Diversity and Distributions

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Beta diversity response to stress severity and heterogeneity in sensitive versus tolerant stream diatoms

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Abstract

Aim: Severity and heterogeneity of stress are major constraints of beta diversity, but their relative influence is poorly understood. Here, we addressed this question by examining the patterns of beta diversity in stress-sensitive versus stress-tolerant stream diatoms and their response to local versus regional factors along gradients of stress severity and heterogeneity.

Location: The Adirondack region of New York.

Methods: Beta diversity was measured as multivariate dispersion of communities across high stress, low stress, and high + low stress (heterogeneous) environments, encompassing 200 stream samples. Null models were implemented to assess community similarity relative to randomly assembled communities and the importance of local assembly processes versus the regional species pool.

Results: The overall beta diversity was influenced by a combination of severity and heterogeneity of stress, while beta diversity of sensitive species increased with heterogeneity. Beta diversity of tolerant species did not vary with either severity or heterogeneity of stress. Heterogeneity decreased community similarity relative to the null expectation in all groups of species. Stress reduced the importance of local assembly mechanisms for the overall beta diversity and sensitive species beta diversity. In contrast, the importance of local assembly mechanisms increased with stress regarding beta diversity of tolerant species.

Main conclusions: Beta diversity responded to both severity and heterogeneity of stress, but turnover along these gradients was mostly driven by sensitive species. The overall beta diversity and beta diversity of sensitive species became more constrained by the depauperate regional species pool, as opposed to local assembly mechanisms. While heterogeneous stress contributed to beta diversity, severe stress suppressed beta diversity through elimination of sensitive species. Therefore, an increase in beta diversity in an environmentally-stressed region may serve as a forewarning for future loss of sensitive species, should the stress continue to intensify.

KEYWORDS
acidification, beta diversity, diatoms, heterogenization, homogenization, null model, stress

1 | INTRODUCTION

With the continued migration of both ecological research and applied biodiversity conservation towards a more integrative, meta-community framework (Leibold et al., 2004), there has been an overwhelming increase of interest in the measurement (Anderson et al., 2011; Tuomisto, 2010a, 2010b), underpinning mechanisms (Baselga, 2010; Chase & Myers, 2011), and benefits of beta diversity (Lamy, Legendre, Chancerelle, Siu, & Claudet, 2015; van der Plas et al., 2016), or the variation in species composition among localities. Beta diversity provides a broader picture of diversity because it shows the connection between alpha (or local) diversity and gamma (or regional) diversity (Socolar, Gilroy, Kunin, & Edwards, 2016).

Due to the inherent dependence of beta diversity on alpha and gamma diversity, it can be difficult to unravel how local assembly processes influence the metric (Chase & Myers, 2011). Broadly speaking, local communities are consequences of both deterministic (i.e., niche selection) and stochastic (i.e., dispersal, ecological drift) processes, but the relative importance of these processes can vary across systems. When deterministic factors prevail, localities with similar environmental conditions are expected to have similar communities, and consequently, low beta diversity. In contrast, completely stochastic communities should not be related to environmental variables and may display variable beta diversity depending on the level of dispersal (Mouquet & Loreau, 2003; Qian, 2009). One complication in inferring the significance of these processes from direct measures of beta diversity is that a reduction in alpha diversity will cause communities to become more dissimilar due to mere probability (Chase & Myers, 2011). Similarly, high gamma diversity can result in communities being more dissimilar due to random sampling effects, that is, smaller subsets of a larger regional species pool residing in different localities are less likely to be similar (Chase & Myers, 2011; Kraft et al., 2011). Advances in null model approaches have made it possible to examine the prominence of deterministic versus stochastic processes operating on communities of very different alpha and gamma diversity (Chase, Kraft, Smith, Vellend, & Inouye, 2011; Kraft et al., 2011).

Environmental heterogeneity and stress are two specific factors shown to influence beta diversity patterns. Heterogeneity is widely shown to increase beta diversity by providing a greater variety of niches (Alahuhta et al., 2017; Astorga et al., 2014). Stress, on the other hand, is often expected to decrease beta diversity by filtering less tolerant species from the regional pool (Chase, 2007; Vellend et al., 2007). In some cases, stress or human disturbance may operate indirectly on beta diversity by reducing habitat heterogeneity and associated niche opportunities (Passy & Blanchet, 2007; Siqueira, Lacerda, & Saito, 2015). Despite the expectation of reduced beta diversity in stressed systems, this negative trend is not always the case. At least a few studies have demonstrated an increase in beta diversity with stress or disturbance (Fugère, Kasangaki, & Chapman, 2016; Hawkins, Mykrä, Oksanen, & Vander Laan, 2015; Libório & Tanaka, 2016; Mykrä, Tolkkinen, & Heino, 2017). Reduced alpha diversity, loss of taxa, and decreased occupancy of once common

species are often cited as explanations for this increase in beta diversity. Given the impact of stress on alpha diversity, null models are clearly necessary to distinguish whether local assembly processes differ between disturbed and undisturbed systems (Myers, Chase, Crandall, & Jiménez, 2015).

In this study, we use acidification as a model for testing how severity and heterogeneity of stress influence beta diversity and local assembly processes. While acidification is widely known to negatively affect alpha diversity (Nierzwicki-Bauer et al., 2010; Stockdale et al., 2014), its consequences for beta diversity are not as clear. On the one hand, variability in pH can contribute to environmental heterogeneity, resulting in higher beta diversity (Gutiérrez-Cánovas, Millán, Velasco, Vaughan, & Ormerod, 2013; Hawkins et al., 2015). On the other hand, acidification may homogenize communities if it narrows the pH range among habitats (Van Dam, Suurmond, & ter Braak, 1981). Furthermore, acidification is expected to impose a strong environmental filter on species composition, but it is unknown whether the relative importance of deterministic versus stochastic processes varies in reality between acid-impacted and non-impacted streams.

The goals of our study were threefold. Our first goal was to disentangle the effects of acidification stress and heterogeneity on measures of beta diversity, emphasizing variation in species abundance (Bray–Curtis) and species occurrence (Jaccard). Our second goal was to determine the influence of acidification stress and heterogeneity on the relative importance of deterministic versus stochastic processes and local assembly mechanisms versus the regional species pool by using null models to control for differences in alpha and gamma diversity, respectively. Our third goal was to test whether the response of beta diversity and the importance of local assembly processes differ between acid-sensitive and acid-tolerant species under conditions varying in acidification stress and heterogeneity. We examined diatom communities in the acid-sensitive Adirondack region of New York, where streams undergo episodic acidification following spring snowmelt and are least acidified during summer base flow. Differences in watershed contribution of organic matter and acid neutralizing capacity cause streams to differ in susceptibility to acidification (Lawrence et al., 2007), resulting in spatial heterogeneity in pH during both high and base flow conditions. As discussed above, acidification stress is expected to decrease beta diversity, yet heterogeneity in pH may cause higher species turnover.

