Original Research Article

The fox and the beach: Coastal landscape topography and urbanisation predict the distribution of carnivores at the edge of the sea

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ABSTRACT

Mitigating the impact of invasive species is a global conservation challenge, which requires an understanding of the factors that drive the distribution, abundance, and ecological interactions of invaders. Red foxes (*Vulpes vulpes*) are a widespread and abundant invasive omnivore in Australia. They are common in dunes and coastal areas that abut marine shorelines, which provide abundant food resources in the form of carrion. They are considered a key threatening process to Australia's biodiversity. The global literature posits that foxes use a broad mix of habitats, leading to an expectation of few consistent associations of foxes with landscape attributes and human uses of beaches and coastal dunes — this is the fundamental hypothesis tested here.

Fox distribution was comprehensively mapped in Eastern Australia (108 km of shoreline, 192 sites, 6900 h of wildlife camera footage) and related (general additive models) to a range of potential drivers (e.g. topographic features, habitat types, urbanisation, connectivity, dogs, fox removal) on ocean beaches.

Notwithstanding the catholic nature of red foxes elsewhere, here we show that habitat use by red foxes along ocean beaches is not indiscriminate: more foxes occur on beaches backed by high dunes and large expanses of natural vegetation. Conversely, significantly fewer foxes occur where natural dune habitats have been lost to urban areas. Fox removal did not affect fox distributions.

Foxes are functionally important carnivores in coastal landscapes, and their disjunct distribution demonstrated by us suggests a spatially heterogeneous functional signal in coastal food-webs. More broadly, sandy beach ecosystems, interspersed by urban development, dominate many coasts, offering a rich bio-geographic tapestry to test how models of fox habitat choice articulate into invasive species management and food-web interactions.

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1. Introduction

"Hide Fox and all after"

Hamlet (W. Shakespeare)

Invasive carnivores impact native species, biodiversity, and ecological functions in many ecosystems globally and have geographic ranges that are expanding (Capinha et al., 2015; Seebens et al., 2018). Reducing the undesirable impacts of invasive carnivores is, therefore, a global conservation challenge, requiring multi-faceted approaches informed by robust data on species biology and ecology (Doherty et al., 2015a, 2016). Species management at the landscape-scale must be based on a solid understanding of the main biophysical features that shape species distributions (Thuiller and Miaud, 2007; Tingley et al., 2013). Identifying habitat features consistently associated with invasive species occurrence is essential to achieve targeted and cost-effective species management (Block et al., 2011; Tingley et al., 2013; Plotz et al., 2016; Law et al., 2017).

Red foxes (*Vulpes vulpes*) are one of the most detrimental invasive carnivores in Australia (Doherty et al., 2016). Due to their broad environmental tolerances, extraordinary adaptability, and wide trophic niches, red foxes are the most widely distributed terrestrial carnivore globally (Marks and Bloomfield, 2006; Southgate et al., 2007; Scott et al., 2014; Mumma et al., 2017). Foxes have a multi-facetted habitat use.; they are common in urban areas (Duduś et al., 2014; Scott et al., 2014; Villaseñor et al., 2014), occur in forests, grasslands, and mountains (Cavallini and Lovari, 1991; Weber and Meia, 1996; Sidorovich et al., 2006; Brito et al., 2009; Janko et al., 2012; Molina-Vacas et al., 2012; Petrov et al., 2016; Sacks et al., 2017)), and forage along marine shorelines (Gallant et al., 2013). Their spatial distribution and activity can be influenced by apex carnivores (e.g. dingoes) and free-roaming ('feral') domestic dogs (Wikenros et al., 2017). Red foxes readily use human paths and roads to disperse and as foraging corridors, suggesting that anthropogenic changes to landscapes increase connectivity and possibly the habitat quality for foxes (Towerton et al., 2016).

Despite decades of work on red fox ecology and a sizeable body of literature on their habitat use, there is no consensus on factors influencing the distribution of the species. For example, urbanisation can affect red fox distributions, but either more or fewer foxes have been reported in cities; similar disparities are evident for grassland areas, forests, and mountainous habitats (Baker and Harris, 2007; Pereira et al., 2012; Duduś et al., 2014; Scott et al., 2014). Red foxes are common on ocean beaches globally, where they reportedly forage mainly on beach-cast carrion (Huijbers et al., 2013, 2015, 2016). Key factors shaping fox distributions in these coastal settings are, however, unknown.

