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Modelling spatial biodiversity in the world's largest mangrove ecosystem—The Bangladesh Sundarbans: A baseline for conservation

Swapan Kumar Sarker, Richard Reeve, Nirmal K. Paul, Jason Matthiopoulos

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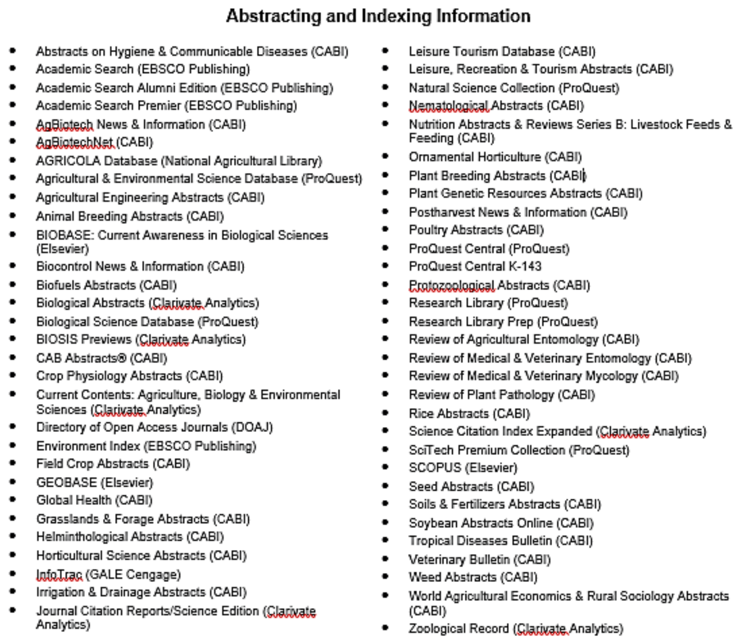

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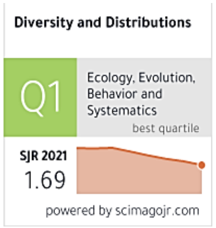

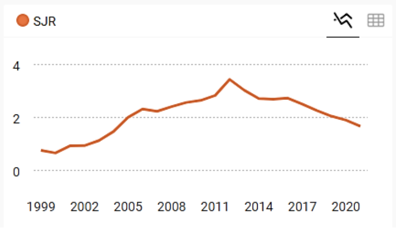

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DDI-2018-0408: Invitation to Review for Diversity and Distributions

1 message

Christian Estrada <onbehalfof@manuscriptcentral.com> Tue, Sep 25, 2018 at 3:25 PM
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MANUSCRIPT DETAILS
TITLE: Modelling spatial biodiversity in the world’s largest mangrove ecosystem - the Sundarbans: A baseline for conservation

ABSTRACT:
Aim Mangrove forests are amongst the most threatened and rapidly vanishing, but poorly-understood ecosystems. We aim to uncover the variables driving mangrove biodiversity and produce baseline biodiversity maps for the Sundarbans world heritage site – the Earth’s largest mangrove ecosystem.
Location The Sundarbans, South Asia.
Methods We collected species abundance, environmental and disturbance data from 110 permanent sample plots covering the entire Bangladesh Sundarbans (6017 km2). We applied generalized additive models to determine the

key variables shaping the spatial distributions of mangrove diversity and community composition. Biodiversity maps were constructed using covariate-driven habitat models and their predictive performances were compared with covariate-free (i.e. direct interpolation) approaches to see whether the inclusion of habitat variables bolster spatial predictions of biodiversity or if we can rely on direct interpolation approaches when environmental data are not available.
Results Historical forest exploitation, disease, siltation and soil alkalinity were the key stressors causing loss of alpha and gamma diversity in mangrove communities. Both alpha and gamma diversity increased along the downstream-to-upstream and riverbank-to-forest interior gradients. Mangrove communities subjected to intensive past tree harvesting, disease outbreaks, and siltation were more homogeneous in species composition (beta diversity). In contrast, heterogeneity in species composition increased along decreasing salinity and downstream-to-upstream gradients. We find that the surviving biodiversity hotspots (comprising many globally endangered tree species) are located outside the established protected area network and hence open to constant human exploitation, and we therefore suggest bringing them immediately under protected area management.
Main conclusions We provide the first habitat-based modelling and mapping of alpha, beta and gamma diversity in threatened mangrove communities. In general, habitat-based models showed better predictive ability than the covariate-free approach. Nevertheless, the small margin of differences between the approaches demonstrates the utility of direct interpolation approaches when environmental data are unavailable.
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Dr Franz Essl
Handling Editor, Diversity and Distributions
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ΩSpecial Characters

This paper is a well-written case study of modeling spatial biodiversity in the world’s largest mangrove ecosystems (mangrove of Sundarbans). The hypothesis and method applied appears sound and the paper clearly describes the findings and discussion which is an important contribution to protection (reforestation and rehabilitation) and management in this area and other mangrove areas include for implementation REED+. Just a little suggestion for improving the paper: - Page 4 line 50: Abbreviation of PSPs need to write fully in the first time - Page 6, line 13-16: what method did you use to determine the concentrations of the variables? Should be clearly but just written in short. - Page 30, Fig 3. North arrow symbols for the map should be placed at each map. After revising it, I suggest this paper is ready for publication.

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Christian Estrada <onbehalfof@manuscriptcentral.com> Thu, Oct 25, 2018 at 9:41 AM
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24-Oct-2018

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Abdul Malik <abdulmalik@unm.ac.id>

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2 messages

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Best regards,

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Modelling spatial biodiversity in the world's largest mangrove ecosystem—The Bangladesh Sundarbans: A baseline for conservation

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Editor: Franz Essl

Abstract

Aim: Mangrove forests are among the most threatened and rapidly vanishing, but poorly understood ecosystems. We aim to uncover the variables driving mangrove biodiversity and produce baseline biodiversity maps for the Sundarbans world heritage site—the Earth's largest contiguous mangrove ecosystem.

Location: The Bangladesh Sundarbans, South Asia.

Methods: We collected species abundance, environmental and disturbance data from 110 permanent sample plots (PSPs) covering the entire Bangladesh Sundarbans (6,017 km^2). We applied generalized additive models to determine the key variables shaping the spatial distributions of mangrove diversity and community composition. Biodiversity maps were constructed using covariate-driven habitat models, and their predictive performances were compared with covariate-free (i.e., direct interpolation) approaches to see whether the inclusion of habitat variables bolster spatial predictions of biodiversity or whether we can rely on direct interpolation approaches when environmental data are not available.

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Main conclusions: We provide the first habitat-based modelling and mapping of alpha, beta and gamma diversity in threatened mangrove communities. In general, habitat-based models showed better predictive ability than the covariate-free approach. Nevertheless, the small margin of differences between the approaches

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Modelling spatial biodiversity in the world's largest mangrove ecosystem - the Sundarbans: A baseline for conservation

Journal:	*Diversity and Distributions*
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Manuscript Type:	Biodiversity Research
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Modelling spatial biodiversity in the world's largest mangrove ecosystem - the Sundarbans: A baseline for conservation

Running head: Mangrove biodiversity in the Sundarbans

ABSTRACT

Aim Mangrove forests are amongst the most threatened and rapidly vanishing, but poorly-understood ecosystems. We aim to uncover the variables driving mangrove biodiversity and produce baseline biodiversity maps for the Sundarbans world heritage site – the Earth's largest mangrove ecosystem.

Location The Sundarbans, South Asia.

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Keywords Biodiversity conservation, endangered species, generalized additive models, habitat rehabilitation, protected area, sea-level rise.

1. INTRODUCTION

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Tropical and subtropical mangrove forests (between 30° N and 30° S) provide numerous ecosystem services and support coastal livelihoods worldwide (Lee et al., 2014). However, they are amongst the most threatened and rapidly vanishing habitats on Earth (Polidoro et al., 2010; Richards & Friess, 2016). The mangrove biome has already lost about 50% of its coverage since the 1950s (Feller et al., 2010), and IUCN has listed 40% of mangrove tree species as Threatened (Polidoro et al., 2010). Increasing anthropogenic pressures and anticipated sea level rise (SLR) are likely to alter the structure and functions of the remaining endangered mangrove forests (Duke et al., 2007), in particular, the Sundarbans UNESCO world heritage site - the Earth’s largest mangrove ecosystem.

Making spatial predictions of biodiversity is important for pinpointing the locations or communities requiring immediate or long-term protection and conservation actions, in evaluating threats to those communities, and in monitoring spatial distributions and temporal dynamics in biodiversity (Socolar et al., 2015). A variety of biodiversity modelling approaches (e.g. stacked species distribution models, macroecological models, ordination, and stochastic models – Ferrier & Guisan, 2006; Mateo et al., 2017) have been applied to understand the spatial patterns of species richness and composition in different forest ecosystems (e.g. neo-tropical, boreal and temperate forests). However, their application to mangrove forests is limited (but see Record et al., 2013) due to the scarcity of field data (Ellison, 2001), thus resulting in poor understanding of mangrove biogeography.

Each of the three established components of biodiversity (alpha, beta and gamma – Whittaker, 1960) characterizes different fundamental attributes of natural communities, and therefore has specific conservation implications. For example, spatial maps of alpha diversity can help in specifying the most species-rich habitats while beta diversity maps can determine the most heterogeneous communities, where protecting larger areas will encompass more biodiversity. Similarly, gamma diversity measures can identify the overall areas with the highest biodiversity. Thus far, mangrove biodiversity studies have mostly relied on alpha diversity, and in particular species richness (Ellison, 2001; Record et al., 2013; Osland et al., 2017) which, by ignoring the variability in species relative abundances, has known weaknesses in identifying areas for prioritisation (Veach et al., 2017). At a regional scale, mangrove plant communities may look spatially homogeneous because mangrove forests are relatively species-poor compared to the upland tropical forests. However, at finer scales, considerable heterogeneity in vegetation structure becomes apparent (Farnsworth, 1998). Therefore, looking at how the components of biodiversity respond to biotic and abiotic variables is important for constructing more informative and practically useful biodiversity maps.

