MANAGEMENT APPLICATIONS



Drivers of Ecological Condition Identify Bright Spots and Sites for Management Across Coastal Seascapes

Ben L. Gilby¹ · Lucy A. Goodridge Gaines² · Hayden P. Borland² · Christopher J. Henderson² · Jesse D. Mosman² · Andrew D. Olds² · Hannah J. Perry²

Received: 31 August 2022 / Revised: 14 February 2023 / Accepted: 15 February 2023 / Published online: 1 March 2023 © The Author(s) 2023

Abstract

Disentangling natural and anthropogenic effects on ecosystem condition can uncover bright spots in urban landscapes that are performing above expectations and so are potential sites for conservation or benchmarking, as well as sites performing below expectations that should be the focus of management. In this study, we tested for correlations between metrics indexing ecological condition (focusing on habitat-forming species) and a suite of spatial and environmental variables at 373 sites across four ecosystems (mangroves, seagrass, saltmarsh and rocky outcrops) and 13 estuaries in southeast Queensland, Australia. Ten condition metrics across the four ecosystems correlated with variables indexing the seascape context of sites, with condition metrics typically higher at sites more connected to natural features including the estuary mouth and mangroves. Urbanisation affected only two metrics, with rocky outcrop oyster cover being 75% lower at sites near extensive urbanisation and algae cover being highest at sites with intermediate urbanisation. We identified patterns in at least two variables from each ecosystem, meaning that decisions need to be made regarding optimal ecosystem states. Overall, management sites were more common than bright spots, with 50% more management sites in mangroves, 42.8% more in seagrasses, 38.5% more in saltmarshes and no bright spots in rocky outcrops (however, 10.3% of rocky outcrop sites were bright spots under an alternate ecosystem state model). We found that patterns in habitat condition across coastal seascapes can be predicted using spatial modelling approaches, and that these models can be readily used to prioritise management actions across the entire regions.

Keywords Estuaries · Wetlands · Restoration · Quantitative · Target ecosystems · Spatial

Introduction

The ecological condition of ecosystems across landscapes affects their support for animals and valuable ecosystem services (Gratwicke and Speight 2005; Kovalenko et al. 2012). Therefore, understanding patterns in ecological condition, *ca.* 'state' in the Driver-Pressure-State-Impact-Response framework and quantified as the structure, function and biodiversity of ecosystems, is an important underpinning of

Communicated by Charles T. Roman

Ben L. Gilby bgilby@usc.edu.au

effective management (Jakobsson et al. 2021; Patrício et al. 2016; Pollock et al. 2017). For example, many ecosystems rely on the growth and persistence of habitat-forming species (e.g. Orth et al. 1984; Vozzo et al. 2021), but these can vary significantly in structure and condition across landscapes due to the combined effects of human pressures (i.e. that can negatively affect condition), management interventions (i.e. that can positively affect condition) and the natural drivers of key species (Asner et al. 2021; Delarue et al. 2015; Jenkins et al. 2021). Disentangling these effects to more accurately predict ecological condition across landscapes, or imply how condition might change in response to impacts or management interventions (Goodridge Gaines et al. 2020; Perry et al. 2023; Stoddard et al. 2006), might be instructive in optimising management across landscapes (Gilby et al. 2021; Murray 2010).

While ecosystem extent and two-dimensional connectedness can typically be mapped effectively across landscapes, mapping layers often cannot or do not reflect spatial variation

¹ School of Science, Technology and Engineering, University of the Sunshine Coast, Petrie 4502, QLD, Australia

² School of Science, Technology and Engineering, University of the Sunshine Coast, Maroochydore DC 4558, QLD, Australia

in ecological condition, and therefore their value for animals and ecosystem services (Nagendra et al. 2013). Similarly, the resolution of such data might be lower than is useful for some planning processes (Mills et al. 2010; Nel et al. 2009). This presents a challenge for managers seeking to maximise biodiversity and ecosystem services, as prioritising locations for conservation actions or management that reduces impacts is difficult from mapping alone (Ferrari et al. 2018; Ferrier 2002). Low resolution or inaccurate mapping can necessitate on-ground assessments and ground truthing which are expensive and time consuming. However, metrics that index ecological condition like the size and density of habitat-forming species are likely to vary predictably across landscapes (e.g. Elliott et al. 2022; Gilby et al. 2020; Heatherington and Bishop 2012; Henderson et al. 2017), and variables explaining their distribution might be useful management surrogates (Ferrier 2002; Hunter Jr et al. 2016; Lindenmayer et al. 2015). Once these patterns are established, management authorities might seek to conserve or manage locations which perform either better (i.e. bright spots) or more poorly (i.e. management sites) than expected (Cinner et al. 2016; Frei et al. 2018).

The concept of bright spots, sites that exceed expectations given natural and anthropogenic drivers, is increasingly common in ecology (Cinner et al. 2016; Frei et al. 2018). Bright spots should not simply be considered areas that are pristine and/or have low levels of human impact. Bright spots can also be areas where management actions have succeeded in improving ecological condition above expectations, or where natural drivers mediate the effects of broader impacts (Cinner et al. 2016). Identifying bright spots is useful for allocating conservation efforts (Queirós et al. 2021), or for identifying areas where management has been successful (Frei et al. 2018). Conversely, management sites, also known as dark spots, are locations which perform below expectations given natural and anthropogenic drivers (Cinner et al. 2016; Frei et al. 2018). Management sites could, for example, have been missed by management actions, or be experiencing an unidentified and localised impact (Cinner et al. 2016). Identifying bright spots also reflects an increasing recognition that effective management requires both effective conservation at sites with good remnant conditions and optimised restoration or management at sites with comparatively poorer conditions (Possingham et al. 2015).

The structure and condition of habitats is a result of the combined effects of natural environmental variables and the additional and overlying effects of human impacts and management interventions at multiple spatial scales (Gilby et al. 2020; Halpern et al. 2012). For example, a forest will have a particular density and composition of trees and extent of undergrowth given the environmental conditions of a particular site (Chapman et al. 1997). While human pressures might affect values at some sites, other sites will have lower

than average condition values simply due to ambient environmental conditions that are beyond management control. Intensively managing sites with naturally lower condition values might therefore be a poor investment. Expected versus observed approaches are often used in ecological monitoring and most efficiently contribute to prioritisation processes when they use readily available ecological information (Turner et al. 2015). For example, spatial information about the distribution of ecosystems (e.g. coarse mapping layers and satellite imagery) and key environmental metrics (e.g. water quality, rainfall, temperature) is often readily, and publicly, available, and can be useful in optimising management plans (Gilby et al. 2021; Pressey et al. 2000; Turner et al. 2015).

Impacts associated with expanding and increasing human populations have resulted in replaced, fragmented and degraded coastal ecosystems globally (Halpern et al. 2012; O'Hara et al. 2021). This has increased demand for management interventions that reverse or mediate impacts globally (Duarte et al. 2009; O'Hara et al. 2021). The ecological condition of many coastal ecosystems pivots on the structure and condition of habitat-forming plant species like mangroves, seagrasses and saltmarsh plants and habitat-forming and reef-building invertebrates like oysters and other shellfish. The effects of many natural and anthropogenic impacts that modify the ecological condition of these ecosystems are, however, not homogenous across coastal landscapes, meaning that some sites are more heavily impacted, while others are potential bright spots within more broadly impacted areas (Li et al. 2021; O'Hara et al. 2021). Natural drivers of habitat structure and condition like tides, sea level and propagule availability also vary spatially across coastal seascapes. Coastal seascapes are comprised of a variety of heterogeneously arranged ecosystems which respond to natural and anthropogenic drivers of ecosystem condition in unique ways (Gilby et al. 2020; Pittman 2018). Together, the heterogeneous distribution of impacts and ecosystems across coastal seascapes makes them the ideal test systems for frameworks seeking to identify patterns in ecological condition and to optimise the selection of management sites and actions.

The ecological condition of coastal ecosystems significantly modifies their capacity to support ecosystem services, and so has become an increasing focus for coastal managers (Barbier 2015; Gilby et al. 2020; Patrício et al. 2016). Identifying locations in landscapes in good ecological condition that should be prioritised for conservation or management actions, or that might be used for ecological benchmarking, is a mechanism for optimising management actions (Cinner et al. 2016; Frei et al. 2018). In this study, we quantify the effects of natural and anthropogenic drivers on metrics indexing ecological condition in four key estuarine ecosystems: mangrove forests, seagrass meadows,

saltmarsh and rocky outcrops. We test for correlations between environmental variables that quantify urbanisation, connectivity and tides on key metrics of ecological condition within these ecosystems and identify locations in estuaries where either (1) sites are performing as expected given model fits of the effects of key environmental variables, (2) sites are performing better than expected given models, thereby identifying sites as bright spots for conservation or baselining, or (3) sites are performing below expectations given models, and so should be the target of management actions like ecological restoration (Fig. 1). Analyses undertaken in this study can be extended to similar applications across marine and terrestrial landscapes where trade-offs exist in the allocation of management actions across landscapes.

