






# The fish–mangrove link is context dependent: Tidal regime and reef proximity determine the ecological role of tropical mangroves

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## Abstract

Tropical mangroves are known to support fish production, but natural variability in the link between mangrove habitats and fish populations undermines our ability to manage, conserve and restore this ecological relationship. This is largely due to undefined context-dependence in the use of mangroves by fish. We collected a spatially extensive dataset of 494 mangrove fish assemblages using standardised Remote Underwater Video surveys of mangrove edge habitats from five environmentally heterogeneous regions in the Indo-Pacific. We used machine learning methods to define contextual limits of the use of mangroves by reportedly mangrove-affiliated fish. We found that tidal range and proximity to coral reefs were the most important contextual predictors of the use of mangroves by most taxa. We established data-driven threshold values for important contextual predictors of the use of mangroves by fish, offering new insights into the variable role played by tropical mangroves in supporting fish life histories. Where

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mangroves occur as part of reef seascapes in regions with limited tidal range (<1.5m), they appear to serve an important juvenile habitat function for a wide spectrum of reef fish. In regions with substantially larger tidal ranges, mangroves appear to only support certain reef species with coastal life histories. Coastal and estuary fish were able to use mangroves in a wide variety of non-reef contexts. We demonstrate that key thresholds in environmental context can govern the functional role of mangroves, with strong implications for the role of other habitats in coastal seascapes.

#### KEYWORDS

ecogeography, ecological value, habitat, nursery ground, RUVs, seascape

## 1 | INTRODUCTION

Environmental decision-making often relies on a conceptual understanding of the ecological roles and functions of different habitat types. How well those concepts are grounded in robust ecological understanding will determine the quality of those decisions (Chan & Satterfield, 2020; Fu et al., 2013). Many habitat types are recognised as performing critical ecological functions for animals, which in turn support ecosystem functioning. For instance, tree hollows provide nesting sites for woodland vertebrates (Gibbons et al., 2002) and corals provide structural complexity that regulates fish productivity (Rogers et al., 2014). Without these habitats, the fauna that require them can become scarce (Cockle et al., 2011; Pratchett et al., 2008), which in turn can alter ecosystem function and resilience. These ecological functions have been incorporated into environmental decision-making through ecosystem-based management (Arkema et al., 2006), and into social and economic decision-making through versatile concepts like ecosystem services (Carpenter et al., 2009). Quantifiable and mappable attributes, like vegetation type or coral cover, often stand in as proxies for critical ecological functions in these arenas, but how well they represent these ecological functions in any given circumstance often remains untested.

Ecological relationships, such as those between fauna and habitat, are particularly context dependent, and therefore particularly susceptible to fundamental issues of transferability (Bradley et al., 2020). In the coastal marine environment, there is evidence of context dependence in fauna-habitat relationships for macroalgae, mangrove, soft sediment flats, salt marsh and seagrass habitats (reviewed in Bradley et al., 2020). For these habitats, there is substantial variation in habitat use by fishes over both small (e.g. metres) and large scales (e.g. between regions), which appears to be driven by variations in environmental conditions (Bradley et al., 2019, 2021; Dubuc, Waltham, et al., 2019; Igulu et al., 2014; Ziegler et al., 2019). This is distinct from attributes of the habitats themselves, like structural complexity, which is now well understood. While the influence of some environmental factors is well understood in isolation, the interplay of different contextual factors is poorly understood, which inhibits reliable predictions of habitat use and habitat function, and therefore ecological value. Directly addressing context dependence,

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through studies that define the contextual limits of ecological relationships, leads to increased understanding, prediction and generalisation in ecology (Catford et al., 2022). Practitioners need clear guidelines about the roles and functions of different habitat types in their local area, such as threshold values in environmental conditions that indicate whether particular concepts are appropriate. In this study, we use a context-dependence framework to identify thresholds in relationships between tropical mangroves and fishes; information that will help avoid regionalisation errors in mangrove fish-related concepts, such as ecosystem services concepts.

Mangroves provide a useful system to study context dependence in fauna–habitat relationships. Several key ecological roles are attributed to mangroves (Lee et al., 2014; Sanchirico & Mumby, 2009). Mangroves are considered an integral part of coastal and estuary ecosystems, serving as important habitats for coastal and estuary fish around the world (Blaber, 2013; Whitfield, 2017). Mangroves are also considered an important part of nearshore coral-rich tropical marine seascapes, supporting key ecosystem functions that are linked to reef resilience (Olds et al., 2012). Their use by reef fish is often related to specific life-history stages and strategies. Mangroves are important nursery habitat for reef fish (Mumby et al., 2004; Nagelkerken et al., 2002), stepping stones in the tripartite life histories of fish that make ontogenetic migrations between coastal/estuary areas and reefs (Russell & McDougall, 2005) and are frequented by adult reef fish (Barnes et al., 2012; Sarnbrook et al., 2019). However, the extent and patterns of use by fish vary widely.

There is a history of controversy over the importance of mangroves for fish. In the early 2000s, there was vigorous debate over the question of whether mangroves were important nursery and feeding habitats, with compelling evidence from some regions and conflicting evidence from others (reviewed in Nagelkerken, 2009). It is now clear that the use of mangroves by fish can vary widely (Castellanos-Galindo et al., 2012; Kimirei et al., 2011; Sheaves, 2012, 2017), with direct consequences for their ecological roles (Lee et al., 2014). This presents a major stumbling block in understanding the extent to which mangroves might enhance local fisheries, due to a lack of location-specific data (Hutchison et al., 2015). This leads to serious problems with valuing the contribution of mangroves to fisheries (Sheaves et al., 2020), and actively prevents the implementation of ecosystem-based concepts by environmental managers (Arnold, 2013; Himes-Cornell et al., 2018).

A more appropriate and tractable set of questions is *where* are mangroves important, for what kinds of fish, and how can we predict this? Extensive work in the Indo-Pacific and Tropical Atlantic has shown that mangrove use may vary both at the regional level, according to climate and tidal regime (Castellanos-Galindo & Krumme, 2015; Igulu et al., 2014), which broadly determine the availability of the forest and estuarine influence, and also at the landscape level, according to qualities of the surrounding seascape (Pittman et al., 2007), and where mangrove habitat is positioned in that seascape (Dorenbosch et al., 2007), particularly in relation to seagrass and coral reefs. Local patch-scale factors are also important

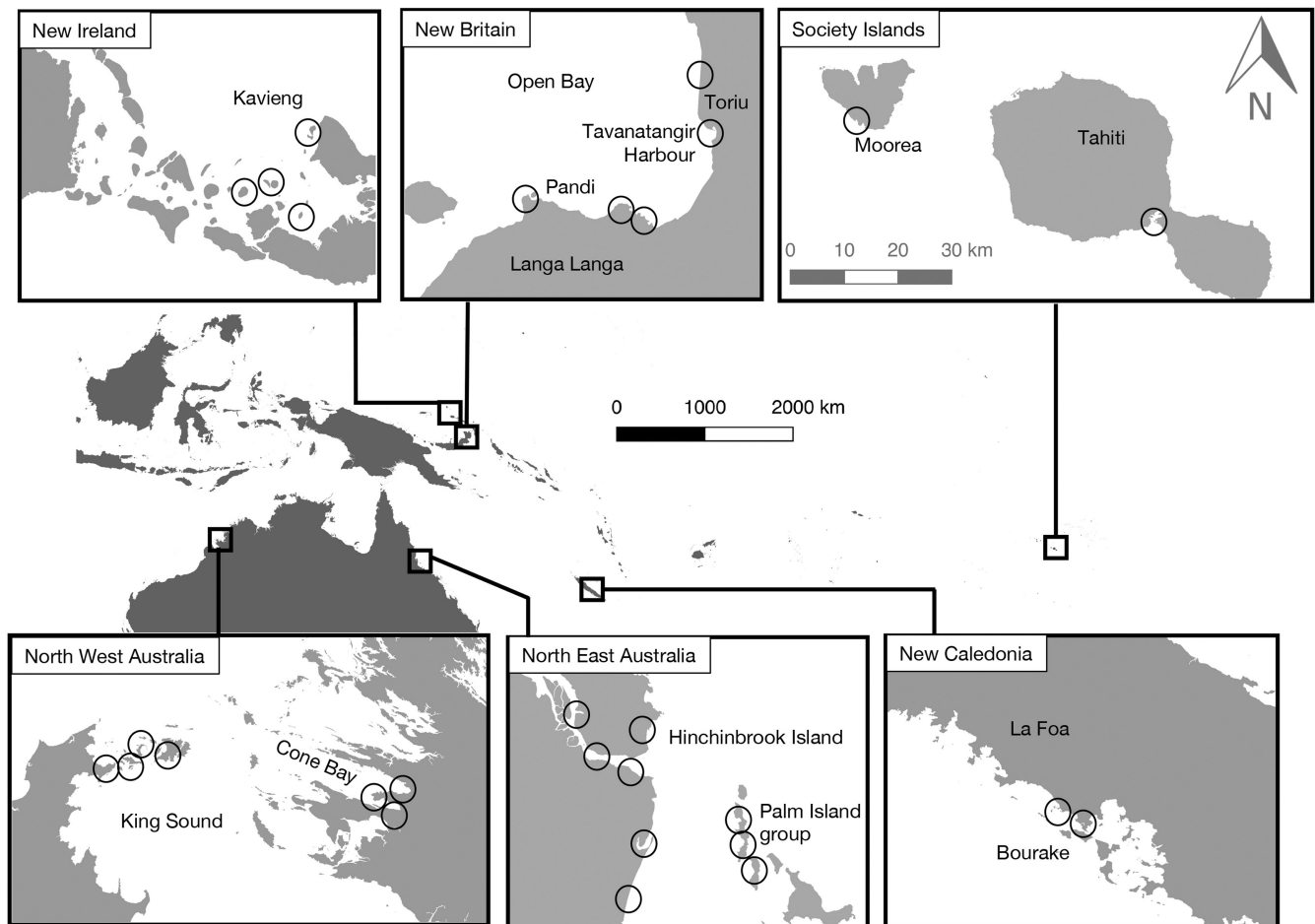
determinants of mangrove use, particularly water qualities like salinity, turbidity and dissolved oxygen (Dubuc, Baker, et al., 2019; Ley et al., 1999), which can exclude fish species based on their level of tolerance; water depth, which can exclude fish based on body size (Dubuc, Waltham, et al., 2019; Ellis & Bell, 2004); substratum, which can relate to feeding opportunities (Barnes et al., 2012; Blaber & Milton, 1990); and surrounding habitats (Wanjiru et al., 2023), all of which are in some way the product of regional (e.g. climate, tide, sedimentary and geomorphic) and landscape factors. Meta-analysis has demonstrated that country of study explains 70% of the variation in the link between mangroves and fisheries (Carrasquilla-Henao & Juanes, 2017). This finding provides tangible guidelines; it is safer to use local knowledge of mangrove–fisheries dependence than to extrapolate knowledge from other countries. This is because environmental factors associated with countries, such as climate, tide, freshwater flow and geomorphology, are likely responsible for spatial patterns in the strength of the fishery–mangrove relationship (Carrasquilla-Henao & Juanes, 2017).

