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Weighting effective number of species measures by abundance weakens detection of diversity responses

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Abstract

1. The effective number of species (ENS) has been proposed as a robust measure of species diversity that overcomes several limitations in terms of both diversity indices and species richness (SR). However, it is not yet clear if ENS improves interpretation and comparison of biodiversity monitoring data, and ultimately resource management decisions.

2. We used simulations of five stream macroinvertebrate assemblages and spatially extensive field data of stream fishes and mussels to show (a) how different ENS formulations respond to stress and (b) how diversity–environment relationships change with values of q, which weight ENS measures by species abundances.

3. Values of ENS derived from whole simulated assemblages with all species weighted equally (true SR) steadily decreased as stress increased, and ENS-stress relationships became weaker and more different among assemblages with increased weighting.

4. The amount of variation in ENS across the fish and mussel assemblages that was associated with environmental gradients decreased with increasing q.

5. *Synthesis and applications*. Species diversity is valued by many human societies, which often have policies designed to protect and restore it. Natural resources managers and policy makers may use species richness and diversity indices to describe the status of ecological communities. However, these traditional diversity measures are known subject to limitations that hinder their interpretation and comparability. The effective number of species (ENS) was proposed to overcome the limitations. Unfortunately, our analyses show that ENS does not improve interpretability of how species diversity responds to either stress or natural environmental gradients. Moreover, incorporating the relative abundance of individuals in different species (evenness) into diversity measures as implemented in ENS can actually weaken detection of diversity responses. Natural resources managers and policy makers therefore need to be cautious when interpreting diversity measures, including ENS, whose values are jointly influenced by richness and evenness. We suggest that both researchers and practitioners measure and report three aspects of diversity (species richness, evenness, and composition) separately when assessing and monitoring the diversity of ecological communities.

1 | INTRODUCTION

There is a critical need to assess and monitor biodiversity as human activities increasingly alter ecosystems (Buckland, Magurran, Green, & Fewster, 2005; Pereira & Cooper, 2006). One important aspect of biodiversity is species diversity – the variation in the numbers and relative abundances of species in a community (Chao, Chiu, & Jost, 2014; Gaston, 1996; Simpson, 1949). Historically, different indices (see Hurlbert, 1971; Patil & Tallie, 1982; Peet, 1974) have been used to quantify species diversity, assess effects of human disturbances on communities, and sometimes guide conservation planning (e.g., Harris, Milligan, & Fewless, 1983; Usher, 1986). Effective use of these indices depends on the extent to which they provide interpretable and comparable measures of the actual species diversity present at different locations. Species richness (SR), the simplest measure of species diversity, is often strongly related to both natural environmental variation (Hannisdal & Peters, 2011; Rosenzweig, 1995) and human-caused disturbance (Dudgeon et al., 2006; Vaughn, 2010). However, different diversity indices often respond inconsistently to both natural environmental gradients and human-caused disturbance (e.g., Cairns & Pratt, 1993; Prendergast, Quinn, & Lawton, 1999; Sheehan, 1984). Subsequent analyses have shown that indices differ in their mathematical properties and hence the degree to which they scale with our conceptual notion of what species diversity means (Jost, 2007; Lande, 1996). These differences may confound comparisons of diversity across studies and affect interpretation of how communities respond to natural environmental heterogeneity and human-caused stresses.