Methods

Study Region and Sites

We quantified the ecological condition of mangrove forests, seagrass meadows, saltmarsh and rocky outcrops in 13 estuaries in southeast Queensland, Australia (Fig. 2), in the austral winter of 2020. Estuaries were selected within the study region because they (1) are relatively evenly geographically separated (Fig. 2A) and (2) represent the range of human impact intensities and extents present in estuaries in the region (Fig. 2B, C). The four focal ecosystems were selected as they (1) are common attributes of estuarine seascapes of the region (Gilby et al. 2018a); (2) are an important focus for local management programs so are subject to targeted management and restoration efforts; and (3) have been shown in previous studies, both within the study region (e.g. Gilby et al. 2018a; Goodridge Gaines et al. 2022; Perry et al. 2023) and beyond (e.g. Gedan et al. 2009; Gilby et al. 2020), to be affected by the frequency and intensity of human impacts at multiple spatial scales. Up to 10 sites of each ecosystem were positioned as evenly as possible from the estuary mouth to the upstream limit of tidal influence in each system. Sites were positioned at least 50 m apart to reduce spatial interdependence. This rule determined the number of replicates of some ecosystems in some estuaries (see Table S1). For example, in a hypothetical estuary where only a single, small (< 50 m long) patch of seagrass is present, then only one seagrass site could be surveyed in this estuary.

Ecological Condition Surveys

Given that each ecosystem has fundamentally different habitat structure, ecological condition metrics were different for each ecosystem. The methods used followed those used in previous studies within the region (Goodridge Gaines et al. 2020, 2022; Perry et al. 2023). At mangrove forest sites, we established a 10×10 m quadrat, in which we quantified the number, type and diameter at breast height (DBH) of each mangrove tree. Mangrove canopy height and canopy cover were also recorded at each site (Table 1, part A). At seagrass sites, we established a 10×10 m quadrat along the edge of each seagrass meadow and within this randomly placed four 50×50 cm quadrats, within which we measured the percent cover of each species of seagrass, the number and average length of eelgrass Zostera muelleri (henceforth Zostera) shoots (Table 1, part B). At saltmarsh sites, we established a 10×10 m quadrat and estimated the total vegetation cover and vegetation species richness within this broader quadrat. We also placed four randomly positioned 50×50 cm quadrats within this broader quadrat to measure average vegetation height and the cover of the most common saltmarsh plant species in the region, salt couch Sporobolus virginicus (Table 1, part C). The species richness of vegetation communities was also quantified at both mangrove and saltmarsh sites (but not at seagrass sites due to only two species of seagrass being present in these estuaries; Zostera and Halophila ovalis) because sensitive species are understood to reduce in presence at sites following key impacts like floods and

Fig. 1 Conceptual diagram illustrating how quantifying spatial patterns in ecological condition metrics can be used to identify potential bright spots (circles) that are performing better than expected, and locations whose conditions fall below what would be expected given environmental conditions, and so might require management through actions like ecological restoration (squares). Shaded blue areas represent 95% confidence intervals





Fig. 2 Map of surveys estuaries (A) and sites (B, C) in southeast Queensland, Australia, with insets of exemplar low (B) and high (C) urbanisation estuaries

Ecological condition metric	Definition	Model family	
A. Mangroves			
Mangrove tree abundance	The number of mangrove trees per 10×10 m quadrat	Negative binomial (log link)	
Mangrove species richness	The number of mangrove species present within each 10×10 m quadrat	Poisson (log link)	
Mangrove forest canopy cover	A visual estimate of the canopy cover (as a proportion) of each site, estimated from the middle of each 10×10 m quadrat	Beta (logit link)	
Mangrove forest canopy height	The height (in m) of the tallest mangrove tree within each 10×10 m quadrat	Gaussian (log link)	
Mangrove tree diameter at breast height	The average diameter at breast height (DBH; in cm) of all mangrove trees within the 10×10 m quadrat, calculated by measuring tree circumference at 1.3 m from the ground, and dividing by Pi	Negative binomial (log link)	
B. Seagrasses			
Zostera muelleri cover	Average cover (as a proportion) of <i>Zostera muelleri</i> within four ran- domly deployed 50×50 cm quadrats at each 10×10 m site	Beta (logit link)	
Zostera muelleri shoot height	Average shoot height (in cm) of <i>Zostera muelleri</i> within four randomly deployed 50×50 cm quadrats at each 10×10 m site	Gaussian (log link)	
Zostera muelleri shoot density	Average shoot density (as number of shoots per 0.25 m^2) of <i>Zostera muelleri</i> within four randomly deployed $50 \times 50 \text{ cm}$ quadrats at each $10 \times 10 \text{ m}$ site	Gaussian (log link)	
C. Saltmarsh			
Total vegetation cover	Total cover (as a proportion) of live saltmarsh within each 10 \times 10 m site	Beta (logit link)	
Average vegetation height	Average vegetation height (in cm) within four randomly deployed 50 \times 50 cm quadrats at each 10 \times 10 m site	Gaussian (log link)	
Vegetation species richness	The number of saltmarsh plant species within each 10×10 m site	Poisson (log link)	
Sporobolus virginicus cover	Average cover (as a proportion) of salt couch <i>Sporobolus virginicus</i> within four randomly deployed 50×50 cm quadrats at each 10×10 m site	Beta (logit link)	
D. Rocky outcrops			
Algae cover	Total algae cover (as a proportion) across the rocky outcrop	Beta (logit link)	
Oyster cover	Total oyster cover (as a proportion) across the rocky outcrop	Beta (logit link)	
Barnacle cover	Total barnacle cover (as a proportion) across the rocky outcrop	Beta (logit link)	

 Table 1
 Ecosystems surveyed, and the ecological condition metrics tested, their definitions and the family used to calculate the corresponding model

trampling. Finally, at rocky outcrops, we measured the size (length, width and height, in m) and complexity (on a scale of 1–5, with 1 = low complexity, 5 = high complexity) of the rocks themselves, before visually estimating the cover of barnacles, oysters and algae across the entire outcrop (Table 1, part D). All surveys were conducted in a window of 1 h either side of a daytime low tide. No two ecological condition metrics within an ecosystem were strongly correlated (i.e. Pearson's *R* coefficients > 0.7 and < -0.7).

Environmental Variables

As each ecosystem is structured by different environmental attributes of coastal seascapes, like depth, tidal inundation and proximity to other ecosystems, we tailored environmental variables to each ecosystem. This meant that the environmental variables tested for each ecosystem were different to each other. Variables were chosen based on evidence of effects from the literature and an associated hypothesis about how variables could affect ecosystem condition within this region (see detail for each variable and associated hypothesis in Table 2).

Environmental variables could be broadly grouped into three categories. Firstly, we used spatial variables that indexed the connectivity of sites to natural features of the estuary like the estuary mouth, the highest astronomical tide line and adjacent ecosystems like mangroves. This was measured in three ways: the proximity of sites to these features as a fish would swim throughout an estuary (i.e. not Euclidean distances), the area of key features around the site (within 50, 100, 500 and 1000 m buffers) and the area of ecosystems across the entire catchment in which the site was located. Secondly, we measured the proximity and extent of urbanisation for each site, using the same three metrics as detailed above for natural features of estuaries (i.e. distance; area within 50, 100,

Table 2 Explanatory variables included in models, their justification for inclusion in this study and the ecosystems for which they were tested against condition indicators

Variable	Definition and justification	Ecosystems tested
Distance to estuary mouth	The distance (in m) from the site to the middle of the channel at the estuary mouth, measured as a fish would swim around river bends etc. Distance to the estuary mouth affects salinity, tidal range, currents and accessibility to propagules (Gilby et al. 2018a)	Mangroves, seagrass, saltmarsh, rocky outcrops
Distance to highest astronomical tide (HAT) line	The distance (Euclidean, in m) of sites to the highest astronomical tide line derived from government-sourced habitat maps (Queensland Government 2022). Distance to high tide line is a proxy for inundation by incoming tides and therefore the provision of propagules to vegetated ecosystems. For example, saltmarshes at higher elevations far from the estuarine channel would be nearer to the high tide line and receive less inundation time and fewer propagules. The measure also indexes the likelihood of being impacted by boat wash within estuaries	Mangroves, seagrass*, saltmarsh
Distance to urbanisation	The distance (in m) of sites to the nearest urbanisation derived from government- sourced urbanisation maps (Queensland Government 2021), measured as a fish would swim around river bends etc. The proximity of sites to urbanisation affects levels of pollution, sediment supply and stormwater runoff, and the levels of other general human impacts (like trampling) in coastal seascapes (e.g. Brook et al. 2018)	Mangroves, seagrass, saltmarsh, rocky outcrops
Area of urbanisation	The area (in ha) of urbanisation derived from government-sourced urbanisation maps (Queensland Government 2021). Initially quantified at distances of 50, 500 and 1000 m from each site, but simplified to 500 m, as 50 m scales covaried with distance to urbanisation, and 500 and 1000 m scales correlated with each other in all ecosystems. The amount of urbanisation near a site affects levels of pollution, sediment supply and stormwater runoff, and the levels of other general human impacts (like trampling) in coastal seascapes (e.g. Gilby et al. 2018a)	Mangroves, seagrass*, saltmarsh, rocky outcrops
Catchment urbanisation	The area (in ha) of urbanisation derived from government-sourced urbanisation and catchment boundary maps (Queensland Government 2021) across the catchment in which the site is located. The amount of urbanisation across a catchment affects levels of pollution, sediment supply and stormwater runoff, and the levels of other general human impacts (like trampling) in coastal seascapes (e.g. Henderson et al. 2019)	Mangroves, seagrass*, saltmarsh, rocky outcrops

Table 2 (continued)

