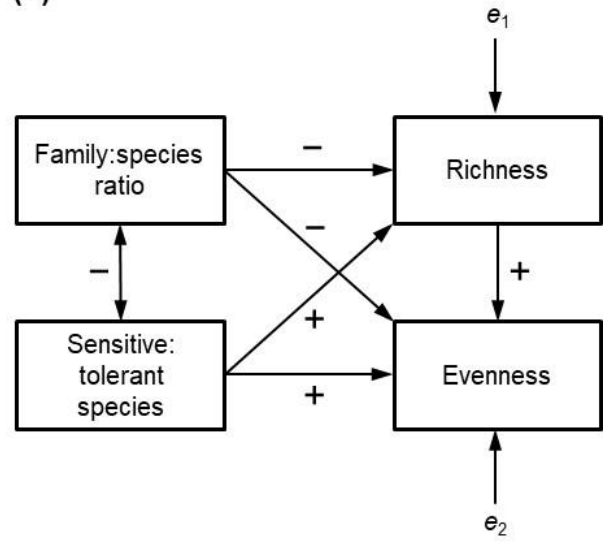
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(a)



(b)



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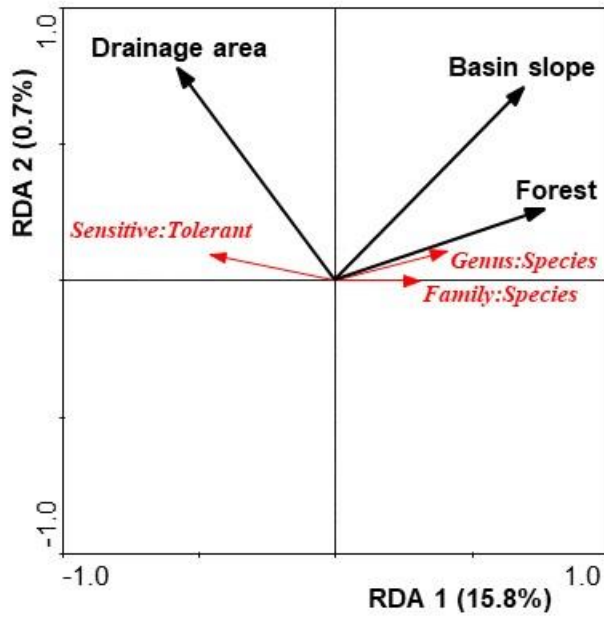
