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Field-measured variables outperform derived alternatives in Maryland stream biodiversity models

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Abstract

Aim: In order to map patterns of biodiversity in support of conservation efforts, statistical models require environmental variables with full coverage across the study area, typically in the form of gridded surfaces derived from GIS, remote sensing or via interpolation. However, derived variables may not be as physiologically relevant or as representative of on-the-ground conditions as field-measured variables. Here, we examine differences in the abilities of derived and field-measured variables to explain and predict biogeographical patterns of freshwater fish and benthic invertebrate communities.

Location: Maryland first- through fourth-order streams, USA.

Methods: We fit generalized dissimilarity models to fish and benthic invertebrate occurrence data (n = 2,165 site-years sampled over 18 years) using one set of field-measured predictors collected concurrent and collocated with faunal sampling, two sets of derived predictors (one representing local and one representing upstream conditions) or a combination. We then compared how well models explained and predicted spatial turnover in taxonomic composition (beta diversity).

Results: For all regions (four physiographic regions and the state as a whole) and for both fish and benthic invertebrates, models fit with field-measured variables were more explanatory and usually more predictive than models fit with derived variables. Within the category of derived predictors, those accounting for upstream conditions were more explanatory and predictive than local-scale versions.

Main conclusions: Although derived variables are most commonly used to describe and map biodiversity, they may be broadly inferior to field-measured variables as predictors in low-order stream biodiversity models. Collection of field-measured data and development of derived data that consider upstream conditions and capture physiologically relevant environmental characteristics are likely to improve our capability to predict and explain spatial patterns of low-order stream biodiversity.

KEYWORDS
benthic invertebrates, community-level model, freshwater fish, generalized dissimilarity model, predictor variables, species distribution model

1 | INTRODUCTION

Effective conservation requires knowledge of the spatial distribution of biota of interest (Dudgeon et al., 2006), but biological census data are typically sparse relative to the extent of areas of concern (Ferrier, Drielsma, Manion, & Watson, 2002; Hawkins & Norris, 2000; Leathwick et al., 2011). In an attempt to overcome this issue, statistical modelling and mapped environmental variables are often used to extrapolate biological patterns to unsampled areas (Elith & Leathwick, 2009; Ferrier & Guisan, 2006). The reliability of such spatial predictions is strongly related to how well the environmental variables characterize conditions that influence species distributions. Therefore, choosing relevant environmental predictor variables remains one of the most universal challenges in modelling geographical patterns of biodiversity (Araújo & Guisan, 2006; Synes & Osborne, 2011; Williams, Belbin, Austin, Stein, & Ferrier, 2012).

Previous studies have explored multiple aspects of variable selection (Austin, 2002), including variable resolution and extent (Austin & Van Niel, 2011; Mackey & Lindenmayer, 2001; Morley & Karr, 2002; Peterson, Sheldon, Darnell, Bunn, & Harch, 2011; Wang, Lyons, & Kanehl, 2003), collinearity between variables (Braunisch et al., 2013) and the method used to retain or eliminate variables from models (Mac Nally, 2000; Pearce & Ferrier, 2000). While most studies emphasize the maximization of model accuracy and predictive ability (e.g., Bucklin et al., 2015; Esselman & Allan, 2010), few have asked a more fundamental question: Are we considering the most biologically relevant predictors in the first place (but see Austin & Van Niel, 2011)? Addressing this question has become more urgent as conservation planning increasingly relies on predictions of spatial patterns of biodiversity under novel future conditions (Fitzpatrick et al., 2011; Maguire, Blois, Nieto-Lugilde, Fitzpatrick, & Williams, 2015; Mokany & Ferrier, 2010).

Theory predicts that variables with a direct physiological influence should be more relevant for modelling patterns of biodiversity than variables with an indirect influence mediated by associations with proximal forces (Austin, 2002; Williams et al., 2012). For example, stream temperature should be a stronger predictor of fish distributions than latitude or altitude, although they are correlated. However, direct, physiologically relevant predictors often require field measurement and are therefore difficult to produce in the full-coverage layers necessary for prediction across space (Frederico, De Marco, & Zuanon, 2014). For this reason, most predictive models rely on environmental variables derived from GIS, remote sensing or interpolation, which are less likely to be physiologically relevant (Austin, 2002) and often suffer from scaling issues (Cord, Meentemeyer, Leitão, & Václavík, 2013; Lechner, Langford, Bekessy, & Jones, 2012).

The disparity between derived and field-measured predictors is likely to be particularly severe in streams, whose relatively small size places them beyond the realm of many remote sensing techniques (Elmore, Julian, Guinn, & Fitzpatrick, 2013) and for which dendritic habitat geometry (Grant, Lowe, & Fagan, 2007), heterogeneous environmental conditions (Dettinger & Diaz, 2000) and integration of upstream influences (Nelson et al., 2009) make interpolation of point measurements into the continuous surfaces needed for predictive mapping a challenge.

Here, we examine differences in the abilities of derived and field-measured variables to explain and predict biogeographical patterns of freshwater fish and benthic invertebrate communities in first- through fourth-order streams in Maryland, USA. To assess variable importance, we modelled patterns of beta diversity using generalized dissimilarity modelling (GDM; Ferrier, Manion, Elith, & Richardson, 2007). GDM considers all species in an assemblage regardless of rarity and statistically selects, weights and transforms candidate environmental variables such that they best represent biological patterns. Our results highlight the inherent challenges of stream biodiversity modelling, but suggest that gains in model performance can be achieved by including field-measured predictors, using derived variables that integrate upstream conditions, and developing physiologically relevant predictors.

2 | METHODS

2.1 | Study region

We considered first- through fourth-order streams in Maryland west of the Chesapeake Bay (see Fig. S1) and used Elmore et al.'s (2013) stream map to define stream locations. The area has strong gradients in population density, land cover, elevation and geology. Population density ranges from east to west from 2604.7 people km^{-2} in the heavily urbanized coastal lowlands around Baltimore to 17.7 people km^{-2} in the forested, mountainous watersheds of Garrett County (World Media Group, 2014). Thus, for a relatively small area, the study region is characterized by substantial environmental gradients that span an array of stream habitat types and five physiographic provinces. Following convention, we divided Maryland into three regions: the Coastal Plain (C), the Piedmont (P) and the Highlands (Utz, Hilderbrand, & Boward, 2009). Because a portion of the westernmost Highlands region drains into the Youghiogheny and Ohio Rivers rather than into the Chesapeake Bay, we further divided that region into the Chesapeake (H) and Youghiogheny (Y) basins. We modelled each of these four regions separately, recognizing the role of their unique geologic character and history in governing biotic distributions and influential habitat variables (Melles, Jones, & Schmidt, 2014). To examine how variable importance changes with spatial extent, we also fit state-level (S) models that combined data from the four individual regions, making five areas total.