Recently, Jost (2007) built on the ideas of Hill (1973) to identify ways to assess species diversity in consistent ways (Chao, Chiu, et al., 2014; Chao, Gotelli, et al., 2014). This work was motivated by recognition that species diversity indices do not typically measure diversity as conceptualized by ecologists, here referred to as true diversity, which Jost (2007) and Tuomisto (2010, 2011) argues is best thought of as the number of equally common species in a community. These indices are usually correlated with true species diversity measures, but their properties differ from those of true species diversity – e.g., doubling the number of equally common species will usually not result in a doubling of an index value (hereafter, the doubling property). To avoid these scaling issues, Jost (2006, 2007) recommends that ecologists use effective number of species (ENS) measures, or Hill Numbers, which satisfy the doubling property, when assessing species diversity. The ENS is the number of equally-common species required to give a particular value of an index. For example, the Simpson Diversity Index (D) is calculated as $\sum(p_i)^2$, where $p_i = n_i/N$, n_i = the abundance of species i, and N = the total number of individuals in a sample. Its ENS is calculated as $1/D$. Jost (2007) also found that a single framework, $\lambda = \sum(p_i)^q$, with ENS defined as $\lambda^{1/(1-q)}$, provided a unified way to represent both SR and many diversity indices. The coefficient q controls the weights of common and rare species in ENS characterizations (e.g., $q = 0$ for SR, q converging to 1 ($q \rightarrow 1$) for the Shannon–Wiener Index or H', and $q = 2$ for Simpson D). Changing q-values produces a family of Hill Numbers. Theoretically, ENS-based measures possess two other important properties: (a) they allow α and β diversity to vary independently from one another across regions with different gamma diversities and (b) a given ENS value denotes the same amount of diversity so that the within-community and among-community components can be directly compared (Jost, 2007). Because of these strengths, ENS measures have been generalized to include phylogenetic and functional diversities (Chao, Chiu, et al., 2014). Also, ENS measures with $q > 0$ (hereafter ENS⁺) appear to have an additional advantage. Their values are less dependent on sampling effort than SR (Beck & Schwanghart, 2010), and they can be more easily adjusted for under-sampling (Chao, Gotelli, et al., 2014). These properties of ENS should provide more interpretable and comparable assessments of biodiversity compared with SR and indices such as Shannon's H' and Simpson's D (Jost, 2007). ENS has been increasingly used for biodiversity monitoring, assessment, and conservation planning (Appendix S1). However, to our knowledge, no empirical studies have systematically and comprehensively documented how comparable different ENS measures are in terms of how they respond to either known alteration in assemblage composition or environmental variables known to influence biodiversity.

In this study, we empirically examined how different ENS measures (including SR) respond to both known alteration in assemblage diversity and naturally occurring environmental heterogeneity. We first examine how different ENS measures calculated for five stream macroinvertebrate assemblages respond to simulated alteration of their composition and species' abundances. Simulated data are useful for assessing system behaviour, because properties of the data are known (Gauch & Whittaker, 1976; Minchin, 1987). We also determined how strongly different ENS measures derived from surveys of stream fish and mussel assemblages are associated with environmental variation within a region. We address two specific questions: how does q affect (a) inferences regarding the response of diversity to assemblage alteration and (b) the strength of ENS-environment associations. Answering these questions will help identify which ENS-based measures provide sensitive, consistent, interpretable, and comparable assessments of species diversity for use in biodiversity monitoring and conservation planning.

2 | MATERIALS AND METHODS

We used three datasets to evaluate the behaviour of SR and other ENS measures. The first dataset describes the response of five stream macroinvertebrate assemblages to simulated impairment (Cao & Hawkins, 2005). The other two datasets describe how stream fish and mussel assemblages, respectively, vary across streams that span a wide range of environmental conditions (Cao, Hinz, Metzke, Stein, & Holtrop, 2016; Cao et al., 2015).

2.1 | Simulated macroinvertebrate assemblages

The macroinvertebrate dataset has been described in detail in a previous publication (Cao & Hawkins, 2005). We used large (~16,000–23,000 individuals) benthic samples to represent the known (true) initial macroinvertebrate assemblages at five minimally-disturbed streams in the Pacific Northwest region of the USA. Most individuals were identified to the genus level but some could only be identified to family or higher levels, a common constraint in macroinvertebrate surveys, because the immature stages of most invertebrates cannot be routinely identified to a finer taxonomic resolution (Merritt, Cummins, & Berg, 2007). We refer to all taxa as "species" out of convenience. These reference-condition assemblages contained 39–54 species (Appendix S2: Table S2), and differed markedly in taxonomic composition (Jaccard Coefficient = 0.43–0.61), evenness (Pielou J = 0.53–0.71; Cao & Hawkins, 2005), and species accumulation curves (Appendix S2: Figure S2a).

In our simulation, we assumed that individual species responded to human-caused stress in direct proportion to their empirically determined environmental tolerances (e.g., Hering et al., 2010; USEPA, 2006). Mechanistic-based simulations of species responses to natural environmental factors, human stressors, and other species would have probably produced theoretically robust responses from which to generalize, but such simulations are not feasible at this time because of our limited understanding of the individual, population, and community ecology of most species of macroinvertebrates. However, to compare the behaviour of ENS measures, it was more important to produce known, plausible changes in assemblage composition and structure than to capture the effects of all processes that can influence diversity patterns.