Variable	Definition and justification	Ecosystems tested
Water depth	The water depth at the deployment time of the cameras, measured using a Garmin depth sounder. Sites were sampled in a period of 2 h either side of high tide, and so depth was measured within this time period at each site. Water depth can affect the likelihood of light reaching the benthos and driving plant and/or algae growth (Dennison 1987)	Seagrass, rocky outcrops
Distance to mangroves	The distance (in m) of sites to the nearest mangrove forest edge derived from government-sourced habitat maps (Queensland Government 2022), measured as a fish would swim around river bends etc. The distance of sites to mangroves has been shown in previous studies in the region to significantly affect fish assemblages, and this could have consequences for condition metrics through processes like carbon or nutrient subsidies (Goodridge Gaines et al. 2022)	Seagrass, rocky outcrops
Area of mangroves	The area of mangroves (in ha) derived from government-sourced habitat maps (Queensland Government 2022). Initially quantified at distances of 50, 500 and 1000 m from each site, but simplified to 500 m, as 50 m scales covaried with distance to mangroves, and 500 and 1000 m scales correlated with each other in all ecosystems. The area of mangroves near a site has been shown in previous studies in the region to significantly affect fish assemblages, and this could have consequences for condition metrics through processes like carbon or nutrient subsidies (Henderson et al. 2021)	Mangroves, seagrass, saltmarsh, rocky outcrops
Area of intertidal flats	The area of intertidal flats (in ha) derived from government-sourced habitat maps (Queensland Government 2022). Quantified at distances of 500 m to match those included in models for area of mangroves and urbanisation (see above). Greater intertidal flat area near a site reduces seascape heterogeneity, and results in sites that are more isolated from other ecosystems and over greater distances by movement across intertidal flats (Goodridge Gaines et al. 2022)	Mangroves, seagrass, saltmarsh, rocky outcrops
Rocky outcrop complexity	A measure from 1 to 5 (1 = low complexity, 5 = high complexity) indexing the overall habitat complexity of rocky outcrop sites. Values were made consistently between sites by benchmarking photographs against initial surveys conducted in two estuaries (Maroochy and Mooloolah) with extensive rocky outcrops. More complex and rugose rocky outcrops provide more locations for the affixing of invertebrates and algae (Borland et al. 2021)	Rocky outcrops

 Table 2 (continued)

Variable	Definition and justification	Ecosystems tested
Area of focal ecosystem	The area of the focal ecosystem (i.e. seagrass for seagrass models and saltmarsh for saltmarsh models) derived from government-sourced habitat maps (Queensland Government 2022). Initially quantified at distances of 50, 500 and 1000 m from each site, but simplified to 500 m, as all correlate with each other. Greater area of each habitat provides greater access to propagules to individual sites within estuaries (Gilby et al. 2018a)	Seagrass, saltmarsh
Area of focal ecosystem across catchment	The area of the focal ecosystem (i.e. seagrass for seagrass models and saltmarsh for saltmarsh models) derived from government- sourced habitat maps (Queensland Government 2022) across the catchment in which the site is located. Greater area of each habitat provides greater access to propagules to individual sites within estuaries (Henderson et al. 2019, 2021)	Mangroves, seagrass*, saltmarsh
Light penetration	Light penetration (in m) as measured by a standard 30-cm diameter Secchi disc during the high tide preceding habitat condition surveys. Higher light penetration indicates greater likelihood of light reaching the benthos and driving plant and/or algae growth (Dennison 1987)	Seagrass*, rocky outcrops

Variables with symbol * next to them covaried (R > 0.7 or < -0.7) with other variables in the analysis for the given ecosystem and so were removed

500 and 1000 m buffers; and area across the catchment). Buffer distances for quantifying local area-based metrics were chosen based on the span of likely effect of these variables at the local scale, while also accounting for the fact that we included the entire catchment extent of key ecosystems for some variables (e.g. for saltmarsh and mangrove condition metrics). Crucially, however, several of these spatial scales covaried, resulting in their removal from the final models (see detail in Table 2). Finally, we measured the effects of water depth (quantified at high tide on the day of surveys using a Garmin depth sounder attached to the survey boat) and light penetration (quantified at high tide on the day of surveys using a standard 30-cm Secchi disc) as these variables are considered important for the ecological condition of seagrass meadows and rocky outcrops. Prior to including variables in statistical models, all variables were checked for collinearity using Pearson's R coefficients; where variables correlated (i.e. *R* either > 0.7 of < -0.7), variables were excluded from analyses based on the strength of underlying hypotheses for each variable (i.e. variables with the least likely effect on condition were removed).

Statistical Analyses

We identified correlations between each condition metric for each ecosystem separately (i.e. from Table 1) with the selected environmental variables for each ecosystem (i.e. from Table 2) using generalised additive mixed models (GAMMs) in the mgcv package (Wood 2022) of R (R Core Team 2022). All models included the variables listed in Table 2 for each ecosystem, plus the random variable of 'Estuary', being the estuary in which sites were located. Distance metrics were included in models as the natural log of the real value to reduce the effects of outliers in these measures (Wood 2006). Model overfitting was reduced by restricting model fits to three knots or fewer (i.e. k = 3) and by running all possible combinations of four or fewer variables using the MuMIn package (Barton 2018). Best-fit models were those with the lowest Akaike's information criterion (AIC) values. Weighted AIC values were calculated for each best-fit model to allow for comparisons across metrics. All best-fit models were checked for spatial autocorrelation using Moran's I using the ape package (Paradis and Schliep 2019) and for GAMM concurvity and model assumptions using the in-built capacity of *mgcv*, with no effects found. Only significant variables in the resulting best-fit models were plotted. Model families for each dependent variable are listed in Table 1. Negative binomial error structures were chosen over Poisson and Gaussian distributions for mangrove tree abundance and mangrove tree DBH, respectively, due to better model fits and model assumption satisfaction.

Once best-fit models were identified and plotted, we determined the value of ecological condition metrics that each site should have given region-wide patterns and the 95% confidence bands around these values using the predict function in mgcv, the full best-fit model for each metric and the raw environmental variables for each site. We identified whether sites could be considered potential bright spots or management sites, or whether the site was performing as expected based the confidence intervals of each model. Here, sites that fall within the confidence intervals of GAMM models are performing as expected (Fig. 1, blue triangle). Sites with values that fall below modelled confidence intervals for the given site's attributes are sites that might be considered targets for management and/or restoration (Fig. 1, red squares). Conversely, sites with values that fall above modelled confidence intervals for the given site's attributes are considered bright spots (Fig. 1, yellow circles). These calculations amount to a predicted versus observed quantification of the values for each condition metric. In essence, we use GAMMs to identify what the condition of sites should be, on average, given all variables in the best-fit model for that metric across the region, and then calculate whether the site is performing as expected, or significantly above or below average. These new habitat condition categories (i.e. bright spot, performing as expected, and manage) were then plotted against significant variables for each metric and summarised using proportions across estuaries and habitats.

Results

Patterns in Mangrove Ecological Condition

Mangrove tree abundance was best explained by the area of mangroves within 500 m of each site (Table 3, part A; Fig. S1). The estuary in which the site was located also had a significant effect on relationships. Here, the highest abundance of mangrove trees was found at sites with the greatest extent of mangroves nearby (Fig. 3A).

Mangrove species richness was best explained by the area of mangroves within 500 m of each site (Table 3, part A). The estuary in which the site was located also had a significant effect on these relationships. However, none of these variables were statistically significant. Mangrove forest canopy height was best explained by the combined effects of the distance of sites to both the estuary mouth and the HAT line and the area of intertidal flats nearby (Table 3, part A; Fig. S1). The estuary in which the site was located also had a significant effect on these relationships. Here, only distance to the estuary mouth had a significant effect on patterns, with mangrove canopy height being highest at sites nearest to the estuary mouth (Fig. 3B).

Mangrove forest canopy cover was best explained by the combined effects of the distance of sites to both urbanisation and the HAT line and the area of mangroves nearby (Table 3, part A; Fig. S1). The estuary in which the site was located also had a significant effect on these relationships. Here, only distance to the HAT line and the area of mangrove had a significant effect on overall patterns, with canopy cover being highest at sites furthest from the HAT line (Fig. 3C) and with the largest area of mangrove nearby (Fig. 3D).

Mangrove tree diameter at breast height was best explained by the combined effects of the distance of sites to both the estuary mouth and HAT line and the area of mangrove nearby (Table 3, part A). However, none of these variables were statistically significant.

Patterns in Seagrass Ecological Condition

Zostera shoot height was best explained by the area of intertidal flats nearby (Table 3, part B; Fig. S2). The estuary in which the site was located also had a significant effect on these relationships. Here, *Zostera* shoot height was highest at sites with the greatest extent of intertidal flats nearby (Fig. 3E).

Zostera shoot density was best explained by the combined effects of the distance of sites to the estuary mouth and the area of mangroves nearby (Table 3, part B; Fig. S2). The estuary in which the site was located also had a significant effect on these relationships. Here, Zostera shoot density was highest at sites with the lowest extent of mangroves nearby (Fig. 3F) and furthest from the estuary mouth (Fig. 3G).

Zostera cover was best explained by the combined effects of the area of intertidal flats and mangroves nearby (Table 3, part B; Fig. S2). The estuary in which the site was located also had a significant effect on these relationships. Here, Zostera cover was highest at sites with between 2.5 and 2.5 ha of intertidal flats nearby (Fig. 3H) and with the lowest extent of mangrove nearby (Fig. 3I).

Patterns in Saltmarsh Ecological Condition

Saltmarsh total vegetation cover was best explained by the distance of sites to the estuary mouth (Table 3, part C). The estuary in which the site was located also had a significant effect on these relationships. However, none of these variables were statistically significant.