A contextual understanding of the mangrove fish relationship, informed by comparable data from different environmental contexts, will allow us to build more meaningful models of the ecological value of mangroves, mangrove fisheries enhancement, and other supporting services that are critical to effective management. Building on existing location-specific understanding of mangrove fish in the Indo-Pacific, we use a unique dataset of comparable field surveys from across environmentally heterogeneous regions to directly assess context dependence in the use of mangroves by fishes. We fill an important gap around thresholds in the ecological role of mangroves. The first step in this direction is to understand in which environmental contexts certain types of fauna are typically present or absent—that is, their distribution in environmental space. We examine potential context dependence in the presence of key fish groups in tropical mangroves across the Indo-Pacific based on a range of factors determined as important in previous studies. To minimise the well known influence of structural habitat qualities on our models of environmental dependence, we have focused entirely on *Rhizophora* prop-root mangrove habitat, a common and widely studied mangrove habitat (Nagelkerken et al., 2008). We ask: are there predictable patterns of environmental dependence for key fish–habitat relationships? In asking this question we aim to provide the first data-derived guidance on context dependence in the link between mangroves and fish.

## 2 | METHODS

### 2.1 | Study sites

Study sites throughout the Indo-Pacific at similar tropical latitudes were chosen to represent the breadth of variation present in environmental contexts inhabited by *Rhizophora* mangroves (Figure 1). Regions represent almost the full range of variation in tidal range experienced in the Indo-Pacific, from 0.5 m in The Society Islands to



**FIGURE 1** Geographical distribution of study sites across the Indo-Pacific region. The middle panel displays the location of study regions within the Indo-Pacific. Inset boxed maps display each of the five study regions, with the Bismarck Archipelago region shown across two panels (New Ireland and New Britain, Papua New Guinea). Within each boxed map, black circles show the location of sampling sites. Each boxed map is identically scaled and oriented (scale bar located in the Society Islands map).

11 m in North West Australia. *Rhizophora* mangroves were sampled in a range of different locations to cover the range of variation in environmental contexts within each study region. This range differed in each region (Table 1) due to differences in climate and geomorphology, as well as the relative dominance of *Rhizophora* mangroves. For example, in islands of the Bismarck Archipelago, *Nypa fruticans* dominated brackish estuaries that extended far inland (i.e. far from coastal reefs), whereas in North East Australia, *Rhizophora* mangroves were abundant in brackish estuaries far from reefs. These sampling imbalances reflect natural variation in environmental context. This unavoidably confounds extremes in particular variables with region, and this was considered in the choice of analysis and interpretation of results.

## 2.2 | Remote underwater video

Unbaited remote underwater videos (RUVs) provide a low-disturbance snapshot of the fauna naturally associated with coastal habitats. All video surveys were conducted in prop-root

habitat of mangroves of the genus *Rhizophora*, and were within the first 2 m of the seaward edge of the forest. RUVs were collected when the forest was inundated, with a roughly even distribution across flood, high and ebb tidal states and rarely during low tide. This was captured in the variable 'tidal direction' (see Figure S1) and included in analysis. All video units across all locations were unbaited and deployed for at least 15 min, at least 20 m apart. This minimum sampling distance is favoured to achieve high-replication RUV studies (e.g. Bradley et al., 2019), but it does not completely guarantee spatial independence, particularly for large cursorial fishes. Therefore, most samples in this dataset were separated by >50 m. All video units consisted of an underwater camera positioned parallel to the horizon, attached to a weighted landing frame that raised the camera off the substratum. Only samples with a visibility range of greater than 0.5 m were retained. This produced 494 video samples for analysis, from across our five regions (for regional breakdown, see Table 1). For optimal and consistent comparison of fish assemblages, 15 min of video was watched from each video sample (following Piggott et al., 2020). Species presence-absence and species richness data were extracted for use in



TABLE 1 Regional sampling details of *Rhizophora* video samples, including environmental parameters and associated meta-data.

Region	Tidal range	Tidal pattern	Sampling period	Yearly average rainfall, climate	Salinity: Range sampled	Distance to reef: Range sampled	Coordinates	n
Society Islands (French Polynesia)	0.5 m	Semi-diurnal with diurnal inequality	Oct 2017	1800 mm, Tropical monsoon climate	32–34 ppt	230 m–360 m	17° S 149° W	55
Bismarck Archipelago (Papua New Guinea)	1.1, 1.2 m	Mixed	New Britain: Sept–Nov 2015 & 2016, New Ireland: April 2018	3700 mm, Tropical monsoon climate	19–35 ppt	3 m–1 km	4° S 151° E	123
New Caledonia	1.8 m	Semi-diurnal with diurnal inequality	Jan–May 2016 & 2017	1250 mm, Tropical savanna climate	31–33 ppt	20–460 m	22° S 166° E	80
North East Aust.	3.9 m	Semi-diurnal with diurnal inequality	June–Dec 2014, 2015 & 2016	2237 mm, Tropical monsoon climate	14–35 ppt	30 m–25 km	18° S 146° E	176
North West Aust.	8.9, 10.8 m	Semi-diurnal	Oct 2015–Aug 2016, June 2017	500 mm, Tropical semi-arid climate	34–35 ppt	200 m–8 km	16° S 123° E	60

Note: Climate data from [www.climate-data.org](http://www.climate-data.org) accessed on October 2022. Tidal pattern data from [data.shom.fr](http://data.shom.fr), accessed on October 2022. Where sites within regions differed in max tidal range, both the highest and lowest values are given.

statistical analyses. Abundance data were avoided due to the out-sized influence of highly abundant taxa on total fish group abundance. This sampling method is not appropriate for small gobiiform fishes and cryptic fishes, therefore this group and their relationship with mangroves are not assessed in this study.

### 2.3 | Seascape life-history strategy categorisation

Fish detected in RUVs were identified to the lowest taxonomic grouping possible, and where possible, juvenile stages were differentiated from adult stages, using stage-specific colour patterns and other morphological characteristics (following Bradley et al., 2019, 2021). We examined two distinct sets of fauna—coastal–estuarine fauna, which are not associated with reefs, and reef-associated fauna, which are found specifically associated with coral reefs at some point in their life cycle. For these reef fish, given the known life-history specificity of the role of mangroves, we assessed adults separately from juveniles. We also distinguished between species that are reef associated throughout their life-history (referred to here as 'juvenile reef specialist fish') from species that are known to typically use non-reef habitats at some point in their life cycle (referred to here as 'multihabitat reef fish' following Sambrook et al., 2019). Using a simple classification scheme, this produced four distinct groups of fish (see Table S1). The 'coastal-estuarine fish' group were individuals of any life stage of taxa that had a reported association with coastal–estuarine areas and no reported association with coral reefs throughout their life history. The 'adult reef fish' group was fish that were visually identified as adults in RUVs that had a reported association with reef habitat during their adult phase. The 'juvenile reef specialist fish' group were fish that were visually identified as juveniles in RUVs that had a reported association with reef habitat, and that were not typically known to use non-reef habitats as either adults or juveniles. The 'juvenile multihabitat reef fish' group were fish that were visually identified as juveniles in RUVs that had a reported association with reef habitat during adult life phases, and that were known to use non-reef areas during some part of their non-planktonic life history.

