

Biotic Constraints and Hydroperiod Drivers of Mangrove–Saltmarsh Zonation in a Microtidal Estuary

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Research Article

Keywords: tidal wetlands, predictive mapping, conditional prediction, sea level rise, joint species distribution model, saltmarshes, mangroves

Posted Date: July 15th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-10272380/v1>

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Additional Declarations: No competing interests reported.

Abstract

Coastal wetland zonation reflects interactions among tidal hydrology, microtopography, and species' physiological tolerances. However, the realized structure of mangrove–saltmarsh ecotones may also depend on biotic constraints not captured by abiotic suitability alone. Here we integrate locally calibrated microtopography, a quasi-dynamic tidal hydroperiod reconstruction, and a joint species distribution model (GJAM) to examine environmental and residual species associations among dominant intertidal vegetation at Towra Point Nature Reserve, southeastern Australia. Using 874 field-surveyed points across tidal flats, mangroves, saltmarsh, and supratidal vegetation, we identify hydroperiod metrics—especially maximum dry period and growing-season inundation frequency—as primary drivers of zonation. After accounting for these environmental gradients, strong negative residual associations persist between *Avicennia marina* and lower saltmarsh species, consistent with competitive exclusion across narrow elevation bands. These findings indicate that species interactions may constrain saltmarsh presence in microsites that appear environmentally suitable, suggesting that biotic filtering may influence future mangrove–saltmarsh transitions under sea-level rise. Our integrative field-based modelling approach highlights the combined role of tidal regime, microtopography, and species relationships in shaping estuarine vegetation patterns.

Introduction

Intertidal wetlands, including tidal flats, mangroves, saltmarshes and supra-tidal forests, are essential coastal ecosystems that provide a range of critical services. These wetlands play key roles in carbon sequestration, coastal protection, biodiversity support, water filtration and sediment stabilization (Barbier et al., 2011; Möller et al., 2014). Along the east coast of Australia, the intertidal zone comprises seagrass meadows and unvegetated tidal flats lowest in the tidal plane. These zones experience the most frequent and longest periods of tidal inundation. At slightly higher elevations, mangrove forests thrive in frequently inundated, saline conditions, while saltmarshes, dominated by herbaceous and graminoid vegetation, occur higher on the tidal plane with less frequent inundation and variable salinity regimes (Keith 2004). Forested swamps, such as those containing swamp oak (*Casuarina glauca*), are typically supra-tidal, but are tolerant of occasional inundation and variable salinity regimes (Grieger et al. 2023; Keith and Scott 2005).

Intertidal estuarine wetlands have experienced substantial historical losses in area and condition through drainage and reclamation, followed by conversion to industrial, port, agricultural and urban development (Davidson 2014; Schuerch et al. 2025). Intertidal wetlands now face an additional chronic and accelerating climate change induced threat: namely sea-level rise. Contemporary sea-level rise is accelerating and is projected to intensify hydrological stress across intertidal wetlands (Cazenave and LeCozannet 2014; Fox-Kemper et al., 2021; Frederikse et al., 2020).

The threat of sea-level rise has particularly profound implications for hydrologically responsive intertidal vegetation zones which occupy a narrow elevation gradient (Haigh et al. 2019). Intertidal zones are likely

to experience increasing inundation frequency and duration if sea-level rise outpaces vertical accretion rates (e.g. Thorne et al. 2018). Landward migration, where intertidal zones shift inland and subtidal extents increase, is widely predicted at a regional scale in estuarine wetlands (e.g. Thorne et al. 2018; Wen et al. 2023). The phenomenon of mangrove species encroachment into upslope saltmarsh habitat has been observed in recent decades, with increasing inundation, soil compaction, and CO₂ enrichment postulated as key drivers (Rogers et al. 2006; Saintilan and Rogers 2015; Saintilan and Williams 1999).

Regional and global projections of coastal wetland change under sea-level rise have successfully identified broad-scale patterns of vulnerability and potential migration corridors based on geomorphic and hydrological constraints (e.g., Borchert et al., 2018; Schuerch et al., 2018; Schuerch et al., 2025; Wen et al., 2023). These frameworks provide a critical "abiotic baseline" for assessing accommodation space. However, these models generally assume that vegetation will occupy all hydroperiod-suitable elevations. This assumption conflates the fundamental niche with the realized niche and may systematically overestimate habitat availability where competitive exclusion occurs. In effect, vegetation is treated as passively filling available physical space. This assumption neglects the distinction between the fundamental niche and the realized niche, which is sharply defined by biotic interactions—such as competition, facilitation, and dispersal limitation—that decouple local zonation from regional abiotic trends (Pennings & Callaway, 1992; Bertness & Leonard, 1997; LaFond-Hudson & Sulman, 2023).

Across the full intertidal–supratidal gradient, sharp vegetation boundaries are frequently maintained not only by inundation thresholds but also by competitive exclusion and vegetation-mediated feedbacks. For example, canopy shading by mangroves may competitively preclude saltmarsh species from physiologically suitable elevations (Saintilan & Rogers, 2015), while facilitation among high-marsh graminoids may ameliorate hypersalinity, allowing persistence in stressful supratidal zones (Bertness & Leonard, 1997). Consequently, abiotic-only projections likely misrepresent the pace and spatial configuration of community shifts, such as mangrove encroachment or the retreat of supratidal forests. To improve the accuracy of future vegetation forecasts, we must move beyond abiotic envelopes and explicitly quantify how interspecific dependencies modify the hydro-geomorphic requirements of wetland species.

This requires a modelling framework capable of disentangling environmental filtering from biotic constraints. Joint Species Distribution Models (JSDMs) offer a robust solution by estimating residual species associations alongside environmental responses (Clark et al., 2017; Pollock et al., 2014). In this study, we integrate high-resolution topographic data with a JSDM to develop an ecologically-predictive approach for coastal vegetation distributions. Specifically, we:

- Quantify fine-scale hydrological and topographic gradients across the transition from tidal flats to supratidal forests.
- Model species–environment relationships using a joint species distribution framework to capture the realized niche.

- Assess whether residual species associations indicate biotic constraints that may modify vegetation zonation beyond abiotic suitability.

By identifying the realized constraints on species distributions, this study aims to refine our capacity to predict future vegetation patterns in dynamic coastal wetlands facing accelerating sea-level rise.

Methods

Study sites

Towra Point Nature Reserve, situated on the southern shores of Botany Bay in New South Wales, Australia (Fig. 1), encompasses one of the most extensive and ecologically valuable tidal wetland complexes in the Sydney region. Designated as a Ramsar site, the reserve features a dynamic mosaic of tidal flats, mangroves, saltmarshes and supra-tidal and terrestrial forests that support diverse plant and animal communities (Australian Littoral Society 1977). Species patterns within the reserve are closely tied to topographic variation, which governs local hydrological regimes such as inundation frequency and soil salinity. Unvegetated tidal flats and seagrass beds occur at the lowest mapped intertidal elevations. The next lowest intertidal vegetation zone is dominated by the grey mangrove *Avicennia marina*. Mid- to upper-elevations are dominated by saltmarsh species which exhibit distinct zonation along fine-scale elevation or edaphic gradients (Keith 2004). Lower saltmarsh species are typically the halophyte *Sarcocornia quinqueflora* and graminoid *Sporobolus virginicus*. The upper saltmarsh is dominated by the rush *Juncus kraussii*. At higher elevation, the supra-tidal swamp oak forest (*Casuarina glauca* overstorey) dominates with terrestrial forest communities occurring beyond regular tidal inundation. Ecologists have used Towra Point Nature Reserve to study invertebrate-vegetation interactions (Bishop et al. 2012; Saintilan and Mazumder 2010). However, surprisingly few studies have addressed multi-species plant interactions in the intertidal zone. Clarke and Hannon (1971) used a glasshouse experiment to infer competitive exclusion of *S. quinqueflora* by both *A. marina* and *J. kraussii*. In addition, Kelleway et al. (2016) demonstrated lateral mangrove encroachment into saltmarsh vegetation communities. Our study extends those findings by using empirical field data to model multispecies plant associations. The planar profile and banded species zones at Towra Point make this site an ideal setting to investigate the role of topography and biotic interactions in shaping plant distributions across tidal wetland habitats. The predictive work is pertinent as sea-level rise and mangrove expansion continue to occur in response to global climate change.