2.2 | Biological data

Fish and benthic invertebrate occurrence data were from the Maryland Department of Natural Resources' Maryland Biological Stream Survey (MBSS; Stranko et al., 2007). The MBSS follows standardized protocols to sample 75-m segments of non-tidal first-through fourth-order streams (Stranko et al., 2007). In three sampling periods over 18 years (1994–2011) and with excellent spatial coverage of the study area (Fig. S1), the MBSS collected occurrence data for approximately 100 fish species and 600 invertebrate taxa. We used data for 86 native fish identified to species (Johnston, 2014) and 581 invertebrate taxa identified to family or genus at 2,165 unique site-years. To ensure that all survey points coincided with Elmore

et al.'s (2013) mapped streams, we used custom scripts to snap site locations to the nearest stream cell along flow lines. When possible, points farther than 300 m from stream cells or located on flat terrain without clear flow direction were manually moved to a stream location using site descriptions recorded on MBSS datasheets. Points that could not reliably be snapped to streams were excluded from the study.

2.3 | Environmental predictor variables

2.3.1 | Field-measured variables

Field-measured environmental variables were collected by the MBSS at survey locations coincident with faunal sampling (Stranko et al.,

2007). They include stream measurements relating to flow and gradient, in-stream habitat, and water temperature and chemistry (Table 1). We omitted unordered categorical variables and variables with five or fewer ordered categories to accommodate GDM's use of environmental distances in model fitting (Ferrier et al., 2007). To maintain sample sizes, we also omitted any field-measured variable lacking measurements for at least 1,000 site-years. After variable omission, we retained only site-years with a complete suite of measurements for the analyses.

2.3.2 | Derived variables

Our derived variables attempt to characterize aspects of the abiotic environment likely to influence the occurrence of aquatic organisms

Variable code	Description
Flow and Gradient	
ST_GRAD	Stream gradient (%), measured from the downstream boundary of the sample segment to the upstream boundary with an inclinometer (1995–2004) or a level (2007–2009)
DischargeCFS	Summer stream flow (cubic feet per second), standard transect method
Habitat	
INSTRHAB	In-stream fish habitat structure rating (0–20)
EPI_SUB	Epifaunal substrate rating (benthic invertebrate habitat, 0–20)
VEL_DPTH	Velocity/depth diversity rating (0–20)
POOLQUAL	Pool/glide/eddy quality rating (0–20)
RIFFQUAL	Riffle/run quality rating (0–20)
EMBEDDED	Embeddedness: percentage that gravel, cobble and boulder particles are surrounded by sediment or flocculent material
SHADING	Percentage of segment that is shaded
AESTHET	Trash rating (0–20)
MAXDEPTH	Maximum depth in sample reach (cm)
AVGWID	Average wetted width of the 1, 25, 50 and 75 m points of the sample segment (m)
AVGTHAL	Average thalweg depth of the 1, 25, 50 and 75 m points of the sample segment (cm)
AVG_VEL	Average velocity of the 1, 25, 50 and 75 m points of the sample segment (m/s)
Water Chemistry	
PH_LAB	Spring pH, measured in the laboratory
COND_LAB	Spring conductance (µmho/cm), laboratory
ANC_LAB	Acid-neutralizing capacity (µeq/L), laboratory
DOC_LAB	Dissolved organic carbon (mg/L), laboratory
SO4_LAB	Sulfate (mg/L), laboratory
NO3_LAB	Nitrate nitrogen (mg/L), laboratory
TEMP_FLD	In situ summer water temperature (°C)
DO_FLD	In situ dissolved oxygen (mg/L)
PH_FLD	In situ summer pH
COND_FLD	In situ summer conductance (µmho/cm)

TABLE 1 Field-measured variables collected by the MBSS at survey locations and considered as environmental predictor variables in generalized dissimilarity models

while emphasizing both local- and watershed-scale physical characteristics. The derived variables were either developed using GIS and/or remote sensing data or downloaded from online databases. All derived variables are temporally invariant and were created at or resampled to 10 m resolution to match the scale of Elmore et al.'s (2013) stream maps.

The derived variables (Table 2) represent as comprehensive a set of environmental variables as reasonably could be developed using available datasets for the study region. Few are direct analogues of the field-measured variables, and they were not intended to be: our goal was to assess field-measured and derived environmental variables in groups, as they are typically used in biodiversity models, rather than to engage in head-to-head comparisons between individual predictors. Indeed, a major difference between field-measured and derived variables is the environmental characteristics they are able to capture, which makes most direct, individual comparisons impossible (e.g., consider the potential for derived surrogates of water chemistry variables). Additionally, as there are typically multiple environmental variables in biodiversity models, we must consider the full complements of variables to understand both variable set synergies and shortcomings; comparisons of individual variables would yield fragmented results.

Our derived variables are topographic, hydrographic, land use/cover, or related to soils or climate (Table 2). Topographic variables characterize landscape shape and, by extension, stream channel shape and related characteristics, such as flow speed and substrate type (Melles et al., 2014). We used a 10 m digital elevation model (DEM) from the National Elevation Dataset (Gesch et al., 2002; Julian, Elmore, & Guinn, 2012) to derive all topographic variables. Hydrographic variables capture flow and network characteristics, such as the residence time of water in watersheds, the relative importance of terrestrial and aquatic inputs, and the area of available connected habitat (Elmore et al., 2013). We used the Terrain Analysis Using Digital Elevation Models toolset (Tarboton, 2014) to derive eight-way flow direction and accumulation (i.e., watershed size), and we measured stream length and network density from Elmore et al.'s (2013) stream map. To characterize urban effects on streams, we also used a set of "stream burial" variables that quantify the extent to which stream segments have been paved over or directed into culverts, pipes or concrete-lined ditches (Elmore & Kaushal, 2008). Burial-related variables were calculated using the 2001 National Land Cover Database impervious surface map (Homer et al., 2007) and USGS 30-cm aerial photography (Elmore & Kaushal, 2008).

