



Using alpha, beta, and zeta diversity in describing the health of stream-based benthic macroinvertebrate communities

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Abstract. Ecological monitoring of streams has frequently focused on measures describing the taxonomic, and sometimes functional, α diversity of benthic macroinvertebrates (BMIs) within a single sampled community. However, as many ecological processes effectively link BMI stream communities there is a need to describe groups of communities using measures of regional diversity. Here we demonstrate a role for incorporating both a traditional pairwise measure of community turnover, β diversity, in assessing community health as well as ζ diversity, a more generalized framework for describing similarity between multiple communities. Using 4,395 samples of BMI stream communities in California, we constructed a model using measures of α , β , and ζ diversity, which accounted for 71.7% of among-watershed variation in the mean health of communities, as described by the California Streams Condition Index (CSCI). We also investigated the use of ζ diversity in assessing models of stochastic vs. niche assembly across communities of BMIs within watersheds, with the niche assembly model found to be the likelier of the two.

Key words: ζ diversity; benthic macroinvertebrates; biotic integrity; diversity indices; landscape diversity; watershed health; zeta diversity.

INTRODUCTION

Stream ecosystems provide a number of ecological services for human activities, ranging from supporting populations of native species to moderating the delivery of nutrients to coastal ecosystems (Anderson et al. 2002, Dudgeon et al. 2005). It has also been recognized that monitoring the health of aquatic stream communities is of importance not just to the functioning of the immediate environment, but to downstream ecosystems and communities impacted by events such as harmful algal blooms (Carpenter et al. 1998, Paerl et al. 2016). However, given the close proximity of many riparian systems to agricultural and urbanized land, such communities are frequently stressed by human activity in the surrounding watershed (Urban et al. 2006, Tonkin et al. 2016). Such stress can take a variety of forms depending on the geographic scope and intensity of land use, such as increased nutrient levels from agricultural runoff or increases in sediment load from upstream erosion (Sala et al. 2000, Allan 2004, Dudgeon et al. 2005, Abell et al. 2007, Strayer and Dudgeon 2010). Ecological stress has been found to be associated with a decline in local (α)

stream community diversity (Hendrickx et al. 2007, Petrin et al. 2008, Heino 2009). Local stream communities are not isolated, being connected through mechanisms such as dispersal, and may more accurately be considered part of a regional-scale metacommunity (Grönroos et al. 2013, Socolar et al. 2016). There is importance then in considering both local and regional measures of biodiversity (Socolar et al. 2016), as well as regional gradients in environmental and anthropogenic activity, in shaping community structure across watersheds (Shade et al. 2008, Rawi et al. 2013, Brendonck et al. 2015, Tonkin et al. 2016).

One approach to assessing the impacts of environmental gradients, both natural and anthropogenic, across a set of stream communities is to consider the regional-scale (γ) diversity of the communities in question (Heino 2009). γ diversity has the advantage of being straightforward to calculate, being the product of the average local-scale diversity (α) and pairwise similarity between local communities (β) (Whittaker 1972). Measures of diversity within (i.e., α), and between or among (i.e., β and γ) communities, have been commonly used in describing stream communities (Vander Vorste et al. 2017). However, such measures are limited in fully describing diversity in groups of more than two samples (Chao et al. 2008). For example, estimates of β diversity are biased towards

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the turnover of rare types of organisms (Latombe et al. 2017).

To address this limitation, we incorporated a new measure, zeta (ζ) diversity, in our study of a set of California stream communities. ζ diversity describes the overlap in categories shared between multiple samples (Fig. 1; Hui and McGeoch 2014). In our study, these categories are defined either by membership of unique taxa or of a particular functional feeding group. Using this framework, one can describe the mean degree of overlap in unique categories among N samples (ζ_N) across a given set of samples. From this metric one can then define the mean α diversity, as defined by categorical richness, across a sample set as ζ_1 , while the mean β diversity, as defined by Jaccard’s similarity index (Jaccard 1900), can then be defined as $\zeta_2/(2 \times \zeta_1 - \zeta_2)$ (Hui and McGeoch 2014). What is novel is that the ζ diversity framework enables measurement of diversity involving three or more sampled communities, which cannot be determined using solely α and β diversity. For example, the loss of categories of taxa found across most samples in an environment can be a useful indicator of widespread environmental degradation (Gaston and Fuller 2008, Pond 2012).

Here we propose the utility of ζ diversity in describing variations in the composition of BMI communities in streams over the entire state of California. We demonstrate the role of a number of factors in shaping ζ diversity, such as variation in the natural landscape (sample site altitude), as well as levels of human impact (land use upstream of sample sites). Using samples (Fig. 2)

collected by the State of California’s Surface Water Ambient Monitoring Program (SWAMP), we also investigated trends in how ζ diversity declines with the number of sampled communities (namely, ζ order). How ζ diversity declines with ζ order can allow for a test of likelihood for two models of community assembly, either a stochastic process (Munoz et al. 2008) or one driven by a niche differentiation process (Scheiner et al. 2011). Given prior observations about how local environment (Siqueira et al. 2012, Astorga et al. 2014) and predation (Chase et al. 2009) have shaped BMI community structures our expectation was to observe dominance of niche differentiation processes over stochastic ones. We then demonstrated how various measures of ζ diversity can be used to describe the health of communities of BMIs as described by the California Streams Condition Index (CSCI; Rehn et al. 2015, Mazor et al. 2016). ζ diversity, as a generalized extension of α and β diversity, has the potential to both better illustrate, at the watershed scale, trends in turnover as well as a more general framework for assessing the health of groups of BMI communities.

MATERIALS AND METHODS

Scope of data

The initial scope of data covered in this analysis consists of 4,984 stream samples from 2,997 unique geographic locations across the state of California, constituting a 23-yr period (1994–2016). Every sample contains the following data: BMIs enumerated and