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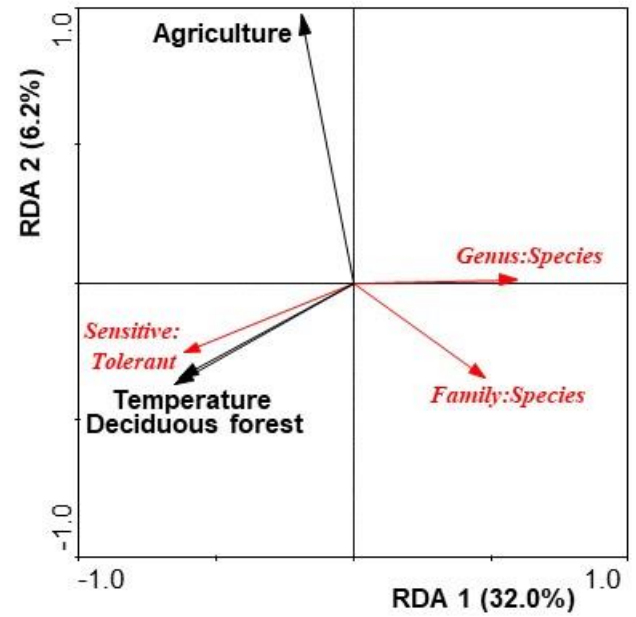
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(a)



(b)



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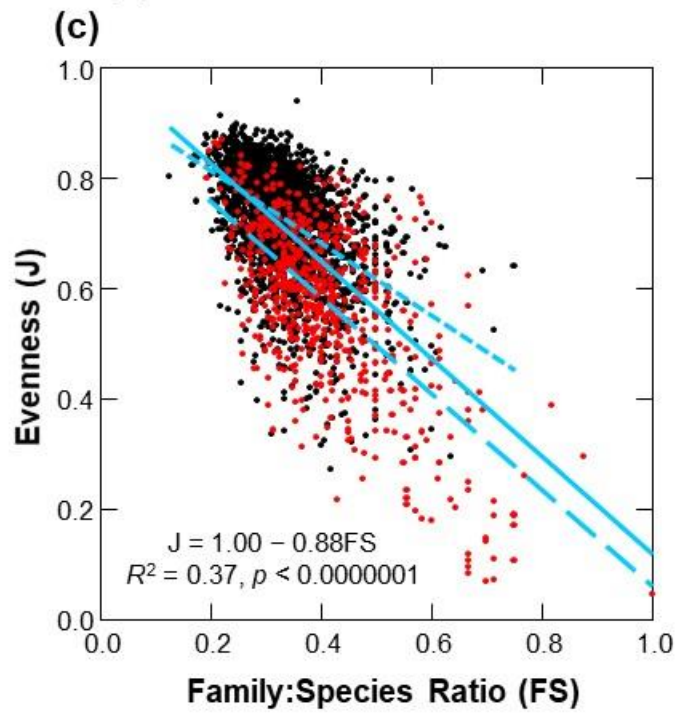
