RESEARCH ARTICLE

Low redundancy and complementarity shape ecosystem functioning in a low-diversity ecosystem

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Abstract

1. Ecosystem functioning is positively linked to biodiversity on land and in the sea. In high-diversity systems (e.g. coral reefs), species coexist by sharing resources and providing similar functions at different temporal or spatial scales. How species combine to deliver the ecological function they provide is pivotal for maintaining the structure, functioning and resilience of some ecosystems, but the significance of this is rarely examined in low-diversity systems such as estuaries.

2. We tested whether an ecological function is shaped by biodiversity in a low-diversity ecosystem by measuring the consumption of carrion by estuarine scavengers. Carrion (e.g. decaying animal flesh) is opportunistically fed on by a large number of species across numerous ecosystems. Estuaries were chosen as the model system because carrion consumption is a pivotal ecological function in coastal seascapes, and estuaries are thought to support diverse scavenger assemblages, which are modified by changes in water quality and the urbanization of estuarine shorelines.

3. We used baited underwater video arrays to record scavengers and measure the rate at which carrion was consumed by fish in 39 estuaries across 1,000 km of coastline in eastern Australia.

4. Carrion consumption was positively correlated with the abundance of only one species, yellowfin bream *Acanthopagrus australis*, which consumed 58% of all deployed carrion. The consumption of carrion by yellowfin bream was greatest in urban estuaries with moderately hardened shorelines (20%–60%) and relatively large subtidal rock bars (>0.1 km^2).

5. Our findings demonstrate that an ecological function can be maintained across estuarine seascapes despite both limited redundancy (i.e. dominated by one species) and complementarity (i.e. there is no spatial context where the function is delivered significantly when yellowfin bream are not present) in the functional traits of animal assemblages. The continued functioning of estuaries, and other low-diversity ecosystems, might therefore not be tightly linked to biodiversity, and we suggest that the preservation of functionally dominant species that maintain functions in these systems could help to improve conservation outcomes for coastal seascapes.

1 | INTRODUCTION

Animals perform a range of important ecological functions (e.g. herbivory, predation, scavenging), which shape the condition of their habitats, structure food webs and underpin the capacity of ecosystems to resist, or recover from, disturbance (Estes et al., 2011; Poore et al., 2012). It is widely accepted that ecological functions are tightly linked to biodiversity (i.e. variation in species, their physical traits and genes), and positive correlations between animal diversity and the delivery of an ecological function have been reported in terrestrial, freshwater and marine ecosystems, particularly in high-diversity systems such as tropical rainforests or coral reefs (Hooper et al., 2005; but see Gamfeldt & Roger, 2017). Human actions have, however, modified landscapes globally, which can cause significant and widespread shifts in species composition, and declines in biodiversity and the delivery of particular ecological functions (Chapin III et al., 2000; Grimm, Faeth, et al., 2008; Halpern et al., 2008; Lohbeck, Bongers, Martinez-Ramos, & Poorter, 2016). Maintaining critical ecological functions is, therefore, an important goal for most conservation and restoration initiatives, but it is not always clear which species perform key functions, and how changes in animal diversity or the abundance of key species correlates with ecological functions in some systems (Lindgren et al., 2016; Srivastava & Vellend, 2005; Wohl, Arora, & Gladstone, 2004).

Biodiversity can positively influence the delivery of an ecological function because multiple species often compete to use the same resources, and different taxa also vary in terms of their sensitivity to disturbance (e.g. physiological tolerances, habitat requirements, level of harvesting pressure; Cardinale et al., 2012; Loreau & de Mazancourt, 2013). In ecosystems with high diversity (e.g. coral reefs or tropical rainforests), multiple species can coexist by using the same resources and performing an identical ecological function (i.e. high functional redundancy), or by using different resources and providing distinct functions (i.e. limited functional redundancy; Bellwood, Hoey, & Choat, 2003; Loreau, 2004; Mori, Furukawa, & Sasaki, 2013). Species that access similar resources might use these in different contexts, and can therefore perform a similar ecological function at distinct times or locations (i.e. high functional complementarity; Brown et al., 2015; Cardinale et al., 2012; Loreau & de Mazancourt, 2013). Thus, functional redundancy and complementarity are important components of animal assemblages, which help to maintain the structure, functioning and resilience of ecosystems to environmental change (Cardinale et al., 2012; Duffy et al., 2015). Well-known examples that illustrate the functional effects of these trophic attributes include the overlapping niches of herbivorous fishes on coral reefs (Brandl & Bellwood, 2014), mammalian predators in terrestrial forests (Ripple et al., 2014) and avian scavengers on ocean beaches (Huijbers et al., 2016), which promote diversity and help to sustain an important ecological function within highly modified landscapes (Elmqvist et al., 2003; Mori et al., 2013). Different ecological functions represent important aspects of a food web and the wider context of an ecosystem and the functions within are needed to fully understand redundancy or complementarity within an ecosystem (de Jonge, Schückel, & Baird, 2019). Redundancy and complementarity might, however, be sensitive to impacts from some human actions, including overharvesting, eutrophication and urbanization, particularly when these stressors result in the loss of multiple species that contribute to maintaining an important ecological function (Grimm, Foster, et al., 2008; Pauly, Christensen, Dalsgaard, Froese, & Torres, 1998). Similar responses in redundancy and complementarity would be expected to be seen in heavily modified landscapes (e.g. city parks or modified estuaries), where previously natural habitats have been replaced with shoreline armouring or artificial structures (Dafforn et al., 2015; Olds, Frohloff, et al., 2018a). These impacts of human change may therefore limit redundancy or complementarity within food webs and therefore, alter how a function is delivered or maintained within an ecosystem (Lohbeck et al., 2016; Lowenstein, Matteson, & Minor, 2015).