Red foxes occur in an extraordinary broad range of landscapes, including sandy beaches and coastal dunes (Brown et al., 2015; Bingham et al., 2018; Schlacher et al., 2019). It follows, that 'coastal foxes' may be posited to show multifarious patterns of habitat use. Notwithstanding the reported catholic nature of fox habitat use, we can test three specific predictive hypotheses based on known fox behaviour and habitat attributes:

1) urban areas increase habitat quality for red foxes at intermediate urban density (e.g. more food), but become inimical at high urban density (e.g. fewer den sites, dogs, disturbance);
2) greater man-made connectivity of the landscape (e.g. roads, beach access points) is favourable to foxes because these landscape transformations create better dispersal networks and opportunities to access foraging sites (e.g. beach-cast carrion);
3) taller coastal dunes covered with more intact natural vegetation generally are less disturbed by humans and form better den sites, thus supporting more foxes.

Knowing the outcome of these conceptual models articulates tangibly to conservation and wildlife management. Because red foxes are an invasive species of high conservation concern in Australia, they attract massive investments in control programs, including 'fox eradication' efforts in coastal areas (Saunders et al., 2010). Thus, by identifying specific landscape contexts and attributes that 'beach foxes' are consistently associated with, invasive species management can be more targeted.

2. Methods

2.1. Study area

We mapped red foxes across a broad ambit of coastal landforms, habitat types, and degrees of urbanisation, along 108 km of coastline in Eastern Australia (Fig. 1; northern limit: 25.97°S, 153.16 °E; southern limit: 26.81°S, 153.14°E). The marine shores of the study area were predominately ocean-exposed sandy beaches, interspersed by a few small rocky headlands and
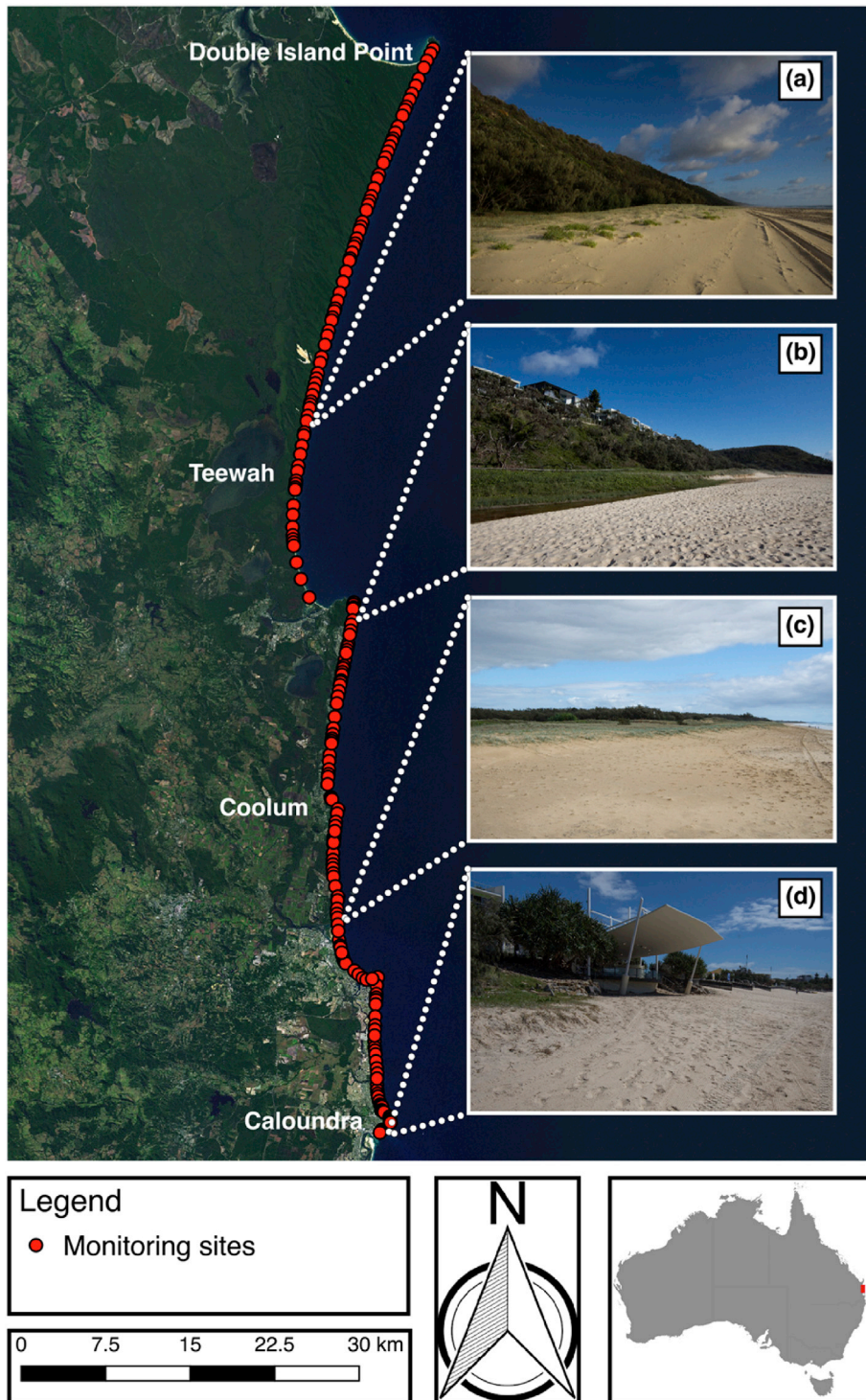
Fig. 1. Location of red fox survey sites (n = 192) in SE Queensland, Australia. Insets show examples of variation in landforms and development intensities, (a) high dunes and no urbanisation, (b) high dunes and moderate urbanisation, (c) low dunes and no urbanisation, and (d) low dunes and high urbanisation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