We therefore modelled the response of each species to stress as a linear function of each species' empirically estimated tolerance value (TV) as: $Y_{ij} = X_j[1 - C_i(1 - TV_j)]$, where X_j = the original abundance of a species j, Y_{ij} = the abundance of species j at stress level i, and TV_j = the tolerance value of species j. Tolerance values (as positive real numbers) of the 70 species observed across the five assemblages ranged from 0 (*most sensitive*) to 5 (*most tolerant*; see Cao & Hawkins, 2005 for details). In this dataset, TV values are approximately equivalent to the optima of species along a generalized gradient of environmental change. A species' abundance will not change with increasing stress if TV = 1, will decrease if TV < 1, and will increase if TV > 1. With increasing stress (C), sensitive species were reduced in abundance or eliminated, whereas abundances of more tolerant

species either remained unchanged or increased. The assemblages were increasingly stressed by increasing the C-value from 0 to 2 at intervals of 0.2 (Cao & Hawkins, 2005). The multi-species responses to stress that we observed in these simulated assemblages were realistic (Appendix S3) and should therefore provide a powerful means for understanding how derived assemblage-level indices respond to assemblage alteration (Cao & Hawkins, 2005). The simulation can be implemented with an R-script provided in Appendix S4.

We also characterized different aspects of species and assemblage tolerance. We measured the correlation between species TVs and their relative abundances (p_i) at C = 0 to help us understand if sensitivity to stress is related to how common (or rare) species are, which could inform us if the use of a profile of ENS measures might provide insights into the responses of common and rare species to increasing stress as previously suggested (Morris et al., 2014). We also documented how overall assemblage tolerance changed with increasing stress by calculating the average TV, measured as $\sum(TV_j \times n_j)/N$, at the 11 stress levels for each assemblage.

2.2 | Regional relationships between two types of stream assemblages and their environments

We compiled field data on two stream assemblages: fish and mussels. The fish data were obtained from a fisheries database managed by the Illinois Department of Natural Resources and is described in detail in Cao et al. (2016). A total of 163 species were recorded across the 937 sites, and sample SR varied between 5 and 40 (M = 18.9). The mussel dataset is based on a state-wide survey conducted in 2010–2015 (Cao et al., 2015). Thirty-nine species were collected from 915 sites, and sample SR ranged from 0 to 19 (M = 5.9). Our analyses of ENS-environment relationships were based on a large set of candidate variables describing climate, geology, land use, topography, soil, stream size, and connectivity to other water bodies (Appendix S5). Most variables were expressed at both watershed and riparian-zone scales. For fish ENS modelling, we used the same 66 candidate environmental variables selected by Cao et al. (2016) for modelling fish abundance in the same region (Appendix S6), and for mussel ENS models, we used the 69 candidate variables used by Cao et al. (2015) in modelling mussel abundance (Appendix S7).

2.3 | ENS evaluation

To answer question 1 (response to known assemblage alteration), we calculated ENS values at 11 q values (0–2 at 0.2 intervals) from all individuals in the simulated macroinvertebrate assemblages at each of 11 stress (C) levels (also 0–2 at 0.2 intervals). We then calculated Spearman correlation coefficients between ENS values and stress levels for each of the 11 ENS-stress datasets and plotted ENS values against C to visualize the relationships. We were particularly interested in determining if the ENS-stress relationship was consistent across assemblages, in which case the ENS-stress relationship would be considered general and independent of initial assemblage composition.

To answer question 2, i.e., relationships with natural environmental and land-use variables (hereafter, environmental variables for brevity), we used random forests regression (Breiman, 2001; Cutler et al., 2007; RANDOMFOREST v4.6-10, R package 3.1.2) to model the relationships between each of 21 versions of ENS ($q = 0$–2 at 0.1 intervals) and environmental variables for both the fish and mussel data. We used all predictors, progressively increasing the number of candidate predictors used in each split (i.e., mtry), and built five replicate models at each mtry level until the mean pseudo-R^2 across the replicates stabilized (R^2 increase <0.01). The mtry value that produced the stable R^2 was used to build the final model. We measured the relative importance of a variable in predicting ENS values as the % increase in mean standard error (%MSEI) in the prediction after values of the variable were randomized across samples (Cutler et al., 2007). The higher the %MSEI is, the more important a variable is in predicting ENS. We then calculated Pearson correlation coefficients (r) between the q-values used to calculate ENS measures and the %MSEI associated with each candidate predictor variable. A high and positive correlation means the importance of a variable in predicting ENS increased with q-value, and vice versa.

3 | RESULTS

3.1 | Response of assemblages to simulated stress

The simulation produced marked changes in both the number of species and species composition (Cao & Hawkins, 2005). On average, the initial assemblages lost 40% of their species at $C = 2$ (Appendix S2), and the similarity (Bray–Curtis Index) in species composition between initial and stressed ($C = 2$) assemblages dropped by 35% on average (Cao & Hawkins, 2005), indicating both substantial species loss and changes in species composition of the assemblages.

