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Seascape diversity and configuration shape habitat selection across multiple coastal ecosystems

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ABSTRACT

Many species move among habitats to feed, shelter, reproduce, and disperse, linking ecosystems across land and seascapes. In coastal ecosystems, fish movements throughout ontogeny connect habitats to form interlinked seascapes. The concepts of nursery habitats and ontogenetic habitat shifts are widely accepted, but how seascape features shape habitat use across coastal ecosystems during different life stages remains unclear. To address this, we surveyed fish from six habitat types with stereo-remote underwater video stations to examine how the spatial attributes of coastal ecosystems influence habitat use. Surveys were completed four times over two years and encompassed 180 sites along 200 km of the inshore Great Barrier Reef, Australia. Key fisheries taxa, including species of Lutjanus, Lethrinus, and Choerodon, exhibited clear ontogenetic shifts, moving from mangroves and back-reef habitats to coral reefs at larger body sizes. Variation in the spatial properties of coastal seascapes, principally the composition and configuration of habitats, was tightly linked to changes in the distribution and abundance of these species at different sizes. These strong seascape effects were evident across all habitats and sizes examined and were consistently more important than variation in habitat cover. Our findings strongly support the seascape nursery concept, demonstrating how the spatial diversity, composition and configuration of habitats can influence the abundance and distribution of coastal fishes and that interconnected habitats are critical for species undergoing ontogenetic shifts. Implementing effective management strategies for these species and their habitats will require protecting seascape features such as high habitat diversity and conserving well-connected patches.

1. Introduction

Many species use multiple ecosystems throughout their lives, moving among different or similar habitat patches in varying locations to feed, shelter, reproduce or disperse (Doherty and Driscoll, 2018; Shaw, 2020). These movements link ecosystems and populations through space and time, on land and in the sea, and often support the delivery of key functions and services for people, such as pollination, propagule dispersal, nutrient cycling and fisheries catch (Massol et al., 2011; Kool et al., 2013; Palola et al., 2025). Multi-habitat use is particularly pervasive in coastal seascapes, where a diversity of organisms move among shallow biogenic habitats with changes in tidal, diel and seasonal cycles, and in response to changing resource needs throughout their lives (Nagelkerken, 2009; Sheaves, 2009; Pittman, 2018). For example, coral reef fishes move into mangroves at high tide to feed, or mobile marine invertebrates use seagrass meadows as a refuge during the day before foraging over unvegetated sands at night (Nagelkerken and van der Velde, 2004; Olds et al., 2018). The juveniles (i.e. individuals smaller than the species-specific length at maturity) of many fish species that are targeted in wild-harvest fisheries use a range of inshore coastal ecosystems (e.g. seagrass, mangroves, saltmarsh, macroalgae) as nursery habitats before undertaking ontogenetic migrations to access offshore habitats (e.g. coral reefs, deeper coastal waters) where they reside as adults (Gillanders et al., 2003; Heck et al., 2003; Minello et al., 2003;

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Sheridan and Hays, 2003; Xing et al., 2025). The nursery functions of shallow submerged vegetation communities have been recognised for centuries (Beck et al., 2001; Sheaves et al., 2015). However, the formal nursery habitat hypothesis was introduced in 2001, proposing that nursery habitats support higher juvenile abundance, densities, growth, and survival, and contribute more individuals to adult populations than other habitats (Beck et al., 2001). The concept of nursery habitats has since expanded from an initial focus on the relative values of individual habitats, to a broader framing that encompasses the complementary values of multiple different habitats linked by migration (Dahlgren et al., 2006; Nagelkerken et al., 2015; Sheaves et al., 2015; Bradley et al., 2019). This seascape nursery definition integrates findings from research on nursery habitats and key ideas from the discipline of landscape ecology, and has been widely discussed as a framework for understanding habitat linkages in coastal systems (Nagelkerken et al., 2015). However, few studies have examined how spatial attributes (e.g. connectivity, diversity, and spatial configuration of habitat patches) may shape seascape utilisation throughout ontogeny by coastal fishes (Litvin et al., 2018; Trackenberg et al., 2024).

Tropical coastal seascapes comprise a mosaic of structurally complex habitat-forming species, including seagrass, mangroves, macroalgae and coral reefs, which are connected by the movement of water, energy and organisms (Nagelkerken, 2009; Boström et al., 2011; Henderson et al., 2017a). Coastal ecosystems are characterised by distinct habitat features and often support unique species pools as coastal fish move among multiple ecosystems for various purposes (Pittman and McAlpine, 2003; Whitfield, 2017; Bradley et al., 2024; Moustaka et al., 2025). For example, a diversity of fish species travel between alternative intertidal and subtidal habitats with the tidal cycle to feed, move among patches of the same habitat to avoid unfavourable environmental conditions or migrate from shallow coastal, to deeper inter-reef habitats with ontogenetic changes in resource requirements (Sheaves, 2009; Berkström et al., 2012; Pittman and Olds, 2015; Dunne et al., 2023). These movements link habitats across coastal seascapes, forming interconnected seascape nurseries that deliver joint habitat functions to support the early development of many fish species through a range of juvenile and sub-adult life stages (Nagelkerken et al., 2015; Olds et al., 2018). The inherent values of coastal seascapes for coastal fish are likely shaped by variation in the ecological condition, spatial context, composition, arrangement and connectivity of the ecosystems they encompass (Sheaves et al., 2015; Olson et al., 2019; Swadling et al., 2022; Moustaka et al., 2024b). This is because these seascape attributes can influence access to food resources, availability of refuge from predators, and the capacity of juveniles fishes to move among habitats (Olds et al., 2018; Bradley et al., 2019). Furthermore, these seascape attributes are key characteristics of diverse coastal systems, linked to variation in biodiversity, ecological functions, and the delivery of ecosystem services, and are particularly important to the distribution, diversity, and abundance of many coastal fishes (Olds et al., 2016; Sievers et al., 2020; Pittman et al., 2021). While ontogenetic habitat shifts are widely recognised, empirical data to quantify and conceptualise spatial patterns of multi habitat use remain limited for many species and habitats (Nagelkerken et al., 2015; Bradley et al., 2019; Fulton et al., 2020; Xing et al., 2025). This means that sizeable gaps remain in our knowledge of how the habitat values of multiple different coastal ecosystems coalesce to support a range of fish species throughout ontogeny.

We examined how the spatial properties of coastal seascapes shape patterns of multi-habitat use by fish on the inshore Great Barrier Reef in eastern Australia. This region supports a diverse mix of ecosystems in different environmental settings, including mangroves on the mainland coast, inter-reef seagrass meadows and isolated patch reefs, as well as clearwater island mangroves, fringing coral reefs and macroalgae dominated back-reef environments that border granitic islands (Barnes et al., 2012; Bradley et al., 2017; Bradley et al., 2019). Additionally, many of these areas are managed as no-take or partially protected zones of the Great Barrier Reef Marine Park and the Great Barrier Reef Coast Marine Park. We (1) quantified ontogenetic patterns of habitat use across the study seascape, and (2) examined the potential effects of emergent seascape properties (i.e. connectivity, composition, configuration, context and scale) on fish species within each habitat. Our intent was to investigate potential seascape effects on the use of multiple habitats throughout ontogeny, so we focussed on the early life stages of fisheries target species that are known to move between different ecosystems as they transition from juvenile to adult habitats (Kimirei et al., 2013; Perry et al., 2018; Bradley et al., 2019). We first tested for differences in fish size among habitats to identify potential patterns of ontogenetic shifts across three key genera; *Lutjanus*, snappers; *Lethrinus*, emperors; and *Choerodon*, tuskfish, and then examined the relative importance of seascape features and benthic habitat composition in shaping spatial patterns in their distribution and abundance. This study is a much-needed step towards describing how seascapes can influence the value of coastal ecosystems across multiple habitats throughout ontogeny and aims to examine whether the diversity and configuration of ecosystems can shape how fish use distinct habitats across at differing life stages.

