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Phylogenetic diversity efficiently and accurately prioritizes conservation of aquatic macroinvertebrate communities

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Citation: Weglarz, K. M., W. C. Saunders, A. Van Wagenen, and W. D. Pearse. 2021. Phylogenetic diversity efficiently and accurately prioritizes conservation of aquatic macroinvertebrate communities. Ecosphere 12(3):e03383. 10.1002/ecs2. 3383

Abstract. Land degradation is a leading cause of biodiversity loss, and understanding its consequences on freshwater ecosystems remains a priority for improving the effectiveness of restoration practices and ecosystem assessments. Freshwater monitoring programs use macroinvertebrates to assess the biotic effects of degradation and management actions, often using the ratio of observed to expected taxa at a site—O/E for this purpose. Despite the power of the O/E approach, large amounts of data are required to generate an expectation and it can be difficult to define a threshold value for degraded sites. An alternative assessment tool is phylogenetic diversity, which is widely used in academic biology but rarely applied in management despite empirical correlations between phylogenetic diversity and management targets such as ecosystem structure and function. Here, we use macroinvertebrate data from 1400 watersheds, collected since 1998, to evaluate the potential for phylogenetic metrics to inform evaluations of management practices. These watersheds were chosen because their low disturbance levels and high habitat heterogeneity have made them problematic to assess with O/E. Phylogenetic diversity detected degradation of assemblages and was sensitive enough to parse impacts to inform management actions. This is particularly notable given the phylogenetic metrics, unlike O/E, did not require additional "baseline" data. Site disturbance and broader environmental drivers strongly predicted site phylogenetic structure, providing management objectives to increase site quality. We call on others to consider using phylogenetic diversity to complement existing O/E schemes, particularly in systems where O/E is insufficient to prioritize management objectives.

Key words: aquatic; biological assessment; macroinvertebrates; metric; monitoring; phylogenetic diversity.

Received 26 August 2020; accepted 3 November 2020. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

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Declines in biodiversity are associated with subsequent loss of ecosystem services (Butchart et al. 2010, Cardinale et al. 2012). This is a particular concern in freshwater ecosystems, which are highly vulnerable (Millennium Ecosystem Assessment 2005). These ecosystems support food web processes and nutrient cycling, purify and supply high-quality freshwater resources,

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regulate sediment and nutrient transport across the landscape, and provide an array of cultural services (Vörösmarty et al. 2010, Macadam and Stockan 2015). Since the late 1800s, when the link between human health and water quality was formally recognized by the scientific community, freshwater systems have been monitored for conservation and restoration purposes (Bonada et al. 2006). While land degradation is recognized as a leading cause of biodiversity loss (Newbold et al. 2015), understanding its consequences on freshwater ecosystems is priority for making evidenced-based management decisions (IPBES 2018). This knowledge gap persists in spite of the well-recognized link between land and water management (Bossio et al. 2010), making it difficult to determine the effectiveness of restoration practices (Feld et al. 2011, Melland et al. 2018). To assess the impact of these practices on the biotic community, many monitoring programs survey aquatic macroinvertebrates because these organisms are abundant, provide anywhere from 20% to 100% of the energy budget to consumers, and are sensitive to changes in water chemistry in predictable ways (Bonada et al. 2006, Macadam and Stockan 2015). Beyond serving as a biomonitoring tool, macroinvertebrates are integral to decomposition and nutrient cycling and support \$31.4 billion in recreational fishing in the United States alone (Prather et al. 2013). Unfortunately, the impact of improved management efforts on freshwater biodiversity, particularly macroinvertebrates and fish, can be difficult to detect owing to the time required for these organisms to return to improved habitats (Meals et al. 2010).

Many monitoring programs rely on macroinvertebrates to assess the biotic effects of degradation because they are relatively easy to collect and identify, and track disruptions more closely than other taxonomic groups (Cairns and Pratt 1993, Bonada et al. 2006, Friberg et al. 2011). Due to their ubiquity in monitoring, a number of metrics have been developed to evaluate the status of macroinvertebrate assemblages (Woodiwiss 1964, Balloch et al. 1976, Cairns and Pratt 1993, Resh and Rosenberg 1993, Bonada et al. 2006, Hellawell 2012). Often, these metrics measure ecological structure and are similar to, or based upon, measures of species richness (Yates et al. 2014). One of the more commonly adopted families of these metrics compares the number of