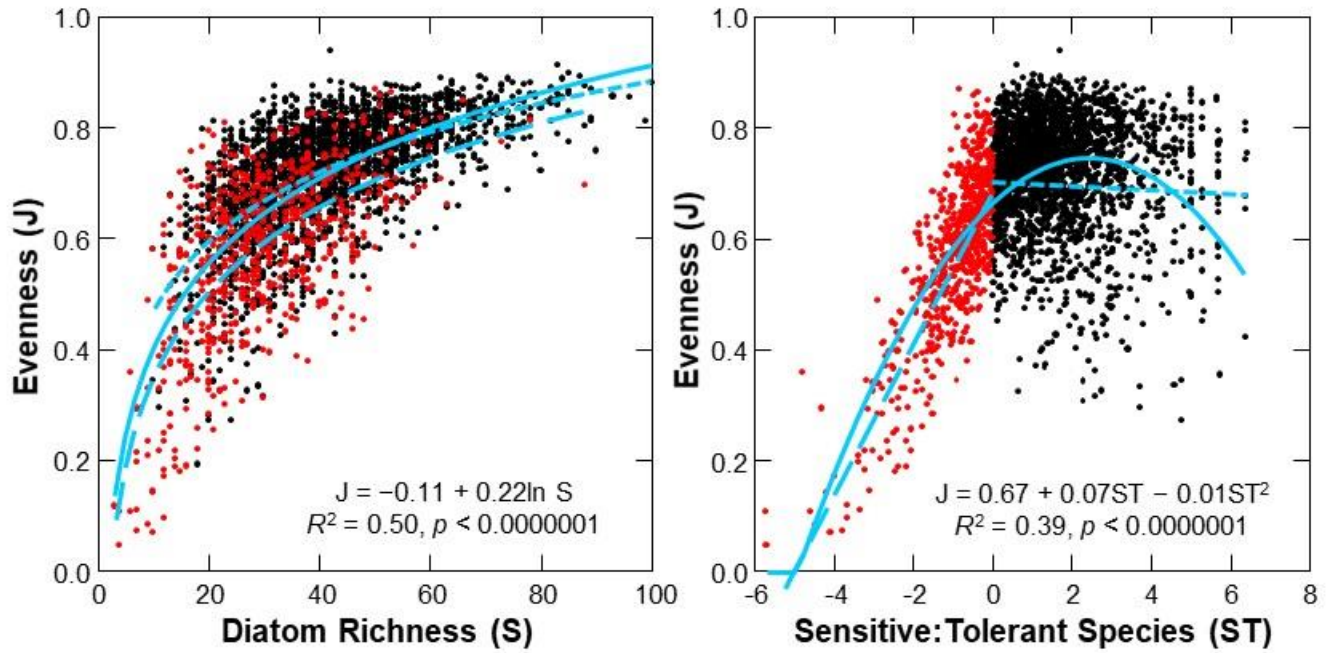
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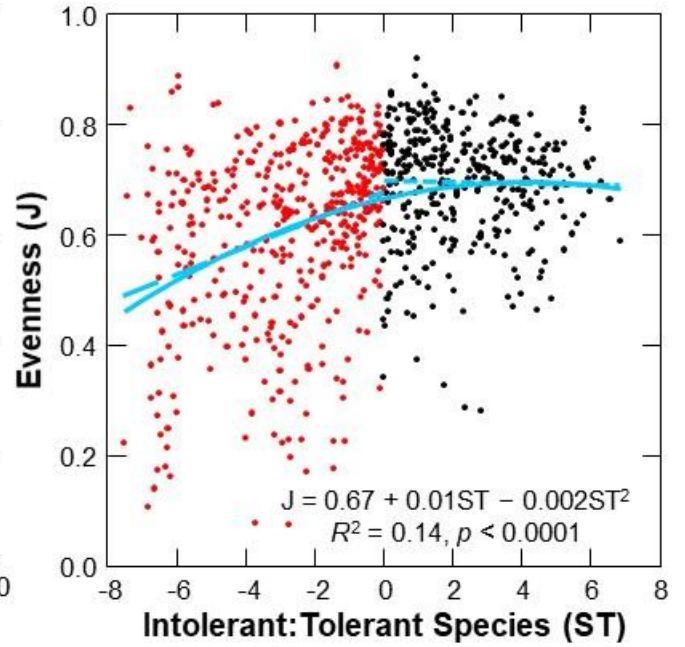
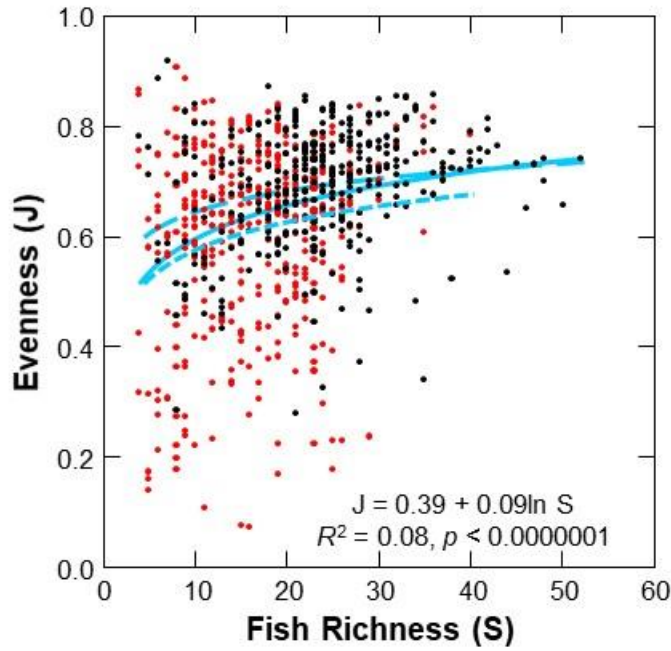
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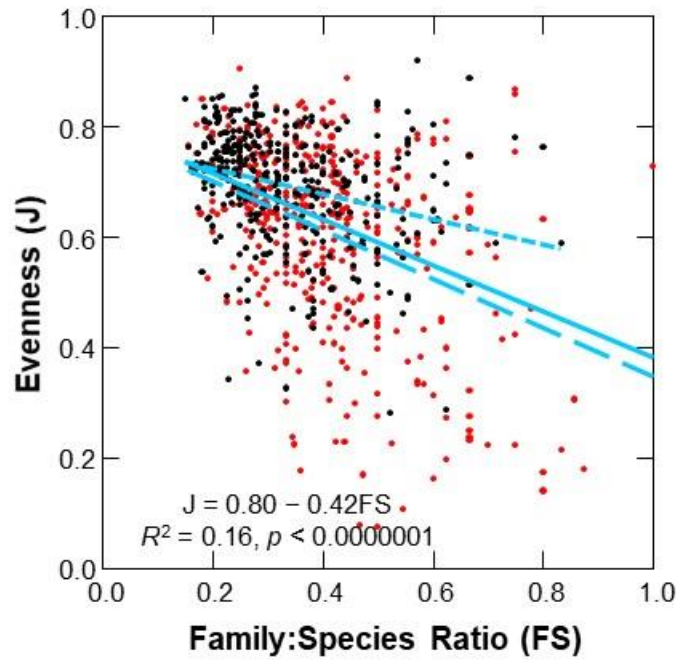
