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## Dimensions of biodiversity in Chesapeake Bay demersal fishes: patterns and drivers through space and time

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**Abstract.** Biodiversity has typically been described in terms of species richness and composition, but theory and growing empirical evidence indicate that the diversity of functional traits, the breadth of evolutionary relationships, and the equitability with which individuals or biomass are distributed among species better characterize patterns and processes within ecosystems. Yet, the advantages of including such data come at the expense of measuring traits, sequencing genes, and counting or weighing individuals, and it remains unclear whether this greater resolution yields substantial benefits in describing diversity. We summarized a decade of high-resolution trawl data from a bimonthly trawl survey to investigate spatial and seasonal patterns of demersal fish diversity in the Chesapeake Bay, USA, with the goal of identifying areas and times of mismatch between different dimensions of diversity, and their response to environmental forcing. We found moderate to strong positive relationships among all metrics of diversity, and that functional and phylogenetic differences were well-reflected in an index derived from taxonomic (Linnaean) hierarchy. Compared with species richness and species diversity, functional, phylogenetic, and taxonomic indices peaked later in the year, which was a consequence of the distribution of biomass among functionally and evolutionarily divergent species. Generalized additive models revealed that spatial, temporal, and environmental variables explained roughly similar proportions of deviance across all aspects of diversity, suggesting that these three factors do not differentially affect the functional and phylogenetic aspects of community structure. We conclude that an index of diversity derived from taxonomic hierarchy served well as a practical surrogate for functional and phylogenetic diversity of the demersal fish community in this system. We also emphasize the importance of evenness in understanding diversity patterns, especially since most ecological communities in nature are dominated by one or few species.

**Key words:** demersal fishes; environmental drivers; estuaries; evenness; functional diversity; phylogenetic diversity; species richness; taxonomic diversity.

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## INTRODUCTION

Biodiversity has long been described in terms of species richness and composition, but it is increasingly recognized that species' roles in ecosystems are intrinsically linked to their functional and phylogenetic differences. Unlike traditional measures of diversity, functional and phylogenetic approaches recognize that species vary by degrees, i.e., that some species are more functionally or phylogenetically similar than others (Webb et al. 2002, McGill et al. 2006). Consequently, these approaches allow for a finer understanding of ecological patterns, the mechanisms driving observed patterns and maintenance of diversity in nature (Webb et al. 2002, Petchey and Gaston 2006), and the role of diversity in ecosystem processes (Hooper et al. 2005, Srivastava et al. 2012). Yet, these advantages come with a tradeoff in effort, as calculations of functional and phylogenetic diversity require considerable additional data beyond simple species counts. While functional and phylogenetic methods are being increasingly applied across systems and taxa (Cadotte et al. 2011), it remains unclear when and where investment in functional and phylogenetic information yields the greatest benefits when characterizing biodiversity.

Functional diversity (hereafter FD) quantifies the community-wide variation in organismal *functional traits*. For our study, we define a functional trait as any character that influences how an organism interacts with its environment and/or other organisms. Our definition is closest to that proposed by Violle et al. (2007) in that we consider functional traits to be morphological, physiological, and life historical indicators of fitness at the individual level. However, we also include traits related to performance that contribute to ecosystem processes as well, such as body mass, and thus more closely resemble *effect traits* as defined by Lavorel and Garnier (2002). Incorporating information on multiple kinds of traits (functional, effect, etc.) can provide deeper insight into differences among organisms at the community level (e.g., Petchey et al. 2007, Devictor et al. 2010).

A trait-based approach to diversity is attractive because functional traits can, in principle, be directly linked to ecosystem processes (Díaz and

Cabido 2001). Thus, FD may provide stronger predictions about those processes than richness alone (e.g., Cadotte et al. 2009). Calculation of FD requires identification of traits that are relevant to the pattern or process under investigation, although there is often a lack of consensus as to what constitute relevant traits for many taxa (Petchey and Gaston 2006). Since trait measurements can be a costly and/or time-intensive process, most traits used in calculations of FD to date are relatively easy to obtain. However, they may not provide the most direct link to fitness or performance (so-called *soft traits*, sensu Hodgson et al. 1999).

Phylogenetic diversity (hereafter PD) quantifies the amount of unshared evolutionary history within an assemblage, and is used with the assumption that underlying evolutionary variation among organisms is an indicator of functional dissimilarity (Webb et al. 2002). As such, PD is often invoked as a holistic measure of diversity, especially if relevant functional traits are not known or measured (Srivastava et al. 2012). For this reason, PD has been shown to be a better predictor of ecosystem functioning than FD in some cases (Cadotte et al. 2009, but see Flynn et al. 2011). This approach assumes that functional differences are evolutionarily conserved, but a comprehensive review of 26 different datasets showed that only 60% of 103 ecological traits exhibited significant phylogenetic signal (Freckleton et al. 2002). These synthetic results, coupled with those from more recent individual studies (e.g., Flynn et al. 2011), suggest that the utility of PD as a surrogate for FD may vary depending on the organisms, their traits, and the scale of the investigation (Srivastava et al. 2012).

A larger roadblock to the widespread use of phylogenetic approaches is that robust molecular phylogenies are not always available, and DNA sequencing can be cost prohibitive or difficult. Several studies have suggested substituting existing Linnaean taxonomy as a proxy for phylogeny (Clarke and Warwick 1998, Shimatani 2001, Crozier et al. 2005, Ricotta 2005, Maherali and Klironomos 2007, Ricotta et al. 2012), or at least using taxonomy to inform poorly resolved phylogenies (Davies et al. 2012). With taxonomy, researchers can easily draw on centuries worth of rigorous data. However, taxonomic distances

may not wholly reflect evolutionary relationships suggested by molecular phylogeny, especially when species have originated recently and/or radiated rapidly (Crozier et al. 2005). Moreover, discrete taxonomic levels (e.g., genus, family, etc.) limit the resolution of evolutionary differences compared to those derived from continuous DNA sequence variation and thus may not provide much insight when species within an assemblage are closely related. In the case of microbes, evolutionary relationships may not be easily defined without the use of molecular tools (Wayne et al. 1987). There have been few direct tests of whether measures of diversity derived from a taxonomic hierarchy—which we refer to as taxonomic diversity (hereafter, TD)—provide similar inferences to PD (see Ricotta et al. 2012).

In addition to functional and phylogenetic differences among species, the relative abundance or biomass of species, defined as evenness, also influences ecosystem processes and may have strong implications for the interpretation of FD and PD (reviewed in Hillebrand et al. 2008). Evidence suggests that communities with a more even distribution of individuals or biomass among species alters biodiversity patterns (Stuart-Smith et al. 2013) and enhances ecosystem processes (Wilsey and Potvin 2000, Kirwan et al. 2007), although there have been comparatively few examples of how evenness modifies the inferences made from FD or PD in particular. In terrestrial grasslands, indices of FD and PD that did not incorporate relative abundance were better predictors of ecosystem processes than those that did (Mouillot et al. 2011*b*, Cadotte et al. 2012). Similarly, the inclusion or exclusion of relative abundance information did not alter areas of spatial mismatch of FD and PD in a bird assemblage (Devictor et al. 2010). However, turnover in dominant species altered the functional structure of estuarine fish communities after disturbance, despite no change in species richness (Villéger et al. 2010). Additionally, incorporating information on both functional traits and relative abundances shifted global diversity hotspots of reef fish diversity towards temperate regions (Stuart-Smith et al. 2013). Thus, it appears that in at least some circumstances, evenness may play an important role in altering the relationships between FD, and potentially PD, and more traditional indices of

diversity.

Here, we investigated how different dimensions of diversity explain spatial and seasonal patterns in the demersal fish community in the Chesapeake Bay, the largest estuary in the USA. Chesapeake Bay is characterized by a strong spatial gradient in salinity driven by tidal exchange with the Atlantic Ocean at the mouth and riverine input, and experiences some of the most extreme intra-annual fluctuations in temperature in the world (Murdy and Musick 2013). The Bay provides valuable economic, ecological, and recreational resources, and supports numerous fisheries (Murdy and Musick 2013). Approximately 350 fish species have been reported in the Chesapeake Bay, although many of these species are vagrants from freshwater or marine habitats, and are not found regularly (Jung and Houde 2003, Murdy and Musick 2013). Some species are only present in the Bay for a portion of the year to feed and/or spawn, spending the rest of their time offshore (Murdy and Musick 2013). We focus here on 50 species of bottom-dwelling fishes that represent the average annual demersal fish community in the Chesapeake Bay.

A recent study characterized spatial and temporal patterns in species richness and Simpson diversity in Chesapeake Bay demersal fishes using high-resolution data from 10 years of fisheries-independent bottom trawl data (Buchheister et al. 2013). They found that species richness and composition were primarily structured along strong environmental gradients, principally salinity, temperature, and dissolved oxygen, with highest richness at the northern and southern ends of the Bay's mainstem channel (Buchheister et al. 2013). Given that an increasing number of studies have found strong disagreement in spatial patterns between species richness, functional, and/or phylogenetic diversity (Petchey et al. 2007, Devictor et al. 2010, Mouillot et al. 2011*a*, Safi et al. 2011, Stuart-Smith et al. 2013), we supplemented the trawl survey data presented in Buchheister et al. (2013) with newly collected functional trait and genetic information.

Our specific objectives were to compare and contrast patterns in species richness, evenness, Gini-Simpson, functional, phylogenetic, and taxonomic diversity through space and time, and to identify the unique contributions of space, time, and environmental variables to diversity using

generalized additive models and deviance partitioning. We expected to find areas of spatial and temporal mismatch among the different measures of diversity based on previous investigations of estuarine (Villéger et al. 2010, 2012) and marine fishes (Mouillot et al. 2011a), as well as other ecological communities (Petchey et al. 2007, Devictor et al. 2010, Safi et al. 2011, Stuart-Smith et al. 2013). Based on well-delineated evolutionary relationships among species within this system, and evidence from other systems (Ricotta et al. 2012), we expected PD and TD to be suitable proxies for one another. Given the strong dominance of a small number of species in this system (Jung and Houde 2003, Buchheister et al. 2013), we predicted evenness would play a large role in determining diversity patterns. Finally, we expected to find strong spatial, temporal, and environmental signal in patterns of diversity, as has been shown previously with richness in this system (Buchheister et al. 2013) and estuarine systems in general (Odum 1988).

## METHODS

### *ChesMMAP survey*

Data for this study were obtained from the Chesapeake Bay Multispecies Monitoring and Assessment Program (ChesMMAP; Latour et al. 2003, Bonzek et al. 2010). This program conducts a bottom trawl survey that operates bimonthly from March to November, and monitors the relative abundance, biomass, age- and size-structure, and trophic interactions of demersal fishes within the mainstem waters of the Chesapeake Bay. Here, we present analyses of data from the years 2002–2011. The ChesMMAP survey employs a stratified random design, with strata determined by water depth and latitude, the latter dividing the Bay roughly by salinity regime (ranging from euryhaline at the mouth to oligohaline at the head). The survey samples approximately 80 randomly selected stations per bimonthly cruise, with the number of stations proportional to the area of each stratum. At each station, a twenty-minute tow is performed with an otter trawl (7.6-cm mesh in the cod end), which targets late-juvenile and adult fishes. Vessel GPS and trawl mensuration gear are used to quantify the area swept for each tow. Finally, measurements of temperature, salinity, dissolved

oxygen, and depth are also collected at each station.

Following Buchheister et al. (2013), we omitted any species that were not adequately sampled by the survey gear (i.e., excluded all pelagic species and any demersal species with < 10 individuals or < 1 kg captured). This exercise left a total of 50 species for this analysis that together accounted for > 99% of the total biomass sampled by the survey (see Table A1 for the full list of species used in the analyses). We further omitted any tows that contained ≤ 1 species (19% of all tows), as these samples did not inform us about diversity and yielded values of evenness that were not interpretable. Ultimately, we were left with a total of 2,530 independent tows across all months and years.

### *Calculating diversity*

To calculate diversity, we used Rao's quadratic entropy (hereafter  $Q$ , Rao 1982). Rao's  $Q$  is calculated as:

$$Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^S d_{ij} p_i p_j \quad (1)$$

where  $S$  is the number of species (richness),  $p_i$  is the relative abundance of species  $i$ ,  $p_j$  is the relative abundance of species  $j$ , and  $d_{ij}$  is the distance (functional, phylogenetic, etc.) between species  $i$  and  $j$ .  $Q$  is therefore the average difference between individuals in each tow. Most relevantly, the distances  $d_{ij}$  can be derived from any measure of dissimilarity, including functional and phylogenetic (Shimatani 2001, Botta-Dukát 2005). Thus, Rao's  $Q$  provides a unifying calculation with which to investigate and compare across the different dimensions of diversity.

For the analysis presented in the main text, we chose to weight by relative biomass instead of relative abundance. Biomass is a better proxy for ecological processes such as production and trophic transfer (Brett and Groves 1979), and has recently been shown to better predict biodiversity patterns in marine demersal fauna than abundance (Certain et al. 2013). However, we also calculated  $Q$  using relative abundance and presence-absence data to facilitate comparisons among the different weighting schemes, and to relate back to previous studies.

For purposes of interpretability and compara-

bility, we converted values of  $Q$  into ‘effective numbers’ (Jost 2006) using the following equation:

$$Q_{\text{eff}} = \frac{1}{1 - Q}. \quad (2)$$

This transformation yields the ‘effective number’ of species in the sample if all species were equally abundant and maximally distinct. Effective numbers have several ideal attributes, including the ‘doubling property,’ which states that if two communities have the same diversity  $X$  but no shared species, then their combined diversity is  $2X$  (Jost 2006). Additionally, as long as distances are ultrametric (i.e., between 0 and 1), then effective numbers can be interpreted identically and directly compared across all dimensions of diversity, including richness (Pavoine et al. 2005, Jost 2006).

We calculated richness as the number of species captured at a given station. For our index of species diversity, we standardized the distances  $d_{ij}$  to either 0 (individuals belong to the same species) or 1 (different species). In this case,  $Q$  collapses to the well-known Gini-Simpson index (Ricotta and Szeidl 2006). In the event that species are all present in equal proportions, then the Gini-Simpson index will be equal to species richness. For evenness, we calculated the relative evenness index from Jost (2010):

$$\text{RLE} = \frac{\ln(Q_{\text{Gini-Simpson}})}{\ln(S)}. \quad (3)$$

The relative evenness index is analogous to Pielou’s evenness and is bound between 0 (maximally uneven) and 1 (maximally even).

To derive functional distances, we first measured and scored 25 functional traits for all 50 species. Functional traits included continuous measures of morphology (e.g., Villéger et al. 2010), estimates of diet composition (e.g., Petchey et al. 2007, Devictor et al. 2010), and life history characteristics. As the 25 traits contained both continuous and categorical values, we calculated Gower distances (Gower 1971) using the correction from Podani (1999) to account for ordered traits. We then employed hierarchical agglomerative clustering to produce an ultrametric functional dendrogram (Petchey and Gaston 2002). To account for the sensitivity of the dendrogram to the clustering algorithm used, we employed the

approach suggested by Mouchet et al. (2008) of using multiple algorithms and choosing the one that best preserves the original, non-ultrametric distances (Mérigot et al. 2010). Finally, we extracted the ultrametric distance matrix from the dendrogram and scaled by the maximum so that all values were between 0-1 before calculating  $Q$ . (See Appendix A for a more detailed discussion of trait selection, measurement, and dendrogram reconstruction).

To derive phylogenetic distances, we constructed a gene tree as a proxy for a molecular phylogeny, using cytochrome oxidase I (*COI*) sequences. Sequence data were available on GenBank for 34 species in the dataset. We extracted, amplified, and sequenced *COI* for a further 3 species, and substituted congeneric relatives for the remaining 13 species. We aligned all sequences, including five outgroups from GenBank, using the online alignment tool MUSCLE (Edgar 2004). The aligned sequences were used to construct a maximum-likelihood gene tree using the program RAXML (v.2.2.3, Stamatakis 2006). To convert the tree to ultrametric, we estimated absolute evolutionary rates using penalized-likelihood and verified the rates using a data-driven cross-validation criterion (Sander-son 2002). Scaling by the absolute rate fixed the age of the root at 1, making the tree ultrametric. The pairwise distance matrix was extracted from the ultrametric tree and divided by the maximum so all values were between 0 and 1 before calculating  $Q$ . (See Appendix A for a detailed discussion of sequencing protocol, congener selection, and phylogeny construction.)

To test whether molecular phylogenetic data provided more information than Linnaean taxonomy, we obtained classification information for all 50 species using the latest accepted taxonomy from the Integrated Taxonomic Information System (<http://www.itis.gov>). Distances were computed as the number of nodes separating each pair of species on the hierarchy (Clarke and Warwick 1998), weighted by the proportional decrease in taxon richness at each successive level on the hierarchy (Clarke and Warwick 1999). Since these distances were already ultrametric (Pavoine et al. 2005), they were not transformed before calculating  $Q$ . With this approach, we preserve the definition of ‘taxonomic diversity’ (TD) as put forth by Shimatani

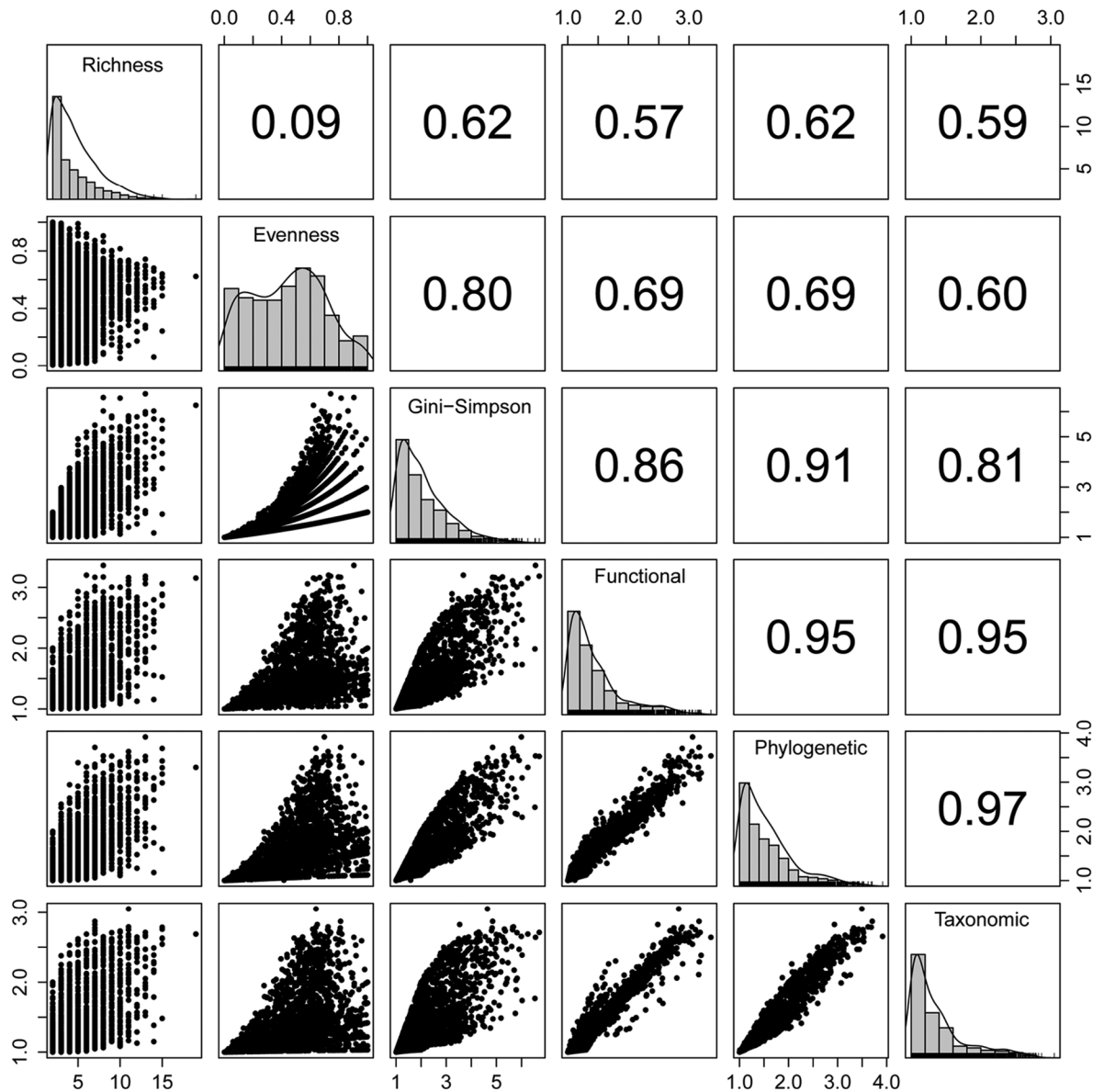


Fig. 1. Scatterplot matrix of each diversity index against the others (lower triangle), frequency histogram for a given index (diagonal), and Spearman's rank correlation coefficient (upper triangle). Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative biomass.