observed taxa (O) to a modeled expectation (E) of taxa at a given site (O/E; Wright 1995, Hawkins et al. 2000, Hawkins 2006). This metric became widely applied in management with the development and adoption of the River Invertebrate Prediction and Classification System (RIV-PACS) (Wright 1995, Wright et al. 2000), which has since been modified for regions outside of the UK (Smith et al. 1999, Hawkins et al. 2000, Yuan et al. 2008, Moya et al. 2011). Such O/E approaches are comparable across systems and relatively easy for managers to interpret (Wright 1995, Wright et al. 2000, Hawkins 2006), but, like all approaches, O/E metrics have potential caveats. They are less sensitive to degradation in heterogeneous environments (Hargett et al. 2007), and uncertainty associated with expectations of potential invertebrates present is often not reflected in the final O/E metric (but see de Zwart et al. 2006). Further, standards for what constitutes a degraded O/E are often subjective, and statistical deviation from this baseline can be difficult to determine (Hämäläinen et al. 2018). The problem is even more acute given variation (and uncertainty; see Introduction) in expectations of site richness: Sites may have the same O/E value even when they have drastically different values of E. For instance, a site with an $\frac{O}{E}$ of $\frac{4}{5}$ and another with an $\frac{O}{E}$ of $\frac{80}{100}$ represent the same O/E value of 0.8, but it is unclear whether this value conveys the same information about species losses for both sites. As is the case with plankton, sites with low species richness may have less functional redundancy than those with high richness (Kruk et al. 2016). Thus, the loss of a single species at the site with the lower E value may mean the absence of an entire functional group, while the impacts of losses at a site with higher richness may be insulated by redundancy. This highlights what is perhaps most critical, and O/E does not consider the kinds of species that are present or absent. The functional diversity of macroinvertebrates reflects an ecosystem's health and productivity (Schmera et al. 2017), and it would be useful, as others have suggested (e.g., Friberg et al. 2011, Yates et al. 2014), for metrics to reflect this, particularly for management purposes.

Even though integrating functional and structural metrics should improve detection of environmental degradation (Yates et al. 2014), macroinvertebrate modeling has been slow to incorporate phylogenetic diversity, which can serve as a proxy for functional diversity (Faith 1992, Webb et al. 2002, Cavender-Bares et al. 2009, Tucker et al. 2017). This is surprising, since much of modern eco-phylogenetic methods were developed from taxonomic metrics developed for macroinvertebrates (reviewed in Pearse et al. 2014; see Izsáki and Papp 1995; Wright 1995). Incorporating the evolutionary history of species (phylogeny) into macroinvertebrate monitoring provides the opportunity to incorporate information about the kinds of species within an ecosystem. Under the assumption that more distantly related species have fewer functional traits in common (but see Mayfield and Levine 2010, Swenson 2013), phylogenetic diversity metrics can reveal the structure (Cadotte et al. 2009), stability (Cadotte et al. 2012, Craven et al. 2018), and primary productivity (Cadotte et al. 2008, Flynn et al. 2011), of ecosystems while highlighting when certain species loss or gain will have an oversized impact on ecosystem function (Strauss et al. 2006, Lessard et al. 2009, Pearse et al. 2015b). Yet, phylogenetic diversity or evolutionary distinctiveness are rarely incorporated into applied conservation, restoration, and management programs (Díaz et al. 2013, Pearse et al. 2015b, Tucker et al. 2017, Cadotte and Tucker 2018), with the notable exception of the EDGE of Existence program (Isaac et al. 2007, Isaac and Pearse 2018). By incorporating phylogenetic diversity metrics into biomonitoring, management programs can gain further insight into ecological processes occurring using the same information already necessary to calculate metrics such as O/E.

The goal of this study was to outline the potential of phylogenetic metrics for macroinvertebrate conservation and monitoring programs, particularly in systems where traditional metrics struggle to provide informative assessments. To accomplish this, we use a well-established, successful monitoring program as a case study: the PACFISH/INFISH Biological Opinion Effectiveness Monitoring Program (PIBO). PIBO's goal is to determine the effectiveness of aquatic conservation strategies in riparian and aquatic systems in the Northwestern United States and has sampled stream reaches in over 1400 watersheds

every five years since the late 1990s (see Fig. 1; Henderson et al. 2005, Archer et al. 2012). Owing to macroinvertebrates' nature as the primary prey resource for imperiled salmonids, the program's macroinvertebrate assemblage data provide a direct link between sites' physical characteristics and the broader biotic community. Yet, most analyses of the PIBO dataset have focused on physical habitat measures (e.g., Kershner et al. 2004a; Al-Chokhachy et al. 2011, 2016), and an attempt to evaluate the causal conceptual model underpinning the use of O/E in PIBO found it could not be used to quantify the impacts of anthropogenic drivers on biological condition (Irvine et al. 2015). Here, we apply phylogenetic diversity metrics to the macroinvertebrate data within the PIBO dataset to demonstrate their usefulness to biomonitoring programs. We highlight how analyses of these metrics can be used to better inform future management practices at PIBO sites where O/E ratios were inadequate. As a case study, we test whether site disturbance correlates with measures of phylogenetic diversity and whether these metrics can be used to parse the drivers of biological condition at sites where O/E has not been sufficient. We focus on the analysis of three phylogenetic diversity metrics, Faith's PD, SES_{MPD}, and SES_{MNTD}, and a detailed description of these metrics can be found in the methods. We evaluate the ability of these metrics, in comparison with O/E, to generate actionable management insights in a low disturbance system where O/E has struggled.

