Can we increase our confidence about the locations of biodiversity 'hotspots' by using multiple diversity indices?

N. TOLIMIERI,[1],† A. O. SHELTON,[1] B. E. FEIST,[1] AND V. SIMON[2]

[1]Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service,
National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard E, Seattle, Washington 98112 USA
[2]Fisheries Resource Assessment and Monitoring Division, Northwest Fisheries Science Center, National Marine Fisheries Service,
National Oceanic and Atmospheric Administration, 2725 Montlake Boulevard E, Seattle, Washington 98112 USA

Abstract.   Some have suggested that targeting conservation efforts on biodiversity hotspots—areas of exceptionally high diversity—is the most efficient way to use limited resources to protect the most or rarest species. Moreover, the preservation of biodiversity is a focus for resource management and conservation because of the links between biodiversity and ecosystem function. However, there are many ways to define biodiversity and a plethora of diversity indices. Do these indices agree on where biodiversity hotspots are, and by extension, where conservation should take place? Here we use a habitat modeling approach to map spatial and temporal patterns in five community metrics of the demersal fish community in the California Current Large Marine Ecosystem: species density, species evenness, taxonomic distinctness, functional divergence and total biomass. Depth, bottom temperature, sediment grain size, and distance to hard substratum were included as covariates in the model. All indices showed strong spatial patterns and relationships with depth. Spatial patterns for functional divergence and total biomass varied among years, but other indices did not show temporal variation. We identified hotspots as cells where at least one index was in the top 5% or 10% of its range. There was minimal spatial overlap among 10% hotspots for the five indices. Over 40% of the study area was classified as a biodiversity hotspot by at least one metric. However, no area was identified as a hotspot by all five metrics, and only slightly more than one percent of the coast was identified as within a hotspot for three or more metrics. Since different indices represent various aspects of diversity, our results caution against the uninformed use of these indices in the identification of biodiversity hotspots. Instead, we must define our objectives and then choose the relevant metrics for the problem.

Key words: functional diversity; groundfish; marine spatial planning; species density; species evenness; taxonomic distinctness.

† E-mail: nick.tolimieri@noaa.gov

INTRODUCTION

Biodiversity has a central place in natural resource management and conservation. Preservation of biodiversity is a goal for both ethical (Davidson 2013, Doak et al. 2014) and functional (Palumbi et al. 2009) reasons. Ecologically diverse communities are more productive, have greater resilience to disturbance, and improved ecosystem services relative to less diverse communities (Worm et al. 2006, Stachowicz et al. 2007, Duffy 2009, Palumbi et al. 2009). Therefore, sustaining

biodiversity should play a foundational role in determining ecosystem-based management (EBM). Palumbi et al. (2009) go so far as to suggest that biodiversity should serve as a "national master variable to enable EBM." Such assertions motivate detailed discussion of spatial and temporal patterns of biodiversity and the best use of biodiversity measures in a management setting (Worm et al. 2005, Tolimieri 2007, Palumbi et al. 2009, Anderson et al. 2013).

Biodiversity hotspots—areas of high diversity and/or endemism—have received the lion's share of attention as management targets for conservation (Myers 1988, 2003, Myers et al. 2000, Araujo and Williams 2001, Araujo 2002, Kareiva and Marvier 2003, Mittermeier et al. 2003, Worm et al. 2003, Selig et al. 2014). Proponents of the concept suggest that focusing conservation efforts on biodiversity hotspots is the most efficient way to use limited resources to protect the most or rarest species (Myers et al. 2000, Myers 2003). However, others note that hotspots are often associated with species' range margins and transition zones (Turpie et al. 2000, Araujo and Williams 2001, Araujo 2002) where species may already be at the limits of their environmental tolerances and less likely to prosper than in the core of their distributions. Moreover, hotspot analyses were initially conceived at global scales identifying 18–25 regions of high richness/endemism (Myers 1988, Myers et al. 2000). To be useful, finer-grained maps of diversity are needed; conservation is conducted on the local or regional scale not the continental scale. Furthermore, we have known for more than a century that tropical latitudes harbor more species (von Humboldt 1808, Darwin 1862, Wallace 1878), and recent analyses, while improving the precision of such early work, are mostly focused on documenting this broad-scale pattern instead of providing information that can be used in a management setting (e.g., Tittensor et al. 2010, Stuart-Smith et al. 2013).

A more serious problem is that while biodiversity is often equated with species richness or endemism (Reid 1998, Myers et al. 2000, Worm et al. 2003), in truth it is a broader, more complex, and nuanced concept (Norton 1994, Purvis and Hector 2000, Sarkar 2005). It "encompass[es] variation at levels of complexity from within species to across ecosystems" (Sala and Knowl-ton 2006) and includes both structural (richness, evenness) and functional components (Callicott et al. 1999). For example, biodiversity spans biological scales from genetic diversity within species (e.g., Hilborn et al. 2003) to counts of species (e.g., Tolimieri 2007), and to higher taxonomic (Clarke and Warwick 1998, 1999, Tolimieri and Anderson 2010), phylogenetic (May 1990, Faith 1992, 1994) and functional relationships (Schleuter et al. 2010). The wide range of diversity indices used by ecologists begs the question: Do these indices agree on where biodiversity hotspots are, and by extension, where conservation should take place?

Here we quantify patterns of demersal fish biodiversity off the west coast of the United States using an extensive time series of systematic fisheries-independent trawl surveys. We use a habitat modeling approach to document spatial and temporal patterns in multiple metrics of biodiversity. Specifically, we (1) characterize five distinct aspects of the groundfish community: species density, species evenness, taxonomic distinctness, functional diversity, and total biomass, (2) develop predictive maps to illustrate spatial patterns of variation for each metric and ask if these patterns vary across years, (3) compare the areas identified as 'high diversity' by each metric to see if multi-species metrics agree on high-value areas along the coast, and (4) discuss the use of such multi-species metrics for basic ecological insight and in the context of EBM and marine spatial planning.