Field Survey

A total of 874 survey points (including 46 on tidal flats) were captured across the vegetation communities on an eastern section of Towra Point Nature Reserve in October and November 2024. All sample points were located at the eastern side of a causeway (Fig. 1). Points were acquired using an approximate grid overlay so that data representation in each vegetation zone was roughly proportional to

the area of each zone. Points were captured with a Leica GS07 GNSS smart antenna (Leica Geosystems AG, Heerbrugg, Switzerland) using RTK corrections connected to the Leica SmartNet service (± 10 mm horizontal precision and ± 20 mm vertical precision). The antenna was affixed to a 2m staff. We followed approximate transect lines across the terrain with intervals of approximately 10 m between each point. At each point, latitude, longitude and elevation positional data were stored and species identities were recorded within an estimated 10 cm diameter area of the staff base. If bare ground dominated ($> 50\%$) the area of interest, its presence was recorded. Our focus was on rapid acquisition of species distributions across the elevation gradient. We therefore acquired species presence-absence information in the vicinity of the elevation measurement only.

Topographic variables

The 1-meter LiDAR DEM (digital elevation model) was acquired during April – July 2024 using a RIEGL miniVUX-3UAV drone (Riegl, Austria), flown at 20–24 km/hr at a height of 40–70 m above ground (measureaustralia.com.au). There are known issues with the accuracy of LiDAR DEM over vegetated areas (Hladik and Alber, 2012). As this study focuses on fine scale topography, we locally calibrated the LiDAR DEM using RTK elevation data to resolve fine-scale topographic variation we corrected the bias in the original LiDAR DEM using our field RTK elevation data. First, we compiled a map of intertidal vegetation zones by manually delineating and digitising vegetation communities from recent high resolution aerial photography (Nearmap Australia Pty Ltd January 2025 image). We then used LiDAR DEM with the field RTK elevation information to build a machine learning generalized additive mixed model (GAMM) in R 4.3.2 (R Development Core Team, 2023). With the fine-tuned GAMM ($R^2 = 0.982$), we then created a bias-corrected DEM. A total of 13 morphological variables, including distance to channel network, channel network base level, morphological feature, plan, profile and total curvatures and a topographic wetness index (Supplementary Materials Table A1), were computed using SAGA GIS (Conrad et al., 2015). These variables regulate salinity and hydrology gradients in the tidal wetlands through modulating flow direction, water, sediment and porewater salinity (Friedrichs and Perry, 2001).

Tidal regime reconstruction

A water level logger (HOB0-U20L-04 Onset, Bourne, USA) was installed at the main channel tidal flat (Fig. 1, ASL – 0.421m) to record tidal level at 15-minute intervals for approximately one year (2/02/2024–31/01/2025). This year-long duration captures intra-annual variation in the tidal regime, but does not capture inter-annual, ocean current or eustatic sea-level variations (Rogers and Krauss 2019). To reconstruct the spatial hydrological regime across a tidal wetland landscape, we integrated the 1-m digital elevation data (DEM) with the water level records using a combination of spatial and time series analysis in R (R Development Core Team, 2023). The core objective was to derive key inundation metrics at every pixel of the DEM domain, characterizing the frequency, duration and variability of tidal flooding relevant to wetland species patterns and ecosystem processes.

First, we extracted the unique ground elevation values from the DEM and identified the spatial coordinates (x, y) corresponding to each elevation. For each distinct elevation level, we simulated the local hydrological regime by referencing it against a continuous water level time series recorded by the tidal flat water level logger. The water depth at each time step was calculated as the difference between the measured water level and the target elevation. These water depth time series were then processed using the *TidalCharacteristics()* function from the “Tides” package (Cox and Schepers, 2018), which automatically detects tidal cycles and extracts key hydrological metrics such as inundation duration (*ITTsum*), dry duration (*DTTsum*), inundation frequency (*IFsum*), tidal amplitude (*TRmean*), and average inundation heights (*IHsum* and *IHcsum*). This approach is computationally efficient because the hydrological metrics only need to be calculated once for each unique elevation in the DEM grid and are then assigned to all equivalent elevations in the grid. The approach assumes, however, that the wetland inundates and emerges as if the tide rises and falls as a horizontal water surface across the entire wetland (i.e. the bathtub assumption). Figure A.1 demonstrates that this is a reasonable assumption for the defined study area at Towra Point.

To ensure ecological relevance, especially for plant phenology and growth, we separately evaluated hydrological metrics for the growing season, defined as the period from September 1 to March 31 (inclusive) (Morgan et al., 2016). This was achieved by subsetting the water level time series to this date range and reapplying the *TidalCharacteristics()* function to calculate growing-season-specific metrics including inundation frequency, proportion of time inundated, and mean tidal amplitude.

Additionally, custom metrics were derived directly from the water depth time series, including the standard deviation of inundation depth, which reflects hydrological variability. By looping through all elevations and mapping the resulting metrics back to their corresponding DEM pixels, we generated continuous spatial layers of hydrological regime variables (a total of 12 layers, Supplementary Material Table A2), suitable for further ecological modelling, classification or landscape-level analyses.

Joint species distribution model

To analyze species-environment relationships, we used Generalized Joint Attribute Modelling (GJAM), a multivariate Bayesian framework designed for joint species distribution modelling (Clark et al., 2017). GJAM models species occurrences simultaneously, accounting for residual correlations among species while incorporating environmental predictors. This approach is particularly useful for presence-absence data, as it allows for interspecific dependencies to be estimated alongside species-specific responses to environmental variables (Clark et al., 2017).

In this study, we applied GJAM to plant presence-absence data collected from our field survey. We used topographic predictor variables such as distance to the channel network, plan and profile curvatures, and relative slope position, as well as tidal regime predictor variables (e.g., inundation frequency, maximum dry period) derived from the corrected DEM and water level logger data. These predictors characterize fine-scale variation in habitat structure and hydrological conditions. We removed highly correlated

environmental variables using the *VIF* function (Variance Inflation Factor) from the “usdm” package (Naimi et al. 2014). We removed these variables to prevent model overfitting (Johnson et al., 2023), ensure stable parameter estimation (Ovaskainen and Abrego, 2020), and improve model transferability (Wunderlich et al., 2025). In addition, to ensure the comparability of the fitted coefficients, all predictor variables were scaled and standardized (i.e. the z-score normalization) before model fitting.

To accommodate potential non-linear responses, we sequentially incorporated spline terms for environmental covariates (Hastie and Tibshirani, 1990) and selected the final model with the smallest deviance information criterion (DIC) (Spiegelhalter et al., 2014). This approach explicitly captures non-linear, unimodal, or other curvilinear relationships between species and their environment (Ovaskainen and Abrego, 2020). We assumed high detection probability for dominant canopy and ground-layer species during intensive field surveys, and therefore did not incorporate detection sub-models.

The model used the “gjam” R package (Clark et al., 2017), with posterior inference conducted via Gibbs sampling. Environmental coefficients and species associations were estimated from the posterior distribution.

Thresholding GJAM probability to binary presence/absence maps

To convert the continuous species occurrence probabilities predicted by the GJAM model into binary presence–absence maps, we applied the Lowest Presence Threshold – Robust (LPT-R) method (Pearson et al., 2007). LPT-R is a conservative thresholding approach designed to reduce the influence of outlier presence records, such as those arising from misidentification, vagrant individuals, or atypical environmental conditions (Dorm et al., 2025). Rather than assigning the minimum predicted probability at observed presence sites (as in traditional LPT), LPT-R selects a lower quantile (5th percentile in this study) of predicted suitability values at known presence locations as the threshold. This ensures that high-confidence presences are retained, while reducing overprediction into marginally suitable areas. The LPT-R threshold was calculated independently for each species using the predicted posterior mean probabilities from the GJAM model, and binary maps were generated by applying these thresholds across the prediction grid. This method is particularly suited for species distribution modelling in dynamic environments such as tidal wetlands, where conservative delineation of suitable habitat is ecologically justified. The LPT-R approach has been proposed as a robust alternative to common statistical thresholds in SDM post-processing (Dormann et al., 2022; Liu et al., 2005).