Where consensus could not be reached on taxonomic identity, individuals were assigned to the level of taxonomic grouping (e.g. genus) where consensus was achieved. Where consensus could not be reached on life-history stage (i.e. juvenile or adult), a conservative approach was taken to assigning juvenile status. For this reason, the 'adult reef fish' group likely contains subadults that are no longer visually distinguishable from adults. Individuals that could not be confidently assigned to a specific group were not included in analysis.

Information for ecological and life-history categorisation of each species was gathered via FishBase (Froese & Pauly, 2017), refined using relevant species guides (Allen, 1985; Allen et al., 2012) and primary research (Newman & Williams, 1996), and further supplemented by the expertise of relevant authors.

## 2.4 | Contextual variables

A range of different variables were used to examine context dependence, namely salinity, distance to reef, tidal range, tidal state, biophysical typology, substratum and depth. Table 2 provides a detailed description of each variable, the methodology used to measure each variable and the associated hypothesis as to why each could be important in determining the use of mangrove habitat by fish (Table 2; see Supplementary Methods for Text S1 for details).

Correlations between variables and imbalances in the dataset (see Figure S1) are representative of natural variation and do not violate underlying assumptions in the machine-learning analyses employed. Results were interpreted with these imbalances in mind.

## 2.5 | Statistical analysis

### 2.5.1 | Forest classification

We used Random Forest classification, a high-accuracy machine learning technique, to determine variable importance and model the relationship between contextual variables and fish groups. Random Forest is a non-parametric statistical classifier that employs classification trees to partition data into homogeneous subgroups using predictor variables, until no further reduction in group heterogeneity can be achieved (Breiman, 2001). Random Forest grows many trees, each with a randomised subset of data and predictor variables, and then tests each tree with the observations in the respective excluded data (out-of-bag [OOB]). Aggregating the proportions of OOB predictions across the entire 'forest' of trees allows for the estimation of probability of class membership based on predictor variables without the dangers of over-fitting associated with single trees. The contribution of each variable to model accuracy (variable importance) is determined by comparing the misclassification rates when using actual and randomly permuted values for each predictor variable (Cutler et al., 2007). To visualise the relationship between predictor variables and the response variable, we used the feature contribution method (Palczewska et al., 2014), which extracts the influence of the variable of interest on the prediction for each observation from the Random Forest model.

To examine context dependence in the presence of each fish group, we built a Random Forest model for each fish group, calculating variable importance and the feature contributions of each contextual variable. Numeric variables were binned to avoid over-fitting. Using species richness data of the fish group as the response factor, Random Forests of 5000 trees were grown, weighted by the prior proportion of presence versus absence of the fish group. For each Random Forest, the OOB error rates were calculated to evaluate model fit, and variable importance was calculated using the permutation process described above. Feature contributions were calculated for each predictive variable, however, only the two most important variables were selected for

interpretation to avoid the use of variables that contribute little to model accuracy. In feature contribution plots, the influence of the predictor variable on class prediction (species richness of the fish group) was displayed for each observation, along with an average for each value of the contextual variable to aid visualisation of the relationship, from which goodness of fit was calculated (Welling et al., 2016). This provides a model of the relationship between a fish group and *Rhizophora* habitat. A strong positive contribution indicates an increased likelihood of encountering species of that fish group, and strong negative contribution indicates a reduced probability of encountering species of that fish group. A contribution close to zero indicates that the variable had little influence on prediction at that value. Collinearity among variables does not reduce prediction accuracy but must be considered in the interpretation of the resulting model. All analyses were performed using R version 3.3.3 (R Core Team, 2017). Random Forests were built using the 'randomForest' package (Liaw & Wiener, 2002), and feature contribution plots were displayed with the 'forestFloor' package (Welling et al., 2016).

### 2.5.2 | Species-specific analyses

We selected a subset of species from our dataset for individual examination of mangrove dependence. These species all feature in the scientific literature as being highly mangrove affiliated as juveniles (see below). This was done for two reasons—to understand how individual species and life stages that are thought to be mangrove affiliated responded to the variables identified as important in fish group analysis, and to explore patterns within the juvenile multihabitat reef fish group, which did not display consistent context-dependent effects in Random Forest analysis. Many of the species previously identified in the scientific literature as mangrove-affiliated fall within the juvenile multihabitat reef fish group.

The species selected for individual examination had to meet the following criteria: (1) They have been defined as mangrove affiliated as juveniles in the scientific literature. This was based on species identified in meta-analysis by Zu Ermgassen et al. (2020). (2) They must be well distributed across the geographic range that we examined (i.e. absences are not due to absence from the region). (3) They must be well represented in our dataset (>10 occurrences). Following these criteria, we identified nine species for individual examination: *Gerres filamentosus*, *Lutjanus fulviflamma*, *Lutjanus argentimaculatus*, *Lutjanus russellii*, *Monodactylus argenteus*, *Siganus fuscescens*, *Siganus lineatus*, *Terapon jarbua* and *Sphyrna barracuda*. Where possible, we distinguished between early and late juvenile phases. For some species, it is not possible to distinguish juveniles from adults in video samples, and in these cases, we examined presence of the species as a whole. We examined species' presence across two contextual variables, tidal range and distance to reef, for each species. These contextual variables

TABLE 2 Factors used in Random Forest analyses of fish group presence.

Factor	Description	Method	Unit	Hypothesis
Salinity	Salinity value of site during sampling period	Measured via conductivity or refractometry (for details, see Text S1)	Parts per thousand (ppt)	Fish may be restricted in their use of habitat based on specific salinity tolerances or preferences (Harrison & Whitfield, 2006; Whitfield et al., 2006).
Distance to reef	Shortest path between video sample and the closest patch of reef	GPS position and satellite imagery (for details, see Text S1)	Log metres	The use of mangroves by reef fish may depend on their ability to access reef habitats, either daily or within their life cycle, and this may be constrained by distance (Dorenbosch et al., 2007; Jones et al., 2010; Pittman et al., 2007).
Tidal range	The location's maximum tidal range	Values were derived from tidal gauge data and predictions (see Text S1)	Log metres	Differences in tidal regime are likely to have a substantial impact on the relationship fish have with mangrove forests. Tidal range determines frequency and inundation of the forest, and the amount of hydrological energy experienced in the forest (Baker et al., 2015), which may lead to different habitat use strategies (Igulu et al., 2014; Sheaves, 2005).
Tidal direction	Categorisation of tidal state at the time of sampling: ebb, flood, slack high and slack low	Values were derived from tidal gauge data and predictions (see Text S1)	Categorical	Use of the mangal forest by fish is likely to be responsive to tidal state, with spatial and temporal strategies corresponding to different tidal states (Sheaves, 2005).
Biophysical typology	Setting of the sampling location combining sedimentary (terrigenous or carbonate) and geomorphic (open coast or estuarine) characteristics	GPS position and satellite imagery	Categorical	Geomorphic setting determines important ecosystem functions, influencing the range of goods and services associated with mangrove forests (Ewel et al., 1998). Here, we use the biophysical typology presented in Worthington et al. (2020). These categories also likely broadly correlate with a range of other landscape factors, including composition and configuration of the local seascape, known to determine patch use by fish (Boström et al., 2011).
Substratum	Categorisation of substratum using four categories: coral rubble, rock, sand and mud	Visual assessment	Categorical	Differences in substratum can influence the quality and quantity of invertebrate prey in the forest (Hsieh, 1995), and therefore may affect the feeding potential of mangroves.
Depth	Vertical distance from the water surface to the bottom of the camera base at the time of sampling	Acoustic depth sounder or taut rope length during camera retrieval	Metres	Water depth can restrict access to mangrove habitat based on fish body depth or behaviour. This could determine both the presence of individuals themselves, and by excluding their predators at shallow depths, determines the refuge value of mangrove habitat (Ellis & Bell, 2004). This variable provides a measure of forest inundation independent of tidal state.

were chosen based on their importance in Random Forest analysis of fish groups. Two-dimensional contextual spaces were constructed based on these two variables and the distribution of sampling effort across these variables. Species and life-stage presence were then plotted across this space, using the 'ggplot2' package (Wickham, 2016) in R.

### 3 | RESULTS

#### 3.1 | Overall

We observed 209 fish species across our 494 mangrove RUV samples. Using contextual variables, we were successfully able to model the occurrence and species richness of three different fish groups in tropical mangroves—juvenile reef specialist fish, adult reef fish and coastal–estuarine fish—but not juvenile multihabitat reef fish. Across these three groups, Random Forest models explained 38%, 49% and 44% of the variability in species richness respectively.