MATERIALS AND METHODS

Data source

We used data from the Northwest Fisheries Science Center's (NWFSC) U.S. West Coast Bottom Trawl Survey of Groundfish Resources off Washington, Oregon, and California (Fig. 1; Bradburn et al. 2011, Keller et al. 2012). The survey is a depth-stratified, random sample that spans approximately 32–48.5° N and 55–1300 m (see Bradburn et al. [2011] for a detailed discussion of the sampling design). Each trawl represents a standardized 15-minute tow. We used 5743 samples collected between 2003 and 2011, encompassing 313 taxa identified to species. The area swept by each trawl was calculated for each tow and ranged from 0.008 to 0.045 km^2 (median: 0.017). We only included hauls deemed
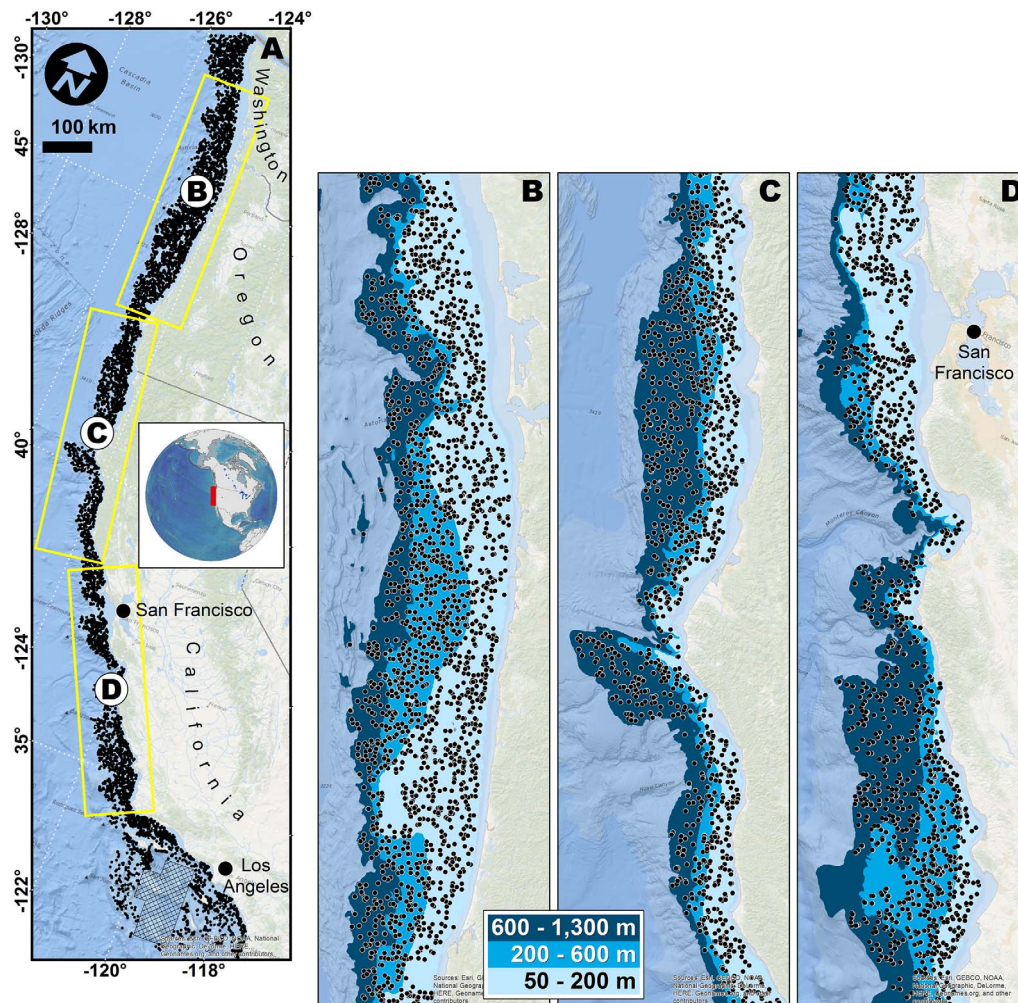
Fig. 1. Locations of fisheries-independent trawls and depth contours (insets) for (A) the entire sampled area and (B) northern, (C) central and (D) southern sections as indicated by the yellow rectangles in (A). Hatched area in the south is the Cowcod Conservation Area.

acceptable for stock assessment and used only individuals identified to species (with two exceptions, see Appendix: Data source and species identification). Note that because bottom trawls selectively sample fish (e.g., small fish fit through the trawl mesh and are not observed) and habitats (trawls cannot sample high-relief, rocky habitat), our results are limited to the assemblage of fishes caught by the trawl survey.

Community metrics

We calculated five multi-species community metrics from the observed trawl data: (1) species density, (2) species evenness, (3) taxonomic distinctness, (4) functional divergence, and (5)

total biomass. The first four are diversity metrics and each captures a distinct aspect of diversity in the fish community. Thought not a diversity metric, we include total biomass as a fifth community metric. Importantly, all of these metrics can be calculated for a single sample. We outline each metric below and present the mathematical calculations for each metric in the appendix.

Species density is the number of species per area (Gotelli and Colwell 2001). Species density contrasts with species richness, which is the absolute number of species observed in an exhaustive sample of an area. Species density is a more easily estimated and conservation-rele-

vant metric (Worm et al. 2003) in part because it indicates the number of species affected by any spatial management. We calculated species density as the number of species per trawl and included swept area in the analyses as a covariate to account for differences in trawl area (see below).

Simpson diversity (Simpson 1949) is a measure of species evenness (or more technically equitability; Tuomisto 2012). Simpson diversity (λ) varies between zero and one and gives the probability that two individuals selected from a sample will be of the same species; thus evenness increases as λ decreases. Here we use a common variant, the Gini-Simpson index ($1 - \lambda$), so that evenness increases as the index approaches one, and $1 - \lambda$ is the probability of an interspecific encounter (Hurlbert 1971). We calculated the Gini-Simpson index (hereafter, species evenness) using the 'vegan' package in R 3.0.1 (R Core Team 2013).

Average taxonomic distinctness summarizes the diversity of a sample based on the evolutionary relatedness among species. It is the mean of all species-to-species distances through a taxonomic tree for all pairs of species within a sample and represents the taxonomic breadth of the sample (Clarke and Warwick 1998, 2001). We calculated taxonomic distinctness using the 'vegan' package in R 3.0.1 (R Core Team 2013) as in Tolimieri and Anderson (2010) and scale taxonomic distinctness between zero and 100 with higher values indicating increase taxonomic diversity in a sample.

Functional diversity is a measure of the range and distribution of "what organisms do in communities" (Schleuter et al. 2010). It is assumed to be a better indicator of productivity and vulnerability than is species diversity because it measures the complementarity and redundancy of co-occurring species. We used functional divergence (Villéger et al. 2008) as a metric of functional diversity. Functional divergence quantifies variance in functional types and indicates the degree of resource differentiation and competition (Schleuter et al. 2010). That is, it measures the distribution of abundance within the volume of functional trait space occupied by the species in the community (Schleuter et al. 2010). We calculated functional diversity using the 'FD' package in R 3.0.1 (R Core Team 2013)

Table 1. A list of the habitat covariates included in the statistical models.