2. Methods

2.1. Study location

We surveyed coastal fish assemblages at 180 sites along 200 km of coastline in eastern Australia, from Mission Beach (−17.880503, 146.111277) in the north to Townsville (−19.221570, 146.797890) in the south (Fig. 1). This region encompasses coastal waters adjacent to the mainland and several island groups (Family Islands, Hinchinbrook Island and surrounding islands, Palm Islands, Magnetic Island) and is characterised by heterogeneous seascapes comprising a diverse mix of mangrove forests, seagrass meadows, macroalgae beds, unvegetated sand, fringing coral reefs and isolated patch reefs (Barnes et al., 2012; Bradley et al., 2019). These habitats are spread across a variety of management zones within the Great Barrier Reef Marine Park and Great Barrier Reef Coast Marine Park, including marine reserve zone (no-take areas where fishing is prohibited), conservation park zone (partial protection from fishing), and general use zones (open to recreational and commercial fishing) (Fig. S1) (Frisch et al., 2012; Emslie et al., 2015). We conducted four separate surveys between August 2022 and March 2024 in which we aimed to sample all 180 sites on each event, but this was not always possible due to poor conditions (unsuitable sea state or water clarity) (Table S1). We surveyed six different habitat types: coastal mangroves (estuarine mangroves on the mainland), island mangroves (clear-water mangroves on islands), seagrass (inter-reef soft sediments that were dominated by seagrass), back-reef environments (lagoons or flats between islands and their fringing reefs that were dominated by macroalgae), fringing reefs (reefs fringing around high continental islands, dominated by hard coral) and isolated reefs (isolated patch reefs that were not connected to islands or their fringing reefs, dominated by hard coral) (Fig. S1, Fig. S2). These habitat patches ranged from small areas of tens of square meters to extensive continuous expanses covering several square kilometres with benthic cover ranging from sparse, low cover to highly dense cover. The number of sites varied among habitats: coastal mangroves ($n = 18$), island mangroves ($n = 21$), seagrass ($n = 33$), back-reef ($n = 35$), fringing reef ($n = 40$), and isolated reef (n = 33). Sites and habitats were selected in partnership with Manbarra, Wulgurukaba, Bandjin, Djiru, Girramay, Gulngay, Nywaigi and Warrgamay Aboriginal Traditional Owners to capture the full extent of variation in habitat, seascape and management zones across this region. Seagrass was, however, excluded from further examination as no target species were sufficiently abundant to permit analysis. Data from isolated and fringing reefs were pooled and were examined as “reefs” in all analyses as the size of target species did not differ between these reef types.

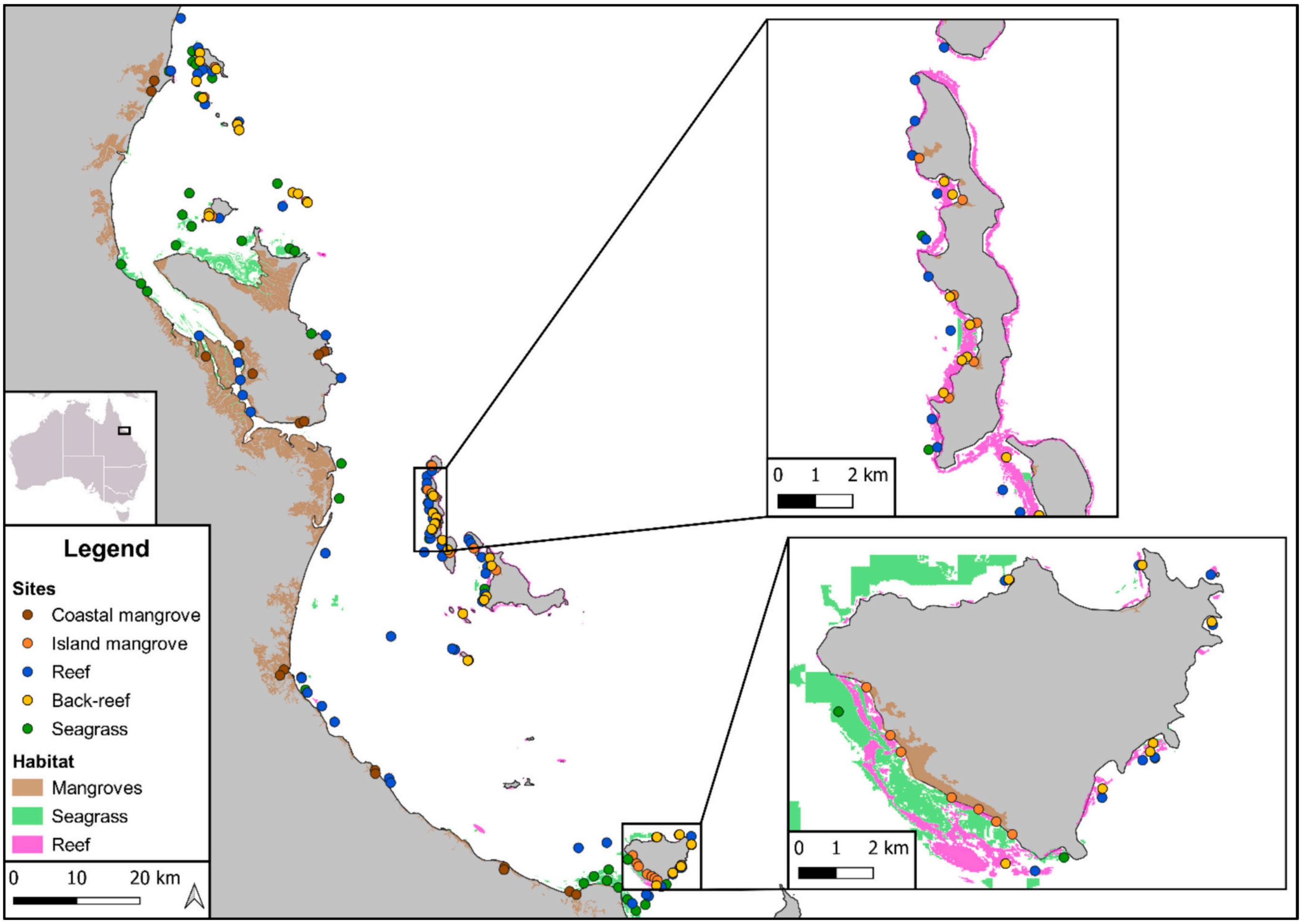

Fig. 1. Location of study sites and habitats in eastern Australia. Insets illustrate variation in seascape connectivity, composition, configuration, and context across the study region. Habitat layers have been clipped to a 10 km extent of the study area.

2.2. *Surveying and measuring fish assemblages*

Fish assemblages were surveyed using stereo remote underwater video stations (stereo-RUVS) consisting of a stainless steel frame deployed on the seabed containing a pair of forward-facing GoPro video cameras precisely mounted for accurate stereo geometry with 500 mm basal separation and 5 degrees of inward convergence (see Langlois et al., 2020). RUVS are widely used to examine the value of different habitats for coastal fishes because they efficiently sample fish species from all sizes (Bradley et al., 2017; Leslie et al., 2017), and the absence of bait decreases the chance of attracting individuals from other habitats (Borland et al., 2022). Five replicate stereo-RUVS were deployed at each site ($n = 3290$ replicates across all four events) and each consisted of 15 min of continuous undisturbed footage, which has previously been shown to be an effective time period for sampling juvenile and sub-adult fishes in a range of coastal habitats within the region (Bradley et al., 2019; Piggott et al., 2020). Replicates were separated by a minimum distance of 50 m to minimise the likelihood of sampling the same individual on multiple replicate deployments at a site (Gilby et al., 2018). All stereo-RUVS were deployed during daylight hours over high tide in intertidal habitats (i.e. coastal and island mangroves) and over low tide in subtidal habitats (i.e. fringing and isolated reefs, back-reef). Stereo-RUVS videos were first processed using Facebook AI Research's Detectron2 (Wu et al., 2019); a next generation library that provides state-of-the-art detection and segmentation (Abdusalomov et al., 2023). This AI network was successfully trained to detect fish in videos with high accuracy (prioritising the reduction in false-negative detections, Text S1). Stereo-RUVS footage that contained fish was then analysed using EventMeasure™ software with all fish identified to the lowest possible taxonomic level (SeaGIS Pty Ltd, 2020). Counts of species abundance were based on the *MaxN* statistic, which records the maximum number of individuals of the same species that can be seen in one frame on video footage from each deployment (Harvey et al., 2007).

To determine whether, and how, key fisheries target species use different habitats at different average sizes, we measured the fork length (from the tip of the snout to the caudal fork) of each fish. Fork length was chosen over total length because these measurements are often more easily definable across a range of species and are also not prone to inaccuracies for individuals that have lost parts of their caudal fins (Langlois et al., 2020). Fisheries target species were measured from each video at the time of *MaxN* using EventMeasure™ software (Rees et al., 2021). Prior to each sampling event, stereo-RUVs were calibrated using the software CAL (SeaGIS Pty Ltd, 2020) to ensure the accuracy of measurements. Individual measurements with a root mean square

(RMS) value greater than 20 mm were excluded from further analysis, as these values are considered imprecise (Langlois et al., 2020; Marrable et al., 2023). Fish that could not be accurately measured from the stereo-RUV footage, typically due to poor camera positioning, partial visibility, or fish orientation, were also excluded. We then compiled the maximum total length from Fishbase (Froese and Pauly, 2024), minimum size limit required for legal harvest in the region from the Queensland Government (Queensland Government, 2024) and fork length at maturity from published literature (Table S2). If fork length data were unavailable, it was calculated using conversions from total length or standard length (Froese and Pauly, 2024).