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(c)



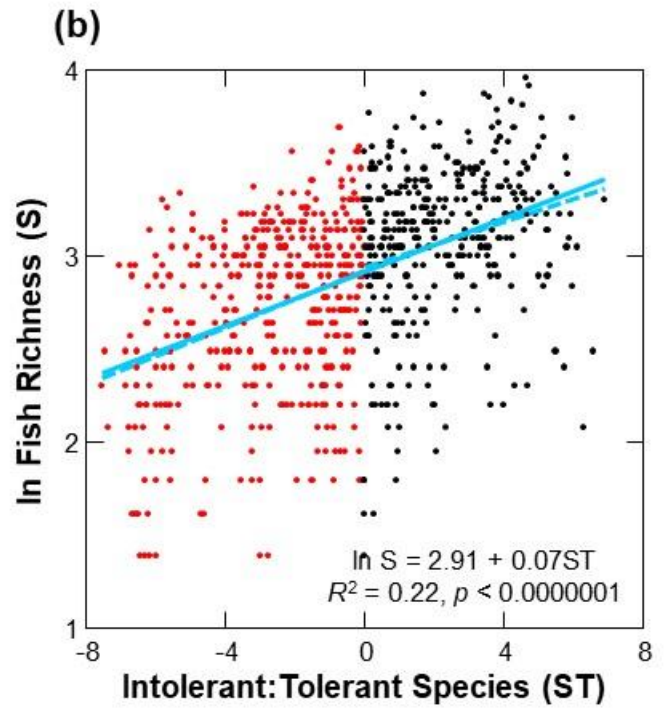
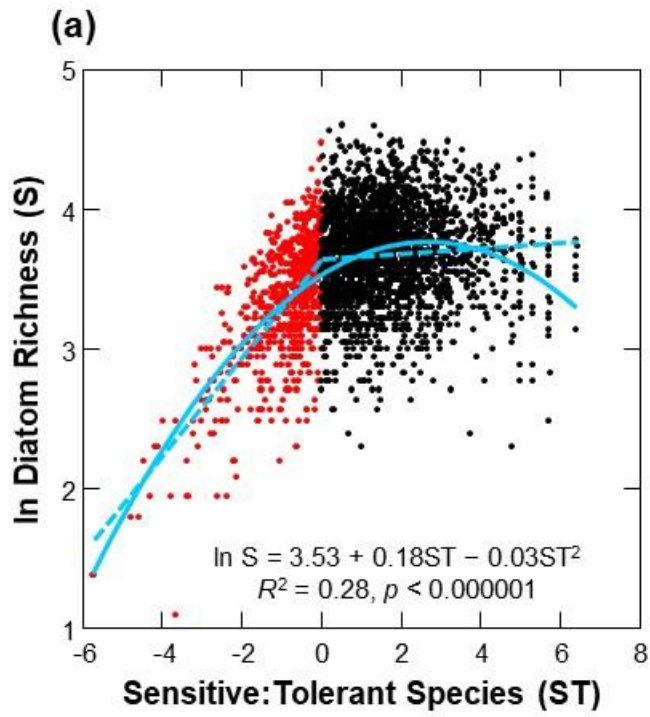
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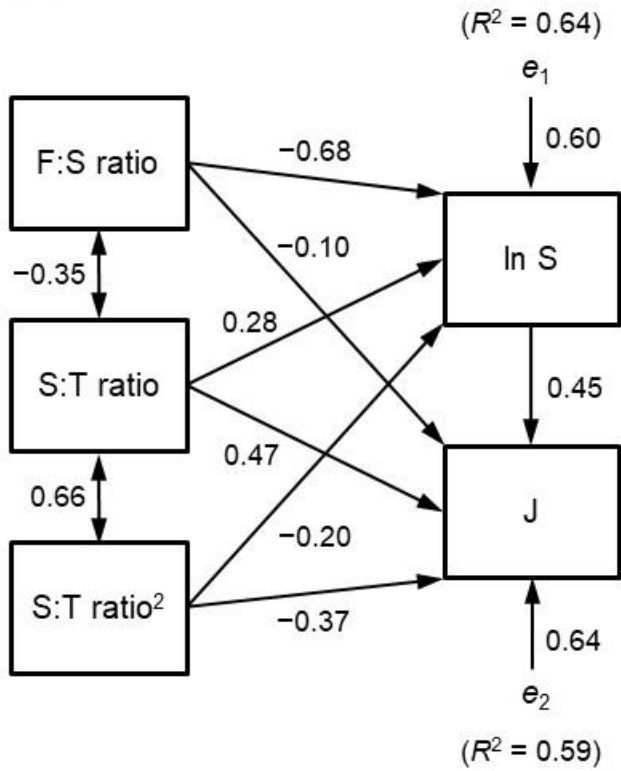