Habitat covariates	Forms included in the model
Depth (m)	$\log(\text{depth})$, $\log(\text{depth})^2$
Bottom temperature (C)	bottom temperature, (bottom temperature)^2
Sediment grain size, Φ scale†	grain size, (grain size)^2
Distance to nearest rocky outcrop (km)	$(\text{km})^{0.5}$

Note: Swept area (km^2) is included as a covariate in all models to account for variation in sampling effort.
  † Φ scale (Krumbein and Sloss 1963).

based on the diets of 49 species (Dufault et al. 2009) that made up 86% of all the biomass in the trawls (Appendix: Table A1). We omitted 158 trawls when calculating functional divergence because there were fewer than three species with diet data in those trawls making it impossible to calculate the metric.

Finally, we calculated the total biomass for each trawl by simply summing the biomass of all species in a haul. While not a diversity metric per se, total biomass is a general community metric indicating that some areas support more fishes than others. It is relevant because aiming conservation efforts at areas of high biodiversity but low biomass may not achieve management goals.

Habitat covariates

We used four continuous habitat covariates as potential predictor variables: average water depth of the trawl, bottom temperature, distance to nearest hard bottom, and sediment grain size. Average water depth and bottom temperature were directly measured on each survey trawl, while distance to nearest rocky bottom patches larger than one ha and sediment grain size were calculated from existing geospatial data layers (NMFS 2013). We considered linear and quadratic terms for water temperature, sediment grain size, distance to rock and the natural logarithm of depth (see Table 1). Additionally, we included the swept area of the trawl as an estimated covariate because community metrics will not scale linearly with effort. Thus we could not simply include effort as an offset (Gotelli and Colwell 2011). Note, there are many other potential habitat covariates that could contribute to community metrics—most notably deep water corals, spong-

es, and other biogenic habitats (Krigsman et al. 2012). We did not have sufficient data across the coast to include these potential covariates as predictor variables.

Statistical models for community metrics

We implemented spatial generalized linear models (Diggle et al. 1998, Wikle et al. 1998, Royle and Wikle 2005, Shelton et al. 2014) to estimate the relationship between habitat variables and each community metric and produce predictive maps for each diversity metric. We used the same generalized linear model structure for all five diversity metrics. However, because the metrics have different statistical properties, we used specific exponential family and link functions for each metric (Appendix: Table A2). We illustrate our statistical approach using species density and provide details for the other metrics in the appendix. Importantly, our approach accounts for spatial autocorrelation and avoids the assumption that the multiple trawls occurring in distinct habitats represent independent samples of an identical fish community. This is a common, unacknowledged assumption in diversity analyses that bin samples arbitrarily based on coarse latitudinal grids (Cheung et al. 2009, Tittensor et al. 2010).

We modeled species density at location s and time t as a Poisson random variable, $Z(s, t)$, whose mean parameter $\mu(s, t)$ is a function of environmental covariates. We wrote this model as a spatial generalized linear model

$$\mathbf{Z}(s,t)|\mu(s,t) \sim \text{Poisson}(\mu(s,t))$$
$$log(\mu(s,t)) = \mathbf{X}(s,t)\boldsymbol{\beta} + w(s,t) \qquad (1)$$

where $\mathbf{X}$ is a design matrix of environmental covariates, $\boldsymbol{\beta}$ is a vector of regression coefficients, and w is a spatially random effect that provides local adjustment to the mean and captures the effect of unobserved covariates and autocorrelation. For simplicity, we considered only models with main fixed effects (i.e., no interactions between covariates) and time-invariant habitat relationships (i.e., no interactions between year and continuous covariates). This structure allowed the spatial random variable w to absorb the variability that may arise from model misspecification.

We modeled w as a smooth spatial surface, $w \sim$ $MVN(0, \mathbf{C}_w(d, \theta, \sigma^2)$, where MVN is the multivariate normal distribution, $\mathbf{C}_w(d, \theta, \sigma^2)$ is a covariance matrix based on an isotropic exponential model with range parameter θ that controls the correlation between points as a function of distance, d, and σ^2 is the spatial variance (Cressie and Wikle 2011).

We accounted for variation among years by testing two covariance structures for w. First, we compared allowing the spatial field to vary among years by making the covariance matrix, $\mathbf{C}_w(d, \theta, \sigma^2)$, block-diagonal with elements comprised of year-specific spatial covariance matrices (see Appendix). Second, we considered a model with a single shared spatial field for all years. Estimating a single field is equivalent to ignoring the temporal component of the data and assuming all of the observations occurred in the same year. For all models we estimated a single θ and a single σ^2, so the scale and magnitude of spatial correlation is considered similar among years.

We used Bayesian methods to implement all of our models and used predictive process models to reduce model dimension and abbreviate computing time (Banerjee et al. 2008, Finley et al. 2009, Latimer et al. 2009, Shelton et al. 2014). We did standard assessments of model convergence and compared models using log-scoring (Krnjajić et al. 2008, Draper and Krnjajic 2010, Draper 2013). As Hooten and Hobbs (2015) note there is not an agreed-upon method for Bayesian model comparison. We discuss the benefits and limitations of the approach taken here in the Appendix.

To generate predictive maps for each metric, we created a 2×2 km resolution regular grid for the region between the 50 and 1,300 m isobaths from the US/Mexico border to the US/Canada border. We then generated a predicted value for each metric using the covariate values and spatial location at the center of grid cell. We made all predictions for a standard trawl area of 0.01 km^2 (1 hectare). We did not generate predictive values within California Cowcod Conservation Area 1 (CCA West; hatched region in Fig. 1), as the trawl survey vessels do not sample in this region.

Identifying biodiversity hotspots for different metrics and their overlap

We compared the predictive maps for the five metrics to identify locations where the diversity metrics agreed on high-value areas. Any given 2 × 2 grid cell was tagged as a hotspot if the value for a given metric was in the top 5% or 10% of its observed range (we refer to these as 5% and 10% hotspots, respectively). We then compared maps of these 5% and 10% hotspots among metrics to determine the proportion of the habitat identified as a hotspot by one to all five of the metrics. We recognize that any definition of a hotspot is arbitrary and note that other percentile cutoffs are potentially reasonable. We also produced maps of the overlap between the 10% hotspots in order to illustrate the location of cross-metric hotspots.