To test the separate effects of severity and heterogeneity of stress (hereon also referred to as high versus low stress and high versus low heterogeneity) on beta diversity and local assembly processes, we examined these factors across (a) high acidity streams sampled during the period of spring acidification (representative of high stress but low heterogeneity), (b) low acidity streams sampled during the period of base flow (representative of low stress but low heterogeneity), and (c) a combination of low and high acidity streams from each sampling period (representative of high heterogeneity). In relation to our first goal, we had four different hypotheses (i.e., competitive predictions) regarding the response of beta diversity to stress versus heterogeneity. We predicted that if beta diversity were most controlled by heterogeneity, we would observe the highest beta diversity across a

heterogeneous pH gradient which included both high and low acidity streams (hypothesis 1). We predicted that if the effects of stress overrode heterogeneity, we would observe the lowest beta diversity across high acidity streams and the highest beta diversity across low acidity streams (hypothesis 2). If stress and heterogeneity interact to affect beta diversity, we predicted observations where hypotheses 1 and 2 were each partially supported, that is, both pH heterogeneity and decreased acidity would increase beta diversity (hypothesis 3). If beta diversity does not vary with acidification stress or heterogeneity, we would conclude that neither impacts beta diversity (hypothesis 4). Regarding our second goal, we predicted that the importance of deterministic assembly would increase with both acidification stress and heterogeneity, being least notable across low-stress streams. Additionally, we expected that the role of the regional species pool would become more prominent under acid stress due to elimination of acid-sensitive species. With respect to our third goal, we predicted that beta diversity of acid-sensitive species would be most affected by variation in acidification stress and heterogeneity, with deterministic processes and regional species pool effects also being more important to sensitive relative to tolerant species.

2 | METHODS

2.1 | Study region, sampling, and laboratory protocols

The study region is located in the Black and Oswegatchie River basins that lie within the western portion of the Adirondack Park in upstate New York (Figure 1), one of the most impacted regions by inorganic acid deposition in the United States (Sullivan, 2015). Our preliminary analysis included 156 streams sampled between 29 and 31 March 2004 and 167 streams sampled between 16 and 18 August 2004. The 323 samples were collected from 185 unique streams, that is, 138 streams sampled in both August and March, 29 streams sampled only in August, and 18 streams sampled only in March. These sampling periods coincided with snowmelt in March and base flow in August, with streams being much more acidic in March (Lawrence, et al., 2008). The geographic span of the study area was 4,585 km^2. Most of the study streams were first order and none were nested (i.e., flowing into one another). Water temperature was measured in the field, while in the laboratory water samples were analysed for pH, water colour, conductivity, and concentrations of dissolved organic carbon (DOC), inorganic monomeric Al (Al_{im}), organic monomeric Al (Al_{om}), all major cations and anions (Ca^{2+}, Cl^-, F^-, K^+, Mg^{2+}, Na^+, NH_4^+, NO_3^-, and SO_4^{2-}), and SiO_2. Diatoms were collected from all available substrates (i.e., stones, macrophytes, and sediments) in each locality, digested with acids in the laboratory, mounted in permanent slides, and identified to species in 300 frustule counts. In addition, we classified species as acid-sensitive and acid-tolerant based on ecological preferences (Camburn & Charles, 2000; DeNicola, 2000; Furey, Lowe, & Johansen, 2011; Lange-Bertalot, Bak, & Witkowski, 2011; Van Dam, Mertens, & Sinkeldam, 1994). Species with circumneutral, alkaliphilous, and alkalibiontic preference (pH ≥ 7) were classified as acid-sensitive. Acidobiontic, acidophilous, and indifferent species were classified as acid-tolerant. While in some contexts, pH tolerance may also refer to species that prefer alkaline pH (Alahuhta et al., 2017; Hawkins et al., 2015), alkalinity was not a problem in this
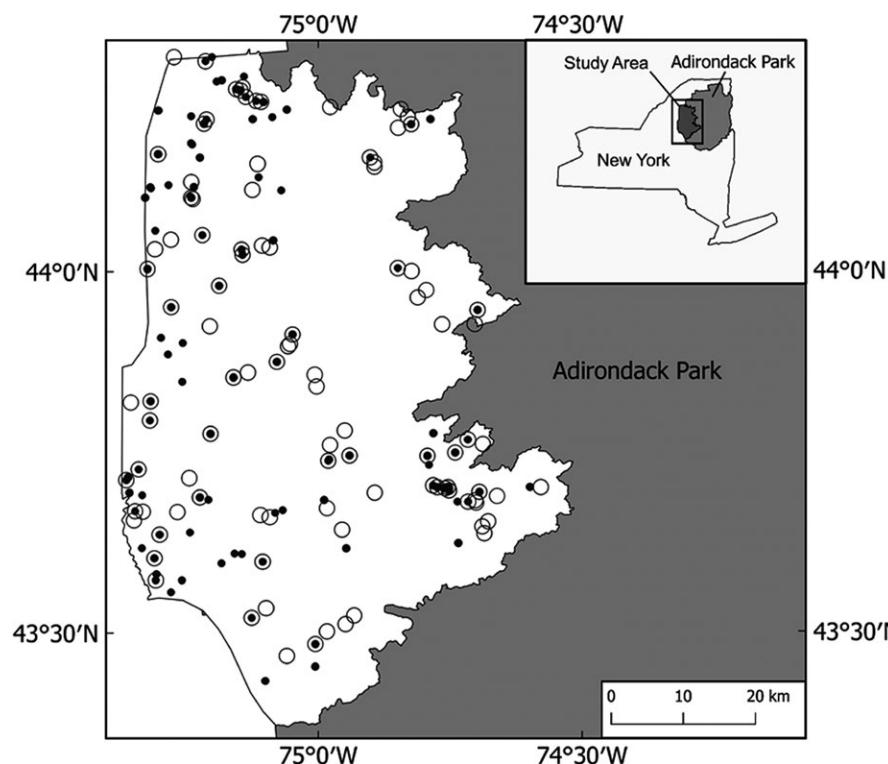

FIGURE 1 Map of the study region in the Black and Oswegatchie River basins in the Adirondack Park, New York. The open circles and black dots indicate locations of streams selected to be in the four groups used in our analysis. The open circles represent streams that were sampled in March 2004, and the black dots represent streams that were sampled in August 2004. Black dots within open circles indicate streams that were sampled in both months

acid-sensitive region. Therefore, for simplicity, we use the terms tolerant versus sensitive to refer to species that are respectively acid-tolerant versus acid-sensitive in our study. Given the high temporal turnover and rapid response of periphyton communities to new environments, as demonstrated in experimental studies (Hirst, Chaud, Delabie, Jüttner, & Ormerod, 2004; Larson & Passy, 2013; Larson, Adumatioge, & Passy, 2016), diatoms are excellent reflectors of current environmental conditions. Thus, diatoms collected in March and August may be considered reflective of the community reactions to the physical and chemical circumstances at the time of sampling.

2.2 | Establishing stream groups based on stress and heterogeneity

Our goal was to group streams into categories that would allow us to test the effects of low stress, high stress, and heterogeneous stress on the regional diversity of diatoms. To determine which of the measured environmental variables were most likely to create stress gradients for diatoms, we ran stepwise redundancy analysis (RDA) with 999 Monte Carlo permutations across all 323 samples. Prior to the RDA, all variables except pH were ln-transformed and species with <1% maximum relative abundance were excluded. The first two variables selected were pH and Al_{im}, which explained 11.2% of the variance in diatom distributions (38.6% of the total explainable variance). Additional variables had only minor contributions to the overall variance (Appendix S1). Therefore, we determined that pH and Al_{im} were the dominant measured environmental gradients for diatoms in this system. Since pH and Al_{im} had a correlation of −0.82, we proceeded to use pH as the basis for categorizing our streams into low heterogeneity groups with high versus low stress and high heterogeneity groups consisting of a combination of high-stress and low-stress streams. Outside of the broad awareness that pH was the strongest gradient influencing species composition in the RDA, we had no prior knowledge of species composition or diversity of the selected groups.

Our classification scheme was as follows (Appendix S2). For each month, streams were ranked by pH. The high-stress group (HS_{Mar}) was created by randomly selecting 50 out of the 75 most acidic streams sampled in March 2004, when acidification was the most severe. The low-stress group (LS_{Aug}) was formed by randomly selecting 50 of the 75 least acidified streams sampled during base flow in August 2004. High heterogeneity groups, consisting of a combination of 25 low acidity (low stress) and 25 high acidity (high stress) streams, were created for each sampling month. The high heterogeneity March group (HH_{Mar}) was constructed by conjoining the 25 most acidic streams not selected for the HS_{Mar} group with the 25 least acidic streams during that period. The high heterogeneity August group (HH_{Aug}) was synthesized from a composite of the 25 least acidic streams not selected for the LS_{Aug} group and the 25 most acidic streams from that period.