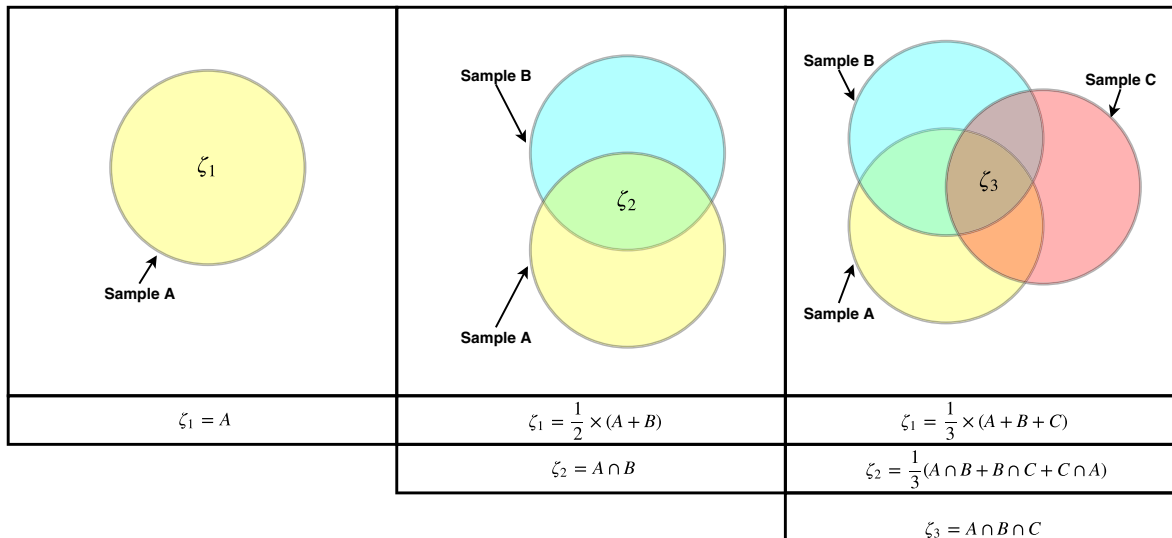


FIG. 1. An illustration of the first three orders of ζ diversity. The mean number of unique categories of organisms per sample, a measure of α diversity, is represented by the value ζ_1 . In comparing two or more samples, the average number of unique categories held in common between any two samples is represented by the value ζ_2 . The mean value then of β diversity, as described by Jaccard distance (Jaccard 1900), for sets of two or more samples is $\zeta_2/(2 \times \zeta_1 - \zeta_2)$ (Hui and McGeoch 2014). For sets of three or more samples, the value of ζ_3 represents all of the unique categories held in common between three samples. This process can be extended to N samples, allowing for a determination of the values ζ_1 through ζ_N .

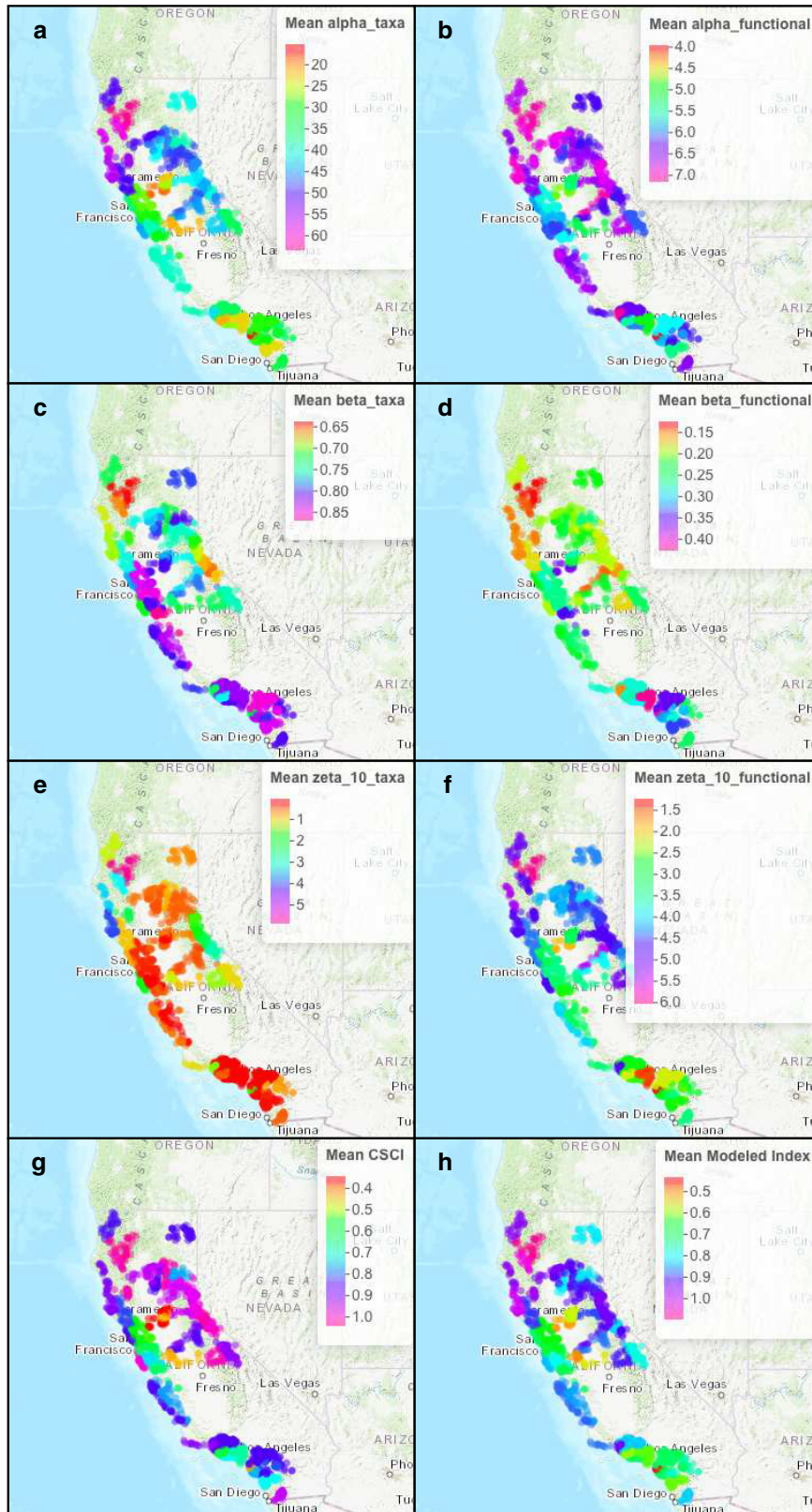


FIG. 2. The mean values per HUC 8 watershed of (a) α_{taxa} , (b) $\alpha_{\text{functional}}$, (c) β_{taxa} , (d) $\beta_{\text{functional}}$, (e) $\zeta_{10, \text{taxa}}$, (f) $\zeta_{10, \text{functional}}$, (g) California Streams Condition Index (CSCI), and (h) modeled health index.

sorted to a standardized level (generally a genus-level identification except chironomids, which were identified to subfamily; Richards and Rogers 2006), a bioassessment index score based on a composite of taxonomic and functional diversity within BMI assemblages known as the California Stream Condition Index (CSCI), sample site altitude in meters, and the percent developed land use (agricultural, urban, and managed landscapes) within a 5-km clipped buffer of the watershed upstream of the sampling site. We used the CSCI as our measure of community health as it has been extensively validated across the state of California, and has been used as the primary bioassessment tool used to assess beneficial uses in California and regulatory compliance with National Pollutant Discharge Elimination System (NPDES) programs (Mazor et al. 2016). Sites were assigned to hydrologic regions (hereafter referred to as “watersheds”) at different regional scales defined by the U.S. Geological Survey Hydrologic Unit Code (HUC), a standardized watershed classification system developed by the U.S. Geological Survey that organizes watersheds in a nested hierarchy by size (Seaber et al. 1987). Each HUC is assigned a geographically unique numerical ID, with geographic scale decreasing in increments of two digits from a regional (HUC 2) to subwatershed (HUC 12) scale. Our initial data contained 118 HUC 8, 22 HUC 6, 14 HUC 4, and 3 HUC 2 watersheds. We designated HUC 8 watersheds as the minimum geographic scale for investigating patterns of diversity.

Sample group selection

To investigate patterns in our measures of α , β , and ζ diversity we first constructed equally sized groups of samples from within each HUC 8 watershed. We chose watersheds with at least 25 unique samples as having sufficient data density for meaningful analysis. This filtering reduced our overall data set from 4,984 to 4,395 unique samples. We then randomly subsampled 25 stream samples within each of the remaining 56 HUC 8 watersheds. For analysis of trends in sample diversity, this process was repeated 100 times. For each group of 25 samples, we calculated the mean sample site altitude (altitude), the mean percent developed upstream land use (land use), and for mean geographic separation distance in meters between samples (distance) we used the *dism* function within the R package *geosphere* (Hijmans, 2016).