2.3. *Quantifying benthic habitat cover, visibility and depth*

We surveyed the cover and composition of seagrass, back-reef and reef habitats at each site using drop-cameras (Carter et al., 2021b). Drop-cameras comprise a SpotX video camera mounted above an aluminium frame that encapsulated a 50 × 50 cm quadrat over the benthos. Benthic photo-quadrats were taken from five replicate drop-camera deployments at each location where stereo-RUVs were deployed. Drop-camera deployments were always conducted after stereo-RUV sampling to minimise disturbance to fish assemblages. Benthic photo-quadrats were separated by at least 2 m with all five drops covering a total area of <10 m^2. The mean percent cover of habitat-forming species (i.e. hard coral, soft coral, seagrass and macroalgae) was then calculated from the drop-camera footage (Table S3, Fig. S2). Drop-cameras could not be used to record variation in the cover of mangroves, therefore, mangrove canopy cover was estimated within a 10 × 10 m plot (positioned to align the outer edge of each quadrat with the mangrove fringe) at each location where stereo-RUVS were deployed in mangrove forests (Table S3, Fig. S2) (Goodridge Gaines et al., 2022; Mosman et al., 2023). The mangrove forests surveyed were dominated by red mangroves (Rhizophora stylosa), with other species occurring only rarely, as such, variation in species composition was minimal. Water column visibility was quantified by estimating the distance (in meters) visible within the field of view of the stereo-RUV footage, rounded to the nearest 0.1 m and water depth was recorded using the vessel sounder at the time stereo-RUVs were deployed.

2.4. *Seascape analysis*

To examine how different seascape features influence the abundance of key fisheries targets across habitats we measured a range of spatial metrics, which are known to influence the distribution, abundance and diversity of juvenile and adult fish in coastal seascapes (Dorenbosch et al., 2004; Olds et al., 2013; Pittman, 2018; Moustaka et al., 2024b) (Table S3). All spatial metrics were quantified in QuantumGIS (QGIS Development Team, 2022) from publicly-available benthic habitat maps. Mangrove maps were sourced from the Queensland Government (Queensland Government, 2019), reef maps were sourced from Allen Coral Atlas (Allen Coral Atlas, 2022) and seagrass maps were sourced from eAtlas data catalogue (Carter et al., 2021a).

Spatial metrics were grouped into four classes based on the spatial properties of the seascape they describe, and included: seascape configuration, seascape composition, seascape connectivity and seascape context (Boström et al., 2011; Pittman et al., 2021) (Table S3). All spatial metrics, except for distance measures that describe variation in seascape context, were quantified from the area and isolation of habitats in buffers that were placed at multiple scales (i.e. 100 m, 250 m, 500 m, and 1000 m) around each survey site (Martin et al., 2018; Moustaka et al., 2024a). Seascape studies need to be scaled to the mobility of the species of interest (Grober-Dunsmore et al., 2009), therefore, these four buffer sizes were chosen to represent seascape variation across multiple scales and to encompass the daily home ranges of key fisheries target species (i.e. snappers: Lutjanus, emperors: Lethrinus and tuskfish: Choerodon) at different life stages (Sheaves, 1993; Pittman et al., 2007; Kendall et al., 2011; Olds et al., 2012; Green et al., 2014). There was, however, strong collinearity among spatial metrics that were computed at different scales (Pearson's correlation coefficient ≥ 0.7), so all subsequent analyses focussed on metrics quantified at the 250 m and 1000 m scales (Dormann et al., 2013). Seascape configuration metrics were quantified separately for each habitat for which benthic maps were available (i.e. mangrove, reef, seagrass) using the proximity index, which is calculated by summing the area of each habitat patch divided by the square of its edge-to-edge distance from its nearest neighbour within the specified buffer size (Olds et al., 2012; McGarigal et al., 2023) (Table S3). Seascape composition metrics were then quantified as seascape diversity using the Shannon-Wiener evenness index, which is calculated as diversity and evenness in the extent of all habitats within the specified buffer size (Shannon, 1948; Moustaka et al., 2024a) (Table S3). Seascape connectivity metrics were quantified by integrating both the area and distance of each habitat type in each seascape and was calculated as the geometric mean of proximity indices for mangrove, seagrass, and reef within the specified buffer size (Olds et al., 2012) (Table S3). Seascape context metrics were quantified by measuring the distance (m) from each stereo-RUVs deployment to the nearest reef, mangrove forest, and seagrass meadow that did not overlap land, this was chosen over Euclidean distance as it reflects the distance a fish would swim (Martin et al., 2015; Berkström et al., 2020) (Table S3). To standardise scales in the units of measurement among different metric types, each seascape metric was converted to a percentage, with values ranging between 0 and 100 %. For example, a reef proximity index of 100 % describes the site with the largest and most well-connected reef patch in the study area, and a seascape diversity of 100 % describes the site with the most diverse and even number of patches of all three habitats (mangroves, seagrass, and reefs) within that specified buffer size.

2.5. *Data analysis*

All analyses other than deriving seascape metrics were conducted in R 4.4 (R Core Team, 2024). Eleven fisheries target species met our criteria for analysis (Table S2), which required that they (1) are known fisheries targets in the region, (2) are known to undertake ontogenetic shifts among habitats, and (3) differed in size among the habitats examined in this study. As a result, the primary target species of the reef line fishery in the region, coral trout (*Plectropomus* spp.) along with other target species (e.g. *Lutjanus sebae, Lutjanus malabaricus*), did not meet the criteria for further analysis. To investigate ontogenetic shifts in habitat utilisation by key fisheries target species, we tested for differences in average size (fork length mm) of each species among habitats using generalised linear mixed models (GLMMs) via the *glmmTMB* package (Brooks et al., 2017). Additionally, we ran models to examine differences in the abundance of these species across habitats. Best-fit models were selected using reverse stepwise simplification, based on Akaike Information Criterion (AIC) and were those with the lowest AIC values. GLMMs were assessed for normality of residuals, homogeneity of variance, outliers, and over-dispersion and were fitted with a Gaussian distribution for size models and a negative binomial distribution for abundance models. All GLMMs included habitat as a fixed effect, and survey event (i.e. four different survey events), protection (i.e. the different management zones within the study area) and site as random effects. Protection was included as a random effect, rather than a fixed effect, because examining the performance of different management zones on the size of each species was not the focus of this study, but we still needed to account for their potential influence in our models. Pairwise comparisons of fork length between habitats were then conducted using estimated marginal means derived from GLMMs with the *emmeans* package in R (Lenth, 2024). Contrasts were calculated for each species to quantify differences in average size between habitats, identifying which specific habitat pairs had significantly different average sizes.

We then focused subsequent abundance analyses on these same species, but only within the habitats where size differences had been detected in the first step, examining the influence of seascape metrics and benthic cover on their abundance. This was done using a full-subsets (FSS) approach and generalised additive mixed models (GAMMs) using the *FSSgam* (Fisher et al., 2018) and *mgcv* packages (Wood, 2022) in R. The FSS GAMM approach fits all possible combinations of variables and calculates the AICc (Akaike Information Criterion corrected for small sample sizes) for each model (Fisher et al., 2018). To avoid overfitting, best-fit models were limited to a maximum of three explanatory variables (Zuur et al., 2009) and were restricted to three knots or fewer (i.e. k = 3). Predictor combinations with Pearson's correlation coefficients ≥ 0.28 or ≤ -0.28 were not permitted in the same model to minimise collinearity, as strong correlations can inflate variances and bias estimates (Graham, 2003; Fig. S3). Separate model sets were constructed for each habitat type to ensure that only ecologically relevant predictors were included. Predictor variables were plotted and assessed for normality and spread of values and variables with a poor spread were transformed (log transformation) or removed (if the transformation did not resolve the issues) before analysis. All GAMMs included protection, survey event, visibility and depth as random effects (Wood, 2006; Harrison, 2014). Protection was treated as a random effect to account for unmeasured variability among management categories while maintaining focus on environmental predictors. Whilst depth is an important factor influencing fish distributions throughout ontogeny, in our study the small within habitat differences did not warrant treating it as a fixed effect. Latitude and longitude were included as a tensor product smooth in all models to address spatial autocorrelation. All GAMMs were fitted with a tweedie distribution. Models were first fitted using maximum likelihood (ML) to enable AICc based comparisons across models with different fixed effects (Zuur et al., 2009). Best-fit models were then refitted using restricted maximum likelihood (REML) for final parameter estimation and plotting (Moustaka et al., 2025). Models with ΔAICc <2 were considered equally supported, and best models were selected from this subset based on parsimony, model weight, and variable importance scores. The relative importance of predictor variables was determined by summing the weight for each variable that was included in best-fit models (Anderson and Burnham, 2004). Model validation followed standard GAMM diagnostics, including checks for residual patterns, concurvity, and spatial autocorrelation. Model fit and assumptions were evaluated using diagnostic checks in the *DHARMa* package (Hartig, 2016).