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Constructing maps of biodiversity indices is important in order to investigate spatio-temporal variations in natural communities, to locate habitats or communities or species that require immediate protection and to support spatially explicit conservation planning (Devictor et al., 2010). Both habitat-based and covariate-free (direct interpolation methods such as Kriging) approaches have been used for mapping biodiversity indices. Although covariate-free approaches have been criticized for low predictive ability (Granger et al., 2015), the relative performance of the approaches has rarely been tested using field data.

Testing the ‘zonation’ hypothesis (i.e. the distinct ordering of tree species along the shore-to-inland gradient, Ellison et al., 2000) and explaining the ‘biodiversity anomaly’ (i.e. why mangrove plant species richness drops along the latitudinal gradient, Ricklefs et al., 2006), have been the key agendas dominating the mangrove biodiversity literature in the last two decades. While such studies have substantially improved our insight into species sorting and richness, limited attention has been paid to understanding how abiotic, biotic and historical anthropogenic pressures have contributed to spatial variations in mangrove diversity and composition. Such knowledge gaps have obstructed the success of conservation initiatives in many tropical coastal regions (Lewis, 2005) such as the Sundarbans.

This study focused on the threatened mangrove plant communities of the Sundarbans which are under severe threat from historical forest exploitation, habitat degradation and future climate change impacts (Sarker et al., 2016). Using a newly introduced abundance-based framework for biodiversity partitioning (Reeve et al., 2016) and a habitat-based biodiversity modelling approach, our overarching goal was to uncover the influences of fine-scale habitat conditions and historical events in shaping the current spatial distributions of alpha, beta and gamma diversity. Our more specific questions include: What are the key drivers of mangrove biodiversity? How do the predictive abilities of covariate-driven habitat models compare with those of covariate-free direct interpolation approaches? Where are the biodiversity hotspots in the Sundarbans currently located? Are these hotspots well protected? Finally, we demonstrate and discuss the potential applications of these novel insights and biodiversity maps for future mangrove research, biodiversity protection, monitoring, and spatial conservation planning.

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2. METHODS

2.1 Study system

The Sundarbans (10,017 km^2), a part of Earth's largest delta, the Ganges-Brahmaputra, is distributed in Bangladesh and India. Due to its outstanding universal ecological and economic value, the Bangladesh part of the Sundarbans (21°30′ - 22°30′N, 89° 00′ – 89°55′E, 6017 km^2) was declared a UNESCO world heritage site in 1997 (Gopal & Chauhan, 2006). It was also declared a Ramsar wetland ecosystem under the Ramsar Convention in 1992 (Chowdhury et al., 2016a). The Sundarbans is washed by the tide twice a day, and freshwater flowing from the Ganges and the opposing saltwater influx from the Bay of Bengal together control its hydrology (Wahid et al., 2007). The climate is humid tropical with four main seasons: pre-monsoon (March–May), monsoon (June–September), post–monsoon (October–November) and the dry winter season (December–February). The average annual precipitation is 1700 mm and the mean temperatures in pre-monsoon, monsoon, post-monsoon and dry winter are 29, 30, 26 and 20°C, respectively (Chowdhury et al., 2016b).

2.2 Tree and environmental data collection

Abbreviation of PSPs need to write fully in the first time

We collected tree data from the 110 PSPs (100 × 20 m, divided into 5 20 × 20 m subplots) covering all salinity zones (i.e. hypo-, meso-, and hypersaline zones) and forest types (see Iftekhar & Saenger, 2008) in the Bangladesh Sundarbans. The Bangladesh Forest Department (BFD) established these PSPs (Fig. 1) in 1986. As part of the 2008 – 2014 surveys, our team, together with the BFD tagged every tree (d.b.h ≥ 4.6 cm at 1.3 m from the ground) with a unique tree number and recorded tree counts for the PSPs. In total, we recorded 49,409 trees from 20 mangrove species (see Appendix S1 in Supporting Information).

[Figure 1]

In 2014 (January – June), we collected 9 soil samples from each PSP (soil depth = 15 cm) adopting a soil sampling design (See Appendix S1 in Supporting Information) to account for the within-plot variations in soil variables. We then determined soil sand, silt and clay percentages, salinity, pH, oxidation reduction potential (ORP), $NH_{4,}$ P, K, Mg, Fe, Zn, Cu and sulphide concentrations. For each soil variable, we recorded the average reading from 9 soil samples.

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We retrieved 5 elevation readings (above-average sea level) from each PSP using the available digital elevation model (accuracy at pixel level = ±1 m) (IWM, 2003) and then averaged them to account for sampling error. We also calculated the “upriver position” (URP), the straight-line distance of each PSP from the river-sea interface (Duke et al., 1998) and classified their position as – (i) ‘downstream’, representing the lower third (0 - 33% upriver from the sea – Bay of Bengal), (ii) ‘intermediate’, representing the middle third (34 - 66% upriver from the sea), and (iii) ‘upstream’, representing the upper third (67 - 100% upriver from the sea) of the estuarine system. This classification system is useful for understanding variability in diversity and species compositions along the downstream (saltwater dominated river system) - upstream (freshwater dominated river system) gradient.

2.3 Covariate selection

We followed Twilley & Rivera-Monroy's (2005) mangrove-centric conceptual framework to construct a biologically informative variable set for our mangrove biodiversity models. This framework integrates abiotic and biotic constraints to explain vegetation structure and productivity at local and regional scales. The abiotic constraints comprise resources, regulators and hydroperiod. Resources (i.e. nutrients) are assimilated by trees. Here, we selected three essential plant macro-nutrients - soil NH_4, P and K – for their critical roles in mangrove growth and development (Reef et al., 2010). Regulators are non-resource variables that control tree eco-physiology (Guisan & Thuiller, 2005). Here, we selected soil salinity, pH and silt. Hydroperiod (i.e. inundation frequency, duration, and depth) controls the regional and local hydrology that in turn influence species distributions in coastal environments (Crase et al., 2013). PSP-level hydroperiod data were unavailable, so we used elevation as a proxy of the likely variation in hydroperiod across the region.

Biotic interactions (e.g. competition or facilitation) between plants can influenc composition at a local scale (Howard et al., 2015). Competitive exclusion competitors in stressed mangrove habitats may lead to species-poor mangrove com dominated by a single or few opportunistic species (Saenger, 2002). To account for such influences, initially, we considered two candidate biotic variables: (i) 'community size' – total number of individuals in each PSP, and (ii) total basal area in each PSP. Diversity models using basal area as a covariate had lower explanatory powers, compared to models with 'community size (CS)'. Therefore, we selected CS as a proxy of biotic interactions.

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We incorporated URP of each PSP in our covariate set to account for the influence of the river systems on species composition along the downstream-upstream gradient. In riverine estuaries, tidal inundation levels, soil physical and chemical properties can significantly vary along the riverbank - inner forest gradient, which influences colonization success and survival of mangrove plants (Berger et al., 2008). To account for such variations, we included the straight-line distance of each PSP from the nearest riverbank (henceforth DR).

Tropical coastal ecosystems are prone to both natural and anthropogenic disturbances (Feller et al., 2017). Natural disturbances (such as tree disease and mortality) and anthropogenic disturbances (such as tree harvesting) offer opportunities for tree recruitment through gap creation, thus influencing vegetation composition (Duke, 2001). To account for the influences of natural and human disturbances on current diversity and species composition, we incorporated historical harvesting (HH) and disease prevalence (DP) as covariates in our models. Here, HH and DP represent the total number of illegally harvested and diseased (for example, 'top dying' disease (dieback of the foliage and twigs in part of the crown) of *Heritiera fomes*, 'heart rot' disease of *Xylocarpus. mekongensis* etc.) trees in each PSP from historical records (1986 to 2014). Finally, using Variance Inflation Factors (VIF, Robinson & Schumacker, 2009) we checked for multi-collinearity in our covariates (see Appendix S2) and removed covariates leading to VIF greater than 2.5. This led to the removal of ORP from our covariate set (see Appendix S2).

2.4 Biodiversity partitioning

For partitioning biodiversity, we used Rényi's generalised relative entropy (Rényi A., 1961), an extension of Hill (1973), Jost (2006; 2007) and Leinster and Cobbold's (2012) notions of ecosystem diversity. Implemented in Reeve et al's 2016 framework, this allows us to partition the alpha, beta and gamma diversity of an ecosystem (called a *metacommunity*) into its *subcommunity* components, thus allowing comprehensive and consistent quantification and modelling of all biodiversity components in a spatial context.

In this study, each PSP represents a *subcommunity* (SC), and the combined PSPs form the *metacommunity* (MC). This approach allows us to understand and easily compare the species diversity and composition in every single SC in relation to the MC (the whole Sundarbans ecosystem). We measured SC alpha, beta, and gamma diversity. Here, the normalised alpha diversity index (denoted $\overline{\alpha}$) represents the diversity of a single SC (PSP) in isolation. The normalised beta diversity index (denoted $\overline{\rho}$) measures representativeness and assesses how well a SC represents the species composition of its MC. It is maximised (1) when the MC is homogenous, and a SC's species composition is identical to that of the MC and therefore represents it perfectly. Low $\overline{\rho}$ therefore suggests high spatial heterogeneity in species composition within the MC, and high $\overline{\rho}$ suggests spatial homogeneity.

The gamma diversity (denoted γ) is the conventional gamma diversity (Hill, 1973; Jost, 2006; Leinster & Cobbold, 2012) at the MC level that reflects the total species diversity in an unpartitioned ecosystem. The framework partitions the MC gamma diversity into SC gamma diversity that measures each PSP's average contribution to (or influence on) the MC diversity per tree. This diversity measure combines the alpha diversity of a SC with its beta diversity to form an assessment of the overall contribution of the PSP to the MC (Reeve et al., 2016).