#### 3.2 | Juvenile reef specialist fish

Tidal range was the single most important variable determining the species richness of juvenile reef specialist fish (Figure 2a). Locations with low tidal ranges of  $\leq 1$  m amplitude were more likely to have higher species richness, and this group was likely to be either species poor or absent altogether at tidal ranges above this (Figure 2b). Distance to reef was also important, with this group likely to be absent in locations greater than 100 m away from reefs (Figure 2c).

#### 3.3 | Juvenile multihabitat reef fish

The Random Forest model produced for this group had low explanatory power (<18%) and is not presented, given the lack of ecological interpretability. This group comprises species with diverse habitat-use strategies, with potentially conflicting responses to contextual variables. In the 'species analyses' section, we examine some widely distributed species that have been identified in previous studies as 'mangrove-affiliated' as juveniles.

#### 3.4 | Adult reef fish

The most important variable determining the species richness of adult reef fish in mangrove forests was substrate type (Figure 3a). Coral rubble substrate increased the probability of mangroves containing a high species richness, whereas in mangroves with mud and sand substrates, species in this group were more likely to be absent (Figure 3b). Perhaps unsurprisingly given their affinity with reef systems, distance to reef was also an important driver, with this group likely to be absent in locations greater than 100 m away from reef areas (Figure 3c).

#### 3.5 | Coastal–estuarine fish

The most important variable in determining the species richness of coastal–estuarine fish in mangrove forests was distance to reef (Figure 4a). Unlike our reef fish-associated groups, this group was likely to be absent at locations close to reefs (<300 m). The further away from reefs, the more variable the results (Figure 4b). Water depth was also of high importance to this group (Figure 4c), with species likely to be present in shallow water (<50 cm) and rare or absent in deeper water (>150 cm). Modelling suggested that salinity was also a dominant driver of species richness in this group, with these species more consistently present in reduced salinities.

#### 3.6 | Species-specific analyses

For species identified as 'mangrove affiliated' as juveniles, the environmental context under which they are found in mangroves varied on a species-by-species basis.

#### 3.7 | Lutjanidae

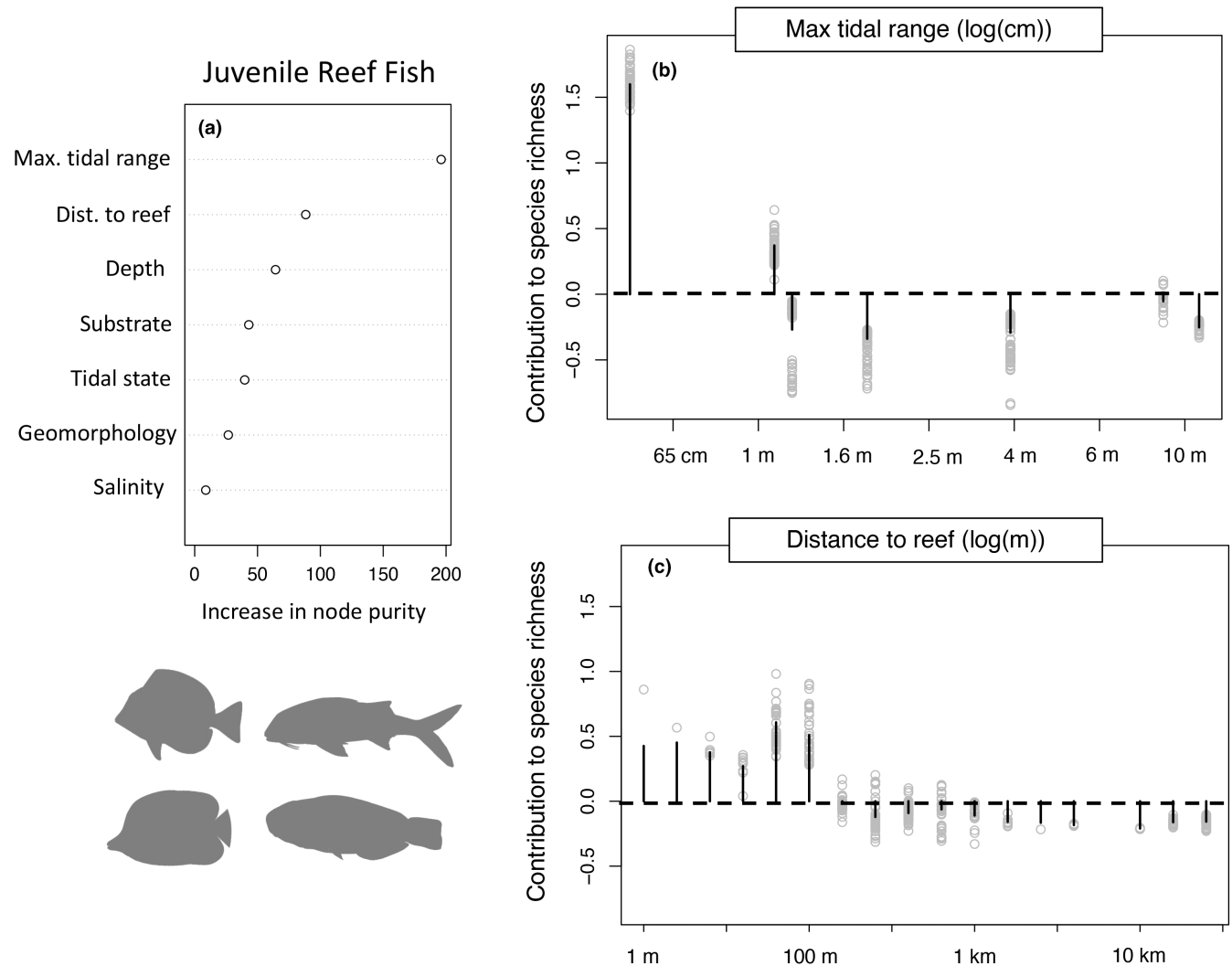
Juvenile snappers (*Lutjanus*) from the multihabitat reef fish group displayed different levels of environmental context dependence. *Lutjanus fulvus* and *Lutjanus fulviflamma* (Figure 5) were present in mangroves only at lower tidal range locations (micro to meso), usually close to reefs. Furthermore, the occurrence of *Lutjanus fulvus* early juveniles in mangroves was restricted to micro-tidal locations. While both these species are reportedly mangrove associated as juveniles, they are conspicuously absent from mangroves in macrotidal contexts. *Lutjanus argentimaculatus* (Figure 5) occurred in mangroves across different tidal ranges, but importantly, occurrences of early juveniles in mangroves were restricted to micro-tidal locations. *Lutjanus russellii* (Figure 5) juveniles were present in mangroves across different tidal ranges (in regions where they are known to occur).

#### 3.8 | Siganidae

Juvenile *Siganus fuscescens* (Figure 6), reportedly mangrove associated, was usually found only in mangroves from micro-tidal locations. *Siganus lineatus* (Figure 6) was present across the spread of variability in tidal range and distance to reef where it is distributed. Note that neither species is distributed in French Polynesia.

#### 3.9 | Other mangrove-affiliated species

*Gerres filamentosus* (Figure 7) was only found in mangroves some distance from reefs, and occurred across the spread of variability in tidal range where it is distributed. *Monodactylus argenteus* (Figure 7) occurred across the spread of variability in tidal range and distance



**FIGURE 2** Random Forest prediction model of juvenile reef specialist fish species richness in mangrove habitat, which explains 38.18% of variability. Variable importance, measured as the mean decrease in model accuracy when a variable is removed from the model (a), and feature contribution plots for (b) maximum tidal range and (c) distance to reef. In feature contribution plots, grey points show the influence of the contextual variable on class prediction for each observation and the length of black bars represent means, indicating the magnitude of positive or negative contribution for each value of the feature variables.

to reef where it is distributed. *Sphyræna barracuda* (Figure 7) only occurred in mangroves in larger tidal ranges, despite being distributed throughout all study locations. Despite being widely distributed, *Terapon jarbua* (Figure 7) only occurred in mangroves in micro-tidal locations (it is not distributed in French Polynesia).