Results

The spatial models for the five community metrics showed strong spatial patterning across the coast (Fig. 2). All five metrics show strong associations with depth (Table 2), and all except taxonomic distinctness showed strong relationships with observed bottom temperature (Table 2). Sediment grain size played a minor role in determining the two metrics. Model selection did not include distance to rock as a predictor of any metric. In all cases, models that included the spatial smoothing term w outperformed nonspatial models. Model comparison indicated that there was no evidence for temporal variability among years for three of the metrics: species density, species evenness, and taxonomic diversity. For each of these metrics, the preferred model used a single shared spatial field (Table 2). In contrast, the preferred models for the functional divergence and total biomass included a unique spatial field for each year. The fact that the spatial field varied among years indicates that the location of unusually high or low values of biomass and functional divergence differed among years. To directly compare the three metrics that showed no temporal variation and the two that did, we calculated an across-year average for total biomass and functional divergence by averaging the predictions for each grid cell and each individual year (Fig. 2). We present the predicted maps for total biomass and

functional divergence by individual year in the Appendix (Figs. A1 and A2).

Patterns with depth varied among metrics. For example, species density was higher at shallow depths in southern waters (e.g., near San Francisco Bay) but higher at intermediate depths in northern waters. Species evenness showed a broadly similar pattern to species density in terms of variation with depth. Functional divergence was highest at shallower areas while taxonomic distinctness was higher at depth (Fig. 2).

The geographic location of hotspots for each metric also varied (Fig. 3). Species density was highest in the vicinity of San Francisco Bay where hotspots were on the shelf. However, species density hotspots were deeper on the slope to the north. Species evenness hotspots were widely distributed but may have been more prevalent north of Cape Blanco. Patterns for taxonomic distinctness were primarily depth related but there were large hotspots south of Point Conception in the south. Functional divergence hotspots were all located from roughly Cape Blanco north with the exception of two small hotspots around Cape Mendocino and just south of Monterey Bay. Biomass hotspots were all found from the Monterey Bay (N 36°30′) and north.

There was little overlap in the locations of hotspots identified by the five metrics (Fig. 4). Over 40% grid cells were classified as a biodiversity hotspot by at least on metric. However, there were no cells identified as hotspots by all five metrics and only slightly more than 1% were identified by three or more metrics.

All of the areas identified as 10% hotspots by three or more metrics were in northern waters off the Oregon and Washington coast (Fig. 4). The southernmost three-metric hotspot was off Cape Blanco. A second was just south of Astoria Canyon with a third just north of Grays Canyon. The only four-metric hotspot of any size was in the vicinity of Heceta and Stonewall Banks with another small four-metric 10% hotspot north of Gray's Canyon.

The greatest overlap between pairs of metrics were for (1) species density and evenness (24%), (2) species evenness and functional diversity (25%), and (3) species density and functional diversity (19%, Fig. 4). Taxonomic distinctness overlapped only trivially with the other four
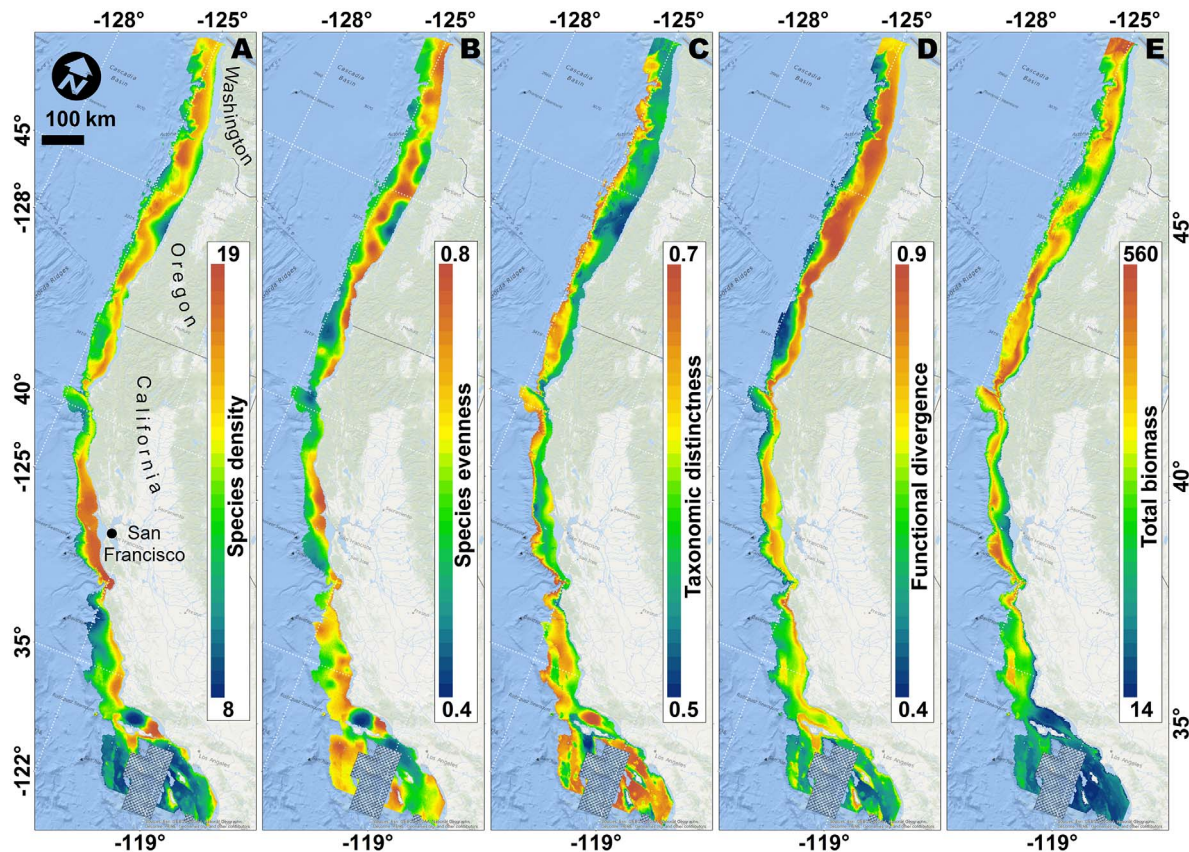
Fig. 2. Spatial patterns for five diversity metrics: (A) species density (no. species ha^{-1}), (B) species evenness, (C) taxonomic distinctness, (D) functional divergence and (E) total biomass (kg ha^{-1}). All metrics are projected in 2 × 2 km grid cells.

metrics.