Sample acquisitions and classifications

Slightly more than one-half (55%) of the BMI samples were collected following the reach-wide protocol of (Peck et al. 2006); the other samples were collected with targeted riffle protocols, which produce comparable data (Gerth and Herlihy 2006, Herbst and Silldorff 2006, Rehn et al. 2007). For most of the available data, taxa were identified to genus, although this level of effort (as

well as the total number of organisms per sample) varied among samples, necessitating standardization of BMI data. Membership of a particular taxon to a functional feeding group was done using CAMLnet (Ode 2003). Using these methods, we assigned all identified BMIs to one of 334 unique taxonomic groups and 8 unique functional feeding groups.

Calculating the CSCI

The CSCI is a predictive measure of community health at a given site that compares observed taxa and metrics to values expected under reference conditions based on site-specific landscape-scale environmental variables, such as watershed area, geology, and climate (Mazor et al. 2016). This index comprises two sets of measurements using a standardized taxonomy for BMI communities (Richards and Rogers 2006): the first being a ratio of observed-to-expected taxa (O/E), and the second a predictive multi-metric index (pMMI) made of six metrics related to ecological structure and function of the BMI assemblage describing the site’s community. The CSCI, and its components, were designed to have minimal influence from major natural gradients, and can therefore be used as a measure of biological conditions with a consistent meaning in different environmental settings (Reynoldson et al. 1997, Hawkins et al. 2010).

Land use

The type and geographic extent of land use in the upstream vicinity of each sampling site data is derived from the National Land Cover Data set (Homer et al. 2007). The type of land use attributed to human activity is measured by the total percent of land cover in a designated area dedicated to agriculture, urbanization, or otherwise managed vegetative landscapes such as golf courses. The sum of all of these measures is applied to each sample site using a 5-km watershed-clipped buffer upstream of a stream sampling site using ArcGIS tools (version 10.3; Environmental Systems Research Institute, Redlands, California, USA; Mazor et al. 2016). Land use data are derived for all sample sites using satellite measurements acquired in the year 2000. It should be noted that the samples in our study were located in areas where the percent developed land use did not change significantly over the range of time covered in this study ($r^2 = -0.02$, P not significant).

Statistical analysis

The diversity measures we used in this study, separately calculated for samples categorized both by taxonomic groups as well as functional feeding groups, were mean α diversity, β diversity, the ζ diversity decline power-law exponent (b), and the mean number of groups held in common across 10 samples (ζ_{10}). Both measures

of α and ζ diversity were calculated using the R package ZETADIV (Latombe et al. 2016), with the mean α diversity per group of samples calculated as ζ_1 . The mean value of β diversity, as determined from the Jaccard distance, was calculated per group of samples using the `vegdist` function in the R package `vegan` (Oksanen et al. 2013). To then determine the contribution of each of our experimental factors to our observed variation in β diversity we performed a 1,000 permutation PERMANOVA using the `adonis` function in the R package `vegan` (Oksanen et al. 2013).

To investigate how similar on average our samples were within groups, as described by ζ diversity, we then tested two models, a power-law of the form $\zeta_N = \zeta_1 N^{-b}$ and an exponential of the form $\zeta_N = \zeta_1 e^{b(N-1)}$, in describing how overlaps between samples declines with ζ order. The ζ diversity decline exponent, b , is a measure of the dissimilarity within a sample set with a greater value of b indicating a greater overall dissimilarity between constituent samples across a multi-site assemblage. We fitted these models to the first 10 orders of ζ within a given set of 25 stream samples. The first 10 orders of ζ diversity, ζ_{10} , were chosen as this was sufficient to show an asymptotic “floor” for the average number of unique taxa or functional feeding group held in common across a sample set. Support for each model was determined using an Akaike Information Criterion (AIC) score within ZETADIV.

For each set of 25 samples, the AIC score was found to be significantly less for the power-law model than the exponential decline model for community compositions described either by taxonomic ($P < 10^{-4}$) or functional feeding groups ($P < 10^{-4}$), as measured by a Wilcoxon signed-rank test. As a further check on the support for a power-law model describing ζ diversity decline, we repeated this analysis using the same sample groups, but with count data randomly reassigned to the taxonomic and functional groups present in those same sample groups. Repeating a comparison of the AIC scores for both models for this randomized data produced ζ diversity curves more likely to be described by an exponential decay model for both taxonomic ($P < 10^{-4}$) and functional diversity ($P < 10^{-4}$), which supports the assertion of taxa being distributed via stochastic process producing an exponential model of ζ diversity decay (Hui and McGeoch 2014). Subsequently, the power-law model was then selected as the likelier of the two in describing the decay in ζ diversity with ζ order.

Our measure of α diversity was compared against altitude, land use, and distance using the `lm` function in the stats R package (v3.5.1 Team, 2018). This same package was used to construct a best-fit linear model to predict the mean CSCI score of a set of samples given their diversity measures. To determine the relative importance of each factor in a linear model the function `calc.relimp` was used within the `relaimpo` R package (Grömping 2006).

To construct a linear model to best predict the ecological health of a set of samples, as measured by their mean

CSCI value, we first applied a backwards elimination method in selecting significant diversity parameters (Pearman 1997, Snodgrass 1997). In comparing the AIC scores of each linear model after the removal of a parameter, we dropped two parameters, b_{taxa} and $b_{\text{functional}}$, as they made no significant contribution in predicting mean CSCI score. The resulting linear involves six parameters: α_{taxa} , $\alpha_{\text{functional}}$, β_{taxa} , $\beta_{\text{functional}}$, $\zeta_{10, \text{taxa}}$, and $\zeta_{10, \text{functional}}$.

RESULTS

Trends within diversity measures

From our analysis of 100 permutations on 56 within-watershed groups of samples we observed four general trends between our measures of diversity (α_{taxa} , $\alpha_{\text{functional}}$, β_{taxa} , $\beta_{\text{functional}}$, $\zeta_{10, \text{taxa}}$, and $\zeta_{10, \text{functional}}$) and environmental parameters (altitude, land use, and distance). Both the mean taxonomic and functional richness per sample have a negative correlation with environmental stress, described either by a rise in land use or a decline in altitude (Fig. 3a and d, Appendix S2: Fig. S1a and d). There is negative correlation between the mean level of similarity within a group between samples and the mean level of environmental stress (Fig. 3b, c, e, and f, Appendix S2: Fig. S1b, c, e, and f). There is also a negative correlation between the mean level of similarity within a group between samples and the mean geographic distance between samples (Fig. 3g–i, Appendix S2: Fig. S1g–i). On a watershed scale, coefficients describing the strength and significance of the relationships between measures of community diversity and turnover with environmental metrics indicate distance appears not to underlie much of the variation in our measures of diversity as compared to either altitude or land use (Appendix S1: Table S1–S2).