Following Hill (1973), Jost (2006; 2007) and Leinster and Cobbold's (2012), the values of all the biodiversity measures are moderated by a viewpoint parameter, q, taking a value between 0 and ∞ representing how conservative the measure is in accounting for species abundance. For $\overline{\alpha}$ and γ, the diversity at $q = 0$ measures species richness; at $q = 1$ measures the exponential of Shannon entropy (Shannon, 1948); and at $q = 2$ measures the inverse of Simpson's concentration index (Simpson, 1948). For all analyses, we present the results using the above three q values (0, 1, and 2), writing them as ${}^{0}\overline{\alpha}$, ${}^{1}\overline{\rho}$, ${}^{2}\gamma$, etc.

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2.5 Biodiversity modelling

We constructed generalized additive models (GAMs, Wood, 2011) to quantify how the different biodiversity components responded to different variables. Guided by data and using non-parametric smoothing functions, GAMs can capture response-predictors relationships without a priori knowledge of the functional form of these relationships (Guisan & Thuiller, 2005). These advantageous features of GAMs are well suited for uncovering unknown biodiversity-environment linkages in dynamic ecosystems such as the Sundarbans where multiple environmental gradients have interactive effects on species distributions (Sarker et al., 2016). All analyses were done in R version 3.2.3 (R Core Team, 2016). Biodiversity GAMs were built using cubic basis splines with the Gamma error distribution using the 'mgcv' package version 1.8 - 7 (Wood, 2011). Model selection and model averaging were carried out using the 'MuMIn' package version 1.15.1 (Barton, 2015). Biodiversity measures were calculated using the 'rdiversity' package version 1.0 (Mitchell & Reeve, 2017).

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We exhaustively fitted GAMs for each diversity index with all possible combinations of covariates. Then we ranked the fitted GAMs using the second-order AIC (AICc) because the ratio between sample size and the number of covariates was < 40 (Burnham & Anderson, 2002). Models whose $\mathrm{AIC_c}$ had values less than 2 units from the best model ($\Delta\mathrm{AIC_c} <2$) were retained as competing models (Burnham & Anderson, 2002). The relative support for each of the competing models was then determined using their Akaike weights ($\mathrm{AIC_{cw}}$, vary between 0 to 1, and the sum of all $\mathrm{AIC_{cw}}$ across the competing models is 1). To reduce model selection uncertainty and bias, we then conducted model averaging to predict the diversity indices. To determine the strength of the covariates, we ranked them based on their Relative Importance (RI) values. RI of each covariate was calculated by totalling the $\mathrm{AIC_{cw}}$ of the models in which the covariate was included. RI values vary between 0 and 1, where 0 specifies that the target covariate is not included in any of the competing models while 1 means that the covariate is included in all competing models. We measured goodness-of-fit of the biodiversity models using the R^2 (coefficient of determination) statistic between the observed and estimated values of the diversity indices.

2.6 Biodiversity mapping

We applied two different approaches to make spatial biodiversity predictions. First, we used our habitat-based models (GAMs) and interpolated covariate surfaces to produce model-

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averaged predictions. Second, we used a direct interpolation method, Ordinary kriging (OK), that simply relied on the empirical spatial autocorrelation between neighbouring PSPs (did not consider environmental covariates) to make purely spatial predictions. We compared these two approaches because environmental data collection is challenging, whereas tree surveys are conducted annually at the PSPs. Hence, it is useful to know how close the predictions of the habitat-based biodiversity models were compared to direct interpolation methods. The size of each grid-cell of the interpolated surfaces was 625 m^2 (25m × 25m). We compared the predictive abilities of GAMs with OK, using the normalized root mean square error (NRMSE) statistic derived from a leave-one-out cross-validation (LOOCV) procedure. For normalization, the root mean square error statistic was divided by the range of the actual diversity values. OK was performed using the ‘gstat’ package version 1.0 - 26 (Pebesma, 2004) in R.

The largest mangrove protected area network (PAN) comprising three Wildlife Sanctuaries (WS) – East WS, West WS, and South WS, has been operational in the Sundarbans since the 1970s. To evaluate its capacity to support the remaining biodiversity hotspots in the Sundarbans, we superimposed this onto our biodiversity maps. All the biodiversity maps were constructed using the ‘raster’ package version 2.4 - 18 (Hijmans, 2017) in R.

3. RESULTS

3.1 Habitat-based biodiversity models

The explanatory power and the goodness-of-fit of the alpha, beta and gamma diversity GAMs varied when we increased weight on species relative abundances (q = 0, 1 and 2) in the subcommunities (SCs). ${}^{1}\overline{\alpha}$ (Shannon entropy) GAM explained more deviance (DE = 71%) and showed a better fit to the data (Adj. R^2 = 0.71) compared to those for ${}^{0}\overline{\alpha}$ (species richness) and ${}^{2}\overline{\alpha}$ (Simpson’s concentration) (Table 1), suggesting that, for alpha diversity, the model with a moderate focus on species relative abundances in the SCs (i.e. $q = 1$) could capture more signal compared to the models that only considered species presence-absence ($q = 0$) or offered more importance to the more dominant species ($q = 2$) in the SCs. Like ${}^{1}\overline{\alpha}$, the ${}^{1}\gamma$ GAM could capture more signal than ${}^{0}\gamma$ and ${}^{2}\gamma$ GAMs. In contrast, for beta diversity, with DE = 65% and Adj. R^2 = 0.70, the ${}^{2}\overline{\rho}$ GAM captured more signal than the ${}^{0}\overline{\rho}$ and ${}^{1}\overline{\rho}$ GAMs, implying that our covariates could more successfully explain the variability in species composition across the SCs when the variability was mostly contributed by more dominant species.

[Table 1]

3.2 Drivers and responses of biodiversity components

The relative importance (RI) of the covariates in influencing biodiversity indexes also varied when we changed weight on species relative abundances in the SCs. For example, while historical harvesting (HH) had no influence on ${}^{0}\overline{\rho}$ (possibly due to high number of shared species between SCs or HH did not lead to species extirpation), it had stronger effects on ${}^{1}\overline{\rho}$ and ${}^{2}\overline{\rho}$, indicating that the influence of past tree harvesting in shaping current community composition becomes clearer when we account for the variability in species relative abundances across the SCs. In general, several abiotic and biotic drivers had combined effects on the spatial distributions of the biodiversity indexes. SC alpha diversity was mainly influenced by CS, URP, DR and silt (Table 1, Appendix S3). CS, URP, salinity, HH, silt and DP were the predominant drivers for spatial variations in SC beta diversity. SC gamma diversity was mostly influenced by CS, URP, salinity, DR, HH, pH and silt.

The partial response plots of the best alpha, beta, and gamma diversity GAMs (for q = 0, 1 and 2) showed similar relationships across the models (Fig. 2, Appendix S3). While alpha diversity (for ${}^{1}\overline{\alpha}$) increased with increasing DR (> 1500 m) and URP (> 80%), it decreased with increasing HH (> 175 tree cuts/0.2 ha), silt (> 20%), CS (> 450 trees/0.2 ha) and pH (> 7.25). The response of alpha diversity varied for different nutrients. The K concentration that maximised ${}^{1}\overline{\alpha}$ was 5.5 gm Kg^{-1} whilst increasing soil P (> 35 mg Kg^{-1}) was related to decreasing ${}^{1}\overline{\alpha}$. Mangrove communities showed increasing representativeness (for ${}^{2}\overline{\rho}$) i.e. homogeneity in species composition with increasing HH (> 150 tree cuts/0.2 ha), silt (> 20 %), DP (> 25 diseased trees/0.2 ha), and CS (> 450 trees/0.2 ha). In contrast, communities showed decreasing representativeness i.e. increasing heterogeneity in species composition with increasing salinity (> 6.5 dS m^{-1}) and URP (> 70%). Gamma diversity (for ${}^{1}\gamma$) showed strong positive responses to increasing DR (> 1000 m), salinity (> 8 dS m^{-1}), and URP (> 70%), and negative responses to increasing HH (> 175 tree cuts/0.2 ha), silt (> 20%), CS (> 500 trees/0.2 ha) and pH (> 7.25).

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[Figure 2]

3.3 Biodiversity maps

Spatial alpha, beta and gamma diversity maps produced via GAMs are presented in Fig. 3. Alpha diversity maps (first row) uncovered that hotspots in species richness ($q = 0$), Shannon entropy ($q = 1$) and Simpson's concentration ($q = 2$) were restricted to the northern (specifically, the Kalabogi region) and eastern (specifically the Sharankhola region) Sundarbans. Beta (second row) and gamma (third row) diversity maps revealed that the entire Sundarbans looks homogeneous when we only looked at species presence or absence ($q = 0$) i.e. not accounting for the between-species variability in relative abundances. Allowing increasing weight on species abundance ($q = 1$ and 2) revealed that the most heterogeneous mangrove communities and the communities that contributed most to the overall biodiversity of the ecosystem were restricted to the northern upstream habitat. Additionally, our maps indicated that the established protected area network (PAN) does not currently include the most diverse (i.e. biodiversity hotspots) and heterogeneous mangrove communities. Prediction error was always reduced by the use of environmental covariates, but particularly for predictions of alpha and gamma diversity. In case of beta diversity, while the predictive ability of the GAM was better than that of Kriging for ${}^{0}\overline{\rho}$ and ${}^{1}\overline{\rho}$, both approaches had almost similar prediction error for ${}^{2}\overline{\rho}$ (Table 2).

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[Figure 3]

[Table 2]

4. DISCUSSION

This study provides a baseline quantification and habitat-based modelling of alpha, beta and gamma diversity of threatened mangrove communities. Contrary to the common assumption that one or two straightforward environmental gradients (salinity and inundation) control mangrove biodiversity (Ellison, 2001), our results revealed that several environmental drivers, biotic interactions and historical events contribute to the emergence of observed spatial patterns of mangrove diversity and species composition. The high explanatory and predictive power of our biodiversity models confirm their usefulness in constructing spatially explicit predictions of species diversity and composition. The ability of the models to reveal previously unknown linkages between the biodiversity components and abiotic, biotic and disturbance variables have yielded novel biological insights and thus now prompt many ecological questions for future studies.