To capture in-stream sediment loads and aspects of water chemistry, we used the Natural Resources Conservation Service's Soil Survey Geographic Database (Soil Survey Staff, n.d.). Silt–clay % influences run-off potential and proneness to flash flooding, soil erodibility and bulk density are related to stream sediment load, and soil pH and bedrock depth can affect water chemistry. We used annual mean surface air temperature from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) to characterize climate.

Land use and land cover also have strong influences on stream biota (Allan, 2004) and therefore are some of the most commonly used predictors of water quality and biotic assemblages in streams (e.g.,

Allan, 2004; Harding, Benfield, Bolstad, Helfman, & Jones, 1998; Utz, Hilderbrand, & Raesly, 2010; Van Sickle & Johnson, 2008). To quantify land cover/use influences, we used forest, canopy cover, wetland, agriculture and impervious surface maps from the 2001 National Land Cover Database (Homer et al., 2007). Impervious surface and canopy cover were mapped as continuous percentages; others were considered present or absent.

We developed multiple versions of these derived variables differing in their spatial attributes: local, spatially weighted accumulated or non-weighted accumulated. Local derived variables reflect the region containing or directly adjacent to an MBSS survey site. For non-hydrographic variables, local variables were calculated in a 30 × 30 m window (3 × 3 10 m pixels) around the site. If the variable was hydrographic, we calculated the local versions using stream cells in a 30 × 10 m window (one pixel upstream, one downstream and the site location).

Spatially weighted and non-weighted accumulated variables characterize the influence of upstream conditions on downstream pixels. Non-weighted accumulated variables quantify the average value of a variable for the entire upstream basin, defined by eight-directional flow path and flow accumulation rasters (Tarboton, 2014). In contrast, spatially weighted accumulated variables account for the unequal influences of each upstream pixel on a particular downstream pixel (Johnson, McNair, Srivastava, & Hart, 2007; Peterson et al., 2011; Sheldon et al., 2012; Van Sickle & Johnson, 2008). Weighted versions of the five land covers (forest, wetland, agriculture, canopy cover and impervious surface) were calculated using an inverse distance weighting scheme adapted from Peterson et al.:

$$\%LU = \frac{\sum_{i=1}^{n} I(k)W_i FA_i}{\sum_{i=1}^{n} W_i FA_i} \times 100,$$

where LU is the land use of a given class, W_i is the weight given to an upstream pixel, i, according to its distance from the nearest stream (here [distance + 1]$^{-1}$), and FA_i is the number of pixels that flow into pixel i (flow accumulation weight). In the case of categorical land uses, $I(k)$ is an index equal to one for the pixels classified as the land use of interest and zero for all other pixels. In the case of land uses with continuous scores, $I(k)$ is equal to the continuous value. Thus, we weighted land pixels through which more water flows and that are closer (by flow distance) to the stream pixel of interest more heavily than farther land pixels through which less water flows.

When fitting models, we grouped non-weighted and spatially weighted accumulated variables together as "accumulated derived." As such, we compared three variable sets: field-measured variables collected by the MBSS in situ (F, Table 1), local derived variables (L, Table 2) and accumulated derived variables (A, Table 2).

2.4 | Statistical modelling

We compared the abilities of the three variable sets to explain and predict patterns of stream biodiversity using GDM, a nonlinear matrix

TABLE 2 Derived variables considered as predictors in generalized dissimilarity models. Local versions characterize conditions directly adjacent to stream pixels (1 × 3 pixels or 3 × 3 pixels); accumulated versions characterize either mean upstream conditions ("accumulated") or upstream conditions where each pixel is weighted by flow path distance to the stream and number of contributing pixels ("weighted acc."). All variables were created at or resampled to 10 m

Variable code	Version	Description. Source
Topographic		
slp	Local	Slope (degrees). NED DEM
	Accumulated	
plan	Local	Transverse curvature at cell perpendicular to flow direction (1/100 elevation units). NED DEM
	Accumulated	
prof	Local	Longitudinal curvature at cell parallel to flow direction (1/100 elevation units). NED DEM
	Accumulated	
Hydrographic		
dem10mp	Local	Eight direction flow raster (1 = East, 2 = SE, etc.). TauDEM
dem10mad8	Accumulated	Number of 10 × 10 m cells that flow into the cell. TauDEM
str_len	Local	Length of stream (km). Elmore et al. (2013) map
	Accumulated	
str_den	Accumulated	Upstream network density (km/km^2). Elmore et al. (2013) map
confluence_num	Accumulated	Number of stream segments that come together on a cell. Elmore et al. (2013) map
str_blen	Local	Length of stream burial (km). Burial probability classified using NLCD 2001 30 m ISA layer
	Accumulated	
bp_2001	Local	Burial probability (0–1). Determined using NLCD 2001 30 m ISA layer
str_bp	Accumulated	Burial probability accumulated (0–1). Determined using NLCD 2001 30 m ISA layer
str_blen_den	Accumulated	Upstream burial density (km/km^2). Determined using NLCD 2001 30 m ISA layer
Land Use/Land Cover		
isa	Local	Proportion impervious surface area, 0–1. NLCD 2001 30 m ISA layer
	Accumulated	

(Continues)

TABLE 2 (Continued)

Variable code	Version	Description. Source
isa_fls_nor	Weighted acc.	
cc	Local	Proportion canopy cover, 0–1. NLCD 2001 30 m
	Accumulated	canopy cover data
cc_fls_nor	Weighted acc.	
for	Local	Forest presence, 0 or 1. NLCD 2001 30 m
	Accumulated	forest data, forest = {41,42,43}
for_fls_nor	Weighted acc.	
ag	Local	Agriculture presence, 0 or 1. NLCD 2001
	Accumulated	30 m LULC data, agriculture = {81,82}
ag_fls_nor	Weighted acc.	
wet	Local	Wetland presence, 0 or 1. NLCD 2001 30 m
	Accumulated	LULC data, wetlands = {90,95}
wet_fls_nor	Weighted acc.	
Soils		
sicl	Local	Proportion of soil volume (0–1) that is below 63 μm in texture. SSURGO, 0.6 ha
	Accumulated	
kfw	Local	Soil erodibility (K value). SSURGO, 0.6 ha
	Accumulated	
bd	Local	Bulk density indicator of soil compaction (g/cm^3). SSURGO, 0.6 ha
	Accumulated	
brd	Local	Distance from soil surface to top of bedrock layer (cm). SSURGO, 0.6 ha
	Accumulated	
ph	Local	Relative acidity or alkalinity of a soil sample. SSURGO, 0.6 ha
	Accumulated	
Climate		
sat	Local	Annual mean temperature (°C*10). WorldClim 2.5 arc-minutes, Bioclim variable 1
	Accumulated	