(2001), and note that this definition of TD is distinct from that used by Devictor et al. (2010) and Villéger et al. (2010), for example, who instead use 'taxonomic diversity' to refer to an index of species diversity (analogous to our Gini-Simpson index).

#### Statistical analysis

To explore the relationships among different indices of diversity, we calculated Spearman's rank correlation ( $r_s$ ). This index tests for a monotonic relationship between two variables but does not assume bivariate normality (Quinn and Keough 2002), a condition which was lacking between some of our variables (see Fig. 1). Values



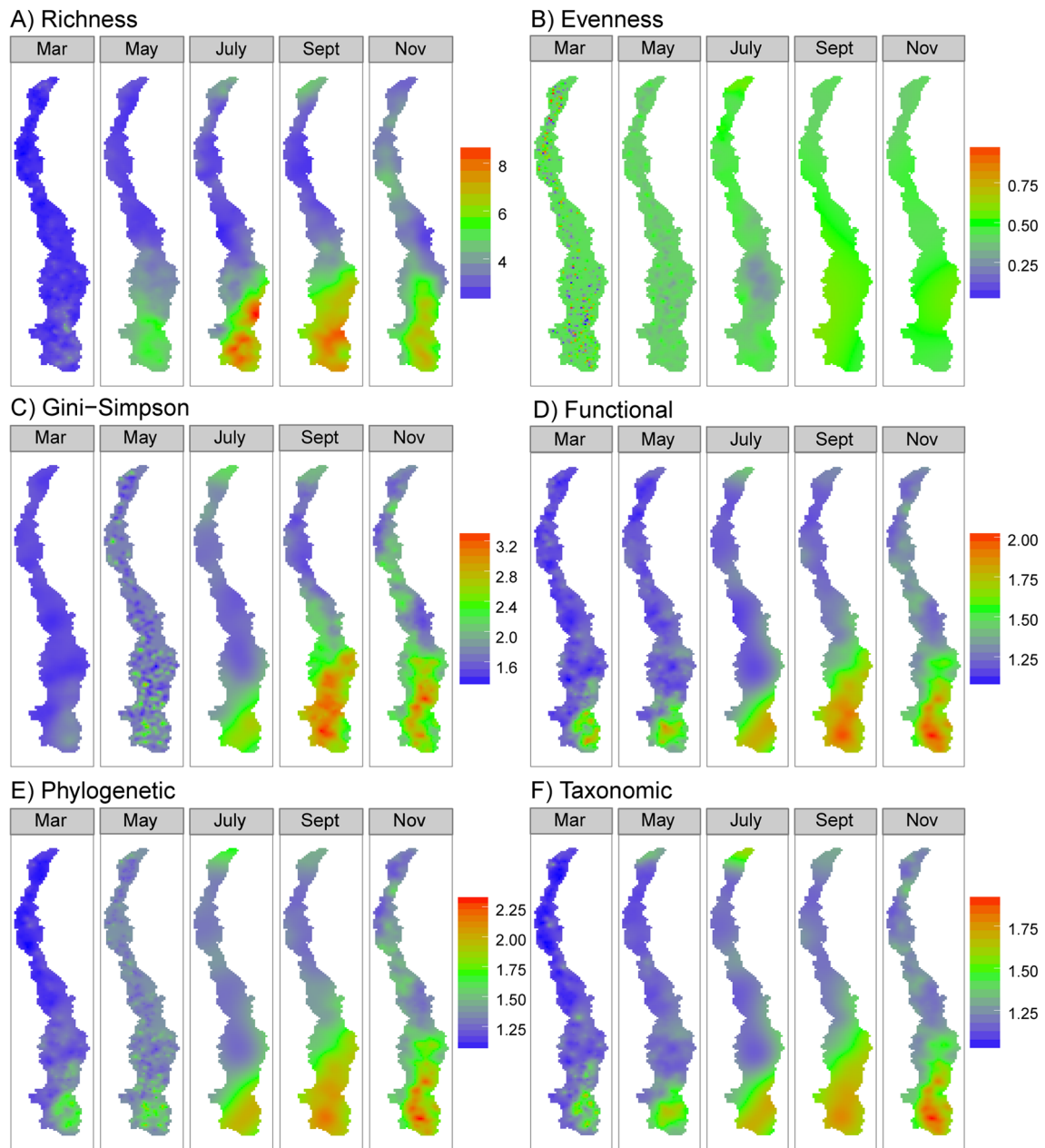


Fig. 2. Kriging interpolation of each diversity index along the mainstem of the Chesapeake Bay, for the five months of the trawl survey and across all years. Warm colors indicate high values of diversity, cool colors indicate low values. The scales for panels A and C–F are in units of effective numbers of species; the scale for panel B is units ranging from 0 (maximally uneven) to 1 (maximally even). Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative biomass.

of  $r_s$  were deemed significantly different (i.e., there is no monotonic relationship between two variables) based on the test in Best and Roberts (1975).

To investigate phylogenetic and taxonomic

signal in functional traits, we calculated matrix correlations between the functional, phylogenetic, and taxonomic distance matrices using Mantel's test. Mantel's test of matrix correlations

removes the potentially confounding effect of richness and evenness on the relationships between FD, PD, and TD, and because it is based on distances, allows for the evaluation of signal across multiple functional traits simultaneously, including those that are not continuous (Pavoine et al. 2013).

To examine spatial and intra-annual trends in the different dimensions of demersal fish diversity, we first interpolated diversity for each month of the survey using ordinary kriging. This approach accounts for the spatial structure of the response, and has been used to address similar questions in the past (e.g., Devictor et al. 2010, Safi et al. 2011). All responses were log-transformed to better meet the assumptions of normality of errors and constant variance, except for evenness, which was arcsine-square root transformed. Predicted values were then back-transformed for plotting. In addition to interpolating the raw values, we also extracted and interpolated the residuals of each index fitted against each of the others using generalized additive models (GAMS, to account for nonlinearities, see below). The plotting of interpolated residuals allowed us to better visualize potential areas of mismatch between the different indices of diversity (e.g., Safi et al. 2011). To further clarify these mismatches, we plotted line graphs of the mean local diversity for each stratum of the sampling design, i.e., the average of all tows within a given region of the Bay (see legend of Fig. 3).

To understand the drivers of diversity patterns, we fitted generalized additive models (GAMs) to each index separately. GAMs provided a general and flexible modeling framework in which the effects of continuous covariates were modeled using non-parametric smoothing functions, and categorical factors were modeled parametrically to determine their mean effect sizes (Wood 2006, Zuur et al. 2009). We evaluated multiple explanatory variables and classified them into three general components of influence: temporal factors (encompassing year and month), spatial variables (latitude and longitude), and environmental covariates (salinity, water temperature, dissolved oxygen, and water depth). The fully parameterized GAM was therefore defined as:

$$y_i = a + \alpha_1(\text{YEAR}) + \alpha_2(\text{MONTH}) + g_1(\text{LONG, LAT}) \times \text{MONTH} + g_2(\text{SAL}) + g_3(\text{TEMP}) + g_4(\text{DO}) + g_5(\text{DEPTH}) + e_i \quad (4)$$

where  $y_i$  is the calculated diversity for station  $i$ ,  $\alpha$ 's are the estimated mean effects for each level of year (YEAR) and month (MONTH), and  $g$ 's are nonparametric smoothing functions for each covariate, including salinity (SAL), temperature (TEMP), dissolved oxygen (DO), and water depth (DEPTH). We incorporated a separate longitude-latitude (LONG, LAT) smoother ( $g_1$ ) for each month to account for any potential space-time interaction in the data following Buchheister et al. (2013). Thin plate regression splines with shrinkage terms were used as the basis to smooth all covariates. The intercept,  $a$ , scales the model prediction to the appropriate level of the response because each smooth estimate ( $g$ ) is constrained to average to 0 over the entire dataset (Ciannelli et al. 2008). The residual error,  $e_i$ , was assumed to be independent and identically distributed with a mean of zero and constant variance. No predictors were sufficiently collinear to warrant dropping from the analysis (see also Buchheister et al. 2013).

This model was fitted to richness using a Poisson distribution and a log-link, while all other indices were log-transformed (except evenness which was arcsine-square root transformed) and fitted to a normal distribution. Graphical and statistical analyses indicated that differences in sampling effort (area swept) did not have discernible effects on diversity across stations and that all tows were sufficiently long to capture a representative sample of biological diversity. Therefore no offset was necessary to account for sampling effort in the GAMs (Zuur et al. 2009).

In order to assess the relative explanatory power of each component, we calculated partial deviances by sequentially removing suites of predictors from the full model (Eq. 4) corresponding to indicators of space, time, or environment, repeated this procedure for all possible permutations, averaged the deviances for all models in which a predictor appeared, and finally calculated a standard error (e.g., Schmiing et al. 2013). The partial deviances are therefore the proportion of total explained deviance of the model uniquely explained by space, time, or the

environment, accounting for the other predictors in the model. This approach is analogous to variance partitioning approaches in a linear modeling framework (Legendre and Legendre 1998), only extended to non-linear models. We performed all analyses in R (v.3.0.1, R Development Core Team 2013) using the following packages: *ape* (Paradis et al. 2004), *automap* (Hiemstra et al. 2009), *clue* (Hornik 2013), *ggplot2* (Wickham 2009), and *mgcv* (Wood 2011).

## RESULTS

### Comparing dimensions of diversity

Across all tows and dates, we found a moderate positive association between species richness and other components of diversity ( $0.57 \leq$  Spearman's rank correlation  $r_s \leq 0.62$ ; Fig. 1). Evenness (computed from relative biomass) was strongly related to the other dimensions ( $0.69 \leq r_s \leq 0.80$ , Fig. 1). Integrating both richness and evenness in the Gini-Simpson index, we found still stronger positive relationships with FD, PD, and TD ( $0.81 \leq r_s \leq 0.91$ ; Fig. 1). Using presence-absence data revealed a slightly diminished but still strong relationship between the Gini-Simpson index and FD, PD, and TD ( $0.69 \leq r_s \leq 0.87$ ; Appendix B: Fig. B2), suggesting that the relationships between these dimensions were only marginally affected by the inclusion of relative biomass. Finally, FD, PD, and TD were nearly redundant in describing demersal fish diversity in this system ( $0.95 \leq r_s \leq 0.97$ ; Fig. 1), and weighting by presence-absence did not alter this conclusion ( $0.89 \leq r_s \leq 0.92$ ; Appendix B: Fig. B2). All values of Spearman's  $r_s$  were significantly different from zero ( $P < 0.001$ ). Mantel correlations confirmed that functional distances between species were strongly conserved in phylogenetic and taxonomic distances ( $0.74 \leq$  Mantel's  $R \leq 0.87$ ). Consistent with our initial hypothesis, the strongest matrix correlation occurred between taxonomic and phylogenetic distances ( $R = 0.87$ ).

### Spatial and seasonal patterns in diversity

Despite the moderate to strong correlations among the different dimensions of fish diversity across all samples, we did identify areas and times of incongruence. Richness was highest at the mouth of the Bay during July and September,

decreased in the middle Bay, and increased again at the head of the Bay (Figs. 2A, 3A). This pattern of higher richness at the two extremes of the salinity gradient adhered to a well-established pattern along estuarine gradients (Odum 1988).

Evenness peaked early in the year (Figs. 2B, 3B), although this trend can be explained by the fact that most communities during March were composed of few species (Fig. 2A). Evenness was lowest in the middle Bay during May and July (Figs. 2B, 3B) due to the overwhelming dominance of Atlantic croaker (*Micropogonius undulatus*), and increased in this region during September and November with the migration of *M. undulatus* out of the Bay (Figs. 2B, 3B). In the upper Bay, evenness decreased slightly from July to November, tracking the increasing dominance of white perch (*Morone americana*) and the concomitant migration of euryhaline fishes, such as spot (*Leiostomus xanthurus*) and weakfish (*Cynoscion regalis*), out of the Bay at the end of the summer (Figs. 2B, 3B).

The Gini-Simpson index, our measure of species diversity that incorporated both richness and evenness, peaked in September in the lower Bay and decreased in November (Figs. 2C, 3C). This peak was again largely attributable to the migration of the biomass-dominant species, *M. undulatus*, out of the Bay after July. While composition and distribution of biomass remained fairly consistent among the remaining species during this time, the loss of such a large amount of biomass with *M. undulatus* manifested as an increase in evenness. It is for this reason that the Gini-Simpson index was lower than would be expected from species richness in the lower Bay during July, and higher than would be expected in September based on residuals from this relationship (Fig. 4A).

Functional, phylogenetic, and taxonomic diversity showed largely identical patterns. All three of these dimensions peaked through November in the lower Bay, which is later in the year than for richness (July) or Gini-Simpson diversity (September, Figs. 2D–F, 3D–F). The later peak in FD, PD, and TD was attributable to the more even distribution of biomass among functionally and evolutionarily divergent species. In July, *M. undulatus* accounted for nearly 50% of the biomass in the lower Bay. By September, 35% of the biomass was dominated by two species in

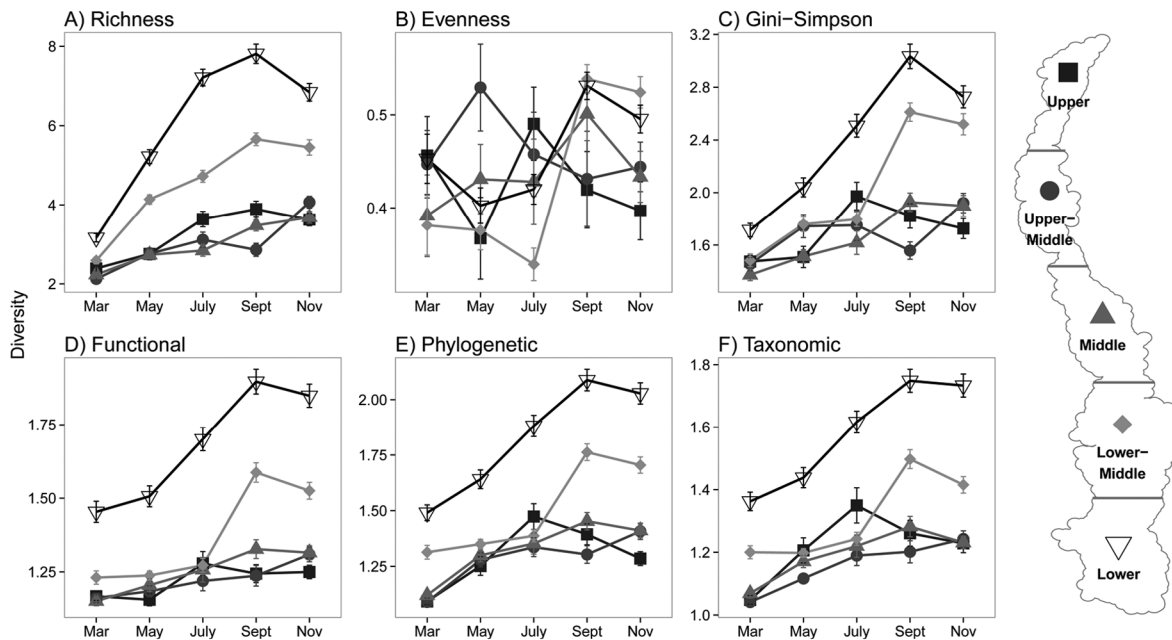


Fig. 3. Plot of mean local diversity (i.e., tow-level) for each region of the Chesapeake Bay. Regions corresponds to each of the strata used in the sampling design and capture the estuarine salinity gradient (see legend), with near marine salinity at the mouth and near freshwater at the head. The scales for panels A and C–F are in units of effective numbers of species; the scale for panel B is units ranging from 0 (maximally uneven) to 1 (maximally even). Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative biomass. Error bars are  $\pm 1$  SE.

the family Sciaenidae, *M. undulatus* and *L. xanthurus*, which are also very similar functionally (Appendix A: Fig. A2). By November, 60% of the biomass was dominated by *L. xanthurus*, summer flounder (*Paralichthys dentatus*), and clearnose skate (*Raja eglanteria*), all of which are more distant functionally and phylogenetically than the dominant species in earlier assemblages (Appendix A: Figs. A2, A3). To that end, weighting by presence-absence produced patterns that mirrored species richness (Appendix B: Fig. B7). Thus, incongruences between species-level indices of diversity and those that incorporate functional, phylogenetic, or taxonomic differences are largely driven by the distribution of biomass among divergent species. It is also important to note that the scale of FD, PD, and TD are all much lower than the Gini-Simpson index or richness, indicating that there was considerable functional, phylogenetic, and taxonomic redundancy within these assemblages, especially during the summer months (Figs. 2, 3).

There were some interesting but comparatively

minor deviations among functional, phylogenetic, and taxonomic diversity. FD was higher than expected based on PD and TD during March at the mouth of the Bay (Fig. 4B, C). This mismatch was due to spiny dogfish (*Squalus acanthias*) being more distant functionally than evolutionarily from two co-occurring elasmobranchs, smooth dogfish (*Mustelus canis*) and clearnose skate (*Raja eglanteria*) (Appendix A: Figs. A2–A4). FD was also higher than expected from TD, and to a lesser degree PD, in the lower Bay during September and throughout the Bay during November (Fig. 4B, C). This pattern was due to the large contribution to biomass by two ray species in the same genus, *Gymnura altavela* and *G. micrura*, which are two- and five-times more distant functionally than they are phylogenetically and taxonomically, respectively (Appendix A: Figs. A2–A4). Finally, FD was lower than expected from both PD and TD during May and July at the head of the Bay (Fig. 4B, C), as the three dominant species in terms of biomass at those times (*L. xanthurus*, *M. undulatus*, and *M.*

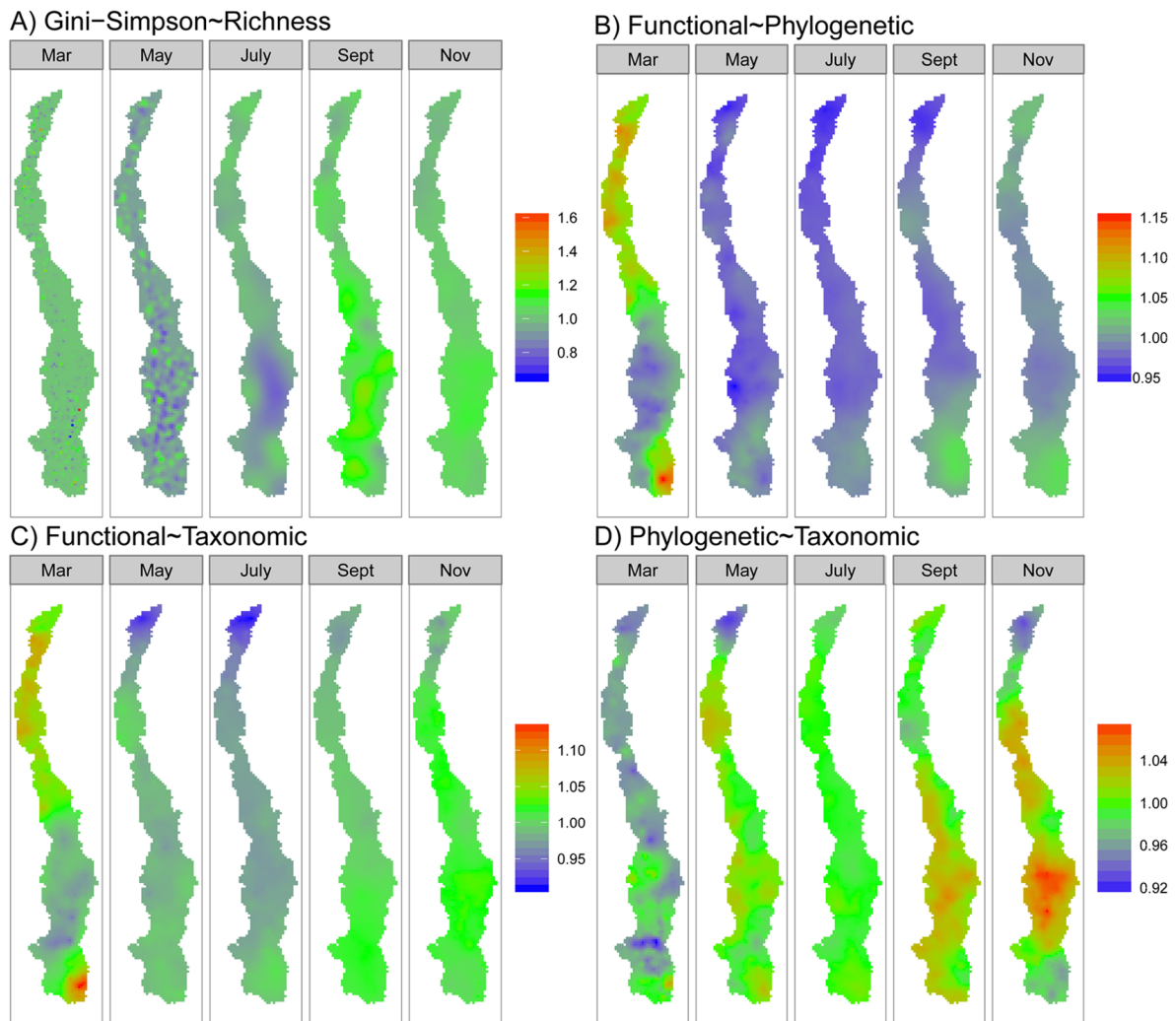


Fig. 4. Kriging interpolation of the residuals from generalized additive models of (A) Gini-Simpson diversity against richness, (B) functional diversity against phylogenetic diversity, (C) functional diversity against taxonomic diversity, and (D) phylogenetic diversity against taxonomic diversity, for each month of the trawl survey and across all years. Warm colors indicate higher than expected diversity, cool colors indicate lower than expected. All indices were weighted by relative biomass.