4.1 Drivers and responses of biodiversity components

Inclusion of URP in the best biodiversity GAMs suggest a strong influence of the downstream/upstream gradient in shaping spatial distributions of all aspects of biodiversity in the Sundarbans. Alpha diversity, SC contribution to the overall diversity of the ecosystem (gamma) and heterogeneity of the communities (beta) increased along the downstream/upstream gradient (URP > 65%), suggesting downstream and intermediate-stream areas are no more suitable for many salt-intolerant species (e.g. *H. fomes*) that were abundant in the past (Gopal & Chauhan, 2006) while the late successional upstream areas are the most suitable habitats for widespread coexistence of salt-intolerant, salt-tolerant and many rare species, corroborating the previous findings of Sarker et al. 2016.

Inclusion of CS in all the best GAMs demonstrates the importance of including at least proxies of biotic variables in habitat-based biodiversity models. Increasing CS significantly contributed to decreasing SC alpha and gamma diversity, and increasing homogeneity in species composition (beta), providing a strong signal for biotic filtering in harsh estuarine settings. From the response plots (Figures 2, S2 & S3), it appears that this pattern arises when SCs have > 450 trees. These SCs are, indeed, distributed in the north-western and south-western hypersaline habitats and Sarker et al. (2016) reported super dominance of small-diameter and early-successional generalists (*E. agallocha* and *C. decandra*) there. On the other extreme, northern hyposaline mangrove communities which are dominated by large-diameter, late-successional specialists (e.g. *H. fomes* and *X. mekongensis*) are usually less populated and support many associated rare endemics, thus are more diverse and distinct than the densely populated hypersaline communities (Fig. 3).

Our analyses uncovered a strong impact of HH and DP in shaping current distributions of the biodiversity components in the Sundarbans, implying the importance of integrating past disturbance events in habitat-based models for more accurate predictions. We detect a significant negative effect of HH on alpha and gamma diversities, although DP has no visible

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effect. This discrepancy may be related to local extinction of many rare endemics during past formal and informal logging activities and high DP (top-dying and heart rot diseases) in the specialists (i.e. *H. fomes* and *X. mekongensis*) (Banerjee et al., 2017) that might not lead to their extirpation but reduced their relative abundances in a higher amount compared to the generalists. However, for beta diversity, both HH and DP contributed to increasing homogeneity in species composition across the SCs (Fig. 2). This again indicates that the diseases have not infected all trees equally rather, they have only infected and removed a few specialists such as *H. fomes* (top-dying disease) and *X. mekongensis* (heart rot disease) which have resulted in increasing homogeneity in the mangrove communities. Therefore, by using the approach of Reeve et al. (2016) to look at how DP simultaneously affects alpha, beta and gamma diversity, we are now able to get indications of the pathogenicity of the disease (i.e. whether it is a generalist and infects and removes all species equally or it is specialised on specific host species). Mangrove habitats with past logging history are commonly nutrient-poor, absorb higher amounts of heavy metals, and are prone to species invasion (Ngole-Jeme et al., 2016). Harvesting- and disease-induced tree mortalities have created many large as well as small forest gaps in the Sundarbans. Intriguingly, the large diameter tree species (i.e. *H. fomes* and *X. mekongensis*) that still dominate the less saline habitats, recruit poorly in the forest gaps (Iftekhar & Islam, 2004). Instead, these forest gaps are increasingly colonized by the disturbance specialists (e.g. *C. decandra*) (Mukhopadhyay et al., 2015). Therefore, increasing colonization and dominance of disturbance specialists in the historically disturbed SCs are the possible mechanisms responsible for increasing similarity among mangrove communities. This result somewhat contrasts with the Intermediate Disturbance Hypothesis which states that diversity of coexisting species is maximum at intermediate intensities of disturbance (Connell, 1978).

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Highly silted mangrove communities in the Sundarbans are not only poor in alpha and gamma diversities but also almost similar in species composition (Fig. 2). These results are in agreement with Mitra & Zaman (2016), reporting limited growth and regeneration of many mangroves due to sediment burial of aerial roots in the Sundarbans. Sediment burial of aerial roots (inhibits root aeration) is a major reason for worldwide mangrove mortality (De Deurwaerder et al., 2016). However, at species level, sensitivity of individual species to sediment burial can vary substantially. For example, Thampanya et al. (2002), in their experimental work on Thailand mangroves, observed 100% mortality in *Avicennia officinalis*, 70% in *Rhizophora mucronata*, and 40% in *Sonneratia caseolaris* under extreme sediment accretion level (32 cm). The Sundarbans is an active delta where the river network annually transports about 2.4 billion tons of sediments (Mitra & Zaman, 2016). Therefore, future research is required to understand species-specific sensitivities and adaptations (e.g. modified rooting architecture) to siltation because this will help to forecast which species may colonize the newly formed islands, and which are compatible for replanting in future siltation scenarios.

Although in their pioneering work, Ellison et al. (2000) found no evidence for 'zonation' in the Sundarbans, we detect a clear pattern of increasing alpha and gamma diversities along the riverbank/forest interior gradient. Communities that are at least 1500 m away from the riverbank have higher alpha diversity and 800 m away have higher gamma diversity compared to the near-bank communities (Fig. 2), implying late successional forest interior communities are more diverse than the early successional riverbank communities.

Salinity has been considered a key constraint limiting species richness in coastal ecosystems (Feller et al., 2010). It appears from our analyses that salinity has no effect on species richness although the importance of salinity slightly increased for Shannon entropy and Simpson concentration, implying the role of salinity becomes clearer when we account for between-species variability in relative abundance. Considering beta diversity, increasing salinity contributes to increasing compositional heterogeneity among the SCs (Fig. 2). This pattern suggests high plot-to-plot variation in composition in the degraded saline soils for population declines and range contraction of many salt-intolerant specialists (e.g. *H. fomes*) and increasing colonization success of the salt-tolerant generalists such as *E. agallocha* and *C. decandra* (Iftekhar & Saenger, 2008; Aziz & Paul, 2015; Mukhopadhyay et al., 2015).

Nitrogen (N), phosphorus (P), and potassium (K) were found to be the important soil nutrients limiting mangrove forest structure in coastal areas in Brazil, Florida, and South Africa (Lovelock et al., 2006; Naidoo, 2009; Da Cruz et al., 2013). Interestingly, these resource variables received less support in our biodiversity models, reconfirming the high importance of regulators and historical disturbances in structuring mangrove communities (Twilley & Rivera-Monroy, 2005).

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4.2 Mangrove biodiversity maps

Our biodiversity maps for the Sundarbans (Fig. 3) reveal that currently the most species-rich (${}^{0}\overline{\alpha}$) mangrove communities are confined to the northern (specifically, Kalabogi) and eastern (specifically, Sarankhola) regions. Due to the proximity of Baleshwar and Posur rivers, these areas receive greater amount of freshwater than the rest of the ecosystem, thus securing suitable conditions for many salt-intolerant and rare plant species. The remaining ecosystem is relatively species-poor. ${}^{1}\overline{\alpha}$ (Shannon entropy) and ${}^{2}\overline{\alpha}$ (Simpson's concentration index) maps not only show similar patterns but also pinpoint the areas – the north-western and south-western Sundarbans – where the super-dominance of generalists has resulted in lower alpha diversity. These areas are prone to regular saltwater flooding and high salinity fluctuation which together were found to inhibit regeneration and growth of many species (Ghosh et al., 2016). Spatial variability in beta diversity becomes clearer when more weight was put on the dominant species (${}^{1}\overline{\rho}$, ${}^{2}\overline{\rho}$), compared to the rare species (${}^{0}\overline{\rho}$). In general, the most heterogenous communities and the communities that contribute most to the overall biodiversity of the whole ecosystem (${}^{0}\gamma$, ${}^{1}\gamma$, ${}^{2}\gamma$), are currently restricted to the northern upstream habitats supporting tree species facing the risk of local (*X. mekongensis*) and global (*H. fomes*) extinction (Sarker et al., 2016).

Restricted distributions of diverse and distinct mangrove communities in a few specific areas clearly indicate for historical pressures on Sundarbans's floral composition, as reported by many (Gopal & Chauhan, 2006; Aziz & Paul, 2015; Ghosh et al., 2016). The freshwater supply from the transboundary rivers into the Sundarbans has substantially declined (3700 m^3/s to 364 m^3/s) since the construction of the Farakka dam (1974) in India (Mirza, 1998). The average soil salinity has already increased by 60% since 1980 (Aziz & Paul, 2015). Illegal harvesting of trees and heavy siltation in the internal channels are ongoing (Rahaman et al., 2015). Therefore, our findings lead us to conclude that additional harvesting, siltation, cuts in freshwater supply and range expansions of the generalists under projected SLR (Karim & Mimura, 2008) may convert the whole Sundarbans into a species-poor homogeneous ecosystem.

The existing approaches for biodiversity mapping without including environmental data [i.e. (i) predicting diversity from stacked species distribution layers, and (ii) estimating a diversity index in few sites and then predicting these estimated values for an entire study area using

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geostatistical interpolation methods] are shown to produce inaccurate spatial predictions of diversity indices (Granger et al., 2015). In this study, in general, the environmental data-driven GAMs showed better predictive ability than the covariate-free direct interpolation method (Table 2), thus, supporting the inclusion of fine-scale environmental, biotic and historical disturbance data for more accurate mapping of biodiversity indices when these data are available. However, similar performances of these approaches in predicting ${}^{2}\overline{\rho}$, and small differences in prediction error for ${}^{0}\overline{\alpha}$ (species richness) and ${}^{0}\gamma$, indicates the utility of direct interpolation methods when environmental data are not available.

