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Research

Landscape transformation alters functional diversity in coastal seascapes

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The ecological impacts of landscape modification and urbanisation have transformed the composition of plant and animal assemblages, and altered the condition of ecosystems globally. Landscape transformation influences the spatial distribution of species and ecological functions by selecting for generalist species with wide ecological niches, which can adapt to opportunities in highly-modified environments. These effects of landscape modification can shape functional diversity on land, but it is not clear whether they have similar functional consequences in the sea. We used estuaries as a model system to test how landscape transformation alters functional diversity in coastal seascapes, and measured how variation in level of urbanisation, catchment modification and habitat loss influenced fish diversity across thirty-nine estuaries in eastern Australia. Fish were surveyed with baited remote underwater video stations and functional diversity was indexed with three metrics that describe variation in the functional traits and niche space of assemblages. The extent of landscape transformation in the catchment of each estuary was associated with variation in the functional diversity of estuarine fish assemblages. These effects were, however, not what we expected as functional diversity was highest in modified estuaries that supported a large area of both urban and grazing land in their catchments, were bordered by a small area of natural terrestrial vegetation and that contained a moderate area of mangroves. Zoobenthivores and omnivores dominated assemblages in highly-modified estuaries, and piscivorous fishes were common in natural waterways. Our results demonstrate, that the modification and urbanisation of ecosystems on land can alter functional diversity in the sea. Intense landscape transformation appears to select for abundant generalists with wide trophic niches, and against species with specialised diets, and we suggest that these changes might have fundamental consequences for ecosystem functioning in estuaries, and other highly modified seascapes.

Keywords: ecosystem functioning, estuary, fish, functional ecology, generalist, urbanisation



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Introduction

Humans like to live near coastlines and many of our cities occupy prominent positions adjacent to major estuaries (Seto et al. 2012, Duarte et al. 2013, Strain et al. 2019). These urban estuaries, and the coastal seascapes in which they are embedded, are among the most modified environments globally (Dafforn et al. 2015, Firth et al. 2016, Bugnot et al. 2019). Many are dominated by armoured shorelines and are routinely dredged to improve their navigability (Waltham and Connolly 2011, Heery et al. 2017, Munsch et al. 2017). Urban estuaries are also frequently characterised by low habitat diversity and poor water quality because natural ecosystems are replaced with hard structures, and nutrients, sediments and other contaminants wash into estuaries from their catchments (Bishop et al. 2017, Freeman et al. 2019, Henderson et al. 2019a). These effects of urbanisation homogenise biotic assemblages and food-webs in the sea, as they do on land (Aronson et al. 2014, Brice et al. 2017, Heery et al. 2017, Moore and Olden 2017). They can also modify the spatial distribution of ecosystem services and ecological functions, but it is not clear how these functional consequences of urbanisation are linked to changes in species diversity or assemblage composition (McPhearson et al. 2016, Concepción et al. 2017, Mayer-Pinto et al. 2018, Olds et al. 2018a).

Landscape transformation modifies the composition of plant and animal assemblages by filtering species based on their diet and habitat requirements, and their physiological and behavioural characteristics (Lefcheck et al. 2016, Barnum et al. 2017, Concepción et al. 2017, Ibáñez-Álamo et al. 2017). Urban environments favour generalists over specialists, because species with wide ecological niches can better capitalise on the range of feeding and sheltering opportunities that cities provide, and the extreme physical conditions that often characterise highly-modified environments (Knapp et al. 2008, Clavel et al. 2011, Moore and Olden 2017). These effects of landscape transformation might, therefore, also modify the functional diversity of flora and fauna (i.e. variation in their physiological, behavioural and morphological traits) in urban settings (Villéger et al. 2010, Mouillot et al. 2013, Gagic et al. 2015, Thornhill et al. 2018). Species with distinct phenotypic and behavioural traits typically occupy different ecological niches, and therefore perform divergent roles in ecosystems (Gamfeldt et al. 2015, Oliver et al. 2015, Lohbeck et al. 2016). Changes in the functional diversity of plant and animal assemblages in urban and agricultural environments, thus provide a mechanism through which landscape fragmentation can alter the spatial distribution of ecosystem functions and services (Villéger et al. 2010, Brice et al. 2017, Ibáñez-Álamo et al. 2017). Research has linked landscape modification with changes in functional diversity in terrestrial forests and in freshwater streams, describing variable effects for plants (Knapp et al. 2008, Nock et al. 2013, Brice et al. 2017), and largely negative consequences for invertebrates, fish and birds (Barnum et al. 2017, Concepción et al. 2017, Moore and

Olden 2017, Oliveira Hagen et al. 2017). These potential functional effects may also result from coastal urbanisation, and from the transformation of terrestrial landscapes that border estuaries and their catchments, but they have not been widely tested in the sea.