High functional redundancy and complementarity might be particularly common in the oceans, where omnivory is pervasive (Bascompte, Melián, & Sala, 2005; Stachowicz, Bruno, & Duffy, 2007; Thompson, Hemberg, Starzomski, & Shurin, 2007), and most species migrate (i.e. tidally, diurnally, ontogenetically) across seascapes to access resources in different habitats (Gillanders, Able, Brown, Eggleston, & Sheridan, 2003; Nagelkerken, 2009; Olds, Nagelkerken, et al., 2018b). Changes in redundancy or complementarity within faunal assemblages may also change across latitudinal gradients, where increased biodiversity closer to the tropics may result in higher levels of functional redundancy or complementarity in these systems (Willig, Kaufman, & Stevens, 2003). Pervasive omnivory and increases in biodiversity may result in a high likelihood of overlapping functional niche space (i.e. redundancy), and extensive temporal and/or spatial partitioning of resource pools (i.e. complementarity; Duffy et al., 2015; Micheli & Halpern, 2005). It has, however, also been suggested that low redundancy and high complementarity can characterize animal assemblages and ecological functions on coral reefs (Brandl & Bellwood, 2014; D'agata et al., 2016), in kelp forests (Ling, Johnson, Frusher, & Ridgway, 2009; Micheli & Halpern, 2005) and over seagrass meadows (Duffy et al., 2015; Reynolds et al., 2018), where herbivory and piscivory are frequently performed by a small suite of species (Bellwood et al., 2003; Duffy et al., 2015; Martin et al., 2018). New research suggests that low redundancy and high complementarity might also be features of animal assemblages in estuaries, coastal bays and on ocean beaches (Bingham et al., 2018; Gilby, Tibbetts, & Stevens, 2017;

Olds, Frohloff, et al., 2018a). It is not clear, however, whether these are prominent, and widespread attributes of coastal food webs, or how functional niche space changes in response to habitat transformation, heavy harvesting pressure or pollution.