4.3 Conservation applications

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Sea level rise is likely to have drastic impacts on riverine and sea-dominated mangrove forests worldwide, particularly, the Sundarbans. Under the projected SLR range by 2100 (30 – 100 cm) which is significantly higher than the global range (26 – 59 cm) (Karim & Mimura, 2008), the Sundarbans is likely to lose 10 – 23% of its present area (Payo et al., 2016) with alteration to soil biogeochemistry (Banerjee et al., 2017) and estuarine hydrology (Wahid et al., 2007). Given the severity of these future environmental impacts on Sundarbans, identifying the existing and future environmental stressors of mangrove biodiversity is important. We detect siltation, soil salinity and pH as the dominant environmental stressors responsible for decreasing mangrove diversity (Table 1, Fig. 2 & Appendix S3). These novel habitat insights and our biodiversity maps have valuable applications in designing and implementing climate-smart mangrove enhancement (reducing abiotic stresses that caused biodiversity loss), restoration (restoring specific areas where certain mangrove species/distinct assemblages previously existed) and reforestation initiatives in the Sundarbans. Previous studies (McKee & Faulkner, 2000; Lewis, 2005; Kodikara et al., 2017) show that considerable uncertainty remains in rebuilding the degraded mangrove habitats to their previous state. However, our results about the key stressors and their spatial distributions can help the forest managers about deciding which mangrove communities or which stressors to target for future reforestation and rehabilitation initiatives.

Our biodiversity maps (Fig. 3) reveal that the established protected area network (PAN), covering 1397 km^{2}, does not include the biodiversity hotspots. Having restricted distributions in the northern and eastern regions, these hotspots support the remaining populations of many globally endangered tree species (Sarker et al., 2016). These biodiversity hotspots are very close to local communities and vulnerable to opportunistic tree harvesting (Iftekhar & Islam, 2004), so we suggest bringing them under protected area management for their immediate protection and long-term conservation of the threatened species living there.

Our results have important implications for devising nutrient enrichment programs in coastal ecosystems. The negative response of alpha diversity to increasing soil P and K concentrations suggest that the mangroves of the Sundarbans may suffer from nutrient toxicity in highly silted hypersaline habitats. Previous nutrient enrichment programs in many coastal regions resulted in widespread mortality of many plant species (Lovelock et al., 2009). Therefore, we suggest for taking extreme cautions while implementing nutrient enrichment programs in the Sundarbans and elsewhere. Further, we advocate for experimental and field-based studies that explicitly investigate the responses of individual mangrove species to nutrients under different environmental settings.

Bangladesh, a signatory of the major conservation related conventions (e.g. World Heritage Convention, Ramsar Convention, Convention on Biological Diversity), have recently developed the 'Biodiversity National Assessment and Program of Action 2020' to assess and monitor its forest resources and to enforce appropriate actions to reduce further exploitation of these resources. Bangladesh has also formulated National Conservation Strategy (2016-2031) to foster development through the conservation and enhancement of natural resources within the framework of sustainable development, particularly as envisioned under the Sustainable Development Goals (SDG) (MoEF, 2016). The country has also ratified the 'Bangladesh Biodiversity Act 2017' to stop illegal trade of forest flora and fauna. It has also adopted a SMART (Spatial Monitoring and Reporting Tool) patrol management system since 2015 to expand the scope of its current mangrove protection efforts. Our baseline biodiversity maps can guide these valuable conservation, biodiversity protection and monitoring initiatives. In addition, these maps can contribute to successful implementation of the REDD+ (Gardner et al., 2012) initiatives for enhancing carbon stock (through biodiversity conservation) as well as financial returns.

5. CONCLUSIONS

This study provides the first comprehensive and coherent quantification and habitat-based modelling of alpha, beta and gamma diversity in threatened mangrove communities in the

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world's largest mangrove ecosystem. We find that several environmental drivers, biotic interactions and historical events have combined effects on the biodiversity components. Specifically, historical harvesting, increasing community size, siltation, salinity intrusion, disease, soil alkalinity and nutrient toxicity are the dominant stressors responsible for reducing mangrove diversity. Although habitat-based models showed better predictive ability than the covariate-free approach, the small margin of differences between the approaches demonstrates the utility of direct interpolation approaches when environmental data are unavailable. Our baseline biodiversity maps uncover that the most diverse and distinct mangrove communities (biodiversity hotspots), comprising many globally endangered tree species, have restricted distributions in the freshwater-dominated northern and eastern regions. Although these biodiversity hotspots are susceptible to human exploitation, they are not included in the existing PAN, thus suggesting for an immediate expansion of the protected area. We believe details on the drivers and their capacity to influence mangroves' diversity and composition, and our baseline biodiversity maps, collectively, will contribute to designing and implementing climate-smart mangrove enhancement, restoration, reforestation and nutrient enrichment initiatives. In addition, our maps can guide the existing and future mangrove biodiversity protection, monitoring and REDD+ initiatives. The existing PSP network covers 83% (20 out of 24) of the true mangrove species in the Sundarbans, suggesting that future studies may need to extend their sampling efforts beyond the current PSP network. Elevation, as a proxy of hydroperiod, received the least support in our models. Given that projected SLR is likely to alter the regional hydrology with changes in soil-biogeochemistry, we suggest adding hydroperiod as a predictor in future biodiversity models when these data become available.

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DATA ACCESSIBILITY

The species abundance data used in this study were gathered from the Management Plan Division (MPD) of the Bangladesh Forest Division (BFD). We and MPD together collected the environmental data. Data were used in our analyses with permission by the responsible administrators of the MPD. Data can be accessed upon request from MPD (nirmal@bforest.gov.bd).

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Table 1. Results of GAMs for nine diversity measures. Summaries of model fit in rightmost three columns are only shown for the best model (DE = deviance explained). Numbers in the main part of the table (enclosed in box) represent the Relative Importance (RI) of each covariate. Dark-shaded cells highlight covariates that were retained in the best model for each biodiversity index. Light-shaded cells represent covariates retained in other models within the candidate set. Dashed boxes indicate no participation of that covariate in any of the candidate models. The covariate short-hands are: community size (CS), upriver position (URP), salinity, distance to riverbank (DR), historical harvesting (HH), acidity (pH), silt concentration, disease prevalence (DP), soil total phosphorus (P), soil potassium (K), elevation above average-sea level (ELE), and soil NH_4.

Diversity types		CS	URP	Salinity	DR	HH	pH	Silt	DP	P	K	ELE	NH_4	AIC cw	DE (%)	Adj-R^2
α	$^0\bar{\alpha}$	1	1	--	0.57	0.40	--	0.08	0.06	--	0.34	--	--	0.16	41	0.45
	$^1\bar{\alpha}$	1	1	0.20	1	0.82	0.80	1	--	0.80	0.80	--	--	0.42	71	0.71
	$^2\bar{\alpha}$	1	1	0.28	0.15	0.11	0.40	--	--	1	0.72	0.42	--	0.28	68	0.65
β	$^0\bar{\rho}$	0.71	0.21	1	0.58	--	--	--	0.94	0.66	0.61	--	--	0.12	51	0.51
	$^1\bar{\rho}$	1	1	0.86	0.25	0.93	0.47	0.35	1	0.29	--	--	--	0.22	58	0.42
	$^2\bar{\rho}$	1	1	0.84	0.46	1	0.84	1	0.84	0.83	0.67	--	0.46	0.37	65	0.70
γ	$^0\gamma$	1	1	0.36	1	0.30	0.91	0.30	1	0.10	--	0.18	0.27	0.12	75	0.86
	$^1\gamma$	1	1	1	1	1	1	1	0.35	0.65	--	0.65	0.65	0.65	86	0.90
	$^2\gamma$	1	1	0.73	1	1	--	1	--	0.72	0.72	--	--	0.28	72	0.74

Table 2. Comparison of predictive accuracy (through leave-one-out cross validation) of the habit-based (GAMs) and Kriged diversity models using normalized root mean square error (NRMSE) of the predicted versus the actual diversity values. NRMSE is expressed here as a percentage, where lower values indicate less residual variance.

Diversity types		GAMs	Kriging
		NRMSE (%)	
Alpha	${}^{0}\overline{\alpha}$	16.52	18.40
	${}^{1}\overline{\alpha}$	14.41	16.03
	${}^{2}\overline{\alpha}$	14.44	16.22
Beta	${}^{0}\overline{\rho}$	20.95	24.66
	${}^{1}\overline{\rho}$	19.21	21.69
	${}^{2}\overline{\rho}$	23.83	23.44
Gamma	${}^{0}\gamma$	12.99	17.05
	${}^{1}\gamma$	9.90	11.33
	${}^{2}\gamma$	10.75	13.15