Mean TV values for the original assemblages ($C = 0$) ranged from 0.65 to 0.94 ($M = 0.80$), and values gradually increased with increasing stress (TVs = 1.18–2.07 [$M = 1.46$] at $C = 2$). Considering that a species with TV = 1 is insensitive to stress, the stressed assemblages were ultimately dominated by more tolerant species. Two or three of the top 5 dominant species in the original assemblages ($C = 0$) were highly sensitive ones (mean TVs = 0.41–0.51), and they were replaced by much more tolerant species (mean TVs = 2.1–4.95) at the highest stress level ($C = 2$).

We also found weakly negative correlations between species' TVs and relative abundances at $C = 0$ ($-0.19 \leq r \leq -0.11$), indicating that neither abundant nor rare species were consistently sensitive or tolerant to stress. Rare species had a large range of TV values, whereas abundant species were either sensitive (TV well below 1) or relatively insensitive to stress (TV close 1) (see Appendix S2: Figure S2b), implying that stress did not consistently affect one abundance group more than another.

3.2 | ENS responses to assemblage alteration

The response of ENS values to the simulated stress strongly depended on q (Figure 1). SR (ENS at $q = 0$) gradually decreased with increasing stress in all assemblages ($-0.98 \leq$ Spearman $r_s \leq -0.89$). However, as q increased, ENS-stress relationships increasingly diverged from one another across the five assemblages (Figure 1, Table 1). For two assemblages (PT and TP), ENS at high q declined with stress, but for the other three assemblages ENS at high q either increased or peaked along the stress gradient. For example, at site MK, ENS values peaked at $C = 1.4$ when q was ~1 or greater.

3.3 | ENS-environment relationships

ENS-environment relationships were strongest at q between 0.0 and 0.2 for both fish (pseudo-R^2 ~0.36) and mussel datasets (pseudo-R^2 ~0.52). Pseudo-R^2 steadily declined to ~0.11 for fish and 0.38 for mussel as q increased from 0.3 to 2.0 (Figure 2), a result consistent with the observation that ENS-stress relationships were often weak at high q (cf. Figure 1). The key environmental predictors for ENS measures remained largely consistent across a range of q-values, including watershed size, growing-degree day, and % of urban land in the watershed (Appendices S6 and S7), although the most important predictors differed to some extent between the two assemblages. However, the importance (%MSEI) of those predictors steadily decreased with increasing q for 55 of 66 predictors for fish ENS, and 55 of 69 predictors for mussel ENS, including all critical ones as indicated by high %MSEI (Appendices S6 and S7). The importance of the other predictors slightly increased with q, but those predictors contributed little to the models (i.e., much lower average %MSEI). In other words, with increasing q the ENS-environment associations became weaker while providing no new information regarding factors affecting diversity.