We then further investigated the contributions of our experimental factors to the observed variations in β diversity using a PERMANOVA with 1,000 permutations. We found altitude ($F_{1, 4315} = 58.8$, $P < 10^{-4}$) and upstream land use ($F_{1, 4315} = 32.8$, $P < 10^{-4}$) accounted for more of the variation in β diversity than either HUC 8 watershed ($F_{41, 4315} = 7.3$, $P < 10^{-4}$) or sampling year ($F_{22, 4315} = 8.4$, $P < 10^{-4}$). As a result, our focus was on the role of land use, distance, and altitude within HUC 8 watersheds in describing patterns of diversity. We also determined, in line with prior observations (Vander Vorste et al. 2017), that variations in β diversity tended to increase with geographic scale, with it increasing from ($F_{6, 4315} = 11.9$, $P < 10^{-4}$) with HUC 6 watersheds, to ($F_{7, 4315} = 38.9$, $P < 10^{-4}$) at HUC 4 watersheds, and ($F_{1, 4315} = 133.4$, $P < 10^{-4}$) at HUC 2 watersheds.

Linear models of diversity and health

Using six parameters, α_{taxa} , $\alpha_{\text{functional}}$, β_{taxa} , $\beta_{\text{functional}}$, $\zeta_{10, \text{taxa}}$, and $\zeta_{10, \text{functional}}$, a linear model was constructed to best predict the mean value of the CSCI score for a

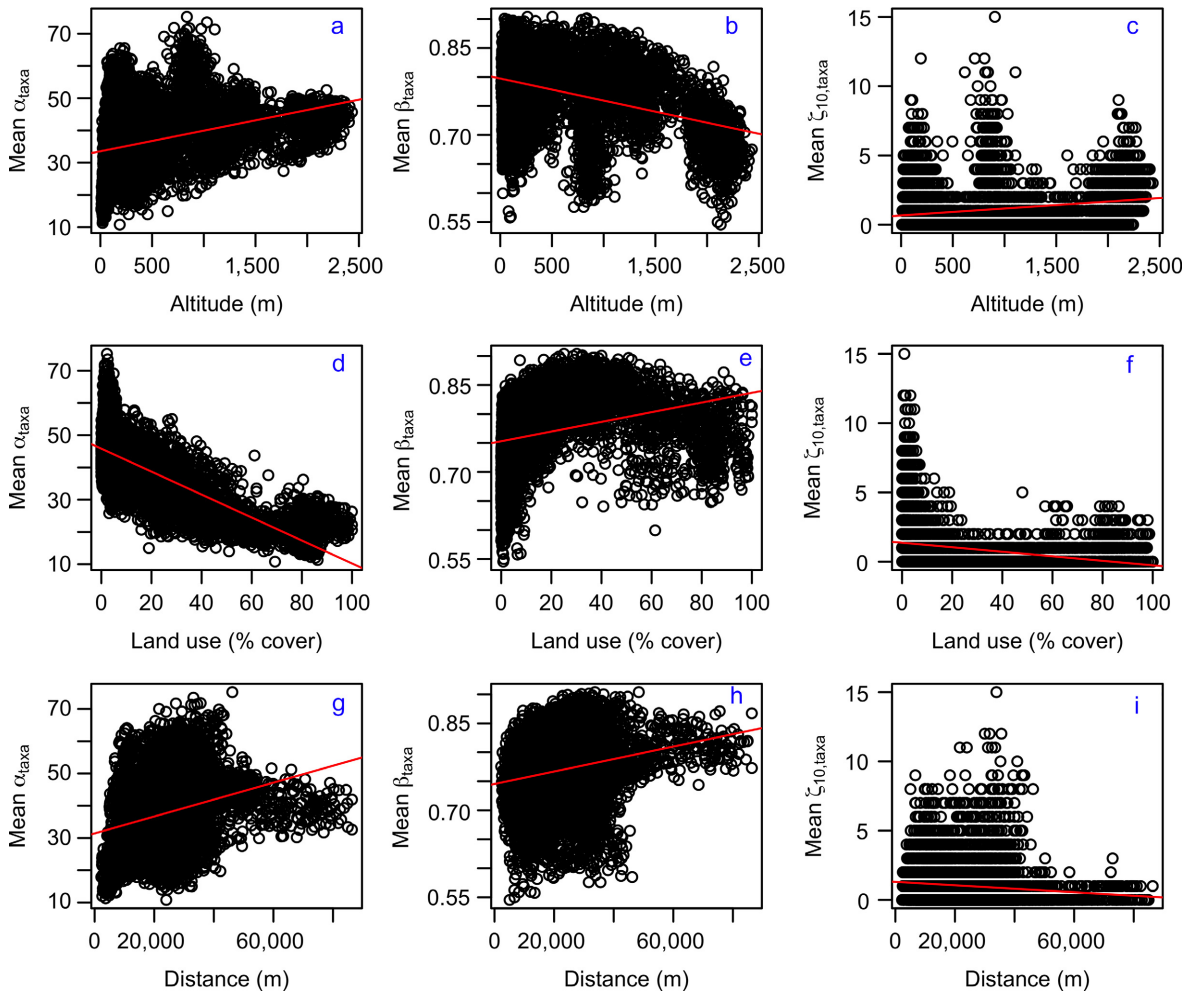


FIG. 3. Trends in the mean values per HUC 8 watershed of α_{taxa} , β_{taxa} , and $\zeta_{10,\text{taxa}}$ vs. changes in altitude, land use, and distance. Note that a rise in β or a decline in ζ_{10} diversity indicates a greater level of dissimilarity between samples within a group.

set of samples (Table 1). The functional relationship between the mean CSCI score per sample group and the remaining diversity parameters are as follows:

$$\begin{aligned} \text{MeanCSCI} = & -0.3 + 6.2 \times 10^{-3} \times \alpha_{\text{taxa}} + 0.2 \times \alpha_{\text{functional}} \\ & - 0.6 \times \beta_{\text{taxa}} + 1.0 \times \beta_{\text{functional}} - 6.5 \times 10^{-3} \\ & \times \zeta_{10,\text{taxa}} + 1.7 \times 10^{-2} \times \zeta_{10,\text{functional}} \end{aligned}$$

This model was found to explain 71.7% of the observed variation in the mean value of the CSCI score for a set of samples. This modeled health index was found to vary in accordance with altitude, land use, and distance for a set of samples in a similar fashion as the mean CSCI score (Table 2, Fig. 4).

DISCUSSION

We found ζ diversity, as an extension of established measures of diversity, to play a potential in role in both

TABLE 1. The relative importance of various diversity parameters in our modeled stream health index.

Parameters	$F_{1, 5568}$	P	Relative importance (%)
α_{taxa}	1.2×10^4	$<10^{-4}$	32.5
$\alpha_{\text{functional}}$	1,151	$<10^{-4}$	36.7
β_{taxa}	21.9	$<10^{-4}$	6.3
$\beta_{\text{functional}}$	690.6	$<10^{-4}$	10.3
$\zeta_{10,\text{taxa}}$	19.4	$<10^{-4}$	3.1
$\zeta_{10,\text{functional}}$	50.5	$<10^{-4}$	11.2

the investigation of BMI community assembly processes as well as assessing the health of groups of BMI communities. In determining a greater likelihood for a power law vs. exponential decay model for how ζ diversity declines with ζ order, we found BMI communities in California streams are more likely to assembled via a niche differentiation rather than a stochastic process. While both measures of α and β diversity were found to

TABLE 2. The relative importance of altitude, land use, and distance in describing linear models of the mean value of the California Streams Condition Index (CSCI) and modeled index per HUC 8 watershed.