We tested for the relationship between biodiversity and the ecosystem function of carrion consumption (e.g. the consumption of dead necromass prior to it becoming unpalatable, sensu Porter & Scanes, 2015) in a low-diversity ecosystem by measuring how carrion consumption by fish varies in estuaries. We chose scavenging as the ecological function of interest, because the consumption of carrion is performed by a wide variety of scavengers, therefore likely being linked to variations in biodiversity that occur across gradients of anthropogenic change or latitude (Barton, Cunningham, Lindenmayer, & Manning, 2013; Nowlin, Vanni, & Yang, 2008). Carrion is a highly nutritious food resource, which is readily consumed by a range of species from a number of trophic levels, most of which are highly adaptive to changes in resource availability (Beasley, Olson, & DeVault, 2012; Wilson & Wolkovich, 2011). While there are few obligate scavengers in estuaries, many species will scavenge opportunistically (Olds, Frohloff, et al., 2018a; Porter & Scanes, 2015). Scavenger assemblages might, therefore, be characterized by high functional complementarity (Brown et al., 2015; Huijbers et al., 2015). Relative to their low diversity, estuaries would be expected to support diverse scavenger assemblages because a large proportion of the assemblage consume carrion opportunistically (e.g. they also perform other functions, from herbivory to predation) due to the regular supply of animal carcasses, which wash-in with run-off from the land (Elliott et al., 2007; Hyndes et al., 2014; Porter & Scanes, 2015). Fish are key scavengers in estuaries, and the rate at which they consume carrion has been linked to changes in water quality, fishing pressure and the modification and urbanization of estuarine shorelines (Olds, Frohloff, et al., 2018a; Porter & Scanes, 2015; Webley, 2008). However, despite the diversity of potential scavengers in estuaries, it appears that carrion consumption could be dominated by a relatively small pool of omnivorous fish species (Olds, Frohloff, et al., 2018a). We measured the rate at which carrion was consumed by fish in estuaries across 1,000 km of coastline in eastern Australia (Figure 1). Our aim was to test how scavenger assemblages, and the function of carrion consumption, change among natural and urban seascapes, latitudinal and species diversity gradients. We extended on work completed in Olds, Frohloff, et al. (2018a), where urbanization was found to supplement carrion consumption in estuaries and there appeared to be complementarity among the species that performed the function. We chose to extend this work into estuaries that (a) had a greater area of natural habitats and reduced urban influence (Henderson et al., 2019a) and (b) were located in more tropical locations, where we expected there to be a greater diversity of scavengers (Willig et al., 2003). Estuaries in this region encompass gradients in both the area of natural fish habitats, the extent of shoreline transformation and armouring, and occur across a large latitudinal gradient, thus allowing for a further test of these effects (Gilby, Olds, Connolly, et al., 2017; Martin et al., 2018; Meynecke, Poole, Werry, & Lee, 2008; Waltham & Connolly, 2011).
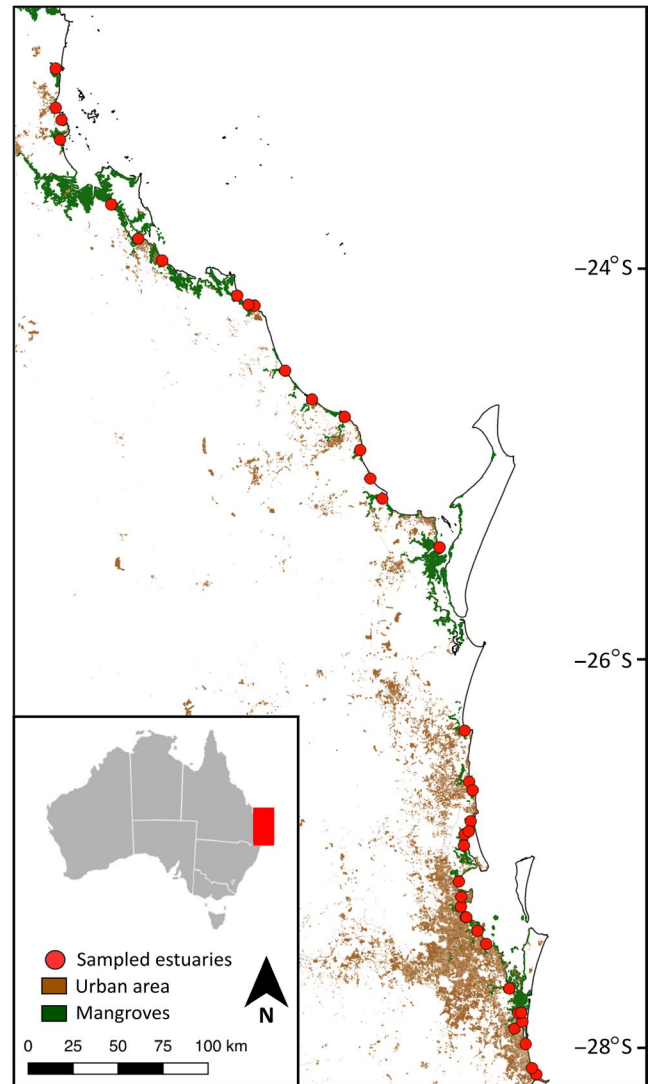

FIGURE 1 Location of the 39 study estuaries in eastern Australia

2 | MATERIALS AND METHODS

2.1 | Study seascape

We surveyed fish assemblages and quantified carrion consumption across 39 estuaries in Queensland, Australia (Figure 1). These estuaries stretch over approximately 1,000 km of coastline, from Water Park Creek in the north (−22.9°S, 150.7°E) to Currumbin Creek in the south (−28.7°S, 153.3°E), and range from natural systems with abundant intertidal mangroves and subtidal rocky fish habitats, to highly urbanized waterways where most shorelines have been hardened with artificial structures (Figure 1; Gilby, Olds, Yabsley, et al., 2017).

2.2 | Scavenger surveys

Scavenging fishes were surveyed with baited remote underwater video stations (BRUVS) in the Austral winter. BRUVS consisted of

a high definition GoPro camera, mounted on a 5-kg weight and a bait bag, which was held 0.5 m in front of the camera on a PVC pipe, and were baited with 500 g of pilchards *Sardinops sagax*. BRUVS sampled 10 sites in each estuary (*n* = 390), which were spaced evenly (separated by 250 m) from the mouth to the point where salinity had declined to 30 psu (Gilby, Olds, Yabsley, et al., 2017; Olds, Frohloff, et al., 2018a). BRUVS were deployed for 1 hr, within 2 hr of high tide and in water depths of 1.5–2 m, over un-vegetated muddy or sandy substrates within 30 m of mangroves (Martin et al., 2015). Scavenger abundance, species richness and assemblage composition were determined using the *MaxN* statistic (Harvey, Cappo, Butler, Hall, & Kendrick, 2007; Wraith, Lynch, Minchinton, Broad, & Davis, 2013).