Table 3 Summary of best-fit generalised additive models (GAMs) for each ecological condition metric (as detailed in Table 1)

Metric	Best-fit model variables			Model <i>R</i> ² value and AIC weight
A. Mangroves				
Mangrove tree abundance*	Area of mangroves $\chi^2 = 4.21, P = 0.04, I = 0.7$			$R^2 = 0.3, w = 0.11$
Mangrove species richness*	Area of mangroves $\chi^2 = 5.98, P = 0.09, I = 0.62$			$R^2 = 0.1, w = 0.05$
Mangrove forest canopy height*	Distance to estuary mouth $F = 3.8, P = 0.03, I = 0.65$	Distance to HAT line $F = 2.2, P = 0.13, I = 0.32$	Area of intertidal flats F = 2.4, P = 0.13, I = 0.31	$R^2 = 0.41, w = 0.06$
Mangrove forest canopy cover*	Distance to HAT line $\chi^2 = 4.2, P = 0.04, I = 0.59$	Area of mangroves $\chi^2 = 4.8$, P = 0.02, I = 0.56	Distance to urban $\chi^2 = 4.6, P = 0.15, I = 0.4$	$R^2 = 0.12, w = 0.05$
Mangrove tree diameter at breast height	Distance to estuary mouth $\chi^2 = 4.76, P = 0.13, I = 0.6$	Distance to HAT line $\chi^2 = 4.85, P = 0.2, I = 0.75$	Area of mangroves $\chi^2 = 5.76, P = 0.06, I = 0.64$	$R^2 = 0.15, w = 0.07$
B. Seagrass				
Zostera muelleri shoot height*	Area of intertidal flats F = 7.28, P < 0.01 , I = 0.92			$R^2 = 0.63, w = 0.18$
Zostera muelleri shoot density*	Distance to estuary mouth $F = 4.56$, $P = 0.03$, $I = 0.55$	Area of mangroves F = 5.17, P = 0.02, I = 0.85		$R^2 = 0.32, w = 0.05$
Zostera muelleri cover*	Area of intertidal flats $\gamma^2 = 8.32$, $P = 0.02$, $I = 0.67$	Area of mangroves $\gamma^2 = 6.1$, $P = 0.01$, $I = 0.66$		$R^2 = 0.18, w = 0.1$
C. Saltmarsh	λ,,	λ,,		
Total vegetation cover*	Distance to estuary mouth $\chi^2 = 1.57, P = 0.2, I = 0.43$			$R^2 = 0.01, w = 0.03$
Vegetation species richness*	Distance to estuary mouth	Area of saltmarsh across catchment	Area of intertidal flats	$R^2 = 0.01, w = 0.02$
	$\chi^2 = 4.89, P = 0.02, I = 0.52$	$\chi^2 = 3.04, P = 0.08, I = 0.31$	$\chi^2 = , P = 0.05, I = 0.47$	
Average vegetation height*	Distance to estuary mouth	Area of saltmarsh across catchment		$R^2 = 0.39, w = 0.1$
	F = 4.33, P = 0.01, I = 0.8	F = 2.7, P = 0.09, I = 0.42		
Sporobolus virginicus cover	None- null model			N/A
D. Rocky outcrops				
Algae cover*	Water depth $\chi^2 = 21.47, P < 0.001, I = 0.79$	Area of urban $\chi^2 = 6.35, P = 0.03, I = 0.56$	Area of intertidal flats $\chi^2 = 5.22, P = 0.02, I = 0.81$	$R^2 = 0.69, w = 0.4$
Oyster cover	Water depth $\gamma^2 = 4.3 P = 0.04 I = 0.55$	Area of urban $\gamma^2 = 10.2 P < 0.01 I = 0.96$		$R^2 = 0.46, w = 0.16$
Barnacle cover	None- null model	$\lambda = 10.2, 1 \le 0.01, 1 = 0.90$		N/A

Models with symbol * also included the random variable estuary in the best-fit model. Italics and bold indicate significant variables

I importance values for each variable, as derived from the sum of weighted AIC values for all models containing the specific variable, *W* weighted AIC values for the best-fit model

Saltmarsh vegetation species richness was best explained by the combined effects of the distance of sites to the estuary mouth, the area of saltmarsh across the catchment and the area of intertidal flats nearby (Table 3, part C). The estuary in which the site was located also had a significant effect on these relationships. Here, only distance to estuary mouth and area of intertidal flats had significant effects on patterns, with vegetation species richness being highest at sites with greater extent of intertidal flats nearby (Fig. 4A) and nearer to the estuary mouth (Fig. 4B).

Saltmarsh average vegetation height was best explained by the combined effects of the distance of sites to the estuary mouth and the total extent of saltmarsh across the catchment (Table 3, part C; Fig. S3). The estuary in which the site was located also had a significant effect on these relationships. Here, only distance to the estuary mouth had significant effects on patterns, with average vegetation



Fig. 3 Generalised additive model outputs of significant variables from best-fit models for **A** mangrove tree abundance, **B** mangrove forest canopy height, **C**, **D** mangrove forest canopy cover, **E** Zostera blade height, **F**, **G** Zostera shoot density and **H**, **I** Zostera cover. For

full best-fit model details, see Table 2. Grey bands indicate 95% confidence intervals. Small, vertical lines on the *X* axis indicate the values for individual replicates

height being highest at sites between 5000 and 6000 m from the estuary mouth (Fig. 4C).

No variables were included in the best-fit model for *Sporobolus virginicus* cover (Table 3, part C).

Patterns in Rocky Outcrop Ecological Condition

Algae cover on rocky outcrops was best explained by the combined effects of water depth at high tide and the area



Fig. 4 Generalised additive model outputs of significant variables from best-fit models for **A**, **B** saltmarsh vegetation species richness, **C** average saltmarsh vegetation height, **D**–F rocky outcrop algae cover

and **G**, **H** rocky outcrop oyster cover. For full best-fit model details, see Table 2. Grey bands indicate 95% confidence intervals. Small, vertical lines on the *X* axis indicate the values for individual replicates

of urbanisation and intertidal flats nearby (Table 3, part D). The estuary in which the site was located also had a significant effect on these relationships. Here, algae cover was highest at sites with greater water depth (Fig. 4D) with between 30 and 40 ha of urbanisation nearby (Fig. 4E) and the lowest extent of intertidal flats nearby (Fig. 4F).

Oyster cover on rocky outcrops was best explained by the combined effects of water depth at high tide and the area of urbanisation nearby (Table 3, part D). The estuary in which the site was located also had a significant effect on these relationships. Here, oyster cover was highest at shallower sites (Fig. 4G) with lower extent of urbanisation nearby (Fig. 4H).

No variables were included in the best-fit model for barnacle cover (Table 3, part D).

Identifying Bright Spots and Potential Management Interventions

We identified three condition metrics in mangrove forests that were significantly explained by our environmental variables: mangrove tree abundance, mangrove canopy height and mangrove canopy cover. For tree abundance, bright spots accounted for 21.7% of all sites surveyed, while management sites accounted for 37.2% of sites surveyed (Table S2A). Bright spots were typically less common than management sites, with 21.6 and 37.2% of sites identified on average per estuary, respectively (Table S2A). All estuaries contained both bright spot and management sites for mangrove tree abundance. For canopy height, bright spots accounted for 15.5% of all sites surveyed, while management sites accounted for 28.7% of sites surveyed (Table S2B). Bright spots were again less common than management sites, with 15.4 and 28.7% of sites identified on average per estuary, respectively (Table S2B). Both the Pumicestone and Noosa systems lacked bright spots for this variable. For mangrove canopy cover, bright spots accounted for 42.6% of all sites surveyed, while management sites accounted for 33.3% of sites surveyed (Table S2C). Bright spots were more common than management sites, with 42.4 and 33.6% of sites identified on average per estuary, respectively (Table S2C). All estuaries contained both bright spot and management sites for mangrove canopy cover. Overall, only 4.7% of sites surveyed were categorised as bright spots according to all these criteria across the region, with these sites located in the Mooloolah, Caboolture, Albert, Logan and Tallebudgera systems (Fig. 5A, Table S2D).