Methods

Data collection

The PIBO program collects data from within the Interior Columbia River and Upper Missouri River Basins at reach-scale sites (160–400 m stream lengths). Sites designated as "reference" (minimally managed) are primarily located in watersheds that have little history of, or no obvious, mining, recent grazing (within 30 yr), timber harvest (<5%), and minimal road density within the watershed (<0.5 km/km²). Macroinvertebrates are sampled from eight fast-water habitats per site and combined into a composite sample using the protocol recommended by the Center for Monitoring and Assessment of



Fig. 1. The distribution of the 1667 PIBO sampling sites across the Interior Columbia and Upper Missouri River Basins. Sites include 1409 standard sites that are sampled every five years, 100 pilot sites, and 158 contracted or special program sites.

Freshwater Ecosystems at Utah State University (Hawkins et al. 2000). Taxa are identified by the BLM/USU National Aquatic Monitoring Center in Logan (Utah). Physical measures of the environment, such as the frequency of large wood, total dissolved solids, bank-full width, and pool frequency, are sampled concurrently across the PIBO sites. For a complete description of these variables and field methods used, see Kershner et al. (2004*b*) and Archer et al. (2012). Here, we analyze PIBO data collected between 2001 and 2017 across 1667 sites, of which 1477 (88%) were sampled more than once.

Measures of site disturbance

All following analyses were conducted in R (3.5.1; R Core Team 2018), data are publicly available through PIBO, and code for analyses is available in (Data S1). To build a macroinvertebrate phylogeny, we searched the TimeTree of Life (Hedges et al. 2015) for species and their congeners, and then added missing species into this phylogeny using dating information from congeners using the "bind-replace" algorithm (*congeneric.merge* in *pez;* Pearse et al. 2015*a*). The resulting phylogeny contained 161 of the 363 insect taxa in the PIBO data; this was the best

coverage we could achieve given many species were identified only to genus (260) and the paucity of genetic data available. Across the 9 insect orders represented in the PIBO dataset, the percent of taxa included ranged from 8.2% (Plecoptera) to 75% (Megaloptera), with Lepidoptera entirely dropped as there was only one species in the dataset (Appendix S1: Table S1). The strong performance of our phylogenetic metrics, despite this lack of data, makes our demonstration of the power of phylogenetic metrics, if anything, conservative. However, we note that phylogenetic diversity analyses are resilient to randomly missing species (Isaac and Pearse 2018). Using this phylogeny, we calculated Faith's PD, a measure of the total phylogenetic branch lengths found within an assemblage and biologically comparable to species richness (Faith 1992). We also calculated SES_{MPD} , a measure of the average distance between pairs of species within an assemblage (Webb et al. 2002, Kembel 2009), and SES_{MNTD} , a measure of the phylogenetic distance between most closely related species (Kembel et al. 2010). Both of these metrics provide a measure of the extent to which assemblages contain closely or distantly related species. These measures of phylogenetic structure have been linked to

ecosystem structure and function (Webb et al. 2002, Cavender-Bares et al. 2006, Cadotte et al. 2009, Cavender-Bares et al. 2009, Flynn et al. 2011).

We calculated these three phylogenetic diversity metrics using pez (Kembel et al. 2010, Pearse et al. 2015a) under a species-label null randomization. This randomization, which permutes species' identities across the phylogeny, creates a purely statistical expectation of SES_{MPD} and SES_{MNTD} values for assemblages, in contrast to the modeled expectation in O/E, which must be predicted from data collected from reference sites. To compare the relative power of O/E and phylogenetic metrics, we also analyzed the O/E metric values that PIBO calculates for management purposes. PIBO calculates O/E by employing a RIVPACS-type predictive model and comparing the number of taxa expected at similar high-quality sites to the number observed at a site (for details, see Irvine et al. 2015). This resulted in metrics for 5033 site-year combinations (1477 of the 1667 sites were surveyed more than once) within the PIBO dataset.