*americana*) are all closer functionally than they are phylogenetically or taxonomically (Appendix A: Figs. A2–A4).

Phylogenetic diversity was less than expected from TD at the head of the Bay during May (Fig. 4D), due to the presence of three species of catfishes—brown bullhead (*Ameiurus nebulosus*), channel catfish (*Ictalurus punctatus*), and white catfish (*Ictalurus catus*)—which are more distant taxonomically from gizzard shad (*Dorosoma cepedianum*) than we recovered in our phylogeny

(Appendix A: Figs. A3, A4). Finally, PD was greater than expected based on TD in the middle Bay during November (Fig. 4D). This outcome was due to the five dominant species (*L. xanthurus*, *M. undulatus*, *M. americana*, *P. dentatus*, and *C. regalis*) being more distant phylogenetically than taxonomically (Appendix A: Figs. A3, A4). The differences among FD, PD, and TD were exaggerated when calculated using presence-absence (Appendix B: Fig. B7), indicating that mismatches among these three aspects of

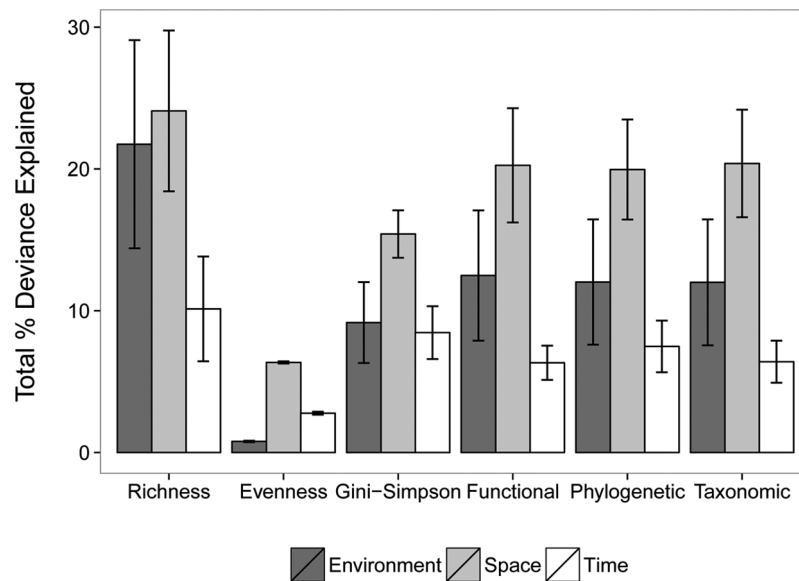


Fig. 5. The partial contributions of space, time, and environment to the total explained deviance from generalized additive models fit to each diversity index. Space was a smoothed combination of latitude and longitude by month, time was a linear combination of month and year, and environment was a smoothed combination of salinity, temperature, dissolved oxygen, and depth. Units are in percentage of total explained deviance, and error bars denote  $\pm 1$  SE on partial deviance estimates (see text for calculations). Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative biomass.

diversity in particular were driven by functional and evolutionary differences among species, and not the distribution of biomass.

Patterns in functional, phylogenetic, and taxonomic diversity weighted by relative abundance (Appendix B: Fig. B4) were muted compared to those weighted by biomass (Fig. 2). This dampening was likely because the most functionally and phylogenetically unique species in our system were elasmobranchs, which are on average much larger than teleosts and also tended to occur in relatively low abundances. Thus, their contribution to diversity was up-weighted when considering relative biomass, but down-weighted when considering relative abundance. A notable exception was FD and TD, which remained consistently high in the lower Bay throughout the year when weighted by relative abundance (Appendix B: Figs. B3, B5), as opposed to peaking in September and November when weighted by relative biomass (Figs. 2D, 3D). This result was due to tows with low abundance of *M. undulatus* that also contained species whose distribution was more even

in terms of individuals than in terms of biomass: *P. dentatus*, *R. eglanteria*, windowpane flounder (*Scophthalmus aquosus*), and spotted hake (*Urophycis regia*). (Additional results corresponding to the different weighting schemes—biomass, abundance, and presence/absence—are presented in Appendix B.)

#### Drivers of observed patterns in diversity

Using generalized additive models, we were able to explain the largest proportion of deviance for richness (56%) and smallest proportion for evenness (9.9%). Roughly the same proportion of total deviance was explained for Gini-Simpson, functional, phylogenetic, and taxonomic diversity (33, 39, 40, and 39% respectively). We divided predictors into suites of variables representing space (latitude and longitude), time (year and month), and environment (salinity, temperature, dissolved oxygen, and depth), and used a deviance partitioning approach to identify the unique contributions of each suite of predictors to diversity. Space explained approximately 24%, time approximately 10%, and environment ap-

proximately 22% of the total explained deviance in richness (Fig. 5). These values were similar in magnitude for Gini-Simpson diversity, FD, PD, and TD, indicating that space, time, and environment have approximately equivalent influence across the various aspects of diversity (Fig. 5). The one exception was evenness, where space accounted for the largest proportion of the total explained deviance at 6.4%, and environment explained the least at <1%. (Values for partial deviances corresponding to the different weighting schemes are given in Appendix B: Table B1.)

## DISCUSSION

Across ten years of survey data on Chesapeake Bay demersal fishes, we found strong agreement between measures of functional, phylogenetic, and taxonomic diversity (Fig. 1), in contrast to what has been shown for birds, mammals, and other marine fishes (Devictor et al. 2010, Mouillot et al. 2011a, Safi et al. 2011). Our results were due to strongly conserved functional traits and evolutionary distances between species within this system. This finding also supported our original hypothesis that measures of diversity derived from taxonomic hierarchy are suitable proxies for those derived from molecular phylogenies (Ricotta et al. 2012).

Incorporating data on the functional traits and evolutionary relatedness of species shifted peaks in diversity to later in the year, as compared to those based on traditional metrics of species richness and diversity (Figs. 2, 3). This result was due to the more even distribution of biomass across functionally, phylogenetically, and taxonomically distinct species, supporting our prediction that well-documented patterns of species dominance in this system would modify the interpretation of FD, PD, and TD. Finally, we found that space, time, and environment explained approximately equivalent proportions of deviance across diversity indices (Fig. 5), suggesting that these extrinsic factors do not differentially affect the various aspects of community diversity.

While we were able to identify several specific regions and months where functional, phylogenetic, and taxonomic diversity differed (Fig. 4), overall these differences were not as striking as have been shown in previous studies (Devictor et

al. 2010, Mouillot et al. 2011a, Safi et al. 2011). There are several possible reasons for this finding. First, our analysis was done on a smaller regional scale ( $10^5$  km<sup>2</sup>), whereas studies addressing similar questions have been conducted on much larger ( $10^7$  km<sup>2</sup>; Devictor et al. 2010, Mouillot et al. 2011a) or even global scales (Safi et al. 2011). A previous study showed that ‘hot-spots’ of avian species richness shifted in space depending on the scale at which the analysis was performed, which was a consequence of the rate at which species accumulated in areas of varying size (Lennon et al. 2001). Extending this idea to functional and phylogenetic diversity, increasing scale may encourage the more rapid accumulation of functionally or evolutionarily unique species. Thus, larger scales may increase the opportunity for mismatch between various dimensions of diversity (Devictor et al. 2010). However, we point out that the scale of our analysis is one that is relevant to management and conservation for this system, particularly within an ecosystem context (Latour et al. 2003).

Second, and related to the issue of scale, the number of species in our study was an order of magnitude lower than in similar investigations using French bird assemblages ( $S = 229$ ; Devictor et al. 2010) and Mediterranean fishes ( $S = 282$ ; Mouillot et al. 2011a), and two orders lower than for global mammalian assemblages ( $S = 4536$ ; Safi et al. 2011), although it is comparable to a study of FD in a community of tropical estuarine fishes ( $S = 62$ ; Villéger et al. 2010). Whereas scale may drive mismatch between different aspects of diversity through mechanisms like increased environmental heterogeneity leading to accumulation of species with contrasting phenotypes and/or evolutionary histories, a larger species pool may do so purely through a sampling effect. In other words, having more species increases the probability that an assemblage will contain a functionally or phylogenetically unique species. This idea argues for a consideration of both scale and the size of the species pool, which are not necessarily independent, when characterizing diversity. However, values of species richness in the Chesapeake Bay are comparable to similar estuarine systems across North America and Europe (Lotze et al. 2006), and other coastal ecosystems are facing threats to local diversity from pollution, climate change, and overfishing

(Sala and Knowlton 2006). Our analysis provides an example of how different dimensions of diversity might behave in similarly depauperate or increasingly species-poor systems.

Beyond issues of scale, the relatively low diversity of our study stems from several additional sources. First, the Bay can be considered a relatively harsh environment in that much of its volume is brackish, and the abiotic environment fluctuates strongly on seasonal or shorter timescales. Many fishes are not adapted to endure the osmoregulatory demands of fluctuating salinities (Day et al. 2012), and this physiological stress imposes strong spatial restrictions on local species richness. This effect is most evident in the lack of overlap in species composition between the near freshwater head of the Bay and the near marine mouth (with the exception of a few cosmopolitan species). Adaptation to varying levels of stress may also be partly responsible for the strong evolutionary conservation of traits revealed by the high Mantel correlations between our functional and phylogenetic matrices. Specifically, 9 of the 50 species in our data set belong to a single family, Sciaenidae, and members typically made up around a quarter to half of the biomass at any given station. Second, many species reside seasonally in the Bay, principally to feed, before migrating to overwintering grounds in the coastal waters of the Atlantic Ocean (Murdy and Musick 2013). As a result, local diversity in the Bay is limited temporally by active dispersal and life history. Finally, we restricted our analyses to demersal fishes to minimize potential bias caused by gear-selectivity (e.g., Villéger et al. 2010). Thus, our findings do not include pelagic or vagrant fishes, but the standardized approach of the survey sampled a large proportion of the dominant species in the Bay (Jung and Houde 2003, Buchheister et al. 2013). Consequently, our results are representative of spatial and temporal patterns in demersal fish diversity in the Chesapeake Bay.

Our analysis also provides strong evidence for the use of taxonomic distances as a proxy for functional and phylogenetic differences among species. While a recent study has proposed the use of taxonomy as a surrogate for phylogeny, they did so using plant assemblages numbering in the hundreds of species (Ricotta et al. 2012).

We demonstrate that this substitution is valid for assemblages with many fewer species. The strong relationship between TD and PD in our study is likely due to the fact that species were taxonomically diffuse, and thus evolutionary distances between species were sufficiently broad to be accurately captured by taxonomy. Had our assemblages been more closely related (e.g., within the same genus), then it is possible that taxonomic hierarchy would be too coarse to delineate the fine-scale differences revealed by molecular methods. Furthermore, our (gene tree proxy for) molecular phylogeny was very close to existing taxonomy. Phylogenetic hypotheses are constantly shifting in light of new (molecular) evidence, and taxonomy is slower to reflect these changes. In our case, evolutionary relationships suggested by phylogeny were already well-delineated by taxonomy, but in cases where phylogenetic evidence conflicts with existing information, it is up to the investigator whether to proceed with potentially dated taxonomic information, or with newer phylogenetic evidence.

Nevertheless, the use of taxonomic hierarchy over functional traits or molecular phylogeny to characterize diversity has important practical implications. Taxonomic data are easily accessible, and calculations of taxonomic diversity are relatively straightforward compared to constructing and extracting indices from molecular phylogenies. Furthermore, while molecular methods are improving in cost and efficiency, there will presumably always be organisms for which robust phylogenies are missing (Crozier et al. 2005, Ricotta et al. 2012). As a result, a common practice is to use taxonomy to resolve incomplete phylogenies (Wiens 2004). In such cases, and in cases where morphological taxonomists have delineated evolutionary differences reflecting phylogenetic signal among species, taxonomy and phylogeny are likely to lead to similar outcomes. Thus, we recommend using taxonomy when robust phylogenetic data are simply not available, when assemblages are taxonomically diffuse, and when taxonomically inferred evolutionary relationships are well-supported.

Our analysis also explicitly shows that the distribution of biomass among functionally or evolutionarily unique species can alter seasonal diversity patterns, specifically in sustaining high



FD, PD, and TD after peaks in species richness and Gini-Simpson diversity have tapered off (Figs. 2, 3; Appendix B). This finding supports the conclusions from previous analyses of groundfish diversity which showed that richness, evenness, and taxonomic differences provide unique information about community structure in the Mediterranean Sea (Mérigot et al. 2007a, 2007b, Gaertner et al. 2010). Our investigation emphasizes the interchangeability of functional or phylogenetic information with taxonomic data within this descriptive framework.

The relationship between evenness and functional and phylogenetic identity may also have implications for ecosystem processes. Theory predicts that the more even distribution of individuals or biomass among functionally complementarity species should enhance ecosystem functioning, although experimental evidence, mostly from grassland plants, is conflicted (Hillebrand et al. 2008). Moreover, recent evidence from tropical reefs and forest systems suggests that less abundant species can have traits that support unique or vulnerable functions (Mouillot et al. 2013). Reconciling the ecosystem implications of abundance- or biomass-distribution among species based on their traits or evolution-ary history is a key issue moving forward.

Our use of generalized additive models revealed relatively consistent effects of space, environment, and time across different dimensions of diversity, suggesting that these three components do not independently affect different aspects of the Chesapeake Bay demersal fish community. However, we did find a larger role for factors relating to space and environment versus those relating to time (Fig. 5). This result once again emphasizes the role of spatially conserved environmental gradients, principally salinity, in driving diversity patterns in the Bay (Buchheister et al. 2013). It also suggests that temporally dependent migration and dispersal may have a smaller influence on the same patterns. While most fishes included in our study migrate in and out of the Bay at some point during their lives, their location within the Bay (and thus their contribution to local diversity) is still largely restricted by their physiological tolerances and preferences (Wagner 1999). The strong influence of environment in mediating dispersal, and thus spatial patterns in communi-

ty diversity, is consistent with findings across many other systems (Cottenie 2005). This result is also consistent with the predictions by Stirling and Wilsey (2001) who posit that diversity indices, such as richness and evenness, will be strongly correlated when dispersal and migration are structuring communities, as is the case in the Chesapeake Bay. However, our analysis also indicated that a large proportion of deviance in diversity was independently explained by environment, suggesting that a role for non-spatially structured environmental variation exists in driving community composition in the Bay. One possible explanation lies with the extent of areas of low dissolved oxygen, which are not as spatially conserved as salinity (although do tend to occur in deep channel of the middle Bay), but which have a strong documented effect on local diversity (Buchheister et al. 2013).

Functional and phylogenetic diversity are increasingly applied in the ecological and conservation literature (Cadotte et al. 2011), yet our results suggest that their usefulness varies among systems. We show for Chesapeake Bay demersal fishes that measures of diversity incorporating taxonomic distances reflect spatial and temporal patterns as well as those that incorporate functional trait or phylogenetic information, and thus may provide a convenient and reliable proxy when phylogenetic data are redundant or unavailable. We also show that the distribution of biomass among functionally and evolutionarily divergent species can significantly alter patterns of diversity. Characterizing large-scale patterns in diversity, especially in relatively species poor systems, will be potentially more accurate and useful when it combines information on species composition, relative abundance or biomass, and existing taxonomic information before moving on to more intensive collection of functional trait and phylogenetic data.

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## SUPPLEMENTAL MATERIAL

### APPENDIX A

#### SUPPLEMENTAL METHODS

##### *Trait selection and measurement*

We assembled information on 28 functional traits relating to biomass accumulation, distribution, food acquisition, locomotion, and reproduction for the 50 most abundant fish species in the ChesMMAP survey during the study period (Table A1). The 28 traits, their functional interpretation, and selected references are provided in Table A2. After examining relationships among continuous traits using Spearman rank correlations, we omitted three traits (indicated with † in Table A2) that were strongly correlated and

represented similar ecological functions to other traits (e.g., mean and maximum biomass).

Fourteen morphoanatomical measurements (Fig. A1, Table A3) were used to derive most ecomorphological traits (see legend, Table A2). The selection of ecomorphological traits was guided largely by the work of Villéger et al. (2010) and references therein, but also by Gatz Jr. (1979a) and Mason et al. (2008). Most morphoanatomical measurements were made directly from approximately 5 individuals of each species (range: 1–7) on museum fish specimens at the Virginia Institute of Marine Science Fish Collection and the Smithsonian Museum of Natural

Table A1. Taxonomic information for all 50 species included in the analysis. Subclass was conserved with class in all cases (Actinopterygii = Neopterygii, Chondrichthyes = Elasmobranchii), and thus were omitted from the table for space.