Estuarine fish assemblages are sensitive to the effects of urbanisation and habitat fragmentation, and fish abundance, diversity and species composition typically change with the modification of estuarine seascapes (Dolbeth et al. 2016, Warry et al. 2018, Yeager et al. 2019). Fish also perform numerous important ecological functions in estuaries (e.g. herbivory, predation, carrion consumption) and the spatial distribution of these functions can, therefore, be modified by the introduction of artificial structures that fragment natural seascapes (Pratt et al. 2015, Mayer-Pinto et al. 2018, Olds et al. 2018a, Yeager et al. 2019). The abundance and diversity of fish from different functional groups varies among estuarine habitats, and can respond to impacts from changes in catchment land-use, overfishing, water quality, habitat loss and fragmentation in distinct ways (Villéger et al. 2010, Whitfield et al. 2018, Olds et al. 2018a). For example, artificial structures provide habitat and feeding opportunities for omnivores and zoobenthivores that consume sessile epifauna (Moreau et al. 2008, Mayer-Pinto et al. 2018), while changes in the area of natural habitats can alter community composition throughout the entire estuary (Gilby et al. 2018, Henderson et al. 2019a). By contrast, the loss of natural habitats from urban estuaries can reduce the suite of feeding opportunities that are available for taxa with narrow trophic niches, such as herbivores and piscivores (Leahy et al. 2011, Warry et al. 2018). Heavy fishing pressure in highly populated areas can also alter the functional characteristics of food-webs by reducing the abundance and diversity of species from higher trophic levels (Pauly et al. 1998). The effects of urbanisation and habitat modification can be positive for some taxa and negative for others, but it is not clear how these changes combine to shape the functional ecology and diversity of fish assemblages in estuaries. We tested whether, and how, the functional diversity of estuarine fish assemblages is modified by spatial variation in both the area of fish habitats in estuaries, and the extent of landscape transformation in their catchments.

Material and methods

Study area

We surveyed fish assemblages at ten sites in the lower reaches of 39 different estuaries ($n = 390$) in eastern Australia, which stretch over 1000 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) (Fig. 1). These estuaries support a diversity of fish habitats, but differ markedly in area of mangrove forests, seagrass meadows, rocky outcrops and armoured shorelines (Meynecke et al. 2008, Martin et al. 2018). They are also distributed along a gradient in the extent to which their

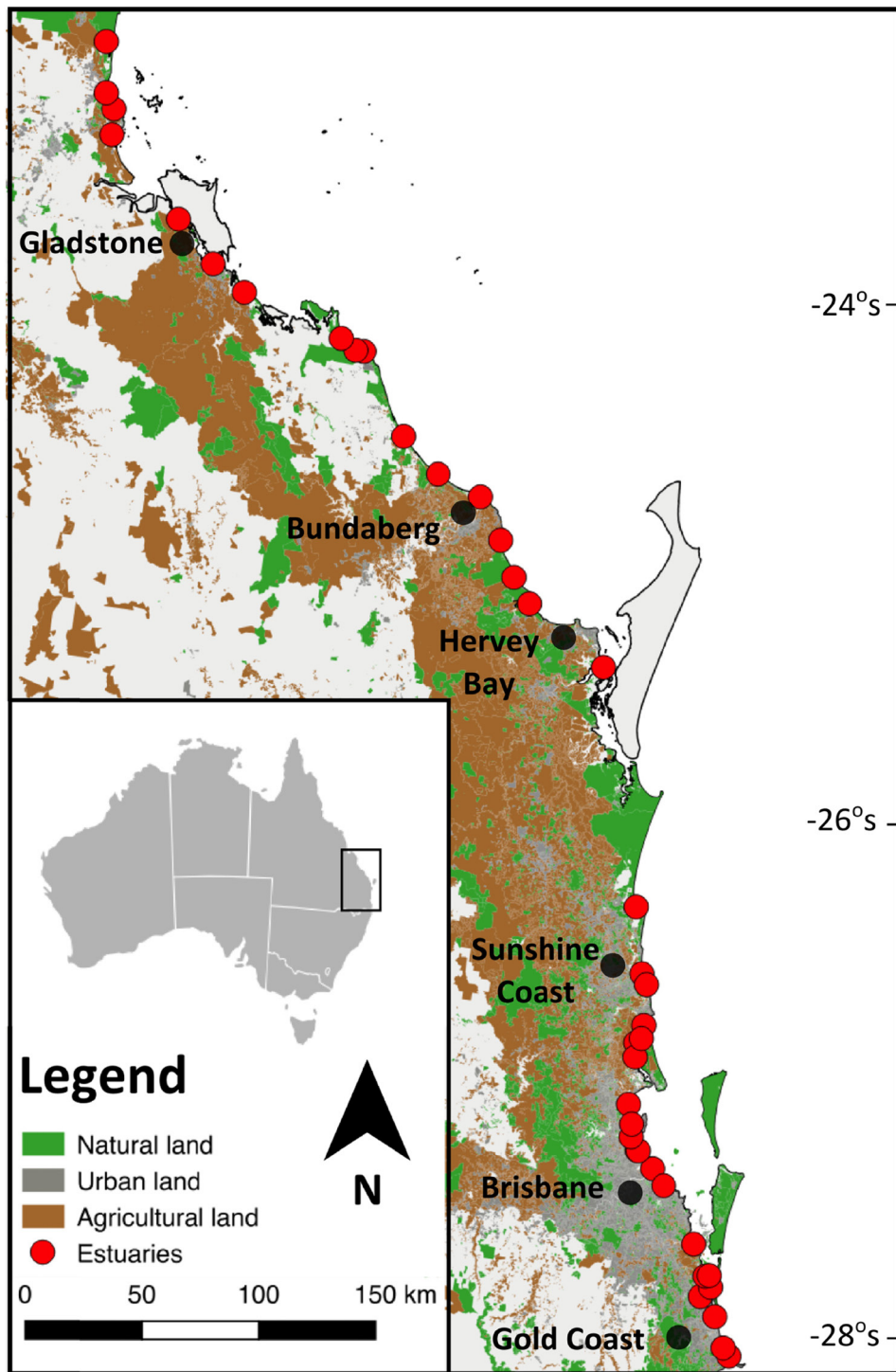


Figure 1. Distribution of natural, urban and agricultural land in the catchments of 39 study estuaries in eastern Australia.

catchments support natural terrestrial vegetation (e.g. remnant vegetation), or have been modified by humans to support cities (i.e. urbanisation) or food production (i.e. grazing, cropping) (Abrantes and Sheaves 2009, Wenger et al. 2016, Olds et al. 2018a).