2.3 | Carrion consumption experiments

Experimental assays have been used widely to measure the consumption of carrion by scavengers in coastal seascapes, particularly on ocean beaches and in estuaries (Huijbers et al., 2015; Porter & Scanes, 2015). We followed the same approach as previous research on carrion consumption in estuaries (Olds, Frohloff, et al., 2018a; Porter & Scanes, 2015; Webley, 2008), and deployed fish carcasses to measure scavenging rates at all sites where BRUVS surveys were conducted. This was done by attaching two pilchards of known weight to the upper surface of each BRUVS bait bag (Olds, Frohloff, et al., 2018a). Pilchards were weighed and then deployed for 1 hr with each BRUVS, and then re-weighed immediately after deployment. Carrion consumption was recorded as the change in pilchard weight during deployment. Scavengers were identified through analysis of BRUVS footage and included all fish species that were observed to feed on deployed pilchards. For each species that consumed exposed pilchards, we recorded the proportion of bait consumed by that species over the entire deployment (Olds, Frohloff, et al., 2018a).

2.4 | Environmental variables

To examine how the level of functional redundancy and complementarity in scavenger assemblages varied among estuaries, we tested for correlations between carrion consumption rates and the extent of both natural (mangrove wetlands, subtidal rock bars) and urban (armoured shorelines) fish habitats. These environments provide important habitat for estuarine scavengers (Olds, Frohloff, et al., 2018a; Porter & Scanes, 2015; Webley, 2008), are characterized by high structural complexity and are both common and stable components of most estuarine seascapes (Bradley, Baker, & Sheaves, 2017; Gilby et al., 2018; Sheaves, Baker, Nagelkerken, & Connolly, 2015). The area of mangrove wetlands and subtidal rock bars and the proportion of hardened shoreline in the sampled reach of each estuary were measured from digitized habitat maps and satellite imagery in Quantum GIS (source: Queensland

Government, Table S1; Gilby, et al., 2017; Olds, Frohloff, et al., 2018a). The area of mangrove wetlands and subtidal rock bars was greatest in northern estuaries, whereas the extent of shoreline armouring was greatest in southern estuaries (see Table S1). Consequently, latitude was included in all analyses to account for potential regional, and water temperature, effects on the distribution of fish habitats, fish abundance and diversity and carrion consumption rates (Willig et al., 2003).

2.5 | Data analysis

We examined functional redundancy and complementarity in scavenger assemblages by testing how both scavenger assemblages and rates of carrion consumption were correlated with spatial variation in the extent of natural (mangrove wetlands, subtidal rock bars) and urban (armoured shorelines) fish habitats. Data were analysed with generalized additive models (GAMs) using the ᴍɢᴄᴠ and MᴜMIɴ packages in ʀ (Bartoń, 2013). Model overfitting was minimized by limiting models to all combinations of four or fewer factors, and by restricting individual models to four or fewer knots (i.e. individual polynomial functions that combine to smooth GAMs; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). Models were compared using Akaike information criterion corrected for finite sample sizes (AIC$_c$) with the MᴜMIɴ package in ʀ. Best-fit models were those with the lowest AIC$_c$ value and those within 2 ΔAIC$_c$ units (Burnham & Anderson, 2002). The relative importance of variables in each model was calculated by summing weighted AIC$_c$ values across all models containing the variable of interest; values closer to one indicate a greater and more consistent association of a predictor and the response variable. We used GAMs to first identify important scavengers, by testing for correlations between carrion consumption rates and both the abundance and species richness of fish that consumed carrion. We then used GAMs to test for potential redundancy or complementarity, by examining whether different scavengers dominated carrion consumption in different seascapes (i.e. in natural and urban fish habitats).

3 | RESULTS

3.1 | Functional redundancy and carrion consumption in estuaries

Thirty-eight fish species consumed carrion in this study (Table S2), with these species varying in their trophic level, size and functional grouping (e.g. omnivores, piscivores or zoobenthivores). Carrion consumption was, however, numerically dominated by only one species, yellowfin bream *Acanthopagrus australis*, which consumed 58% of all deployed necromass (Figure 2; Table S2). Eight other fish species consumed between 1% and 14% of all carrion deployments: banded toadfish *Marilyna pleurostricta* 14%; common toadfish *Tetractenos hamiltoni* 11%; trumpeter whiting *Sillago maculata* 2%; crescent grunter *Terapon jarbua* 2%; silver toadfish *Lagocephalus sceleratus* 2%; blue catfish *Neoarius graeffei* 1%; banded scat