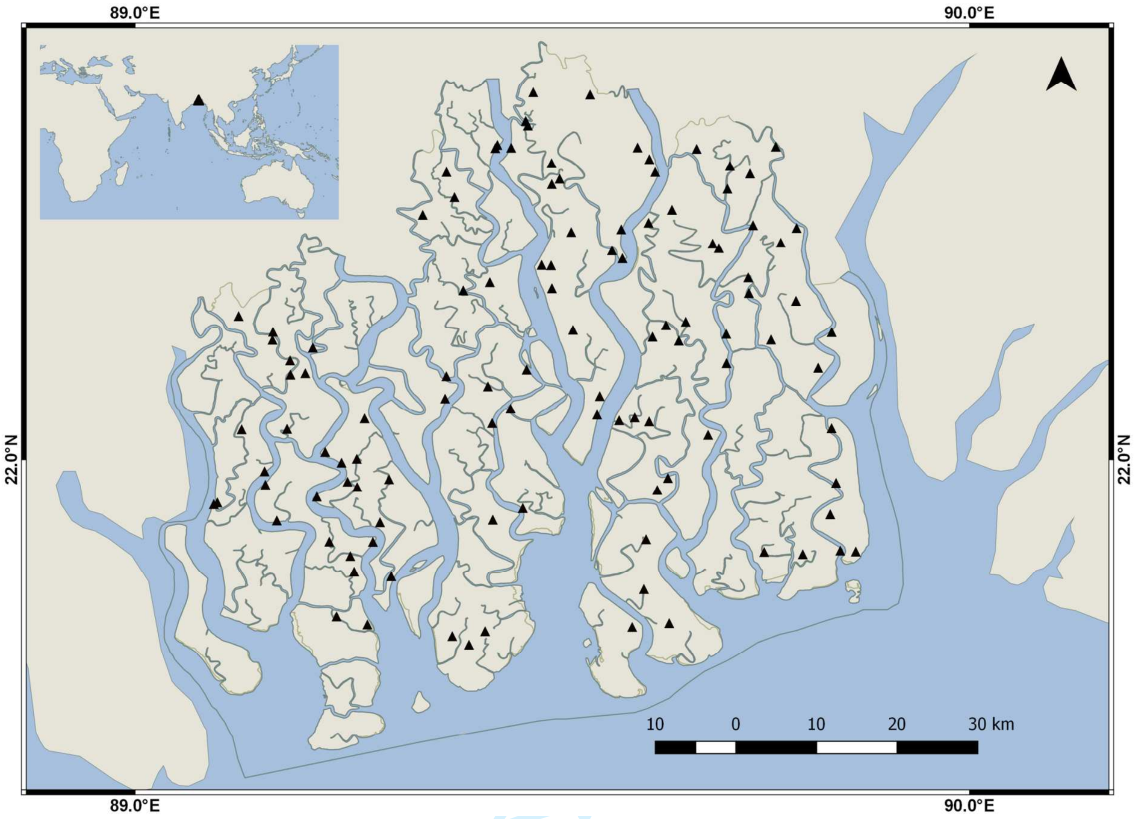

Figure 1. Sampling sites (triangles) in the Sundarbans, Bangladesh. Blue areas represent water bodies.

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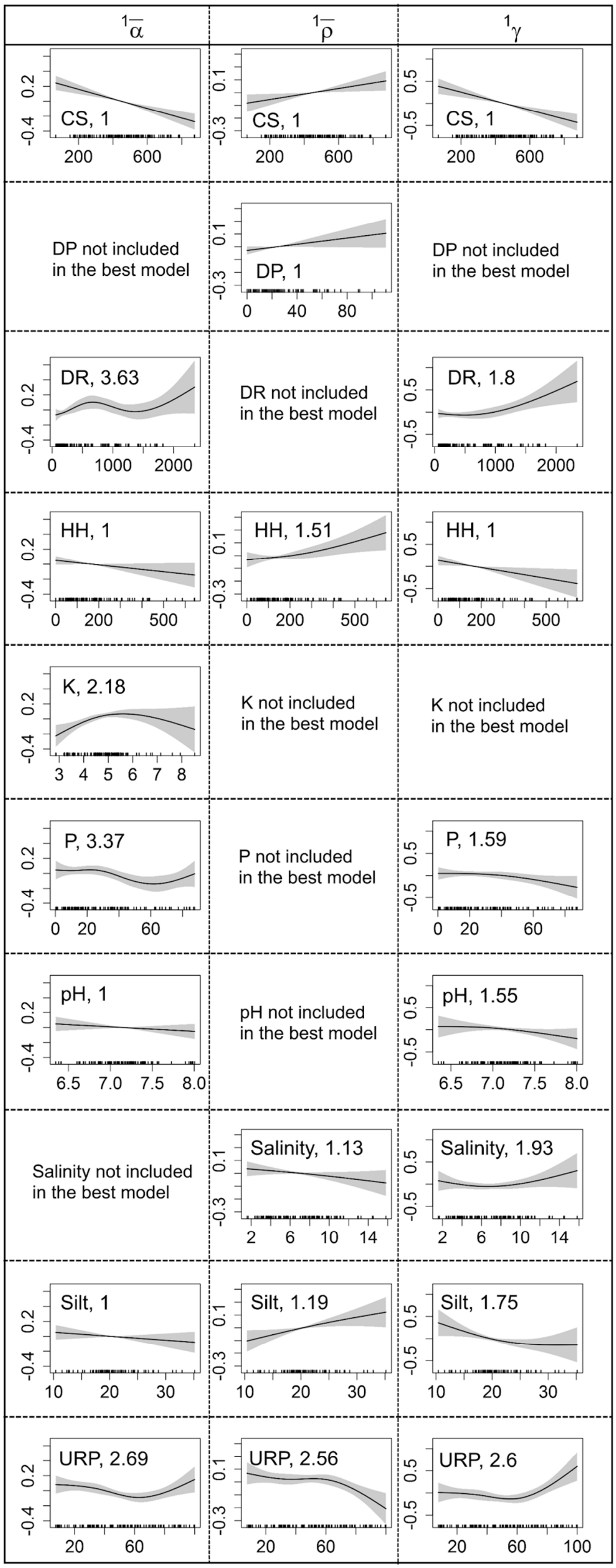
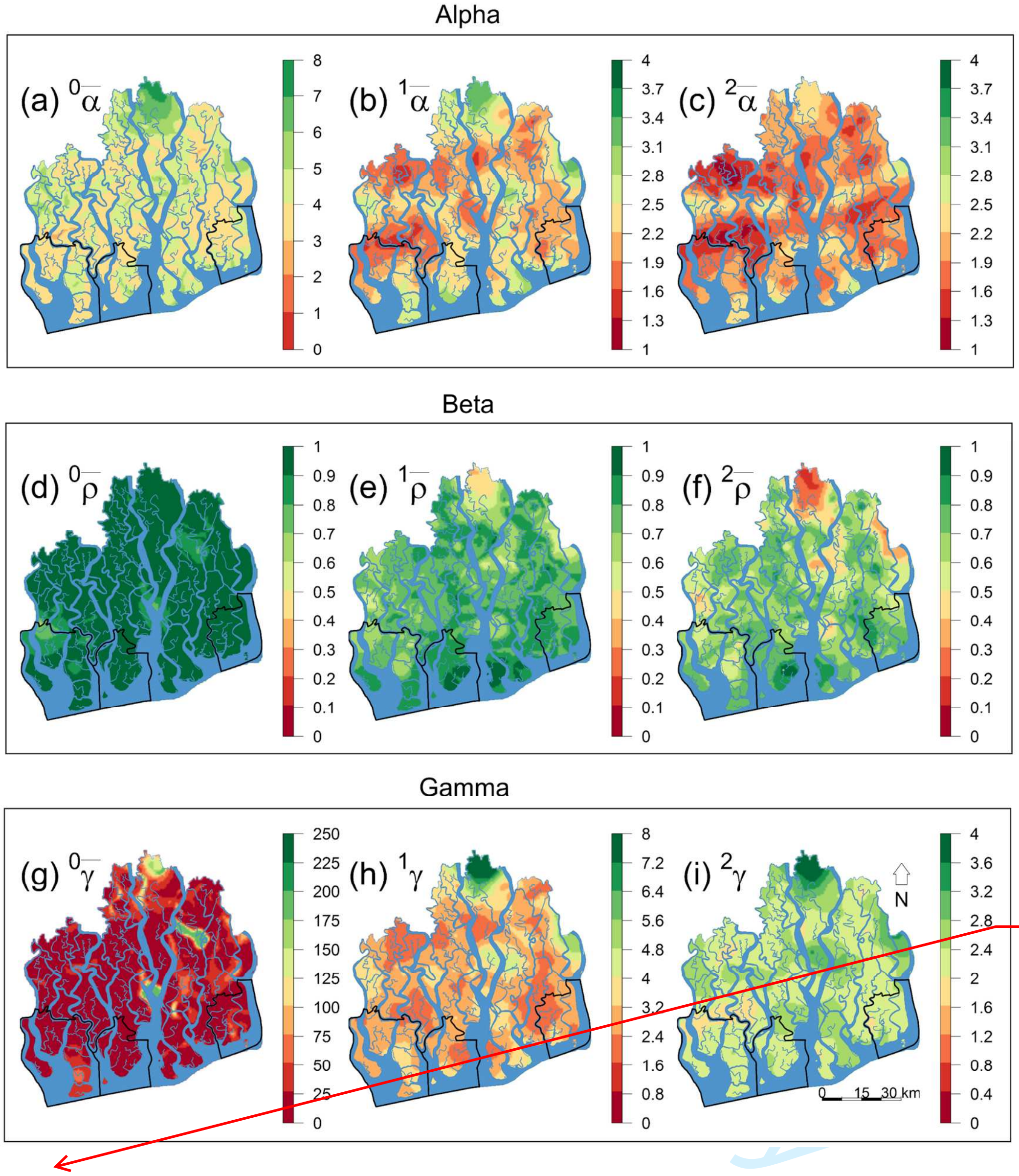


Figure 2. Effects of covariates inferred from our best GAMs fitted to the biodiversity indices for *q* = 1. The solid line in each plot is the estimated spline function (on the scale of the linear predictor) and shaded areas represent the 95% confidence intervals. Estimated degrees of freedom are provided for each smooth following the covariate names. Zero on the y-axis indicates no effect of the covariate on diversity index values. Covariate units: CS = total number of individuals in each plot, URP = % upriver, soil salinity = dS m^{-1}, DR = distance (m) of each PSP from the riverbank, Historical harvesting (HH) = total number of harvested trees in each plot since 1986, silt (%), disease prevalence (DP) = total number of diseased trees in each plot since 1986, P = mg Kg^{-1} and K = gm Kg^{-1}.