estuarine inlets (Fig. 1). Impacts of urbanisation on beaches ranged from minimal (coastal dune systems with vegetation disturbed only by the occasional access path) to heavy modifications (near-complete loss of dune systems (Huijbers et al., 2013). Where present, coastal dunes range in height from 1.7 m to 27.4 m, three major estuaries drain the coastal

floodplain, and reserve areas vary from very small remnants of natural vegetation abutted by houses to large tracts of a national park (Fig. 1); (Schlacher et al., 2015) This heterogeneous mosaic of landscape features, and human modifications to the coastal landscape, are a good system to identify habitat preferences of red foxes in a coastal setting.

2.2. Fox mapping

We determined fox occurrence using motion-detecting camera traps at 192 sites (Fig. 1; Supplementary Material S1). The along-shore dispersion of sites was set by a stratified random design (strata were gazetted beach localities), resulting in a mean distance between camera sites of 547 m (se = 29 m). Fox monitoring followed protocols developed for scavengers on sandy beaches and in coastal dunes (Huijbers et al., 2013, 2015, 2016; Schlacher and Hartwig, 2013; Schlacher et al., 2013; Brown et al., 2015; Maslo et al., 2016b; Bingham et al., 2018). Briefly, two Scoutguard Zero Glow 8M were set at the dune-beach interface and baited with whole fish (mullet, *Mugil cephalus*). All fish were measured (mean = 37.7 cm, se = 0.09), weighed (mean = 531 g, se = 3.68), and tagged before deployment. In this study, carcass weight (GLM, p = 0.19) did not significantly influence the probability of detecting a fox at a camera site. Cameras were deployed over two days during the 2018 austral autumn and early winter (Feb to June). We first set cameras after sunset on day one and then checked them 12 h, replacing the bait when it was removed. Thus, fox presence was detectable over two nights, and occurrence during either nocturnal recording period is treated as a fox being present at a particular locality.

2.3. Environmental variables

We measured 14 environmental variables that have either been identified in the literature as having an influence on red fox distribution (Table 1). Variables encompassed four main categories: i) development and urbanisation; ii) landscape connectivity; iii) geomorphology; and iv) fox control effort (Table 1). Using a similar study design to (Huijbers et al., 2015), we used the average daily home range of red foxes (1.6-km linear distance) as the area around each camera deployment from which values of environmental variables were extracted (Table 1).

2.4. Data analysis

Before model building, we assessed co-linearity between all possible pairs of potential predictors (n = 14) using Pearson's correlations. Where correlation coefficients were >0.7, we retained only one of the two variables. Because roads are thought to provide dispersal conduits for foxes or facilitate access to food (carrion) on roadsides, the total length of all roads in the foxes' home ranges was initially measured; it was, however, highly correlated with several other variables (Fig. S1). As 'number of access points' was a complementary metric of connectivity and did not correlate strongly with any other variable, we retained it as a metric of connectivity. The variables 'reserve area' and 'forest cover' were both essentially the inverse of 'urban land cover', and were highly correlated with several other variables; as such, both were excluded and 'urban land cover' was retained. 'Distance to estuary' was initially predicted to be an index of carrion washed to nearby beaches (and hence relevant to scavenging foxes), but was found to be correlated with several other variables and therefore not included in the full models (Fig. S1). We did not retain 'distance to human settlement' as it is a less comprehensive metric of urbanisation than 'urban land cover' and also collinear with terrain ruggedness. 'Fox control type' (i.e. the type of method used to cull foxes) and 'fox removal' (i.e. the number of individuals culled) were highly correlated. Since fox removal is a direct measure of the *actual* effect of fox control programs, it was retained in our models. The set of predictors used for model building comprised: urban land cover, domestic dog presence, number of beach access points, low-lying areas, water bodies, dune height, terrain ruggedness, and fox removal (Table 1).