Model Performance Assessment

To evaluate the predictive performance of the GJAM model, we used threshold-dependent and threshold-independent metrics. Specifically, we assessed model accuracy using the Area Under the Receiver Operating Characteristic Curve (AUC-ROC), True Skill Statistic (TSS) and the and the F1-score for each

species. This approach ensures robust model assessment by incorporating both probability-based discrimination (AUC) and classification accuracy (TSS and F1-score).

Threshold-Independent Metric: AUC-ROC

The AUC-ROC was calculated to measure the model's ability to discriminate between presence and absence. AUC values range from 0 to 1, where values ≥ 0.7 indicate acceptable model performance, ≥ 0.8 indicate good performance, and values ≥ 0.9 suggest excellent discrimination (Swets, 1988; Manel et al., 2001). AUC was computed for each species using the pROC package in R.

Threshold-Dependent Metric: TSS

To assess classification accuracy, we used the True Skill Statistic (TSS), which considers both sensitivity and specificity. TSS values range from -1 to 1 , where values ≥ 0.4 are considered acceptable, ≥ 0.6 indicate good performance, and values ≥ 0.8 suggest excellent model accuracy (Allouche et al., 2006; Liu et al., 2011). The optimal threshold for presence-absence classification was determined using Youden's index, which identifies the threshold that maximizes the sum of sensitivity and specificity (Youden, 1950).

F1-Score for Model Performance

The F1-score was also used to evaluate model performance, as it provides a balance between precision (positive predictive value) and recall (sensitivity). The F1-score is particularly useful when dealing with imbalanced presence-absence data. It is calculated as:

$$\text{F1-score} = F1 = 2 \times \frac{\text{Precision} \times \text{Recall}}{\text{Precision} + \text{Recall}}$$

$$\text{and Precision} = \frac{TP}{TP + FP} \text{ and Recall} = \frac{TP}{TP + FN}$$

where TP = True Positive, FP = False Positive, TN = True Negative, and FN = False Negative.

F1-score values range from 0 to 1, where ≥ 0.6 is considered acceptable, ≥ 0.7 is good, and ≥ 0.8 suggests highly reliable predictions. A low F1-score (< 0.5) may indicate poor model performance due to class imbalance or prediction errors. The use of F1-score in ecological modelling has been supported by studies such as Sokolova & Lapalme (2009) and Powers (2011).

Permutated variable importance

To evaluate the relative importance of predictor variables in influencing species distribution, we implemented a permutation-based variable importance approach that assesses the effect of each predictor on model predictive certainty. Specifically, we quantified the contribution of each environmental variable by independently shuffling its values and comparing the change in predictive uncertainty—measured as the mean absolute difference in the posterior standard deviation of species composition

(wSe)—relative to predictions from the original fitted model. This procedure was repeated for each predictor while holding all other variables constant, thereby isolating its unique influence. Model predictions were generated using 1,000 posterior samples ($nsim = 1000$) to ensure robust estimation of uncertainty. The resulting importance scores were normalized to yield relative rankings and rescaled to a 1–100 range for interpretability. This approach provides a reliable estimate of each predictor's influence on reducing uncertainty in the multivariate species response modelled by GJAM. The permuted variable importance is a well-established method in machine learning and statistical modelling (Gregorutti et al., 2017; Fisher et al., 2019).

Species association-based condition predictions

We applied the `gjamConditionalParameters()` function to the fitted GJAM model to investigate species co-occurrence structure and potential interspecific associations beyond shared environmental responses. This approach partitions the residual correlation structure of the model to estimate partial correlations between species, conditional on the presence or absence of others in the community (Clark et al., 2017; Wilkinson et al., 2021). For each focal species, we calculated conditional residual associations (A-matrix) by conditioning on the remaining species in the assemblage. This allows the identification of positive or negative associations that may reflect facilitation, competition, or unmeasured ecological filtering. We also extracted the conditional precision (P-matrix), representing the inverse of residual variance, as a measure of how tightly a species' occurrence is constrained by the community context. Significant associations were defined by 95% credible intervals that did not include zero. This method provides a statistical framework for disentangling species co-occurrence patterns from the effects of shared environmental drivers, supporting inference on biotic structuring in community assembly.

Post-Modelling Prediction of Species Distribution Using GJAM

After fitting the Generalized Joint Attribute Model (GJAM), we used the trained model to predict the distribution of grey mangrove (*A. marina*), saltwater couch (*S. virginicus*), beaded glasswort (*S. quinqueflora*), sea rush (*J. kraussii*), and swamp oak (*C. glauca*). Predictions were generated across the study area using new environmental data representing different topographic and hydrological conditions.

To obtain species occurrence probabilities, we applied the posterior mean estimates of model parameters to the new predictor dataset, which included topography variables (e.g., distance to the channel network, minimum and maximum curvatures, relative slope position) and hydrological variables (mean inundation duration, maximum dry period, and growing season inundation frequency). These probability predictions were then converted into binary occurrence values (presence-absence) using species-specific thresholds determined by LPT-R.

Model uncertainty was assessed using posterior predictive intervals, and spatial prediction accuracy was evaluated by comparing predicted distributions with independent validation data. The final binary occurrence maps provide insights into potential habitat suitability under varying tidal regime scenarios.

Results

Vertical Zonation and Species Realized Niches

The distribution of the five dominant wetland species exhibited distinct vertical zonation across the tidal frame, though with notable overlapping physiological tolerances (Fig. 2). *A. marina* occupied the lowest elevation range (Median: 0.49 m AHD), extending from the mudflat boundary into the mid-intertidal zone. *S. quinqueflora* and *S. virginicus* occupied the mid-to-high intertidal positions, while *J. kraussii* and *C. glauca* were restricted to the highest elevations (Fig. 2).

Crucially, the violin plots reveal a substantial "elevation overlap"—particularly between the upper range of *A. marina* and the lower range of *S. quinqueflora*. While *S. quinqueflora* is physiologically capable of occupying lower elevations (indicated by the lower tail of its distribution), its realized niche is truncated relative to *A. marina*. This discrepancy between potential abiotic suitability and observed occurrence indicates that elevation alone does not fully explain zonation patterns.

Model performance

The GJAM with the smallest Deviance Information Criterion (DIC) included ten environmental predictors: the three natural cubic splines of distance to channel network (Distance 1, Distance 2 and Distance3), terrain complexity, maximum and minimum curvature, relative slope position (RSP), mean inundation duration (MID), maximum dry period (MDP), and flood frequency during the growth season (FreqG). The GJAM fitted the survey data well for all species (Table 1). Overall, the model’s performance was excellent according to probability-based metrics (i.e. AUC), and good (TSS, F1-score) according to classification-based metrics. Moreover, none of the species were modelled poorly according to the performance metrics. The model performance for *J. kraussii* was evaluated as highly reliable for both probability- and classification-based metrics, but the performance varied for other species (Table 1).

Table 1
Species-specific model performance at Towra Point Nature Reserve, Australia

AUC	A. marina	S. virginicus	S. quinqueflora	J. kraussii	C. glauca	Mean	Overall
	0.97	0.83	0.80	0.96	0.96	0.91	Excellent
TSS	0.85	0.57	0.46	0.84	0.84	0.71	Good
F1-score	0.85	0.78	0.68	0.83	0.56	0.74	Good

The comparison of species distributions among contemporary aerial photo, mapped and predicted approaches is presented in Fig. 3. Visual inspection shows that there are no major discrepancies in the predicted patterns of distribution in comparison to the mapped distribution. In particular, the predicted distribution of mangroves is similar to the aerial photo.

