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Limited functional redundancy in vertebrate scavenger guilds fails to compensate for the loss of raptors from urbanized sandy beaches

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ABSTRACT

Aim Globally, urbanization is one of the most widespread, intense and ecologically destructive forms of landscape transformation, and it is often concentrated in coastal areas. Theoretically, species losses attributable to urbanization are predicted not to alter overall ecosystem function if functional redundancy (i.e. replacement of function by alternative species) compensates for such losses. Here, we test this expectation by measuring how coastal urbanization affects scavenger guilds on sandy beaches and whether changes in guild composition result either in an overall loss of scavenging efficiency, or in functional compensation under alternative guild structures, maintaining net ecosystem functioning.

Location Fourteen beaches along the east coast of Australia with variable levels of urbanization.

Methods Scavenging communities and rates of carrion removal were determined using motion-triggered cameras at the beach-dune interface.

Results A substantial shift in the community structure of vertebrate scavengers was associated with gradients in urbanization. Iconic and functionally important raptors declined precipitously in abundance on urban beaches. Importantly, other vertebrates usually associated with urban settings (e.g. dogs, foxes, corvids) did not functionally replace raptors. In areas where < 15% of the abutting land had been developed into urban areas, carcass removal by scavengers was often complete, but always > 70%. Conversely, on beaches bordering coastal cities with < 40% of natural vegetation remaining, two-thirds of fish carcasses remained uneaten by scavengers. Raptors removed 70–100% of all deployed fish carcasses from beaches with < 8% urban land cover, but this number dropped significantly with greater levels of urbanization and was not compensated by other scavenger species in urban settings.

Main conclusions There is limited functional redundancy in vertebrate scavenger communities of sandy beach ecosystems, which impacts the system's capacity to mitigate the ecological consequences of detrimental landscape transformations.

Keywords

Carrion, coastal management, functional loss, human impacts, sandy beaches, scavenging, urbanization.

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INTRODUCTION

Functional diversity is a critical component of ecosystem functioning (Cardinale *et al.*, 2006). The broad contention is that if ecosystems show functional redundancy, and thus comprise a suite of species that fulfil similar roles (Lawton & Brown, 1993), the likelihood of losing particular ecosystem functions as a result of biodiversity loss is decreased (Naeem & Wright, 2003; Loreau & Mazancourt, 2013). In particular, different responses to environmental change of functionally equivalent species increase 'response diversity' (Elmqvist *et al.*, 2003), enhancing the capacity of ecosystems to resist disturbances (Mori *et al.*, 2013). In the face of increasing environmental change forced by anthropogenic pressures, maintenance of functional diversity is predicted to be critical for the long-term sustainability of ecosystems (Laliberte *et al.*, 2010).

The requirements of a growing human population are driving a global acceleration in the rate of land use change (Grimm *et al.*, 2008). Urban population growth in particular is expanding at unprecedented rates (Seto *et al.*, 2010), having significant, and potentially irreversible, effects on species diversity and ecosystem functioning (McDonald *et al.*, 2008). Effects of urbanization include losses of species richness (McKinney, 2008), changes in carnivore distributions and abundances (Ordeñana *et al.*, 2010), and elevated extinction rates of plants (Hahs *et al.*, 2009). By contrast, some species thrive in urbanized areas (Shochat *et al.*, 2006; Cardilini *et al.*, 2013; Sushinsky *et al.*, 2013), and these 'urban' species might compensate for potential loss of ecosystem functions in cities (Gonzalez & Loreau, 2009).

Globally, urbanization is widespread, concentrated, and accelerating in the coastal strip (Martínez *et al.*, 2007). Coastal areas also comprise ecosystems that provide important services (e.g. harvestable natural resources, recreation and tourism, storm buffers), which are in part controlled by the distribution and occurrence of species in these ecosystems (Barbier *et al.*, 2011). Changes in species distribution or abundance along urbanized coastlines have been reported across a variety of taxa and geographic areas, including altered invertebrate and fish assemblages near artificial structures (Bulleri & Chapman, 2010; Hubbard *et al.*, 2013), a decline in the abundance of an endangered coastal mammal due to habitat loss (Schmidt *et al.*, 2012) and altered habitat selection of birds on beaches accessible to off-road vehicles (Meager *et al.*, 2012). While these changes manifest as a result of key ecological processes such as recruitment, foraging, competition and predation, empirical data to test the effect of urbanization on important processes in coastal ecosystems remain scarce.