North arrow symbols for the map should be placed at each map

Figure 3. Spatial distributions of SC alpha, beta and gamma diversities (for q = 0 - 2) over the entire Sundarbans generated through GAMs. Higher values of $\overline{\alpha}$ and γ indicate greater species diversity and community contribution to the overall diversity of the ecosystem. Lower values of $\bar{\rho}$ indicate greater heterogeneity in species composition (i.e. community distinctness from the metacommunity) and higher values of $\bar{\rho}$ represent greater representativeness (i.e. homogeneity) in species composition. The black contours represent the three protected areas.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1

Table S1 Taxonomy, global conservation status, and mean abundances of the mangrove species censused in the 110 permanent sample plots in the Bangladesh Sundarbans. *IUCN global population trend, † Not assessed for the IUCN Red List, LC = Least concern, DD = Data deficient, NT = Near threatened, VU= Vulnerable, EN = Endangered, D = Decreasing.

Latin name	**Local name**	**Family**	**IUCN conservation status**	**Global population trend***
Aegiceras corniculatum (L.) Blanco	Khalshi	Myrsinaceae	LC	D
Amoora cucullata Roxb.	Amur	Meliaceae	NA†	NA
Avicennia officinalis L.	Baen	Avicenniaceae	LC	D
Bruguiera sexangula (Lour.) Poiret	Kakra	Rhizophoraceae	LC	D
Cerbera manghas L.	Dagor	Apocynaceae	NA	NA
Ceriops decandra (Griffith) Ding Hou	Goran	Rhizophoraceae	NT	D
Cynometra ramiflora L.	Singra	Fabaceae	NA	NA
Excoecaria agallocha L.	Gewa	Euphorbiaceae	LC	D
Excoecaria indica (Willd.) Müll.Arg.	Batul	Euphorbiaceae	DD	D
Heritiera fomes Buch-Ham.	Sundri	Malvaceae	EN	D
Intsia bijuga (Colebr.) Kuntze	Bhaela	Leguminosae	VU	D
Lumnitzera racemosa Willd.	Kirpa	Combretaceae	LC	D
Hypobathrum racemosum (Roxb.) Kurz	Narikali	Rubiaceae	NA	NA
Pongamia pinnata (L.) Pierre	Karanja	Leguminosae	LC	Stable
Rhizophora mucronata Lam.	Jhana	Rhizophoraceae	LC	D
Sonneratia apetala Buch-Ham.	Keora	Lythraceae	LC	D
Talipariti tiliaceum (L.) Fryxell	Bhola	Malvaceae	NA	NA
Tamarix dioica Roxb.	Nona Jhao	Tamaricaceae	NA	NA
Xylocarpus granatum Koen.	Dhundal	Meliaceae	LC	D
Xylocarpus mekongensis Pierre	Passur	Meliaceae	LC	D

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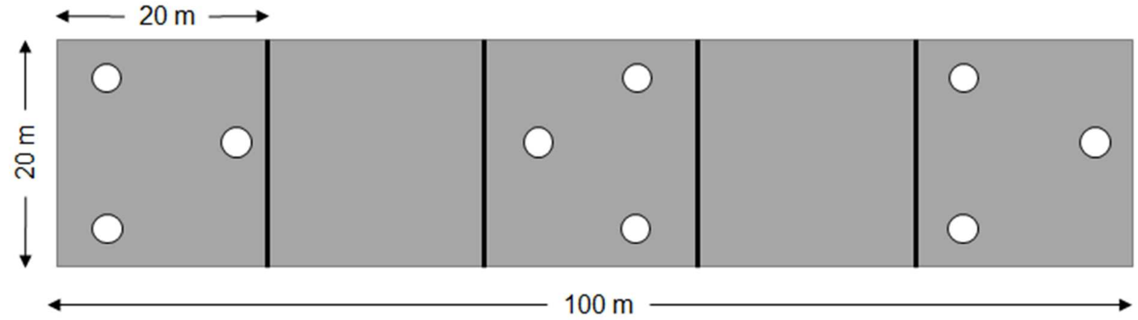

Fig. S1 Soil sampling design. Total 9 soil samples (circles, 0 – 30 cm depth) were randomly (3 samples/subplot) collected in the ends and middle of the 20 x 20 subplots in each PSP**.**

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Appendix S2

Table S2.1 Correlation (expressed as Pearson correlation coefficients) between the covariates.

	HH	DR	Elevation	K	DP	NH_4	P	pH	Salinity	Silt	CS	URP
DR	0.02											
Elevation	-0.07	0.09										
K	0.13	0.10	0.25									
DP	-0.18	0.02	0.16	0.11								
NH_4	0.3	-0.09	0.02	0.18	-0.06							
P	-0.18	-0.19	-0.05	-0.37	-0.02	-0.12						
pH	-0.01	0.00	-0.02	-0.13	-0.05	-0.18	-0.08					
Salinity	-0.22	-0.16	-0.02	-0.16	0.12	-0.29	0.28	-0.03				
Silt	0.09	0.09	0.11	0.11	0.04	0.01	0.02	0.06	-0.05			
CS	-0.16	-0.10	0.09	0.25	0.16	-0.04	-0.02	0.04	0.12	0.08		
URP	0.49	0.15	0.00	0.16	-0.22	0.15	-0.15	-0.15	-0.14	-0.03	-0.35	
ORP	0.06	0.04	0.01	0.20	-0.03	0.25	0.02	-0.89	-0.09	0.03	0.00	0.17

Table S2.2 Stepwise VIF test outputs of the environmental covariates. The covariate short-hands are: community size (CS), upriver position (URP), salinity, distance to riverbank (DR), historical harvesting (HH), acidity (pH), silt concentration, disease prevalence (DP), soil total phosphorus (P), soil potassium (K), elevation above average-sea level (ELE), and soil NH4.

Covariates	VIF
CS	1.33
URP	1.65
Salinity	1.29
DR	1.13
HH	1.50
pH	2.43
Silt	1.09
DP	1.14
P	1.32
K	1.5
Elevation	1.12
NH_4	1.27
ORP	5.58

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Appendix S3

Table S3 Results of GAMs for nine diversity measures. Summaries of model fit in rightmost three columns are only shown for the confidence set models i.e. models with $\Delta AIC_c \leq 2$. + symbol indicates that the covariates were retained and – symbol indicates that the covariates were not retained in the confidence set models for each biodiversity index. The covariate short-hands are: community size (CS), upriver position (URP), salinity, distance to riverbank (DR), historical harvesting (HH), acidity (pH), silt concentration, disease prevalence (DP), soil total phosphorus (P), soil potassium (K), elevation above average-sea level (ELE), and soil NH_4.

Diversity types		CS	URP	Salinity	DR	HH	pH	Silt	DP	P	K	ELE	NH_4	AIC_c	ΔAICc	AICcw
Alpha	${}^{0}\overline{\alpha}$	+	+	--	+	--	--	--	--	--	--	--	--	362.58	0.00	0.16
		+	+	--	--	--	--	--	--	--	--	--	--	362.92	0.34	0.14
		+	+	--	+	+	--	--	--	--	--	--	--	363.25	0.67	0.12
		+	+	--	--	+	--	--	--	--	--	--	--	363.29	0.72	0.11
		+	+	--	--	+	--	--	--	--	+	--	--	363.64	1.07	0.09
		+	+	--	--	--	--	--	--	--	+	--	--	363.83	1.26	0.09
		+	+	--	+	--	--	--	--	--	+	--	--	363.96	1.39	0.08
		+	+	--	+	--	--	+	--	--	--	--	--	364.10	1.53	0.08
		+	+	--	+	+	--	--	--	--	+	--	--	364.14	1.56	0.07
		+	+	--	+	--	--	--	+	--	--	--	--	364.51	1.93	0.06
	${}^{1}\overline{\alpha}$	+	+	--	+	+	+	+	--	+	+	--	--	118.89	0.00	0.42
		+	+	+	+	+	+	+	--	--	--	--	--	120.35	1.46	0.20
		+	+	--	+	+	--	+	--	+	+	--	--	120.42	1.53	0.20
		+	+	--	+	--	+	+	--	+	+	--	--	120.60	1.70	0.18
	${}^{2}\overline{\alpha}$	+	+	+	--	--	+	--	--	+	--	+	--	96.88	0.00	0.28
		+	+	--	--	--	--	--	--	+	+	--	--	97.57	0.69	0.20
		+	+	--	+	--	--	--	--	+	+	--	--	98.18	1.30	0.15
		+	+	--	--	--	--	--	--	+	+	+	--	98.34	1.46	0.14
		+	+	--	--	--	+	--	--	+	+	--	--	98.59	1.71	0.12
		+	+	--	--	+	--	--	--	+	+	--	--	98.72	1.83	0.11
Beta	${}^{0}\overline{\rho}$	+	--	+	+	--	--	--	+	--	+	--	--	-247.97	0.00	0.12
		--	+	+	+	--	--	--	+	+	--	--	--	-247.79	0.17	0.11
		+	--	+	--	--	--	--	+	--	+	--	--	-247.53	0.43	0.09
		+	--	+	--	--	--	--	+	+	--	--	--	-247.50	0.46	0.09
		+	--	+	+	--	--	--	+	+	--	--	--	-247.44	0.53	0.09
		+	--	+	+	--	--	--	+	+	+	--	--	-247.26	0.71	0.08
		--	--	+	--	--	--	--	+	--	+	--	--	-247.06	0.91	0.07
		+	--	+	--	--	--	--	+	+	+	--	--	-246.99	0.98	0.07
		+	--	+	+	--	--	--	--	+	+	--	--	-246.73	1.23	0.06
		+	--	+	+	--	--	--	+	--	--	--	--	-246.73	1.24	0.06
		--	+	+	+	--	--	--	+	+	+	--	--	-246.61	1.36	0.06
		--	--	+	--	--	--	--	+	+	+	--	--	-246.29	1.67	0.05
		+	+	+	--	--	--	--	+	+	--	--	--	-246.06	1.91	0.04
	${}^{1}\overline{\rho}$	+	+	+	--	+	--	+	+	--	--	--	--	-105.82	0.00	0.15
		+	+	+	--	+	+	--	+	--	--	--	--	-105.60	0.21	0.14
		+	+	+	+	+	+	--	+	+	--	--	--	-105.56	0.25	0.13
		+	+	+	+	+	+	--	+	--	--	--	--	-105.31	0.51	0.12
		+	+	+	--	+	--	--	+	--	--	--	--	-104.99	0.83	0.10
		+	+	+	--	+	+	--	+	+	--	--	--	-104.66	1.16	0.08
		+	+	--	--	+	--	--	+	--	--	--	--	-104.50	1.32	0.08
		+	+	+	--	--	--	+	+	--	--	--	--	-104.21	1.60	0.07
		+	+	+	--	+	--	+	+	+	--	--	--	-104.21	1.61	0.07
		+	+	--	--	+	--	+	+	--	--	--	--	-104.00	1.81	0.06
	${}^{2}\overline{\rho}$	+	+	+	--	+	+	+	+	+	+	+	--	-61.93	0.00	0.37
		+	+	+	+	+	+	+	+	+	+	--	+	-61.55	0.39	0.30
		+	+	+	--	+	+	+	+	--	--	--	--	-60.37	1.56	0.17
		+	+	--	+	+	--	+	--	+	--	--	+	-60.20	1.73	0.16