FIGURE 2 Carrion consumption was dominated by yellowfin bream *Acanthopagrus australis*. Yellowfin bream consumed 58% of all carrion deployed in estuaries, by contrast no other species consumed >14% of deployed carrion. Carrion consumption was also positively correlated with the abundance of yellowfin bream, but not fish species richness, or the abundance of any other species. Correlations were tested with general additive models (GAMs): shaded regions indicate 95% confidence intervals
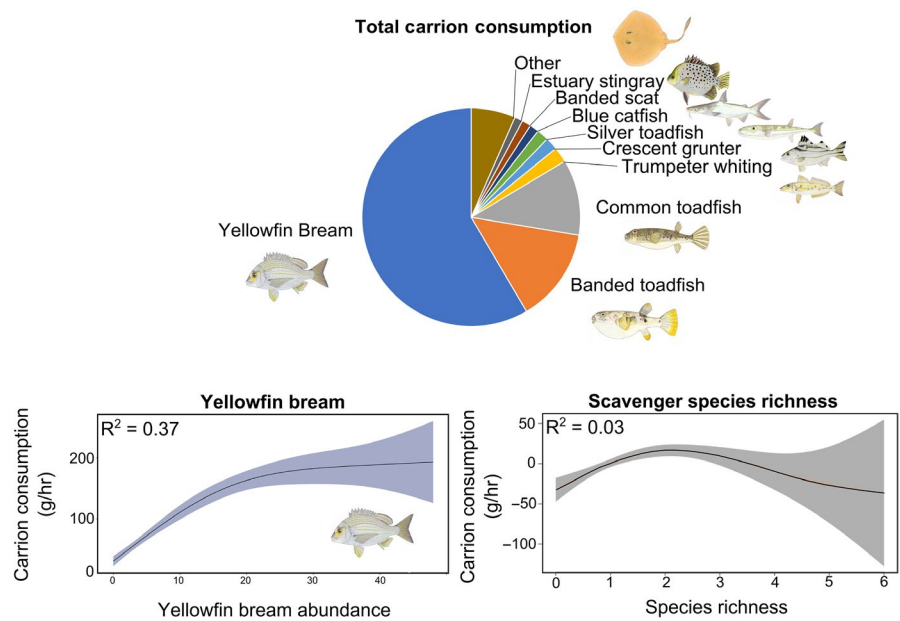
TABLE 1 Generalized additive models (GAMs) testing for correlations between carrion consumption, and the abundance of all fish species that consumed ≥1% of all deployed carrion. *df* = 3 for all species

Common name	Scientific name	*p*	R^2	AIC_c
Yellowfin bream	***Acanthopagrus australis***	**<.001**	**.37**	**4,095**
Banded toadfish	*Marilyna pleurostricta*	.215	.004	4,255
Common toadfish	*Tetractenos hamiltoni*	.893	.000	4,260
Trumpeter whiting	*Sillago maculata*	.163	.005	4,258
Crescent grunter	*Terapon jarbua*	.109	.007	4,257
Silver toadfish	*Lagocephalus sceleratus*	.069	.015	4,255
Blue catfish	*Neoarius graeffei*	.322	.008	4,258
Banded scat	*Selenotoca multifasciata*	.713	.001	4,260

Bold text identifies a significant correlation between a species and carrion consumption.

Selenotoca multifasciata 1%; and estuary ray *Hemitrygon fluviorum* 1% (Figure 2; Table S2).

Carrion consumption in estuaries was characterized by low functional redundancy as changes in the rate of carrion consumption among estuaries were positively correlated with variation in the abundance of only one species, yellowfin bream (Figure 2; Table 1), reaching a maximum asymptote when bream abundance reaches approximately 20 individuals. Carrion consumption was not correlated with variation in the abundance of any other species, or with changes in the richness of scavengers among estuaries (Figure 2; Table 1).

3.2 | Functional complementarity and carrion consumption in estuaries

Carrion consumption in estuaries was characterized by low functional complementarity as the spatial drivers of carrion consumption reflect that of yellowfin bream and not biodiversity or any other species. Spatial variation in the consumption of carrion by scavengers was correlated with changes in the extent of urban shorelines and the area of subtidal rock bars in each estuary (Figure 3; Table 2).

The area of mangrove wetlands and latitude of each estuary were also weakly correlated with carrion consumption, but these variables did not make significant contributions to best-fit models (Figure 3; Table 2). Spatial variation in yellowfin bream abundance was also correlated with the extent of urban shorelines, the area of subtidal rock bars and the latitude of each estuary (Figure 3; Table 2). Overall, both carrion consumption and the abundance of yellowfin bream reached an optimum level in urban estuaries with moderately (20%–60%) hardened shorelines and large subtidal rock bars (>0.1 km^2; Figure 3; Table 2). By contrast, the diversity of scavenging fishes was correlated with latitude, and the area of both mangrove wetlands and subtidal rock bars in each estuary (Figure 3). More scavenging species were present in high latitude (>26°) subtropical estuaries, with abundant mangroves (>13 km^2) and also reached an optimum level at a moderate amount of subtidal rock (0.08–0.1 km^2).