3. Results

3.1. Fisheries target species use multiple habitats during ontogenetic shifts across coastal seascapes

Eleven fisheries target species from three genera (i.e. *Lutjanus*, *Lethrinus* and *Choerodon*) were observed in distinct habitats at different average sizes (Table 1, Fig. 2, Table S4). Four different patterns of nursery seascape use were identified from the size distributions of these species among habitats: (1) a shift from smallest sizes in coastal mangroves to largest sizes on reefs either directly (e.g. *Lutjanus russellii*), or through an intermediate shift to island mangroves (e.g. *Lutjanus argentimaculatus*); (2) back-reef to mangroves and reefs: a shift from back-reef environments at the smallest average size to island mangroves and reefs at the largest average size (e.g. *Lethrinus harak, Choerodon anchorago*); (3) back-reef to reefs: a shift from back-reef environments at the smallest average size to reefs at the largest average size (e.g. *Lutjanus carponotatus*, *Lutjanus vitta, Choerodon schoenleinii*); and (4) non-reef to reefs: a shift from coastal mangroves, island mangroves and back-reefs at the

Table 1

Summary of pairwise contrasts (estimated marginal means) for the fork length of each species between habitats, derived from generalised linear mixed models. The table displays pairwise comparisons of habitats for each species, including the estimated difference in fork length (Estimate), standard error (SE), t-ratio, and *p*-value. Significant contrasts ($p < 0.05$) are bolded and indicate significant differences in fork length between habitats.

Species	Habitat contrasts	Estimate	SE	t-ratio	p-value
Lutjanus argentimaculatus					
	Coastal mangrove/Island mangrove	−109.26	11.48	−9.51	**<0.001**
	Coastal mangrove/Reef	−182.55	24.99	−7.31	**<0.001**
	Island mangrove/Reef	−73.29	25.43	−2.88	**0.01**
Lutjanus carponotatus					
	Back-reef/Reef	−67.61	11.00	−6.13	**<0.001**
Lutjanus russellii					
	Coastal mangrove/Reef	−71.62	29.60	−2.24	**0.02**
Lutjanus fulviflamma					
	Coastal mangrove/Island mangrove	−11.22	12.26	−0.91	0.79
	Coastal mangrove/Back-reef	−7.92	12.46	−0.63	0.92
	Coastal mangrove/Reef	−91.98	24.00	−3.41	**0.004**
	Back-reef/Island mangrove	3.31	6.86	0.48	0.96
	Island mangrove/Reef	−70.75	21.63	−3.27	**0.006**
	Back-reef/Reef	−74.06	21.75	−3.40	**0.004**
Lutjanus vitta					
	Back-reef/Reef	−95.30	34.43	−2.76	**<0.001**
Lethrinus harak					
	Island mangrove/Back-reef	35.89	11.94	3.00	**0.008**
	Island mangrove/Reef	−55.66	31.16	−1.78	0.17
	Back-reef/Reef	−91.55	30.46	−3.00	**0.008**
Lethrinus laticaudis					
	Back-reef/Reef	−160.75	20.03	−8.02	**<0.001**
Lethrinus lentjan					
	Back-reef/Reef	−60.70	25.50	−2.38	**0.04**
Choerodon anchorago					
	Island mangrove/Back-reef	62.17	17.90	3.49	**0.002**
	Island mangrove/Reef	−13.26	20.88	−0.63	0.80
	Back-reef/Reef	−75.44	19.51	−3.87	**<0.001**
Choerodon cyanodus					
	Back-reef/Reef	−111.85	21.57	−5.18	**<0.001**
Choerodon schoenleinii					
	Back-reef/Reef	−53.97	21.46	−2.51	**0.01**

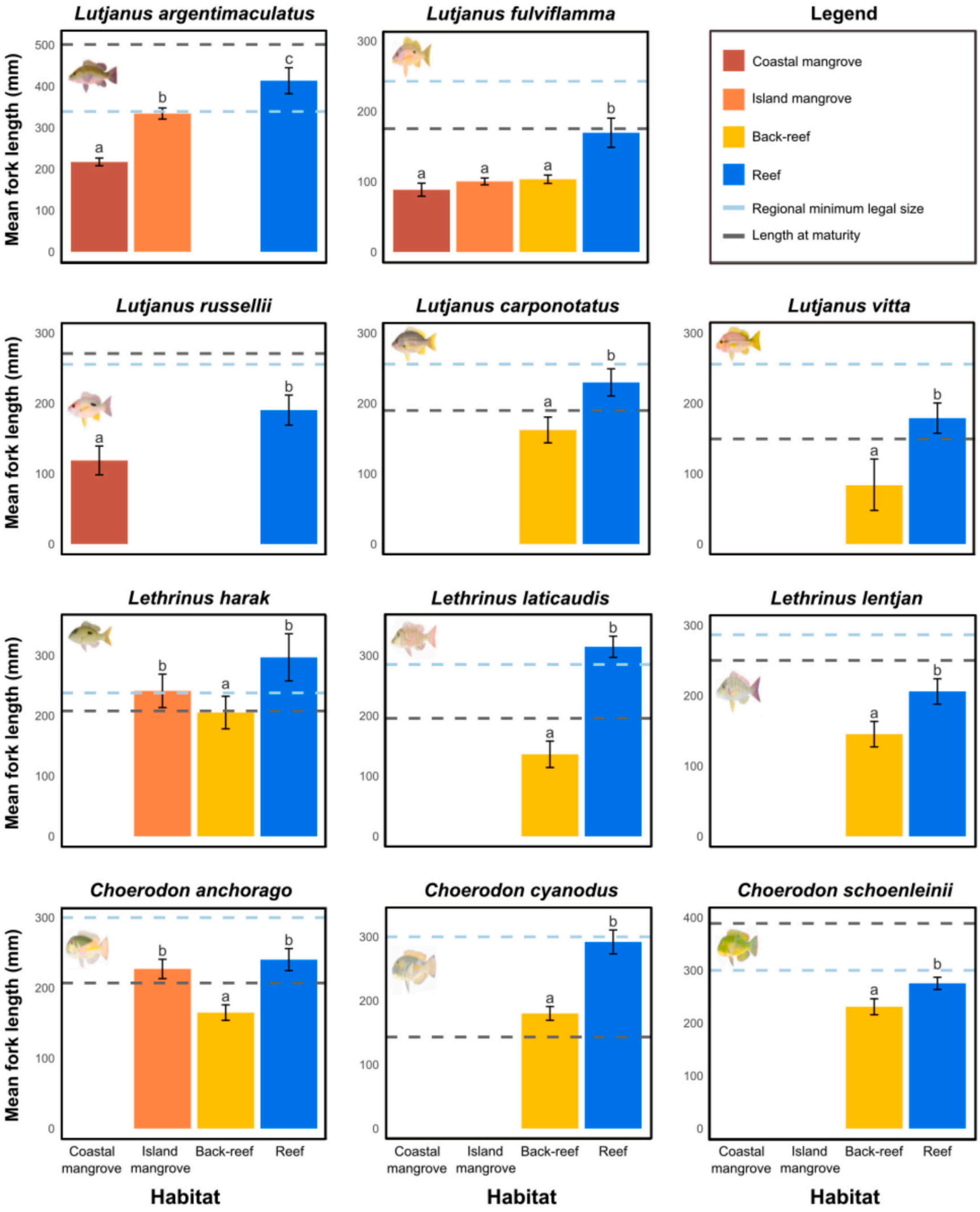

Fig. 2. Mean fork length (mm) of each focal fish species across habitats derived from generalised linear mixed models. Different letters above bars indicate significant differences in average size between habitats identified from pairwise contrasts (estimated marginal means), habitats sharing the same letter are not significantly different. Dashed lines represent regional minimum legal-size limits (blue) and lengths at maturity (grey). Fish images sourced from efishalbum.com. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

smallest average size to reefs at the largest average size *(*e.g. *Lutjanus fulviflamma)* (Table 1, Fig. 2).