As data on fox control effort and fox removal were only available for sites south of Noosa (n = 114; 26.38 S, 153.09 E), we conducted a diagnostic test to determine whether fox control measurably influenced fox presence in our study. This test was done with a Generalised Additive Model (GAM (Hastie and Tibshirani, 2017); containing all remaining environmental predictors (n = 8). Models were based on a binomial distribution, and smooths were constrained to four knots to reduce over-fitting (Burnham and Anderson, 2002; Zuur et al., 2009). The importance of fox control was assessed using multi-model inference (e.g. summed weighted AIC values for each model containing each predictor variable). The variable 'fox control' was the least important predictor of fox presence (importance = 0.17), and was therefore not further tested in the full model runs (i.e. the entire study region) using data on fox occurrence and environmental features for all sites (n = 192). Best fitting models were selected by fitting a maximum GAM containing all remaining environmental predictors and running a multi-model inference, using weighted delta Akaike Information Criterion (AIC) values to compare model fits (Akaike, 1973). Best-fit models were considered to be those within two Δ AIC of the model with the lowest AIC.

3. Results

Although foxes occupied all types of habitats and landscape contexts over a broad geographic swathe (we detected foxes at 97 of 192 sites), three environmental attributes strongly shaped fox distribution: dune height, urban land cover, and terrain rugosity (Table 2; Fig. 2). Dune height was the best predictor of fox presence, with foxes occurring more frequently on beaches backed by dunes 10 m or higher (Fig. 3a). Urbanisation (indexed by the cover of urban land in a typical fox home range) also

Table 1

List of environmental variables used for building GAMS (Generalised Additive Models) relating fox presence to habitat attributes. ([#] calculated following (Huijbers et al., 2015) for a 'typical' fox home range in a coastal area, representing a 1.6 km radius centred on each camera trap sites).

Variable	Units	Definition, Method(s)	Rationale Table S1	Date Source(s)
Urban landscapes				
Urban land cover	percentage surface area[#]	Urban land cover was calculated according to (Huijbers et al., 2015). In brief, we overlaid 265 random points (in a 8 x 8 grid configuration with 4 points per cell) on a satellite image (Google Earth) centred on each of the 192 survey sites. The total area measured was 3.2 km × 3.2 km square to correspond with a typical fox home range in a coastal area (see Huijbers et al., 2015 for full details of the method).	Red foxes use urban environments in many geographic locations (Marks and Bloomfield, 2006; Duduś et al., 2014; Hradsky et al., 2017). Red foxes also readily use man-made structures for shelter and denning sites (Goldyn et al., 2003).	Google Earth satellite imagery
Distance to human settlement	Metres	The minimum linear distance between a camera site and the nearest house.	as above	Google Earth satellite imagery
Domestic dogs	number of individuals detected per camera trap site	The number of domestic dogs present at each camera site.	Den site selection is reported to be negatively associated with the presence of domestic dogs (Marks and Bloomfield, 2006). In Australia, wild dogs and dingoes can also suppress red fox numbers (Letnic et al., 2009, 2011).	camera trap footage (this study)
Connectivity				
Total road length	metres of total road network[#]	The length of all paths and roads.	Roads provide structure for shelter (Goldyn et al., 2003), paths for dispersal and food in the form of roadkill (Trewhella and Harris, 1990; Carter, 2010). Conversely, foxes are killed in vehicle collisions (Gosselink et al., 2003).	GIS, road layer obtained from the Queensland Government (2015).
Access points	number of paths cut through the dunes[#]	The number of private and council-maintained beach access paths that cut through the dunes to reach the beach.	Red foxes readily use man-made tracks and paths (Frey and Conover, 2006; Erb et al., 2012).	Council-maintained beach access points were sourced from Noosa Council and Sunshine Coast Council. Private beach access points were located using Google Earth satellite imagery and marking sections were unmarked walking paths cut through the foredunes.
Reserve area	m²[#]	All areas classified as 'natural' or 'conservation' in the official spatial land-use catalogue of the Queensland Government (2015)	Reserves bordering beaches have been shown to influence red fox distributions (Schlacher et al., 2015).	GIS, conservation and natural areas layer obtained from Queensland Government (2015).
Forest cover	percentage surface cover[#]	see urban land cover above	Forest is a frequently analyses habitat type in studies dealing with habitat choice of red foxes (Hradsky et al., 2017).	Google Earth satellite imagery
Geomorphology				

(continued on next page)

Table 1 (*continued*)