## 4 | DISCUSSION

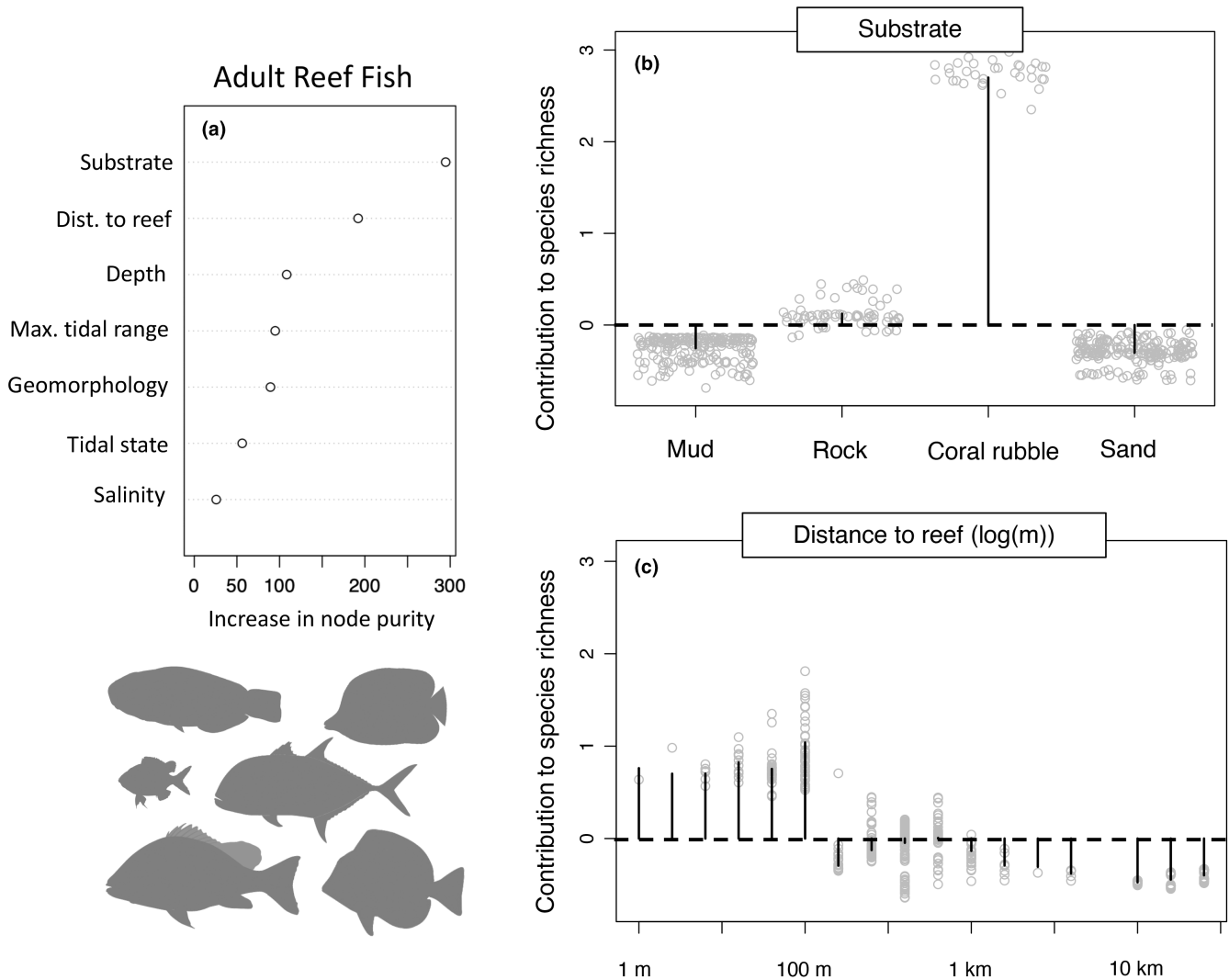
The use of mangroves by fish clearly differs among species and life-history stages, but even within these groups, we show that patterns of habitat use differ among locations. These findings preclude global generalisations of the function of mangroves, as key fish groups were found to use mangroves only under specific conditions. Environmental context was an important predictor of the presence and species richness of fish groups, and the presence of a range of purportedly mangrove-affiliated species was restricted to particular

locations that shared similar environmental conditions. The predictability of mangrove use by fish has two major implications. First, mangroves in similar contexts may share similarities in function, regardless of regional differences in species pools (Bradley et al., 2021; Hemingson & Bellwood, 2018). Therefore, a unified understanding of mangrove habitat function may be possible for certain environmental conditions. Second, it implies that broad differences in environmental context between regions may result in broad differences in habitat function. The role of mangroves as fish habitat is therefore expected to vary according to environmental context.

### 4.1 | Tidal range

Tidal range appears to be a crucial determinant of the presence of juvenile reef fish in general and a range of putatively mangrove associated species. Over half of the species classed as 'mangrove affiliated'

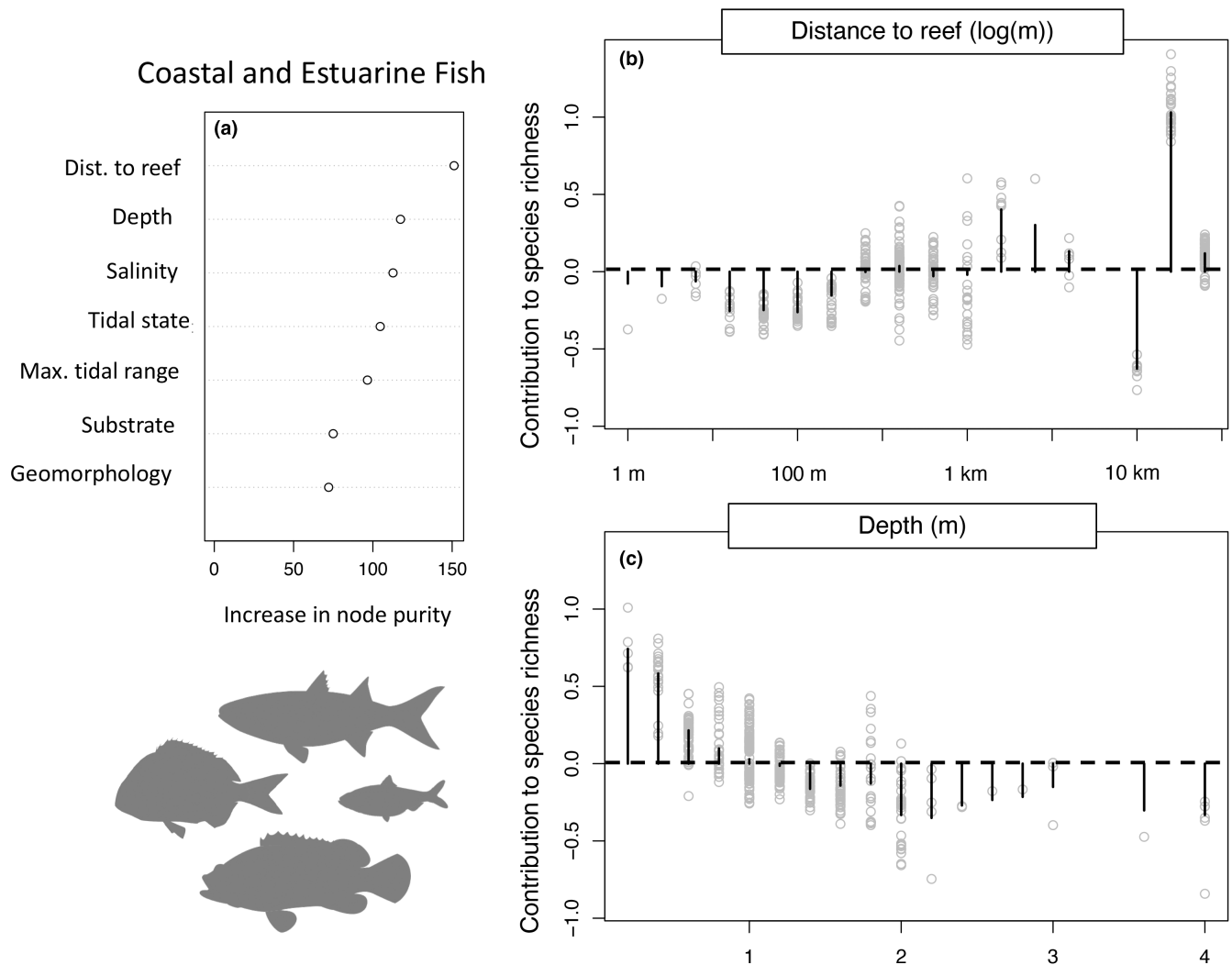




**FIGURE 3** Random Forest prediction model of adult reef fish species richness in mangrove habitat, which explains 48.55% of variability. Variable importance, measured as the mean decrease in model accuracy when a variable is removed from the model (a), and feature contribution plots for (b) maximum tidal range and (c) distance to reef. In feature contribution plots, grey points show the influence of the contextual variable on class prediction for each observation, and the length of black bars represent means, indicating the magnitude of positive or negative contribution for each value of the feature variables.