Hypothetically, if functional redundancy is a common trait of ecosystems, human changes in land use that alter species composition should result in little or no change to ecosystem functioning because of adequate functional replacement (Fig. 1). Alternatively, in systems where functional redundancy is limited, there will be little or no effective

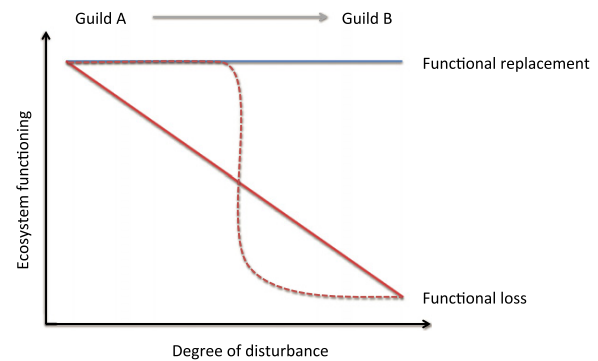


Figure 1 Conceptual model tested in this study. If increased levels of disturbance, for example urbanization, alter the species composition of functional groups (i.e. guilds) that contain functionally equivalent species, overall ecosystem function is maintained through functional replacement of species (blue line). Alternatively, if there is no replacement of the lost species or guild, or if functional diversity in the alternative guild is considerably different from that of the lost guild in undisturbed environments, this could lead to functional loss of ecosystem processes, which might occur either gradually with increasing disturbance (red solid line), or abruptly when a particular threshold for a guild is reached (red dotted line).

compensation for lost species or guilds, leading to substantial changes in ecosystem function overall. An equivalent degradation or loss of ecosystem function will also occur if the traits of the replacement species or guild in disturbed settings differ considerably from those of the original species complement in less disturbed environments (Fig. 1). This loss could occur either gradually with an increase in disturbance, or abruptly when a particular threshold for a species is reached (Scheffer *et al.*, 2001).

Testing competing models for the role of functional redundancy in shaping the consequences of species loss or replacement in altered landscapes requires systems with three key traits: (1) humans have altered the landscape, (2) species' functions are reasonably well known and (3) ecological functions can be accurately measured as a response variable. Sandy beaches possess these traits. Because beaches are found along stretches of coastline with variable intensity of development and urbanization, they represent an ideal system to test the effects of urbanization on ecosystem processes (Schlacher *et al.*, 2012). We chose carrion consumption, or scavenging, as the ecosystem process of interest, because it is a widespread and crucial process in many ecosystems (Nowlin *et al.*, 2008) that is also a prominent and important feature of beaches (e.g. Schlacher *et al.*, 2013a). Moreover, carrion is utilized by a variety of species that are highly adaptive to changes in resource supply (Wilson & Wolkovich, 2011). A comparison of scavenging dynamics on sandy beaches at two extreme levels of urbanization in Australia showed that invasive mammals replaced raptors as scavengers on urban beaches, resulting in a significant decline in scavenging efficiency (Huijbers *et al.*, 2013). We do not know, however, if these

changes occur gradually, or if there is a threshold in the amount of urbanization that abruptly excludes certain scavenger species, changing key functional properties of the system.

In this study, we tested competing conceptual models of how functional redundancy might mediate the consequences of species loss, or replacement, for ecosystem function (Fig. 1). For this, we use the removal of animal carcasses by vertebrate scavengers on sandy beaches over a gradient of coastal urbanization as the test system. Rates of carrion removal (a functional response) were determined at multiple beaches encompassing a gradient of urban development to test: (1) whether scavenger guilds on sandy beaches change structurally with increasing levels of urbanization, and (2) whether such changes result in a gradual or abrupt functional loss of an ecosystem process; or c) whether functional replacement of species within guilds can maintain overall scavenging efficiency of the system.

METHODS

Study sites

This study was conducted on 14 beaches in south-east Queensland and northern New South Wales, Australia, stretching from Rainbow Beach to Byron Bay, covering 340 km of coastline (Fig. 2). This coastline comprises areas that are intensively developed for residential and recreational purposes, such as the Sunshine and Gold Coasts, interspersed

with natural non-urban areas with relatively low levels of human impact, such as North Stradbroke Island. The wide variety in land use and habitat conditions makes this coastline ideal for studying scavenger responses to urbanization.

Land use and vegetation cover of each study site was calculated using a random-point count methodology in Coral Point Count with Excel extensions (CPCe) (Kohler & Gill, 2006). In this software package, a matrix of randomly distributed points can be overlaid on still images. These points are then assigned to predetermined land use categories to estimate coverage of each category.