Class	Superorder	Order	Family	Genus and species
Actinopterygii	Acanthopterygii	Perciformes	Ephippidae	<i>Chaetodipterus faber</i>
Actinopterygii	Acanthopterygii	Perciformes	Labridae	<i>Tautoga onitis</i>
Actinopterygii	Acanthopterygii	Perciformes	Carangidae	<i>Selene setapinnis</i>
Actinopterygii	Acanthopterygii	Perciformes	Carangidae	<i>Selene vomer</i>
Actinopterygii	Acanthopterygii	Perciformes	Haemulidae	<i>Orthopristis chrysoptera</i>
Actinopterygii	Acanthopterygii	Perciformes	Moronidae	<i>Morone americana</i>
Actinopterygii	Acanthopterygii	Perciformes	Moronidae	<i>Morone saxatilis</i>
Actinopterygii	Acanthopterygii	Perciformes	Sciaenidae	<i>Bairdiella chrysoura</i>
Actinopterygii	Acanthopterygii	Perciformes	Sciaenidae	<i>Cynoscion nebulosus</i>
Actinopterygii	Acanthopterygii	Perciformes	Sciaenidae	<i>Cynoscion regalis</i>
Actinopterygii	Acanthopterygii	Perciformes	Sciaenidae	<i>Larimus fasciatus</i>
Actinopterygii	Acanthopterygii	Perciformes	Sciaenidae	<i>Leiostomus xanthurus</i>
Actinopterygii	Acanthopterygii	Perciformes	Sciaenidae	<i>Menticirrhus</i> spp.
Actinopterygii	Acanthopterygii	Perciformes	Sciaenidae	<i>Micropogonias undulatus</i>
Actinopterygii	Acanthopterygii	Perciformes	Sciaenidae	<i>Pogonias cromis</i>
Actinopterygii	Acanthopterygii	Perciformes	Sciaenidae	<i>Sciaenops ocellatus</i>
Actinopterygii	Acanthopterygii	Perciformes	Serranidae	<i>Centropristis striata</i>
Actinopterygii	Acanthopterygii	Perciformes	Sparidae	<i>Archosargus probatocephalus</i>
Actinopterygii	Acanthopterygii	Perciformes	Sparidae	<i>Lagodon rhomboides</i>
Actinopterygii	Acanthopterygii	Perciformes	Sparidae	<i>Stenotomus chrysops</i>
Actinopterygii	Acanthopterygii	Perciformes	Trichiuridae	<i>Trichiurus lepturus</i>
Actinopterygii	Acanthopterygii	Perciformes	Uranoscopidae	<i>Astroscopus guttatus</i>
Actinopterygii	Acanthopterygii	Pleuronectiformes	Achiridae	<i>Trinectes maculatus</i>
Actinopterygii	Acanthopterygii	Pleuronectiformes	Paralichthyidae	<i>Etropus microstomus</i>
Actinopterygii	Acanthopterygii	Pleuronectiformes	Paralichthyidae	<i>Paralichthys dentatus</i>
Actinopterygii	Acanthopterygii	Pleuronectiformes	Scophthalmidae	<i>Scophthalmus aquosus</i>
Actinopterygii	Acanthopterygii	Scorpaeniformes	Triglidae	<i>Prionotus carolinus</i>
Actinopterygii	Acanthopterygii	Scorpaeniformes	Triglidae	<i>Prionotus evolans</i>
Actinopterygii	Acanthopterygii	Tetraodontiformes	Diodontidae	<i>Chilomycterus schoepfii</i>
Actinopterygii	Acanthopterygii	Tetraodontiformes	Tetraodontidae	<i>Sphoeroides maculatus</i>
Actinopterygii	Clupeomorpha	Clupeiformes	Clupeidae	<i>Dorosoma cepedianum</i>
Actinopterygii	Cyclosquamata	Aulopiformes	Synodontidae	<i>Synodus foetens</i>
Actinopterygii	Ostariophysi	Siluriformes	Ictaluridae	<i>Ameiurus catus</i>
Actinopterygii	Ostariophysi	Siluriformes	Ictaluridae	<i>Ameiurus nebulosus</i>
Actinopterygii	Ostariophysi	Siluriformes	Ictaluridae	<i>Ictalurus punctatus</i>
Actinopterygii	Paracanthopterygii	Batrachoidiformes	Batrachoididae	<i>Opsanus tau</i>
Actinopterygii	Paracanthopterygii	Gadiformes	Gadidae	<i>Urophycis regia</i>
Chondrichthyes	Euselachii	Carcharhiniformes	Carcharhinidae	<i>Carcharhinus plumbeus</i>
Chondrichthyes	Euselachii	Carcharhiniformes	Triakidae	<i>Mustelus canis</i>
Chondrichthyes	Euselachii	Myliobatiformes	Dasyatidae	<i>Dasyatis americana</i>
Chondrichthyes	Euselachii	Myliobatiformes	Dasyatidae	<i>Dasyatis centroura</i>
Chondrichthyes	Euselachii	Myliobatiformes	Dasyatidae	<i>Dasyatis sabina</i>
Chondrichthyes	Euselachii	Myliobatiformes	Dasyatidae	<i>Dasyatis say</i>
Chondrichthyes	Euselachii	Myliobatiformes	Gymnuridae	<i>Gymnura altavela</i>
Chondrichthyes	Euselachii	Myliobatiformes	Gymnuridae	<i>Gymnura micrura</i>
Chondrichthyes	Euselachii	Myliobatiformes	Myliobatidae	<i>Myliobatis freminvillei</i>
Chondrichthyes	Euselachii	Myliobatiformes	Rhinopteridae	<i>Rhinoptera bonasus</i>
Chondrichthyes	Euselachii	Rajiformes	Rajidae	<i>Leucoraja erinacea</i>
Chondrichthyes	Euselachii	Rajiformes	Rajidae	<i>Raja eglanteria</i>
Chondrichthyes	Euselachii	Squaliformes	Squalidae	<i>Squalus acanthias</i>

History Fish Collection using calipers with 0.1 mm precision. Exceptions include caudal fin surface area, which was measured digitally from scientific illustrations depicted in Murdy et al. (2002), and caudal fin height, which was measured on both museum specimens and from illustrations in Murdy et al. (2002). Because most morphoanatomical measurements were made on preserved museum specimens, measurements

requiring destructive manipulation of mouth or gill parts were considered, but ultimately not conducted.

#### Functional dendrogram

To calculate functional diversity, we constructed a functional dendrogram using hierarchical agglomerative clustering (Petchey and Gaston 2002), which groups species based on their



Table A2. Description and interpretation of the 28 functional traits measured for all 50 species in the analysis by type.

Trait	Definition (formula or possible values)	Functional interpretation	Explanation	Data source
Food acquisition Dentition*	Describes the type of oral teeth characterizing the anterior jaw: absent = no marginal teeth; elongate = long, slender, sharp (for holding); triangular = flat-bladed, pointed (for cutting); villiform = numerous small, needlelike; caniniform = recurved, conical with sharp points (for grasping and holding); cardiform = numerous short, fine, pointed; incisiform OR brush-like = flat-bladed, non-pointed (for removing prey from surfaces); molariform OR pavement-like = short, dull (for crushing)	Prey type(s) acquired and prey handling		Carpenter 2002; Helfman et al. 2009; McEachran and Fechhelm 1998; Murdy et al. 1997
Eye size*	Eye diameter/head depth	Prey detection (Villéger et al. 2010; adapted from Boyle and Horn 2006)		
Jaw length*	Lower jaw length/head length	Nature and size of food items captured (modified from Sibbing and Nagelkerke 2000)		
Oral gape position*	Mouth height/head depth	Feeding method in the water column (Villéger et al. 2010; adapted from Dumay et al. 2004 and Sibbing and Nagelkerke 2000)		
Diet: annelid worms Diet: arthropods and crustaceans Diet: fishes Diet: miscellaneous/other Diet: molluscs	Proportion by weight (0–1)	The prey resources most important to the consumer; defines the direct functional interactions among species	Mean proportion of stomach content weight comprised of the designated prey item as calculated from ChesMMAP data or from the literature. For ChesMMAP derived data, predator size classes and ontogenetic changes in diet were disregarded.	ChesMMAP Program 2012; Boschung and Mayden 2004; Carpenter 2002; Froese and Pauly 2012; Manooch 2007; Murdy et al. 1997; Ross 2001; and other primary sources§
Locomotion Body transversal shape*	Body depth/body width	Vertical position in the water column and hydrodynamism (Gatz 1979b)		

Table A2. Continued.

Trait	Definition (formula or possible values)	Functional interpretation	Explanation	Data source
Caudal fin aspect ratio*	(Caudal fin height) <sup>2</sup> /caudal fin surface area	Caudal fin use for propulsion and/or direction. A proxy for hydrodynamic efficiency and swimming speed (Nursall 1958)		Murdy et al. 1997 (measured digitally from scientific illustrations)
Caudal peduncle throttling*	Caudal fin height/caudal peduncle width	Caudal propulsion efficiency through reduction of drag (Villéger et al. 2010; from Webb 1984)		
Eye position*	Eye height/head depth	Vertical position in the water column (Mahon 1984; Watson and Balon 1984)		
Pectoral fin position*	Pectoral fin height/body depth	Pectoral fin use for braking and maneuverability (Mason et al. 2008)		
Relative pectoral fin length*	Pectoral fin length/standard length	Pectoral fin use for propulsion (Gatz 1979b)		
Swimming mode*	Describes the efficiency of motor performance as a function of the mechanism of propulsion, from undulatory resistance-based to oscillatory life-based propulsion respectively: 1 = ammiiform; 2 = diodontiform OR rajiform; 3 = labriform; 4 = mobuliform; 5 = tetraodontiform; 6 = anquilliform; 7 = carcharhiniform; 8 = subcarangiform; 9 = carangiform.	Adult swimming ability as speed and acceleration (Webb 1994)		Devincenti et al. 2009; Freadman 1979; Froese and Pauly 2012; Hebrank 1982; Leonard et al. 1999; Parson et al. 2011; judgement calls based on related species, morphology, and video
Biomass accumulation Length-weight growth parameter	unitless	Rate of biomass accumulation	Allometric growth parameter $b$ of the length-weight relationship, $W = a \times L^b$ , where $W$ is fish weight and $L$ is fish length.	ChesMMAP; Bister et al. 2000; Boothby and Avault 1971; Hyle 1976; Reichert 1998; Wigley et al. 2003
Life span	short (1–5 yrs), medium (6–10 yrs), long (11–20 yrs), very long (>20 yrs)	How long a species may persist in the ecosystem	For species lacking published information, life-span categories were assumed based on congeners or general scientific understanding.	Murdy et al. 1997

Table A2. Continued.

Trait	Definition (formula or possible values)	Functional interpretation	Explanation	Data source
Maximum total length†	mm	The greatest achievable size of an individual in nature and its maximum contribution to biomass in the ecosystem	Total length for teleosts and sharks, disc width for batoids.	Murdy et al. 1997
Maximum weight	g	The greatest achievable size of an individual in nature and its maximum contribution to biomass in the ecosystem	The maximum recorded mass of the species.	ChesMMAP; Murdy et al. 1997; IGFA 2012
Mean total length†	mm	The realistic average size of an individual and its average contribution to biomass in the ecosystem	Reflects the species-specific catchability of the trawl gear used for ChesMMAP.	ChesMMAP
Mean weight†	g	The realistic average size of an individual and its average contribution to biomass in the ecosystem		
Distribution Duration of residence	0–5	Annually, how long a species is present and functioning in the ecosystem	The average number of ChesMMAP trawl surveys per year in which at least one individual was found at >1 station (pooling across years, regions, and depths).	ChesMMAP
Month of maximum abundance	3, 5, 7, 9, 11	Seasonally, when a species' biomass and potential impact to ecosystem functioning is the greatest	ChesMMAP cruise month in which the estimated biomass index for the species was the highest. Biomass indices were estimated using a delta-lognormal GLM model with Month, Year, Region, and Depth as factors.	ChesMMAP
Reproduction Development mode	Oviparity, ovoviviparity, viviparity	The amount of provisioning given to eggs and maternal investment in the young	Oviparity: eggs are laid with little to no development within the mother. Ovoviviparity: eggs hatch within the female. Viviparity: unborn young are supplied nourishment through the mother.	EOL 2012; Evans 1981; FLMNH 2012; Froese and Pauly 2012; IUCN 2012; Murdy et al. 1997

Table A2. Continued.

Trait	Definition (formula or possible values)	Functional interpretation	Explanation	Data source
Length at 50% maturity	mm	Speed of maturation: lower values (as a proportion of maximum body size) are indicative of more r-selected species (on the r-K spectrum)	Length at which 50% of females are sexually mature, determined using logistic regression. Disc width was used for rays and skates, and total length for all other species.	ChesMMAP; Ballenger 2011; Boschung and Mayden 2004; Brown 1981; Nammack et al. 1985; Reichert 1998; Ross et al. 1995; Springer 1960; Struhsaker 1969; Waring 1984; White et al. 2003
Spawning location	River, estuary, ocean	Spatial spawning distribution and where young are likely to recruit	The area in which spawning occurs, not necessarily within Chesapeake Bay.	Daiber and Booth 1960; FLMNH 2012; García-Abad et al. 1999; Hildebrand and Cable 1938; Murdy et al. 1997; Packer et al. 2003; Stokes 1980; Wourms 1977
Spawning season	Spring, summer, fall, winter	Temporal spawning distribution and when young are likely to recruit	Season in which the median month of spawning/paturation occurs. Categories are spring (Mar–May), summer (Jun–Aug), fall (Sept–Nov), and winter (Dec–Feb). If the median month fell on a seasonal division, the earlier season was chosen.	Daiber and Booth 1960; FLMNH 2012; García-Abad et al. 1999; Hildebrand and Cable 1938; Murdy et al. 1997; Packer et al. 2003; Stokes 1980; Wourms 1977

*Notes:* Eleven traits were considered ecomorphological (indicated with \*), nine of which were calculated from morphoanatomical measurements described in Table A3 (“dentition” and “swimming mode” were scored as categorical and thus did not require measurements). Three traits were dropped from the final analysis due to high Spearman rank correlations (indicated with †). Traits were directly measured if source is blank. Full references in the ‘Source’ column are provided below.

§ Other primary sources are Bowman et al. 2000, Chao and Musick 1977, Cruz-Escalona et al. 2005, Ellis and Musick 2007, Hansen 1969, Hettler 1989, Johnson and Seaman 1986, Link et al. 2002, Martins et al. 2005, Ross 1989, Scharf and Schlicht 2000, Steimle and Shaheen 1999.

positions in multivariate trait space. Because several different algorithms exist for hierarchical agglomerative clustering (Legendre and Legendre 1998), we used the approach outlined by Mouchet et al. (2008) of building multiple dendrograms using different algorithms, and choosing the one that best preserves the original dissimilarities between species.

First, we computed a dissimilarity matrix between each pair of species from the functional trait data using Gower’s dissimilarity index (Gower 1971). The Gower index is an ideal distance measure because it can incorporate continuous, categorical, and ordinal trait information (after applying the correction from Podani 1999), account for missing trait values, and apply weighting to individual traits. Our trait database represents all three types of data,

and contains some missing values (e.g., the absence of morphological characters relating to the caudal fin in batoids, or skates and rays). Additionally, we chose to downweight the five traits representing different aspects of diet (percent crustaceans, percent fish, etc.), because these traits are not independent. Knowing the percent of the diet composed of molluscs provides some information about the percent of the diet composed of worms; for instance: % worms  $\leq 100 - \%$  molluscs. As a result, we weighted each diet trait by 1/5 so that collectively, they had equal weight to each of the other 24 traits in the trait database. Gower dissimilarities were calculated using the function *gowdis* in the package *FD* (Laliberté and Shipley 2011).

Second, we constructed functional dendrograms from the Gower dissimilarity matrix using

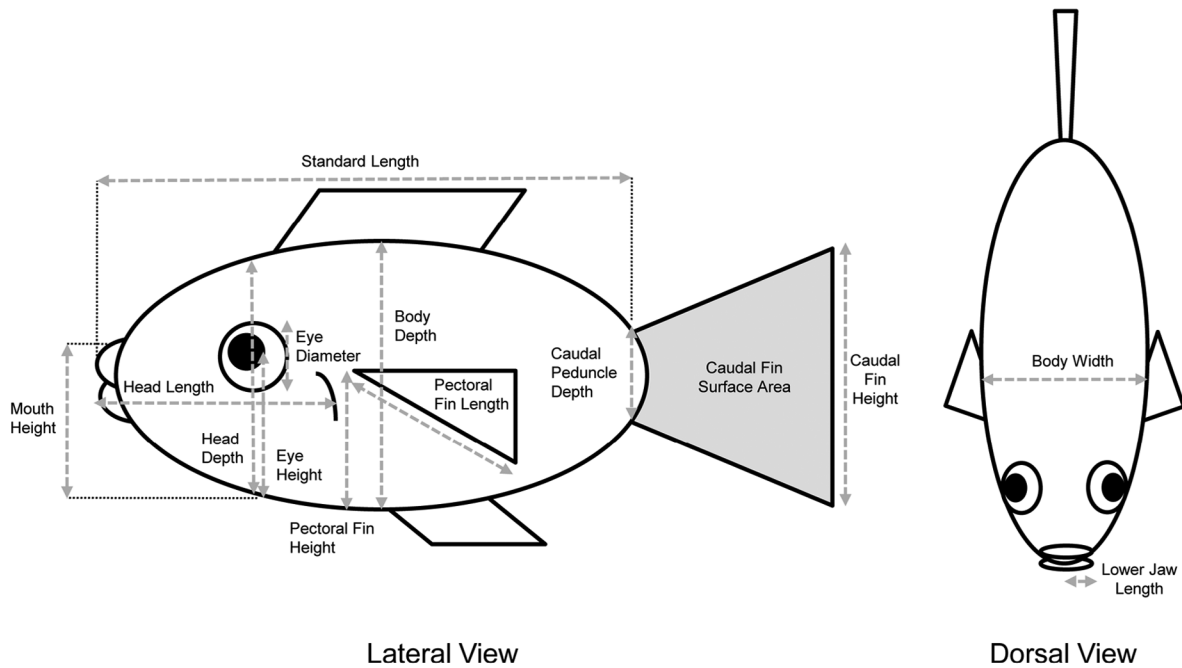


Fig. A1. Conceptual illustration of morphoanatomical measurements conducted on each fish (modified from supplementary material in Villéger et al. 2010). A full description of the measurements, and any exceptions, is provided in Table A2.

the following agglomeration methods: single linkage, complete linkage, Ward's minimum variance, unweighted arithmetic average clustering (UPGMA), and weighted arithmetic average clustering (WPGMA). We omitted two other algorithms suggested by Mouchet et al. (2008)—unweighted centroid clustering (UPGMC) and weighted pair group centroid clustering (WPGMC)—because they are not appropriate for non-metric distances. When used with Gower dissimilarities, these two methods can lead to reversals (or inversions) in the dendrogram that violate the ultrametric property (Legendre and Legendre 1998), and we required the dendrogram to be ultrametric (Pavoine et al. 2005). Dendrograms were built using the function *hclust* in the R *base* package. We also built a consensus dendrogram, which utilized all four clustering algorithms to produce a dendrogram that emphasized areas of agreement between the different algorithms (Mouchet et al. 2008). The consensus dendrogram was built using the function *cl\_consensus* in the *clue* package (Hornik 2013).

Third, we computed the ultrametric distances

from each dendrogram, in which the root-to-tip distance of the dendrogram was scaled to 1 using the function *cl\_ultrametric* in the *clue* package (Hornik 2013). We compared the original distances to the ultrametric distances using a matrix norm, the 2-norm (Mérigot et al. 2010). We then extracted the pairwise distances from the ultrametric dendrogram that best preserved the original distances (i.e., lowest 2-norm value), which was the UPGMA dendrogram, using the function *cl\_dissimilarity* in the *clue* package (Hornik 2013). Finally, we standardized the values so the maximum distance between species equaled 1 (Devictor et al. 2010). The final functional dendrogram is presented in Fig. A2 and is also provided as a Newick-format file.

#### Phylogenetic tree

To maximize data coverage, we queried GenBank to locate sequences available for vouchered specimens included in this study (Table A1). We found that cytochrome oxidase I (*COI*) was available for 34 of our 50 target species. Vouchered tissue samples were available in the Virginia Institute of Marine Science Ichthyology

Table A3. Description of morphoanatomical measurements for a typical teleost fish species, with clarifications and exceptions for flatfishes, batoids (skates and rays), and sharks.

Measurement	Description	Clarifications and exceptions
Body depth	Longest dorsal-ventral distance (excluding any fins) measured perpendicular to the anterior-posterior axis	Flatfishes: Longest dorsal-ventral distance (excluding any fins) measured relative to the fish's orientation lying on sediment (technically equivalent to body width on a "standard" teleost fish).
Body width	Longest lateral width of the fish (from left lateral side to right lateral side)	Flatfishes: Longest width of the fish as it lies on the sediment (technically equivalent to body depth on a "standard" teleost). Batoids: Lateral distance between wing tips (i.e. disc width).
Caudal fin height	Widest dorso-ventral distance of the caudal fin while in a natural position	Batoids and <i>Trichiurus lepturus</i> : Coded as not available (NA); species do not have a true caudal fin.
Caudal fin surface area	Surface area of the caudal fin	
Caudal peduncle depth	Shortest dorso-ventral distance at the caudal peduncle (teleosts) or precaudal notch (sharks)	
Eye diameter	Diameter of the eye measured vertically along the head depth axis	None
Eye height	Distance between the center of the eye to the bottom of the head	Flatfishes: Distance from the center of the non-migrating eye to the sediment side of the fish.
Head depth	Dorso-ventral distance measured through the center of the eye	Batoids: Dorso-ventral distance measured through the eye from the top of the eye to the bottom of the head.
Head length	Distance from snout to posterior end of the operculum, measured along the antero-posterior axis	Batoids and sharks: Distance from the snout to the anterior most gill slit, measured along the antero-posterior axis.
Lower jaw length	Distance from the middle, anterior point of the lower jaw (i.e. dentary in teleosts) to the corner of the mouth (the "end" of the lower jaw complex; i.e. retroarticular in teleosts)	None
Mouth height	Distance from the top of the mouth (closed) to the bottom of the head along the head depth axis	Batoids and sharks: Fixed at zero; mouth is completely inferior.
Pectoral fin height	Dorso-ventral distance from the dorsal most point of the pectoral fin insertion to the ventral side	Batoids and sharks: Fixed at zero. <i>Trinectes maculatus</i> : Coded as NA; pectoral fin is completely reduced.
Pectoral fin length	Longest straight-line distance from the dorsal pectoral fin insertion to the tip of the pectoral fin	Batoids: Distance from the wing tip to the edge of the body cavity, measured along the Body Width axis. Sharks: Straight-line distance measured from the medial, ventral insertion of the pectoral fin to its tip. <i>Trinectes maculatus</i> : Coded as NA; pectoral fin is completely reduced.
Standard length	Straight-line distance from the snout to the posterior end of the hypural bone	Batoids: Measured from the snout to the posterior insertion of the pelvic fin. Sharks: Measured from the snout to the precaudal notch.

Notes: Flatfishes include *Etropus microstomus*, *Paralichthys dentatus*, *Scophthalmus aquosus*, and *Trinectes maculatus*. Batoids include *Dasyatis americana*, *D. centroura*, *D. sabina*, *D. say*, *Gymnura altavela*, *G. micrura*, *Myliobatis freminvillei*, *Rhinoptera bonasus*, *Raja erinacea*, and *R. eglanteria*. Sharks include *Carcharhinus plumbeus*, *Mustelus canis*, and *Squalus acanthias*.