Surveying fish assemblages

Fish assemblages were surveyed with baited remote underwater video stations (BRUVS), which are a standard technique for measuring fish diversity and abundance in most seascapes

because they sample the full variety of species from all trophic groups (Wraith et al. 2013). BRUVS consisted of a high definition GoPro camera mounted to a 5 kg weight, and a bait bag (with 500 g of *Sardinops sagax*) that was held 0.5 m in front of the camera by a PVC pipe (Gilby et al. 2016). All BRUVS deployments lasted for one hour. We standardised for possible effects of salinity on estuarine fish assemblages by only deploying BRUVS in the marine stretch of each estuary, and by spacing deployments evenly between the mouth and the point at which salinity decreased to 30 psu (Olds et al. 2018a). Estuarine fish assemblages are characterised by high spatial (e.g. habitat, seascape context) and temporal (e.g. tide, diel period, season) variability (Sheaves 2009, Nagelkerken et al. 2015). We accounted for these potential confounding effects on fish assemblages by only conducting surveys within two hours of daytime high tides during the austral winter (i.e. when water clarity is highest), and by deploying all BRUVS in water depths of 1.5–2.5 m over non-vegetated muddy or sandy substrate within 30 m of estuarine banks (Gilby et al. 2017, Olds et al. 2018a). While BRUVS are known to bias the abundances of species at mid trophic levels, they are the most suitable method of measuring functional diversity in estuaries due to their ability to sample the full breadth of trophic levels (Wraith et al. 2013). Similarly, we chose to sample over non-vegetated habitats in order to avoid the effects of biasing our results by sampling fish in structurally complex habitats that were not available in all estuaries, or were of reduced quality in some (Gilby et al. 2018, Henderson et al. 2019a). Data to describe fish abundance and diversity was quantified from BRUVS footage using the standard ‘MaxN’ statistic (Henderson et al. 2017).

Measuring environmental attributes

We tested whether, and how, variation in both the extent of landscape transformation and the area of fish habitats shaped the functional diversity of fish assemblages. Catchment land-use spatial layers were collected from the Queensland Government as part of the Queensland Land Use Mapping Program. Land use type was based on the Australian land use and management classification scheme, with catchment land use being quantified by measuring the area of urban (i.e. intensive uses, buildings, impervious surfaces), agricultural (i.e. grazing, cropping) and natural (i.e. remnant terrestrial vegetation) land in the catchment of each estuary with Quantum GIS (Waltham and Connolly 2011, Gilby et al. 2017, Olds et al. 2018a) (Supplementary material Appendix 1 Table A2). The area of structurally complex fish habitat (i.e. mangrove forests, seagrass meadows, rocky outcrops and armoured shorelines) was also measured from digitized habitat maps and satellite imagery in Quantum GIS (Bradley et al. 2017, Gilby et al. 2018, Martin et al. 2018). Urbanisation is often concentrated in certain locations (i.e. the lower reaches of estuaries, or in a small area of some catchments), so we measured the extent of urban development in each catchment at three different scales: estuary, sub-catchment, and catchment (Supplementary material Appendix 1 Table A2). These three measures of urbanisation

were, however, strongly and positively correlated for estuaries across the study area (Supplementary material Appendix 1 Fig. A1). Similarly, we did not include latitude in any of our analyses as it correlated strongly and significantly with the levels of urbanisation in the catchment ($p < 0.001$, $R^2 = 0.85$), levels of grazing in the catchment ($p < 0.001$, $R^2 = 0.35$) and levels of natural land ($p < 0.001$, $R^2 = 0.51$) (Supplementary material Appendix 1 Fig. A2).

Data analysis

Functional diversity was described as variation in the functional traits of fish species (Gagic et al. 2015). We calculated three metrics of functional diversity; functional richness, functional dispersion, functional evenness and species richness using the ‘fundiv’ and ‘FD’ packages in the R statistical environment, and used these metrics to index spatial variation in functional diversity among estuaries (Mason et al. 2005, Laliberté and Legendre 2010). Functional richness (e.g. functional diversity sensu (Petchey and Gaston 2006)), which was calculated using a dendrogram approach because species richness was regularly lower than the number of traits used in the calculation of the functional richness metric, and refers to the diversity of functional niches supported in an ecosystem, with low functional richness suggesting some niches in an assemblage are underutilised (Mason et al. 2005). In order to account for categorical traits, our dendrogram was based on a Gower dissimilarity matrix with clustering based on average trait values (Petchey and Gaston 2006). Functional dispersion refers to the mean distance in multidimensional functional trait space from the centroid of all species in that assemblage, and is weighted for abundance, with low functional dispersion suggesting a decrease in the diversity of functional traits (Laliberté and Legendre 2010). Functional evenness is a measure of the distribution of functional niches across a community and is calculated using the abundances of different species within trait space, with low functional evenness suggesting some niches having a reduced number of individuals performing those functions, while others may contain a large number of individuals performing a similar role (Mason et al. 2005). Data on fish functional traits were extracted from FishBase (Froese and Pauly 2018) using the ‘rfishbase’ package in R (Boettiger et al. 2017). We were interested in the functional ecology of estuarine fish assemblages and, therefore, collected data on the feeding type, body shape, trophic level, body length, body depth, head length, pre-orbital length and eye diameter of each species to describe their potential ecological roles in estuarine food-webs (Supplementary material Appendix 1 Table A3) (Elliott et al. 2007). Our functional diversity dendrogram was then used to partition the estuarine fish assemblage into different functional groupings, based on their positioning in the dendrogram relative to one another (Supplementary material Appendix 1 Fig. A3). Functional groups were assigned to prominent divisions in the tree, where the species in one functional group are separated from all other functional groups by at least two major divisions (Gagic et al. 2015).