Variable	Units	Definition, Method(s)	Rationale Table S1	Date Source(s)
Distance to estuary	Metres	The distance between a camera site and the nearest estuarine inlet.	Estuaries can flush carrion out to sea that can wash up on nearby beaches to benefit foxes foraging near estuaries.	GIS
Low lying areas/wetlands	m$^{2\#}$	The land area below 1 m elevation.	Red foxes forage in palustrine areas of low elevation (Cleve et al., 2011; Carter et al., 2012; Hradsky et al., 2017; Mumma et al., 2017).	GIS, LiDAR layer obtained from Geoscience Australia (2017)
Waterbody	m$^{2\#}$	The area covered by water bodies (excluding the ocean).	Lakes, rivers, creeks and dams can increase the abundance of prey species for foxes (Meisner et al., 2014).	GIS, habitat layer obtained from Queensland Government (2015).
Dune height	Metres	The maximum altitude landwards within a 50 m radius of each camera site.	Hypothesised that taller dunes provide areas less disturbed by humans and dogs and with better den sites.	GIS, LiDAR layer obtained from Geoscience Australia (2017)
Terrain ruggedness	standard deviation of elevation$^{\#}$	The standard deviation of elevation.	Terrain ruggedness can negatively influence red fox abundance (Gallant et al., 2013; Mumma et al., 2017).	GIS, LiDAR layer obtained from Geoscience Australia (2017)
Fox control				
Fox control type	PCA score$^{\#}$	Local government uses five different fox control techniques: trapping, cage trapping, canid pest ejectors, egg baits, and den fumigation. A Principal Component Analysis was conducted on the types of control methods used within a 1.6 km radius of each site. The PC1 score explained 97.1% of the variation in control efforts, with the majority of variation explained by foothold traps.	A combination of different control methods typically yields more culls (Saunders et al., 2010).	The location and type of fox control methods were obtained from local government authority conducting these.
Fox removal	No. individuals	The number of foxes captured and removed in the year leading up our surveys.	More individuals culled is predicted to translate into fewer foxes in fewer areas.	The location and type of fox control methods were obtained from local government authority conducting these.

Table 2
Best-fit generalised additive models (GAMs) relating fox distribution to a range of environmental predictors (cf. Table 1; *** = p < 0.001, ** = p < 0.01, * = p < 0.051, ns = p > 0.05).

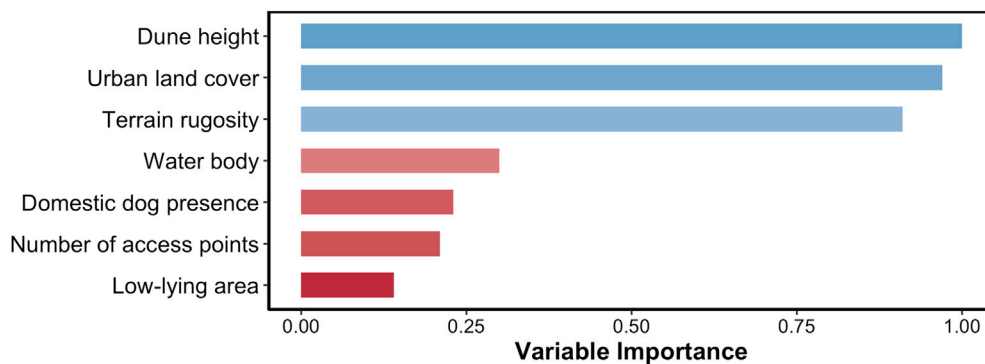| Model	Variable 1	Variable 2	Variable 3	Variable 4	df	ΔAICc
1	Dune height **	Urban land cover **	Terrain rugosity **	Waterbody ns	9	—
2	Dune height ***	Urban land cover **	Terrain rugosity *		8	0.79
3	Dune height **	Urban land cover **	Terrain rugosity *	Domestic dog presence ns	9	0.90
4	Dune height ***	Urban land cover **	Terrain rugosity *	Number of access points ns	9	1.10

Fig. 2. Comparison of the relative importance of modelled environmental variables in predicting fox presence. Importance values are the sum of the weighted AIC values for each GAM model containing that variable. Larger importance values denote a stronger association of fox presence with a particular variable (Importance values < 0.6 are regarded to have little effect in models, and this is reflected by colour (blue > 0.6, red < 0.6) with colour saturation reflecting numerical values). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

strongly influenced fox distributions (Fig. 2), with markedly more foxes found along shorelines characterised by large tracts of natural vegetation than on urban beaches (Fig. 3b). Dunes with a more varied topographic relief supported significantly fewer foxes (Fig. 3c). Other predictors tested were either not significant when included in best-fit models, had low importance values as predictors, or both [e.g. water bodies; domestic dogs, access points (Table 2, Fig. 2)].