Drivers of biotic degradation

To explain potential variation in phylogenetic and O/E metrics, we utilized a range of covariates that describe variation in geoclimatic and anthropogenic drivers across the study area. Appendix S1: Table S2 outlines the explanatory variables used in our analysis. We divided these variables into 'actionable' variables that management practices may affect, and 'non-actionable' which management is unlikely to be able to control as they mostly constitute natural environmental gradients. We included the PIBO program's site designation as 'managed' or 'reference' (see Kershner et al. 2004*a* for more details). We also included the PIBO program's condition index of habitat integrity. This condition index is a numeric score ranging from 0 (worst) to 100 (best), calculated by summing independent index values of six variables: residual pool depth, percent pools, diameter of the 50th percentile streambed particle, percent pool tail fines <6 mm, large wood frequency, and average bank angle (see Al-Chokhachy et al. 2010 for all details). The condition index was developed to describe the relative quality of habitat provided by the physical attributes of a stream channel for anadromous and inland salmonids. As such, it is unlikely to adequately serve as a comprehensive index of habitat integrity for macroinvertebrates. Yet, as this condition index is a summary of a stream's physical environment, we sought to use it to evaluate potential correlation between the physical environment and macroinvertebrate metrics developed here.

With over 40 potential explanatory variables in our dataset, we identified potential drivers of degradation using a two-step approach. First, we used Lasso regression (Tibshirani 1996, Hastie and Efron 2013) to eliminate explanatory variables with minimal sway on response variables. Lasso regression is a machine learning algorithm designed to reduce a large number of potential explanatory variables to a suite of those that are strongly associated with a response variable (Hastie and Efron 2013). Variables with an absolute coefficient of over 0.01 for at least one of the four metrics were considered for inclusion in further analyses. PIBO's habitat condition index was also included in further analyses. With a set of 19 explanatory variables identified by the Lasso regression as potentially important for at least one of our four response variables (Faith's PD, SES_{MPD}, SES_{MNTD}, and O/E), we then used information theoretic criteria to identify the most important predictors of our response variables. To accomplish this, we fit a linear model to these data for each metric and then used the *dredge* function in the package *MuMin* to estimate the importance of each variable on our models (Bartoń 2018). Information theoretic criteria (Burnham and Anderson 2002, 2004) allow for uncertainty in both model specification (which variables are important) and parameters (coefficient estimates) to filter through into model predictions. This allows us to circumvent traditional problems with significance thresholds and their arbitrary decision criteria when dealing with datasets of this size and complexity. Then, we ensured all explanatory variables were Z-transformed prior to analysis, making each variable's coefficient a measure of relative importance (Grueber et al. 2011, Gelman et al. 2014). This makes variable coefficients directly comparable, such that a variable with a coefficient twice that of another variable is twice as important in driving a response variable, and so allows us to generate more actionable insights.

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We fit mixed-effects models, for each metric, using site identity as a random covariate to control for repeated measures from sites through time (Bates et al. 2015). To generate site-specific recommendations useful for PIBO's management purposes, we calculated the random effects of our mixed-effects models (Bates et al. 2015). In a mixed-effects framework, treating each site identity as a 'random' variable controls for uneven sampling of sites while quantifying the impacts of the other explanatory variables. It also generates site-specific estimates for identifying sites with unusually high or low values of our diversity indices (PD, SES_{MPD}, SES_{MNTD}, and O/E) within the context of our model. This method is appropriate for making recommendations within a dataset, but these site-level predictions should not be used to generalize to other nearby sites or to different datasets (as is the case for related random-effects approaches; Robinson 1991; Hadfield et al. 2010). Spatial plotting was conducted using the R packages 'rgdal', 'rgeos', 'raster', and 'ggmap' (Kahle and Wickham 2013; Bivand et al. 2018; Bivand and Rundel 2018; Hijmans 2018).

Results

The stream-reach condition index that PIBO has been using to quantify management impacts at sampled stream reaches is negatively correlated with SES_{MNTD} and SES_{MPD} (Fig. 2). Thus, sites with more intact aquatic habitat tend to correlate with lower measures of these phylogenetic diversity metrics indicating they contain macroinvertebrate communities that are more phylogenetically clustered and have more close relatives. For example, we would expect a site with a high habitat condition index value to have negative SES_{MNTD} and SES_{MPD} scores, both of which indicate that the assemblage contains more phylogenetically closely related taxa than compared with a statistical null expectation. Disturbed sites (*i.e.*, low index scores), by contrast, are more phylogenetically overdispersed, suggesting different ecological assembly as a result of disturbance. O/E showed the strongest significant correlation with site condition index (18.6%). Thus, O/E is a better metric of the condition index than our phylogenetic diversity indices. This is to be expected as O/E uses data from reference sites to calculate expectation, but its performance is comparable to that of SES_{MNTD} and SES_{MPD} . While Faith's PD significantly correlated with the site condition index (0.2%), it was the weakest of the metrics. Faith's PD is the only metric we examined that does not incorporate a statistical expectation of diversity for macroinvertebrate assemblages. It is also the only metric for which 'reference' sites differed from 'managed' sites (Fig. 3). This indicates that references site conditions are not necessarily good benchmarks for macroinvertebrate communities, which may impact the performance of O/E.