Health index	CSCI	Modeled index
Proportion of variation due to altitude	$F_{1, 5571} = 9,243$	$F_{1, 5596} = 3,162$
P_c variation due to altitude	$<10^{-4}$	$<10^{-4}$
Proportion of variation due to land use	$F_{1, 5571} = 1.1 \times 10^4$	$F_{1, 5596} = 6,890$
P_c variation due to land use	$<10^{-4}$	$<10^{-4}$
Proportion of variation due to distance	$F_{1, 5571} = 45.1$	$F_{1, 5596} = 12.5$
P_c variation due to distance	$<10^{-4}$	$<10^{-3}$
Relative importance of altitude (%)	24.0	15.6
Relative importance of land use (%)	73.1	78.7
Relative importance of distance (%)	2.8	5.7
Proportion of variance explained by model (%)	78.3	64.3

explain sizable proportions of variation in the mean CSCI, our measure of BMI community health, within each of the 56 watersheds across California we found the addition of measures of ζ_{10} diversity to improve the ability of our modeled index to account for variation in our measure of BMI community health. As our modeled index uses a more generalized framework composed of presence/absence diversity measures, rather than relying on a set of undisturbed reference communities, we believe there is the potential to utilize the ζ diversity framework in creating community health assessment indices applicable in environments beyond the current geographic scope of the CSCI.

Modeling watershed health and the importance of single and multi-sample measures of diversity

We found both the mean watershed values of α_{taxa} and $\alpha_{\text{functional}}$ to have the greatest relative importance in our model to describe the variation in the mean CSCI on a per watershed basis. Measures of diversity across

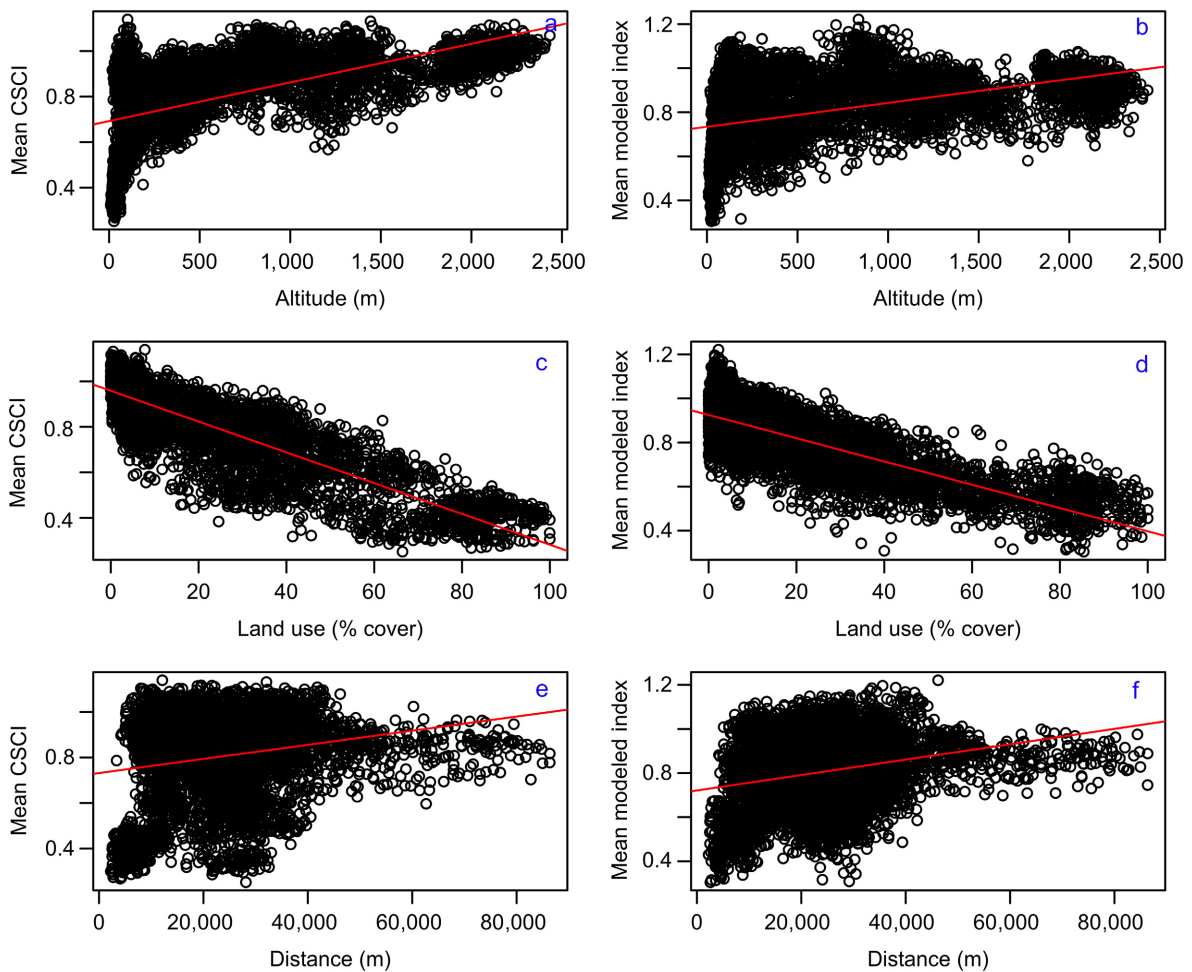


FIG. 4. A comparison of the sample group mean values for the CSCI and modeled index versus sample group mean values for altitude, land use, and distance with linear best fit lines. Both indices show similar behavior in response to changes in altitude, land use, and distance.

multiple samples in a watershed (β and ζ) further improved our model's predictive powers. It is also noteworthy that both β and ζ_{10} diversity have a significant role in our model, although they are potentially capturing two different patterns describing multiple sampled communities. In general measures of diversity that incorporate the overlap between large numbers of communities, such as ζ_{10} diversity, are more sensitive to the presence of common groups of organisms than those that only involve pairwise comparisons, such as β diversity, which are inherently more biased to the presence of rare groups (Latombe et al. 2017). As we observed that both ζ_{10} and β diversity have a significant role in our model of the health of BMI communities across a watershed (Table 1) we propose that the effects of environmental degradation cannot be fully assessed by the loss of rare or common taxa alone, but both must be considered in tandem. We also noted that a sizeable portion of variation in the mean value of the CSCI per watershed could be attributed to our modeled index. As this index is comprised solely of a linear combination of measures α , β , and ζ_{10} diversity it suggests future assessments of the health of BMI communities across a watershed could be done using a more general framework than the one used to devise the CSCI.

Relationships between measures of watershed health and the physical environment

We found that both our modeled index and the CSCI have similar patterns of variation with our measurements of the physical environment (Fig. 4). Variation in the average α_{taxa} and $\alpha_{\text{functional}}$ diversity per watershed appear to underpin a significant portion of the variation of both the CSCI, itself a composite measure of taxonomic and functional richness (Mazor et al. 2016), and our modeled index of watershed health (Table 2). Prior observations support the general trend of the decline in BMI sample diversity associated with a rise in environmental stress at the sample site (Paul and Meyer 2001, Stepenuck et al. 2002, Ourso and Frenzel 2003, Wallace and Biastoch 2016). This has been observed with α_{taxa} and upstream land use (Sponseller et al. 2001, Stepenuck et al. 2002, Allan 2004), α_{taxa} and altitude (Ward, 1986; Jacobsen et al. 1997, Jacobsen 2008), as well as with $\alpha_{\text{functional}}$ and both altitude and land use (Huryn et al. 2002, Finn and Leroy Poff 2005, Heino 2005). Our results then support the utility of using both average α_{taxa} and $\alpha_{\text{functional}}$ diversity per watershed as indicators of the health of their resident BMI communities.