3.1.1. Snappers (Lutjanus)

Five species of snapper (*Lutjanus*) were observed in distinct habitats at different average sizes (Table 1, Fig. 2, Fig. S3). *Lutjanus argentimaculatus* followed the mangroves to reefs pattern of seascape use and varied in size across three habitats; individuals of the smallest average size were found in coastal mangroves (mean FL = 222 mm), individuals of intermediate average size were found in island mangroves (mean FL = 331 mm), and the largest average size was found on reefs (mean FL = 405 mm) (Table 1, Fig. 2, Fig. S4). *Lutjanus fulviflamma* followed the non-reefs to reef pattern of seascape use and varied in size across all four habitats; individuals of the smallest average size were found in coastal mangroves (mean FL = 87 mm), island mangroves (mean FL = 94 mm) and back-reefs (mean FL = 98 mm), and the largest average size was found on reefs (mean FL = 168 mm) (Table 1, Fig. 2, Fig. S4). *Lutjanus russellii* followed the mangroves to reefs pattern of seascape use and varied in size across two habitats; individuals of the smallest average size were found in coastal mangroves (mean FL = 134 mm), and the largest average size was found on reefs (mean FL = 185 mm) (Table 1, Fig. 2, Fig. S4). *Lutjanus carponotatus* and *Lutjanus vitta* followed the back-reef to reef pattern of seascape use, with individuals of the smallest average size found in back-reefs (165 mm and 83 mm FL, respectively) and the largest average size on reefs (230 mm and 178 mm FL, respectively) (Table 1, Fig. 2, Fig. S4).

3.1.2. Emperors (Lethrinus)

Three species of emperor (*Lethrinus*) were observed in distinct habitats at different average sizes (Table 1, Fig. 2, Fig. S5). *Lethrinus harak* followed the back-reef to mangroves and reefs pattern of seascape use and varied in size across three habitats, individuals of the smallest average size were found in back-reefs (mean FL = 205 mm), whilst the largest average size was found in island mangroves (mean FL = 241 mm) and reefs (mean FL = 296 mm) (Table 1, Fig. 2, Fig. S5). *Lethrinus laticaudis* and *Lethrinus lentjan* followed the back-reef to reef pattern of seascape use, with the smallest individuals found in back-reefs (144 mm and 150 mm, respectively) and the largest on reefs (304 mm and 181 mm) (Table 1, Fig. 2, Fig. S5).

3.1.3. Tuskfish (Choerodon)

Three species of tuskfish (*Choerodon*) were observed in distinct habitats at different average sizes (Table 1, Fig. 2, Fig. S6). *Choerodon anchorago* followed the back-reef to mangroves and reefs pattern of seascape use and varied in size across three habitats, individuals of the smallest average size were found in back-reefs (mean FL = 164 mm), whilst the largest average size was found in both island mangroves (mean FL = 227 mm) and reefs (mean FL = 240 mm) (Table 1, Fig. 2, Fig. S6). *Choerodon cyanodus* and *Choerodon schoenleinii* followed the back-reef to reef pattern of seascape use, with the smallest individuals found in back-reefs (181 mm and 227 mm, respectively) and the largest on reefs (292 mm and 281 mm, respectively) (Table 1, Fig. 2, Fig. S6).

3.2. Seascape diversity and configuration shape habitat selection by fisheries target species across multiple coastal ecosystems

Most species were more abundant in their early-stage habitats, where they were observed at smaller average sizes (Table S4, Table S5. These included *Lutjanus argentimaculatus*, *Lutjanus fulviflamma*, *Lutjanus russellii*, *Lutjanus carponotatus*, *Lethrinus lentjan*, *Lethrinus harak*, and *Choerodon cyanodus* (Table S5, Fig. S7). In contrast, *Lutjanus vitta* was more abundant in its largest average size habitat while *Lethrinus laticaudis*, *Choerodon anchorago*, and *Choerodon schoenleinii* showed no significant difference in abundance across habitats (Table S5, Fig. S7). Changes in the diversity and configuration of coastal seascapes were tightly linked to variation in the abundance of these fisheries target species (Table S6- S8, Fig. 3–5). The effects of these seascape attributes on fish abundance were present across all habitats and sizes examined and were consistently stronger than any effects from variation in benthic habitat cover.

3.2.1. Snappers (Lutjanus)

Seascape composition (specifically seascape diversity at the 1 km scale) and seascape configuration (particularly reef proximity index at the 1 km scale) were the primary factors influencing snapper (*Lutjanus*) abundance (Table S6, Fig. 3a). *Lutjanus argentimaculatus* were most abundant in: (1) coastal mangroves with a high mangrove proximity index (1 km scale); (2) island mangroves where there was high mangrove cover (> 50 %), a high reef proximity index (> 30 %) (1 km scale), and high seascape diversity (1 km scale); (3) reefs with high seascape diversity (1 km scale) (Table S6, Fig. 3a & 3b).However, the reef models had both low model weight and low R^2 values, so results should be interpreted cautiously. *Lutjanus fulviflamma* were most abundant in: (1) coastal mangroves with moderate seascape connectivity (20–40 %) (1 km scale) and seascape diversity (250 m); (2) back-reefs that were < 6 km from a mangrove forest, and with a high seagrass cover (> 50 %); (3) island mangroves with a high reef proximity index (1 km scale) and high seascape diversity (1 km scale); and (4) reefs with a high seagrass proximity index (1 km scale) (Table S6, Fig. 3a & Fig. S8). However, the best model for reefs had low weight and a low R^2 and should therefore be interpreted with caution. *Lutjanus russellii* were most abundant in: (1) coastal mangroves with high mangrove cover (> 50 %), moderate mangrove proximity index (30–60 %) (1 km scale) and high seagrass proximity index (250 m scale); and (2) reefs with high seascape diversity (250 m scale) (Table S6, Fig. 3a & Fig. S9). *Lutjanus carponotatus* were most abundant in: (1) back-reefs with high macroalgae cover (> 50 %), a high reef proximity index (> 50 %) (250 m scale) and high seascape diversity (1 km scale); and (2) reefs with moderate hard coral cover (30–60 %) and low seascape diversity (1 km scale) (Table S6, Fig. 3a & Fig. S10). *Lutjanus vitta* were most abundant in (1) back-reefs where the reef proximity index was either low (0–25 %) or high (75–100 %) (1 km scale), there was high seagrass cover and high seascape connectivity (1 km scale); and (2) reefs with high seascape diversity (1 km scale), a moderate reef proximity index (20–40 %) (1 km scale) and moderate hard coral cover (30–60 %) (Table S6, Fig. 3a & Fig. S11).

3.2.2. Emperors (Lethrinus)

Seascape composition (specifically seascape diversity at the 250 m scale) and seascape configuration (particularly reef proximity index at the 250 m scale) were the primary factors shaping the abundance of emperors (*Lethrinus*) (Table S7, Fig. 4a). *Lethrinus harak* were most abundant in: (1) back-reefs with moderate seascape diversity (30–60 %) (250 m scale), a high reef proximity index (250 m scale) and high seagrass cover; (2) island mangroves that were < 50 m from a reef and with a high seascape connectivity (250 m scale); and (3) reefs with high seascape diversity (1 km scale) (Table S7, Fig. 4a & 4b). *Lethrinus laticaudis* were most abundant in: (1) back-reefs with moderate seascape diversity (30–60 %) (250 m scale); and (2) reefs with a high reef proximity index (250 m scale) (Table S7, Fig. 4a & Fig. S12). *Lethrinus lentjan* were most abundant in back-reefs with high macroalgae cover and high reef proximity index (250 m scale); and (2) reefs with a high seascape diversity (250 m scale) (Table S7, Fig. 4a & Fig. S13).