The use of information theoretic criteria to estimate the importance of each explanatory variable revealed that many of the important predictors of O/E, SES_{MPD}, and SES_{MNTD} were the same, while the drivers of PD differed (Fig. 3). Some of the important drivers of SES_{MPD} and SES_{MNTD} are not practical for management interventions, such as stream gradient and latitude. There were, however, several potentially actionable factors related to stream geomorphology (average bankfull width, pool tail fines, and number of pools) and road density (in the reach itself and its surroundings). SES_{MPD} and SES_{MNTD} differed in the size of pool tail fine sediment that affected them, with SES_{MPD} more affected by the cumulative impact of both larger particles (<6 mm) and those than <2 mm, while SES_{MNTD} was affected by both combined and those <2 mm alone.

Using our mixed-effects framework and the same predictor variables, we were able to identify sites with unusually high or low (phylogenetic) metric values that are either under- or over-performing (Fig. 4). This allows managers to identify sites where management actions may have the largest impacts and, using information from the predictor variables, determine what actions should have the most impact. Notably, geographic hotspots and coldspots are visible for all variables, which is likely related to the non-actionable diversity drivers we identified, such as latitude. These geographic inferences are still possible in the absence of designated reference sites and a site condition index score.

Discussion

Assessing and tracking the condition of aquatic and riparian resources on federal lands

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Fig. 2. The relationships between condition index and SES_{MNTD}, SES_{MPD}, Faith's PD, and O/E, showing both managed and reference sites. The results of a linear regression for each of these metrics indicated that site condition index score explained 9.6%, 9.6%, 0.2%, and 18.6% of the variance, respectively. Site condition index score was significantly correlated with all metrics: SES_{MNTD} ($F_{1,4586} = 488.6$, P < 0.0001, $r^2 = 0.096$), SES_{MPD} ($F_{1,4586} = 490.6$, P < 0.0001, $r^2 = 0.097$), Faith's PD ($F_{1,4631} = 12.32$, P < 0.0005, $r^2 = 0.002$), and O/E ($F_{1,4580} = 1049$, P < 0.0001, $r^2 = 0.186$). Thus, O/E is a better metric of the condition index than our phylogenetic diversity indices, which is to be expected as O/E uses additional data to calculate its expectation, but that its performance is comparable to that of SES_{MNTD}, SES_{MPD}, and Faith's PD. However, designation of a site as reference significantly explained only 2.9%, 1.4%, 0.6%, and 5.2% of variance for all metrics, respectively (SES_{MNTD}) ($F_{1,4974} = 116.3$, P < 0.0001, $r^2 = 0.023$), SES_{MPD} ($F_{1,4974} = 68.22$, P < 0.0001, $r^2 = 0.014$), Faith's PD ($F_{1,5031} = 21.87$, P < 0.0001, $r^2 = 0.004$), and O/E ($F_{1,4975} = 272.2$, P < 0.0001, $r^2 = 0.052$)). This indicates that reference site conditions are not necessarily good benchmarks for macroinvertebrate communities.

necessitates tracking changes in sites' abiotic and biotic conditions to ensure management is effective at achieving its objectives. Many previous analyses of the PIBO dataset use physical habitat measures, compared between reference and managed sites, to assess stream health (e.g., Kershner et al. 2004*a*, Al-Chokhachy et al. 2011, 2016). This work identified important drivers of habitat degradation, but did not quantify the biotic response to such disturbances. Efforts to assess biotic response have primarily focused on the vegetation component of the PIBO dataset, examining the impact of grazing on plants (Coles-Ritchie et al. 2007), of plants on stream structure (Roper et al. 2007, Hough-Snee et al. 2015, Hough-Snee et al. 2016), and the physical site factors that predict plant invasion (Al-Chokhachy et al. 2013, Menuz and Kettenring 2013). These studies are a solid foundation for understanding the health of these sites, but as a