Collection for three of the missing species (*Urophycis regia*, *Astroscopus guttatus*, and *Etropus microstomus*). For the 13 species for which both tissue samples and sequence data were unavailable, we substituted COI sequences for closely related congeners (indicated with an asterisk in Table A4). Only one congener was unavailable for *Larimus fasciatus*, in which case we substituted

*Cynoscion nebulosus* based on the phylogeny of Sasaki (1989). In addition to the 50 species, we obtained 5 sequences to serve as outgroup taxa (indicated with a dagger in Table A4). The outgroup taxa were a mixture of Myxiniformes and Pertomyzontiformes, which are basal to Chondrichthyes, and included: *Caspiomyzon wagneri*, *Eudontomyzon lanceolata*, *Ichthyomyzon bdelli-*

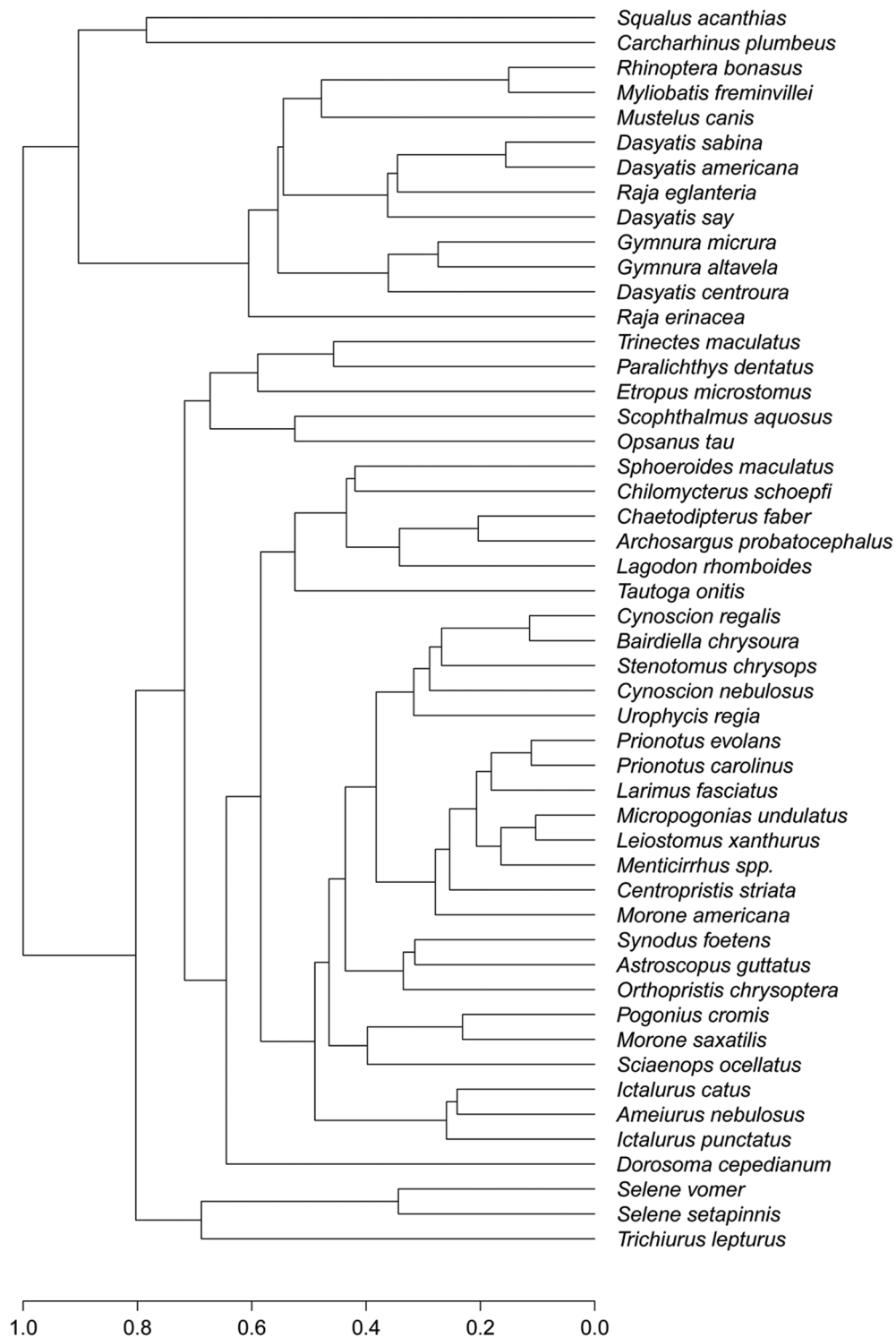


Fig. A2. The final ultrametric functional dendrogram obtained using hierarchical agglomerative clustering (UPGMA).

Table A4. GenBank accession numbers for all 50 species used in the study.

Taxon	GenBank accession no.	Congener	Congener accession no.
<i>Ameiurus nebulosus</i>	HQ557164.1		
<i>Archosargus probatocephalus</i>	HQ024929.1		
<i>Bairdiella chrysoura</i>	GU225147.1		
<i>Carcharhinus plumbeus</i>	HQ171652.1		
<i>Centropristis striata</i>	JN021294.1		
<i>Chaetodipterus faber</i>	FJ583016.1		
<i>Cynoscion nebulosus</i>	JN021296.1		
<i>Cynoscion regalis</i>	EU180145.1		
<i>Dasyatis sabina</i>	JN025277.1		
<i>Dorosoma cepedianum</i>	EU524566.1		
<i>Gymnura micrura</i>	GU225294.1		
<i>Ictalurus punctatus</i>	EU524676.1		
<i>Lagodon rhomboides</i>	HQ557326.1		
<i>Leiostomus xanthurus</i>	HQ024956.1		
<i>Menticirrhus americanus</i>	EU074466.1		
<i>Micropogonias undulatus</i>	HQ024968.1		
<i>Morone americana</i>	HQ024972.1		
<i>Morone saxatilis</i>	HQ024976.1		
<i>Mustelus canis</i>	FJ519630.1		
<i>Orthopristis chrysoptera</i>	GU225422.1		
<i>Paralichthys dentatus</i>	GU440447.1		
<i>Pogonias cromis</i>	EU752167.1		
<i>Raja eglanteria</i>	JF895098.1		
<i>Raja erinacea</i>	JF894905.1		
<i>Sciaenops ocellatus</i>	HQ025012.1		
<i>Scopthalmus aquosus</i>	EU752185.1		
<i>Selene setapinnis</i>	GU225036.1		
<i>Selene vomer</i>	FJ584093.1		
<i>Squalus acanthias</i>	EF539285.1		
<i>Stenotomus chrysops</i>	HQ025017.1		
<i>Synodus foetens</i>	FJ918940.1		
<i>Tautoga onitis</i>	JN313932.1		
<i>Trichiurus lepturus</i>	FJ347953.1		
<i>Trinectes maculatus</i>	JN028438.1		
<i>Ameiurus catus</i> *	...	<i>Ameiurus nebulosus</i>	HQ557164.1
<i>Chilomycterus schoepfi</i> *	...	<i>Chilomycterus antillarum</i>	FJ583138.1
<i>Dasyatis americana</i> *	...	<i>Dasyatis sabina</i>	JN025277.1
<i>Dasyatis centroura</i> *	...	<i>Dasyatis sabina</i>	JN025277.1
<i>Dasyatis say</i> *	...	<i>Dasyatis sabina</i>	JN025277.1
<i>Gymnura altevela</i> *	...	<i>Gymnura micrura</i>	GU225294.1
<i>Larimus fasciatus</i> *	...	<i>Cynoscion nebulosus</i>	JN021296.1
<i>Myliobatus freminvillei</i> *	...	<i>Myliobatus goodei</i>	EU074489.1
<i>Opsanus tau</i> *	...	<i>Opsanus beta</i>	GU225418.1
<i>Prionotus carolinus</i> *	...	<i>Prionotus ophyras</i>	FJ583924.1
<i>Prionotus evolans</i> *	...	<i>Prionotus ophyras</i>	FJ583924.1
<i>Rhinoptera bonasus</i> *	...	<i>Rhinoptera javanica</i>	DQ108133.1
<i>Sphoeroides maculatus</i> *	...	<i>Sphoeroides pachygaster</i>	EU074598.1
<i>Caspiomyzon wagneri</i> †	HQ579126.1		
<i>Eudontomyzon lanceolata</i> †	HQ579127.1		
<i>Ichthyomyzon bdellium</i> †	JN026862.1		
<i>Lampetra geminis</i> †	JN028424.1		
<i>Petromyzon marinus</i> †	EU524273.1		

\* Species replaced by a congeneric relative.

† Species that served as an outgroup.

*um*, *Lampetra geminis*, and *Petromyzon marinus*.

We extracted total genomic DNA from vouchered tissue plugs for *U. regia*, *A. guttatus*, and *E. microstomus* using QIAGEN's DNAEasy tissue kit. We completed PCR amplification using universal primers given in (Folmer et al. 1994). PCR conditions were as follows: an initial 4 minute denaturation at 94°C, followed by 45

cycles of 94°C for 1 min, 45°C for 1 min, and 72°C for 1 min, with a final extension at 72°C for 4 min. We cleaned up successfully amplified products using the QIAquick PCR Purification kit and eluted to a final volume of 25 µl. We used an ABI Sequencing Reaction Protocol and sequenced amplified COI in both directions on an Applied Biosystems 3130xl ABI Prism Genetic Analyzer



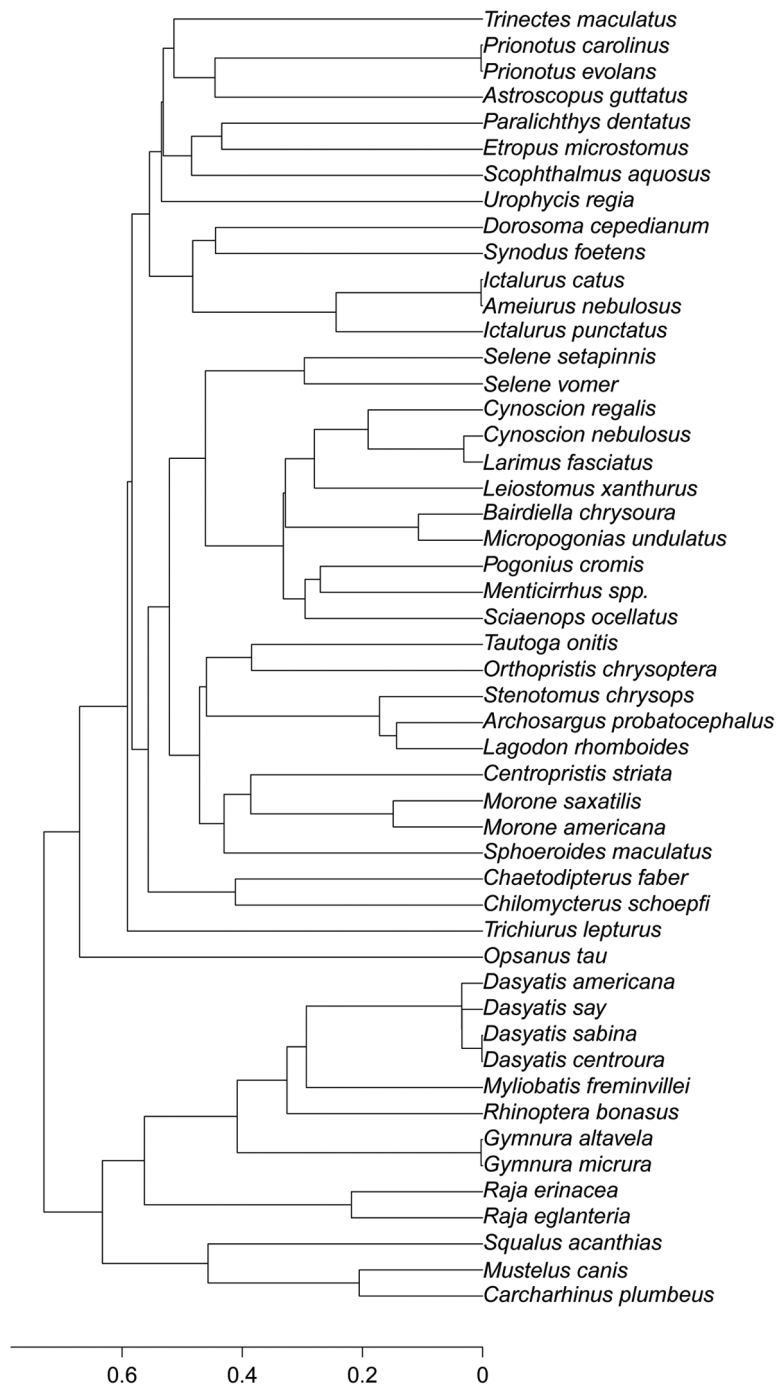


Fig. A3. The final ultrametric phylogenetic tree obtained using maximum-likelihood estimation.

DNA sequencer.

We aligned sequences (including outgroups) using the online alignment tool MUSCLE (Multiple Sequence Comparison by Log-Expectation;

Edgar 2004) with default settings, and adjusted alignments by eye. We used the aligned sequences to construct a maximum-likelihood gene tree using the program RAxML (v.2.2.3, Stamatakis

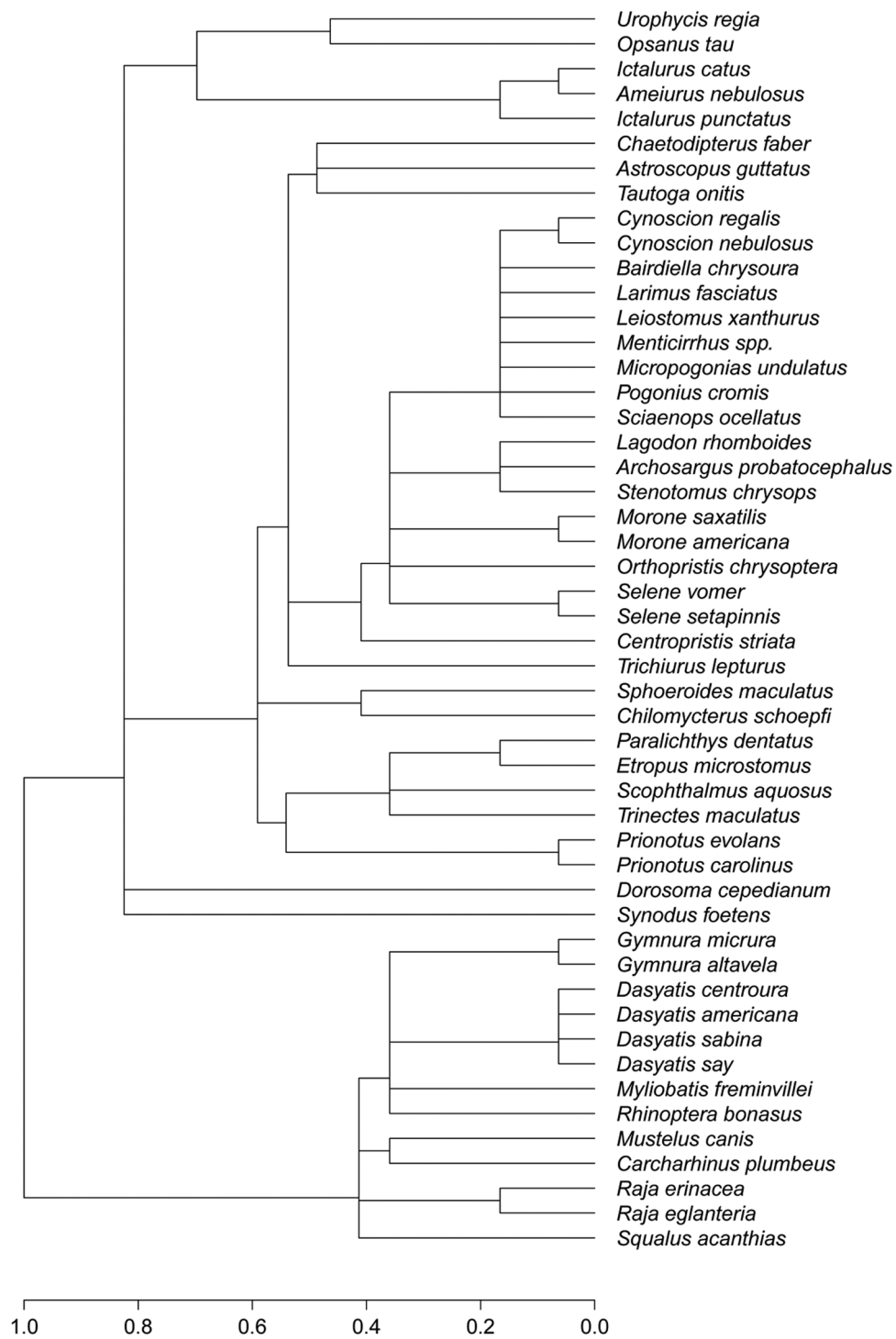


Fig. A4. The final taxonomic tree obtained using methods in Clarke and Warwick (1998).

2006). This program searched for the tree with the best likelihood scores from 200 random maximum parsimony start trees, with GAMMA+P-Invar model of rate heterogeneity and the ML estimate of the alpha-parameter. Node supports were obtained from 999 bootstrapped trees using the rapid hill-climbing algorithm. The tree was rooted using the five outgroups, and we used the gene tree as a proxy for phylogenetic distance among all non-outgroup species.

To convert the tree to ultrametric, we used the function *chronopl* in the *ape* package (Paradis et al. 2004), which estimated divergence times using the penalized likelihood algorithm; lambda (the smoothing parameter) was determined through a data-driven cross-validation procedure (Sander-son 2002). We rooted the ultrametric tree, pruned the outgroups, extracted the cophenetic distance matrix from the ultrametric tree, and standardized the values so the maximum distance between species equaled 1. The final phylogenetic

tree is presented in Fig. A3 and is also provided as a Newick-format file.

#### Taxonomic tree

We first obtained classification information for all 50 species using the latest accepted taxonomy from the Integrated Taxonomic Information System (<http://www.itis.gov>), which are presented in Table A1. The taxonomic tree was constructed from this classification table using the function *as.phylo* in the *ape* package (Paradis et al. 2004). Ultrametric distances were computed as the number of nodes separating each pair of species on the hierarchy (Clarke and Warwick 1998), weighted by the proportional decrease in taxon richness at each successive level on the hierarchy (Clarke and Warwick 1999). We obtained the distances using the function *taxa2dist* with the argument *varstep = TRUE* in the *vegan* package (Oksanen et al. 2013). The final taxonomic tree is presented in Fig. A4 and is also provided as a Newick-format file.

## APPENDIX B

### SUPPLEMENTAL RESULTS

#### Expanded analyses using abundance- and presence/absence-weighted indices

We generated scatterplot matrices to explore the associations between diversity indices—richness, evenness, Gini-Simpson, functional, phylogenetic, and taxonomic diversity—weighted by relative abundance (Fig. B1) and presence/absence (Fig. B2). There were overall weaker associations between components of diversity weighted by relative abundance (Fig. B1) compared to relative biomass (Fig. 1, main text), as indicated by Spearman's rank correlation coefficient ( $r_s$ ). As noted in the main text, this result was likely due to rare but large species driving stronger dominance in terms of biomass than in terms of abundance. However, we emphasize that functional, phylogenetic, and taxonomic indices were all still highly associated ( $0.92 \leq r_s \leq 0.97$ ; Fig. B1), with the strongest relationship again occurring between phylogenetic and taxonomic diversity ( $r_s = 0.97$ ). We also note that, when weighting by presence/absence, the Gini-Simpson index collapses to species richness, hence the perfect correlation (Fig. B2).

We mapped each diversity index weighted by

relative abundance (Fig. B3) and presence/absence (Fig. B4), and constructed corresponding line graphs of mean local diversity by month and region of the Bay (Figs. B5, B6). As noted in the main text, indices weighted by abundance show largely congruent patterns with richness, with the exception of abundance-weighted functional diversity peaking in March as well as November, and taxonomic diversity remaining relatively high throughout the year in the lower Bay (Figs. B3, B5). Again, weighting by presence/absence showed patterns nearly identical to richness (Fig. B4), indicating that mismatches identified in the main text were the function of uneven distribution of biomass (Fig. 2, main text).

We also mapped the residuals of all pairwise combinations of each index against the other, fitted using generalized additive models (GAMs). Combinations of biomass-weighted indices are given in Figs. B7–B9; we note a subset of this figure is represented in Fig. 4 in the main text. Abundance-weighted indices are given in Figs. B10–B12, and presence/absence-weighted indices are given in Figs. B13–B15.