3.2.3. Tuskfish (Choerodon)

Seascape composition (specifically seascape diversity at the 1 km scale) was the primary factor shaping the abundance of tuskfish (*Choerodon*) (Table S8, Fig. 5a). *Choerodon schoenleinii* were most abundant in: (1) back-reefs with high macroalgae cover, that were < 3 km from a mangrove forest and with a high reef proximity index (1 km scale); and (2) reefs with high seascape diversity (1 km scale) and a high reef proximity index (250 m scale) (Table S8, Fig. 5a & 5b). *Choerodon*

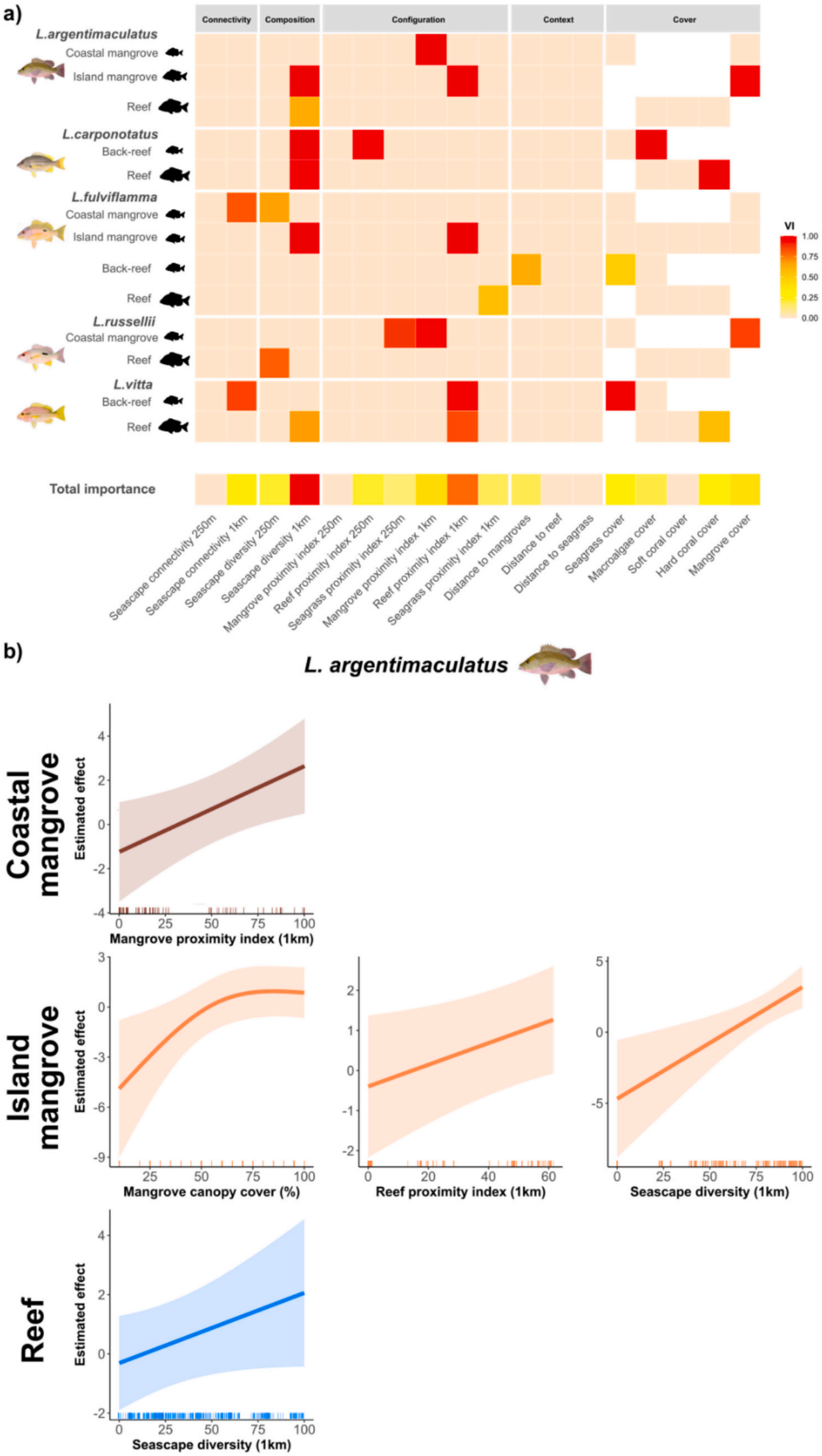

Fig. 3. (a) Heatmap of variable importance values (VI) from best-fit generalised additive mixed models for snapper (*Lutjanus*) species across habitats. The total importance represents the average variable importance for the genus. The dark fish icons represent the average size classes of fish in each habitat. Variables that were not relevant in particular habitats are coloured white. (b) Partial plots illustrating the effects of seascape and benthic habitat metrics on the abundance of *Lutjanus argentimaculatus*, a model species, across different habitats. These plots are derived from best-fit generalised additive mixed models. Fish images sourced from efish album.com. Relationships for other snapper species are available in the Supplementary Material.

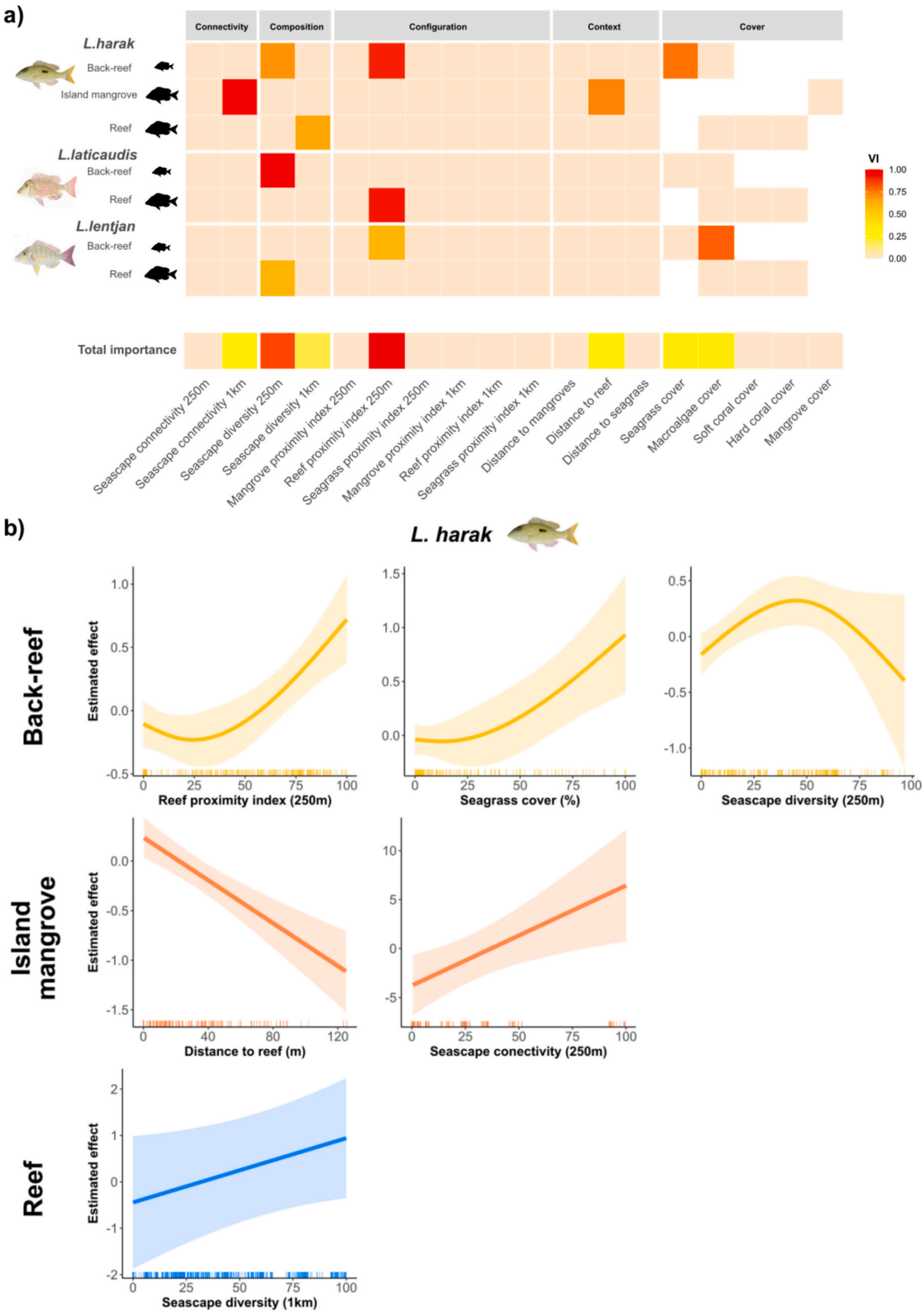

Fig. 4. (a) Heatmap of variable importance values (VI) from best-fit generalised additive mixed models for emperor (Lethrinus) species across habitats. The total importance represents the average variable importance for the genus. The dark fish icons represent the average size classes of fish in each habitat. Variables that were not relevant in particular habitats are coloured white. (b) Partial plots illustrating the effects of seascape and benthic habitat metrics on the abundance of *Lethrinus harak*, a model species, across different habitats. These plots are derived from best-fit generalised additive mixed models. Fish images sourced from efishalbum.com. Relationships for other emperor species are available in the Supplementary Material.