Fig. 3. Plots showing the relative importance of each explanatory variable considered in the model for each metric considered. Coefficient values further from zero (in the either positive or negative direction) indicate that the variable has a greater impact on the overall model. For example, the percent of pool tail fines <2 mm present has nearly twice the influence on the SES_{MNTD} model as pool frequency. Explanatory variables are indicated on the left and are colored by whether or not they are considered potentially actionable by a manager attempting to address habitat degradation. This indicates there are consistently influential actionable explanatory variables.

primary prey source for the imperiled fishes PIBO was designed to monitor, an understanding of the macroinvertebrates of the sites is key to achieving management goals. Initial efforts to evaluate the usefulness of macroinvertebrate O/E ratios in quantifying the impacts of anthropogenic drivers on biological condition failed to find support for the underlying conceptual model for the use of O/E (Irvine et al. 2015). This highlights the need for a more effective metric for measuring the health of macroinvertebrate communities at PIBO sites that, ideally, capitalize on the data this management program already collects.



Fig. 4. Plots showing site-level variation across each metric, highlighting sites with unusually high or low metric values given the variation within the dataset for each explanatory variable. In all cases, sites in yellow should be management priorities. In (a) (SES_{MNTD}) and (b) (SES_{MPD}), sites in blue have more positive values, indicating more distantly related species are found at a site, and values in yellow have more closely related species at a site (more negative values), than would be expected given site conditions (management, disturbance, latitude, and all other variables in our models). Again, given clustering (more negative) is found at more disturbed sites, sites in yellow should be management priorities. In (c) (Faith's PD), sites in yellow have less phylogenetic diversity, and sites in blue more diversity, than would be expected by chance, and thus, sites in yellow are management priorities. Finally, in (d) (O/E) sites in yellow have fewer species observed than expected, while sites in blue have more species than the expectation. We emphasize that, as discussed in the text, these estimates should not be used to generalize management decisions to other sites or data, and should only be considered within the context of this modeling exercise.

Here, we use phylogenetic diversity metrics to quantify the health of macroinvertebrate assemblages at sites within the PIBO dataset and demonstrate these metrics' usefulness in generating actionable insights for land managers. Phylogenetic diversity metrics that incorporate a statistical expectation of diversity (SES_{MPD} and SES_{MNTD}) are more sensitive than those that do not (Faith's PD), complementing the current PIBO focus on taxonomic metrics incorporating

expectations (O/E; an expectation of taxa that may be present at the site derived from the modeling of independently collected data). However, SES_{MPD} and SES_{MNTD} remove the need for management programs to first to collect data for modeling an expectation, easing implementation, particularly in regions where known reference conditions do not exist or have not been determined. These metrics provide similar information on biotic condition using minimal measures of habitat integrity and, using the random-effects method demonstrated here, can highlight sites where management actions will have the greatest impact without the need to designate baselines for what constitutes a degraded site. Below, we discuss the management implications of the drivers we have identified in the data.

Contrasting patterns of phylogenetic and taxonomic diversity

Ratios of observed to expected taxa at a site (O/E ratios) are modified measures of species richness that can be compared across sites and studies (Hawkins 2006). These ratios depend on models of the probability of taxon capture (PC) to predict the expected pool (E), which impacts their performance (Clarke et al. 2003). O/E ratio performance varies depending on the predictor variables used to generate the expectation and the PC thresholds used to calculate E (Hawkins et al. 2000, Hawkins 2006). These dependencies limit the application of O/E ratios to locations where PC models have been developed and adequate predictive data can be collected. There are, however, strong conceptual links between the phylogenetic diversity metrics we use here and previous O/E approaches. Faith's PD augments observed species richness with information about the phylogenetic diversity of those species, and so information about their traits and evolutionary history (Faith 1992). This added information about the kinds of species within a site is useful, and SES_{MPD} and SES_{MNTD} build upon this by incorporating an evolutionary expectation of what a randomly assembled ecological community might resemble (Webb et al. 2002, Kembel 2009). By combining expectations of community structure with information about the kinds of species in an assemblage, we can pick apart the drivers of community assembly and change that are important for determining management actions. As sites are degraded or restored, it is possible for the number of species within a site to remain constant, while the species themselves change; phylogenetic diversity metrics are sensitive to such changes. Critically, in our phylogenetic approach the expected pool comes from the observed data alone: There is no need for comparison sites in order to generate a statistical expectation allowing application of this method in locations that lack PC models. This is a clear

practical advantage in favor of the use of phylogenetic diversity metrics in management programs.