NED DEM, National Elevation Dataset Digital Elevation Model; TauDEM, Terrain Analysis Using Digital Elevation Models; NLCD, National Land Cover Database; ISA, Impervious Surface Area; SSURGO, Soil Survey Geographic Database.

regression technique (Ferrier et al., 2007). GDM relates pairwise dissimilarity in species composition (biological dissimilarity, the response variable, quantified using the Sørensen index; Sørensen, 1948) to a set

of predictor variables describing how sites differ in their environmental conditions (environmental distance) and how spatially isolated they are from one another (geographical distance).

Generalized dissimilarity modelling accommodates two nonlinearities common in large ecological datasets: variation in the rate of compositional turnover of species along environmental gradients (non-stationarity), and the curvilinear relationship between compositional dissimilarity and environmental/geographical distance (Allan, 2004; Dodds, Clements, Gido, Hilderbrand, & King, 2010; Ferrier et al., 2007). The asymptotic nature of compositional dissimilarity metrics is addressed by transforming the scaled relationship between the distance predictors and compositional dissimilarity using a generalized linear model with an exponential link function (Ferrier et al., 2002, 2007). To accommodate non-stationarity in rates of species turnover along gradients, GDM fits flexible, positively monotonic I-splines to each predictor (Ferrier et al., 2007). The shape of the I-spline indicates the rate of biological turnover at each position along the gradient (Ferrier et al., 2007). I-splines thereby provide a means to weight and transform environmental predictor variables objectively such that they best represent biological patterns (Ferrier et al., 2007; Leathwick et al., 2011; Williams et al., 2012). Because GDM assimilates the responses of many species to environmental gradients, we expect that conclusions will be less sensitive to atypical individual species/environment relationships.

We converted occurrence data to presence/absence, which is considered more reliable for benthic invertebrates in the MBSS dataset (Boward & Friedman, 2011). For each year, we considered pairwise comparisons between all sites surveyed in that year. We omitted pairwise comparisons when the year of survey was different to avoid concurrently modelling both temporal and spatial beta diversity. In addition to the environmental predictors, we also included geographical distance between sites as a predictor in all models.

We fit a total of 70 GDMs, including separate models for each combination of area (five), survey taxon (fish, benthic invertebrates) and variable set (seven combinations of three variable groups: F = field-measured variables only, A = accumulated derived variables only, L = local derived variables only, AL = accumulated derived and local derived variables, FA = field-measured and accumulated derived variables, FL = field-measured and local derived variables, and FAL = field-measured, accumulated derived and local derived variables). We removed correlated variables (Pearson or Spearman correlations >|.7|) both within and between each variable set for each region, retaining those variables of correlated sets that we considered most biologically relevant (Austin, 2002; Williams et al., 2012). In the few cases where variables were correlated across sets (i.e., L with A, L with F or A with F), we retained the variable deemed most biologically relevant (Johnston, 2014). Manually choosing candidate variables in cross-group comparisons could bias our results. However, cross-group correlations were rare and only three variables were omitted as a result: accumulated surface air temperature, accumulated soil erodibility and flow accumulation (Table S1). There was only one correlated field-measured/derived pair (Table S1).

After removing correlated variables, we quantified variable importance and tested for statistical significance of individual predictor

variables and the model itself using matrix permutation and backward elimination as implemented in the *gdm.varImp* function in the gdm library (Manion, Lisk, Ferrier, Nieto-Lugilde, & Fitzpatrick, 2016). To test model significance, we first fit GDM using the unpermuted environmental data. Next, we permuted the entire environmental table 100 times and fit GDM to each permuted table. Model significance was determined by comparing the deviance explained by GDM fit to the unpermuted table to the distribution of deviance explained values from GDM fit to the 100 permuted tables. To assess variable significance, this process was repeated for each predictor individually (i.e., only the data for the variable being tested were permuted rather than the entire environmental table). Variable importance was quantified as the percentage reduction in deviance explained between models fit with the variable permuted and unpermuted. The variable with the largest *p*-value was removed, and the process was repeated until all non-significant predictors were removed. To reduce computation time, the state-level models were fit five times using a random 50% subset of site-pairs, rather than once using the entire dataset. We quantified predictor contribution to deviance explained by averaging results from the permutations of these five models; results were consistent across models. All GDM analyses were performed in R version 3.0.1 (R Core Team, 2013).

2.5 | Evaluation of field-measured and derived variable sets

We compared GDM explanatory power and predictive ability within area and taxon (fish or invertebrates), so the only difference between models was predictor variable set. We measured how well models explained faunal beta diversity using percentage deviance explained. We also used deviance partitioning to determine the percentage of explained deviance uniquely attributable to each of the three variable groups for each area–taxon combination (Borcard, Legendre, & Drapeau, 1992; Jones et al., 2013; Whittaker, 1984).

Beyond being explanatory, models useful for management must make accurate predictions to unsurveyed locations. We measured model predictive ability by assessing how well models fit with training data were able to predict withheld test data. For each region/taxon/variable set combination, we randomly partitioned site-pairs 50 times into training (70%) and testing (30%) sets. We fit GDMs using training data and the variables pre-selected by the permutation/backward selection procedure and then predicted compositional dissimilarity to test site-pairs. We assessed predicted compositional dissimilarity using the median error of the predicted versus observed compositional dissimilarity, based on standardized residuals. We compared standardized residuals within area–taxon pairs using Kruskal–Wallis rank sum tests followed by multiple comparison tests.