Importance of environmental variables

Permutation-based analysis of predictor importance revealed differences in the relative contributions of hydrological and morphological variables in this tidal wetland system (Fig. 4). The inundation metrics of Maximum dry period (MDP), Inundation frequency during the growing season (FreqG) and Mean length of each inundation event (MID) were the most influential predictors of species distributions (Table 2). The dominance of these variables in the permutation-based importance analysis emphasises the strong influence of tidal hydrological regimes on species distributions in this intertidal environment.

Table 2
Permutation-based importance of the investigated hydrological and morphological variables using AUC, TSS and F1-score

Variable description		Importance score (%)		
		AUC	TSS	F1-score
MDP	Maximum dry period: longest continuous period without inundation	100	100	85.1
FreqG	Number of inundation events during the growing season (1st September – 31st March)	95.6	98.5	100
MID	Mean duration (hrs) of each inundation event	31.6	39.6	39.4
distance2	Distance to channel network metric: spline 2	20.6	35.6	24.6
distance3	Distance to channel network metric: spline 3	9.7	11.6	20.7
convexity	Terrain surface convexity: either diverging or concentrating water flow	2.4	3.8	11.0
mincurve	Minimum curvature: depression-forming concavity	1.6	6.8	17.2
RSP	Relative slope position: elevation relative to coastal terrain	1.3	6.9	4.2
maxcurve	Maximum curvature: ridge-forming convexity	0.9	0	4.4
distance1	Distance to channel network metric: spline 1	0	4.5	0

While morphological factors such as distance to the tidal channel network (distance2 and distance3), terrain convexity and minimum curvature (mincurve) also contributed to predictions, their influence was moderate (Table 2). Although fine-scale terrain features help structure species at local scales, it is inundation metrics of extended dry periods and inundation frequency and duration that are the primary drivers of species zonation in this coastal wetland ecosystem.

The species-specific effects of hydrology and topography

The GJAM model revealed species-specific responses to hydrological and topographic variables (Fig. 4). These patterns reflect ecological niche differentiation along both topographic and hydrological

gradients. Among the tidal wetland species examined, *A. marina* showed a strong negative association with distance from the channel network, as indicated by significantly negative standardized coefficients for all three distance splines—particularly distance2 (posterior mean ≈ -2.0 , 95% CI excluding zero) and distance3—highlighting its preference for frequently inundated areas. Positive effects of inundation frequency during the growing season (FreqG) and mean inundation duration (MID) further emphasise the reliance of mangroves on persistent tidal inundation (Fig. 4a). Maximum dry period (MDP) was expected to have a negative effect on *A. marina* distributions, yet the model indicated a small positive effect (Fig. 4a). The basis for this result is unclear, possibly reflecting the dominance of inundation frequency (FreqG) and the absence of interaction terms in the model.

S. quinqueflora, a lower saltmarsh species, exhibited negative associations with inundation frequency (FreqG) and maximum dry period (MDP) (posterior mean ≈ -0.7) and moderate uncertainty, suggesting sensitivity to both prolonged inundation and desiccation stress (Fig. 4b). *S. virginicus*, another lower saltmarsh species, showed strongly positive associations with distance from the channel network (distance2 and distance3: posterior means > 2.0 , 95% CIs excluding zero) and negative coefficients for inundation frequency (FreqG), extended dry periods (MDP) and inundation duration (MID), indicating that it favours moderately elevated marsh zones that are neither too wet nor subject to extended dry periods (Fig. 4c).

The upper saltmarsh species, *J. kraussii*, displayed positive responses to distance from channel network (distance2 and distance3: posterior means ≈ 1.5 and 1.0 , respectively) and extended dry periods (MDP), and negative associations with inundation duration (MID: ≈ -1.2), indicating its preference for higher intertidal elevations (Fig. 4d). *C. glauca* exhibited a strong positive association with maximum dry period (MDP). Unexpectedly, it also exhibited a small yet positive association with inundation frequency during the growing season (FreqG) and mean inundation duration (MID) (Fig. 4e). The dominant association with MDP and an absence of defined model interaction terms, limits our capacity to interpret findings for FreqG and MID. Compared with the other intertidal species, *C. glauca* responses were less sharply defined by proximity to tidal channels or slope metrics, indicating a more generalized habitat tolerance within the supra-tidal zone.

These species-specific patterns emphasize the different ecological strategies of tidal wetland species and the potential for predictive mapping to appropriately capture their distributions. The separation of responses along both hydrological and topographic gradients provides strong support for environmental filtering as a structuring force in these coastal wetland communities. These results highlight clear species-specific differences in habitat associations, while also demonstrating the degree of uncertainty in parameter estimates. The wider credible intervals for certain variables suggest uncertainty in species responses or data limitations. The use of standardized coefficients and credible intervals derived from Gibbs sampling in the GJAM framework ensures that uncertainty is appropriately quantified, enhancing the interpretability and robustness of species–environment relationships captured by the model.

Disentangling Environmental Filtering from Biotic Interactions

While hydrological gradients defined the fundamental niche for all species, the Joint Species Distribution Model (GJAM) revealed that biotic interactions significantly constrained the realized niche, particularly at ecotonal boundaries (Fig. 5). After accounting for all shared environmental responses (e.g., elevation, hydroperiod), strong negative residual correlations emerged between the dominant mangrove *A. marina* and lower saltmarsh taxa. Specifically, *S. quinqueflora* exhibited a significant negative dependence on *A. marina* ($p = -0.74$; Fig. 5a, b). This suggests that within the elevation bands where these species physiologically overlap (as observed in Fig. 2), *S. quinqueflora* is competitively excluded by *A. marina*. A similar, though slightly weaker, negative association was observed between *S. virginicus* and *A. marina* ($p = -0.64$). In contrast, positive residual associations were identified in the high marsh, suggesting facilitative mechanisms. *J. kraussii* displayed a positive correlation with *S. virginicus* (0.13). The conditional precision estimates further reinforced this distinction: species with narrow, competitively constrained niches (*S. quinqueflora*, precision = 0.62) were highly predictable based on community composition, whereas the canopy-dominant *A. marina* (precision = 0.36) was structured primarily by physical environmental filters rather than interspecific dependency.

Discussion

Beyond Abiotic Envelopes

Large-scale projections of wetland migration under sea-level rise have been instrumental in identifying broad patterns of vulnerability (Schuerch et al., 2018; Thorne et al., 2018; Wen et al., 2023). These models emphasize elevation capital and accommodation space as dominant controls. Our results confirm that hydroperiod metrics—particularly maximum dry period and growing-season inundation frequency—strongly structure species distributions. However, our results show that "bathtub" models relying solely on elevation will likely overpredict saltmarsh persistence in zones suitable for mangroves, as they fail to account for competitive exclusion (Fig. 6). After accounting for hydroperiod, strong negative residual associations remained between mangroves and lower saltmarsh species. These patterns are consistent with competitive exclusion along stress gradients (Bertness & Leonard, 1997; Emery et al., 2001). Thus, abiotic-only projections likely overestimate the resilience of saltmarshes by assuming they can retreat into any physically suitable upslope accommodation space. Our model suggests that without active management of mangrove encroachment (e.g., via hydrological manipulation), the realized migration corridor for saltmarsh may be significantly narrower than the potential abiotic corridor identified by regional models (e.g., Borchert et al. 2018). By incorporating residual species dependencies, the joint model captured patch-scale exclusion that elevation-based predictions would overlook.

Environmental predictors of intertidal species distributions

Hydrological variables, particularly maximum dry period (MDP), number of inundation events during the growing season and mean length of each inundation event, were dominant drivers of species occurrence at Towra Point Nature Reserve, supporting the paradigm that tidal wetland vegetation is largely structured by hydroperiod and salinity gradients (Pennings et al., 2005; Silvestri et al., 2005). While we did not measure soil salinity directly, the strong explanatory power of MDP may provide a proxy for hypersaline stress in this system. In micro-tidal, sandy wetlands like Towra Point, extended dry periods in depression features increase porewater salinity well beyond seawater concentrations (Ridgway et al., 2012). By capturing this hydrological mechanism, the model indirectly captures variable physiological tolerance of salinity stress. Other studies have similarly identified inundation frequency (Balke et al. 2016) and duration (Balke et al. 2011) as primary determinants of saltmarsh or mangrove vegetation limits. These hydroperiod components appear particularly useful across global studies in discriminating species distributions. Topographic variables such as distance to the channel network, terrain surface convexity, curvature and relative slope position had lower overall importance compared with hydrological variables but were important discriminators at the species level. Our results are consistent with observations that morphological gradients modulate local hydrodynamics and species habitat suitability (He et al., 2011; Fagherazzi et al., 2012a). Topographic features, although secondary in permutation importance, likely act as interaction amplifiers. Small variations in elevation structure localized hydrological contrasts that may tip competitive balances between adjacent species. Thus, topography may not directly filter species; it may define the spatial scale of biotic interactions.