Generalised additive models (GAMs) were used to test for associations between the functional diversity metrics and species richness, and the extent of catchment modification (indexed as the area of urban or agricultural land) and the area of fish habitats (i.e. mangrove forests, seagrass meadows, rocky outcrops and armoured shorelines) among estuaries. GAMs were then fit to test for potential effects on the abundances of fish from each functional group using the most important factors in the previous analyses. Model overfitting was minimised by running models with all possible combinations of four or fewer factors, and by restricting individual models to four polynomial functions or fewer. Models were compared using Akaike information criterion corrected for finite sample sizes (AICc) and assessed for auto correlation using the 'acf' function in R. Best-fit models were those with the lowest AICc value and those within 2 AICc units (Burnham and Anderson 2002). The relative importance of variables in each model was calculated by summing weighted AICc 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. All GAM analyses were conducted using the 'mgcv' (Wood and Wood 2015) and 'MuMIn' (Bartoń 2013) packages in R.

Results

Functional diversity was highest in highly-modified estuaries that supported a large area of both urban (i.e. > 500 km²) and grazing (i.e. > 60 000 km²) land in their catchments, were bordered by a relatively small area of natural terrestrial vegetation

(< 1200 km²), that contained a moderate area of mangroves (i.e. 20–40 km²) (Fig. 2, also see Supplementary material Appendix 1 Fig. A4). The functional diversity of estuarine fish assemblages was associated with variation in both the extent of land-use change in catchments (i.e. urbanisation, grazing, cropping), and the area of complex habitat structures in estuaries (i.e. mangroves, seagrass, rock bars, artificial structure) (Fig. 2, Table 1). Urbanisation in the catchment was the best predictor of functional diversity in estuarine fish assemblages, and this was consistent across all metrics used to index functional diversity (i.e. functional richness, dispersion, evenness and species richness). The area of grazing land and natural vegetation in catchments, and the area of mangrove habitat in estuaries were also important predictors of functional diversity in the majority of best fit models (Fig. 2, Table 1). The area of seagrass in an estuary and the area of cropping land in the catchment also appeared in the best fit models for functional dispersion and evenness respectively (Fig. 2, Table 1). Best fit models for all measures of functional diversity followed similar trends, with urbanisation in the catchment being the best predictor of all functional measures (Table 1). Best fit models for functional dispersion and functional evenness were found to have reduced explanatory power and increased variation in the number of significant models and reduced deviance explained by the models (Table 1).

Our functional trait analyses partitioned the assemblage of estuarine fishes into twelve functional groups (Supplementary material Appendix 1 Fig. A3). These functional groups included three categories of piscivore (i.e. compressiform, fusiform, other), five categories of zoobenthivore (i.e. depressiform, taeniform, compressiform, globiform, fusiform),