Foxes were most common on beaches characterised by taller dunes, low urbanisation and correspondingly large natural areas such as the beaches and dunes north of Noosa (Fig. 4). We recorded a fox site occupancy of 72% (56 of 78 sites) on this 52 km of coastline where the mean urban land cover was 0.1% (se = 0.05) and mean dune height was 13.2 m (se = 0.7 m; Fig. 4). By contrast, the coastline south of Noosa is substantially more developed (mean = 21.2%, se = 1.05), backed by lower dunes (mean = 8.6, se = 0.36), with only small coastal reserves and tidal inlets interspersing a belt of near continual suburbs and small coastal cities. In the 56 km of coastline of this southern section, we recorded red foxes at 41 of 114 sites (36% occupancy; Fig. 4).

4. Discussion

Red foxes are highly adaptable, generalist predators that occur in an extraordinary broad ambit of habitat types, ranging from Arctic seashores to the edge of the Arabian deserts (Marks and Bloomfield, 2006; Southgate et al., 2007; Scott et al., 2014; Mumma et al., 2017). Despite decades of research on habitat use by red foxes, there appears to be little consensus about the principal factors that shape their distributions and habitat selections. Red foxes are a functional component of the food web on many marine shorelines and the abutting terrestrial zones (Bingham et al., 2018), yet habitat use in these settings often remains unknown. Considering the mixed reports of habitat use by this trophic generalist species elsewhere, red foxes may have weak affinities to particular features of the coastal landscape. Nevertheless, here we show that habitat use by red foxes along ocean beaches is not indiscriminate: foxes are more likely to be found on beaches characterised by high dunes and large expanses of natural vegetation. Conversely, foxes are less likely to be found where tall dunes are not contiguous and where dunes have been transformed into urban areas or cities. By contrast, fox distributions were not related to proximity to water bodies, low-lying areas or beach access points, to domestic dog abundances, or council-run fox control programs.