Biotic interactions affecting intertidal species distributions

We observed multiple negative biotic interactions across adjacent vegetation zones. Mangrove (*A. marina*) and lower saltmarsh species (*S. quinqueflora* and *S. virginicus*) exhibited mutual negative interactions. Furthermore, lower saltmarsh species were often distributed in patch monocultures. The adjacent upper saltmarsh (*J. kraussii*) and Swamp oak forest (*C. glauca*) species also depicted negative interactions. These species patterns follow the paradigm of a steep intertidal physical stress gradient generating striking zonation as species competitively dominate at their optimal niche position and are excluded when physical conditions (hydrological and edaphic) exceed stress tolerances (Angelini et al. 2011; Bertness and Leonard 1997). We also found weakly positive interactions between *S. virginicus* and *J. kraussii* at higher elevations of the study area. These species may exhibit facilitative interactions within shared niche spaces, where plant cover can effectively limit evaporative water loss and salt accumulation, in turn ameliorating stressful physical conditions (Bertness and Leonard 1997; He and Bertness 2014). Our observational study has identified sharp patterns of zonation consistent with other intertidal wetlands (e.g. Angelini et al. 2011; Friess et al. 2012; Pennings and Callaway 1992). However, manipulative experiments are required to attribute displacement or co-occurrence to competitive or facilitative interactions or to physiological limitations. In any case, our predictive model successfully captured characteristically strong patterns of intertidal zonation, particularly in the lower intertidal zone.

Methodological innovation and advancements in GJAM

The primary contribution of this study is not methodological novelty *per se*, but demonstration that species interactions must be incorporated in projection models to avoid the problem of systematic bias in sea-level rise impact assessments. While JSDMs have been increasingly applied in community ecology (Ovaskainen et al., 2017), their use in forecasting climate-driven ecotone shifts remains limited. Our results show that including residual covariance changes predicted persistence patterns better than abiotic drivers alone. Unlike traditional species distribution models (SDMs) that treat species independently, GJAM provides a joint modelling framework that estimates residual co-occurrence patterns. Inclusion of residual species associations via conditional prediction enables researchers to assess co-occurrence patterns that may reflect unmeasured ecological filters (Kettunen et al., 2021; König et al., 2021; Ovaskainen et al., 2017). This is especially useful in complex ecological systems like tidal wetlands where plant assemblages are structured by both abiotic stressors and biotic interactions (Fagherazzi et al., 2012b; Taylor et al., 2021). While our analysis does not demonstrate causation, we found evidence of both negative (e.g. *S. quinqueflora* and *A. marina*) and weakly positive (*J. kraussii* and *S. virginicus*) associations among species. Our modelling approach explicitly considers biotic interactions and therefore increases ecological realism of predictive mapping.

This study contributes to the growing body of literature utilising multivariate, probabilistic frameworks in community ecology (e.g., Ovaskainen & Abrego, 2020; Ovaskainen et al., 2017). Compared to latent variable models (e.g., HMSC or BORAL), GJAM's ability to handle non-normal, discrete responses (e.g., presence-absence) with species covariance estimation makes it particularly suitable for systems where detection probability is high, but species abundances are sparse. Furthermore, the integration of quasi-dynamic tidal hydrology reconstruction using logger data and high-resolution DEMs presents a robust approach for linking environmental gradients to biological responses at landscape scales. This offers an advance by accounting for seasonal variability and topographic control of tidal exposure—crucial predictors of vegetation zonation (e.g. Davis et al. 2005; Duke 1990).

Limitations

We identify several limitations associated with the study. Our analysis pertained to a single tidal wetland, and patterns observed may vary in other estuarine or geomorphic contexts. Indeed, the importance of site-level variation in topography, channel configuration and tidal regime on species habitat availability has been recognised by many researchers (e.g. Mossman et al. 2012; Woodroffe et al. 2016). However, our mapping approach should be used within a cascading decision-support framework. We advocate for regional-scale vulnerability assessments to provide a first pass identification and prioritisation of high-value wetlands for further analysis. Our modelling can then be applied to derive accurate map products from empirical and modelled parameters for a subset of intertidal wetlands.

We caution that while the bathtub simplification holds for this marine-dominated, sandy system, it may fail in wetland sites that are large with respect to estuarine water-level gradients and in wetlands sites with complex geomorphology. In such contexts, our JSDM framework would require coupling with a hydrodynamic model of the wetland site of interest.

Our reliance on presence–absence data, while rapidly acquired in the field, limits the ability to detect fine-scale abundance responses, and some potentially influential environmental variables (e.g., soil nutrients and salinity, historical disturbance) were not included. Future work could expand the spatial and temporal scope, incorporate abundance-based models, and explore how species associations evolve under projected climate and land use change scenarios.

While residual correlations are consistent with competitive or facilitative interactions, they do not demonstrate causality. Experimental manipulation would be required to confirm mechanisms. Nevertheless, from a forecasting perspective, capturing these statistical dependencies improves predictive realism regardless of underlying process.

Implications for Coastal Wetland Management

For coastal managers, projections based solely on elevation capital may overestimate the availability of refuge habitat for saltmarsh under sea-level rise. Even where upslope terrain appears hydroperiod-suitable, competitive exclusion by mangroves may restrict realized migration corridors. Management strategies that rely on passive landward retreat may therefore fail to conserve saltmarsh without active intervention, such as hydrological manipulation or targeted mangrove control in priority conservation zones. The strong negative association between *A. marina* and *S. quinqueflora* and *S. virginicus* as well, implies that active intervention, such as funnelling to reduce hydroperiod or targeted mangrove seedling removal (Kelleway et al., 2017), may be required to maintain saltmarsh refugia even in areas that appear geomorphologically suitable. Furthermore, the robust performance of the 'bathtub' hydrological model in this particular system suggests that managers may achieve reliable, site-specific vegetation forecasts using accessible logger data and RTK-calibrated DEMs, without the need for computationally expensive hydrodynamic simulations in settings with similar scale and morphological complexity.

Conclusion

This study demonstrates that while hydroperiod remains the dominant driver of tidal wetland zonation, species interactions significantly constrain realized distributions at mangrove–saltmarsh ecotones. Models that ignore these dependencies risk overestimating saltmarsh resilience and underestimating mangrove expansion under sea-level rise. Integrating joint species modelling with hydrological metrics enhances ecological realism and refines forecasts of climate-driven boundary shifts. Forecasting coastal wetland change under sea-level rise requires explicit consideration of biotic constraints. Incorporating species interactions into predictive models improves spatial realism and strengthens the evidence base for adaptive wetland management.

Declarations

Author Contribution

All co-authors contributed to study conception and design. TM and MH acquired data, while all authors contributed to project implementation. LW conducted formal analysis and interpretation of data. LW wrote the original manuscript draft. All authors substantively edited and revised the manuscript and approved the submitted version of the manuscript.

Acknowledgement

Fieldwork was conducted on country of Dharawal, Dharug and Eora nations with NSW Scientific Licence SL100432. The research was funded under the Marine Estate Management Strategy (MEMS). MEMS is the NSW Government's ten-year Strategy developed by the NSW Marine Estate Management Authority to coordinate the management of the marine estate.

Data Availability

All data supporting the findings of this study are available within the paper and its Supplementary Information.