4 | DISCUSSION

Biodiversity is a key component of many ecosystems and plays a pivotal role in the delivery of numerous ecosystem functions (Bellwood
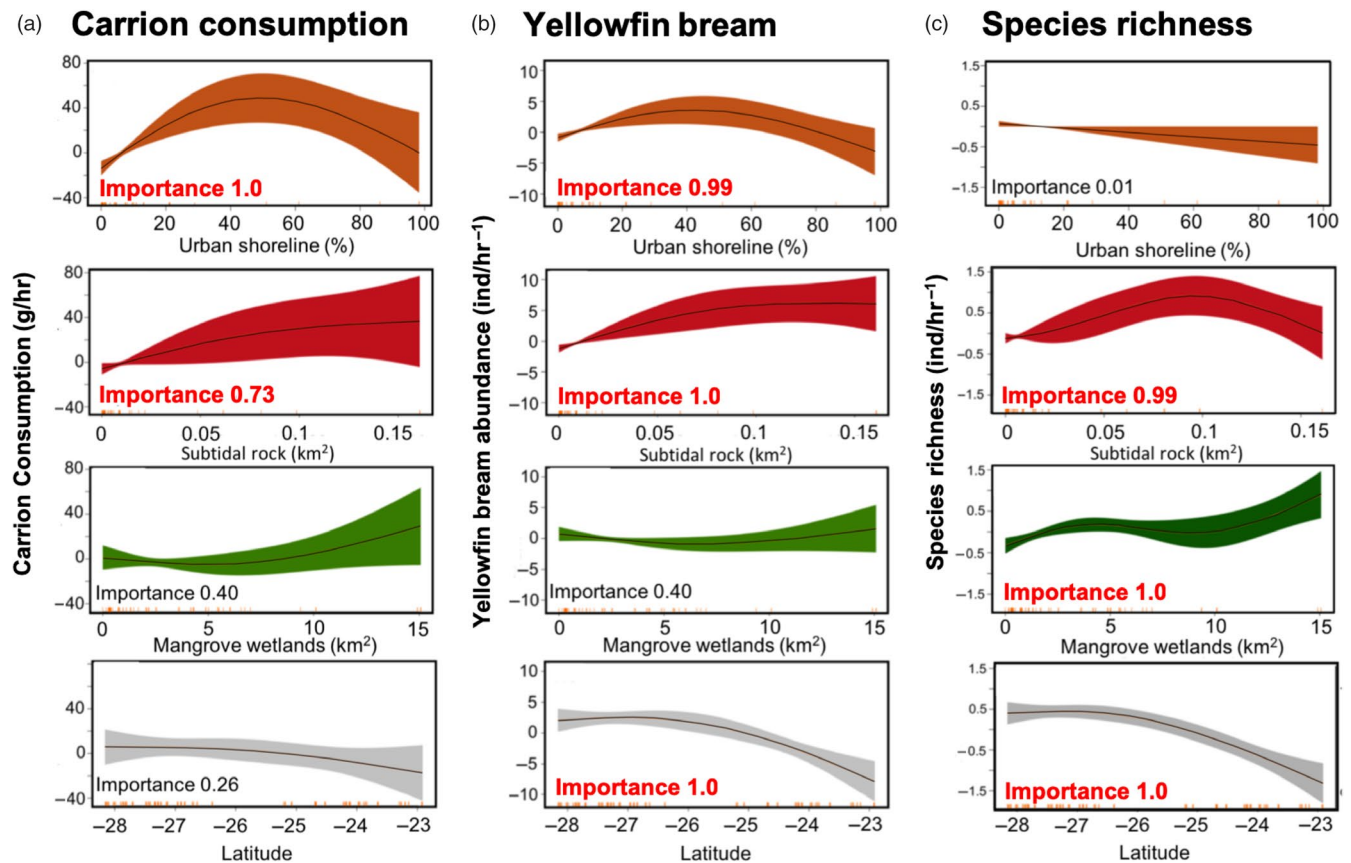
FIGURE 3 Generalized additive models (GAMs) illustrating correlations between: (a) carrion consumption; (b) yellowfin bream abundance; and (c) the species richness of scavengers, the extent of natural and urban fish habitats and latitude. Shaded regions indicate 95% confidence intervals; importance values indicate the contribution of each variable to GAMs. Larger importance values (highlighted in red) indicate stronger correlation with dependent variables; smaller values (i.e. <0.60) have little or no effect