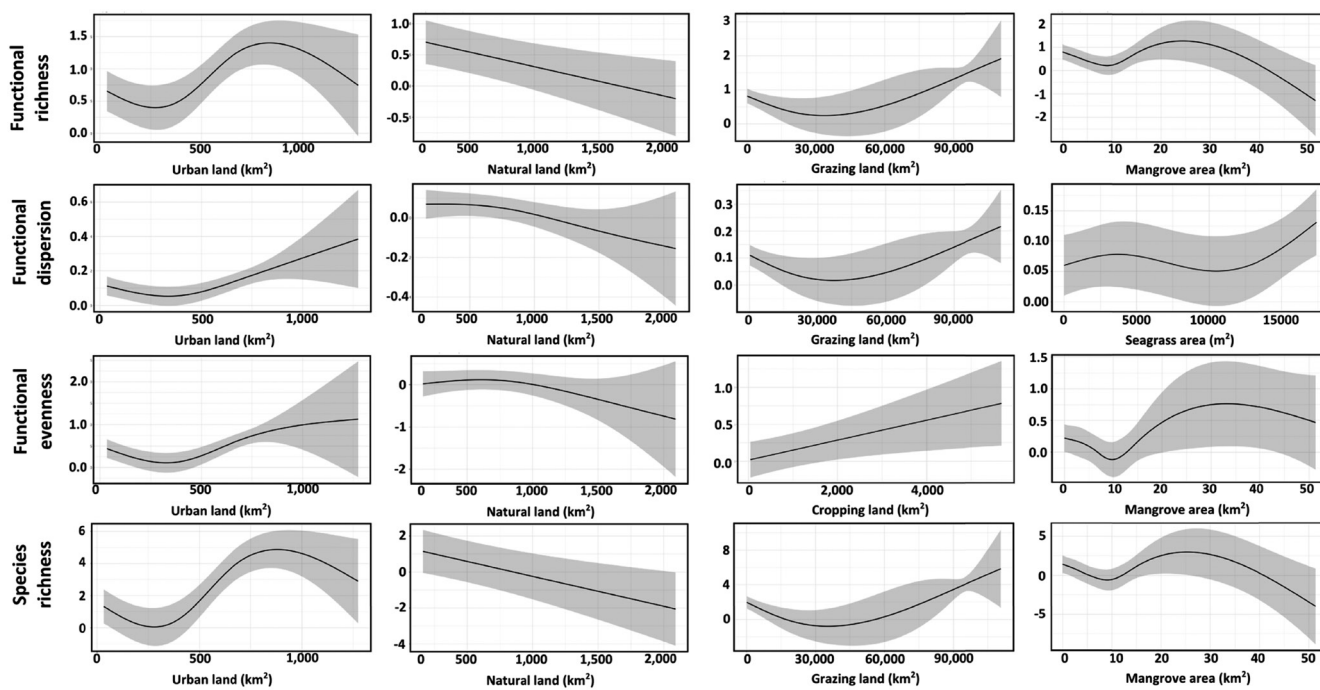


Figure 2. Generalised additive models (GAM) partial plots illustrating associations between functional diversity metrics and significant environmental variables (i.e. catchment land-use types and estuarine habitats). Shaded areas indicate 95% confidence intervals.

Table 1. Best-fit generalised additive models (GAMs) displaying associations between functional diversity metrics and environmental variables (i.e. catchment land-use types and estuarine habitats). Numbers in parentheses indicate the importance and significance of variables in best-fit models. Larger importance values, in bold, indicate stronger associations (values < 0.60 have little or no effect).

Functional diversity metrics	Best fit model	R ²	df	Deviance %	AIC _c
Functional richness	Urban land ^(1.0, p<0.001) + Grazing land ^(0.99, p=0.03) + Mangrove area ^(0.98, p<0.001) + Natural land ^(0.85, p=0.003)	0.19	13	21	549.6
Functional dispersion	Urban land ^(0.95, p=0.001) + Grazing land ^(0.63, p=0.04) + Natural land ^(0.32, p=0.001) + Seagrass area ^(0.32, p=0.013)	0.07	9	10.3	-824.7
	Urban land + Grazing land + Seagrass area	0.06	8		-824.2
	Urban land + Grazing land	0.05	6		-824.0
	Urban land + Grazing land + Natural land	0.05	7		-823.7
	Urban land + Grazing land + Natural land + Mangrove area	0.08	12		-823.4
	Urban land + Grazing land + Seagrass area + Cropping land	0.06	9		-823.3
	Urban land	0.04	4		-823.0
Function evenness	Urban land ^(0.99, p<0.001) + Mangrove area ^(0.92, p=0.01) + Cropping land ^(0.69, p=0.002) + Natural land ^(0.54, p=0.07)	0.13	13	14.2	257.2
	Urban land + Mangrove area + Natural land + Cropping land	0.12	10		257.5
	Urban land + Mangrove area + Cropping land + Grazing land	0.12	10		257.9
	Urban land + Mangrove area + Cropping land	0.10	7		258.8
Species richness	Urban land ^(1.0, p<0.001) + Grazing land ^(1.0, p=0.003) + Mangrove area ^(1.0, p<0.001) + Natural land ^(0.94, p=0.002)	0.23	13	23.9	1421.9

two categories of omnivore (i.e. compressiform, sagitiform), and one category of both zooplanktivores and herbivores (Supplementary material Appendix 1 Table A3, A4). Functional groups had a variable response to the impacts of urbanisation within the catchment. Urbanisation was negatively associated with the abundance of all piscivorous fish categories (see examples in Fig. 3, Table 2, also see Supplementary material Appendix 1 Fig. A5). By contrast, urbanisation was positively associated with the abundance of most small-medium sized zoobenthivores (i.e. depressiform, globiform, fusiform and compressiform zoobenthivores) and sagitiform omnivores (see examples in Fig. 3, Table 2, also see Supplementary material Appendix 1 Fig. A6). Urbanisation did not, however, significantly affect or appear in the best fit models for taeniform zoobenthivores, compressiform omnivores, zooplanktivores or herbivores in the estuaries we studied, with each of these groups having poor model fits and thus were not overly effected by the different land use types (see examples in Fig. 3, Table 2). Estuaries that had lower levels of urbanisation were found to have a higher abundance of piscivorous fish with a larger average maximum total length than those species found in urbanised systems (Supplementary material Appendix 1 Table A4). This was supported by a significant decrease in the average trophic level of fish in estuaries as urbanisation increased (Supplementary material Appendix 1 Fig. A7). The area of mangroves in each estuary, and the area of both grazing land and natural terrestrial vegetation in each catchment, were also significant and important predictors of abundance of most functional groups. The directionality of the effects of mangroves, grazing land and natural terrestrial vegetation were, however, highly variable and often weak associations, and the influence of these features was always secondary to the effects of urbanisation (Fig. 3, Table 2, also see Supplementary material Appendix 1 Fig. A5, A6).