3 | RESULTS

3.1 | Explanatory power

Generalized dissimilarity models explained between 3.1% and 43.7% of the deviance in compositional dissimilarity, depending on variable
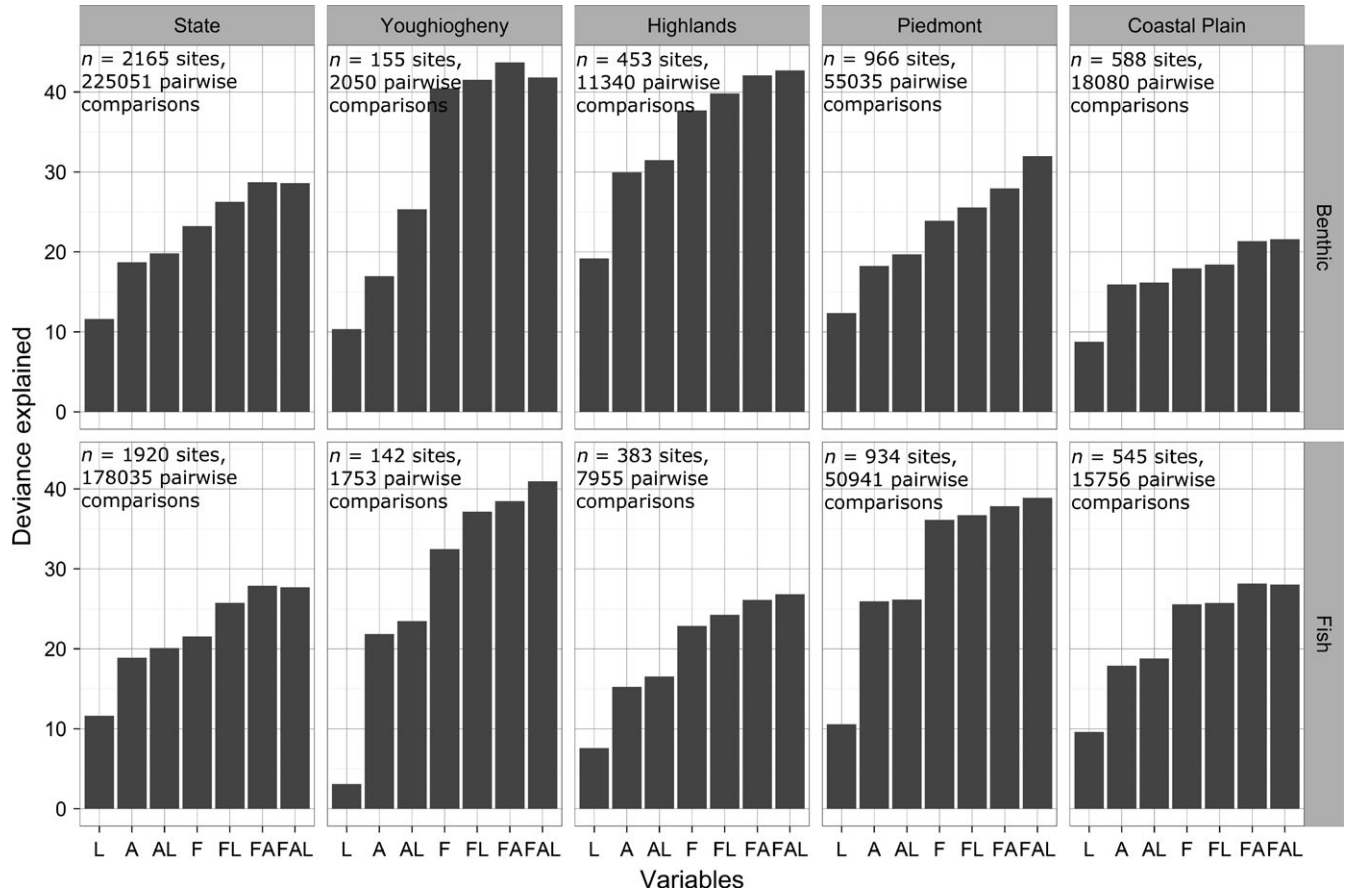
FIGURE 1 Deviance explained values for generalized dissimilarity models in five areas (four regions and statewide) and for both fish and benthic invertebrates. Each panel is an area–taxon pair. F = field-measured, L = local derived and A = accumulated derived variables

set, area and taxon (Figure 1). Across areas, average deviance explained of models built with derived variables (AL) was 22.5% for benthic invertebrates and 21.0% for fish. In contrast, average deviance explained of models built with only field-measured variables (F) was 28.6% and 27.7% for benthic invertebrates and fish. Average deviance explained of models considering variables from all three sets (FAL) was the greatest: 33.3% for benthic invertebrates and 32.5% for fish. Within each area–taxon pair, the model built with only local derived

variables always had the lowest deviance explained, and models that included field-measured variables always had the highest deviance explained.

Deviance partitioning revealed that across areas and taxa, local derived variables uniquely explained no more than 12.6% of the total deviance (total deviance was quantified as deviance explained by the relevant FAL model, Figure 2). Accumulated derived variables uniquely explained between 0.7% and 20.0% of the deviance, and
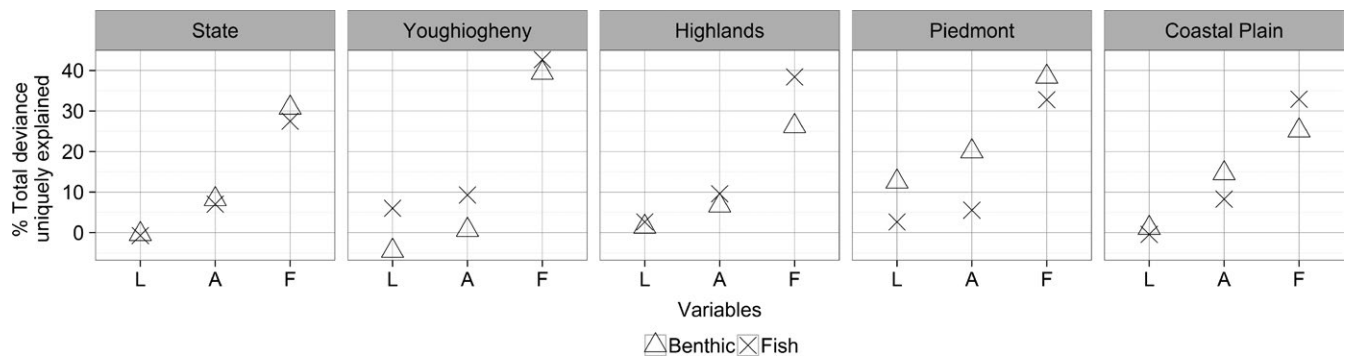

FIGURE 2 Percentage of total deviance (defined as deviance of the FAL model) uniquely explained by each variable set (F = field-measured, L = local derived, A = accumulated derived) for area–taxon pairs. Note that some of the local derived percentages are negative because models were not perfectly nested

field-measured variables uniquely explained between 25.1% and 42.7%.