We ran a second stepwise RDA to determine the dominant variables structuring diatom communities within these four groups, comprising 200 stream samples in total. The three strongest gradients selected were pH, Al_{im}, and temperature, explaining 16.3% of the overall variance (or 50.2% of the explainable variance; Appendix S3). Additional variables each explained very little of the overall variance (≤1.3%); therefore, we proceeded by including only these three dominant gradients in our environmental heterogeneity analysis.

2.3 | Geographic distance and environmental heterogeneity among groups

A permutation test of multivariate dispersions (PERMDISP; Anderson, 2006) with 9,999 permutations was run on the Euclidean distances of Universal Transverse Mercator coordinates to test whether there was significant among-group variance in geographic distance. The dominant environmental variables (pH, Al_{im}, and temperature) were standardized by subtracting the variable mean from each value and dividing by the standard deviation. Then, a second PERMDISP was run on the standardized variables to test for differences in environmental heterogeneity among groups. Principal component analysis (PCA) was performed on the environmental variables to identify dominant gradients of variation (CANOCO 4.5). Analysis of variance (ANOVA) in SYSTAT 12 was used to test for significant differences in pH, Al_{im}, and temperature among the four groups of streams. Post hoc Tukey's multiple comparison tests were performed on all significant ANOVAs ($p < 0.05$).

2.4 | Compositional heterogeneity among groups

PERMDISP was also used to test for heterogeneity in species composition (Anderson, Ellingsen, & McArdle, 2006). We examined both abundance-based Bray–Curtis dissimilarity and presence–absence-based Jaccard dissimilarity. PERMDISP was run on dissimilarity matrices of all species across the four stream groups and then repeated on dissimilarity matrices of only the sensitive and tolerant species. Principal coordinate analysis (PCoA) was employed to visualize compositional heterogeneity among groups. Tukey's post hoc pairwise comparison tests were run for all significant PERMDISP tests ($p < 0.05$). All PERMDISPs were performed in the R package Vegan (Oksanen et al., 2017).

ANOVA was used to test for differences in mean total species richness and species richness of sensitive and tolerant species among the four stream groups. Gamma diversity, or the total number of species found across all streams in a group, was first calculated across all species and then separately for sensitive and tolerant species.

2.5 | Null models

For each stream group, we applied two null models: the Raup–Crick metric developed by Chase et al. (2011) and the null model developed by Kraft et al. (2011). The Raup–Crick metric tests the probability of two communities of a given species richness being more

or less dissimilar from the null (Chase et al., 2011). Thus, this method evaluates the role of deterministic processes in each group, while controlling for differences in alpha diversity among localities. The probability metric is scaled between –1 and 1, with –1 being more similar than any of the null simulations, 1 being more dissimilar than any of the null simulations, and values of 0 being no different than the random expectation. The pairwise Raup–Crick values for each group were based on 9,999 null simulations.

The model by Kraft et al. (2011) is designed to examine deviations from the null while keeping gamma diversity constant, providing a way to assess whether beta diversity in different groups was limited by the regional species pool. This model uses a modified version of Whittaker's multiplicative function ($\beta = 1 - \overline{\alpha}/\gamma$). First, the observed beta diversity is calculated using this function. Then, individuals are shuffled across samples and the mean "null" beta diversity is calculated, based on the number of permutations. The beta deviation is the difference between the observed and mean null beta diversity, divided by the standard deviation of the null beta diversities. Greater deviations indicate that beta diversity is controlled by local processes (e.g., habitat filtering) as opposed to being determined by gamma diversity alone (Kraft et al., 2011). As gamma diversity is maintained in this procedure, smaller deviations suggest that beta diversity is strongly limited by regional processes that affect the size of the species pool.

For our purposes, we added a looping function with resampling to the model by Kraft et al. (2011), in order to calculate a mean beta deviance for each stream group (Appendix S4). For each group, this looping function resampled 50% ($n = 25$) of the samples 999 times, calculating an observed beta diversity for each resampling and then a mean null beta diversity based on 999 reshufflings of individuals among the 25 samples. In this way, 999 beta deviations were calculated by subtracting the mean null beta diversity from the observed beta diversity, then dividing by the standard deviation of the null beta diversities in each of the resamplings.

Both Raup–Crick and Kraft et al. null models were first performed on all species and then separately on the tolerant and sensitive species. Significance in Raup–Crick values and beta deviations across groups was determined using permutational ANOVA with 999 permutations in the RVAideMemoire package in R (Hervé, 2017). Significant ANOVAs were followed by Bonferroni pairwise comparisons using the same package.

3 | RESULTS

3.1 | Geographic distance and environmental heterogeneity among groups

The omnibus p-value for the PERMDISP of Euclidean distance between streams was nonsignificant ($p > 0.10$), with mean within-group distance between streams ranging between 35.6 and 40.8 kilometres. PERMDISP indicated significant differences in environmental heterogeneity across groups ($F = 39.9$, $p = 0.0001$). The Tukey's post hoc pairwise comparisons revealed the highest heterogeneity in HH_{Mar} and HH_{Aug}, followed by HS_{Mar} and LS_{Aug} (Table 1). The first two axes of PCA of environmental variables across the four stream groups explained 95.9% of the sample variance (Figure 2). The first axis was negatively correlated with pH and positively correlated with Al_{im}, while the second axis was negatively correlated with temperature. The HH_{Mar} group was spread across the pH/Al_{im} gradient and negatively correlated with temperature, while the HH_{Aug} group was spread across the pH/Al_{im} gradient and positively correlated with temperature. The HS_{Mar} group was negatively correlated with pH and temperature, while the LS_{Aug} group was positively correlated with pH and temperature.

The ANOVAs testing whether group means for pH ($F = 45.8$, $p < 0.0001$), Al_{im} ($F = 30.6$, $p < 0.0001$), and temperature ($F = 161.7$, $p < 0.0001$) differ among groups were significant. The Tukey's pairwise comparison tests indicated that the two high heterogeneity (HH) groups did not differ in pH or Al_{im} but did differ in temperature. The LS_{Aug} group had the least stressful conditions (highest pH and temperature, and lowest Al_{im}), while the HS_{Mar} group had the most stressful conditions (lowest pH and temperature, and highest Al_{im}, Table 1).

3.2 | Compositional heterogeneity among groups

The PERMDISP analyses revealed that both Bray–Curtis dissimilarity ($F = 7.1$, $p = 0.0004$) and Jaccard dissimilarity ($F = 6.5$, $p = 0.0002$) in the overall species composition (β_{All}) differed across groups. For both abundance-based and presence–absence-based dissimilarity metrics, the HS_{Mar} group had the lowest dispersion, while the other three groups were not significantly different from one another, based on Tukey's post hoc pairwise comparisons.

Variable	HS_{Mar}	HH_{Mar}	LS_{Aug}	HH_{Aug}
Environmental heterogeneity	1.06[a]	1.35[b]	0.42[c]	1.35[b]
pH	4.9[a]	6.0[b]	6.9[c]	5.8[b]
Al_{im} (μmol/L)	5.7[a]	2.8[b]	0.3[c]	2.8[b]
Temperature (°C)	2.8[a]	4.6[b]	14.5[c]	14.9[c]

TABLE 1 Mean environmental heterogeneity measured as standardized Euclidean distance from the centroid, and mean pH, Al_{im}, and temperature of the four stream groups

Note. The high-stress group consists of the most acidic streams sampled in March (HS_{Mar}), the low-stress group consists of the least acidified streams sampled in August (LS_{Aug}), and the high heterogeneity groups are composed of both low and high acidity streams sampled in each month (HH_{Mar} and HH_{Aug}). Values with different superscripts are statistically significant (Tukey's adjusted p-value <0.05).