Phylogenetic diversity is often viewed as a proxy for functional diversity, under the assumption that species that are more distantly related to one another have fewer functional traits in common (Devictor et al. 2010, Mazel et al. 2014, Tucker et al. 2018). This is certainly true, at a coarse scale, for macroinvertebrates: Species within the same genus often resemble one another, but many different families and orders are instantly recognizable. Because environmental stressors alter the structure of a community, they also predictably alter its phylogenetic diversity (Cadotte et al. 2008, Letcher 2009, Burns and Strauss 2011, Flynn et al. 2011, Cadotte et al. 2012). By understanding the phylogenetic structure of healthy communities, we can identify damaged communities. Previous work on Daphnia indicated that disturbed communities tend to be phylogenetically clustered (Helmus et al. 2010), which is thought to reflect the new environmental filtering pressure of the disturbance. However, disturbed PIBO sites (i.e., those with low condition indices) are instead overdispersed, with high SES_{MNTD} scores. Undisturbed communities with clustered structures, such as PIBO sites, occur in other invertebrate systems such as ants, where invasion results in a reduction in clustering as groups of specialists are lost (Lessard et al. 2009). Here, phylogenetic diversity of macroinvertebrate assemblages is measured within each site (locally) and tends to be clustered in less anthropogenically disturbed sites. Since healthy macroinvertebrate communities are clustered at PIBO sites, we suggest that SES_{MPD} and SES_{MNTD} are sensitive enough to pick up on the losses of specialists within these communities, despite that we tested them in a setting with low disturbance where other metrics historically struggle. This phylogenetic clustering most likely reflects the high level of habitat heterogeneity found at PIBO sites, with highly specific habitats that host specialists, further highlighting that phylogenetic diversity metrics may be particularly useful in areas where O/E struggles. In contrast, communities at disturbed sites tended to be more overdispersed-they contain more distantly related species. This pattern would be consistent with the loss of specialist

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species, although we do not explicitly test these hypotheses here. Landscape-scale stressors that reduce site heterogeneity would result in a loss of close relatives, as they are more likely to be functionally similar (Cavender-Bares et al. 2009). The phylogenetic clustering observed likely further reflects the environmental heterogeneity of PIBO sites as assemblages with larger source pools are expected to be more clustered (Cavender-Bares et al. 2006; Swenson et al. 2006; Pearse et al. 2013). Thus, phylogenetic diversity metrics offer a path for large-scale biomonitoring programs to overcome issues that O/E ratios face with habitat heterogeneity, even in settings with low anthropogenic disturbance levels, as it is reflected in the resulting phylogenetic structure of the community.

Management implications of phylogenetic diversity

Improving and maintaining stream health for macroinvertebrates, and thus the imperiled fishes that prey upon them, depend on identifying the actionable factors that most dramatically disrupt these communities. The relationships between the different physical measures of habitat quality that PIBO collects and the metrics we calculated allow us to highlight factors that are most influential on the macroinvertebrate communities, and some that were surprisingly not. The relative influence of these factors can help better target management practices in the future. PIBO's site designation as "reference" is not a significant driver of disruption for O/E and only has a small influence on $\ensuremath{\mathsf{SES}_{\mathsf{MNTD}}}$ and $\ensuremath{\mathsf{SES}_{\mathsf{MPD}}}$ (Fig. 3, coefficient values overlap 0 for O/E and nearly do so for SES_{MNTD} and SES_{MPD}). During the original study design and implementation phase of the PIBO program, reference sites were selected to encompass both the greatest spatial extent possible and the range of variation in habitat conditions resulting from natural disturbances (e.g., wildlife, landslides). Furthermore, not all anthropogenic disturbances (e.g., recreation) were considered in the initial selection of reference sites. As a result, the binary classification of managed/reference alone is apparently insufficient to distinguish between intact and impaired macroinvertebrate assemblages, which indicates these reference communities may not be ideal for calculating E in O/E. In contrast,