(six of the nine species) were no longer associated with mangroves in macrotidal areas. A negative association with tidal range was also responsible for a large proportion of the predictive power in the models for reef fish juveniles. These fish were predictably absent in large tidal range contexts. This is consistent with the results of a global meta-analysis (Igulu et al., 2014) that found a lower tendency for reef fish juveniles to use mangroves in areas with a macro-tidal range. This will have consequences throughout the tropical Indo-Pacific, where tidal range varies widely (Figure 8). For many fish, the magnitude of tidal movement may determine the use of mangroves by altering the balance between the benefits of inhabiting mangroves, and the challenges of undertaking intertidal migrations. Tidal range determines the availability of, and access to mangrove forests in a number of ways, and this has a range of consequences for fish (Sheaves, 2005). First, it determines the duration that mangroves are inundated and available to fish (Baker et al., 2015) and the proportion of time fish

must necessarily spend outside the forest. Second, it determines the depth of water in the mangroves and the duration of flooding (Baker et al., 2015) and consequently, it will determine the duration of any refuge value obtained by utilising mangrove habitat (Paterson & Whitfield, 2000; Rypel et al., 2007). Third, tidal range will determine the magnitude of water movement through the forest. While mangrove structure provides refuge from tidal currents and wave energy (Brinkman et al., 1997; Mazda et al., 1997), with large enough tidal range, the hydrological forces experienced in the forest may eliminate any hydro-dynamic advantages of inhabiting mangroves relative to other habitats and may restrict the use of these areas to fish with higher swimming ability (Fulton et al., 2001). Finally, tidal amplitude is known to regulate levels of dissolved oxygen and the duration of anoxic conditions inside mangrove forests, with larger tides resulting in larger fluctuations in oxygen, which may restrict the use of these habitats to fish with the ability to tolerate low oxygen levels



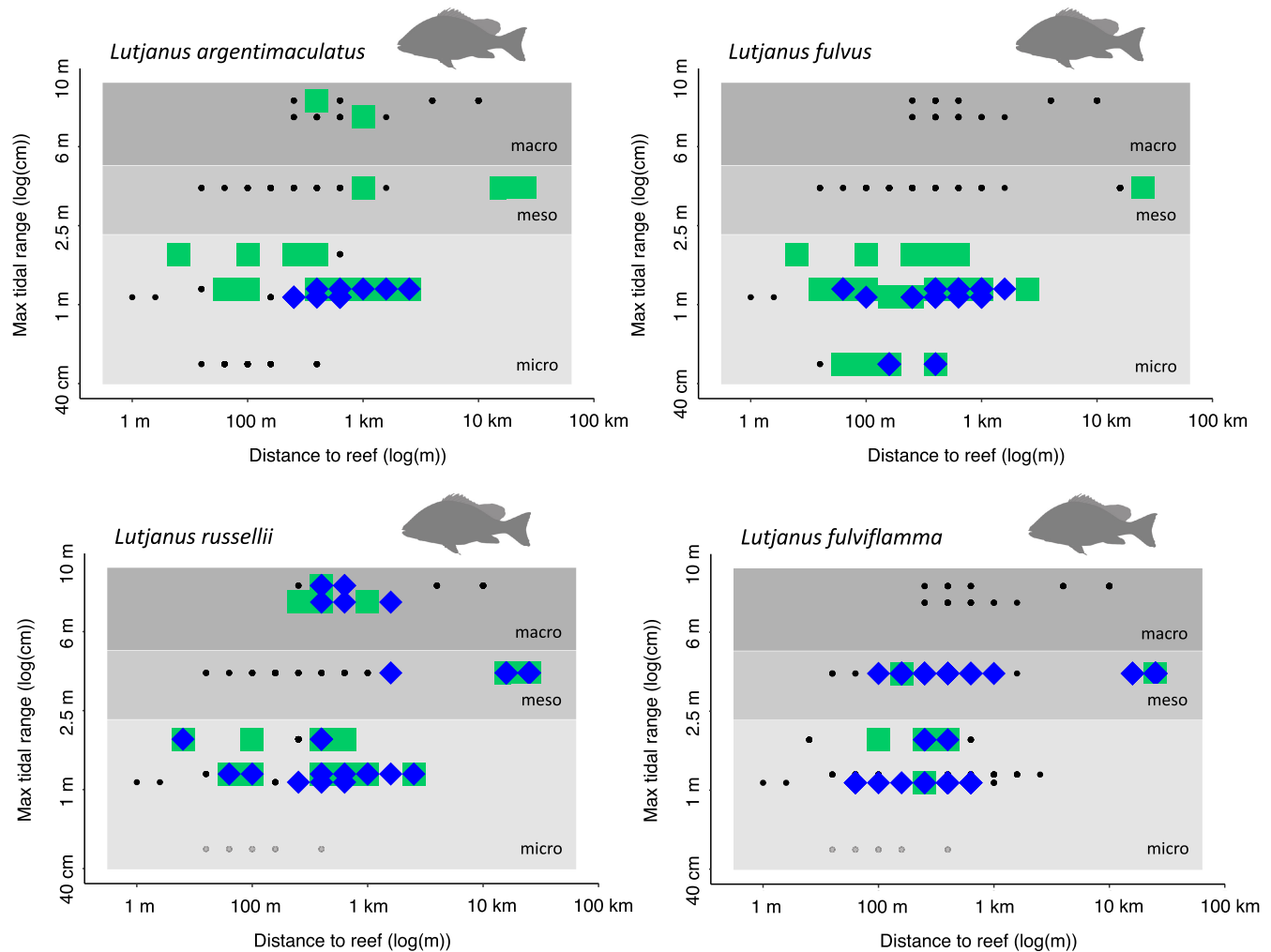
**FIGURE 4** Random Forest prediction model of coastal-estuarine fish species richness in mangrove habitat, which explains 43.49% of variability. Variable importance, measured as the mean decrease in model accuracy when a variable is removed from the model (a), and feature contribution plots for (b) maximum tidal range and (c) distance to reef. In feature contribution plots, grey points show the influence of the contextual variable on class prediction for each observation, and the length of black bars represent means, indicating the magnitude of positive or negative contribution for each value of the feature variables.

(Dubuc et al., 2021; Mattone & Sheaves, 2017). With increasing tidal range, the function of mangrove forests as habitat for particular fish is likely to fluctuate rapidly over small temporal scales (Dubuc, Baker, et al., 2019; Kroeker et al., 2020). For fish that inhabit reefs, the value of using mangroves with large tidal ranges may be relatively low and may come with greater risk of predation. Conversely, in micro-tidal contexts, mangroves appear to provide a relatively stable, permanently submerged complex habitat that can be utilised by juvenile reef fish when proximal to reefs, without the challenges associated with more significant tidal forces.

## 4.2 | Distance to reef

The distance between mangroves and coral reefs was important for all fish groups considered in our study, but responses differed

among these groups. For reef fish, being close to reefs was a key predictor of their presence in mangroves. Coastal-estuarine fish, on the other hand, were negatively associated with distance to reef, typically using mangroves that were over a minimum threshold distance from reefs (>150m). These patterns are probably due to few fish exclusively using mangrove habitats over tidal, diel or ontogenetic cycles (Sheaves, 2009). Therefore, the use of mangroves is likely to depend on proximity to other habitats that fish require at spatial scales relevant to their daily or ontogenetic movements (Nagelkerken et al., 2015). In the case of reef fish, their use of mangroves clearly depends on proximity to reefs, either directly through their requirements for reef habitat (Unsworth et al., 2008) or their general proximity to reef-flat or lagoonal habitats, which over the scales sampled in this study, would co-vary with proximity to reef. This might include appropriate settlement habitats such as coral rubble (Dahlgren & Eggleston, 2000) or subtidal seagrass or



**FIGURE 5** Distribution of four reportedly mangrove-affiliated lutjanids according to tidal range and distance to reef. Black points represent the binned distribution of total mangrove sampling effort across contextual space ( $n=494$ ) and show where species were not present. Grey points show samples from locations where the species is not distributed. Blue diamonds indicate the presence of early juvenile stages, and green squares indicate the presence of late juvenile stages. Where X-axes are in log scale, increasing units of measurement are displayed for ease of interpretation.