FIGURE 2 PCA showing the distribution of the four groups along the environmental gradients selected for this study

These results support hypothesis 3 as beta diversity was equally high in the low stress and high heterogeneity groups (Table 2 and Appendix S5).

The PERMDISP analyses also established differences in dissimilarity of sensitive species ($\beta_{Sensitive}$) among groups: Bray–Curtis ($F = 7.5$, $p = 0.0002$) and Jaccard ($F = 8.5$, $p = 0.0002$). The Tukey's post hoc pairwise comparisons of the Bray–Curtis and Jaccard dissimilarities revealed the highest dispersion in the HH_{Aug} and HH_{Mar} groups and the lowest dispersion in the LS_{Aug} and HS_{Mar} groups.

Since beta diversity of sensitive species decreased as heterogeneity decreased, hypothesis 1 is supported. The PERMDISP for Bray–Curtis dissimilarity of tolerant species ($\beta_{Tolerant}$) was significant ($F = 2.9$, $p = 0.04$), with the dissimilarity of HS_{Mar} being significantly lower than that of HH_{Mar}. The PERMDISP for the Jaccard dissimilarities was nonsignificant. The weak differences in tolerant species dissimilarity among groups (e.g., high heterogeneity groups overlapping with the low and high stress groups) suggests that neither stress nor heterogeneity influenced the distribution of tolerant species (hypothesis 4). A depiction of which pathways (i.e., severity of stress versus heterogeneity of stress) affect β_{All} and $\beta_{Sensitive}$ versus $\beta_{Tolerant}$ is shown in Figure 3.

ANOVA indicated significant among-group differences in total species richness ($F = 24.4$, $p < 0.0001$), sensitive species richness ($F = 28.8$, $p < 0.0001$), and tolerant species richness ($F = 4.9$, $p = 0.003$). The most stressed HS_{Mar} group had the lowest alpha and gamma diversity for all species and sensitive species, while the least stressed LS_{Aug} group had the highest alpha and gamma diversity for both (Table 2). There were not large differences in alpha and gamma diversity of tolerant species across groups, although alpha diversity was significantly lower in the HH_{Mar} group (Table 3).

3.3 | Null models

The Raup–Crick values for all species ($F = 66.7$, $p = 0.001$), sensitive species ($F = 32.3$, $p = 0.001$), and tolerant species ($F = 33.2$, $p = 0.001$) were significantly different across groups. While all the Raup–Crick values were negative (more similar than expected by random chance), the values were significantly less negative in the HH_{Mar} and HH_{Aug} groups relative to the HS_{Mar} and LS_{Aug} groups (Table 3).

TABLE 2 Mean distance to the centroid of the Bray–Curtis and Jaccard similarity indexes across groups for β_{All}, $\beta_{Sensitive}$, and $\beta_{Tolerant}$

Metric	HS_{Mar}	HH_{Mar}	LS_{Aug}	HH_{Aug}	Conclusion
β_{All}					
Bray–Curtis	0.49[a]	0.55[b]	0.53[b]	0.55[b]	Hypothesis 3: Stress severity + heterogeneity
Jaccard	0.46[a]	0.52[b]	0.49[ab]	0.51[b]	Hypothesis 3: Stress severity + heterogeneity
$\beta_{Sensitive}$					
Bray–Curtis	0.54[a]	0.59[bc]	0.55[ab]	0.62[c]	Hypothesis 1: Stress heterogeneity
Jaccard	0.54[ab]	0.57[ac]	0.52[b]	0.60[c]	Hypothesis 1: Stress heterogeneity
$\beta_{Tolerant}$					
Bray–Curtis	0.48[a]	0.53[b]	0.50[ab]	0.52[ab]	Hypothesis 4: Neither stress severity nor heterogeneity
Jaccard	0.40[a]	0.44[a]	0.43[a]	0.43[a]	Hypothesis 4: Neither stress severity nor heterogeneity

Note. Values with different superscripts are statistically different (p-< 0.05) based on Tukey's post hoc pairwise comparisons following a significant PERMDISP. The conclusion column indicates which hypothesis was supported by our results
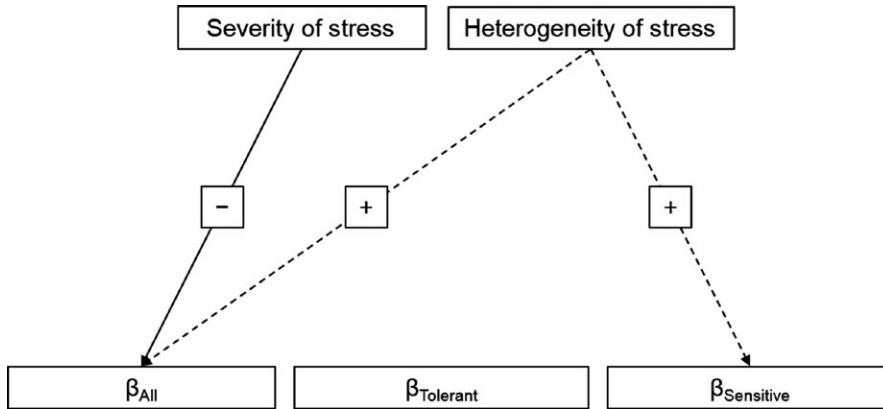
FIGURE 3 Pathways of environmental control on beta diversity in our multivariate dispersion analyses. Pathways representing the severity of stress are solid arrows, and pathways representing the heterogeneity of stress are dashed arrows. Each pathway is marked as positive or negative, depending on the direction of influence

TABLE 3 Alpha and gamma diversity, Raup–Crick, and beta deviation results for all species, sensitive species, and tolerant species in each of the four groups

Metric	HS_{Mar}	HH_{Mar}	LS_{Aug}	HH_{Aug}
All species				
Alpha	18[a]	21[a]	33[b]	27[c]
Gamma	81	101	133	126
Raup–Crick	−0.59[a]	−0.30[b]	−0.48[c]	−0.30[b]
Beta deviation	46.3[a]	68.5[b]	54.6[c]	64.4[d]
Sensitive species				
Alpha	4[a]	9[b]	16[c]	11[b]
Gamma	29	46	68	67
Raup–Crick	−0.33[a]	−0.22[b]	−0.37[a]	−0.18[b]
Beta deviation	10.3[a]	30.1[b]	34.2[c]	27.6[d]
Tolerant species				
Alpha	13[a]	11[b]	13[a]	13[a]
Gamma	37	38	43	41
Raup–Crick	−0.48[a]	−0.36[b]	−0.44[a]	−0.28[c]
Beta deviation	41.2[a]	39.6[b]	26.7[c]	38.6[d]

Note. Values with different superscripts were significantly different ($p < 0.05$) based on ANOVA followed by Tukey's post hoc comparisons for alpha diversity and Permutational ANOVA followed by Bonferroni comparisons for Raup–Crick and beta deviation.

The beta deviations for the Kraft et al. (2011) null model were significantly different across groups for all species ($F = 9,171$, $p = 0.001$), sensitive species ($F = 17,958$, $p = 0.001$), and tolerant species ($F = 4,863$, $p = 0.001$). The most stressed HS_{Mar} group had the lowest beta deviation for all species and sensitive species (Table 3). Beta deviations across groups for the tolerant species were not as drastically different, but the beta deviation was noticeably lower in the least stressed LS_{Aug} group compared to the other groups (Table 3). In summary, Raup–Crick values generally increased (became less negative) with heterogeneity of stress. Beta deviations of all species and sensitive species decreased with severity of stress while those of tolerant species increased with severity of stress (Figure 4).