Discussion

The vast literature on biodiversity and ecosystem function suggests that the conservation of biodiversity may act as a simple and practical tool for implementing EBM (Palumbi et al. 2009). Focusing on biodiversity hotspots has been suggested as a way to maximize our 'bang-for-the-buck' by targeting conservation efforts in areas with the most or most vulnerable species (Myers et al. 2000, Myers 2003). However, the task of identifying hotspots is difficult because biodiversity can be defined in many ways both among and within taxa and at different spatial scales. At scales appropriate to management, there may be little overlap in the hotspots for different taxa or for hotspots defined by richness or endemism (Reid 1998), making it difficult to situate spatial planning tools such as no-take

Table 2. Summary of habitat covariates included in the preferred models for each community metric.

Model	Habitat covariates	Single random field?
Species density	log(depth), log(depth)^2, temperature	Y
Species evenness (Gini-Simpson, $1 - \lambda$)	log(depth), temperature	Y
Taxonomic distinctness	log(depth), log(depth)^2, grain size	Y
Functional divergence	log(depth), log(depth)^2, temperature, temperature^2	N
Total biomass	log(depth), log(depth)^2, grain size, temperature	N

Note: In addition to the covariates listed, all models included an estimated linear effect for the area trawled.
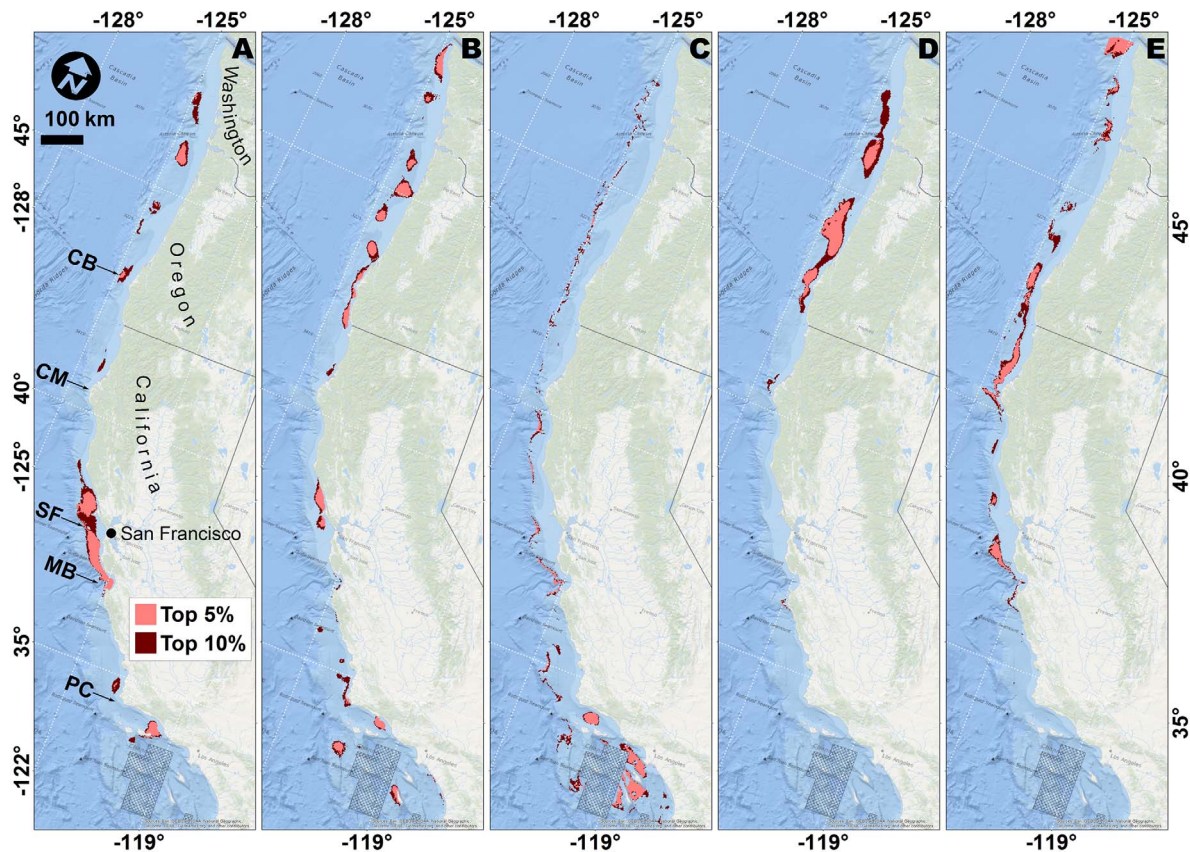
Fig. 3. Location of 5% and 10% hotspots for (A) species density, (B) species evenness, (C) taxonomic distinctness, (D) functional divergence and (E) total biomass. The maps show the areas where each diversity metric was in the top 5% or 10% of its range. CB = Cape Blanco; CM = Cape Mendocino; SF = San Francisco Bay; MB = Monterey Bay; PC = Point Conception.

areas or to target other conservation actions. For example, in Europe (the palearctic), phylogenetic diversity for terrestrial vertebrate groups (amphibians, birds, mammals) shows little overlap due to different evolutionary histories (Zupan et al. 2014). As a result, the evolutionary history of these taxa is unequally represented within the network of European protected areas. Moreover, hotspots may be located in biogeographic transition zones where species are at their range margins (Turpie et al. 2000, Araujo and Williams 2001, Araujo 2002) and species are likely at the limits of their environmental tolerances. Other authors suggest that focusing on hotspots could divert efforts away from other important conservation objectives (Kareiva and Marvier 2003).

Here, we show that five widely used metrics of biodiversity provide disparate information about the fish community and the locations of biodiversity hotspots in waters along the U.S. West Coast. From one perspective, we could conclude that there are no biodiversity hotspots on the U.S. West Coast; there are no areas in which all five metrics are high along the nearly 2,100 km of coastline. Furthermore, only 0.1% of the area was identified as a high value area for four metrics, only 1.3% include three metrics and only 6% included two metrics. This lack of agreement is troubling for the prospect of targeting hotspots for conservation efforts. Moreover, our indices are only a few of the vast number of diversity metrics that could be applied to our data (e.g., Gotelli and Colwell 2001, Schleuter et al. 2010, Anderson et al. 2011). Each would likely provide a different map of high value areas.