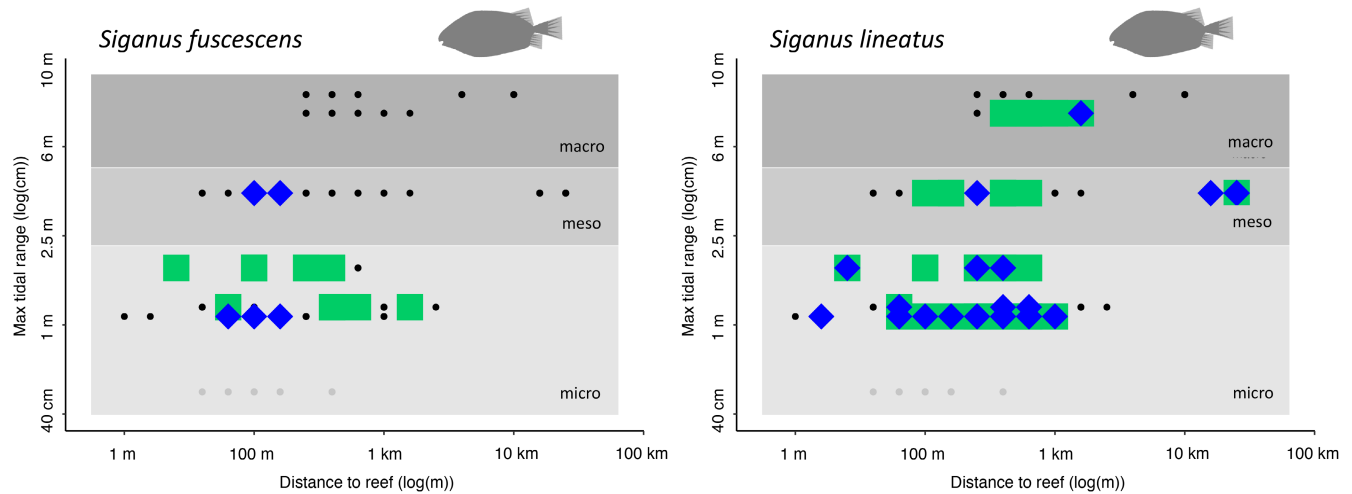
macroalgae (Dorenbosch et al., 2007; Fulton et al., 2020) that may be related to their use of lagoonal nurseries as a whole (Bradley et al., 2019). On the other hand, coastal-estuarine fish might require access to habitats such as coastal rocky headlands or estuarine seagrass (Bradley et al., 2017; Gilby et al., 2018) that may be far from coral reefs.

### 4.3 | Contextual thresholds in the ecological role of mangroves

Our findings define contextual boundaries within which ecological functions are likely to occur. In the following sections, we use the values found in this study to provide a guide for fish-associated ecological roles performed by mangroves (visually summarised in Figure 9). There will necessarily be exceptions to these predictions, and any serious violations of these predictions will help focus our search for predictable patterns and underlying mechanisms.

### 4.4 | Reef fish community enhancement

Mangrove habitat appears to support coral reef fish communities in some contexts, but not others. Mangroves close to reefs in locations where they are almost continuously submerged (e.g. less than 1.5m maximum amplitude) appear to be the most optimal configuration to support a diversity of juvenile reef fish. However, in larger tidal range settings, mangroves were less likely to be used by juvenile reef fishes, including purportedly mangrove-associated reef fish juveniles which use coastal areas. While some adult reef fish were found in mangroves directly adjacent to coral reef habitat (as in Barnes et al., 2012), their use of mangroves overall was limited. These findings have important implications for the link between mangroves and coral reefs. Paradigms about the role of mangroves as nursery grounds for coral reef fishes, which were developed and tested in the reef fringing mangroves of micro-tidal Caribbean and North America (Adams et al., 2006), ring true in this study in similar contexts in the Indo-Pacific (Bismarck Archipelago and The Society Islands), but not



**FIGURE 6** Distribution of two reportedly mangrove-affiliated siganids according to tidal range and distance to reef. Black points represent the binned distribution of total mangrove sampling effort across contextual space ( $n=494$ ) and show where the species was not present. Grey points show samples from locations where the species is not distributed. Blue diamonds indicate the presence of early juvenile stages, and green squares indicate the presence of late juvenile stages. Where X-axes are in log scale, increasing units of measurement are displayed for ease of interpretation.

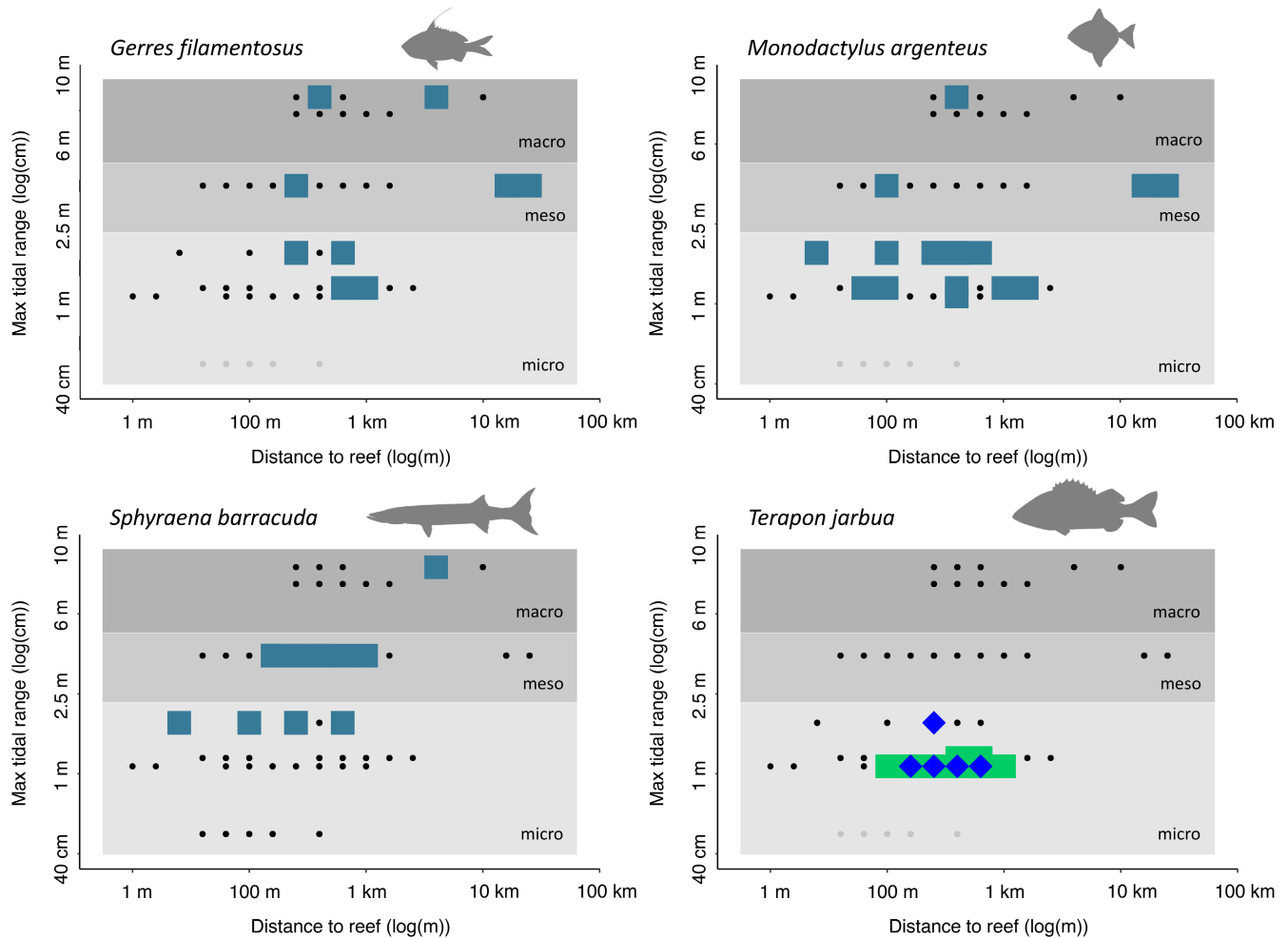
in other contexts in the same biogeographic realm. This complicates fundamental ideas around the ecosystem supporting services of mangroves. In meso and macro-tidal settings, links with other parts of the seascape may be much more important for reef fish, including supposedly mangrove-dependent species (e.g. Sievers, Abesamis, et al., 2020; Sievers, McClure, et al., 2020).

Because the use of mangroves by reef fish depends on environmental conditions, reef-related ecosystem service values attributed to mangroves (Himes-Cornell et al., 2018; Liqueste et al., 2016), including supporting, regulating and provisioning services related to reef fish and their fisheries, will necessarily vary according to environmental context. Where mangroves occur as part of reef seascapes in regions with limited tidal movement ( $<1.5$  m maximum amplitude), they appear to invariably serve as a juvenile habitat and potentially provide a nursery function for reef fish (sensu Adams et al., 2006; Igulu et al., 2014). In the Indo-Pacific, this includes restricted parts of Australia, Papua New Guinea, Solomon Islands, French Polynesia and Indonesia, and beyond our study region boundaries, also includes parts of India, Sri Lanka and Madagascar (Figure 8). This accords with previous studies from these specific locations (e.g. Solomon Islands: Hamilton et al., 2017). With increasing tidal range, mangroves can be used by reef fish, but tend to be less widely integrated into reef ecosystems. In regions with larger tidal ranges, it is likely that mangroves serve as an important habitat in the juvenile phase of some coastal-associated reef fish, but unlikely that mangrove habitat broadly supports a wide variety of reef fish juveniles. Here, the way that reef fauna are able to use the mosaic of habitat features along the coast is constrained by their exclusion from mangroves at low tide (Krumme, 2009). This includes most of northern Australia, parts of Papua New Guinea, most of Southeast Asia and beyond our study region boundaries, parts of India and Madagascar. This accords with previous studies from these locations (e.g. Bradley et al., 2019; Sievers, Abesamis, et al., 2020; Sievers, McClure, et al., 2020).