Best-fit models	R^2	df	AIC_c
Carrion consumption			
Urban shoreline[(1.0)] + Subtidal rock[(0.73)]	.07	5	4,205.5
Urban shoreline[(1.0)] + Subtidal rock[(0.73)] + Mangrove wetland[(0.40)]	.08	6	4,205.7
Urban shoreline[(1.0)] + Subtidal rock[(0.73)] + Latitude[(0.26)]	.08	6	4,206.3
Urban shoreline[(1.0)] + Mangrove wetland[(0.40)]	.07	5	4,207.4
Yellowfin bream			
Urban shoreline[(0.98)] + Subtidal rock[(1.0)] + Latitude[(1.0)]	.15	7	2,546.8
Scavenger species richness			
Subtidal rock[(0.99)] + Mangrove wetland[(1.0)] + Latitude[(1.0)]	.17	9	1,065.3

TABLE 2 Generalized additive models (GAMs) testing for correlations between the extent of fish habitats and latitude on: carrion consumption; yellowfin bream abundance; and the species richness of scavengers in estuaries. All models within 2 AIC_c values of best-fit models are included. Numbers in brackets indicate the relative importance of each variable to best-fit models

et al., 2003; Huijbers et al., 2015). Our results show that the consumption of carrion by estuarine scavengers was not linked to biodiversity and that the delivery of carrion consumption in this ecosystem may be characterized by both low redundancy (e.g. one species correlates with the function rather than biodiversity) and low complementarity (e.g. there is no spatial context where the function is delivered significantly when yellowfin bream are not present). Carrion consumption was positively correlated with the abundance of only one species, yellowfin bream, which consumed the most necromass in urban estuaries with moderately (20%–60%) hardened

shorelines and relatively large subtidal rock bars (>0.1 km²). By contrast, carrion consumption was not correlated with variation in the abundance or necromass consumption of any other species, or with the composition of scavenger assemblages, which were most diverse in high latitude subtropical estuaries (>26°), with abundant mangroves (>13 km²) and a moderate amount of subtidal rock (0.08–0.1 km²). While Olds, Frohloff, et al. (2018a) reported species complementarity between natural and urban estuaries, here we find that across a greater latitudinal extent and with a greater number of natural estuaries in our study, that one species appeared to

dominate the function and was the only species and component of the fish community (e.g. biodiversity) that correlated with the function. Low functional redundancy has been widely reported from animal assemblages in marine ecosystems, for example, on coral reefs (Brandl & Bellwood, 2014; D'agata et al., 2016), in kelp forests (Ling et al., 2009; Micheli & Halpern, 2005) and over seagrass meadows (Duffy et al., 2015; Reynolds et al., 2018). This is, however, the first time that both low redundancy and low complementarity may have been reported for animal assemblages and ecological functions in coastal seascapes (Gamfeldt et al., 2015). Our findings demonstrate that ecological functions may still be maintained across estuarine seascapes despite no influence of biodiversity, resulting in limited redundancy and complementarity in the functional traits of animal assemblages.

It is widely accepted that the functioning of ecosystems is linked to biodiversity (Balvanera et al., 2006; Cardinale et al., 2006; Hooper et al., 2012), but the significance of diversity for particular ecological functions has recently being challenged (Gamfeldt & Roger, 2017; Manning et al., 2018). It is therefore important that we identify where an ecological function is not tightly linked to biodiversity and alter management actions to reflect those that will maintain ecological functions in different contexts or different ecosystems (Henderson, Stevens, et al., 2019; Ripple & Beschta, 2007). We show that the consumption of carrion by estuarine scavengers was not correlated with changes in species diversity, or the composition of scavenger assemblages, but rather with variation in the abundance of a single dominant species. The role of species dominance in functional ecology is gaining traction, and it has been suggested that relatively small pools of species can underpin the provision of several ecological functions (e.g. herbivory, predation) on land, and in the sea (Gamfeldt et al., 2015; Schuldt et al., 2018). Species that dominate key ecological functions are likely to be relatively common (Lohbeck et al., 2016; Winfree, W. Fox, Williams, Reilly, & Cariveau, 2015), and could therefore be important targets for refined spatial management (i.e. harvesting restrictions, species conservation), as their protection might help to maintain the function of interest across landscapes or seascapes (Hunter et al., 2016; Lentini & Wintle, 2015). The dominant scavenger in this study, yellowfin bream, is harvested heavily by both recreational and commercial fishers throughout its range (Curley, Jordan, Figueira, & Valenzuela, 2013; Webley, McInnes, Teixeira, Lawson, & Quinn, 2015), which suggests that carrion consumption may be sensitive to changes in fishing pressure. Because carrion consumption was strongly correlated with variation in the abundance of a single species, which aggregates around urban structures, rock bars and mangroves in estuaries (Clynick, Chapman, & Underwood, 2008; Folpp, Lowry, Gregson, & Suthers, 2013; Meynecke, Lee, & Duke, 2008), careful management of both yellowfin bream and the structurally complex habitats they frequent might help to maintain this important ecological function across disturbed estuaries, while also increasing trophic complexity in food webs (sensu Olds, Frohloff, et al., 2018a). The conservation of common and functionally important species could help to improve management outcomes that focus on enhancing ecological functions in estuaries, and other low-diversity ecosystems (Oliver et al., 2015; Winfree et al., 2015).