Higher, contiguous coastal dunes appear to be a good fox habitat in the study area (Fig. 4). Taller coastal dunes may support higher densities of red foxes as they provide sandy, well-drained soil which are the preferred denning conditions for foxes (Carter et al., 2012). Moreover, some of the high dune sections of the survey area included cliffs or inclines with a slope steeper than 50%. It is plausible that foxes may not readily climb such steep terrain, and hence may occupy the small foredunes in the narrow strip at the seaward edge of the foredunes. In addition, there might be less human activity and greater carrion retention on beaches with tall dunes, theoretically providing better foraging opportunities in these sections. As a consequence, tall contiguous dunes may effectively 'concentrate' foxes in a narrow strip of frontal dunes seawards bordering the
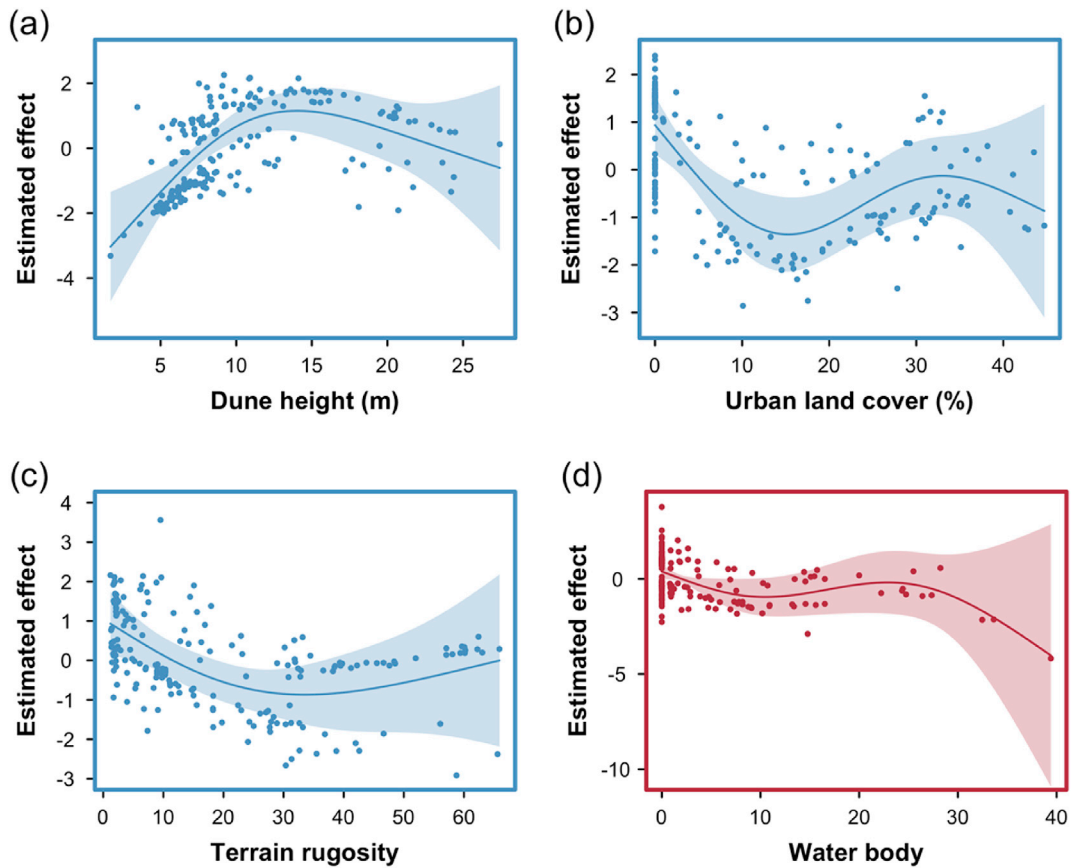
Fig. 3. Relationship of fox occurrence associated with four environmental variables included in the best GAM model: a) dune height, b) urban land cover, c) terrain rugosity, and d) water body area (cf. Fig. 2). Plots are the effects of individual variables, accounting for other predictor variables, estimated by generalised additive models (GAMs); shaded areas show 95% Bayesian intervals. Variables with importance values > 0.6 are plotted in blue, and importance values < 0.6 are plotted in red (cf. Table 2 and Fig. 2). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
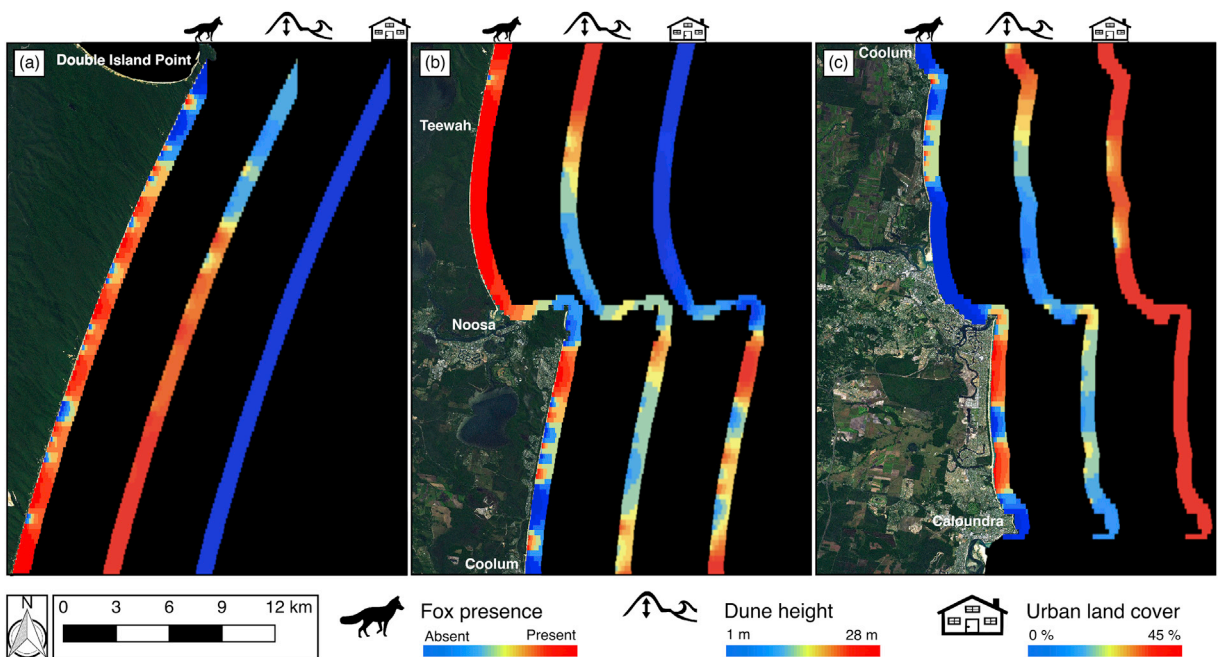

Fig. 4. Variation in fox occurrence in relation to dune height and urban land cover along beaches of the study area. For visual clarity, distributions are shown in three sectors: a) Double Island Point to the north of Teewah (left panel), b) Teewah to Coolum beach (centre panel), and c) Coolum to Caloundra (right panel).

un-vegetated part of the beach. Because foredunes backed by higher primary dunes are also the preferred habitat for many ground-nesting birds, such as oystercatchers and plovers (Meager et al., 2012; Ehmke et al., 2016; Maslo et al., 2016a, 2016b, 2019), landscape features may modify the impact of invasive species on exposed beaches.