3.2 | Predictive ability

Relationships between predicted and observed compositional dissimilarity for all variable sets, all areas, and both fish and invertebrates clustered around the one-to-one line, although in all cases there was considerable scatter (Fig. S2). Kruskal–Wallis rank sum tests showed that within each area and taxon, there were significant differences in how effectively models fit with different variable sets predicted biological dissimilarity among withheld site-pairs (Figure 3, Table S2). Within area/taxon pairs, models that were not significantly different in prediction error tended to be fit either both with or both without field-measured variables (Table S2). Exceptions included cases in which accumulated derived and field-measured variables were similarly predictive. In contrast, predictive ability of models built with only local derived vs. field-measured variables was always significantly different except in three cases: for the statewide fish and Youghiogheny and Coastal Plain benthic invertebrate models.

Overall, the pattern in predictive ability (Figure 3) was similar to the pattern in explanatory power (Figure 1): models built with only local

derived variables almost always had the lowest predictive ability (the average median standardized residual for L models was 0.49), followed by models built with accumulated derived variables (A and AL models both had an average median error of 0.47). Models including field-measured variables had the best predictive ability (F models had average median standardized residual = 0.46), although several individual derived variables were also useful for explanation and prediction (Figure 4, Table S3).

4 | DISCUSSION

Spatial modelling of biodiversity is an important conservation tool for informing management, identifying priority preservation areas (Ferrier, 2002; Margules, Pressey, & Williams, 2002) and understanding impacts of global change (Botkin et al., 2007; Fitzpatrick, Gove, Sanders, & Dunn, 2008; Maguire et al., 2015). However, the utility of models for conservation depends on the extent to which predictor variables are associated with patterns of biodiversity. Overall, we found that in first- through fourth-order Maryland streams, the sorts of derived environmental variables most commonly available for predictive biodiversity mapping (i.e., local-scale derived variables) were inferior to field-based measurements. Derived variables that
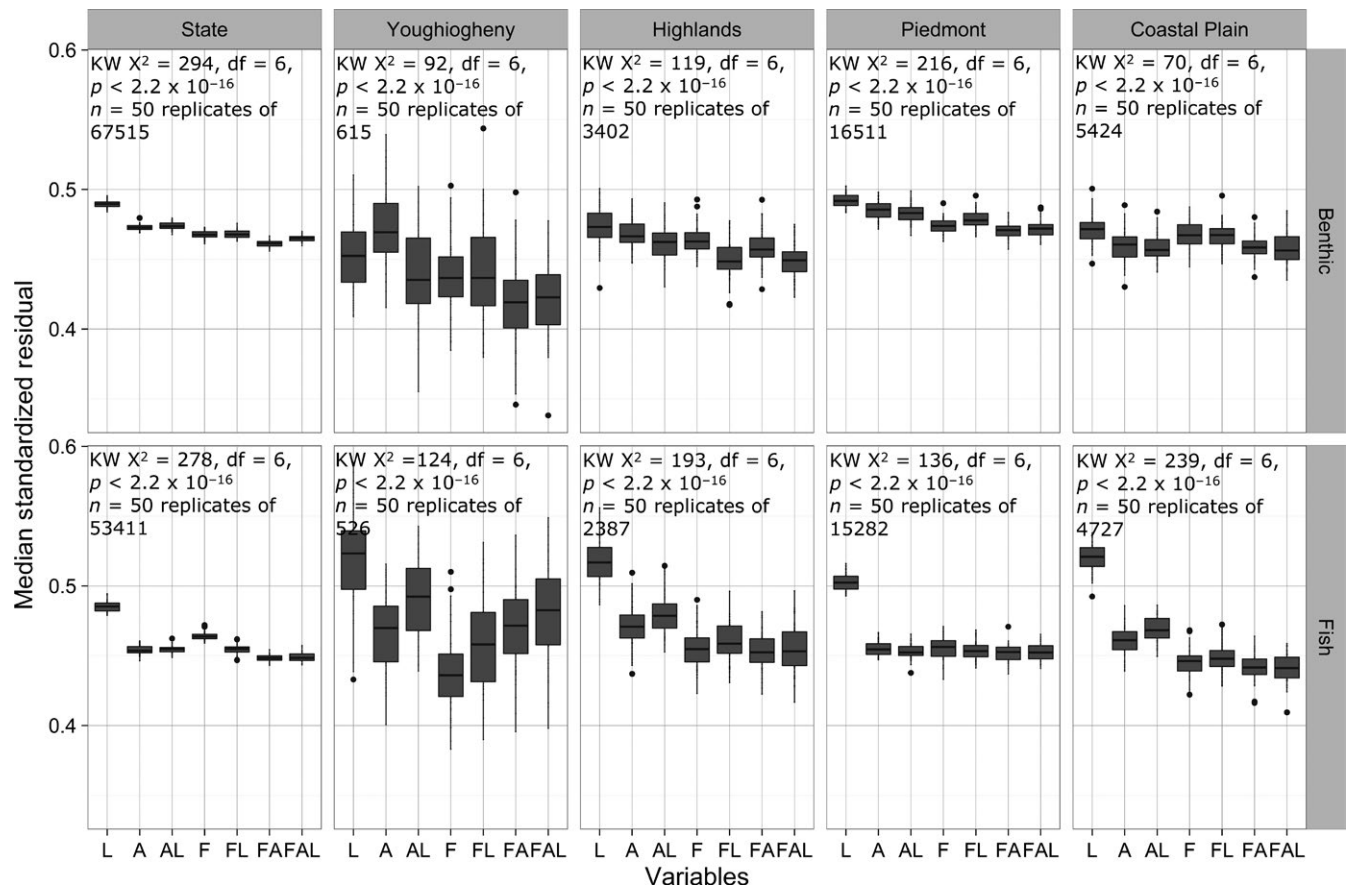