Finally, we applied a deviance partitioning approach to determine the relative contributions

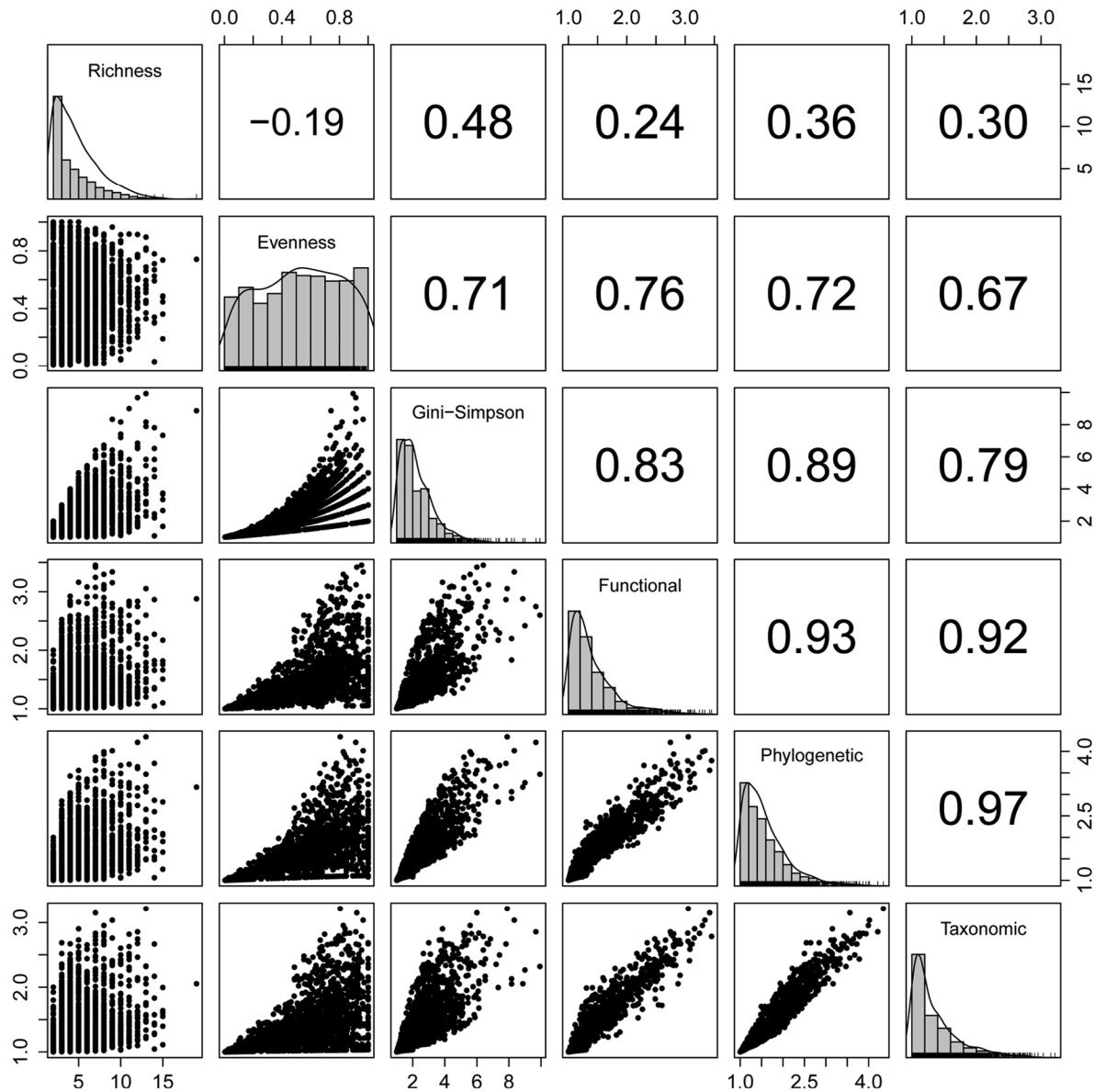


Fig. B1. Scatterplot matrix of each diversity index against the others (lower triangle), frequency histogram for a given index (diagonal), and Spearman's rank correlation coefficient (upper triangle). Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative abundance.

of space, time, and the environment in driving patterns in diversity. Partial deviances and their standard errors are given for all indices and weighting approaches in Table B1. We also

provide barplots of the partial deviances for abundance-weighted (Fig. B16) and presence/absence-weighted indices (Fig. B17) for comparisons with Fig. 5 in the main text.

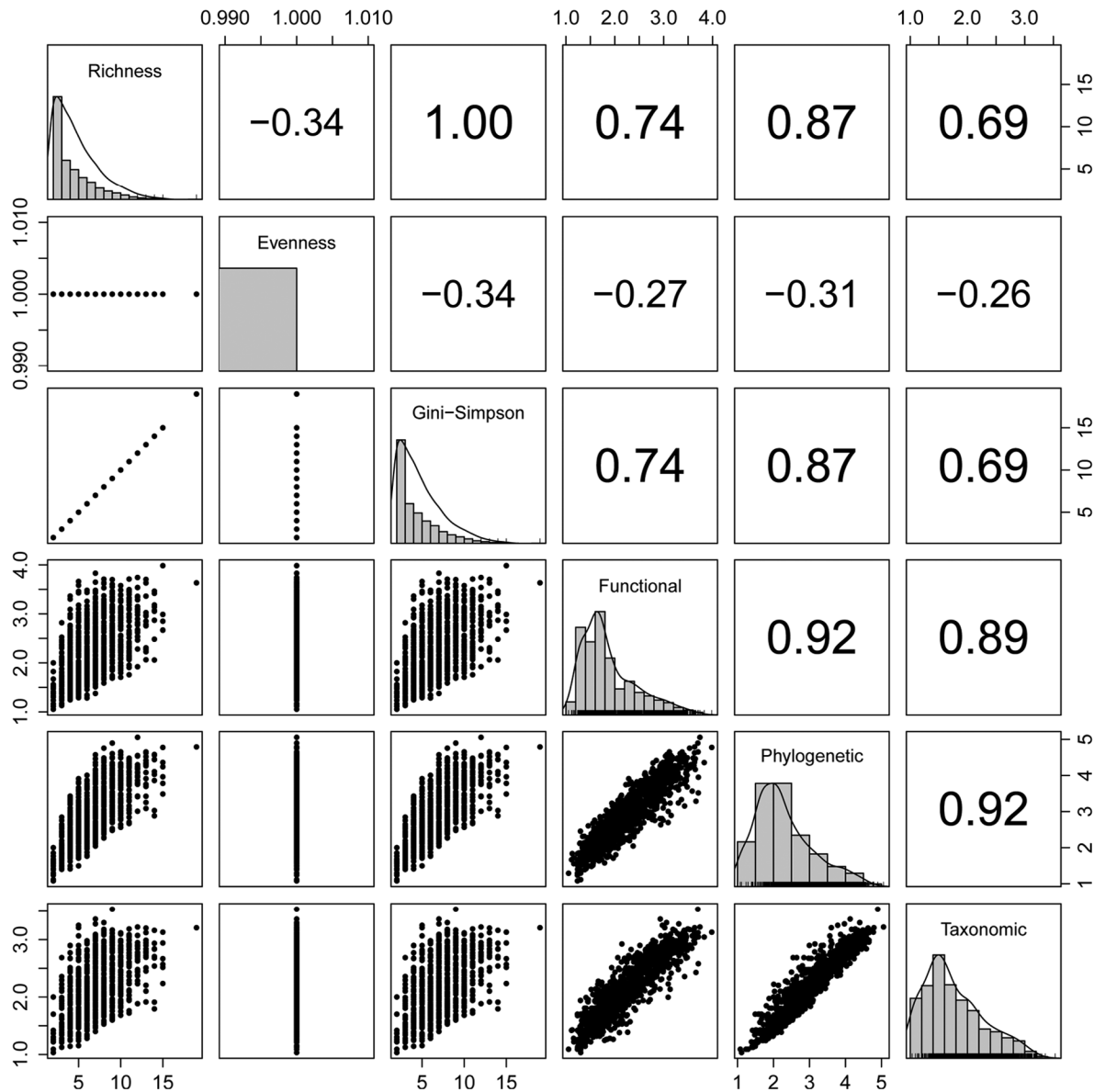


Fig. B2. Scatterplot matrix of each diversity index against the others (lower triangle), frequency histogram for a given index (diagonal), and Spearman's rank correlation coefficient (upper triangle). Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by presence/absence. In this case, the Gini-Simpson index collapses to richness ( $r_s = 1$ ).

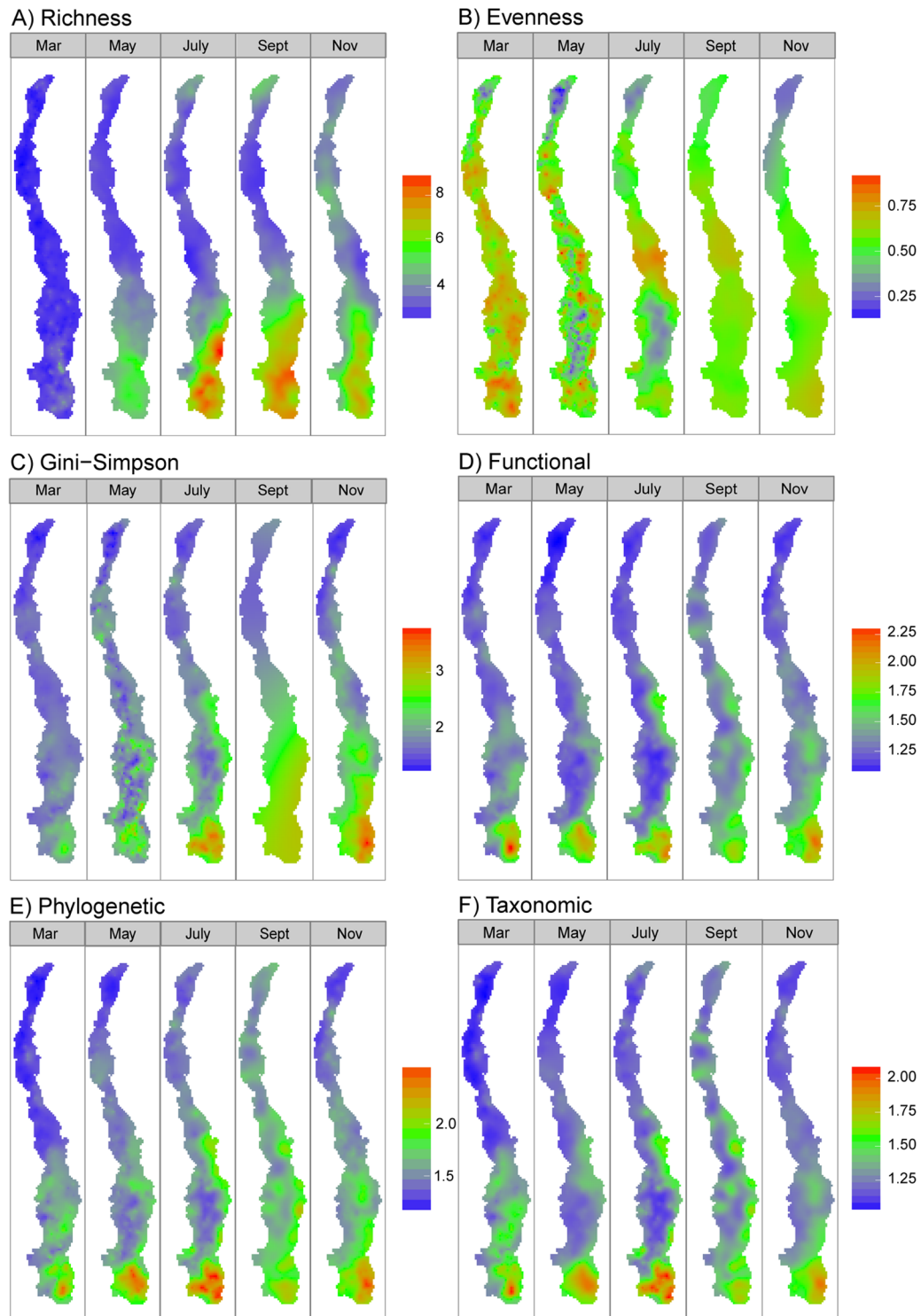


Fig. B3. Kriging interpolation of each diversity index along the mainstem of the Chesapeake Bay, for the five months of the trawl survey and across all years. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative abundance. Interpretation given in legend of Fig. 2, main text.

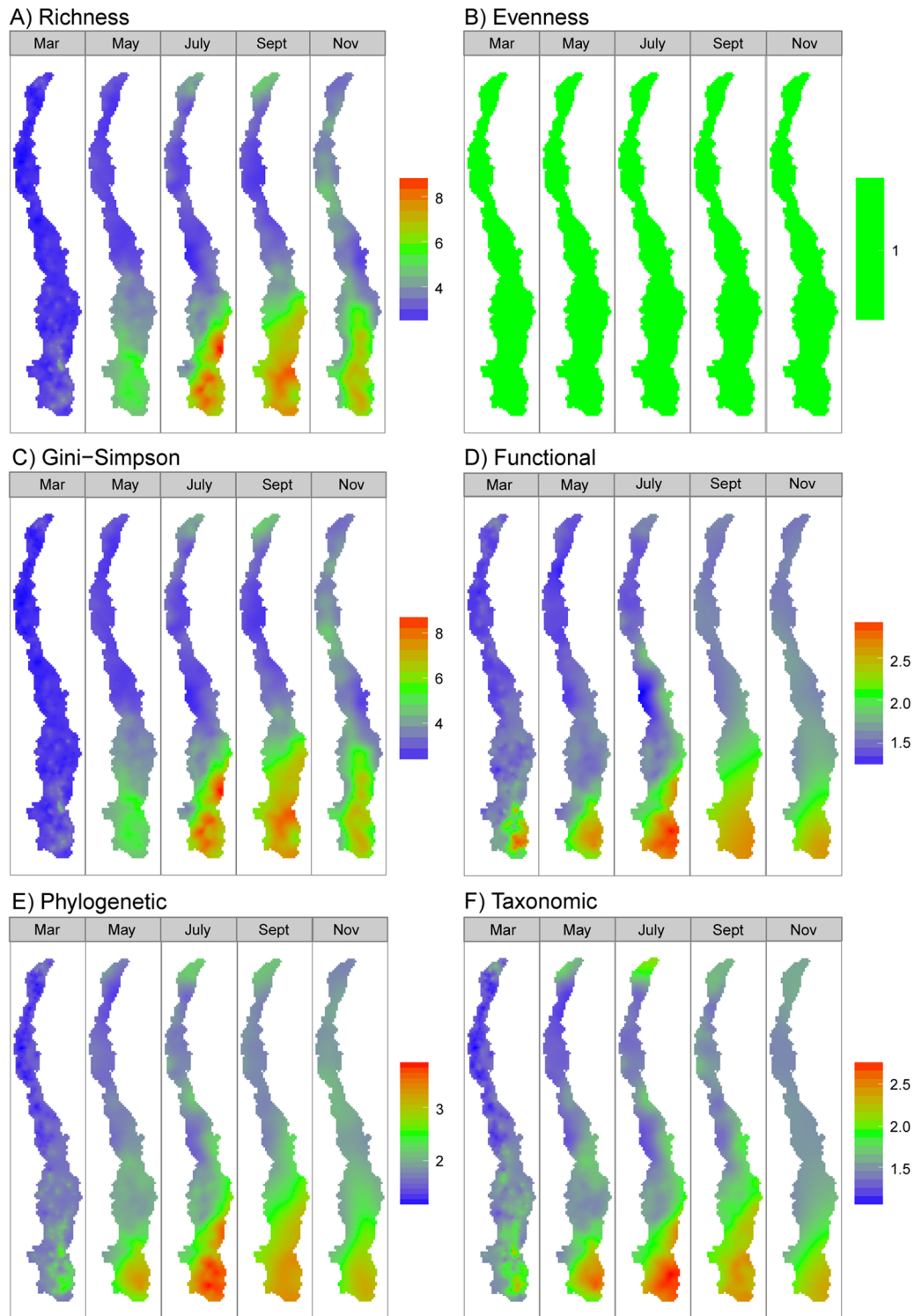


Fig. B4. Kriging interpolation of each index of diversity along the mainstem of the Chesapeake Bay, across the five months of the trawl survey and across all years. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by presence/absence. In this case, values of evenness collapse to 1. Interpretation given in legend of Fig. 2, main text.

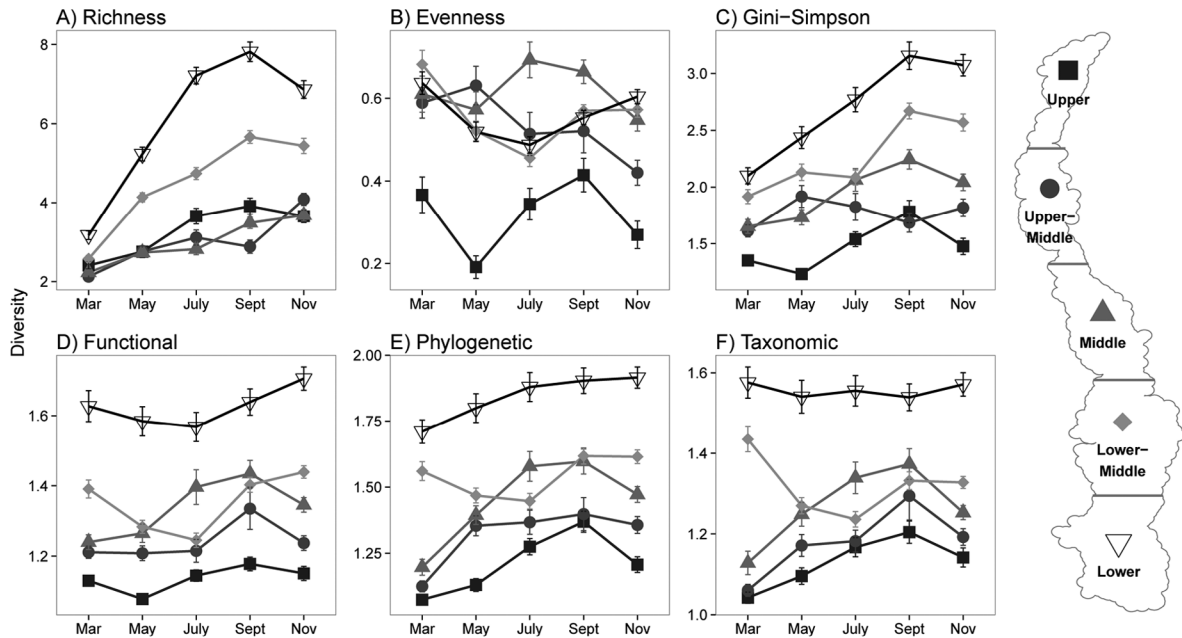


Fig. B5. Line graphs of mean local (tow-level) diversity for each region of the Chesapeake Bay by month, across all years of the survey. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative abundance. Error bars are  $\pm 1$  SE. Interpretation given in the legend of Fig. 3, main text.

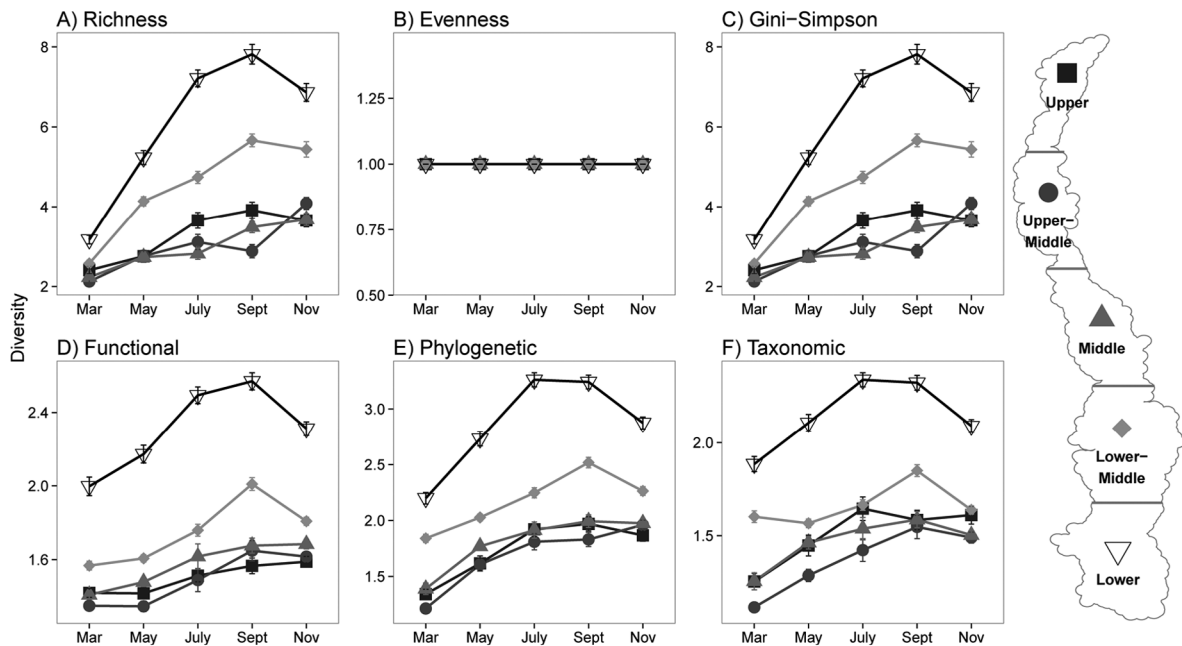


Fig. B6. Line graphs of mean local (tow-level) diversity for each region of the Chesapeake Bay by month, across all years of the survey. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by presence/absence; in this case, values of evenness collapse to 1. Error bars are  $\pm 1$  SE. Interpretation given in the legend of Fig. 3, main text.