4 | DISCUSSION

Consistent with our first objective, we tested four hypotheses regarding how severity versus heterogeneity of stress influence beta diversity. This question has become increasingly important as beta diversity may have contrasting directional responses to stress or disturbance, with different inferences for regional conservation (Socolar et al., 2016). Generally, our results support hypothesis 3, that beta diversity is influenced by a combination of stress and heterogeneity.
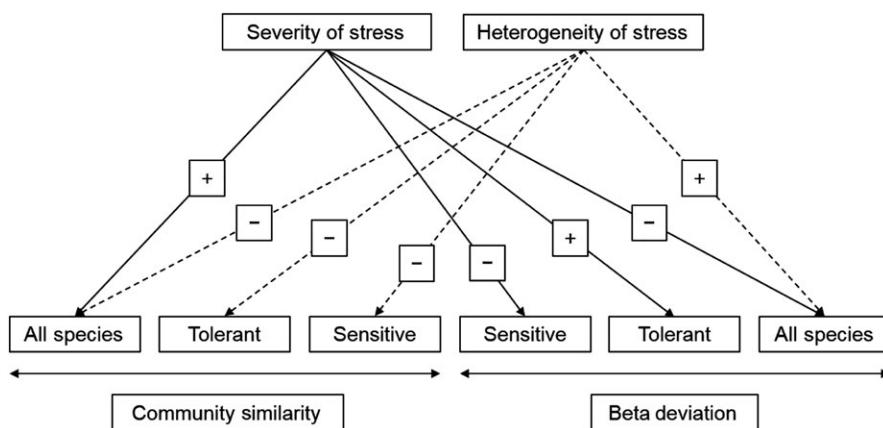

FIGURE 4 Effects of severity and heterogeneity of stress on community similarity (negativity of the Raup–Crick values) and beta deviation of all species, tolerant species, and sensitive species. The solid arrows represent the severity of stress, while the dashed arrows represent the heterogeneity of stress. Each pathway is marked as positive or negative, depending on the direction of influence

Metrics based on species abundances and occurrence suggested that heterogeneity can offset the negative effects of stress to an extent. However, as stress becomes more wide-spread, heterogeneity is lost, resulting in a narrower niche breadth and stronger selection of tolerant species (Chase, 2007). This stronger filtering results in a decrease in β_{All} with severity of stress.

Deconstructing the species pool into guilds may provide insight into how differences in species adaptations influence distributions (Dong et al., 2016; Jamoneau, Passy, Soininen, Leboucher, & Tison-Rosebery, 2018). We showed that relative to β_{All}, $\beta_{Sensitive}$ was more influenced by heterogeneity, confirming hypothesis 1. The high alpha diversity combined with low beta diversity in the low-stress group is suggestive of favourable environmental conditions that allow a larger proportion of the species pool to inhabit each site, resulting in less turnover. This result is consistent with Pither and Aarssen (2005), who found that the composition of acid-sensitive species became more similar across circumneutral and alkaline lakes relative to acidified lakes. In contrast, a more diverse stress gradient, equivalent to an increase in heterogeneity of stress, enhanced beta diversity by breaking up the dominance of sensitive species.

Similarly, studies of macroinvertebrates and fungi have documented altered species prevalence, taxon loss, or decreased alpha diversity as explanations for increased beta diversity with stress or disturbance (Hawkins et al., 2015; Libório & Tanaka, 2016; Mykrä et al., 2017). Notably, Hawkins et al. (2015) observed greater heterogeneity across disturbed sites, in part attributed to low pH or unnaturally high pH relative to reference sites. The mechanism of increased beta diversity for both pH extremes was ascribed to expansion of rare, tolerant species in concurrence with suppression of once common, sensitive species.

In contrast to the findings of Hawkins et al. (2015), tolerant species in our study were common across both high and low stress gradients. The ubiquity of acid-tolerant diatoms in Adirondack streams is seen in their weak variation in abundance-based beta diversity and uniform occurrence-based beta diversity across groups differing in stress severity and heterogeneity. These results, along with the similar alpha and gamma diversity of tolerant species among groups, indicate that acid-tolerant species occur across broad pH ranges in this acid-sensitive region. Our analyses concur with those of Pither and Aarssen (2005), who described tolerant diatom species as pH generalists that exhibit little turnover along pH gradients.

Our second objective was to examine the influence of acidification stress and heterogeneity on community similarity relative to randomly assembled communities and whether these factors alter the constraint of beta diversity by local assembly mechanisms versus the regional species pool. The null model results revealed differences in local assembly patterns after controlling for the effects of alpha and gamma diversity. The mean Raup–Crick values were all more similar than expected in randomly assembled communities, signifying a strong role of environmental filtering, consistent with other diatom studies (Soininen, Jamoneau, Rosebery, & Passy, 2016; Verleyen et al., 2009). The lack of hydrological connectivity in headwater streams, such as in the streams studied here, may further

intensify the importance of species sorting relative to other local assembly mechanisms, including dispersal (Heino, Grönroos, Soininen, Virtanen, & Muotka, 2012; Jamoneau et al., 2018). We had originally predicted that communities would become more deterministic with stress and that this would be partially exemplified by higher community similarity (or more negative Raup–Crick values). These predictions were confirmed only for β_{All}, for which the Raup–Crick value was the lowest (most negative) in the high-stress group. However, the Raup–Crick values for the sensitivity guilds did not differ between the low-stress and high-stress groups. Instead, heterogeneity emerged as the most important factor, introducing more randomness in community composition across all species and within both guilds.

While initial perspectives on community assembly assumed that environmental determinism increases with stress (Chase, 2007), it is now evident that the effect of disturbance on environmental filtering is distinct to the taxon or system. For instance, Mykrä et al. (2017) reported that environmental degradation led to homogenization of bacterial communities but more stochastic fungal communities. Hawkins et al. (2015) observed more stochastic distribution of macroinvertebrates in intermediately disturbed sites, while severe disturbance generated physicochemical heterogeneity and more dissimilar taxonomic composition than predicted by chance. In our system, heterogeneity of stress drove communities closer to a random distribution, and this pattern persisted across guilds. Severity of stress, on the other hand, was less impactful, increasing environmental filtering relative to the null distribution across all species but not among the sensitivity guilds. Incongruent with other studies, environmental filtering remained the dominant control on communities across gradients of stress severity and heterogeneity (i.e., shared occupancy of species was higher than the null expectation in all environments).

In relation to our second and third objectives, we did uncover differences in how the severity and heterogeneity of stress affect local assembly mechanisms, in addition to beta diversity, in sensitive versus tolerant species. We originally predicted that stress would suppress beta diversity by reducing the size of the regional species pool. This pattern was only confirmed for β_{All} and $\beta_{Sensitive}$, which were under weak local assembly but high gamma diversity control in the high-stress group. In contrast, the role of local assembly for tolerant species increased with stress. These diverging trends suggest that at high stress, sensitive species exert disproportionately larger impacts on communities, most likely driven by their diminished regional diversity, when compared to tolerant species. Strong filters on the regional species pool may weaken species-environment relationships that are important in local assembly (Vellend et al., 2007). Our analyses also revealed that species were constrained by local effects in favourable conditions (i.e., more acidic for tolerant species and less acidic for sensitive species) but by the regional pool in unfavourable environments (i.e., less acidic for tolerant species and more acidic for sensitive species). Thus, stress can benefit some species, while restricting others, and depending on their stress tolerance, these species can experience larger or smaller beta

deviations. Consequently, it is appropriate to generalize that species responses to local versus regional effects are determined by species' environmental preference and environmental context, necessitating community deconstruction. Previous studies have recognized the positive link between species sorting and habitat heterogeneity (Astorga et al., 2014; Stegen et al., 2013), but our findings further indicate that the strength of local assembly processes may depend on environmental suitability.