For Review Only

Gamma	$^{0}\gamma$	+	+	--	+	--	+	--	+	--	--	--	--	786.94	0.00	0.12
		+	+	--	+	--	+	--	+	--	--	--	+	787.16	0.22	0.11
		+	+	--	+	--	--	--	+	--	--	--	+	787.53	0.59	0.09
		+	+	--	+	--	+	--	+	--	--	+	--	787.54	0.60	0.09
		+	+	+	+	+	+	--	+	--	--	--	--	787.99	1.06	0.07
		+	+	--	+	--	+	+	+	--	--	--	--	788.01	1.08	0.07
		+	+	+	+	+	+	+	+	--	--	--	+	788.09	1.15	0.07
		+	+	+	+	--	+	--	+	--	--	--	--	788.15	1.22	0.07
		+	+	--	+	+	+	--	+	--	--	--	--	788.20	1.26	0.06
		+	+	+	+	--	+	+	+	--	--	--	--	788.24	1.30	0.06
		+	+	--	+	--	+	+	+	+	--	--	--	788.73	1.79	0.05
		+	+	+	+	+	+	--	+	--	--	+	--	788.74	1.80	0.05
		+	+	+	+	--	+	+	+	+	--	--	--	788.78	1.85	0.05
		+	+	--	+	+	+	--	+	--	--	+	--	788.92	1.99	0.04
	$^{1}\gamma$	+	+	+	+	+	+	+	--	+	--	+	+	279.25	0.00	0.65
		+	+	+	+	+	+	+	+	--	--	--	--	280.51	1.26	0.35
	$^{2}\gamma$	+	+	+	+	+	+	+	--	--	--	--	--	98.50	0.00	0.28
		+	+	--	+	+	--	+	--	+	+	--	--	98.58	0.08	0.27
		+	+	+	+	+	+	+	--	+	+	--	--	98.90	0.40	0.23
		+	+	+	+	+	--	+	--	+	+	--	--	99.05	0.55	0.21

For Review Only

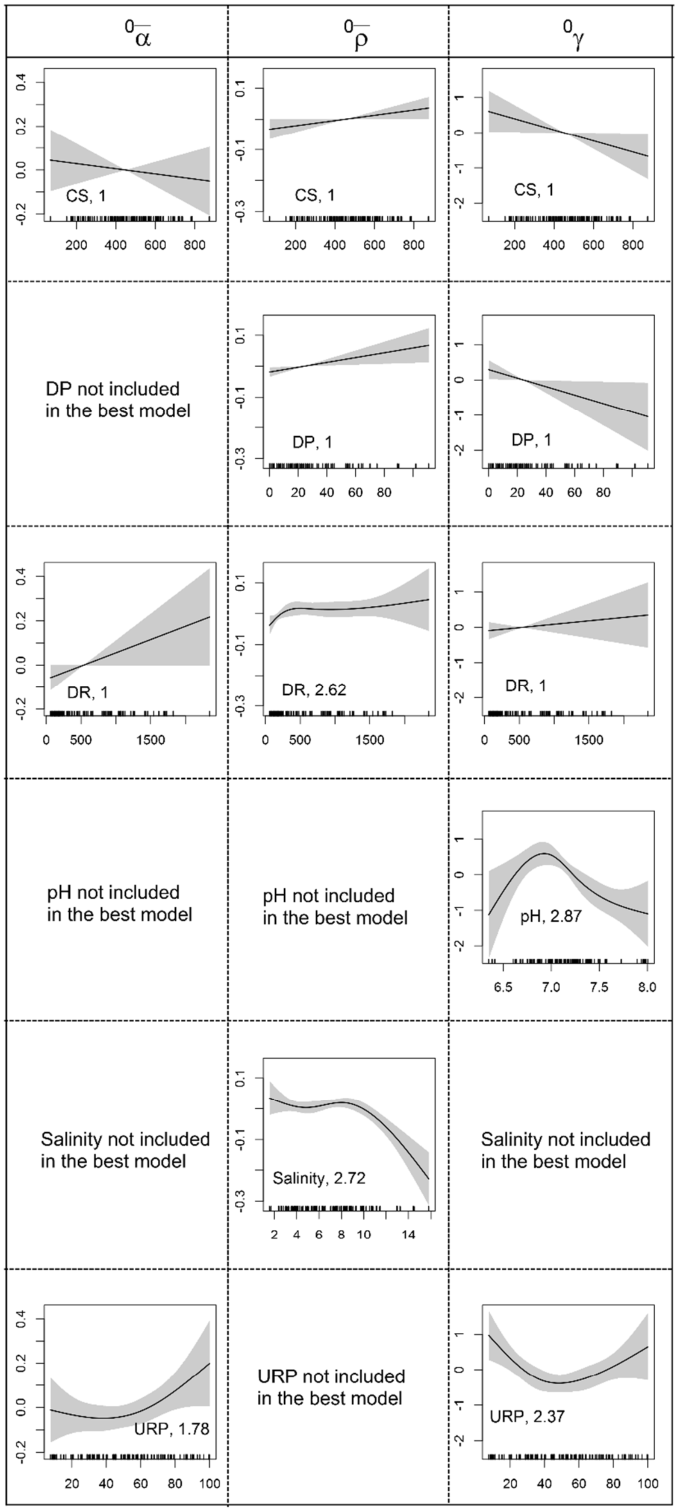

Fig. S3.1 Effects of covariates inferred from our best GAMs fitted to the biodiversity measures for $q = 0$.

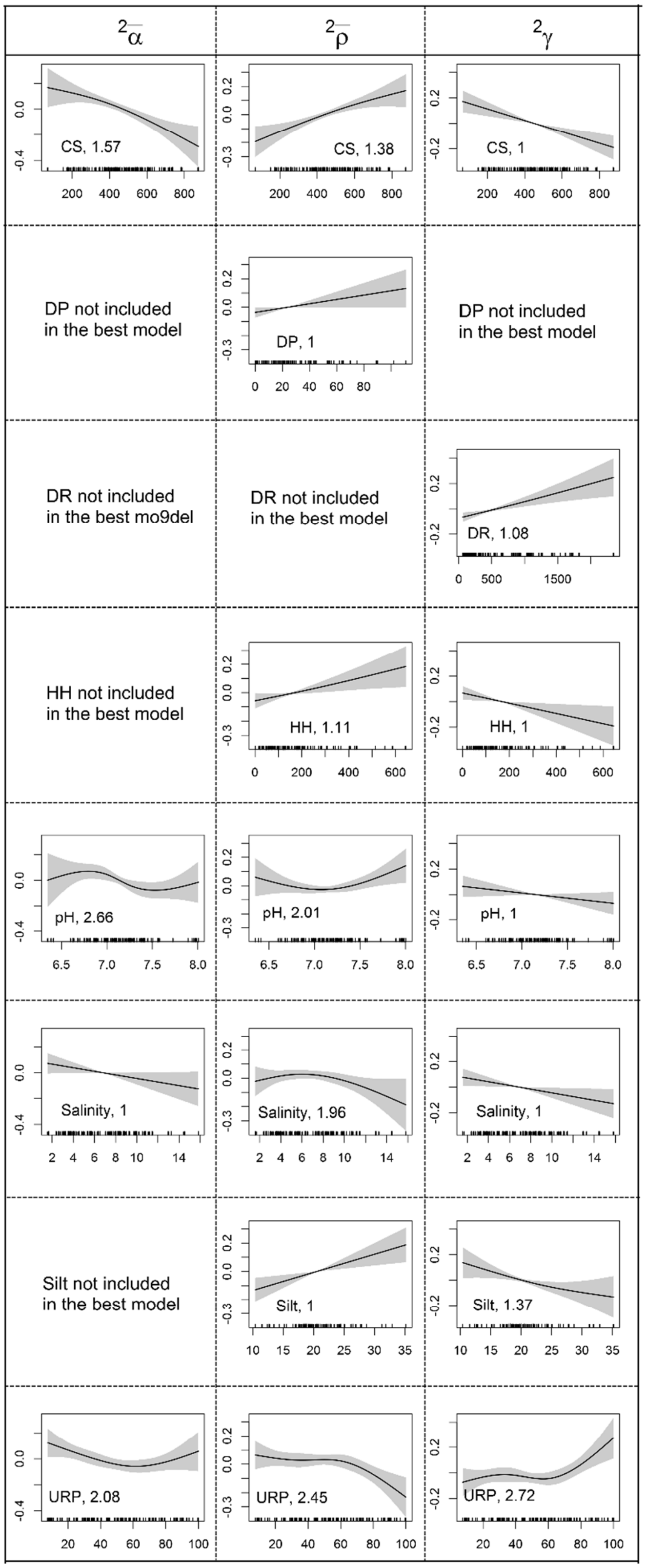

Fig. S3.2 Effects of covariates inferred from our best GAMs fitted to the biodiversity measures for $q = 2$.