Red foxes are part of the urban fauna in many cities globally (Marks and Bloomfield, 2006; Cove et al., 2012; Duduś et al., 2014; Scott et al., 2014; Villaseñor et al., 2014). Yet, in this coastal setting, where a series of peri-urban areas and small coastal cities are interspersed by a few and small natural areas (small rocky headlands, reserves and estuarine inlets), we found that foxes were less frequent on beaches abutted by more urban development. Fox natal den site selection is negatively impacted by the presence of domestic dogs in backyards (Marks and Bloomfield, 2006). As domestic dogs are highly prevalent throughout the entire coastal urban strip, highly urban areas may provide unsuitable habitat for natal denning, reducing red fox density. Although we measured domestic dog presence on beaches seawards of the dunes, this does not necessarily reflect the density of domestic dogs within the adjacent urban area. Furthermore, fox presence at some of the urbanised beaches may be the result of populations of foxes occurring in small pockets of natural vegetation and coastal reserves (Schlacher et al., 2015).

There is support in the literature that proximity to water influences fox distributions in other landscapes (Silva et al., 2009; Cleve et al., 2011; Carter et al., 2012; Hradsky et al., 2017; Mumma et al., 2017). We found no evidence for this, possibly as a consequence of the widespread availability of water in this coastal setting. Foxes are known to use roads and man-made paths for movement; therefore, we tested whether the density of beach access points (a measurement of connectivity (Schlacher et al., 2015) correlated with fox distributions on beaches. Greater connectivity between the beach and the back-area of the dunes did not result in more foxes scavenging along the strandline, emphasising that foxes can use marine shorelines in spatially flexible ways.

Lethal fox 'control' activities are undertaken throughout Australia, the aim being to suppress fox populations by killing individuals (Berry et al., 2013; Kirkwood et al., 2014; Mahon , 2009; Saunders et al., 2010). The practices, while ostensibly targeting red foxes, can also kill domestic animals and native animals, and are therefore regarded as inappropriate in more populated urban areas, including coastal regions (O'Hagan, 2004; Subroy et al., 2018). This practice can, however, result in sporadic, uncoordinated, and reactive culling attempts, despite research demonstrating that small-scale, short-term efforts are ineffective to control foxes (Gentle et al., 2007; Newsome et al., 2014; Saunders et al., 2010; Towerton et al., 2011). We found that fox removal, conducted as part of the local government's invasive species control efforts, did not affect the distribution and abundance of red foxes, despite considerable control efforts in the coastal areas directly bordering ocean beaches.

Invasive carnivores adversely impact many populations of native species (Doherty et al., 2015b, 2016). In Australia, the detrimental impact of red fox populations to native species has been widely and comprehensively documented for decades (Saunders et al., 2004; Abbott, 2011; Anson et al., 2013; Woinarski et al., 2018). Effectively reducing this impact and conserving coastal biodiversity and function is contingent upon the ability to successfully identify key habitat features associated with the distribution of this invasive species (Tingley et al., 2013). In this context, we have shown that red foxes at the edge of the sea are not necessarily as eclectic in their habitat choices as would be commonly surmised based on conventional wisdom that suggests quasi indiscriminate habitat use (Table S1). Instead, tall dunes outside of urbanised sections of the coast appear to be favourable fox habitats in a subtropical landscape dominated by exposed sandy beaches backed by coastal dunes and interspersed by urban development. These landscape attributes form the setting for much of the subtropical and temperate coastline of Australia, offering a vast geographic tapestry to test how models of fox habitat choice can be used to refine invasive carnivore management.

5. Conclusion

Conventional wisdom suggests that red foxes have largely non-specific habitat association, being broad generalists with flexible habitat choices. This thesis is not supported by the distribution patterns of red foxes inhabiting coastal dunes and foraging on sandy beaches at night in SE Queensland. We found that habitat associations are not indiscriminate, but that foxes are more abundant where beaches are backed by taller dunes that are less transformed by urban development. Fox control efforts by the local authority did not influence fox distributions. Foxes are functionally important consumers in coastal food-webs, and the disjunct distributions demonstrated here suggest that their trophic role may be spatially heterogeneous. In the context of invasive species management, our findings provide empirical data to consider spatially refining future investments and transition to more ethical methods.

Data accessibility statement

The data underpinning this paper are available here:
Schlacher, Thomas et al. (2020), Olivia Kimber 2018 Honours Fox Mapping, Dryad, Dataset, https://doi.org/10.5061/dryad.qjq2bvqcn.

Declaration of competing interest

The authors declare no conflict of interest.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2020.e01071.

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