quantitative measures of sites' abiotic condition (in the form of actionable explanatory variables) provide clear evidence that management affects these drivers of macroinvertebrate assemblage. PIBO's overall abiotic site condition index significantly correlates with O/E, SES_{MPD}, and SES_{MNTD}, but while significantly correlating with Faith's PD, the relationship is weak in comparison. This metric is the only of the four diversity metrics that do not incorporate some expectation of diversity. This result demonstrates that a statistical expectation of diversity is a useful component for metrics and is consistent with results from previous studies of the PIBO dataset. Other abiotic factors such as roads in a reach and/or its surroundings are some of the strongest factors influencing community structure. These measures of disturbance yielded similar or better results than site condition index. Road construction increases fine sediment and adversely impacts macroinvertebrates (King 1983, Lenat and Crawford 1994, Wood and Armitage 1997). Pool tails are thought to be important spawning habitat for the fish PIBO monitors (Keller et al. 1990). Measures of fine sediment in these areas, specifically percent pool tail fines present, also reflect this adverse relationship, driving overdispersion nearly as strongly as roads. Because SES_{MPD} reflects broader patterns across the entire phylogeny, this is consistent with habitat filtering of entire lineages on the basis of the percent of pool tail fines <6 mm present, and the percent of pool tail fines <2 mm present driving competition among close relatives, thus having a greater impact on SES_{MNTD}. The bank-full width of the reach is about half as influential as the previously mentioned measures, indicating that overall stream structure has some impact on the communities present. The amount of total dissolved solids (TDS) and percent vegetatively stable banks have a comparatively minor influence on community structure, supporting previous findings that these measures may have little impact on macroinvertebrates and should not be the focus of management actions (Mazeika et al. 2004, Timpano et al. 2010). That TDS were not important in our model does not mean TDS do not influence macroinvertebrates (Clements and Kotalik 2016), particularly as measurement of this variable may be limited by measuring at base flows (Cey et al. 1998). Rather, measures of pool tail fines and roads appear to be better indicators of macroinvertebrate assemblage response to management activities within the PIBO dataset.

Surprisingly, the frequency of large wood had little influence on macroinvertebrate communities when other explanatory variables such as sedimentation are included. Large wood has been hypothesized to be an important moderator of human stressors, specifically sedimentation (Irvine et al. 2015), but does not appear to strongly impact assemblage structure in these data. This indicates that indirect effects of large wood have mostly been accounted for by other explanatory variables in our model. In general, these results suggest that stream macroinvertebrates are consistently sensitive to road density, overall stream structure, and sedimentation. To remediate degraded macroinvertebrate assemblages, managers should focus efforts on actionable factors, such as roads, fine sediment, and the number of pools per kilometer, that have a large influence on community structure.

Simply identifying overdispersed communities does not adequately prioritize sites for management purposes. Community response to disturbance must be driven by physical measures that are 'actionable' and thus may be affected by management practices. Our statistical models identified a number of drivers of diversity in the PIBO data that are not likely to be influenced by management actions but are still important determinants of community structure (see Fig. 3). Of these non-actionable variables, stream gradient, elevation, and latitude are important predictors of SES_{MNTD} and SES_{MPD}, and geographic 'hotspots' and 'coldspots' are visible for all variables in Fig. 4. These variables have nearly double the influence on our models as both fine sediment and road density, reflecting latitudinal gradient in biodiversity (Hillebrand 2004), aquatic insect sensitivity to temperature (Johnson and Jones 2000), and known patterns of decreased diversity in aquatic communities at higher elevations (Altermatt et al. 2013). Even though these variables strongly influence the model, they are a result of site location and thus cannot be addressed by land managers. We suggest that all other things being equal, those sites that are strongly impacted by these factors (i.e., are at high latitudes and are hot), should be a lower

management priority. Some managers may be able to address factors that we designate as nonactionable. For example, grazing is known to impact instream temperatures (Belsky et al. 1999, Hough-Snee et al. 2013, Kovach et al. 2019), and thus, altering grazing intensity could be used to alter temperature and thus help remediate the site. By accounting for what cannot be changed and acting on what can, managers will effectively and efficiently be able to apply these metrics.

O/E has provided strong management insight for decades, but like all approaches it has strengths and disadvantages. Here, we have shown how phylogenetic diversity metrics, which incorporate information on the kinds of species present in assemblages and have less ecological data requirements, can help managers prioritize conservation actions. In this system, we have found phylogenetic diversity, when combined with an analysis targeted at quantifying the potential benefits of management interventions, provides valuable insight to be of great insight for a program that has struggled to pull meaningful conclusions from O/E in the past due to high habitat heterogeneity and low levels of overall disturbance. We encourage others to experiment with these new metrics and approaches, in the hope that they will be of use in other monitoring programs of macroinvertebrates and other taxa.

ACKNOWLEDGMENTS

We are grateful to anonymous reviewers, and the editorial board, for their help improving this manuscript. WDP, KMW, and the Pearse Lab are funded by NSF ABI-1759965, NSF EF-1802605, and USDA Forest Service agreement 18-CS-11046000-041. We would like to thank all the field technicians associated with the PACFISH INFISH Biological Opinion Effectiveness Monitoring Program who collected field data associated with this study. These crews were supervised by Eric Archer and Rick Henderson.

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DATA AVAILABILITY

Data are publicly available by request through the USDA Forest Service PACFISH/INFISH Biological Opinion Monitoring Program (https://www.fs.usda.gov/detail/r4/landmanagement/resourcemanagement/?cid=stelprd 3845865), and the code to conduct analyses is available in the supplemental information.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2. 3383/full