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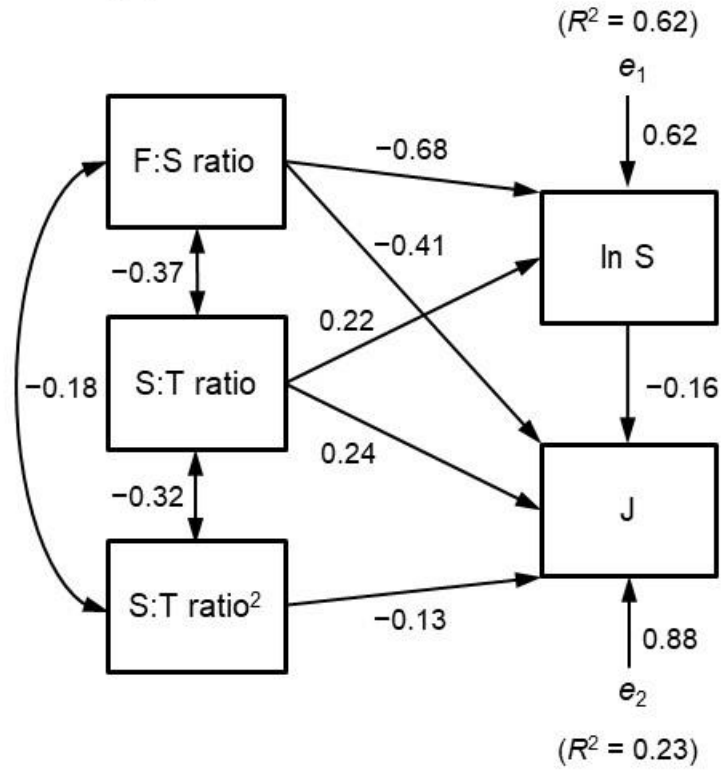
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562

(a)



(b)



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