Many animals consume carrion because it is a nutrient-rich food source that is readily available and easy to obtain (Wilson & Wolkovich, 2011). Prey availability in many ecosystems, including estuaries, is likely to be influenced by a number of spatial, temporal and anthropogenic factors and while many species are opportunistic scavengers, a nutrient-rich food source such as carrion is highly suitable for a number of species (Porter & Scanes, 2015). Scavenger assemblages are therefore, frequently characterized by high diversity in a number of ecosystems (Barton et al., 2013; DeVault, Olson, Beasley, & Rhodes, 2011). We hypothesized that this would also be the case, particularly in tropical estuaries, where diversity was expected to be higher, omnivory is ubiquitous, and carrion is regularly supplied by the flow of carcasses from river discharges (Heck & Valentine, 2007; Olds, Frohloff, et al., 2018a; Stachowicz et al., 2007). Carrion was consumed by 38 fish species, but the function was numerically dominated by yellowfin bream, which consumed 58% of all deployed necromass. When yellowfin bream was not present, carrion consumption decreased and no species replaced the role of the dominant species. Yellowfin bream are common in the estuaries of the study area, they are aggressive omnivores (e.g. highly abundant, not influenced negatively by urbanization and have a larger body size than most other omnivores) with wide trophic niches, and feed opportunistically on a variety of prey items, including detritus, plants (e.g. algae, seagrass), live animals (e.g. infaunal and epifaunal invertebrates, fish) and carrion (Gilby et al., 2018; Meynecke, Poole, et al., 2008; Olds, Frohloff, et al., 2018a; Sheaves et al., 2014). This wide trophic niche, aggressive behaviour and high abundance are likely to give yellowfin bream a competitive advantage over a number of other scavengers in estuaries (Olds, Frohloff, et al., 2018a). Similarly, a number of other species that are opportunistic scavengers in estuaries are likely to be less abundant, target more specified types of prey/carrion or have smaller body sizes, thus potentially being out-competed by species such as yellowfin bream. It has recently been suggested that high species dominance might be a common feature of scavenger assemblages (Inger, Per, Cox, & Gaston, 2016), and the function of carrion consumption appears to be contingent on a small number of common, and opportunistic, trophic generalists across a range of ecosystems, including forests, deserts and coastal dunes (DeVault et al., 2011; Huijbers et al., 2016; Mateo-Tomás, Olea, Moleón, Selva, & Sánchez-Zapata, 2017). In addition to being characteristics of successful scavengers, the behavioural traits (e.g. out-compete other species and highly abundant), broad physiological tolerances (e.g. broad salinity and temperature tolerances) and dietary flexibility (e.g. can feed in a broad variety of natural and urban habitats) of generalist omnviores, like yellowfin bream, might also underpin their successful colonization of urban environments (Bishop et al., 2017; Clavel, Julliard, & Devictor, 2011; Olds, Frohloff, et al., 2018a).

Here, we assessed changes in an ecosystem function across a large latitudinal scale, larger than those of most conservation and management decisions and establishing these patterns for other

ecological functions (e.g. herbivory or predation) should be a focus of future ecological studies. We used this approach rather than the typical Biodiversity–Ecosystem Function (BEF) experimental approach, which typically manipulates the diversity and evenness of community composition, as we were able to assess changes in ecosystem functions because of natural variability in species composition, biodiversity and the area of a number of important habitat variables (Srivastava & Vellend, 2005). Our findings, therefore, demonstrate that ecological functions can be maintained across estuarine seascapes despite both limited redundancy and complementarity in the functional traits of animal assemblages. We show that consumption of carrion by estuarine scavengers was not correlated with changes in species diversity, or the composition of scavenger assemblages, but rather with variation in the abundance of a single dominant species. The functioning of estuaries, and other low-diversity ecosystems, might therefore be tightly linked with the dominance of opportunistic species and not that of biodiversity, and we suggest that the conservation of these functionally important species could help to improve management outcomes for coastal seascapes.

AUTHORS' CONTRIBUTIONS
C.H., B.G., T.S., R.C. and A.O. conceived the idea, C.H., B.G., H.B., T.M. and A.O. performed the research, C.H., B.G., H.B. and A.O. analysed the data and C.H., B.G., T.S., R.C., M.S., P.M., N.F., T.M. and A.O. wrote and drafted the manuscript.

DATA AVAILABILITY STATEMENT
Data for this paper is available from Zenodo: https://doi.org/10.5281/zenodo.3522256 (Henderson et al., 2019b).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.