FIGURE 3 Boxplots of median error of predicted dissimilarities, where each box summarizes 50 median errors based on standardized residuals. F = field-measured, L = local derived and A = accumulated derived variables. For significant differences between boxes within area–taxon pairs, see Table S2
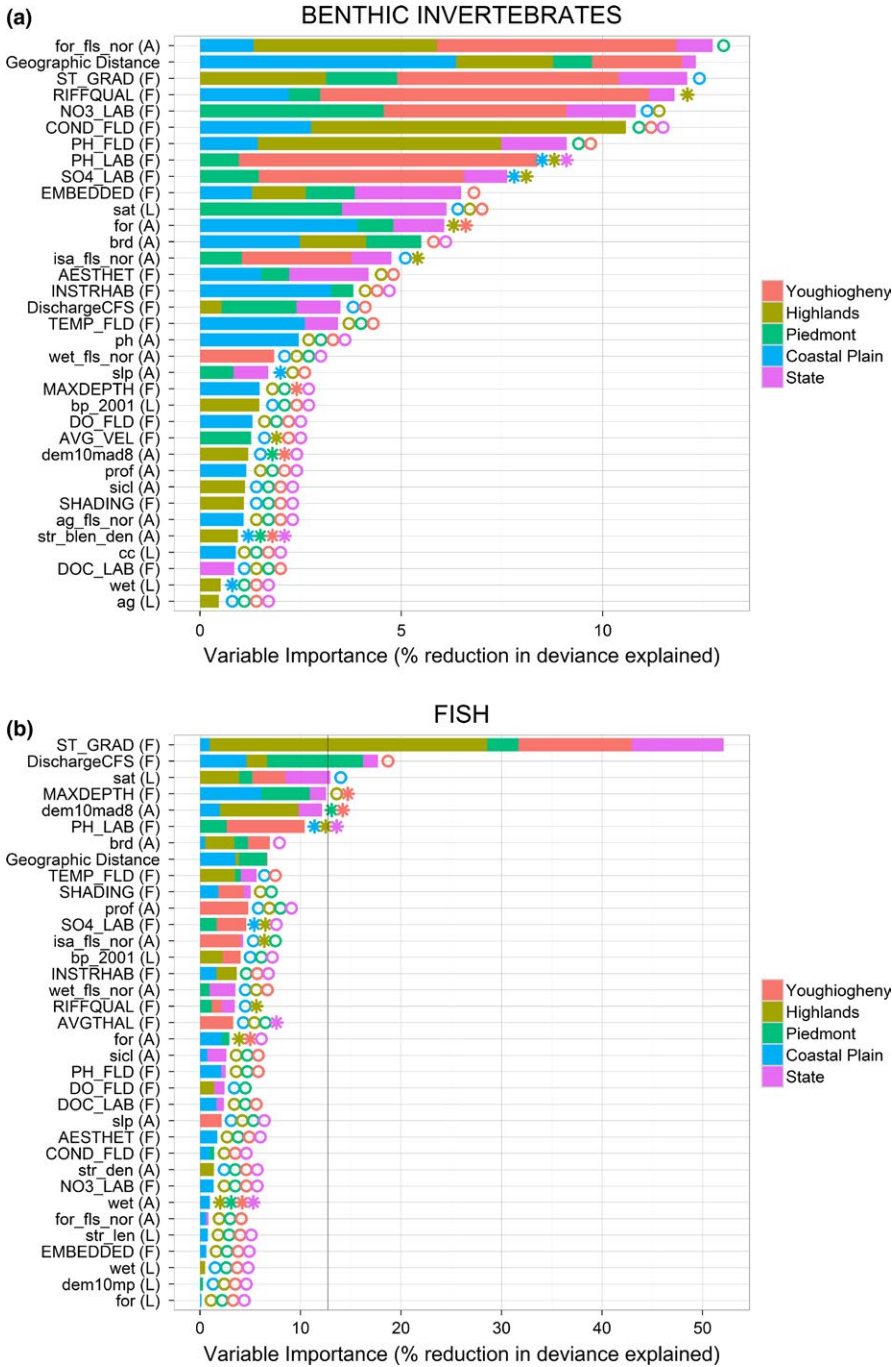
(a)

(b)

FIGURE 4 Importance of predictor variables selected in generalized dissimilarity models for (a) benthic invertebrates and (b) fish when field-measured (F), accumulated derived (A) and local derived (L) variables were candidates. Variable importance is quantified as the percentage reduction in deviance explained when the variable is permuted. Note differences in *x*-axis scales, with the black vertical line in the lower panel indicating the maximum combined value in the upper panel. Symbols next to the bars show whether unselected variables were removed as a result of (o) correlation analysis or (*) by permutation/backward selection

attempted to capture catchment-scale conditions were significantly more explanatory and predictive than their local counterparts, but still tended to be inferior to field measurements. Still, no category of variables was entirely without value, and the best models included representatives from all available variable types. These findings were consistent for both fish and benthic invertebrates across Maryland's varied physiographic regions and in the statewide analysis.

4.1 | Scaling considerations

We expected that the relative importance of variables would change with extent of the region being modelled. However, results from the

statewide analyses broadly agree with regional results. In fact, contrary to expectation, we found that there was a higher number of statistically significant differences between statewide models than between regional models (likely associated with the higher power afforded by the greater number of site-years at the scale of the entire state, Table S2). Congruence of regional and statewide results suggests that failure to include physiologically relevant predictors in low-order stream biodiversity models could have important conservation implications. However, in the context of the consistent results across physiographic regions and the state in this study, it is also important to mention that we expect the relative strengths of field-measured vs. derived variables in stream biodiversity models to be contingent not

only on the spatial extent of the modelled area, but also on stream size and the spatial and temporal scales of the variables themselves.

Our results are most relevant to first- through fourth-order streams in Maryland; practitioners interested in applying stream biodiversity models at other scales may find different results. Analyses of much broader spatial extents (e.g., continental) would be expected to find increased predictive power of broad-scale derived variables while decreasing the feasibility of taking field measurements. For example, a study of third- to sixth-order streams in north-eastern Mesoamerica determined that reach-level, field-measured variables explained less variation in fish occurrences than derived catchment-level data (though the authors acknowledge their results are atypical, Essleman & Allan, 2010).