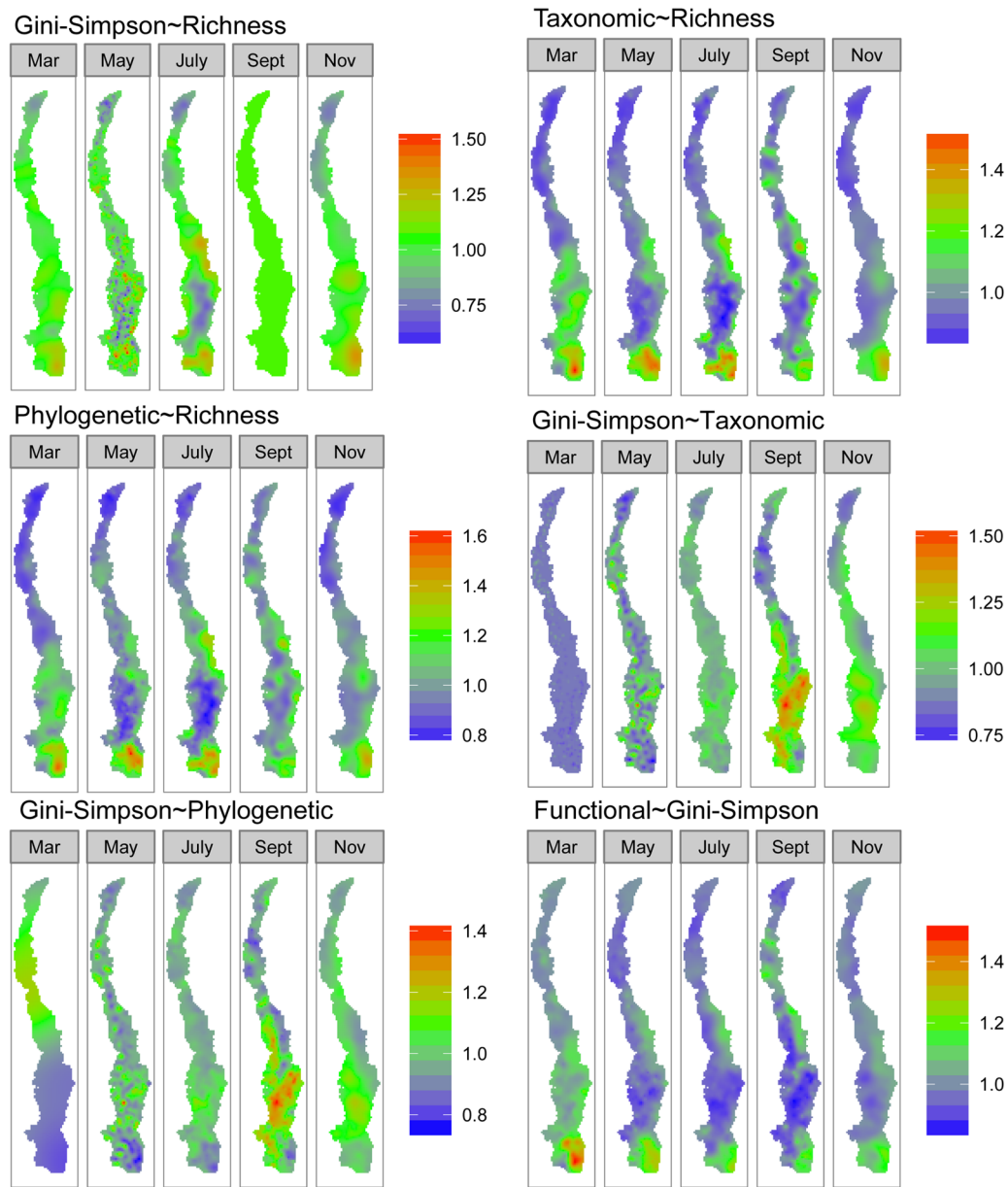


Fig. B7. Kriging interpolation of the residuals from generalized additive models of all pairwise combinations of diversity indices, for each month of the trawl survey and across all years. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative biomass. Figures were broken up for space restrictions. Interpretation given in the legend of Fig. 4, main text.

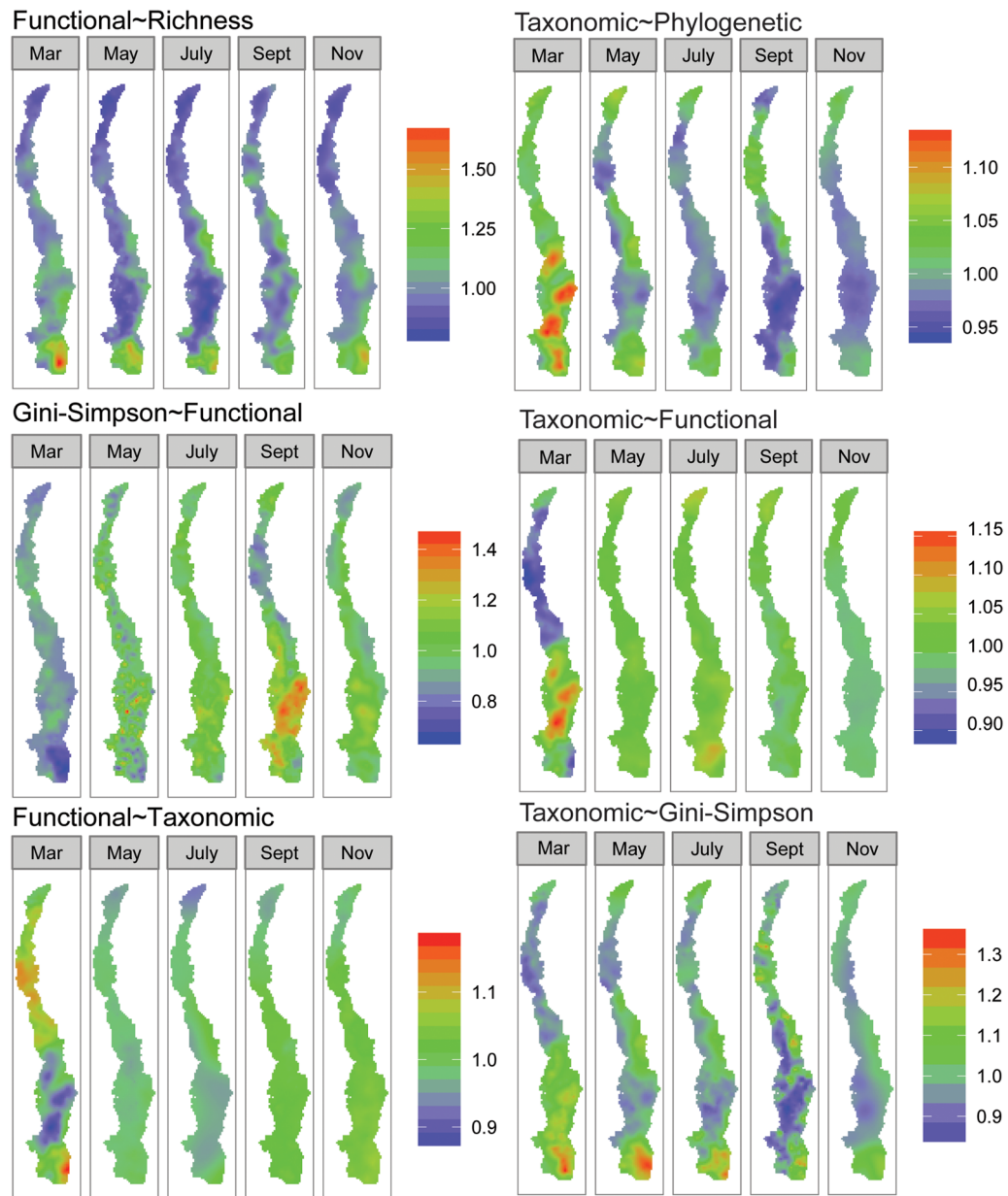


Fig. B8. Kriging interpolation of the residuals from generalized additive models of all pairwise combinations of diversity indices, for each month of the trawl survey and across all years. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative biomass. Figures were broken up for space restrictions. Interpretation given in the legend of Fig. 4, main text.

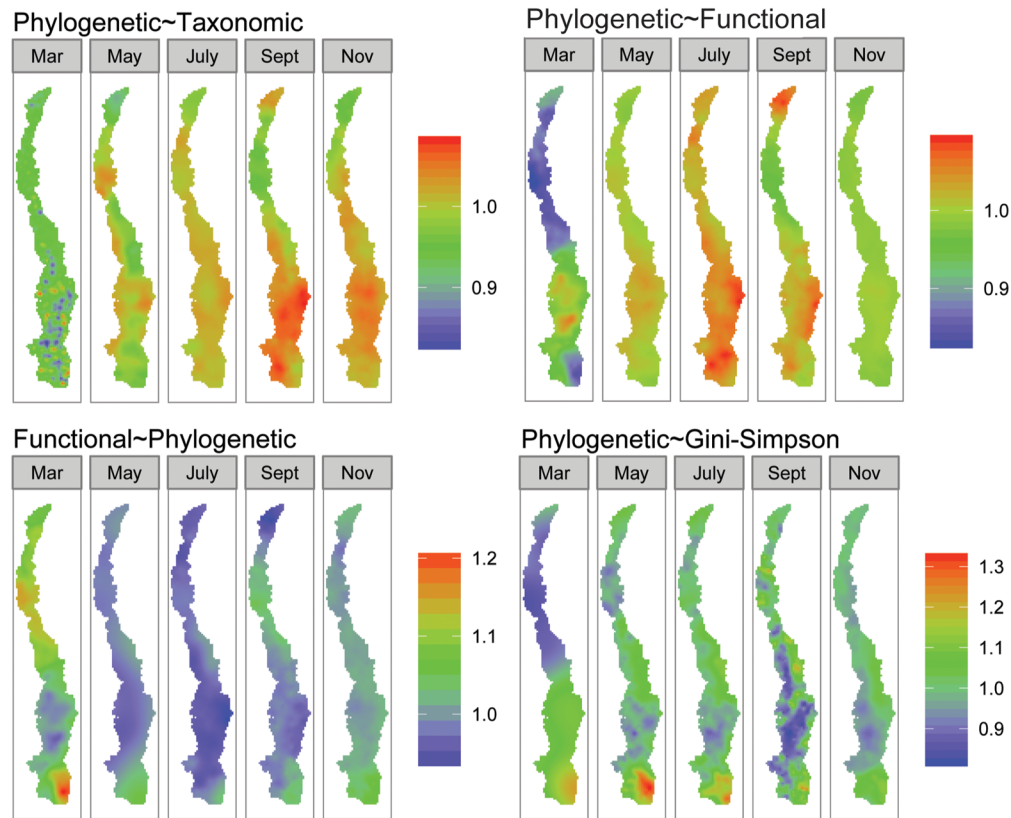


Fig. B9. Kriging interpolation of the residuals from generalized additive models of all pairwise combinations of diversity indices, for each month of the trawl survey and across all years. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative biomass. Figures were broken up for space restrictions. Interpretation given in the legend of Fig. 4, main text.

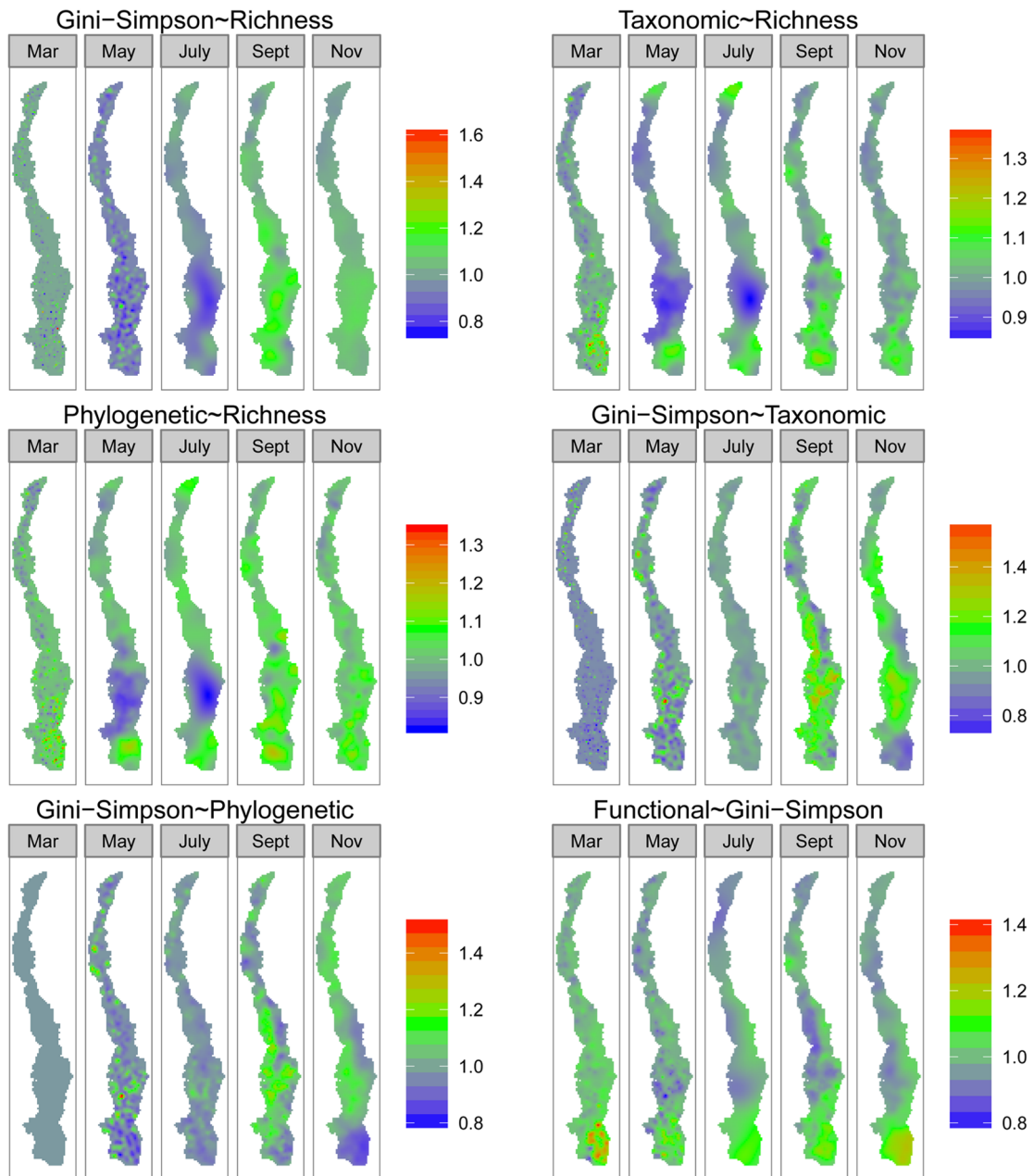


Fig. B10. Kriging interpolation of the residuals from generalized additive models of all pairwise combinations of diversity indices, for each month of the trawl survey and across all years. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative abundance. Figures were broken up for space restrictions. Interpretation given in the legend of Fig. 4, main text.

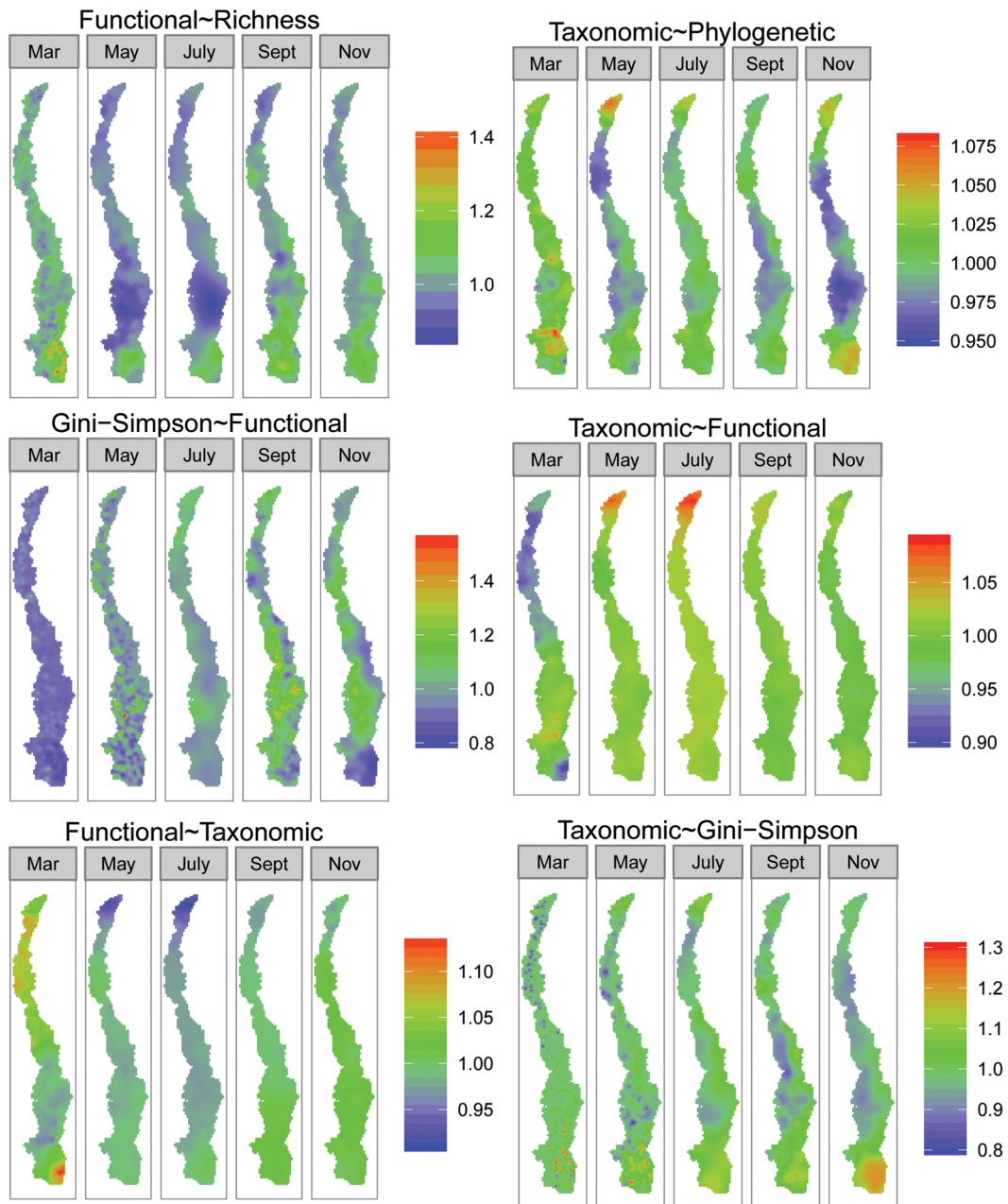


Fig. B11. Kriging interpolation of the residuals from generalized additive models of all pairwise combinations of diversity indices, for each month of the trawl survey and across all years. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative abundance. Figures were broken up for space restrictions. Interpretation given in the legend of Fig. 4, main text.