4 | DISCUSSION

The detrimental effects of human disturbances on species diversity is generally well established (e.g., McGill, 2015; Pimm et al., 2014), but our ability to make standardized comparisons across studies has been compromised by lack of consensus on the definition of species diversity and how best to measure it (Chiarucci, Bacaro, & Scheiner, 2011; Magurran & McGill, 2011; Norton, 1994; Ricotta, 2005). Recent studies have attempted to establish a unified framework for interpreting different diversity measures and relating them to one another (Jost, 2007). The concept of ENS is an essential aspect of this framework. Ecologists have started to explore some of the statistical (e.g., accuracy) and mathematical properties (e.g., doubling and partitioning rules, see Jost 2007, of ENS (Beck & Schwanghart, 2010; Chao, Gotelli, et al., 2014; Chiu, Jost, & Chao, 2014), and have used ENS for both monitoring and conservation planning (Appendix S1), but empirical assessments of the behaviour and comparability of ENS measures has lagged behind theoretical developments. In this study, we showed that ENS measures may not be as comparable across assemblages or as interpretable as expected from theory in their response to either disturbance or environmental
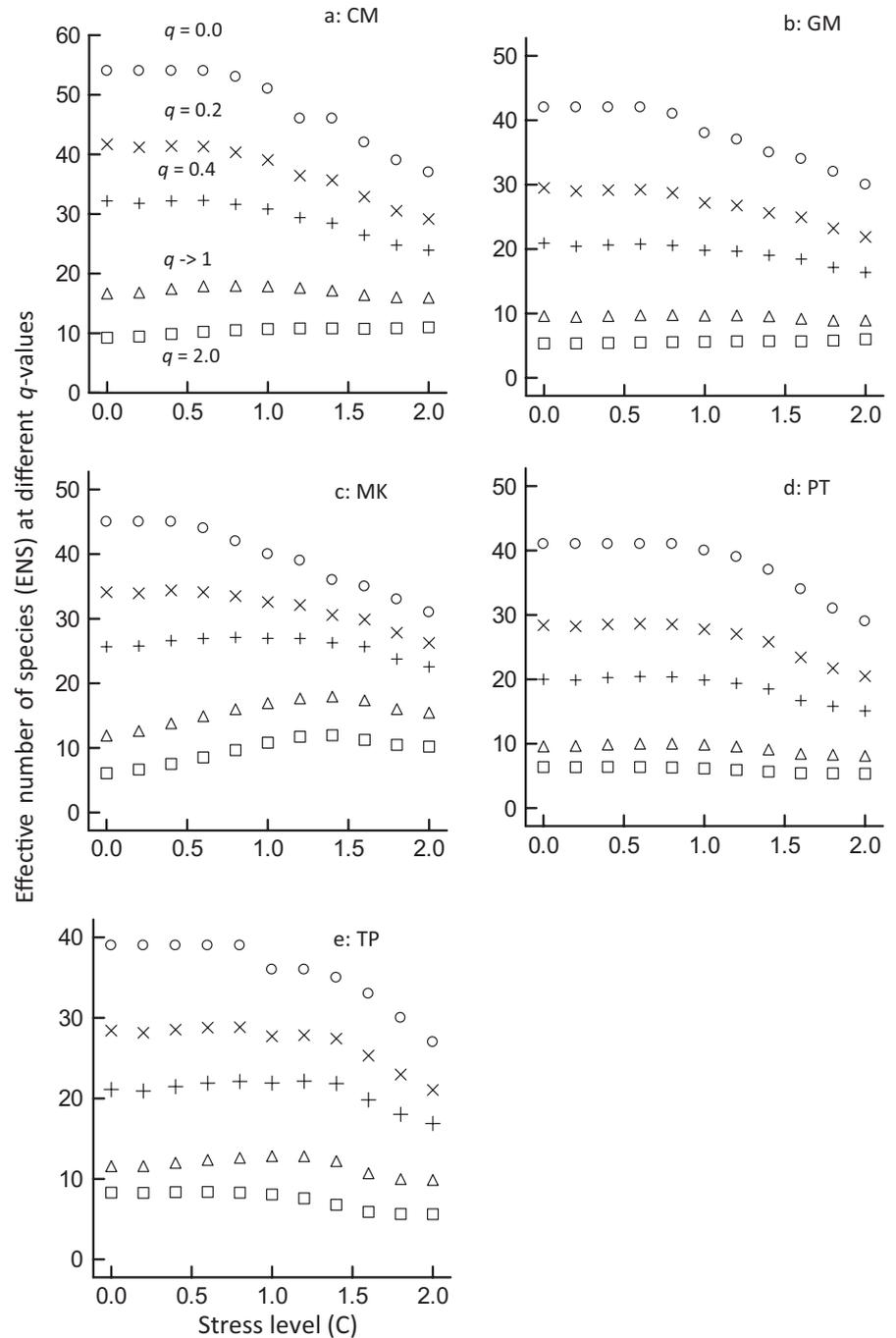
FIGURE 1 (a–e) Response of the effective number of species (ENS) based on five selected levels of q to a simulated stress gradient in five macroinvertebrate assemblages (see Table 1 for assemblage labels)

heterogeneity. Below, we show that our results are consistent with other previous observations and suggest that this behaviour is likely caused by how species relative abundance or evenness is incorporated into ENS measures. We conclude that it may be more useful to base comparisons of species diversity on evenness-adjusted estimates of SR or estimates of the degree to which species abundance distributions deviate from expected distributions.