We identified three condition metrics in seagrass meadows that were significantly explained by our environmental variables: *Zostera* height, density and cover. For *Zostera* height, bright spot sites accounted for 20.8% of total sites surveyed, while management sites accounted for 26.4% of sites (Table S3A). Bright spots were relatively evenly spread between management sites, with 18.1 and 23.3% of sites identified on average per estuary, respectively (Table S3A). The Pine River estuary contained no bright spots or management sites for this metric, mostly due to the lower replication levels in this estuary (Table S1). For *Zostera* density, bright spot sites accounted for 22.6% of total sites surveyed,

0 50 km A. Mangroves **B. Seagrass** Noosa 😑 0% 🛦 0% 📕 10% Noosa – 10% 🔺 20% 📕 20% Maroochy Maroochy Mooloolah 🦲 10% 🔺 10% 📕 0% <mark>●</mark> 0% ▲ 10% <mark>●</mark> 0% ▲17% 10% 33% Pumicestone – 0% 🔺 0% 📕 10% Pumicestone – 0% 🔺 10% 📕 0% Caboolture — 10% 🔺 10% 📕 0% Pine 0% Brisbane - 0% 🔺 20% 📕 0% Pine 0% ▲ 0% ■10% 0% Tingalpa 😑 0% 🔺 0% 📕 10% Albert Logan 🦲 20% 🛦 0% 📕 20% 10% ▲ 10% ■ 10% Pimpama 😑 0% 🔺 20% 📕 20% Pimpama 😑 20% 🔺 20% 📕 20% Nerang 😑 0% 🔺 11% 📕 22% Nerang 😑 0% 🔺 10% 📕 10% Tallebudgera Tallebudgera 10% 🔺 0% 📕 0% 10% 🔺 20% 📕 10% C. Saltmarsh **D. Rocky outcrops** Noosa – 0% 🔺 20% 📕 30% Noosa – 0% 🔺 10% 📕 0% Maroochy Maroochy Mooloolah 😑 0% 🔺 10% 📕 10% 🖕 Mooloolah 🥚 0% 🔺 0% 📕 80% <mark>●</mark> 0% ▲ 30% 0% (20% 100% Pumicestone 0%
30%
20% Pumicestone – 0% 🔺 10% 📕 0% Caboolture 0% 🔺 40% 📕 0% Caboolture 😑 0% 🔺 0% 📕 50% Pine 10% Pine Brisbane - 0% 100% 0% Brisbane 😑 0% 🛦 0% 📕 20% 0% 0% 20% 0% Tingalpa — 20%🛦 30% 📕 0% Tingalpa 😑 0% 🔺 0% 📕 50% Albert Albert Logan — 10% 🔺 20% <mark>=</mark> 20% Logan 😑 0% 🔺 10% 📕 60% 0% 0% ▲ 0% ■ 0% 0% Pimpama – 20% 🔺 40% 📕 10% Pimpama 😑 0% 🛦 0% 📕 33% ▲ 0% ■ 0% Nerang 😑 0% 🛦 0% 📕 0% Nerang 😑 0% 🛦 0% 📕 0% Tallebudgera Tallebudgera 0% 🔺 0% 📕 20% 0% 🔺 10% 📕 10%

Fig. 5 Map of the study estuaries (indicated on the map in black points) with the percentage of sites for A mangroves, B seagrass, C saltmarsh and D rocky outcrops within each estuarine having all sites falling into bright spots (yellow circles), as predicted (blue triangles) and management sites (red squared) for all significant variables. See Tables S2–S5 for a full breakdown of these percentages across all variables and estuaries while management sites accounted for 33.96% of sites (Table S3B). Bright spots were less common than management sites, with 21 and 40.5% of sites identified on average per estuary, respectively (Table S3B). Again, the Pine River estuary contained no bright spots or management sites for this metric, mostly due to the lower replication levels in this estuary (Table S1). For Zostera cover, bright spots accounted for 32.1% of total sites surveyed, while management sites accounted for 35.9% of sites (Table S3C). Bright spots were much less common than management sites, with 29 and 43.3% of sites identified on average per estuary, respectively (Table S3C). Overall, only 5.7% of sites surveyed were categorised as bright spots according to all these criteria across the region, with these sites located in the Noosa, Pimpama and Tallebudgera systems (Table S3D, Fig. 5B). It could be argued that high Zostera density and height metrics are not compatible with each other, and that higher shoot lengths at lower density are the preferred ecosystem state in estuaries (Perry et al. 2023); 7.6% of sites fulfilled these criteria, and these sites occurred in the Nerang, Pumicestone and Tallebudgera systems (Table S3D).

We identified two condition metrics in saltmarsh that were significantly explained by our environmental variables: vegetation height and vegetation species richness. For vegetation height, bright spot sites accounted for 18.3% of total sites surveyed, while management sites accounted for 33.7% of sites (Table S4A). Bright spots were less common than management sites, with 14.6 and 26.9% of sites identified on average per estuary, respectively (Table S4A). The Albert, Brisbane, Mooloolah and Noosa systems lacked bright spots for this variable. For vegetation species richness, bright spot sites accounted for 21.2% of total sites surveyed, while management sites accounted for 33.7% of sites (Table S4B). Bright spots were less common than management sites, with 23.9 and 33.9% of sites identified on average per estuary, respectively (Table S4B). The Brisbane, Maroochy and Nerang systems lacked bright spots for this variable. Overall, only 4.8% of sites surveyed were categorised as bright spots according to all these criteria across the region, with these sites located in the Logan, Pimpama and Pine systems (Table S4C, Fig. 5C).

We identified two condition metrics in rocky outcrops that were significantly explained by our environmental variables: algae and oyster cover. For algae cover, bright spot sites accounted for 17.2% of total sites surveyed, while management sites accounted for 52.87% of sites (Table S5A). Bright spots were much less common than management sites, with 15.1 and 55.2% of sites identified on average per estuary, respectively (Table S5A). The Caboolture, Maroochy, Mooloolah, Pimpama and Pine systems lacked bright spots for this variable. For oyster cover, bright spot sites accounted for 14.9% of total sites surveyed, while management sites accounted for 70.1% of sites (Table S5B). Again, bright spots were much less common than management sites, with 14.3 and 75.1% of sites identified on average per estuary, respectively (Table S5B). The Albert, Brisbane, Caboolture, Logan, Maroochy, Noosa, Pine and Tingalpa systems lacked bright spots for this variable. Overall, no sites surveyed were categorised as bright spots according to both criteria across the region (Table S5C, Fig. 5D). It could be argued that high algae and oyster cover metrics are not compatible with each other, and that higher oyster cover with lower algae cover is the preferred ecosystem state (Gilby et al. 2018b); 10.3% of sites fulfilled these criteria, and these sites occurred in the Mooloolah, Nerang, Pimpama, Pumicestone and Tallebudgera systems (Table S5C).

Discussion

Understanding Patterns in Ecological Condition

The ecological condition of ecosystems, especially of habitat-forming species, has significant implications for the degree to which they support animal assemblages, important ecological functions and valuable ecosystem services (Goodridge Gaines et al. 2020; Gratwicke and Speight 2005; Kovalenko et al. 2012; Orth et al. 1984). Identifying important variables affecting the condition of ecosystems increases our understanding of how natural and human drivers interact to modify ecosystem structure. In this study, we identified significant statistical patterns in ten of 15 ecological condition metrics across four coastal ecosystems in southeast Queensland, Australia. Here, condition metrics were typically correlated with the connectivity of sites to natural features of coastal seascapes like the open sea, mangroves or intertidal flats. This reflects our existing understanding of coastal ecosystems both globally (Pittman 2018; Whitfield 2017) and within the study region (Goodridge Gaines et al. 2020; Henderson et al. 2017), where greater seascape connectivity typically results in better ecological condition, higher abundance and diversity of animals and greater ecological resilience. Only two condition metrics were significantly affected by variables indexing human impacts, with rocky outcrop oyster cover being lower in areas with more extensive urbanisation nearby and rocky outcrop algae cover being highest with intermediate extents of urbanisation nearby. This general lack of effects of human impacts and urbanisation across most ecosystems indicates either that the condition metrics tested here are not broadly affected by the human impacts or that the human impact variables used here did not sufficiently quantify these effects. However, these findings reinforce the notion that maximising landscape connectivity and habitat diversity in the coastal zone is crucial in optimising multiple attributes of

coastal ecosystems (Gilby et al. 2018a; Heatherington and Bishop 2012; Olds et al. 2018; Zamprogno et al. 2016). More thoroughly interrogating the interplay between natural and anthropogenic drivers of ecosystems can improve our understanding of the responses of ecosystems to both pressures and management (Gilby et al. 2020; Goodridge Gaines et al. 2020; Heatherington and Bishop 2012; Van der Stocken et al. 2015), their support of key ecosystem services (Barbier 2015; Whitfield 2017) and to establish more effective abiotic management surrogates for conserving and managing these vital coastal ecosystems (Hunter Jr et al. 2016; Lindenmayer et al. 2015).

The spatial patterns in ecological condition established in this study strongly reflect our ecological understanding of these ecosystems. For example, mangrove tree abundance varied with the area of mangroves nearby in this study. The area of mangroves nearby affects the delivery of propagules and the isolation of sites from other impacts, while intertidal flats can affect local hydrology, propagule supply and site inundation (Van der Stocken et al. 2015). Similar effects likely modified saltmarsh vegetation richness in this study (Huiskes et al. 1995; Lõhmus et al. 2020). While mangrove forests are highly dynamic and constantly renewing, mangrove tree density tends to be lower and trees larger (as measured by canopy height or diameter at breast height) in the most mature mangrove forests (Duke 2001). Crucially, mangrove tree density and size did not correlate strongly in this study (R = 0.42), perhaps indicating that most mangrove forests in this region are of low maturity and have high tree turn over. Whether this is a natural feature of mangrove forests in the region or due to broader impacts requires further investigation. However, such findings highlight the opportunity for bright spots in mangrove tree density to be conserved in the early stages of mangrove forest succession to ensure ongoing stability in ecosystem structure and function (Duke 2001).

Rocky outcrops are crucial ecosystems in estuaries as they are often one of the only hard structure ecosystems present within the broader seascape, thereby providing important opportunities for animals to feed on sessile invertebrates like oysters and important shelter and spawning habitats to a variety of species (Gilby et al. 2018a; Grabowski et al. 2005). In this study, algae cover was higher at deeper water depths, likely due to greater inundation times and lower exposure times driving higher algal biomass to deeper depths. Oysters have very specific tidal ranges in which they can thrive, and the patterns established for oyster cover on rocky outcrops reflect our understanding that oyster abundance declines with increasing greater depth and especially beyond the lowest astronomical tide line where predation on younger oysters is likely more intense (Gilby et al. 2019). Shellfish reef restoration is an increasing focus for managers within this region (Gillies et al. 2018; McAfee et al. 2022),

and these results support the notion that strategic placement of restored shellfish reefs is required to ensure restoration success (Gilby et al. 2019).