We also observed that communities of BMIs tended to have greater degrees of similarity (lower β and higher ζ_{10}) both taxonomically as well as functionally, within watersheds at a higher AL with the opposite trends observed in comparison to land use and distance (Fig. 4, Appendix S2; Fig. S1, Appendix S1; Table S1–S2). Our observed relationship between β diversity and distance,

where a greater geographic distance between samples is associated with greater intersample dissimilarity, is in line with previous observations of communities of stream BMIs (Astorga et al. 2012, Rouquette et al. 2013). However, our observations appear to run counter to previous research indicating a positive correlation between the mean altitude of a set of samples and their degree of community dissimilarity (Finn and Leroy Poff 2005, Frady et al. 2007), as well as a negative correlation with upstream land use (McGoff et al. 2013).

One potential mechanism for the observed correlations with dissimilarity between sampled communities within watersheds, negative with altitude and positive with land use, may be driven by an underlying correlation with habitat heterogeneity. Prior observations support a positive relationship between the β diversity of multi-site assemblages of BMIs and variations in the physical environment; habitat heterogeneity (Shostell and Williams 2007, Astorga et al. 2014, Zhang et al. 2014). Using the standard deviation of land use on a per watershed basis as a proxy for habitat heterogeneity, we find strong correlations with our measures of dissimilarity between communities: β_{taxa} ($r = 0.6, P < 10^{-4}$), $\beta_{\text{functional}}$ ($r = 0.6, P < 10^{-4}$), $\zeta_{10, \text{taxa}}$ ($r = -0.4, P < 10^{-4}$), and $\zeta_{10, \text{functional}}$ ($r = -0.5, P < 10^{-4}$). This suggests a measure such as the standard deviation of land use could be used as a proxy for habitat heterogeneity on a watershed scale (Sponseller et al. 2001, Astorga et al. 2014), and may be a metric to consider in subsequent studies. As this proxy of habitat heterogeneity is negatively correlated with altitude ($r = -0.4, P < 10^{-4}$) this suggests that a decline in habitat heterogeneity with altitude may then be driving our observed decline in dissimilarity between sampled communities within watersheds with altitude. A similar relationship may also underpin the positive correlation between land use and dissimilarity as our measure of habitat heterogeneity is positively correlated with land use ($r = 0.6, P < 10^{-4}$).

ζ Diversity decay and evidence of niche differentiation

Our observations, whereby ζ diversity decays via a power-law with respect to ζ order, support a model of stream community composition being determined more by niche differentiation than by a stochastic assembly process (Scheiner et al. 2011, Hui and McGeoch 2014, Hui et al. 2018). Both our measures of turnover, β and ζ_{10} diversity, are more strongly associated with the standard deviation of land use than altitude within both low and high altitude watersheds (Appendix S1: Tables S3–S4). Treating the standard deviation of land use as a measure of landscape heterogeneity this suggests variability in upstream land use underlies a process of niche differentiation in metacommunities of BMIs on a watershed scale (Winemiller et al. 2010, Astorga et al. 2014, Hammill et al. 2018).

Such niche differentiation, whereby the probability of detecting a member of a particular taxon or functional

feeding group within a particular sample varies across a landscape, is also reflected in the probabilities of detecting members of a particular taxon or functional feeding group within our set of BMI communities. For example, of the 334 unique taxa identified in our data only members of three genera were detected in more than 50% of our samples. These were members of the genera *Baetis* and *Simulium* and the subclass Oligochaeta, which are known to be geographically widespread (Fend et al. 2005). We observed a similar skew in functional diversity with the most common functional group, collector-gatherers, present in only 37.8% of samples while the average functional group was only found in 12.5% of samples. This may be reflective of the relative tolerance of each functional group to the abiotic stressors frequently associated with human dominated land use. Such a case has been observed with members of the collector-gatherer feeding group (Feld and Hering 2007). Although we should note that the BMIs within the family Chironomidae, whose members belong to the collector-gatherer functional feeding group, were aggregated to the level of subfamily rather than genus.

CONCLUSION

Our results indicated that, for multiple communities within watersheds, both the mean values of α_{taxa} and α diversity were found to negatively correlate with mean upstream land use and positively with altitude. This is in line with prior observations of the response of communities of stream BMIs to natural and anthropogenic variation in the environment (Ward 1986, Jacobsen et al. 1997, Sponseller et al. 2001, Huryn et al. 2002, Stepenuck et al. 2002, Allan 2004, Finn and Leroy Poff 2005, Heino 2005, Jacobsen 2008). Such relationships are also observed in the behavior of the CSCI, itself a measure of taxonomic and functional α diversity (Rehn et al. 2015, Mazor et al. 2016). What we have also demonstrated is a relationship between measures of the diversity of our groups of sampled communities, described both by measures of β and ζ_{10} diversity, and variations in the environment, both natural and anthropogenically driven.

As the monitoring of the health of ecological communities transitions from methods utilizing taxonomic diversity of particular groups of indicator taxa, or other forms of diversity such as the functional feeding group memberships utilized in this study, to broader community profiles enabled by metagenomic approaches (Baird and Hajibabaei 2012, Bohmann et al. 2014, Deiner et al. 2016, Jackson et al. 2016) the need arises for a more generalized framework with which to construct measures of single and multi-community health that could incorporate information on the composition of full communities (e.g. bacteria, algae, etc.) in addition to groups of well-defined indicator taxa (Hooper et al. 2003, Takamura et al. 2008, Pignata et al. 2013). What our results illustrate then is the potential for creating a more

generalizable framework for assessing the health of communities using both established measures of diversity, such as α and β , as well as comparisons of larger ensembles of communities enabled by the ζ diversity framework.