4.1 | ENS response to assemblage alteration

In this study, we show for the first time how different ENS measures respond to known assemblage alteration. Our simulations (Figure 1,

Table 1) demonstrated that different measures of ENS can respond differently to disturbance depending on the initial species composition, how sensitive different species are to stress, and the specific ENS measure used. As Cao and Hawkins (2005) illustrated, simulated stress caused both heavy losses of the most sensitive, often initially abundant, species and substantial shifts in overall species composition. In this study, we further showed that increasing stress greatly increased dominance by insensitive or tolerant species and increased average TV in the stressed assemblages. However, contrary to expectation, SR tracked these known effects of stress in a more interpretable way than ENS$^+$ measures. Our analyses did show that ENS$^+$ measures were often less affected by stress than SR and

TABLE 1 Spearman correlations (r_s) between measures of the effective number of species (ENS) based on four q values and simulated stress for five assemblages. ENS-stress correlations were estimated based on both whole assemblage counts and the means of 11 random, 500-count replicate samples from each assemblage

Assemblage	q-value	ENS-stress correlation
Camas Creek (CM)	0.0	−0.95
	0.4	−0.93
	1.0[a]	−0.47
	2.0	0.91
Goodman Creek (GM)	0.0	−0.97
	0.4	−0.93
	1.0	−0.72
	2.0	0.96
Mack Creek (MK)	0.0	−0.98
	0.4	−0.58
	1.0	0.74
	2.0	0.83
Porter Creek (PT)	0.0	−0.89
	0.4	−0.87
	1.0	−0.82
	2.0	−0.94
Trapper Creek (TP)	0.0	−0.91
	0.4	−0.64
	1.0	−0.54
	2.0	−0.90

[a]q converges to 1 (ENS is not definable at $q = 1$).

FIGURE 2 Variation in the amount of variance (R^2) in effective number of species (ENS) estimates explained by random-forests regression models for assemblages of stream fish (blank circle) and mussels (solid circle). ENS was based on q values that ranged from 0 to 2.0 at intervals of 0.1. Sixty-six candidate environmental predictor variables were used in the fish models, and 69 in the mussel models (see Appendix S5)

could even respond oppositely. As such, calculating a profile of different ENV$^+$ measures could therefore be useful in showing how different numbers of equally-abundant species respond to stress, but such an approach may not offer any conceptual advantages over describing how evenness responds to stress. ENS$^+$ does offers some information about characteristics of species abundance distributions and evenness (Chao & Jost, 2015). However, it is more informative and useful to practitioners to directly examine species abundance distributions instead of summarizing a distribution into either a single number (Matthews & Whittaker, 2015) or a set of numbers (ENS$^+$ at different q-values).

ENS$^+$ also can provide information that SR does not when the relative abundances of species in an assemblage change without species loss, which may occur in the early stage of eutrophication or under certain disturbances (Jones, Ripplinger, & Collins, 2017; Rosset et al., 2014). In such cases, ENS$^+$ becomes an index of evenness. However, in the case of aquatic ecosystems at least, responses of assemblages to water-quality or habitat degradation typically involve reduction or loss of sensitive species with no or positive effects on the abundance of tolerant species (Cao, Bark, & Williams, 1997; Hawkins, 2006; Hawkins, Mykrä, Oksanen, & Vander Laan, 2015; Perkins, 1983), a pattern also produced by our simulations. In
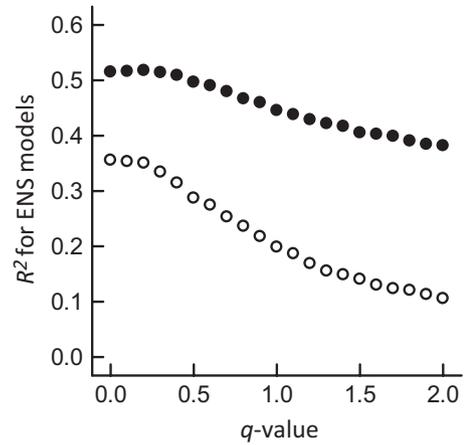
such cases, the response of ENS$^+$ becomes unpredictable, remains the same, increases, or decreases (but most likely less than SR) as showed in Figure 1. Some have suggested ENS profiles can show how abundant or rare species jointly respond to stress (e.g., Morris et al., 2014). However, that is possible only if (a) one abundance group is more tolerant or sensitive than the other and (b) stress benefits neither group. A slower decline in ENS$^+$ than SR would indicate stress mainly affects rare species, whereas an increase of ENS$^+$ would indicate that stress mainly is affecting abundant species (raising evenness). However, the weak correlation between relative abundance and TV in our field data does not support the first assumption, and environmental stress is known to increase the abundance of tolerant species, as we discussed earlier. When abundant and sensitive species are replaced by originally rare and tolerant species, ENS$^+$ will not change so that the second assumption is rarely met either. Therefore, ENS profiles will unlikely offer useful insights into the responses of common or rare species.