This study provides a novel trait-based framework elucidating the pathways of local and regional control on beta diversity in stressed systems. It shows that stress severity versus heterogeneity have differential effects on community similarity, measured when alpha diversity is controlled, and local assembly processes, measured when gamma diversity is controlled. Stress severity constrains local assembly processes, while stress heterogeneity affects community similarity. Our framework further demonstrates that while stress heterogeneity acts upon both guilds in a similar way (increased heterogeneity leads to lower similarity), stress severity impacts only sensitive species, and this pattern persists at the level of the entire community. The diverging effect of stress severity on the strength of local assembly processes highlights the utility of examining the response of these mechanisms within guilds. The beta deviations of sensitive species show declining importance of assembly mechanisms and increased constraint by the regional species pool with stress. While disturbance has been shown to modify beta diversity by favouring some species and limiting others (Hawkins et al., 2015), our study further reveals that these opposing patterns result from differences in how stress affects the intensity of local assembly processes. It is unknown whether stress (or disturbance) has the same effect on local assembly of sensitive versus tolerant species in all systems, but this investigation presents a model for testing the influence of stress in future studies.

The contrasting diversity patterns of sensitive versus tolerant species imply that heterogeneity increased β_{All} through what Socolar et al. (2016) described as "subtractive heterogenization." In other words, alpha diversity of sensitive species declined with acid stress, and the elimination of sensitive species from acid streams in the heterogeneous groups gave rise to higher beta diversity. Many of these sensitive species (i.e., *Achnanthidium minutissimum*, *Meridion circulare*, and *Encyonema* species) are indicators of healthy New York streams (Passy & Bode, 2004). Thus, the consistently high alpha diversity of these species in low-stress streams should be desirable. As Socolar et al. (2016) asserted, the interpretation of beta diversity for conservation management is contextual and must be viewed through the lens of changes in alpha diversity. Given the extremely low alpha diversity and sparse species pool of these positive indicator species in the high-stress group, increased beta diversity due to heterogeneous stress may actually be an early warning sign of environmental degradation that will diminish diversity if allowed to persist (de Juan, Thrush, & Hewitt, 2013). Even in scenarios where gamma diversity is maintained by high species turnover, problems may still arise if functionally important

taxa are absent from disturbed sites (Fugère et al., 2016). For these reasons, changes in beta diversity, even positive ones, may be cause for concern in anthropogenically modified or stressed systems. Our findings affirm the notion that inferences about beta diversity should be made with careful consideration of how shifts in species composition, alpha, and gamma diversity affect the metric. Deconstructing the species pool may provide further insight as to whether stress or disturbance increases beta diversity by disproportionately affecting the distribution of sensitive species.

DATA ACCESSIBILITY

The data supporting the results in this manuscript are archived in Dryad.

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BIOSKETCHES

Katrina Pound received her Ph.D. from the University of Texas at Arlington, where she is currently a postdoctoral researcher. Her research interests are in acid-impacted streams and processes influencing biodiversity.

Gregory Lawrence obtained a Ph.D. in Civil Engineering at Syracuse University after studying the effects of acid rain and clearcutting on stream chemistry at the Hubbard Brook Experimental Forest in New Hampshire. After 3 years as a research professor at the University of Maine, Lawrence joined the New York Water Science Center of the U.S. Geological Survey in Troy, New York, where he has worked since.

Sophia Passy's research explores the origins of species coexistence and abundance inequality across organismal groups in aquatic ecosystems as well as the causes of acidification and its consequences for stream algal communities.

Author contributions: S.I.P. and K.L.P. developed the ideas, K.L.P. analyzed the data, G.B.L. designed the sampling scheme and collected the samples, K.L.P. wrote the article with substantial input by S.I.P.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.
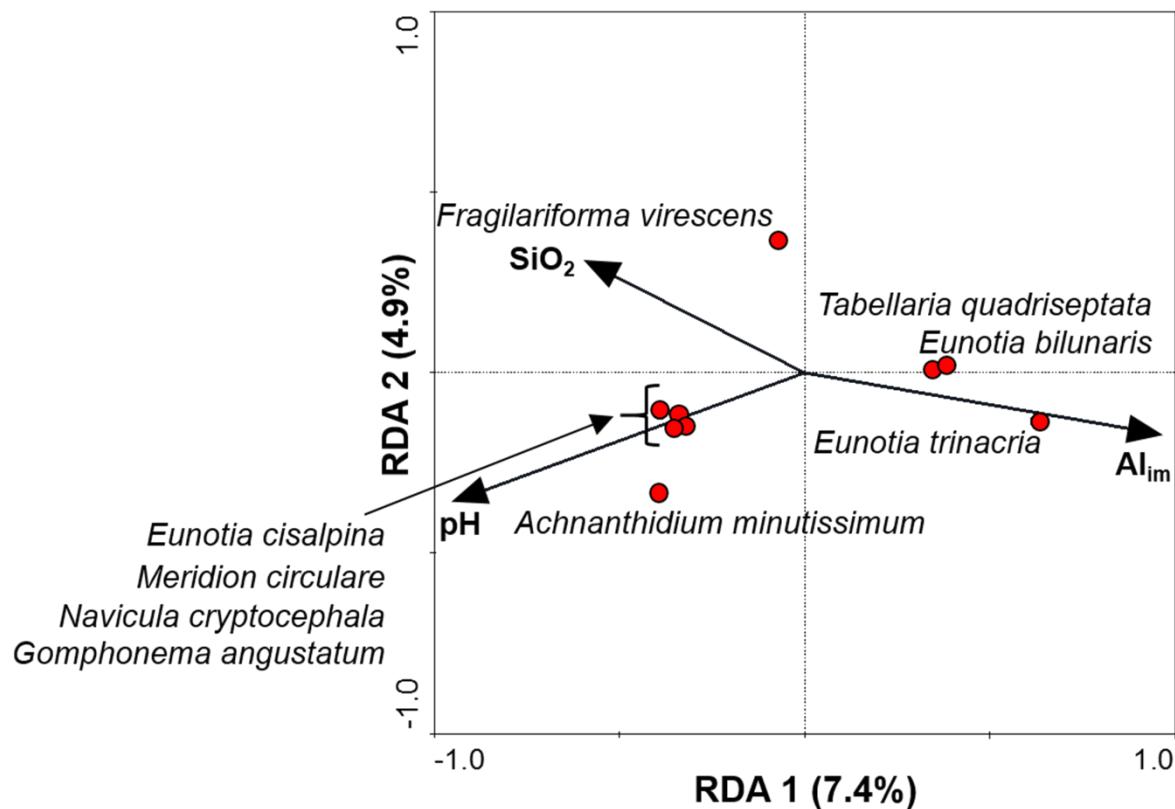
Appendix S1. Redundancy analysis (RDA) ordination of the dominant environmental gradients and selected species from the 323 stream samples from which the four categories were formed.
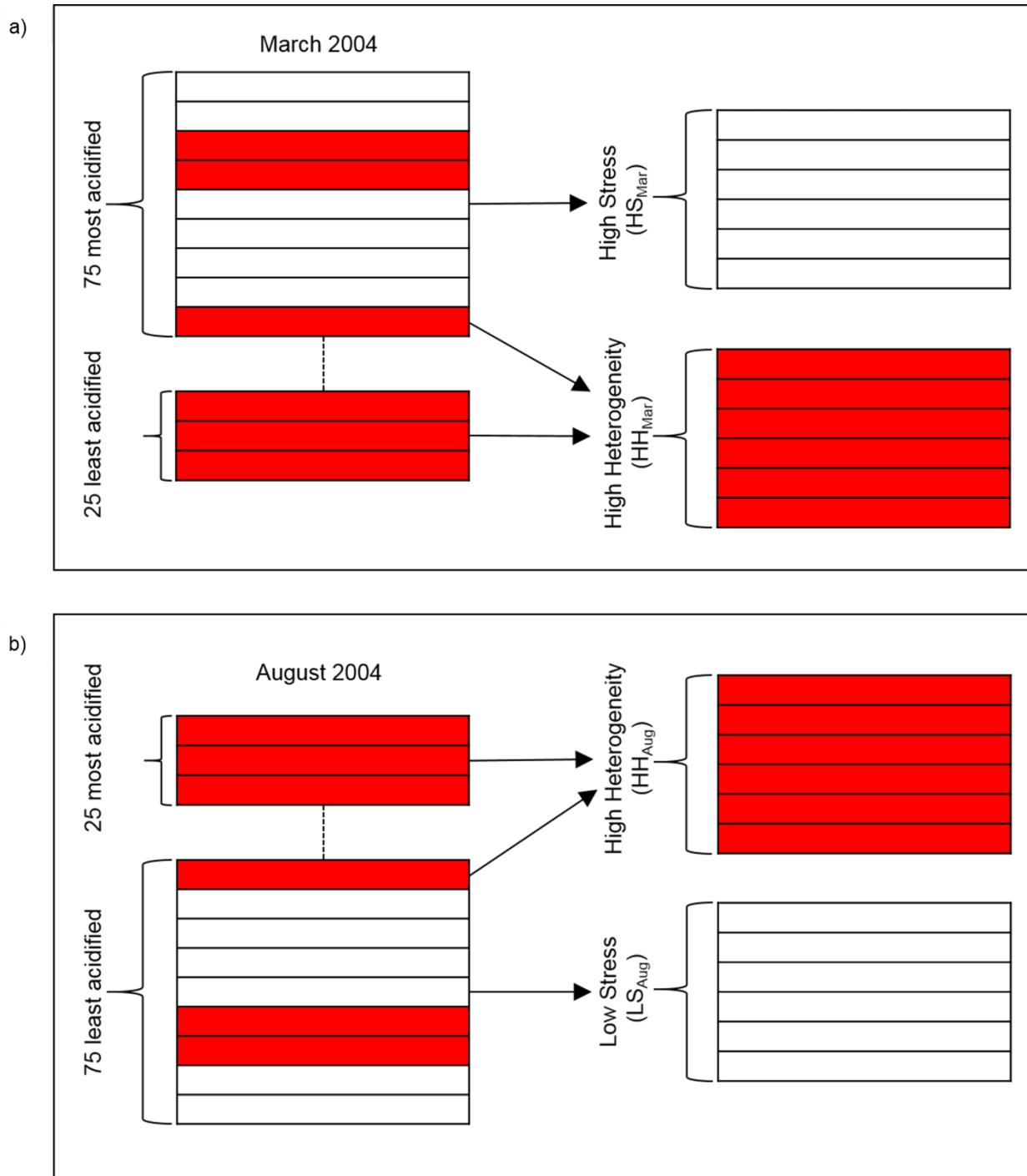
Appendix S2. Visual portrayal of how the streams were selected for the four groups, i.e. high heterogeneity in March (HH$_{Mar}$), high stress in March (HS$_{Mar}$), high heterogeneity in August (HH$_{Aug}$), and high stress in August (HS$_{Aug}$). In both boxes a and b, the red rows represent