Discussion

Landscape modifications alter the distribution of ecological functions and services through changes to the assemblage structure in many ecosystems, but it is not clear how these consequences of urbanisation and fragmentation are linked to changes in functional diversity (Knapp et al. 2008, McPhearson et al. 2016, Ibáñez-Álamo et al. 2017). Impacts on functional diversity have been reported from urban and agricultural environments on land, and in modified streams (Brice et al. 2017, Concepción et al. 2017), but these potential effects of habitat transformation are rarely considered in coastal seascapes (Kelley et al. 2018, Mayer-Pinto et al. 2018). We demonstrate, that there was some association between land-use metrics and species and functional richness, and the abundance of a few key functional groups, however, that variation in other functional metrics and functional groups was not well explained by land-use. The extent to which catchments had been converted to provide land for either urban development, or grazing livestock, was associated with the functional diversity of fish assemblages in adjacent estuaries. The direction of the effects of landscape transformation were, however, not what we expected: functional diversity was highest in estuaries that bordered large areas of either urban or grazing land, and that supported a relatively small area of mangrove habitat. Changes in functional diversity corresponded to divergence in the functional group composition of fish assemblages between highly-modified estuaries and natural waterways. Landscape transformation was positively associated with the abundance of most zoobenthivores and omnivores, and negatively associated with the abundance of all piscivorous fishes and resulted in an overall trophic downgrading of fish communities. These findings lend support to the paradigm that the fragmentation of ecosystems on land can alter biodiversity in the sea (Stoms et al. 2005, Halpern et al. 2009), and agree with

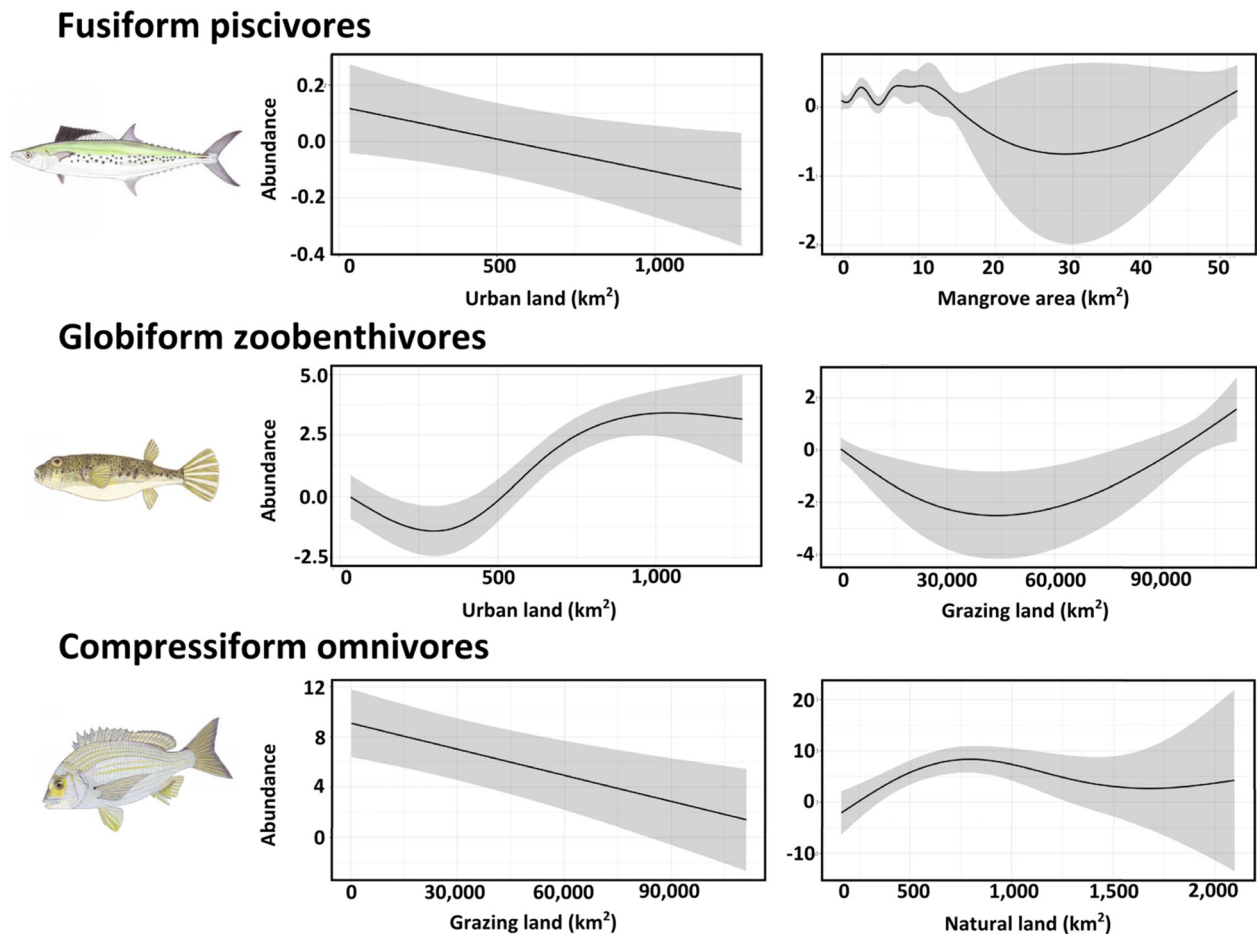


Figure 3. Generalised additive models (GAMs) illustrating associations between representative functional groups and significant environmental variables (i.e. catchment land-use types and estuarine habitat metrics). Shaded areas indicate 95% confidence intervals. See Supplementary material Appendix 1 Fig. A3, A4 for all other GAM models.

findings of previous studies that suggest changes in terrestrial land-use might also have consequences for functional ecology in coastal seascapes (Bishop et al. 2017, Mayer-Pinto et al. 2018, Olds et al. 2018a).