We note that the response of high-q ENS$^+$ measures based on whole assemblages to stress was similar to how SR estimates derived from small samples respond to stress (Cao & Hawkins, 2005). This agreement comes as no surprise because both are strongly influenced by the number of abundant species. However, biodiversity assessments based on small samples are known to poorly capture real differences among assemblages (Cao, Williams, & Larsen, 2002; Chase & Knight, 2013) and effects of disturbances on assemblages (Cao, Williams, & Williams, 1998; King & Richardson, 2002; Cao & Hawkins, 2005). If ENS$^+$ measures based on high q provide no more information than a poor estimate of SR, their use in biodiversity assessment and management is questionable. In addition, we emphasize that the response of ENS to stress in our analysis was based the whole assemblages (i.e., no bias). In reality, ENS is estimated based on samples (e.g., 500 individuals). In other analyses we have performed (Y. Cao & C. P. Hawkins, unpublished data), ENS estimates based on

small sample sizes generally responded to stress similarly as true values, but they were even less consistent among assemblages and replicates than true values. Hence, ENS derived from sample data would be even more problematic than indicated by our simulations.

4.2 | ENS-environment relationships

Ecologists generally agree that spatial variation in species diversity is largely driven by environmental heterogeneity (Guégan, Lek, & Oberdorff, 1998; Hawkins et al., 2003; Tews et al., 2004). Moreover, Molinari (1989) goes so far to argue that the relevancy of species diversity measures should be judged on the degree to which they are correlated with environmental variables. The reduced R^2 for ENS$^+$-environment models that we observed with increasing q (Figure 2, Appendices S6 and S7) indicates that the interpretability of diversity-environment relationships degrades as ENS measures are increasingly weighted by species abundance, which implies their potential value to resource managers varies with q. Certain, Dormann, and Planque (2014) reported similar results for multiple types of assemblages, and Lefcheck et al. (2014) observed that of several ENS and other diversity measures, SR was most strongly associated with environmental variables. It appears that use of high-q ENS measures obscure the responses of less common, and likely more specialized, species to environmental variability. Weak associations between ENS$^+$ measures and environment variables imply that ENS$^+$ measures will not provide the sensitivity needed to fully inform natural resources managers of either current biodiversity status or trends in biodiversity over time. Similarly, use of ENS$^+$ measures may not sufficiently describe how diversity is expected to change with climate change and landscape alteration.

4.3 | Richness, evenness, and diversity

The reasons different forms of ENS respond differently and inconsistently to stress and environmental variation must be rooted in either ecological differences among species or the mathematical properties of different species abundance distributions. As observed in the simulated communities, the specific initial mix of species present in a community (which vary in their tolerances both within and across communities) can influence how ENS measures respond to stress (Figure 1). In addition, the two main elements of species abundance distributions (SR and evenness) can respond to disturbances in different and complex ways – e.g., generally increase, generally decrease, neutral, and vary in the shape (linear, nonlinear) of the response (Mackey & Currie, 2001). Thus, the response of different ENS$^+$ measures to stress is likely to be assemblage-specific, as we observed in this study, because assemblages can naturally differ in their species abundance distributions.

The initial evenness of species abundances and how different species specifically respond to stress and environmental variation appear to differentially influence different ENS measures. In general, human disturbances often reduce SR, but frequently increase evenness (Biswas & Mallik, 2010; Hawkins & Yuan, 2016; Svensson,

Lindegarth, Jonssen, & Pavia, 2012). In these cases, ENS$^+$ estimates may increase, decrease, or remain stable, depending on the balance between the decline in SR and the increase in evenness. This balance can vary with sites, stress levels, and q, as also observed in our simulation (Figure 1). For ENS$^+$ measures to respond consistently to either disturbance or environmental gradients, SR and evenness must be positively correlated. However, empirical studies do not support this assumption (Bock, Jones, & Bock, 2007; MacDonald, Nielsen, & Acorn, 2017; Soininen, Passy, & Hillebrand, 2012; Stirling & Wilsey, 2001). The variable relationships that actually exist between SR and evenness imply that ENS$^+$ measures will be more difficult to interpret than SR, as observed in our modelling of diversity-environment relationships (Figure 2). Based on their observation that SR and evenness were strongly, but negatively, correlated, MacDonald et al. (2017) also concluded that combining SR and evenness as done in ENS$^+$ measure "does not produce measures that consistently align with our intuitive sense of species diversity". Ultimately, we need to understand the biological mechanisms for why individual species, and thus evenness and SR, respond as they do, but our knowledge of the ecological requirements and tolerances of most species is currently sorely incomplete.