streams placed in the HH groups, while the clear rows represent streams selected for the HS_{Mar} and LS_{Aug} groups, respectively. **a)** Selection of the March streams for the HS_{Mar} and HH_{Mar} groups. The left column represents the March streams prior to selection, ordered by increasing pH. Fifty streams were randomly selected for the HS_{Mar} group from the 75 most acidified streams in March. The remaining 25 most acidified streams were then combined with the 25 least acidified streams to form the HH_{Mar} group. **b)** Selection of the August streams for the LS_{Aug} and HH_{Aug} groups. The left column represents the August streams prior to selection, ordered by increasing pH. Fifty streams were randomly selected for the LS_{Aug} group from the 75 least acidified streams in August. The remaining 25 least acidified streams were then combined with the 25 most acidified streams to form the HH_{Aug} group.
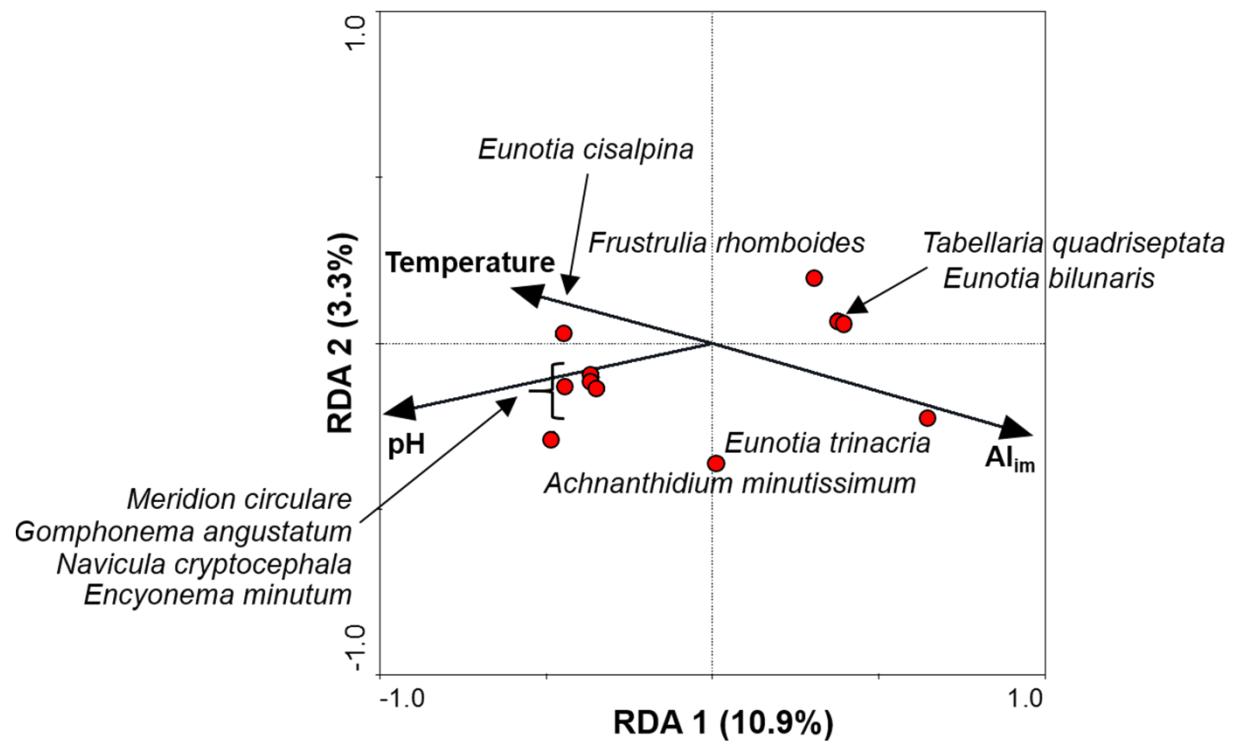
**Appendix S3.** Redundancy analysis (RDA) ordination of the dominant environmental variables and selected species in the 200 samples from the four groups.