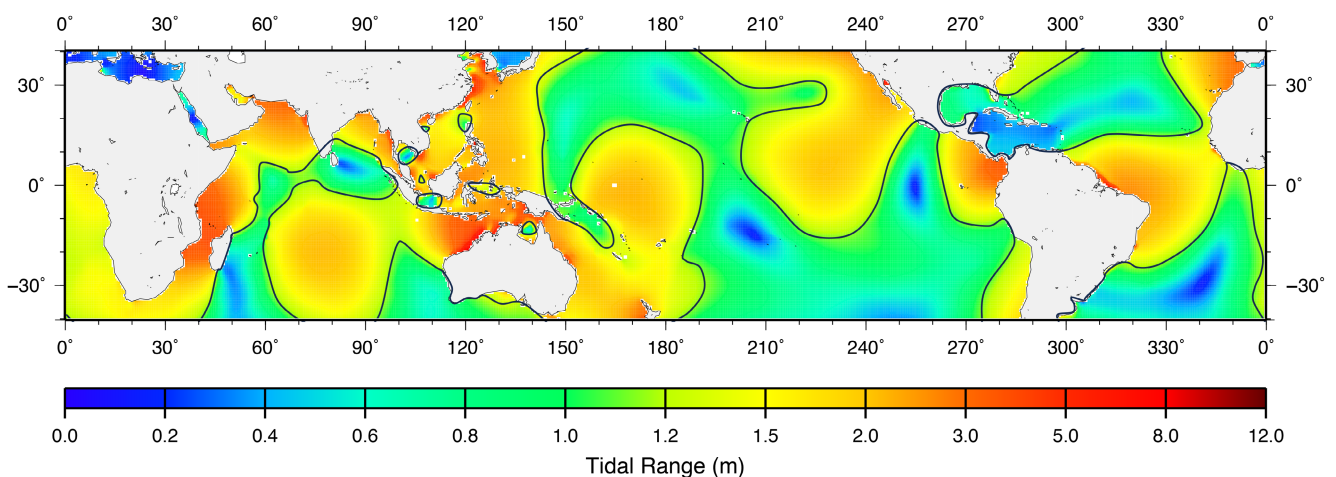
Where are mangroves typically not habitat for reef fish? In macro-tidal regions far from reefs (e.g.  $>3$  km), we predict reef fish to be largely absent from mangroves. This includes large parts of northern Australia and southern Papua New Guinea and Indonesia, as well as parts of Southeast Asia. Even in micro-tidal regions with strong mangrove-reef linkages, reef fish enhancement by mangrove presence appears to quickly disappear at distances larger than a few kilometres (Huijbers et al., 2013; Nagelkerken et al., 2017). There are, however, some species that are known to make extensive large-scale ontogenetic migrations, such as *Lutjanus argentimaculatus* (Russell & McDougall, 2005), and these would be present in mangroves far away from coral reefs. In mangroves rarely used as reef fish habitat, ecosystem support could still be occurring through pathways not examined in this study, for example nutrient or carbon delivery, trophic support or nocturnal use of the forest.

#### 4.5 | Coastal and estuary fish community enhancement

Mangrove habitat appears to provide important habitat for coastal and estuary fish across tidal ranges and regions, with certain conditions strongly influencing their use. Coastal and estuary fish were rarely encountered in mangroves that were part of coral reef seascapes. This is to be expected based on wider ecosystem associations that these species may have with coastal and estuarine habitats not present in coral reef seascapes (Sheaves et al., 2015). Interestingly, mangrove habitat was much more likely to be used by coastal and estuary species when shallow (Dubuc, Waltham, et al., 2019). This implies that water depth has important consequences for the use of mangroves by fish. This supports the idea that fish in these environments specifically utilise shallow water (Paterson & Whitfield, 2000; Rypel et al., 2007), and may follow the shallow water edge as it moves through the forest. This means



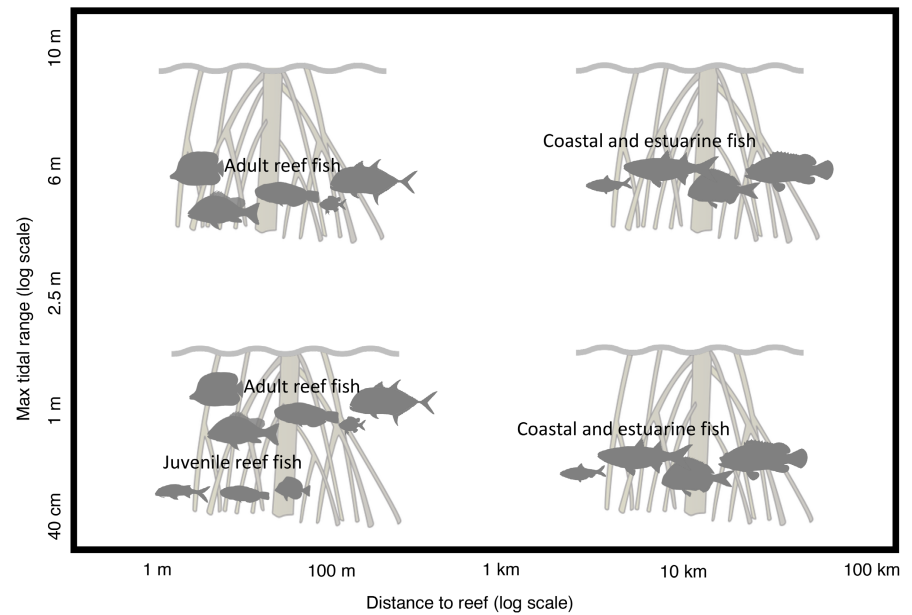
**FIGURE 7** Distribution of mangrove-affiliated species according to tidal range and distance to reef. Black points represent the binned distribution of total sampling effort across contextual space ( $n=494$ ) and show where the species was not present. Grey points show samples from locations where the species is not distributed. In the top left, top right and bottom left panels, blue squares indicate the presence of the species (any life stage). In the bottom right panel, blue diamonds indicate the presence of early juvenile stages and green squares indicate the presence of late juvenile stages. Where X-axes are in log scale, increasing units of measurement are displayed for ease of interpretation.



**FIGURE 8** Variation in tidal range across the tropics and subtropics, with colours in the ocean showing magnitude of tidal range. Black curved line shows the approximate boundary between  $<1.5$  and  $>1.5$  m tidal range identified in this study as important in determining the use of mangroves by fish. Tidal output was reproduced with permission from the National Tidal Centre, Australian Bureau of Meteorology.



**FIGURE 9** Conceptual figure showing the fish groups identified in this study as most likely to be using mangroves as habitat across four quadrants of environmental space based on two contextual variables that were important across different fish groups in our study.



that the value of mangrove habitat is not fixed, but varies according to inundation regimes (Baker et al., 2015). There were important regional differences in the use of mangroves by purportedly mangrove associated species. *Terapon jarbua* was common in micro-tidal regions but conspicuously absent from macro-tidal locations. Clearly, there are important contextual limits on the use of mangroves by certain species. Overall, the use of mangroves by coastal and estuary fish did not appear to shift substantially between regions. Anywhere outside of reef seascapes, we can predict that mangrove habitat can be used by coastal-estuarine fish communities. Here, mangroves appear to provide important habitat for this group, where it may provide important feeding and refuge functions (Blaber, 2008; Nagelkerken et al., 2008). However, the fish community that uses the habitat, including the Gobiiform fishes not examined in this study, and the way that habitat value is generated and delivered, is likely to vary. Because of this complexity, simple value calculations developed in one region and applied broadly, such as fish biomass output per unit area, are likely to be inaccurate.

#### 4.6 | Wider implications

Our study suggests that the ecological roles played by certain habitat or vegetation types can be highly context dependent. Academics and practitioners must recognise that ecological roles may be enabled or constrained by conditions at scales beyond the scope of normal investigation (Andersson et al., 2015; Birkhofer et al., 2015), and that critical ecological relationships may not respond to typical indicators of habitat condition or integrity (Liquete et al., 2016). We hope our work can serve as a blueprint for defining context dependence in the ecological roles of other habitats. Efforts to quantify environmental variation in the ecological role of habitats, such as our work, can be combined with recent technical advances in

mapping environmental variation in key habitats (e.g. Worthington et al., 2020) to produce powerful new tools for guiding research, management and intervention.

#### AUTHOR CONTRIBUTIONS

MB, AD, CP, KS, AH, MD, TL, MG, SW, KC, TH, GM, MT, RB, IN and MS contributed to the ideas, design and manuscript. MB led field sampling in NEA, NWA, PNG and FP. AD led field sampling in NC and NEA. CP led field sampling in NWA. KS led field sampling in PNG. MB, AD, CP, KS and KC performed the video analysis. MB performed the statistical analysis. MB led the writing of the manuscript.

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#### CONFLICT OF INTEREST STATEMENT

The authors wish to declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

The dataset used in this study is available at Research Data JCU: <https://doi.org/10.25903/spkx-3m03>.

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