We recognize the limitations in drawing general inferences from either simulations or field correlations, and our results may not be applicable to all types of stress, taxonomic groups, or habitats. However, useful species-diversity measures need to behave as ecologists intuitively expect them to under most situations, and our results showed that ENS$^+$ measure do not meet this expectation, particularly at the two commonly used q-levels. A more fundamental question is why the number of equally-abundant species (ENS$^+$) is thought to be a true or better measure of species diversity. We agree that the ENS framework conceptually and mathematically unifies different diversity indices, but we question its practical utility with respect to biodiversity conservation/restoration and better understanding relationships between biodiversity and ecosystem functions. We worry that uncritical acceptance and use of ENS$^+$ measures may actually distract research efforts from real challenges in monitoring and conservation, such as those outlined in McGill, Dornelas, Gotelli, and Magurran (2015).

4.4 | Moving forward

Ecologists need to find alternative ways to incorporate species abundances in measures of species diversity that allow meaningful comparisons across space and time. One possibility is to measure the deviance of the assemblage evenness observed with that from an expected evenness value derived from minimally-disturbed and environmentally matched reference sites—an approach comparable to that used in freshwater ecological assessments (e.g., Hawkins, 2006; Hawkins & Yuan, 2016). Another possibility is to estimate the deviation of observed species abundance distributions from well-supported theoretical models, such as log-normal distributions (Hubbell, 2001) or log-series distributions, both of which have been commonly observed in nature (Ulrich, Ollik, & Ugland, 2010). If the specific types of species abundance distributions are strongly associated with either

different taxonomic groups or habitats, as suggested by Ulrich et al. (2010), it should be possible to adjust estimates of SR based on the level of deviation from the expected distribution. In assessing the biological condition of freshwaters, researchers already have attempted to adjust the value of richness-based biological indices based on sample evenness (e.g., Vander Laan & Hawkins, 2014). However, additional studies are needed to fully test these ideas. These suggested methods are fundamentally different from ENS⁺ in how they incorporate evenness. Higher evenness always leads to higher values of ENS^+ due to the evenness principle (Shannon, 1948), but we suggest that SR could be made more comparable when evenness varies by adjusting SR based on the degree to which the observed evenness deviates (positive or negative) from an expected value. For example, consider the case where N species are found at a site with evenness of 0.50, but the expected evenness is 0.40. One might adjust SR by $(1-|0.4-0.5|)$, which gives an adjusted SR value of $N \times 0.9$. The same adjusted SR would occur if the observed evenness is 0.30. Future studies should assess which evenness measures (Jost, 2010) to use and how to best adjust SR. The evenness principle is derived from information theory, and it is the core of ENS^+, but it has never been ecologically justified in the sense of considering why communities of equally-abundant species are ecologically more important or meaningful than others. It seems time for ecologists to rethink this principle in defining and measuring species diversity.

In conclusion, we think that diversity measures that are jointly and differentially sensitive to richness and evenness as in ENS^+ have limited practical application for most biodiversity monitoring and assessment programs, because they cannot be easily interpreted and compared, particularly at high q-levels. We suggest that ecologists and natural resource managers should separately assess and interpret measures of SR, evenness, and composition while researchers continue to work on ways to overcome the weaknesses of SR (Hillebrand et al., 2017; Larsen, Chase, Durance, & Ormerod, 2018) and ENS^+. As a special case of ENS ($q = 0$), SR has all the desirable properties of ENS^+ measures. The main weakness of SR as a measure of species diversity is its strong dependence on sampling effort. Comparability of SR estimates can be improved by either adopting standardized sampling procedures or making post-sampling statistical adjustments. Standardizing sampling effort on sample completeness [referred to as sample representativeness by Cao, Hawkins, Larsen, and van Sickle (2007) and sample coverage by Chao and Jost (2012) may also improve comparisons of SR across space and time. Until we understand how to best standardize sampling effort, rarefaction techniques will likely remain the best option for improving comparability of SR estimates despite their recognized limitations (review by Cao et al., 2007; Gotelli & Colwell, 2001). Statistically extrapolating to the true SR at sites could provide the best comparisons of SR, but extrapolation techniques are not always effective and are typically imprecise (Brose, Martinez, & Williams, 2003; Cao et al., 2007). We think that questions regarding changes in species abundance distributions and community composition are best answered by directly measuring and comparing them, rather than inferring them through ENS measures.

AUTHORS' CONTRIBUTIONS

Both authors designed the study. Y.C. analysed the data and wrote the first draft of the manuscript. Both authors contributed to subsequent revisions and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.7264p69 (Cao & Hawkins, 2019).

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