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Figures

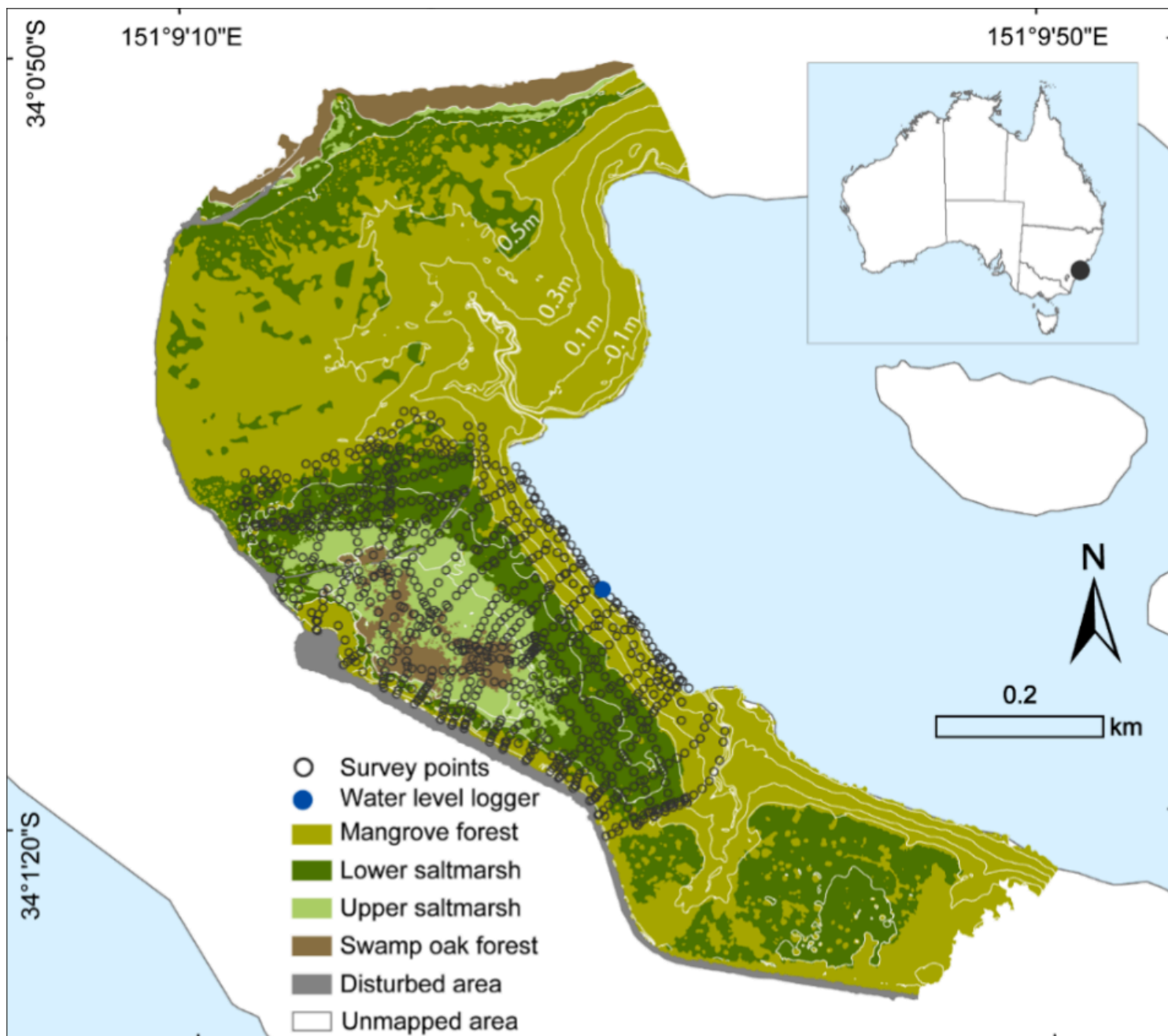


Figure 1

The study site is located at Towra Point Nature Reserve, about 15 km south of Sydney in New South Wales, Australia (inset map). The 874 sample points (RTK point elevations) were placed within the middle of the study area where mangrove, lower and upper saltmarsh, and swamp oak forest form distinct zones along the elevation gradient.

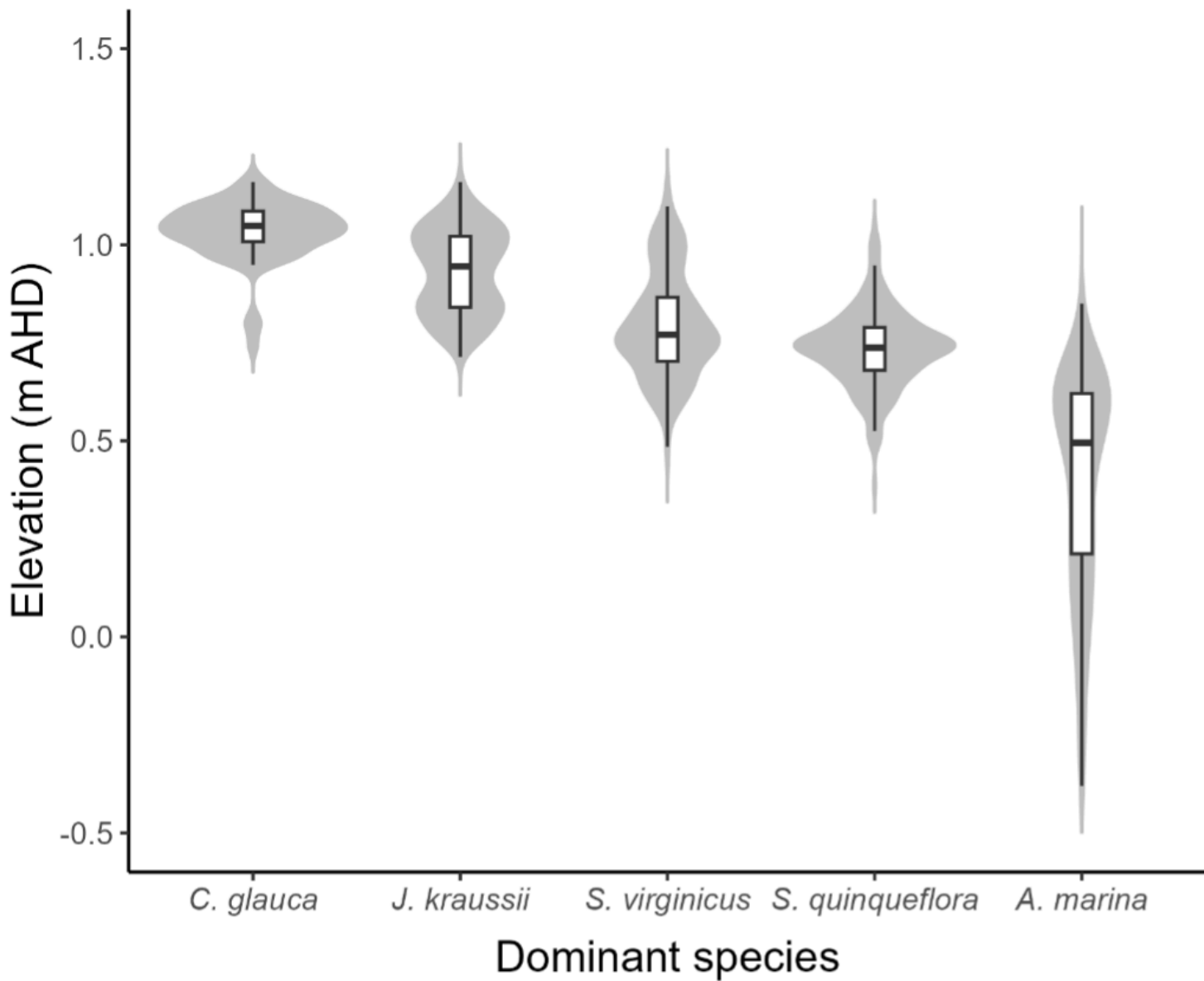


Figure 2

Vertical distribution (m AHD) of dominant tidal wetland species at Towra Point. Thick black lines represent the median elevation, vertical rectangles indicate the interquartile range (IQR), and the shaded 'violin' shapes visualize the probability density of the data.