It is widely accepted that the transformation of landscapes into cities and agricultural lands is associated with pervasive declines in species diversity, and the ecological condition of natural habitats (Grimm et al. 2008, McPhearson et al. 2016). These structural changes do not, however, always have similar functional consequences for assemblages and ecosystems, because many species flourish in modified landscapes, and some of these taxa can dominate pivotal ecological functions (Ibáñez-Álamo et al. 2017, Mayer-Pinto et al. 2018). We show that the functional diversity of fish assemblages is highest in modified estuaries that support a large area of either urban (i.e. > 500 km²) or grazing (i.e. > 60 000 km²) land in their catchments. This finding seems counterintuitive, but it mirrors the results of several studies that have documented high functional diversity in the plant and bird assemblages of cities and farmlands (Nock et al. 2013, Brice et al. 2017, Oliveira Hagen et al. 2017). Functional diversity might be higher in some modified landscapes, than

in their natural counterparts, because these systems offer a diverse suite of habitats (e.g. buildings, roads, rock walls, gardens), which differ fundamentally from those that characterise natural landscapes (Bishop et al. 2017, Concepción et al. 2017, Ibáñez-Álamo et al. 2017). They provide abundant food and shelter for opportunistic species with wide trophic niches (e.g. foxes, racoons, ravens, sea bream), while removing suitable habitat and changing estuarine conditions (e.g. reducing water quality in estuaries) that suit their predators, thus allowing these generalists to dominate assemblages and ecological functions (DeVault et al. 2011, Inger et al. 2016). Modified urban landscapes also reduce the suitability of estuarine ecosystems to naturally forming habitats, with a decrease in the condition or overall area within an ecosystem, limiting the suitability for high trophic level or specialised species in these areas (Villéger et al. 2010, Lefcheck et al. 2016). Engineering urban and agricultural environments to provide diverse habitats and optimising estuarine condition for functional groups that can both cope with disturbances and taxa that are sensitive to change, might therefore help to promote functional diversity and maintain ecological functions across modified landscapes.

Table 2. Best fit generalised additive models (GAMs) displaying associations between the abundance of each functional group and significant environmental variables (i.e. catchment land-use types and estuarine habitats). Numbers in parentheses indicate the importance and the significance of variables in best-fit models. Larger importance values indicate stronger associations (values <0.60 have little or no effect).

Functional group	Best fit	R ²	df	AICc	Deviance %
Negative effects of urbanisation					
Compressiform piscivore	Urban land ^(0.86, p=0.03) + Mangrove area ^(0.95, p<0.001) + Grazing land ^(0.49, p=0.14)	0.15	12	837.6	10.3
	Urban land + Grazing land	0.10	5	838.2	
Fusiform piscivore	Grazing land	0.09	4	839.2	
	Urban land ^(0.72, p=0.02) + Mangrove area ^(0.78, p=0.04) + Grazing land ^(0.57, p=0.13)	0.08	12	408.6	2.4
Other piscivore	Urban land + Mangrove area	0.06	4	409.0	
	Urban land + Natural land	0.06	4	410.4	
	Urban land ^(0.63, p=0.01) + Mangrove area ^(0.96, p=0.006) + Grazing land ^(0.52, p=0.26)	0.04	5	592.5	4.3
	Urban land + Mangrove area + Natural land	0.04	6	593.0	
	Mangrove area + Natural land	0.05	6	593.0	
Positive effects of urbanisation	Mangrove area + Natural land + Grazing land	0.05	7	593.6	
	Urban land + Mangrove area	0.04	4	593.7	
	Urban land ^(0.94, p=0.0001) + Mangrove area ^(1.0, p<0.0001) + Grazing land ^(1.0, p<0.0001) + Natural land ^(0.55, p=0.22)	0.23	12	583.5	8.5
	Urban land ^(1.0, p<0.0001) + Grazing land ^(0.99, p=0.004)	0.14	7	1519.5	0.7
	Urban land + Grazing land + Mangrove area	0.14	8	1520.9	
Compressiform zoobenthivore	Urban land + Grazing land + Natural land	0.14	8	1521.0	
	Urban land + Grazing land + Mangrove area + Natural land	0.14	9	1521.1	
	Urban land ^(0.50, p=15)	0.01	3	1873.2	0.3
	Urban land + Natural land	0.01	4	1874.5	
	Mangrove area	0.01	3	1874.7	
	Grazing land	0.01	3	1874.9	
	Natural land	0.01	4	1875.0	
Fusiform zoobenthivore	Urban land + Mangrove area	0.01	4	1875.0	
	Urban land + Natural land	0.01	6	1875.1	
	Urban land ^(0.89, p=0.008) + Mangrove area ^(1.0, p<0.0001) + Grazing land ^(0.94, p=0.0001) + Natural land ^(0.91, p=0.004)	0.21	18	1329.7	14.5
	Urban land ^(0.72, p=0.04) + Mangrove area ^(0.98, p=0.02) + Natural land ^(0.72, p=0.06)	0.09	8	2055.3	8.0
	Urban land + Mangrove area	0.08	6	2056.4	
Sagittiform omnivore	Mangrove area + Natural land	0.08	7	2056.6	
	No effects of urbanisation				
Taeniform zoobenthivore	Grazing land ^(0.77, p=0.09) + Natural land ^(0.91, p=0.06)	0.05	6	409.3	12.2
	Grazing land + Natural land + Urban land	0.06	7	409.4	
	Grazing land + Natural land + Mangrove area	0.05	7	411.1	
Compressiform omnivore	Grazing land ^(0.97, p=0.0005) + Natural land ^(1.0, p=0.0003) + Mangrove area ^(0.87, p=0.06)	0.13	11	2567.6	1.8
	Grazing land + Natural land	0.11	8	2567.9	
All zooplanktivores	Mangrove area ^(0.63, p=0.07)	0.02	4	3283.5	2.6
	Urban land	0.03	4	3283.7	
	Mangrove area + Urban land	0.03	6	3283.7	
	Urban land + Grazing land	0.03	5	3284.2	
	Mangrove area + Grazing land	0.02	4	3284.5	
	Mangrove area + Urban land + Grazing land	0.04	6	3284.6	
	Mangrove area + Urban land + Natural land + Grazing land	0.04	7	3284.9	
	Mangrove area + Natural land	0.03	5	3285.2	
	Mangrove area + Urban land + Natural land	0.03	6	3285.3	
	All herbivores	Mangrove area ^(0.56, p=0.18)	0.01	3	580.3