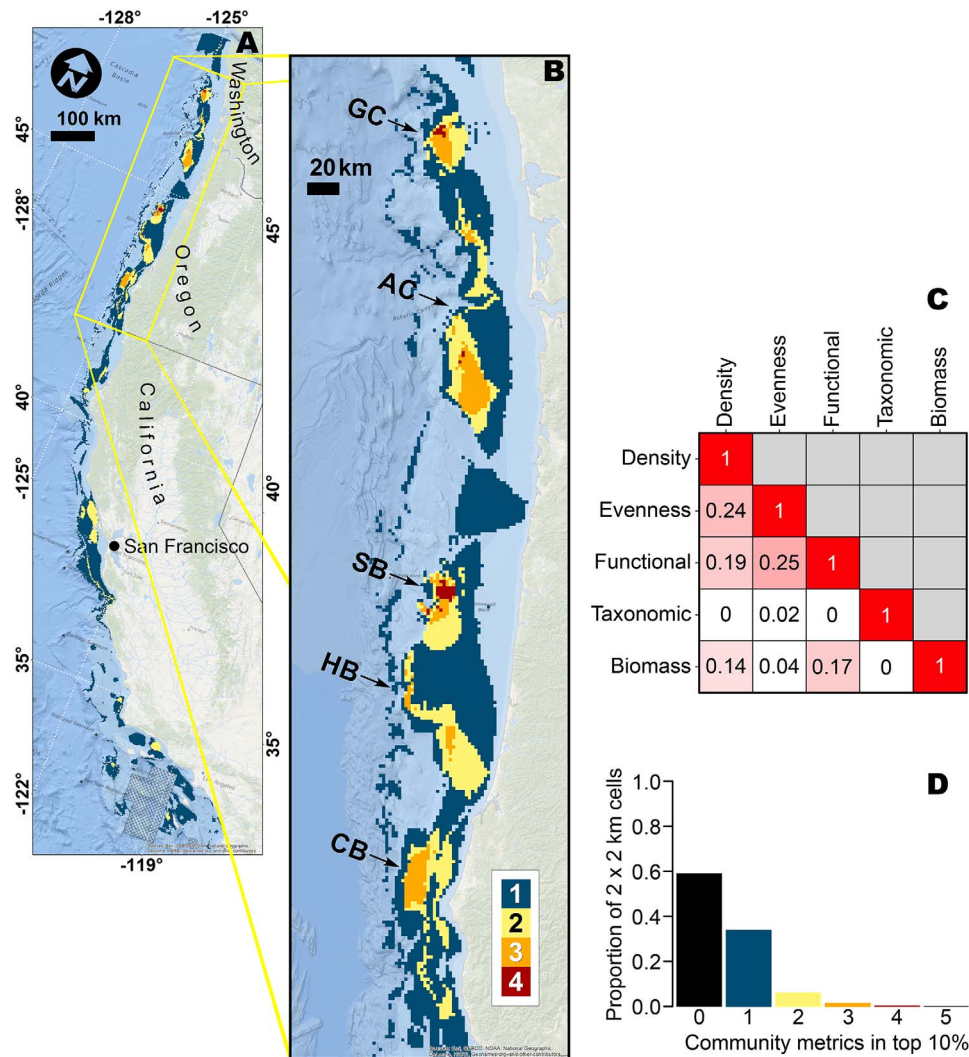From another perspective, the wide-range of

Fig. 4. (A) Overlap in the 10% hotspots for five diversity metrics (species density, species evenness, taxonomic distinctness, functional divergence and total biomass for the U.S. West Coast. (B) overlap in the northern section as indicated by the rectangle in (A). (C) Similarity matrix between five diversity metrics. (D) Summary plot of areal proportion of study area where overlap occurred between the five metrics. GC = Grays Canyon; AC = Astoria Canyon; SB = Stonewall Bank; HC = Heceta Bank; CB = Cape Blanco.

potential diversity maps can help us focus on how we use biodiversity hotspots by pointing to an obvious and thorny problem: managers need to specifically define the aspect of biodiversity they wish to conserve or otherwise manage. Despite the optimism of some authors (e.g., Palumbi et al. 2009), simultaneously optimizing all facets of biodiversity will be impossible in virtually all real-world situations (Reid 1998, Zupan et al. 2014). The identification and

conservation of biodiversity for EBM face the same challenges as those faced in single-species management: spatial planning requires a clear, agreed upon set of goals to manage toward. The development and application of an ever-growing number of diversity metrics does not change this fundamentally important fact.

Each of the metrics used for the fish community off the U.S. West Coast represents a different aspect of biodiversity. For example, targeting

hotspots of species density would protect the greatest number of species per unit area (Myers et al. 2000, Araujo and Williams 2001, but see Araujo 2002, Myers 2003). Alternatively, if the goal is to sustain ecosystem function and services (Palumbi et al. 2009), functional diversity hotspots would be appropriate targets. Focusing management on biomass hotspots would be relevant for goals related to extractive exploitation (fishing) such as the maintenance of spawning stock biomass. Taxonomic diversity maps provide an evolutionary perspective on biodiversity. Each option outlined above could be used to generate management scenarios, but they cannot all be satisfied simultaneously.

The among-year variability in the maps for total biomass and functional divergence, complicates the process of spatial planning; hotspot locations were not consistent over time (Appendix: Figs. A1 and A2). We presented a time-average map of biomass and functional divergence, but the year-to-year variation was considerable for both metrics. Recent analyses of biodiversity have generally been done globally (e.g., Tittensor et al. 2010, Stuart-Smith et al. 2013)—at a scale too large to be practical for spatial management—and ignore temporal changes in biodiversity. For comparison, the entirety of our study region is represented by only three grid cells in the richness patterns characterized by Tittensor et al. (2010). Furthermore, the ability to include temporal changes should be a priority for any biodiversity analyses given the projected changes to environments in the coming years due to global climate change (IPCC 2014).

A criticism of the use of hotspots for conservation is that they may tend to occur in transition zones where species are at their range margins and less likely to prosper than in the core of their range (Turpie et al. 2000, Araujo and Williams 2001, Araujo 2002). There are several biogeographic breaks along the West Coast where assemblage structure changes for marine species and especially groundfishes: Point Conception, Monterey Bay, Cape Mendocino and Cape Blanco (Horn and Allen 1978, Dawson 2001, Horn et al. 2006, Tolimieri and Levin 2006). Overall the concordance between the biogeographic breaks and diversity metrics was not overwhelming. Hotspots were frequently associated with biogeographic breaks, but they also occurred elsewhere (Fig. 3). For example, some species density hotspots were proximate to biogeographic breaks, although, only in the Monterey Bay locale was there a large area of high species density. Notably, the Monterey Bay and Point Conception hotspots for species density had low total biomass (but high historical fishing pressure; Miller et al. 2014). Thus, targeting conservation in these areas would address many species, but not many individuals of each species. Conversely the multiple metric hotspots at Cape Blanco and to the north occurred in areas of high biomass suggesting that they would be more effective locations for conservation efforts. These results emphasize the importance of evaluating multiple diversity metrics. While hotspots for a particular metric were often located near a biogeographic break, many other hotspots were not. For example, there were small hotspots for species evenness near Point Conception and Cape Mendocino and a substantial hotspot near Cape Blanco. However, large 5% hotspots were also common in other locations north of Cape Blanco and south of Point Conception. Patterns for taxonomic distinctness were primarily related to depth and did not show strong latitudinal variation or association with biogeographic features.