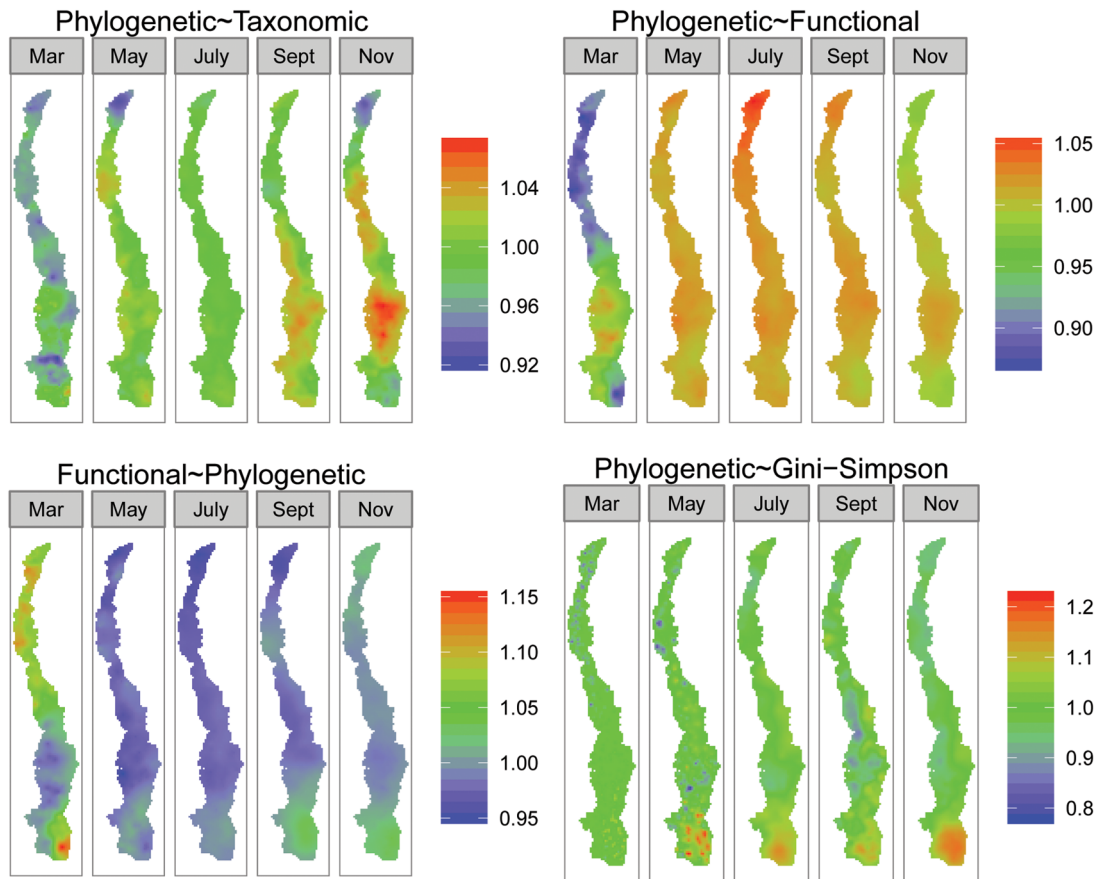


Fig. B12. Kriging interpolation of the residuals from generalized additive models of all pairwise combinations of diversity indices, for each month of the trawl survey and across all years. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative abundance. Figures were broken up for space restrictions. Interpretation given in the legend of Fig. 4, main text.

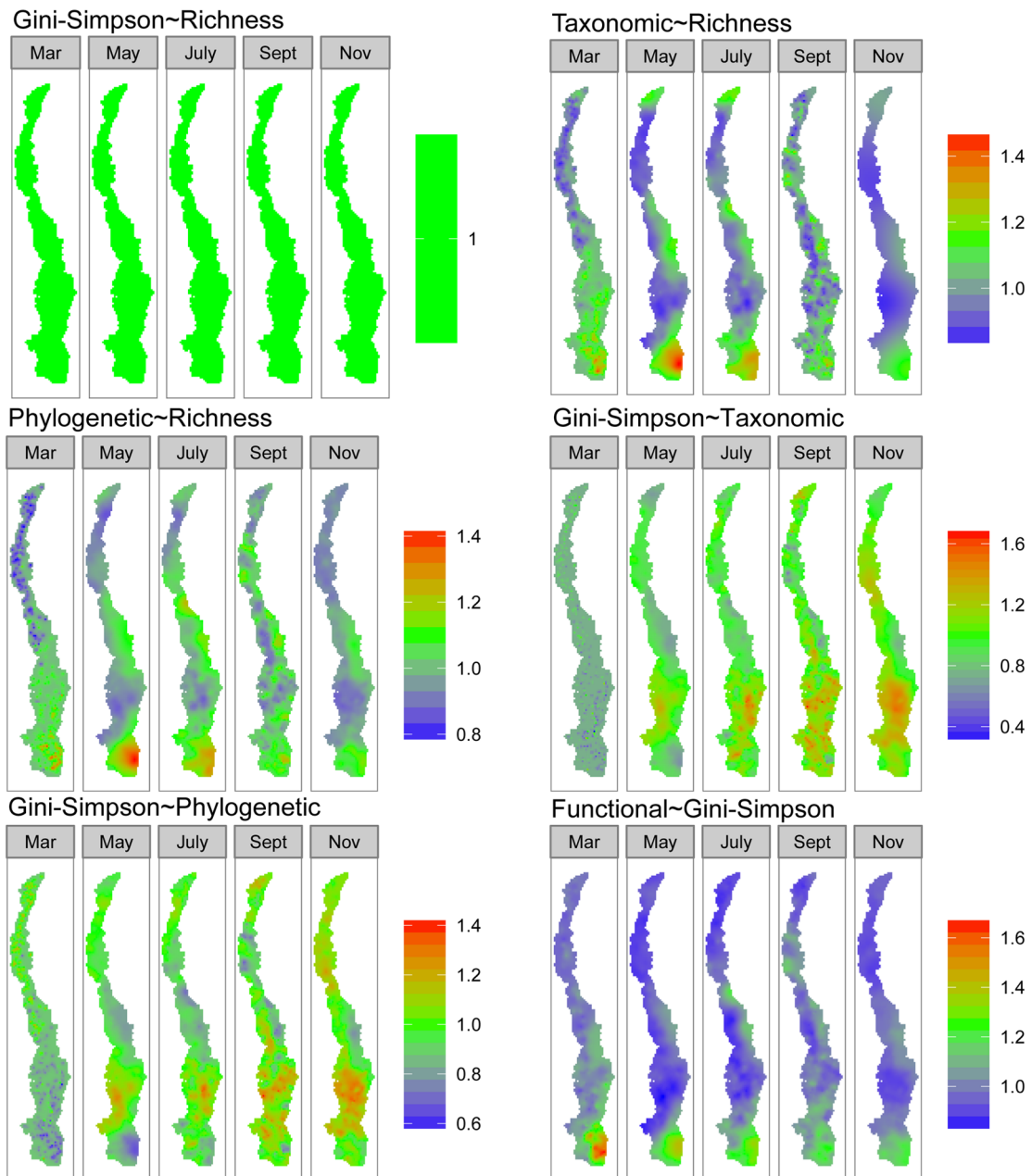


Fig. B13. Kriging interpolation of the residuals from generalized additive models of all pairwise combinations of diversity indices, for each month of the trawl survey and across all years. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by presence/absence. In this case, the Gini-Simpson index collapses to richness, so the fit is perfect and the residual deviance is 0. Figures were broken up for space restrictions. Interpretation given in the legend of Fig. 4, main text.

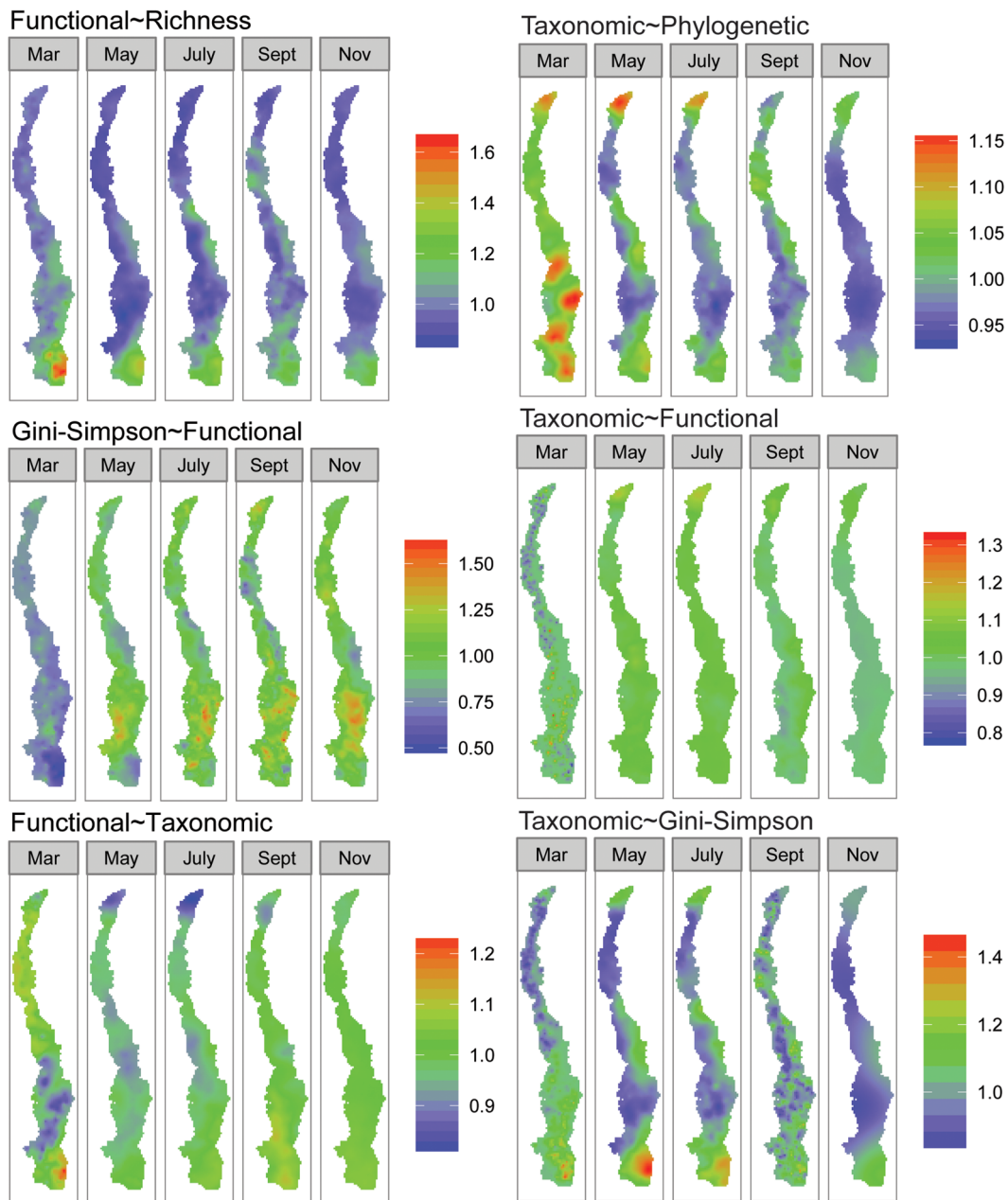


Fig. B14. Kriging interpolation of the residuals from generalized additive models of all pairwise combinations of diversity indices, for each month of the trawl survey and across all years. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by presence/absence. In this case, the Gini-Simpson index collapses to richness, so the fit is perfect and the residual deviance is 0. Figures were broken up for space restrictions. Interpretation given in the legend of Fig. 4, main text.



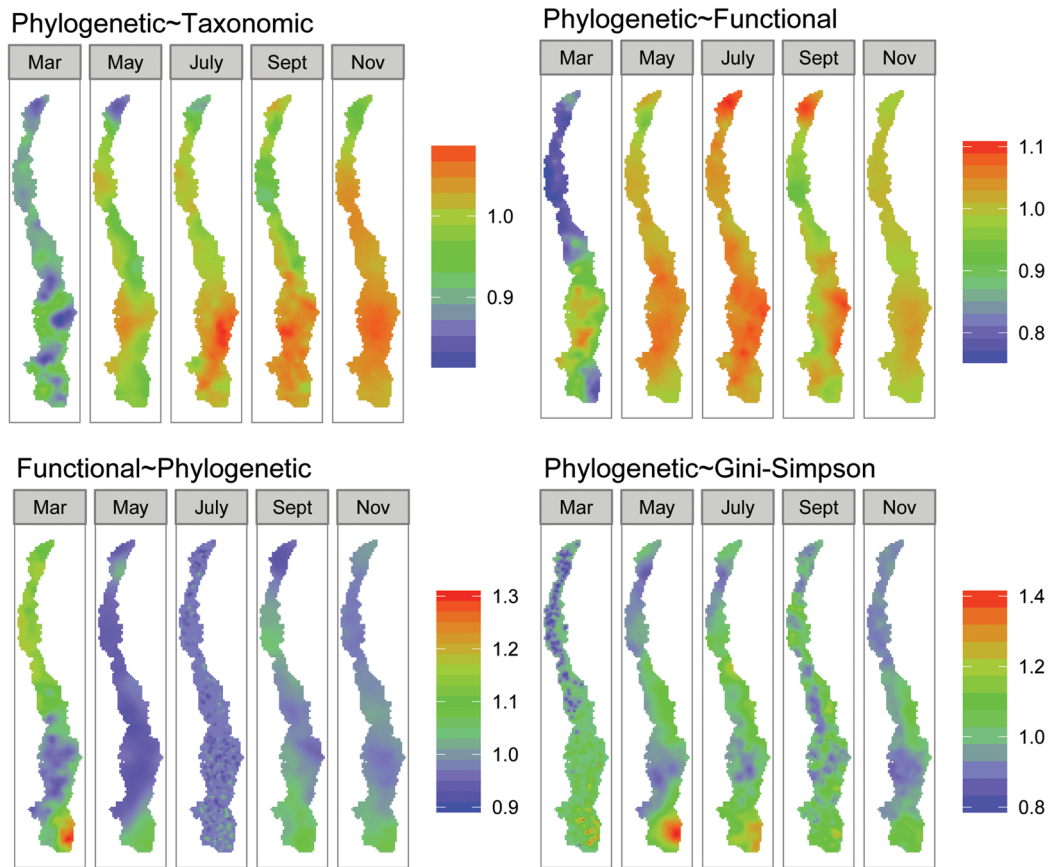


Fig. B15. Kriging interpolation of the residuals from generalized additive models of all pairwise combinations of diversity indices, for each month of the trawl survey and across all years. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by presence/absence. In this case, the Gini-Simpson index collapses to richness, so the fit is perfect and the residual deviance is 0. Figures were broken up for space restrictions. Interpretation given in the legend of Fig. 4, main text.

Table B1. Partial deviances for each diversity index fitted against indicators of space (latitude and longitude), time (month and year), and environment (temperature, salinity, dissolved oxygen, and depth) using generalized additive models. Values are percentages of the total explained deviance  $\pm$  SE.

Diversity index	Weighting	% Total deviance	% Space	% Time	% Environment
Richness	...	56.0	24.0 $\pm$ 5.6	10.1 $\pm$ 3.7	21.8 $\pm$ 7.3
Evenness	Abundance	22.2	14.3 $\pm$ 0.6	2.0 $\pm$ 0.3	5.9 $\pm$ 0.1
Gini-Simpson	Abundance	35.0	19.1 $\pm$ 3.3	4.6 $\pm$ 1.0	11.4 $\pm$ 3.7
Functional	Abundance	40.7	25.4 $\pm$ 4.4	2.1 $\pm$ 0.2	13.2 $\pm$ 4.5
Phylogenetic	Abundance	40.5	23.9 $\pm$ 4.5	2.5 $\pm$ 0.7	14.1 $\pm$ 4.7
Taxonomic	Abundance	40.4	25.7 $\pm$ 0.6	1.5 $\pm$ 0.2	13.2 $\pm$ 4.5
Evenness	Biomass	9.9	6.4 $\pm$ 0.1	2.8 $\pm$ 0.1	0.1 $\pm$ 0.0
Gini-Simpson	Biomass	33.0	15.4 $\pm$ 1.7	8.5 $\pm$ 1.9	9.2 $\pm$ 2.9
Functional	Biomass	39.1	20.3 $\pm$ 4.0	6.3 $\pm$ 1.2	12.5 $\pm$ 4.6
Phylogenetic	Biomass	39.5	20.0 $\pm$ 3.5	7.5 $\pm$ 1.8	12.0 $\pm$ 4.4
Taxonomic	Biomass	38.8	20.4 $\pm$ 3.8	6.4 $\pm$ 1.5	12.0 $\pm$ 4.4
Functional	Presence/absence	56.7	32.7 $\pm$ 7.0	4.5 $\pm$ 1.6	19.4 $\pm$ 7.6
Phylogenetic	Presence/absence	60.6	28.7 $\pm$ 7.8	7.7 $\pm$ 3.3	4.3 $\pm$ 1.7
Taxonomic	Presence/absence	54.6	29.2 $\pm$ 7.5	4.3 $\pm$ 1.7	21.1 $\pm$ 7.9

Notes: Diversity indices were either weighted by abundance, biomass, or presence/absence. Richness is inherently presence/absence and therefore cannot be weighted. When weighted by presence/absence, both evenness and the Gini-Simpson index collapse to richness, and therefore are not included in the table.

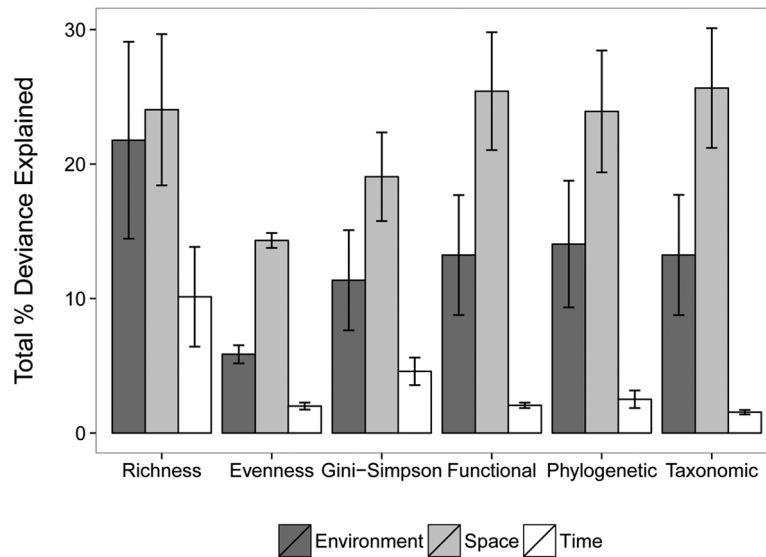


Fig. B16. The partial contributions of space, time, and environment to the total explained deviance from generalized additive models fit to each diversity index. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by relative abundance. Error bars denote  $\pm 1$  SE on partial deviance estimates. Interpretation given in the legend of Fig. 5, main text.

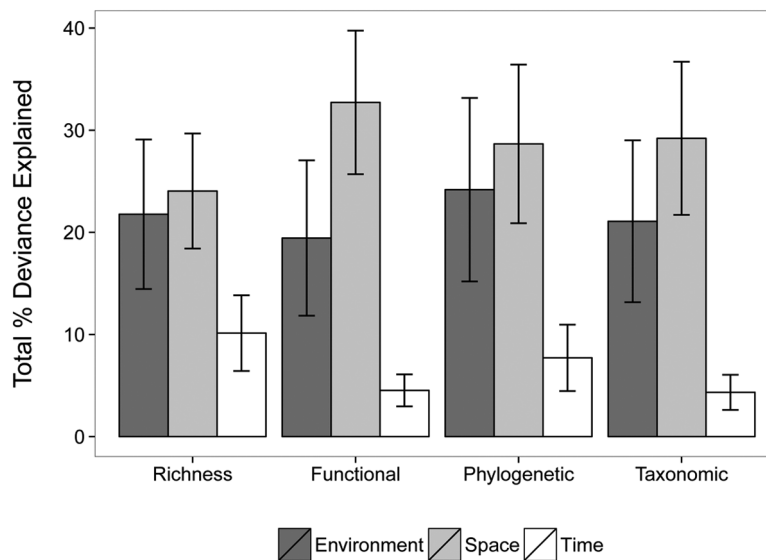


Fig. B17. The partial contributions of space, time, and environment to the total explained deviance from generalized additive models fit to each diversity index. Gini-Simpson, functional, phylogenetic, and taxonomic diversity indices are weighted by presence/absence. A model could not be fit to evenness since the index collapses to 1 using presence/absence data. Additionally, the Gini-Simpson index collapses to richness when using presence/absence data and is likewise excluded. Interpretation given in the legend of Fig. 5, main text.

## SUPPLEMENT

R script containing all data analyses and Newick format ([Ecological Archives C005-001-S1](#)), functional, phylogenetic, and taxonomic trees in