Management Applications

Predictions of ecological condition across landscapes are useful for identifying sites that should be conserved or used for management benchmarking and those that should be the focus of management actions (Cinner et al. 2016; Frei et al. 2018). The distribution of these sites (i.e. bright spots and management sites) was relatively even across estuaries and ecosystems in this study. Given the patterns of bright spots and management sites across both ecosystems and estuaries, this indicates that, broadly, our approach can successfully identify these patterns across multiple ecosystems and management units in coastal seascapes. The key exception was rocky outcrops, where no bright spot locations could be identified when the high values of the two metrics were considered, thereby reflecting our understanding of the degradation of these ecosystems across this region (Diggles 2013). Crucially, however, several rocky outcrop bright spots were identified when considering the high ecosystem state to be comprised of high oyster and low algae cover; this finding highlights the importance of understanding the local ecosystem context in disentangling patterns. The next step in progressing our understanding of these categories is to undertake further field surveys, analyses and engagement with managers to further disentangle exactly why sites are performing better than expected, and vice versa. It may be, for example, that management actions have resulted in meaningful improvements in condition at some bright spots, whereas other bright spots could have environmental conditions not quantified here that mediate the effects of impacts. Further disentangling these effects can assist in selecting specific management actions for underperforming sites.

The analyses conducted in this study have strong potential to (1) help prioritise management actions to underperforming sites; (2) establish high state baseline values to which management can aim; (3) create distribution models of habitat condition across landscapes, thereby improving the resolution of information reflecting habitat condition; and 4) help to optimise the spatial allocation of management efforts and conservation effects across landscapes. The approach undertaken elicits fair comparisons between sites and estuaries because models account statistically for all environmental variables causing variation in each ecological condition metric. This includes the random effect of the estuary in which sites are positioned, thereby indicating potential underlying variables affecting ecological condition at an estuary scale that were not quantified here. Using modern conditions and their drivers across landscapes also results in management outcomes being most relevant for today's conditions and a lesser reliance on management plans being set using historical baselines. This reduces the likelihood of shifting baselines affecting the likelihood of achieving management outcomes. Similarly, accounting for variation in variables that naturally affect ecological condition ensures that management does not implement homogenous or static plans for managing ecosystems across landscapes. Ensuring habitat heterogeneity at multiple spatial scales, from the number and type of plants to the diversity of ecosystems across landscapes, is vital in maximising biodiversity and ensuring support of ecosystem services (Gilby et al. 2020; Pittman 2018).

Ecological Restoration

Human impacts to ecosystems are driving an increased demand for ecological restoration in the coastal zone (Duarte et al. 2020). Setting quantitative ecological targets for restoration that describes the ecological condition of fully restored ecosystems is challenging in many systems because modern conditions in many remnant patches are often affected by human impacts and shifted baselines (Duarte et al. 2009; Soga and Gaston 2018). Models which disentangle these effects, such as those used here, can be used to isolate the effects of human impacts and therefore predict the likely unimpacted values of habitat condition for a given restoration site (Stoddard et al. 2006). However, habitats are not always entirely lost, and human impacts can simply impinge upon the potential for ecosystems to occur in good ecological condition or to support maximum biodiversity or ecosystem services (Barbier 2015). While the recovery of a lost habitat to a fully functioning ecosystem that reflects target ecosystem conditions is often the goal of restoration (Standards Reference Group SERA 2017), management should not overlook potential easy gains made from simply improving remnant ecosystem condition. Indeed, this may result in some of the most financially efficient improvements in ecological condition, biodiversity and ecosystem service delivery possible with relatively small investments potentially resulting in significant ecological benefits, including for fish abundance and biodiversity (Perry et al. 2023). With the global demand and associated funding for ecological restoration rising along with the need for expansive landscape scale restoration, optimising ecological restoration by (1) better selecting target ecosystem condition and (2) better allocating actions to the correct sites using approaches such as the one used here will result in greater outcomes for the given management focus or spend (Gilby et al. 2019, 2021; Standards Reference Group SERA 2017).

Future Challenges and Considerations

Five of the 15 ecological condition metrics tested here were not significantly explained by dependent variables in our analyses. Similarly, models for several of the metrics for which significant patterns were found had low R^2 values. This finding is somewhat surprising as all dependent variables included in this study have been shown in previous studies to have effects on the focal habitats of this study and so are generally accepted to have an impact upon the metrics we tested (see Table 2), but may be an indicator that other variables, not quantified in this study, could be driving differences in the condition of some sites. For example, it is possible that the influence of these predominantly spatial variables might be mediated by the effects of more local environmental metrics like hydrology, physicochemical attributes of the water column and sediment changes and composition (especially over years to decadal scales). These considerations were perhaps not adequately accounted for in this study and are typically not reflected in publicly available mapping, and so often require more specific, time consuming and/or more expensive surveys to quantify them. Indeed, the site-specific nature of many of these variables means that broad-scale management programs seeking to prioritise management across the scale quantified here will simply not have access to such data. While such variables might not have been significant in this study, broad-scale information on these attributes may require specific quantification at multiple spatial scales across these estuaries, and could be the focus of future studies.

A key challenge with the approach undertaken in this study is that surveys were conducted in modern conditions that might already be affected by a shifted baseline (Duarte et al. 2009; Soga and Gaston 2018). In this sense, applying actions based on modelled predictions which are essentially the average predicted condition anticipated given current positions within the broader seascape and environmental conditions could be criticised for being conservatively low in projected outcomes. This approach may also artificially spread the numbers of sites within bright spot, performing as expected and manage categories in our analyses because replicates were used for both model building and for subsequent categorisation. Under broader management scenarios, where thousands of sites might be being considered, this 'self-benchmarking' approach would not be undertaken, and new, independent sites that were not part of initial model construction sites would be placed into the model to determine categorisation. It could be argued that more 'pristine' conditions from outside of a broadly impacted region, or historical values of condition, might be more effective values against which bright spots could be selected. The challenge, of course, is that even when historical data is available, it

can be compromised by issues around shifting baselines, whereby human impacts might have become so severe that setting historical baselines as targets is simply unachievable (Balaguer et al. 2014; Duarte et al. 2009; Higgs and Jackson 2017). Similarly, reasonably comparable 'pristine' conditions are rarely available when setting benchmark or management targets (Simenstad et al. 2006). One way to overcome this would be to account for successional age in models explaining habitat condition metrics in this study (Amici et al. 2013). This was, however, not possible in this region due to a lack of data describing the successional age of sites, a situation not unusual for impacted coastal ecosystems (Elliott et al. 2022). Alternatively, managers could artificially increase target values to ensure that they are not conservatively low. Such approaches are less quantitative and rely strongly on the availability of historical data for benchmarking, or the contributions of significant local knowledge from stakeholders and local experts. However, such processes should be viewed as a positive step in maximising community and stakeholder engagement and in improving environmental management based on good, local historical and ecological knowledge (Phillipson et al. 2012; Reed 2008).

Human pressures are increasing across ecosystems and landscapes globally, driving an increased demand for actions to conserve remnant patches and improve and reconnect disconnected or degraded fragments (Duarte et al. 2020; Halpern et al. 2012; Possingham et al. 2015). In this study, we used quantitative approaches to (1) identify important drivers of ecological condition in coastal ecosystems that might be useful abiotic surrogates, (2) allocate sites to categories according to whether they are performing above, at or below expectations given overall trends and (3) detail how such an approach might be useful in optimising the allocation of management focus across landscapes. We propose such a predicted versus observed approach, which is predicated on a fundamental understanding of the ecology of focal ecosystems, to be a simple way to understand the implications of both anthropogenic impacts and management on ecosystems across most landscapes. Undertaking such analyses using simple and well-established metrics and generally widely available data like mapping layers is a quantitative and efficient method for optimising interventions. This study also has implications for ecological restoration, both in the identification and allocation of actions to sites and in the development of more effective and quantitative restoration targets. Together, undertaking such actions has the potential to improve multiple facets of ecosystem management relatively quickly, and could be considered more broadly.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12237-023-01187-w. Acknowledgements The authors also thank Edward Hay, Tyson Jones, Cody James and Nicholas Ortodossi for their contributions to field surveys.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. This study was funded by Healthy Land and Water and University of the Sunshine Coast.

Data Availability Derived data supporting the findings of this study are available from the corresponding author (BG) on request.