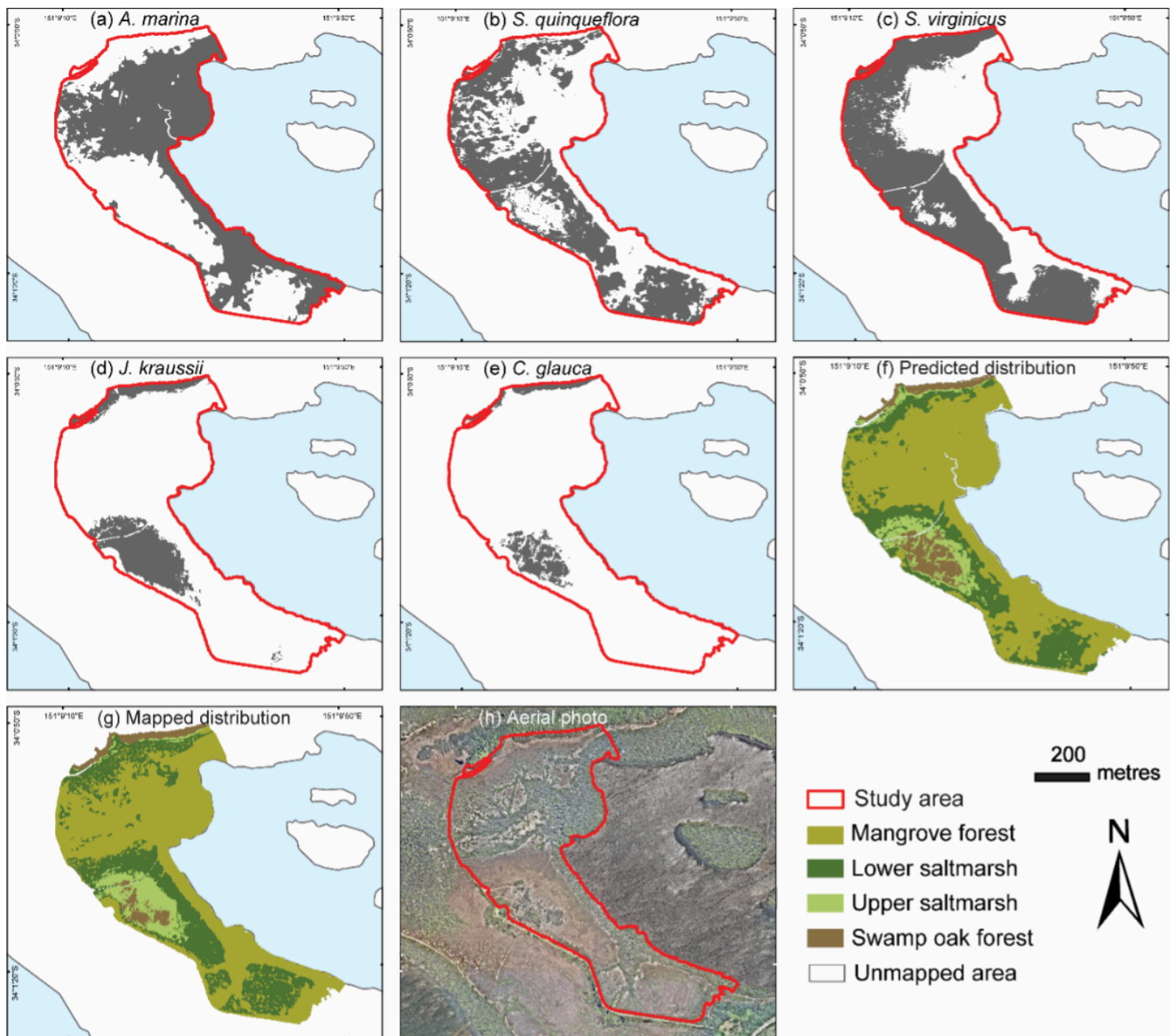


Figure 3

Predicted and observed vegetation distributions at Towra Point Nature Reserve. Panels A–E show binary presence–absence predictions for *Avicennia marina*, *Sarcocornia quinqueflora*, *Sporobolus virginicus*, *Juncus kraussii*, and *Casuarina glauca*, respectively, derived from the fitted GJAM model and thresholded using the LPT-R method. Panel F presents the composite vegetation map (canopy layer) obtained by overlaying species-specific predictions. Panel G shows the independent photo-interpreted vegetation map, and Panel H displays the corresponding aerial imagery (27 January 2025). Spatial agreement between predictions and mapped vegetation demonstrates that the joint model captures observed zonation patterns across the tidal gradient.

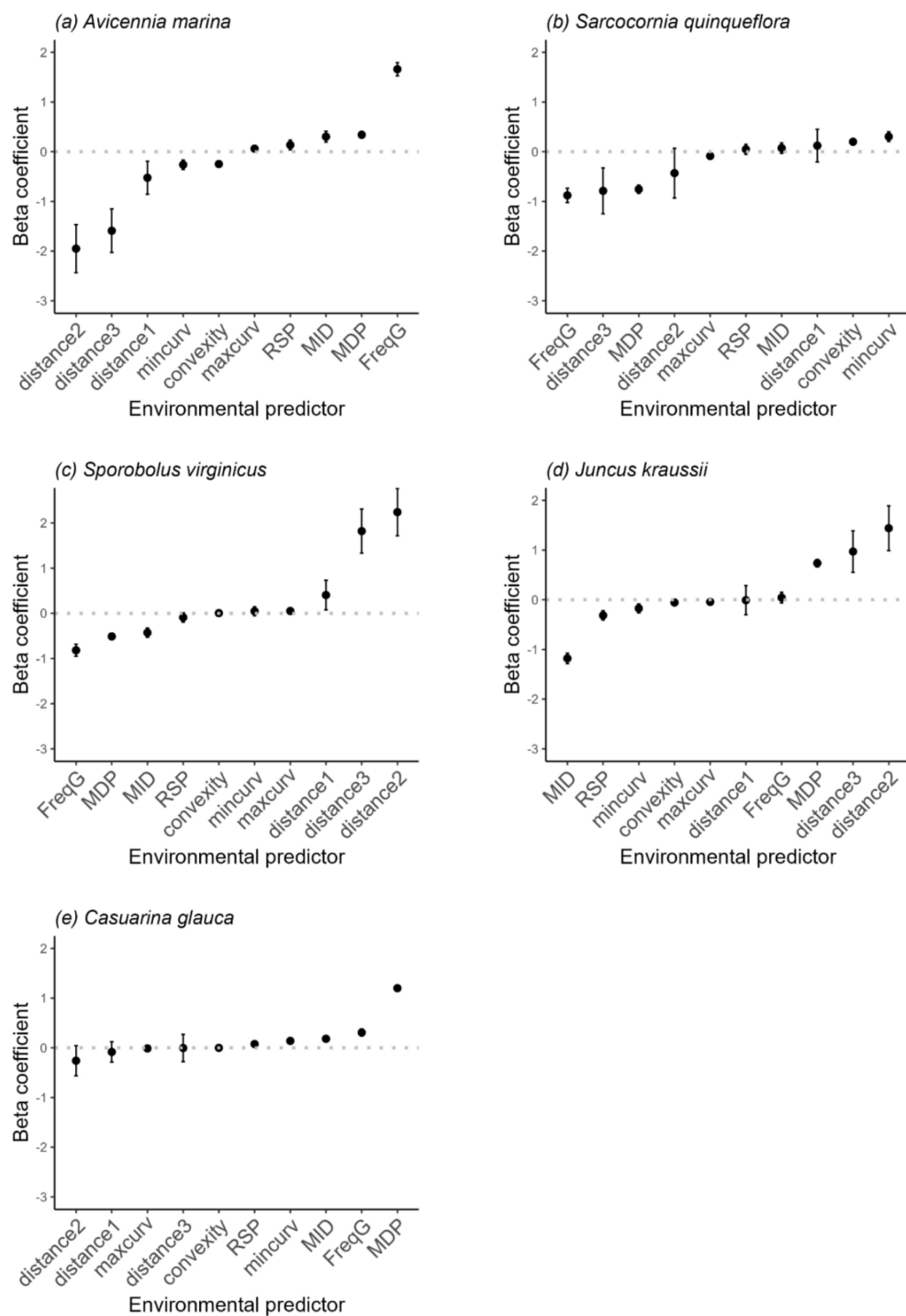


Figure 4

The species-specific effects of the ten most influential hydrological and morphological variables at Towra Point Nature Reserve. Dots are means and vertical bar are 95% credible intervals.