In addition to study area extent and stream size, efficacy of predictor variables in stream biodiversity models is related to their ability to capture a range of spatially nested scales (Frissell, Liss, Warren, & Hurley, 1986). The hierarchical nature of stream networks is an important consideration of our analyses, as spatial relevance is a main distinguishing characteristic of field-measured vs. derived variables. Field-measured variables are necessarily local (though downstream flow ensures that they integrate aspects of upstream influences). In contrast, derived predictors may be either local or calculated at the catchment level. But at which spatial scale should "catchment" be defined? To the extent possible, we attempted to leverage the power of derived variables to capture influences on stream biodiversity at multiple scales by including both local-scale and accumulated derived variables, by inverse distance weighting the land use variables, and with our consideration of variables that define a study site's location in the watershed (str_len, str_den and dem10mad8). Indeed, one of our most striking results is that field-measured variables outperform derived variables *despite* their local scale. However, we acknowledge that we did not exhaust the possibilities for derived variables to capture hierarchical watershed processes, and we recommend that future research consider the utility of derived variables at additional spatial scales (e.g., Stein, Hutchinson, & Stein, 2014).

Finally, it is also clear that stream communities are sensitive to dynamics across time (e.g., Harding et al., 1998), which were not included in either of our variable sets. In cases when temporal dynamics are considered and only derived data are available across time, derived variables would become comparatively more valuable.

4.2 | Evaluation of field-measured and derived variable sets

Despite the above scale-related caveats, this research quantitatively corroborates extensive theoretical work suggesting that environmental measures with direct physiological effects should have greatest predictive power (i.e., Austin, 1980; Dormann et al., 2012; Elith & Leathwick, 2009; Franklin, 1995). The overall superior explanatory and predictive ability of field-measured variables in models is especially compelling given that our derived variables represent an extension of variables previously used in similar applications of GDM to stream biodiversity (Leathwick et al., 2011; Snelder et al., 2012): our base stream map is more realistic than the National Hydrography Dataset (Elmore et al.,

2013), and the stream burial metrics (Elmore & Kaushal, 2008) and land use inverse weighting (Peterson et al., 2011) are relatively novel.

We speculate that in addition to the greater physiological relevance of field-measured variables, their superiority may also be related to the dendritic shape and integrative nature of streams, which makes deriving relevant variables particularly challenging. Interpolation of stream measurements must consider directionality (Peterson et al., 2013), confluence locations (Benda et al., 2004) and connectivity (Grant et al., 2007); myriad small, ephemeral or intermittent channels have been difficult to map using remote sensing tools alone (Elmore et al., 2013); and predictor variables must characterize both upstream and local drivers of biotic distributions (Kratzer et al., 2006; Morley & Karr, 2002; Stanfield & Kilgour, 2013; Urban, Skelly, Burchsted, Price, & Lowry, 2006). Thus, we suggest that the relative strength of field-measured variables is partially related to their greater biotic relevance and partially to the relative weakness of other candidates. This balance could shift in other ecosystems.

In low-order temperate stream systems, however, we expect that our results will be broadly applicable. The physiographic regions of Maryland vary in their natural environments and human population density (Reger & Cleaves, 2008), and the amount of deviance explained by the models developed for this study is on par with that reported by other studies applying GDM to stream biodiversity (Leathwick et al., 2011; Snelder et al., 2012), allowing for differences in length of environmental gradients (Murphy, 2010), available predictors and sample size (Leathwick et al., 2011; Snelder et al., 2012).

The three cases in which local derived predictors were comparable to field-measured predictors demonstrate that there could be situations in which local derived variables are superior. In the case of the Coastal Plain benthic invertebrates, we hypothesize that field-measured variables are performing particularly poorly rather than that local-scale variables are performing well. Field-measured variables represent only the moment of sampling and therefore may be less able to characterize extremes. In the past, Coastal Plain streams have responded more dramatically to drought conditions than streams in Maryland's other regions, experiencing very low flows and standing pools of water (Prochaska, 2005). In the case of the Youghiogheny benthic invertebrates, a low sample size resulted in high variability (Figure 3). Statewide, the finding that local-scale variables were comparable to field-measured variables in fish biodiversity models was unexpected, and more study of this result is warranted.

4.3 | Informing model improvements

Deviance explained by our models was generally low, which raises the question: How might we further improve environmental predictor variables? We suggest that the biodiversity modelling community would benefit by prioritizing derivation of full-coverage environmental variables that capture true physiological drivers of biodiversity distributions and consider the temporal nature and spatially hierarchical structure of flowing waters.

Ultimately, "derived" and "physiologically relevant" need not be mutually exclusive. Development of methods to derive physiologically

relevant predictors available across space and through time is a key goal. Airborne thermal remote sensing measuring stream temperature (e.g., Torgersen, Faux, McIntosh, Poage, & Norton, 2001), lidar quantifying stream depth and structure (e.g., McKean & Isaak, 2009) and hyperspectral measurements mapping stream microhabitats (e.g., Marcus, 2002) are particularly promising avenues. Model improvements to capture the temporal dynamics of streams might involve the inclusion of candidate variables reflecting past land use, temporal trends, or extreme conditions and variability (Harding et al., 1998; Zimmermann, Edwards, Moisen, Frescino, & Blackard, 2007). Spatial improvements could include alternative methods for weighting upstream land use (e.g., Peterson et al., 2011) that account for in-stream as well as overland flow distance (Van Sickle & Johnson, 2008), as well as amending predictors to consider "upstream" at multiple scales (Stein et al., 2014).

5 | CONCLUSIONS

In our low-order stream biodiversity models, field-measured variables were superior to derived variables in explanation and prediction of fish and benthic invertebrate beta diversity, and derived variables considering upstream conditions were consistently superior to local-scale derived variables. Although ours is not the first call for closer consideration of the physiological relevance of candidate predictor variables (e.g., Araújo & Guisan, 2006; Austin & Van Niel, 2011), it is among the first attempts to quantify the differences between models built with different sets of derived and field-measured variables. In the context of increasingly scarce conservation resources (Bottrill et al., 2008) and rapid development of remote sensing technology (Cord et al., 2013), these results suggest we may be able to improve biodiversity models by continuing efforts to develop physiologically relevant predictors.

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BIOSKETCH

Miriam Johnston was a student at the University of Maryland Center for Environmental Science during the development of this work; she is now a PhD candidate at Harvard University. She is broadly interested in the effective application of models to conservation issues.

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