Declarations

Conflict of Interest The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

- Amici, V., E. Santi, G. Filibeck, M. Diekmann, F. Geri, S. Landi, A. Scoppola, and A. Chiarucci. 2013. Influence of secondary forest succession on plant diversity patterns in a Mediterranean landscape. *Journal of Biogeography* 40: 2335–2347.
- Asner, G.P., N.R. Vaughn, S.A. Foo, J. Heckler, and R.E. Martin. 2021. Abiotic and human drivers of reef habitat complexity throughout the main Hawaiian Islands. *Frontiers in Marine Science* 8: 631842.
- Balaguer, L., A. Escudero, J.F. Martin-Duque, I. Mola, and J. Aronson. 2014. The historical reference in restoration ecology: re-defining a cornerstone concept. *Biological Conservation* 176: 12–20.
- Barbier, E.B. 2015. Valuing the storm protection service of estuarine and coastal ecosystems. *Ecosystem Services* 11: 32–38.
- Barton, K. 2018. MuMIN: multi-model inference. *R Package Version* 1 (42): 1.
- Borland, H.P., B.L. Gilby, C.J. Henderson, J.X. Leon, T.A. Schlacher, R.M. Connolly, S.J. Pittman, M. Sheaves, and A.D. Olds. 2021. The influence of seafloor terrain on fish and fisheries: a global synthesis. *Fish and Fisheries* 22: 707–734.
- Brook, T.W., B.L. Gilby, A. Olds, R.M. Connolly, C.J. Henderson, and T.A. Schlacher. 2018. The effects of shoreline armouring on estuarine fish are contingent upon the broader urbanisation context. *Marine Ecology Progress Series* 605: 195–206.
- Chapman, C.A., L.J. Chapman, R. Wrangham, G. Isabirye-Basuta, and K. Ben-David. 1997. Spatial and temporal variability in the structure of a tropical forest. *African Journal of Ecology* 35: 287–302.
- Cinner, J.E., C. Huchery, M.A. MacNeil, N.A. Graham, T.R. McClanahan, J. Maina, E. Maire, J.N. Kittinger, C.C. Hicks, C. Mora, E.H. Allison, S. D'Agata, A. Hoey, D.A. Feary, L. Crowder, I.D. Williams, M. Kulbicki, L. Vigliola, L. Wantiez, G. Edgar, R.D. Stuart-Smith, S.A. Sandin, A.L. Green, M.J. Hardt, M. Beger, A. Friedlander, S.J. Campbell, K.E. Holmes, S.K. Wilson, E. Brokovich, A.J. Brooks, J.J. Cruz-Motta, D.J. Booth,

P. Chabanet, C. Gough, M. Tupper, S.C. Ferse, U.R. Sumaila, and D. Mouillot. 2016. Bright spots among the world's coral reefs. *Nature* 535: 416–419.

- Delarue, E.M.P., S.E. Kerr, and T.L. Rymer. 2015. Habitat complexity, environmental change and personality: a tropical perspective. *Behavioural Processes* 120: 101–110.
- Dennison, W.C. 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. *Aquatic Botany* 27: 15–26.
- Diggles, B.K. 2013. Historical epidemiology indicates water quality decline drives loss of oyster (*Saccostrea glomerata*) reefs in Moreton Bay, Australia. *New Zealand Journal of Marine and Freshwater Research* 47: 561–581.
- Duarte, C.M., D.J. Conley, J. Carstensen, and M. Sanchez-Camacho. 2009. Return to Neverland: shifting baselines affect eutrophication restoration targets. *Estuaries and Coasts* 32: 29–36.
- Duarte, C.M., S. Agusti, E. Barbier, G.L. Britten, J.C. Castilla, J.-P. Gattuso, R.W. Fulweiler, T.P. Hughes, N. Knowlton, C.E. Lovelock, H.K. Lotze, M. Predragovic, E. Poloczanska, C. Roberts, and B. Worm. 2020. Rebuilding marine life. *Nature* 580: 39–51.
- Duke, N.C. 2001. Gap creation and regenerative processes driving diversity and structure of mangrove ecosystems. Wetlands Ecology and Management 9: 267–279.
- Elliott, B.B., A.D. Olds, C.J. Henderson, A.J. Rummell, and B.L. Gilby. 2022. Optimising restoration and rehabilitation using environmental and spatial drivers of plant assemblages. *Landscape and Urban Planning* 226: 104484.
- Ferrari, R., H. Malcolm, J. Neilson, V. Lucieer, A. Jordan, T. Ingleton, W. Figueira, N. Johnstone, and N. Hill. 2018. Integrating distribution models and habitat classification maps into marine protected area planning. *Estuarine, Coastal and Shelf Science* 212: 40–50.
- Ferrier, S. 2002. Mapping spatial pattern in biodiversity for regional conservation planning: where to from here? *Systematic Biology* 51: 331–363.
- Frei, B., D. Renard, M.G. Mitchell, V. Seufert, R. Chaplin-Kramer, J.M. Rhemtulla, and E.M. Bennett. 2018. Bright spots in agricultural landscapes: identifying areas exceeding expectations for multifunctionality and biodiversity. *Journal of Applied Ecology* 55: 2731–2743.
- Gedan, K.B., B.R. Silliman, and M.D. Bertness. 2009. Centuries of human-driven change in salt marsh ecosystems. *Annual Review* of Marine Science 1: 117–141.
- Gilby, B.L., A.D. Olds, R.M. Connolly, P.S. Maxwell, C.J. Henderson, and T.A. Schlacher. 2018a. Seagrass meadows shape fish assemblages across estuarine seascapes. *Marine Ecology Progress Series* 588: 179–189.
- Gilby, B.L., A.D. Olds, C.H. Peterson, R.M. Connolly, C.M. Voss, M.J. Bishop, M. Elliott, J.H. Grabowski, N.L. Ortodossi, and T.A. Schlacher. 2018b. Maximising the benefits of oyster reef restoration for finfish and their fisheries. *Fish and Fisheries* 19: 931–947.
- Gilby, B.L., A.D. Olds, C.K. Duncan, N.L. Ortodossi, C.J. Henderson, and T.A. Schlacher. 2019. Identifying restoration hotspots that deliver multiple ecological benefits. *Restoration Ecology* 28: 222–232.
- Gilby, B.L., M.P. Weinstein, R. Baker, J. Cebrian, S.B. Alford, A. Chelsky, D. Colombano, R.M. Connolly, C.A. Currin, I.C. Feller, A. Frank, J.A. Goeke, L.A. Goodridge Gaines, F.E. Hardcastle, C.J. Henderson, C.W. Martin, A.E. McDonald, B.H. Morrison, A.D. Olds, J.S. Rehage, N.J. Waltham, and S.L. Ziegler. 2020. Human actions alter tidal marsh seascapes and the provision of ecosystem services. *Estuaries and Coasts* 44: 1628–1636.
- Gilby, B.L., A.D. Olds, C.J. Brown, R.M. Connolly, C.J. Henderson, P.S. Maxwell, and T.A. Schlacher. 2021. Applying systematic conservation planning to improve the allocation of restoration actions at multiple spatial scales. *Restoration Ecology* 29: e13403.

- Gillies, C.L., I.M. McLeod, H.K. Alleway, P. Cook, C. Crawford, C. Creighton, B. Diggles, J. Ford, P. Hamer, G. Heller-Wagner, E. Lebrault, A. Le Port, K. Russell, M. Sheaves, and B. Warnock. 2018. Australian shellfish ecosystems: past distribution, current status and future direction. *PLoS ONE* 13: e0190914.
- Goodridge Gaines, L.A., A.D. Olds, C.J. Henderson, R.M. Connolly, T.A. Schlacher, T.R. Jones, and B.L. Gilby. 2020. Linking ecosystem condition and landscape context in the conservation of ecosystem multifunctionality. *Biological Conservation* 243: 108479.
- Goodridge Gaines, L.A., C.J. Henderson, J.D. Mosman, A.D. Olds, H.P. Borland, and B.L. Gilby. 2022. Seascape context matters more than habitat condition for fish assemblages in coastal ecosystems. *Oikos* 8: e09337.
- Grabowski, J.H., A.R. Hughes, D.L. Kimbro, and M.A. Dolan. 2005. How habitat setting influences restored oyster reef communities. *Ecology* 86: 1926–1935.
- Gratwicke, B., and M.R. Speight. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology* 66: 650–667.
- Halpern, B.S., C. Longo, D. Hardy, K.L. McLeod, J.F. Samhouri, S.K. Katona, K. Kleisner, S.E. Lester, J. O'Leary, M. Ranelletti, A.A. Rosenberg, C. Scarborough, E.R. Selig, B.D. Best, D.R. Brumbaugh, F.S. Chapin, L.B. Crowder, K.L. Daly, S.C. Doney, C. Elfes, M.J. Fogarty, S.D. Gaines, K.I. Jacobsen, L.B. Karrer, H.M. Leslie, E. Neeley, D. Pauly, S. Polasky, B. Ris, K. St Martin, G.S. Stone, U.R. Sumaila, and D. Zeller. 2012. An index to assess the health and benefits of the global ocean. *Nature* 488: 615–620.
- Heatherington, C., and M.J. Bishop. 2012. Spatial variation in the structure of mangrove forests with respect to seawalls. *Marine* and Freshwater Research 63: 926–933.
- Henderson, C.J., B.L. Gilby, S.Y. Lee, and T. Stevens. 2017. Contrasting effects of habitat complexity and connectivity on biodiversity in seagrass meadows. *Marine Biology* 164: 117.
- Henderson, C.J., B.L. Gilby, T.A. Schlacher, R.M. Connolly, M. Sheaves, P.S. Maxwell, N. Flint, H.P. Borland, T.S.H. Martin, B. Gorissen, and A.D. Olds. 2019. Landscape transformation alters functional diversity in coastal seascapes. *Ecography* 43: 138–148.
- Henderson, C.J., B.L. Gilby, E. Stone, H.P. Borland, and A.D. Olds. 2021. Seascape heterogeneity modifies estuarine fish assemblages in mangrove forests. *ICES Journal of Marine Science* 78: 1108–1116.
- Higgs, E.S., and S.T. Jackson. 2017. The role of history in restoration ecology. In *Routledge handbook of ecological and environmental restoration*, 66–75. Routledge.
- Huiskes, A.H.L., B.P. Koutstaal, P.M.J. Herman, W.G. Beeftink, M.M. Markusse, and W. De Munck. 1995. Seed dispersal of Halophytes in tidal salt marshes. *Journal of Ecology* 83: 559–567.
- Hunter, M., Jr., M. Westgate, P. Barton, A. Calhoun, J. Pierson, A. Tulloch, M. Beger, C. Branquinho, T. Caro, J. Gross, J. Heino, P. Lane, C. Longo, K. Martin, W.H. McDowell, C. Mellin, H. Salo, and D. Lindenmayer. 2016. Two roles for ecological surrogacy: Indicator surrogates and management surrogates. *Ecological Indicators* 63: 121–125.
- Jakobsson, S., M. Evju, E. Framstad, A. Imbert, A. Lyngstad, H. Sickel, A. Sverdrup-Thygeson, J.P. Töpper, V. Vandvik, L.G. Velle, P.A. Aarrestad, and S. Nybø. 2021. Introducing the index-based ecological condition assessment framework (IBECA). *Ecological Indicators* 124: 107252.
- Jenkins, M.R., J.M. Cummings, A.R. Cabe, K. Hulthen, M.N. Peterson, and R.B. Langerhans. 2021. Natural and anthropogenic sources of habitat variation influence exploration behaviour, stress response, and brain morphology in a coastal fish. *Journal of Animal Ecol*ogy 90: 2446–2461.