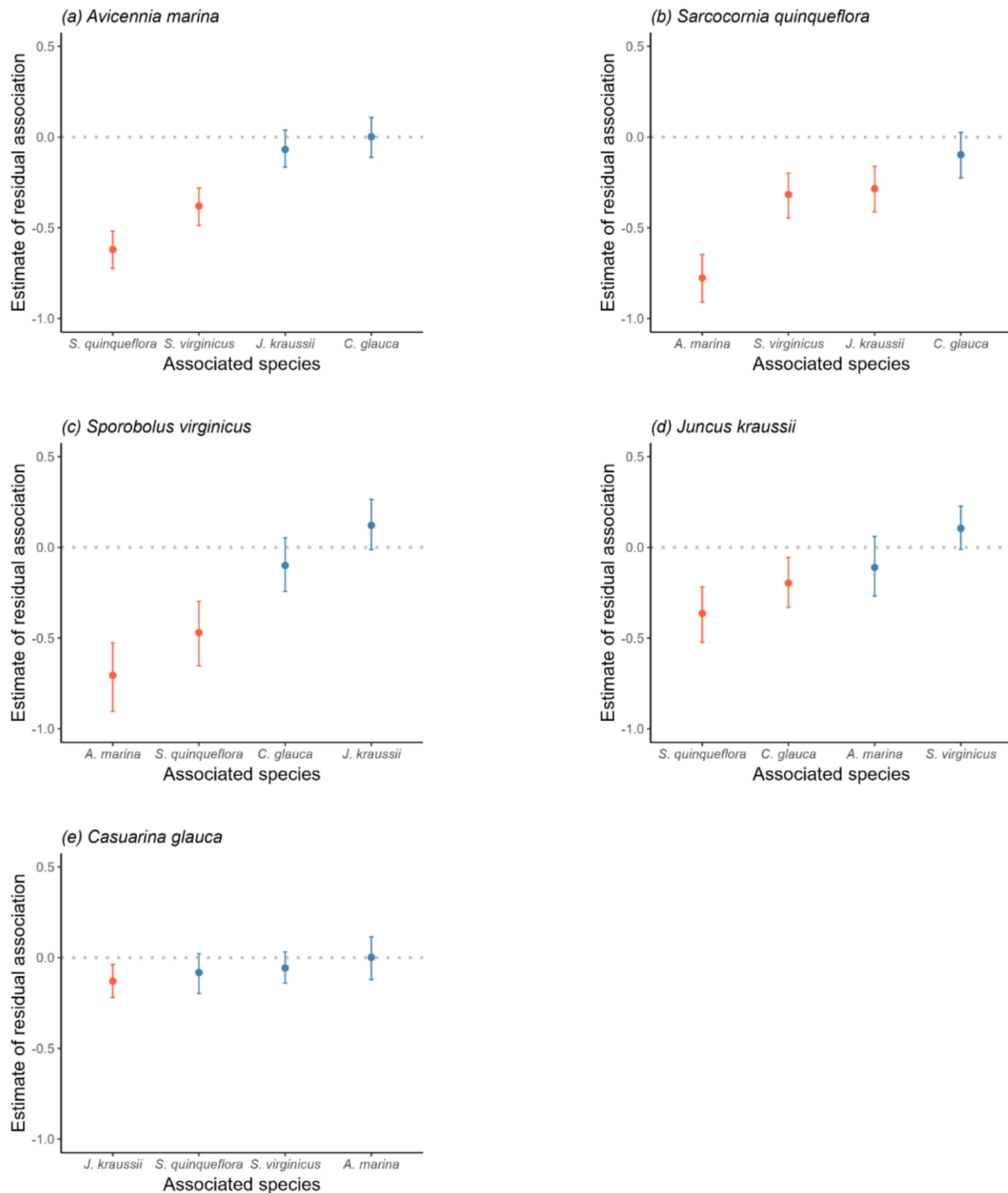


Figure 5

The species associations based on the conditional predictions of the fitted GJAM model represent the likely occurrence of target species given the other species present. Target species are (a) *Avicennia marina*; (b) *Sarcocornia quinqueflora*; (c) *Sporobolus virginicus*; (d) *Juncus kraussii*; (e) *Casuarina glauca*. The y-axis (Estimate of residual association) indicates the strength and direction of association, with negative values meaning avoidance and positive values suggesting co-occurrence. Dots are mean and

the vertical bars are 95% CIs (credible intervals). Red indicates a significant ($p < 0.05$, i.e., the estimate CIs do not include zero) relationship.

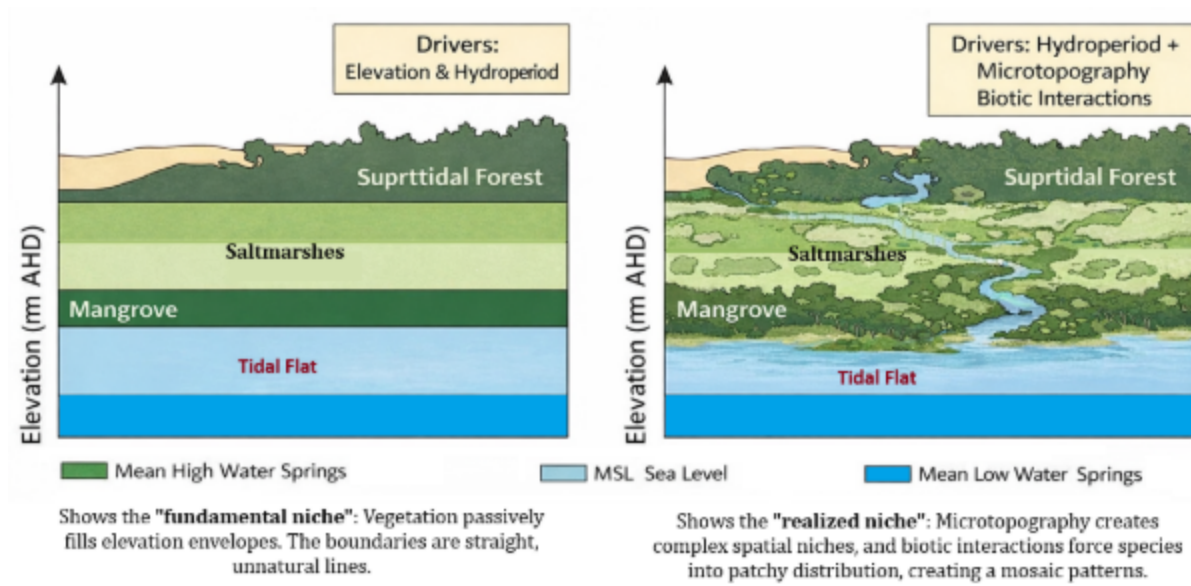


Figure 6

Conceptual comparison of coastal wetland zonation predicted by an abiotic-only model versus a Joint Species Distribution Model (JSDM). Left: Abiotic-Only Prediction: Standard models rely on regional elevation and hydroperiod thresholds, (the fundamental niche), resulting in predictions of smooth, parallel vegetation bands. Right: JSDM Prediction: By integrating abiotic drivers (hydroperiod and topography) with biotic interactions, the JSDM predicts a complex, realistic mosaic pattern (the realized niche). Note the intertwining of mangrove and saltmarsh ecotones: topographic features amplify local hydrological gradients, while competitive exclusion restricts saltmarsh from theoretically suitable abiotic zones.

Supplementary Files

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- [S1S2Topographicandhydrologicalvariables.docx](#)