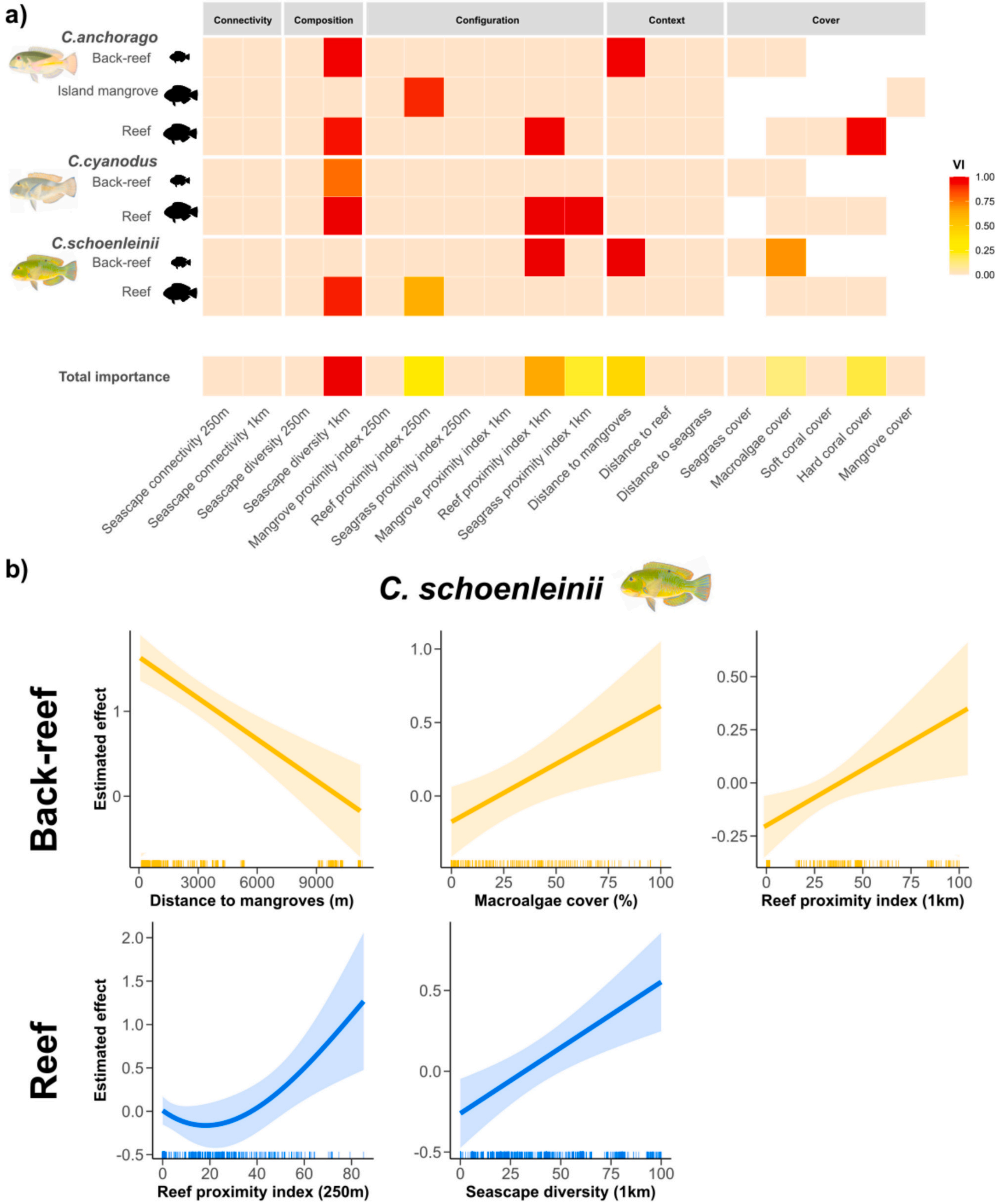

Fig. 5. Heatmap of variable importance values (VI) from best-fit generalised additive mixed models for snapper (*Choerodon*) species across habitats. The total importance represents the average variable importance for the genus. The dark fish icons represent the average size classes of fish in each habitat. Variables that were not relevant habitats are coloured white. (b) Partial plots illustrating the effects of seascape and benthic habitat metrics on the abundance of *Choerodon schoenleinii*, a model species, across different habitats. These plots are derived from best-fit generalised additive mixed models. Fish images sourced from efishalbum.com. Relationships for other tuskfish species are available in the Supplementary Material.

anchorago were most abundant in: (1) back-reefs with high seascape diversity (1 km scale), that were moderately distant from mangroves (3–6 km); (2) island mangroves with a high reef proximity index (250 m scale); and (3) at reefs with low seascape diversity, a moderate reef proximity index (20–40 %) (1 km scale) and high hard coral cover (Table S8, Fig. 5a & Fig. S14). *Choerodon cyanodus* were most abundant in: (1) back-reefs with either low (0–25 %) or high (75–100 %) seascape diversity (1 km scale); and (2) reefs with a moderate seagrass proximity index (1 km scale), a low seascape diversity (1 km scale) and a high reef proximity index (1 km scale) (Table S8, Fig. 5a & Fig. S15).

4. Discussion

In this study, we report ontogenetic habitat shifts by key fisheries target species and identify patterns of multi-habitat use across seascape nurseries to inform the management and protection of their vulnerable early life stages. We demonstrate that changes in the composition (i.e. seascape diversity) and configuration (particularly reef proximity index) of coastal seascapes can strongly influence variation in the abundance of coastal fishes across body sizes. In most cases, environments characterised by higher seascape diversity (i.e. comprising a large area and even mix of different habitat types) and greater reef proximity (i.e. close to a large area of reef) supported higher abundances of fisheries target species. However, responses were not consistent across all species, with some exhibiting non-linear or negative relationships with these variables. Our findings provide strong support for the seascape nursery concept (Nagelkerken et al., 2015; Sheaves et al., 2015), which views habitats as interconnected ecosystems, but has rarely been tested with empirical data to examine how variation in spatial patterns and processes influence habitat use across seascape nurseries (Lefcheck et al., 2019; Trackenberg et al., 2024). We agree that habitats should be conceptualised as individual components of inter-connected seascapes and suggest that describing the effects of seascape composition and configuration on target species abundance and diversity will help to improve the efficacy of management actions for these important species and their habitats.

Ontogenetic habitat shifts are common for many fish species (Nagelkerken et al., 2000; Kimirei et al., 2011; Dunne et al., 2023) and such migrations can occur at a range of scales, from movements along freshwater to marine gradients to movements among patches in local habitat mosaics (Sheaves et al., 2015). We illustrate shifts throughout ontogeny between multiple habitats by fisheries target species with all species found on reefs at their largest body sizes. We identify four different patterns of nursery seascape use: (1) mangroves to reefs; (2) back-reef to mangroves and reefs; (3) back-reef to reefs; and (4) non-reef to reefs. The five species of snapper (*Lutjanus*) examined in this study exhibited the most variation in nursery seascape use and utilised the highest diversity of habitat types across different life stages (i.e. mangroves to reefs, back-reef to reefs and non-reef to reefs), whilst the three species of emperor (*Lethrinus*) and tuskfish (*Choerodon*) used fewer habitat types with distributions that were largely centred around back-reef environments in reef-island seascapes (i.e. back-reef to island mangroves and reefs and back-reef to reefs). These size-based patterns were supported by the abundance analyses, which revealed that spatial drivers such as proximity to mangroves and seascape diversity often predicted abundance in ways consistent with the inferred ontogenetic pathways. For instance, species that shifted from mangroves to reefs tended to be more abundant on reefs with a high seascape diversity, while species linked to back-reef to reef pathways responded more strongly to connectivity to reefs and seascape diversity. It is well established that structurally complex habitat-forming species, like mangroves, seagrass and macroalgae, can function as nurseries for a range of juvenile fishes (Beck et al., 2001; Mumby et al., 2004; Nagelkerken, 2009; Whitfield, 2017; Fulton et al., 2020). Their value for juvenile fish, however, can depend on their spatial context and environmental conditions in wider seascapes (Bradley et al., 2019; Bradley et al., 2024; Moustaka et al., 2024b; Sievers et al., 2024; Moustaka et al., 2025). As coral reefs are often the final adult habitat for many species, their potential value as nurseries, or intermediate stop-over habitats, for juveniles and sub-adults is rarely considered (Lefcheck et al., 2019). In this study, reefs consistently supported the largest sizes of all species, however, based on the small sizes we recorded, many of these individuals were still likely juveniles or sub-adults. This finding highlights that inshore reefs can function as important habitats for juvenile fish, with their spatial attributes influencing their habitat value (Olds et al., 2012; Berkström et al., 2020). Our results also show that the smallest sizes of all focal species were found in either coastal mangroves (e.g. *Lutjanus argentimaculatus, Lutjanus russellii*), back-reef environments (e.g. *Lethrinus harak* and *Choerodon schoenleinii*), or both habitats (e.g. *Lutjanus fulviflamma*). These patterns suggest that coastal mangroves and back-reefs are critical for early-stage juveniles, and that connectivity between these and other ecosystems, which are used at larger body sizes, are pivotal for supporting fish across coastal seascapes (Adams et al., 2006; Whitfield, 2017; Moustaka et al., 2025). Identifying how ontogenetic shifts link seemingly isolated ecosystems across space and time is critical for effective fisheries management and the conservation of target species that rely on inshore nurseries in interconnected seascapes (Nagelkerken et al., 2015; Sheaves et al., 2015; Galaiduk et al., 2017).