Original Data

Individual 1	Species A	Sample 1
Individual 2	Species C	Sample 1
Individual 3	Species E	Sample 1
Individual 4	Species B	Sample 2
Individual 5	Species E	Sample 2
Individual 6	Species C	Sample 2
Individual 7	Species B	Sample 3
Individual 8	Species A	Sample 3
Individual 9	Species A	Sample 3
Individual 10	Species B	Sample 4
Individual 11	Species E	Sample 4
Individual 12	Species D	Sample 4

Step 1

Select 50% of samples →

Calculate Observed β on Subsample:
$$\beta_{observed} = 1 - \bar{\alpha}/\gamma$$

Individual 1	Species A	Sample 1
Individual 2	Species C	Sample 1
Individual 3	Species E	Sample 1
Individual 10	Species B	Sample 4
Individual 11	Species E	Sample 4
Individual 12	Species D	Sample 4

→ Shuffle Individuals Across Subsamples →

Calculate Null β:
$$\beta_{Null} = 1 - \bar{\alpha}/\gamma$$

Individual 2	Species C	Sample 1
Individual 12	Species D	Sample 1
Individual 11	Species E	Sample 1
Individual 1	Species A	Sample 4
Individual 3	Species E	Sample 4
Individual 10	Species B	Sample 4

Step 2
Shuffle subsample and recalculate β_{null} 999 times

→

Step 3
Calculate $\beta_{deviation}$:
$(\beta_{observed} -$ Mean $\beta_{null})/\beta_{SD}$

→

Step 4
Repeat Subsampling and Previous Steps 999 Times

→

Step 5
Use Permutational ANOVA to Test for Differences in $\beta_{deviation}$ Among Groups

Appendix S4. Schematic figure showing the steps of the null model analysis after Kraft et al. (2011). **Step 1:** 50% of the samples were taken from the original dataset and $\beta_{observed}$ was calculated. **Step 2:** Individuals were shuffled among the samples and β_{null} was calculated 999 times. **Step 3:** Calculate $\beta_{deviation}$ as the difference between $\beta_{observed}$ and mean β_{null}, divided by the standard deviation of β_{null}. **Step 4:** Repeat the subsampling and previous steps 999 times. **Step 5:** Use Permutational ANOVA to test for differences in $\beta_{deviation}$ among groups.

a) Bray-Curtis
All Species ($p = 0.0004$)
HH$_{Mar}$ HH$_{Aug}$ LS$_{Aug}$ HS$_{Mar}$

b) Bray-Curtis
Sensitive species ($p = 0.0002$)
HH$_{Aug}$ HH$_{Mar}$ LS$_{Aug}$ HS$_{Mar}$

c) Bray-Curtis
Tolerant species ($p = 0.04$)
HH$_{Mar}$ HH$_{Aug}$ LS$_{Aug}$ HS$_{Mar}$

d) Jaccard
All Species ($p = 0.0004$)
HH$_{Mar}$ HH$_{Aug}$ LS$_{Aug}$ HS$_{Mar}$

e) Jaccard
Sensitive species ($p = 0.0002$)
HH$_{Aug}$ HH$_{Mar}$ HS$_{Mar}$ LS$_{Aug}$

f) Jaccard
Tolerant species (NS)
HH$_{Mar}$ HH$_{Aug}$ LS$_{Aug}$ HS$_{Mar}$

6
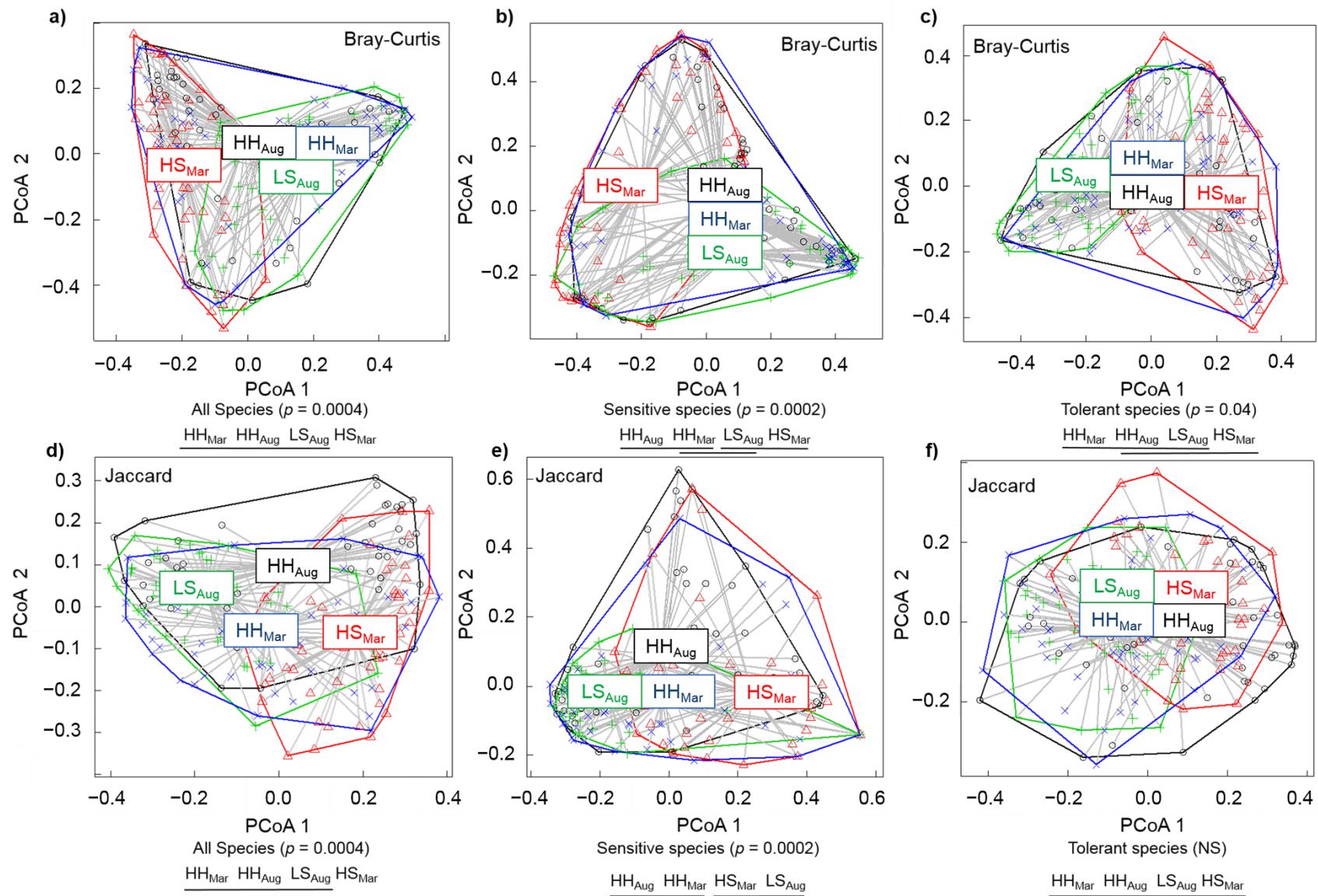
Appendix S5, a-f. Principal Coordinate Analyses (PCoA) of resemblance matrices of the four groups of streams, using Bray-Curtis (top row) and Jaccard (bottom row) dissimilarity of all species (a and d), sensitive species (b and e), and tolerant species (c and f). The p-values indicate the omnibus statistic for the permutation test of multivariate dispersion (PERMDISP). Underneath each plot, the stream groups are listed in order of descending value of mean dissimilarity (i.e., beta diversity). Underlined groups were not statistically different in the Tukey's post hoc pairwise comparisons. For the sensitive and tolerant species analyses, samples with abundance of zero across all species were necessarily removed prior to the analysis (e.g., n = 49 samples for the HH_{Mar} group in b, c, e, and f and n = 46 samples for the HS_{Mar} group in b and e). All other groups had n = 50 samples across all analyses.