- Kovalenko, K.E., S.M. Thomaz, and D.M. Warfe. 2012. Habitat complexity: approaches and future directions. *Hydrobiologia* 685: 1–17.
- Li, Y., Y. Sun, and J. Li. 2021. Heterogeneous effects of climate change and human activities on annual landscape change in coastal cities of mainland China. *Ecological Indicators* 125: 107561.
- Lindenmayer, D., J. Pierson, P. Barton, M. Beger, C. Branquinho, A. Calhoun, T. Caro, H. Greig, J. Gross, J. Heino, M. Hunter, P. Lane, C. Longo, K. Martini, W.H. McDowell, C. Mellin, H. Salo, A. Tulloch, and M. Westgate. 2015. A new framework for selecting environmental surrogates. *Science of the Total Environment* 538: 1029–1038.
- Lõhmus, K., T. Balke, M. Kleyer, and P. Török. 2020. Spatial and temporal patterns of initial plant establishment in salt marsh communities. *Journal of Vegetation Science* 31: 1122–1132.
- McAfee, D., I.M. McLeod, H.K. Alleway, M.J. Bishop, S. Branigan, S.D. Connell, C. Copeland, C.M. Crawford, B.K. Diggles, J.A. Fitzsimons, B.L. Gilby, P. Hamer, B. Hancock, R. Pearce, K. Russell, and C.L. Gillies. 2022. Turning a lost reef ecosystem into a national restoration program. *Conservation Biology* 36: e13958.
- Mills, M., R.L. Pressey, R. Weeks, S. Foale, and N.C. Ban. 2010. A mismatch of scales: challenges in planning for implementation of marine protected areas in the Coral Triangle. *Conservation Letters* 3: 291–303.
- Murray, C. 2010. Effective policy evaluation: refining design processes for coastal ecosystem condition indicators. *Coastal Management* 38: 681–687.
- Nagendra, H., R. Lucas, J.P. Honrado, R.H. Jongman, C. Tarantino, M. Adamo, and P. Mairota. 2013. Remote sensing for conservation monitoring: assessing protected areas, habitat extent, habitat condition, species diversity, and threats. *Ecological Indicators* 33: 45–59.
- Nel, J.L., D.J. Roux, R. Abell, P.J. Ashton, R.M. Cowling, J.V. Higgins, M. Thieme, and J.H. Viers. 2009. Progress and challenges in freshwater conservation planning. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19: 474–485.
- O'Hara, C.C., M. Frazier, and B.S. Halpern. 2021. At-risk marine biodiversity faces extensive, expanding, and intensifying human impacts. *Science* 372: 84–87.
- Olds, A.D., I. Nagelkerken, C.M. Huijbers, B.L. Gilby, S.J. Pittman, and T.A. Schlacher. 2018. Connectivity in coastal seascapes. In *Seascape* ecology, ed. S.J. Pittman, 261–291. Oxford: John Wiley and Sons.
- Orth, R.J., K.L. Heck, and J.V. Van Montfrans. 1984. Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. *Estuaries* 7: 339–350.
- Paradis, E., and K. Schliep. 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35: 526–528.
- Patrício, J., M. Elliott, K. Mazik, K.-N. Papadopoulou, and C.J. Smith. 2016. DPSIR–Two decades of trying to develop a unifying framework for marine environmental management? *Frontiers in Marine Science* 3: 177.
- Perry, H.J., L.A. Goodridge Gaines, H.P. Borland, C.J. Henderson, A.D. Olds, J.D. Mosman, and B.L. Gilby. 2023. Identifying optimal values of coastal habitat condition for management and restoration. *Estuarine, Coastal and Shelf Science* 282: 108250.
- Phillipson, J., P. Lowe, A. Proctor, and E. Ruto. 2012. Stakeholder engagement and knowledge exchange in environmental research. *Journal of Environmental Management* 95: 56–65.
- Pittman, S.J. 2018. Seascape ecology. Oxford: Wiley Blackwell.
- Pollock, L.J., W. Thuiller, and W. Jetz. 2017. Large conservation gains possible for global biodiversity facets. *Nature* 546: 141–144.
- Possingham, H.P., M. Bode, and C.J. Klein. 2015. Optimal conservation outcomes require both restoration and protection. *PLoS Biology* 13: e1002052.

- Pressey, R.L., T.C. Hager, K.M. Ryan, J. Schwarz, S. Wall, S. Ferrier, and P.M. Creaser. 2000. Using abiotic data for conservation assessments over extensive regions: quantitative methods applied across New South Wales, Australia. *Biological Conservation* 96: 55–82.
- Queensland Government. 2021. Queensland landuse mapping program. Brisbane, Australia: Queensland Government. https://qldspatial. information.qld.gov.au/. Accessed Dec 2021.
- Queensland Government. 2022. Regional ecosystem mapping. Brisbane, Australia: Queensland Government. https://qldspatial. information.qld.gov.au/. Accessed June 2022.
- Queirós, A.M., E. Talbot, N.J. Beaumont, P.J. Somerfield, S. Kay, C. Pascoe, S. Dedman, J.A. Fernandes, A. Jueterbock, and P.I. Miller. 2021. Bright spots as climate-smart marine spatial planning tools for conservation and blue growth. *Global Change Biology* 27: 5514–5531.
- R Core Team. 2022. *R: A language and environment for statistical computing, ed.* Vienna, Austria: R Foundation for Statistical Computing.
- Reed, M.S. 2008. Stakeholder participation for environmental management: a literature review. *Biological Conservation* 141: 2417–2431.
- Simenstad, C., D. Reed, and M. Ford. 2006. When is restoration not? Incorporating landscape-scale processes to restore self-sustaining ecosystems in coastal wetland restoration. *Ecological Engineering* 26: 27–39.
- Soga, M., and K.J. Gaston. 2018. Shifting baseline syndrome: causes, consequences, and implications. *Frontiers in Ecology and the Environment* 16: 222–230.
- Standards Reference Group SERA. 2017. National standards for the practice of ecological restoration in Australia, 2nd ed. Society for Ecological Restoration Australasia. www.seraustralasia.com. Accessed June 2017.
- Stoddard, J.L., D.P. Larsen, C.P. Hawkins, R.K. Johnson, and R.H. Norris. 2006. Setting expectations for the ecological condition of streams: the concept of reference condition. *Ecological Applications* 16: 1267–1276.
- Turner, W., C. Rondinini, N. Pettorelli, B. Mora, A.K. Leidner, Z. Szantoi, G. Buchanan, S. Dech, J. Dwyer, M. Herold, L.P. Koh, P. Leimgruber, H. Taubenboeck, M. Wegmann, M. Wikelski, and C. Woodcock. 2015. Free and open-access satellite data are key to biodiversity conservation. *Biological Conservation* 182: 173–176.
- Van der Stocken, T., D.J. De Ryck, B. Vanschoenwinkel, E. Deboelpaep, T.J. Bouma, F. Dahdouh-Guebas, and N. Koedam. 2015. Impact of landscape structure on propagule dispersal in mangrove forests. *Marine Ecology Progress Series* 524: 95–106.
- Vozzo, M.L., V.R. Cumbo, J.R. Crosswell, and M.J. Bishop. 2021. Wave energy alters biodiversity by shaping intraspecific traits of a habitat-forming species. *Oikos* 130: 52–65.
- Whitfield, A.K. 2017. The role of seagrass meadows, mangrove forests, salt marshes and reed beds as nursery areas and food sources for fishes in estuaries. *Reviews in Fish Biology and Fisheries* 27: 75–110.
- Wood, S.N. 2006. *Generalized additive models: an introduction with R*. Chapman and Hall/CRC.
- Wood, S. 2022. mgcv: mixed GAM computation vehicle with GCV/AIC/ REML smoothness estimation. R package version 1.8–36.
- Zamprogno, G.C., M.M.P. Tognella, V.D.S. Quaresma, M.B.D. Costa, S.S. Pascoalini, and G.F.D. Couto. 2016. The structural heterogeneity of an urbanised mangrove forest area in southeastern Brazil: influence of environmental factors and anthropogenic stressors. *Brazilian Journal of Oceanography* 64: 157–172.