The high functional diversity of fish assemblages in modified estuaries was driven by the dominance of small and medium-sized zoobenthivores and omnivores in these systems. Common zoobenthivores and omnivores that

characterised estuaries bordering urban and agricultural lands included sting rays (*Dasyatidae*), silver biddies (*Gerreidae*), guitarfish (*Glaucostegidae*), grunter (*Haemulidae*), garfish (*Hemiramphidae*), wrasse (*Labridae*), moray eels

(Muraenidae), mullet (Mugilidae), sea bream (Sparidae), perch (Terapontidae) and toadfishes (Tetraodontidae). Species from these fish families have been widely reported from estuaries in highly urbanised catchments, and are able to capitalise on the reduced predator availability, increased feeding opportunities and artificial habitats that dominate urban seascapes, and cope with increased fishing pressure and reductions in water quality (Chapman and Blockley 2009, Bishop et al. 2017, Olds et al. 2018a). Most species feed on either detritus, vegetation, invertebrates, or small fishes (Baker and Sheaves 2005, Elliott et al. 2007, Waltham and Connolly 2007), and shelter over soft sediments or in a range of natural and artificial habitats that offer high vertical relief and structural complexity (Sheaves 2005, Potter et al. 2015, Gilby et al. 2018). We did, however, not sample over complex habitats within estuaries, which may further influence the functional composition of species in the urbanised estuaries (Gilby et al. 2018, Henderson et al. 2019a). Functional diversity was lower in natural estuaries with larger mangrove forests, but these seascapes were also characterised by an abundance of large piscivores. Common piscivores in natural estuaries included trevally (Carangidae), lates perch (Latidae), snappers (Lutjanidae), flathead (Platycephalidae), threadfin (Polynemidae), tailor (Pomatomidae), mackerel (Scombridae), grouper (Serranidae) and barracuda (Sphyraenidae). These fish are meso and apex predators and occupy the highest trophic levels in many subtropical and tropical estuaries (Sheaves 2009, Rosenblatt et al. 2013, Gilby et al. 2017). Many of these fish species that were negatively impacted by urbanisation are of high fisheries value (78%), while the majority of those that benefitted from the same landscape changes are not fisheries target species (22%). Most species move among a diverse range of high-relief natural habitats in estuaries (e.g. rocky and coral reefs, mangrove forests, seagrass meadows) (Nagelkerken et al. 2015, Bradley et al. 2017, Olds et al. 2018b). Many can also reside in artificial habitats (i.e. under jetties, around pylons, or over armoured shorelines), but they are typically less abundant in highly-modified systems, which support low habitat diversity and food-webs comprised of a greater abundance of lower trophic level species (Byrnes et al. 2007), restrict passage to the open sea, and often experience high fishing pressure from humans that live in adjacent towns and cities (Connolly 2003, Sheaves et al. 2014, Olds et al. 2018a). The impacts of landscape transformation on functional diversity, therefore, likely result from broad differences in water quality, predator abundance, habitat diversity and condition and connectivity between natural and modified seascapes, which exert combined effects on the range of feeding and sheltering opportunities that these estuaries provide for fishes.

Our findings provide empirical evidence that the transformation of coastal landscapes by humans can be associated with functional diversity in adjacent marine ecosystems. Functional diversity was, however, greatest in highly-modified estuaries, which supported an abundance of species with wide trophic niches and broad habitat requirements. The prevailing

conditions in these systems appear to favour the dominance of generalists over species with specialized diets and habitat needs, and we suggest that intense urbanisation might, therefore, have fundamental consequences for the functional ecology of estuaries, and other highly modified ecosystems.

Data deposition

Data available from the USC Research Bank: <<https://dx.doi.org/10.25907/5d93f7c7d6013>> (Henderson et al. 2019b).

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Supplementary material (Appendix ECOG-04504 at <www.ecography.org/appendix/ecog-04504>). Appendix 1.