The spatial positioning of habitats (i.e. their connectivity, composition, configuration and context) in coastal seascapes can alter patterns in the abundance, diversity and distribution of many fish species (Olds et al., 2018; Peterson et al., 2024), but it is less clear how these seascape attributes influence fish assemblages at distinct life stages (Olson et al., 2019; Berkström et al., 2020; Swadling et al., 2024). We report strong effects of the spatial composition (diversity) and configuration (relative area and isolation) of habitats in coastal seascapes and show that these seascape attributes were consistently more important than differences in benthic habitat composition in shaping the distribution and abundance of fisheries target species. Variation in seascape composition and configuration influenced the abundance of key fisheries target species in all habitats, and fish abundance was mainly highest in areas that were characterised by high seascape diversity and by a high proximity index for reef, mangroves or seagrass (i.e. there was a large area of these habitats close to focal patches). Previous research has reported positive effects of connectivity, configuration and context on fish abundance and diversity in many seascapes (Grober-Dunsmore et al., 2007; Henderson et al., 2017b; Sievers et al., 2020). This highlights the ecological importance of seascape diversity and configuration, as access to a mosaic of habitat types can provide complementary resources for feeding, growth and predator avoidance (Olds et al., 2018; Berkström et al., 2020). These processes help explain why abundance was often highest in areas where multiple habitats occurred in close proximity. Furthermore, we extend this knowledge of seascape ecology by illustrating consistency in spatial effects, both among ecosystems and across fish species and life stages. It was anticipated that the spatial scale over which each species might respond to seascape features would correlate with changes in individual body size (and associated variation in mobility characteristics, energy needs and relative predation risk) (Kramer and Chapman, 1999), but this was not the case as seascape effects scaled with species identity and were instead quite consistent across body sizes (Pittman et al., 2007). The primary responses of snapper (*Lutjanus*) and tuskfish (*Choerodon*) species examined in this study to seascape features mostly occurred at the largest scale (1 km), whereas the primary responses of emperor (*Lethrinus*) species mostly occurred at the smallest scale (250 m). These results suggest that different species respond to seascape patterns at distinct scales, and the consistency of species (and genera) responses among habitats and sizes indicates that these effects might result from selective use of seascape features, rather than from size-related changes in fish mobility or incidental variation in the spatial scale of fish habitats.

Seascape composition and configuration were consistently the most significant features in predicting variation in the abundance of fisheries target species, but the cover of habitat forming species (i.e. seagrass, macroalgae, coral, mangroves) was also important for some species. It is well established that a higher cover of habitat-forming species can be crucial for the juveniles of some fish species, with denser cover providing essential structural complexity, modifying the availability and complementarity of food resources, and altering predation risk for juvenile fish in vegetated habitats (Whitfield, 2017; Wilson et al., 2017; Lefcheck et al., 2019; Fulton et al., 2020). In this study, the cover of habitat-forming species (i.e. the cover of seagrass, macroalgae and mangroves) was correlated with the abundance of fisheries target species in mangroves and back-reef environments, and these effects were particularly strong and positive when species were at their smallest sizes. We recorded the juveniles of fisheries target species in a diversity of habitat-forming vegetation, including in seagrass, macroalgae and mangroves, but most observations were restricted to intertidal and shallow subtidal waters (i.e. back-reef and mangroves). By contrast, deeper seagrass meadows that grew over soft sediments between reefs supported very few juveniles of the species focused on in this study. These deeper inter-reef seagrass meadows could not be included in our analyses, due to the extremely low abundance and highly patchy distribution of certain species, but we suggest that they might still function be important for the juveniles of other fisheries target species. For example, the early juveniles of *Lutjanus malabaricus* ($<$ 10 cm) were only detected in deep seagrass meadows, which are likely dispersed widely across these large, patchy meadows. Whilst seascape composition and configuration were the most important factors affecting the distribution and abundance of fisheries target species in this study, our results also highlight an important role of high-cover, habitat-forming ecosystems for the early juveniles of some species. Our findings also show that management strategies that focus on capturing both seascape attributes and the cover of habitat forming species will be essential for supporting fish in seascape nurseries.

We show that species targeted by fisheries can use multiple interconnected habitats throughout their lives and show how changes in the diversity and configuration of these habitats can be the most significant attributes for predicting fish distributions through their early life histories, and across seascapes. We report effects of seascape attributes on the abundance of fish at differing life stages across multiple habitats, but our results are limited to patterns in fish abundance and size. Future research should examine whether, and how, these findings influence additional components of the nursery role hypothesis (e.g. fish growth, survival, productivity) at the scale of multiple species and ecosystems (Beck et al., 2001; Lefcheck et al., 2019; Moustaka et al., 2024b; Trackenberg et al., 2024; Xing et al., 2025). Other approaches, such as acoustic telemetry and otolith microchemistry, could be useful in quantifying habitat use throughout ontogeny to further evaluate these mechanisms. One limitation of this study is that coral and macroalgal reefs could not be distinguished in the available seascape habitat layers. Therefore, higher-resolution seascape maps that differentiate between coral and macroalgal habitats would be valuable for future research. Nevertheless, our findings illustrate the need for multi-scale, and multi-habitat, approaches when assessing and managing fish habitats and seascapes, and highlight how seascape attributes can play a pivotal role in determining how, and where, fisheries target species utilise multiple ecosystems as chains of linked habitats throughout their lives (Nagelkerken et al., 2015; Pittman and Olds, 2015; Swadling et al., 2024). We suggest that managing a singular habitat in isolation may not be effective without considering the spatial context of the surrounding seascape and alternate habitats that species will use throughout ontogeny (Sheaves et al., 2006; Nagelkerken et al., 2015; Litvin et al., 2018). Therefore, maintaining connected seascapes with diverse habitat types is vital for supporting the development and growth of species targeted by fisheries as they undertake ontogenetic habitat shifts (Olds et al., 2012; Berkström et al., 2020; Swadling et al., 2022). We therefore suggest that management should prioritise conserving habitat diversity, protecting large and well-connected patches, and ensuring linkages between mangroves, seagrass, and reefs. Emphasising these spatial attributes of seascape composition and configuration will help optimise management actions in coastal ecosystems.

CRediT authorship contribution statement

Jesse D. Mosman: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Hayden P. Borland:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Ashley J. Rummell:** Writing – review & editing, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Christopher J. Henderson:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Sam Allan:** Writing – review & editing, Investigation, Data curation. **Alec Bannam:** Writing – review & editing, Investigation, Data curation. **Stacy L. Bierwagen:** Writing – review & editing, Funding acquisition, Conceptualization. **Michael J. Bradley:** Writing – review & editing, Funding acquisition, Conceptualization. **Alex B. Carter:** Writing – review & editing, Investigation, Funding acquisition, Data curation, Conceptualization. **Daniela M. Ceccarelli:** Writing – review & editing, Funding acquisition, Conceptualization. **Robert Coles:** Writing – review & editing, Funding acquisition, Conceptualization. **Michael J. Emslie:** Writing – review & editing, Funding acquisition, Conceptualization. **Ben L. Gilby:** Writing – review & editing, Funding acquisition, Conceptualization. **Lucy A. Goodridge Gaines:** Writing – review & editing, Formal analysis. **Edward J. Hay:** Writing – review & editing, Investigation, Data curation. **Katrina Kaposi:** Writing – review & editing, Data curation. **Dmitry A. Konovalov:** Writing – review & editing, Data curation. **Theo Murphy:** Writing – review & editing, Investigation, Data curation. **Jordan C. Murray:** Writing – review & editing, Data curation. **Marcus Sheaves:** Writing – review & editing, Funding acquisition, Conceptualization. **Timothy M. Smith:** Writing – review & editing, Investigation, Funding acquisition, Data curation, Conceptualization. **Marcus Stowar:** Writing – review & editing, Funding acquisition, Conceptualization. **Andrew D. Olds:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

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Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.111558.

Data availability

Data will be made available on request.

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