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LITERATURE CITED

- Abell, R., J. D. Allan, and B. Lehner. 2007. Unlocking the potential of protected areas for freshwaters. *Biological Conservation* 134:48–63.
- Allan, J. D. 2004. Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology and Systematics* 35:257–284.
- Anderson, D., P. Glibert, and J. Burkholder. 2002. Harmful algal blooms and eutrophication: Nutrient sources, composition, and consequences. *Estuaries* 25:704–726.
- Astorga, A., J. Oksanen, M. Luoto, J. Soininen, R. Virtanen, and T. Muotka. 2012. Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? *Global Ecology and Biogeography* 21:365–375.
- Astorga, A., R. Death, F. Death, R. Paavola, M. Chakraborty, and T. Muotka. 2014. Habitat heterogeneity drives the geographical distribution of β diversity: the case of New Zealand stream invertebrates. *Ecology and Evolution* 4:2693–2702.
- Baird, D. J., and M. Hajibabaei. 2012. Biomonitoring 2.0: a new paradigm in ecosystem assessment made possible by next-generation DNA sequencing. *Molecular Ecology* 21:2039–2044.
- Bohmann, K., A. Evans, M. T. P. Gilbert, G. R. Carvalho, S. Creer, M. Y. Knapp, W. Douglas, and M. De Bruyn. 2014. Environmental DNA for wildlife biology and biodiversity monitoring. *Trends in Ecology & Evolution* 29:358–367.
- Brendonck, L., M. Jocqué, K. Tuytens, B. V. Timms, and B. Vanschoenwinkel. 2015. Hydrological stability drives both local and regional diversity patterns in rock pool metacommunities. *Oikos* 124:741–749.
- Carpenter, S., N. Caraco, D. Correll, R. Howarth, A. Sharpley, and V. Smith. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecological Applications* 8:559–568.
- Chao, A., L. Jost, S. C. Chiang, Y. H. Jiang, and R. L. Chazdon. 2008. A two-stage probabilistic approach to multiple-community similarity indices. *Biometrics* 64:1178–1186.
- Chase, J. M., E. G. Biro, W. A. Ryberg, and K. G. Smith. 2009. Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities. *Ecology Letters* 12:1210–1218.
- Deiner, K., E. A. Fronhofer, E. Mächler, J. C. Walser, and F. Altermatt. 2016. Environmental DNA reveals that rivers are conveyor belts of biodiversity information. *Nature Communications* 7:12544.
- Dudgeon, D., et al. 2005. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81:163.
- Feld, C. K., and D. Hering. 2007. Community structure or function: effects of environmental stress on benthic macroinvertebrates at different spatial scales. *Freshwater Biology* 52:1380–1399.

- Fend, S. V., J. L. Carter, and F. R. Kearns. 2005. Relationships of field habitat measurements, visual habitat indices, and land cover to benthic macroinvertebrates in urbanized streams of the Santa Clara Valley, California. *American Fisheries Society Symposium* 47:193–212.
- Finn, D. S., and N. Leroy Poff. 2005. Variability and convergence in benthic communities along the longitudinal gradients of four physically similar Rocky Mountain streams. *Freshwater Biology* 50:243–261.
- Frady, C., S. Johnson, and J. Li. 2007. Stream macroinvertebrate community responses as legacies of forest harvest at the H.J. Andrews experimental forest, Oregon. *Forest Science* 53:281–293.
- Gaston, K. J., and R. A. Fuller. 2008. Commonness, population depletion and conservation biology. *Trends in Ecology & Evolution* 23:14–19.
- Gerth, W. J., and A. T. Herlihy. 2006. Effect of sampling different habitat types in regional macroinvertebrate bioassessment surveys. *Journal of the North American Benthological Society* 25:501–512.
- Grömping, U. 2006. Relative importance for linear regression in R: the package relaimpo. *Journal of Statistical Software* 17:1–27.
- Grönroos, M., J. Heino, T. Siqueira, V. L. Landeiro, J. Kotanen, and L. M. Bini. 2013. Metacommunity structuring in stream networks: roles of dispersal mode, distance type, and regional environmental context. *Ecology and Evolution* 3:4473–4487.
- Hammill, E., C. P. Hawkins, H. S. Greig, P. Kratina, J. B. Shurin, and T. B. Atwood. 2018. Landscape heterogeneity strengthens the relationship between β -diversity and ecosystem function. *Ecology* 99:2467–2475.
- Hawkins, C. P., J. R. Olson, and R. A. Hill. 2010. The reference condition: predicting benchmarks for ecological and water-quality assessments. *Journal of the North American Benthological Society* 29:312–343.
- Heino, J. 2005. Functional biodiversity of macroinvertebrate assemblages along major ecological gradients of boreal headwater streams. *Freshwater Biology* 50:1578–1587.
- Heino, J. 2009. Biodiversity of aquatic insects: spatial gradients and environmental correlates of assemblage-level measures at large scales. *Freshwater Reviews* 2:1–29.
- Hendrickx, F., et al. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. *Journal of Applied Ecology* 44:340–351.
- Herbst, D. B., and E. L. Silldorff. 2006. Comparison of the performance of different bioassessment methods: similar evaluations of biotic integrity from separate programs and procedures. *Journal of the North American Benthological Society* 25:513–530.
- Hijmans, R. J. 2016. *geosphere*: spherical trigonometry. R package version 1.5-5. See <https://cran.r-project.org/package=geosphere>
- Homer, C., J. Dewitz, J. Fry, M. Coan, N. Hossain, C. Larson, N. Herold, A. McKerrow, J. N. VanDriel, and J. Wickham. 2007. Completion of the 2001 national land cover database for the conterminous United States. *Photogrammetric Engineering and Remote Sensing* 73:337.
- Hooper, H. L., R. M. Sibly, T. H. Hutchinson, and S. J. Maund. 2003. The influence of larval density, food availability and habitat longevity on the life history and population growth rate of the midge *Chironomus riparius*. *Oikos* 102:515–524.
- Hui, C., and M. A. McGeoch. 2014. Zeta diversity as a concept and metric that unifies incidence-based biodiversity patterns. *American Naturalist* 184:684–694.
- Hui, C., W. Vermeulen, and G. Durrheim. 2018. Quantifying multiple-site compositional turnover in an Afrotropical forest, using zeta diversity. *Forest Ecosystems* 5:15.
- Hury, A. D., V. M. Butz Hury, C. J. Arbuckle, and L. Tsomides. 2002. Catchment land-use, macroinvertebrates and detritus processing in headwater streams: taxonomic richness versus function. *Freshwater Biology* 47:401–415.
- Jaccard, P. 1900. Contribution au problème de l'immigration postglaciaire de la flore alpine. *Bulletin de la Société Vaudoise des Sciences Naturelles* 36:87–130.
- Jackson, M. C., et al. 2016. Recommendations for the Next Generation of Global Freshwater Biological Monitoring Tools. *Advances in Ecological Research* 55:615–636. <https://doi.org/10.1016/BS.AECR.2016.08.008>
- Jacobsen, D. 2008. Low oxygen pressure as a driving factor for the altitudinal decline in taxon richness of stream macroinvertebrates. *Oecologia* 154:795–807.
- Jacobsen, D., R. Schultz, and A. Encalada. 1997. Structure and diversity of stream invertebrate assemblages: the influence of temperature with altitude and latitude. *Freshwater Biology* 38:247–261.
- Latombe, G., M. A. McGeoch, D. A. Nipperess, and C. Hui. 2016. *zetadiv*: functions to compute compositional turnover using ζ diversity. R package version 1.1.1. <https://cran.r-project.org/package=zetadiv>
- Latombe, G., C. Hui, and M. A. McGeoch. 2017. Multi-site generalised dissimilarity modelling: using ζ diversity to differentiate drivers of turnover in rare and widespread species. *Methods in Ecology and Evolution* 8:431–442.
- Mazor, R., A. Rehn, P. Ode, M. Engeln, K. Schiff, E. Stein, D. Gillett, D. Herbst, and C. Hawkins. 2016. Bioassessment in complex environments: designing an index for consistent meaning in different settings. *Freshwater Science* 35:249–271.
- McGoff, E., A. G. Solimini, M. T. Pusch, T. Jurca, and L. Sandin. 2013. Does lake habitat alteration and land-use pressure homogenize European littoral macroinvertebrate communities? *Journal of Applied Ecology* 50:1010–1018.
- Munoz, F., P. Coutron, and B. R. Ramesh. 2008. Beta diversity in spatially implicit neutral models: a new way to assess species migration. *American Naturalist* 172:116–127.
- Ode, P. 2003. List of Californian macroinvertebrate taxa and standard taxonomic effort. California Department Fish and Game. http://www.safit.org/Docs/CABW_std_taxonomic_effort.pdf
- Oksanen, J., et al. 2013. *vegan*: Community ecology package. <http://CRAN.R-project.org/package=vegan>
- Ourso, R. T., and S. A. Frenzel. 2003. Identification of linear and threshold responses in streams along a gradient of urbanization in Anchorage, Alaska. *Hydrobiologia* 501:117–131.
- Paerl, H., et al. 2016. Mitigating cyanobacterial harmful algal blooms in aquatic ecosystems impacted by climate change and anthropogenic nutrients. *Harmful Algae* 54:213–222.
- Paul, M. J., and J. L. Meyer. 2001. Streams in the urban landscape. *Annual Review of Ecology and Systematics* 32:333–365.
- Pearman, P. B. 1997. Correlates of amphibian diversity in an altered landscape of Amazonian Ecuador. *Conservation Biology* 11:1211–1225.
- Peck, D. V., et al. 2006. Environmental Monitoring and Assessment Program—Surface Waters Western Pilot study: field operations manual for wadeable streams. EPA/620/R-06/003. Office of Research and Development, US Environmental Protection Agency, Corvallis, Oregon, USA.
- Petrin, Z., G. Englund, and B. Malmqvist. 2008. Contrasting effects of anthropogenic and natural pH in streams: a meta-analysis. *Proceedings of the Royal Society B* 275:1143–1148.
- Pignata, C., et al. 2013. Application of European biomonitoring techniques in China: Are they a useful tool? *Ecological Indicators* 29:489–500.