The maintenance of biodiversity is important for both ethical and practical reasons. Technical advances in statistics and mapping will allow improved identification of biodiversity hotspots that can help us in targeting conservation dollars and management activities. However, our results caution against their uninformed use because different diversity metrics differ in the identification of high-diversity areas. We first need to define our objectives and then choose the relevant metrics for the problem. A diversity of diversity metrics is only helpful if they can provide actionable information for well-defined goals. Claiming that we should manage ecosystems for the benefit of biodiversity in general is not helpful and may obscure profitable avenues to pursue toward sustainable management. Nevertheless, well-motivated, spatio-temporal methods applied to diversity metrics have an important role to play in determining conservation priorities and actions.

LITERATURE CITED

Anderson, M. J., et al. 2011. Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. Ecology Letters 14:19–28.

Anderson, M. J., N. Tolimieri, and R. B. Millar. 2013. Beta diversity of demersal fish assemblages in the North-Eastern Pacific: interactions of latitude and depth. PLoS ONE 8:1:15.

Araujo, M. B. 2002. Biodiversity hotspots and zones of ecological transition. Conservation Biology 16:1662–1663.

Araujo, M. B., and P. H. Williams. 2001. The bias of complementarity hotspots toward marginal populations. Conservation Biology 15:1710–1720.

Banerjee, S., A. E. Gelfand, A. O. Finley, and H. Sang. 2008. Gaussian predictive process models for large spatial data sets. Journal of the Royal Statistical Society B 70:825–848.

Bradburn, M. J., A. Keller, and B. H. Horness. 2011. The 2003 to 2008 U.S. West Coast bottom trawl surveys of groundfish resources off Washington, Oregon, and California: estimates of distribution, abundance, length, and age composition. NOAA technical memorandum, NMFS-NWFSC-114. U.S. Department of Commerce, Washington, D.C., USA.

Callicott, J. B., L. B. Crowder, and K. Mumford. 1999. Current normative concepts in conservation. Conservation Biology 13:22–35.

Cheung, W. W. L., V. W. Y. Lam, J. L. Sarmiento, K. Kearney, R. Watson, and D. Pauly. 2009. Projecting global marine biodiversity impacts under climate change scenarios. Fish and Fisheries 10:235–251.

Clarke, K. R., and R. M. Warwick. 1998. A taxonomic distinctness index and its statistical properties. Journal of Applied Ecology 35:523–531.

Clarke, K. R., and R. M. Warwick. 1999. The taxonomic distinctness measure of biodiversity: weighting of step lengths between hierarchical levels. Marine Ecology Progress Series 184:21–29.

Clarke, K. R., and R. M. Warwick. 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. Marine Ecology Progress Series 216:265–278.

Cressie, N., and C. K. Wikle. 2011. Statistics for spatio-temporal data. Wiley, Hoboken, New Jersey, USA.

Darwin, C. 1862. The voyage of the Beagle. Doubleday, Garden City, New Jersey, USA.

Davidson, M. D. 2013. On the relation between ecosystem services, intrinsic value, existence value and economic valuation. Ecological Economics 95:171–177.

Dawson, M. N. 2001. Phylogeography in coastal marine animals: a solution from California? Journal of Biogeography 28:723–736.

Diggle, P. J., J. A. Tawn, and R. A. Moyeed. 1998. Model-based geostatistics. Journal of the Royal Statistical Society: Series C 47:299–350.

Doak, D. F., V. J. Bakker, B. E. Goldstein, and B. Hale. 2014. Moving forward with effective goals and methods for conservation: a reply to Marvier and Kareiva. Trends in Ecology and Evolution 29:132–133.

Draper, D. 2013. Bayesian model specification: heuristics and examples. Pages 409–431 in D. P. Damien, N. G. Polson, and D. A. Stephens, editors. Bayesian theory and applications. Claredon Press, Oxford, UK.

Draper, D., and M. Krnjajic. 2010. Calibration results for Bayesian model specification. Bayesian Analysis 1:1–43.

Dufault, A. M., K. Marshall, and I. C. Kaplan. 2009. A synthesis of diets and trophic overlap of marine species in the California Current. NOAA Technical Memorandum NMFS-NWFSC-103. U.S. Department of Commerce, Washington, D.C., USA.

Duffy, J. E. 2009. Why biodiversity is important to the functioning of real-world ecosystems. Frontiers in Ecology and the Environment 7:437–444.

Faith, D. P. 1992. Conservation evaluation and phylogenetic diversity. Biological Conservation 61:1–10.

Faith, D. P. 1994. Phylogenetic pattern and the quantification of organismal biodiversity. Philosophical Transactions of the Royal Society B 345:45–58.

Finley, A. O., H. Sang, S. Banerjee, and A. E. Gelfand. 2009. Improving the performance of predictive process modeling for large datasets. Computational Statistics and Data Analysis 53:2873–2884.

Gotelli, N. J., and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters 4:379–391.

Gotelli, N. J., and R. K. Colwell. 2011. Estimating species richness. Pages 39–54 in A. E. Magurran and B. J. McGill, editors. Frontiers in measuring biodiversity. Oxford University Press, New York, New York, USA.

Hilborn, R., T. P. Quinn, D. E. Schindler, and D. E. Rogers. 2003. Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Sciences USA 100:6564–6568.

Hooten, M. B., and N. T. Hobbs. 2015. A guide to Bayesian model selection for ecologists. Ecological Monographs 85:3–28.

Horn, M. H., and L. G. Allen. 1978. A distributional analysis of California coastal marine fishes. Journal of Biogeography 5:23–42.

Horn, M. H., L. G. Allen, and R. N. Lea. 2006. Biogeography. Pages 3–25 *in* L. G. Allen, D. J. Pondella II, and M. H. Horn, editors. The ecology of marine fishes: California and adjacent waters. University of California Press, Berkley, California, USA.

Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. Ecology 52:577–586.

IPCC [Intergovernmental Panel on Climate Change]. 2014. Climate change 2014: impacts, adaptation, and vulnerability. Part B: regional aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Kareiva, P., and M. Marvier. 2003. Conserving biodiversity coldspots: recent calls to direct conservation funding to the world's biodiversity hotspots may be bad investment advice. American Scientist 91:344–351.

Keller, A. A., J. R. Wallace, B. H. Horness, O. S. Hamel, and I. J. Stewart. 2012. Variations in eastern North Pacific demersal fish biomass based on the U.S. west coast groundfish bottom trawl survey (2003–2010). Fisheries Bulletin 110:205–222.

Krigsman, L. M., M. M. Yoklavich, E. J. Dick, and G. R. Cochrane. 2012. Models and maps: predicting the distribution of corals and other benthic macroinvertebrates in shelf habitats. Ecosphere 3:art3.

Krnjajić, M., A. Kottas, and D. Draper. 2008. Parametric and nonparametric Bayesian model specification: a case study involving models for count data. Computational Statistics and Data Analysis 52:2110–2128.

Krumbein, W., and L. Sloss. 1963. Stratigraphy and sedimentation. Second edition. W. H. Freeman, San Francisco, California, USA.

Latimer, A. M., S. Banerjee, H. Sang, Jr, and E. S. Mosher. 2009. Hierarchical models facilitate spatial analysis of large data sets: a case study on invasive plant species in the northeastern United States. Ecology Letters 12:144–154.

May, R. M. 1990. Taxonomy as destiny. Nature 347:129–130.

Miller, R. R., J. C. Field, J. A. Santora, I. D. Schroeder, D. D. Huff, M. Key, D. E. Pearson, and A. D. MacCall. 2014. A spatially distinct history of the development of California groundfish fisheries. PLoS ONE 9(6):e99758.

Mittermeier, R. A., G. A. B. da Fonsec, T. Brooks, J. Pilgrim, A. Rodrigues, and N. Myers. 2003. Hotspots and coldspots. American Scientist 91:384–384.

Myers, N. 1988. Threatened biotas: 'hotspots' in tropical forests. Environmentalist 8:187–208.

Myers, N. 2003. Biodiversity hotspots revisited. BioScience 53:916–917.

Myers, N., R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonesca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403:853–858.

NMFS [National Marine Fisheries Service]. 2013. Groundfish essential fish habitat synthesis: a report to the Pacific Fishery Management Council. NOAA, National Marine Fisheries Service, Northwest Fisheries Science Center, Seattle, Washington, USA.

Norton, B. G. 1994. On what we should save: the role of cultures in determining conservation targets. Page 466 *in* P. L. Forey, C. J. Humphries, and R. I. Vane-Wright, editors. Systematics and conservation evaluation. Clarendon Press, Oxford, UK.

Palumbi, S. R., et al. 2009. Managing for ocean biodiversity to sustain marine ecosystem services. Frontiers in Ecology and the Environment 7:204–211.

Purvis, A., and A. Hector. 2000. Getting the measure of biodiversity. Nature 405:212–219.

R Core Team. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reid, W. V. 1998. Biodiversity hotspots. Trends in Ecology and Evolution 13:275–280.

Royle, J. A., and C. K. Wikle. 2005. Efficient statistical mapping of avian count data. Environmental and Ecological Statistics 12:225–243.

Sala, E., and K. Knowlton. 2006. Global marine biodiversity trends. Annual Review Environmental Resources 31:93–122.

Sarkar, S. 2005. Biodiversity and environmental philosophy: an introduction. Cambridge University Press, New York, New York, USA.

Schleuter, D., M. Daufresne, F. Massol, and C. Argillier. 2010. A user's guide to functional diversity indices. Ecological Monographs 80:469–484.

Selig, E. R., W. R. Turner, S. Troëng, B. P. Wallace, B. S. Halpern, K. Kaschner, B. G. Lascelles, K. E. Carpenter, and R. A. Mittermeier. 2014. Global priorities for marine biodiversity conservation. PLoS ONE 9:e82898.

Shelton, A. O., J. T. Thorson, and E. J. Ward. 2014. Spatial, semi-parametric models improve estimates of species abundance and distribution. Canadian Journal of Fisheries and Aquatic Sciences 71(11):1655–1666.

Simpson, E. H. 1949. Measurement of diversity. Nature 163:688.

Stachowicz, J. J., J. F. Bruno, and J. E. Duffy. 2007. Understanding the effects of marine biodiversity on communities and ecosystems. Annual Review of

Ecology and Systematics 38:739–766.

Stuart-Smith, R. D., et al. 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. Nature 501:539–542.

Tittensor, D. P., C. Mora, W. Jetz, H. K. Lotze, D. Ricard, E. V. Berghe, and B. Worm. 2010. Global patterns and predictors of marine biodiversity across taxa. Nature 466:1098–1101.

Tolimieri, N. 2007. Patterns in species richness, species density, and evenness in groundfish assemblages on the continental slope of the US Pacific coast. Environmental Biology of Fishes 78:241–256.

Tolimieri, N., and M. J. Anderson. 2010. Taxonomic distinctness of demersal fishes of the California current: moving beyond simple measures of diversity for marine ecosystem-based management. PLoS ONE 5:e10653.

Tolimieri, N., and P. S. Levin. 2006. Assemblage structure of eastern pacific groundfishes on the US continental slope in relation to physical and environmental variables. Transactions of the American Fisheries Society 135:317–332.

Tuomisto, H. 2012. An updated consumer's guide to evenness and related indices. Oikos 121:1203–1218.

Turpie, J. K., L. E. Beckley, and S. M. Katua. 2000. Biogeography and the selection of priority areas for conservation of South African coastal fishes. Biological Conservation 92:59–72.

Villéger, S., N. W. H. Mason, and D. Mouillot. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89:2290–2301.

von Humboldt, A. 1808. Ansichten der Natur mit wissenschaftlichen Erlauterungen. J.G. Cotta, Tubingen, Germany.

Wallace, A. R. 1878. Tropical nature and other essays. McMillan, London, UK.

Wikle, C. K., L. M. Berliner, and N. Cressie. 1998. Hierarchical Bayesian space-time models. Environmental and Ecological Statistics 5:117–154.

Worm, B., et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science 314:787–790.

Worm, B., H. K. Lotze, and R. A. Myers. 2003. Predatory diversity hotspots in the blue ocean. Proceeding of the National Academy of Sciences USA 100:9884–9888.

Worm, B., M. Sandow, A. Oschlies, H. K. Lotze, and R. A. Myers. 2005. Global patterns of predator diversity in the open oceans. Science 309:1365–1369.

Zupan, L., M. Cabeza, L. Maiorano, C. Roquet, V. Devictor, S. Lavergne, D. Mouillot, N. Mouquet, J. Renaud, and W. Thuiller. 2014. Spatial mismatch of phylogenetic diversity across three vertebrate groups and protected areas in Europe. Diversity and Distributions 20:674–685.

Supplemental Material

Ecological Archives

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