- Pond, G. J. 2012. Biodiversity loss in Appalachian headwater streams (Kentucky, USA): Plecoptera and Trichoptera communities. *Hydrobiologia* 679:97–117.
- R Core Team. 2018. R: A language and environment for statistical computing. R Core Team, Vienna, Austria.
- Rawi, C. S. M., S. A. Al-Shami, M. R. Madrus, and A. H. Ahmad. 2013. Local effects of forest fragmentation on diversity of aquatic insects in tropical forest streams: implications for biological conservation. *Aquatic Ecology* 47:75–85.
- Rehn, A. C., P. R. Ode, and C. P. Hawkins. 2007. Comparisons of targeted-riffle and reach-wide benthic macroinvertebrate samples: implications for data sharing in stream-condition assessments. *Journal of the North American Benthological Society* 26:332–348.
- Rehn, A. C., R. D. Mazon, and P. R. Ode. 2015. The California Stream Condition Index (CSCI): A New Statewide Biological Scoring Tool for Assessing the Health of Freshwater Streams SWAMP Technical Memo.
- Reynoldson, T. B., R. H. Norris, V. H. Resh, K. E. Day, and D. M. Rosenberg. 1997. The reference condition: a comparison of multimetric and multivariate approaches to assess water-quality impairment using benthic macroinvertebrates. *Journal of the North American Benthological Society* 16:833–852.
- Richards, A. B., and D. C. Rogers. 2006. List of freshwater macroinvertebrate taxa from California and adjacent states including standard taxonomic effort levels. Southwest Association of Freshwater Invertebrate Taxonomists, Chico, California, USA.
- Rouquette, J. R., M. Dallimer, P. R. Armsworth, K. J. Gaston, L. Maltby, and P. H. Warren. 2013. Species turnover and geographic distance in an urban river network. *Diversity and Distributions* 19:1429–1439.
- Sala, O. E., et al. 2000. Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774.
- Scheiner, S. M., A. Chiarucci, G. A. Fox, M. R. Helmus, D. J. McGlenn, and M. R. Willig. 2011. The underpinnings of the relationship of species richness with space and time. *Ecological Monographs* 81:195–213.
- Seaber, P. R., F. P. Kapinos, and G. L. Knapp. 1987. Hydrologic unit maps: US Geological Survey Water Supply Paper 2294. US Geological Survey.
- Shade, A., S. E. Jones, and K. D. McMahon. 2008. The influence of habitat heterogeneity on freshwater bacterial community composition and dynamics. *Environmental Microbiology* 10:1057–1067.
- Shostell, J. M., and B. S. Williams. 2007. Habitat complexity as a determinate of benthic macroinvertebrate community structure in cypress tree reservoirs. *Hydrobiologia* 575:389–399.
- Siqueira, T., L. M. Bini, F. O. Roque, S. R. Marques Couceiro, S. Trivinho-Strixino, and K. Cottenie. 2012. Common and rare species respond to similar niche processes in macroinvertebrate metacommunities. *Ecography* 35:183–192.
- Snodgrass, J. W. 1997. Temporal and spatial dynamics of beaver-created patches as influenced by management practices in a south-eastern North American landscape. *Journal of Applied Ecology* 34:1043–1056.
- Socolar, J. B., J. J. Gilroy, W. E. Kunin, and D. P. Edwards. 2016. How should beta-diversity inform biodiversity conservation? *Trends in Ecology & Evolution* 31:67–80.
- Sponseller, R. A., E. F. Benfield, and H. M. Valett. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. *Freshwater Biology* 46:1409–1424.
- Stepenuck, K. F., R. L. Crunkilton, and L. Wang. 2002. Impacts of urban landuse on macroinvertebrate communities in southeastern Wisconsin streams 1. *JAWRA Journal of the American Water Resources Association* 38:1041–1051.
- Strayer, D. L., and D. Dudgeon. 2010. Freshwater biodiversity conservation: recent progress and future challenges. *Journal of the North American Benthological Society* 29:344–358.
- Takamura, N., et al. 2008. Environmental gradients determining the distribution of benthic macroinvertebrates in Lake Takkobu, Kushiro wetland, northern Japan. *Ecological Research* 24:371–381.
- Tonkin, J., S. Stoll, S. Jähnig, and P. Haase. 2016. Anthropogenic land-use stress alters community concordance at the river-riparian interface. *Ecological Indicators* 65:133–141.
- Urban, M., D. Skelly, D. Burchsted, W. Price, and S. Lowry. 2006. Stream communities across a rural-urban landscape gradient. *Diversity Distributions* 12:337–350.
- Vander Vorste, R., P. McElmurray, S. Bell, K. M. Eliason, and B. L. Brown. 2017. Does stream size really explain biodiversity patterns in lotic systems? A call for mechanistic explanations. *Diversity* 9:26.
- Wallace, A. M., and R. G. Biastoch. 2016. Detecting changes in the benthic invertebrate community in response to increasing chloride in streams in Toronto, Canada. *Freshwater Science* 35:353–363.
- Ward, J. V. 1986. Altitudinal zonation in a Rocky mountain stream. *Archiv für Hydrobiologie Suppl.* 74:133–199.
- Whittaker, R. H. 1972. Evolution and measurement of species diversity. *Taxon*, 2/3:213–251.
- Winemiller, K. O., A. S. Flecker, and D. J. Hoeinghaus. 2010. Patch dynamics and environmental heterogeneity in lotic ecosystems. *Journal of the North American Benthological Society* 29:84–99.
- Zhang, Y., L. Liu, L. Cheng, Y. Cai, H. Yin, J. Gao, and Y. Gao. 2014. Macroinvertebrate assemblages in streams and rivers of a highly developed region (Lake Taihu Basin, China). *Aquatic Biology* 23:15–28.

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