In order to quantify the intensity of urbanization at scales that correspond to the way animals use their environment, we first established the spatial extent of daily home ranges of potential scavenger species. Previous research showed that the most abundant and frequent beach scavengers in this region are mammals (foxes, dogs, rats) and birds (raptors, gulls and crows) (Huijbers *et al.*, 2013; Schlacher *et al.*, 2013a,b). We used the average daily home range of the red fox [1.6-km linear distance, based on (Meek & Saunders, 2000) and (Dekker *et al.*, 2001)] as proxy for daily movement ranges of all mammals, and the linear daily foraging distance of the white-bellied sea eagle [9.2 km, based on (Wiersma & Richardson, 2009)] for birds. A thorough literature review indicated that the daily home ranges of other potential scavenger species would fall within these two ranges, enabling us to assess the effects of urbanization on the maximum area used by groups of scavengers. We used a stratified random method of point specification to quantify

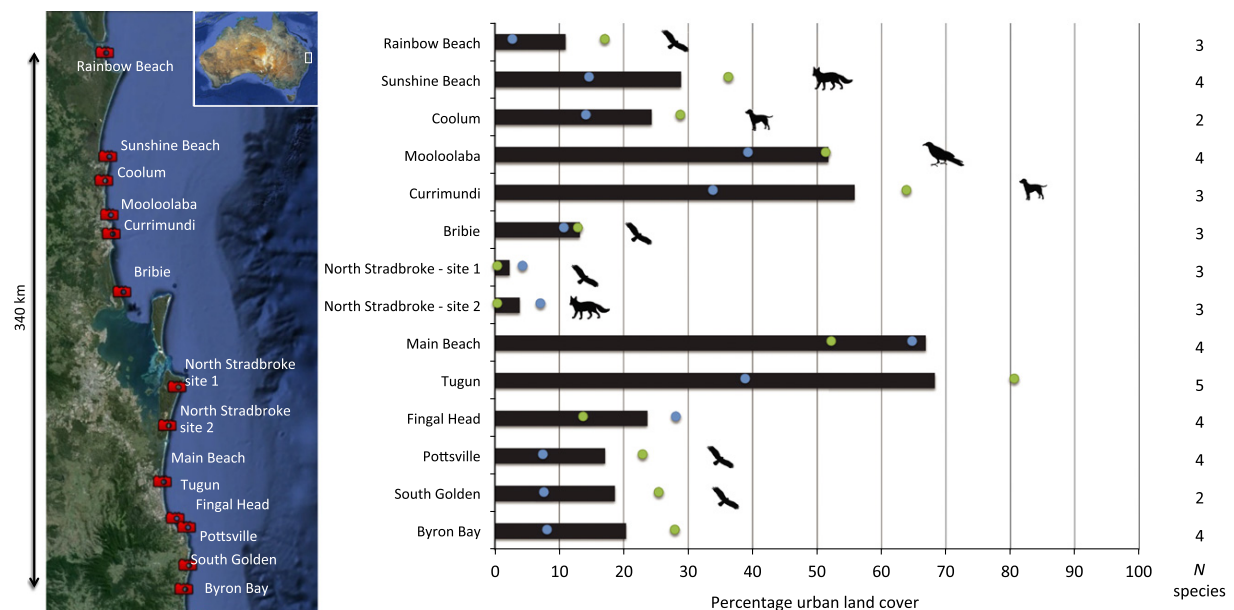


Figure 2 Locations of study sites (left panel) and percentage of urban land cover averaged for raptors and foxes for each site (black bars in right panel). The dots indicate percentage urban land for areas behind the beach that represent the daily home range of foxes (4.6 km², green dots) and raptors (169 km², blue dots). For each site, the dominant scavenger species recorded in our experiment is shown with a silhouette (raptor, fox, dog or crow). For sites without an animal silhouette, more than half of the camera deployments did not capture any scavengers. The column on the right side shows the number of scavenger species recorded per site.

the intensity of urban development within a radius of 1.6 km for the fox home range, and 9.2 km for the raptor home range, around each of the study sites. The centre of this home range was based on the position of the most central camera within the array (see Experimental set-up). A customization option in CPCe allowed the specification of random points on still images retrieved from Google Earth to user-defined land cover codes (see Appendix S1 in Supporting Information for detailed CPC methods).

The percentage of urban land cover ranged from 0% to 92% across our sites and differed per site between the fox and raptor home ranges (Fig. 2). Urban land included all bitumen roads, buildings, industrial areas, public amenities, airports, strongly modified vegetation such as parks and golf clubs, cleared land and landfills. For most sites, the smaller fox home range comprised a higher percentage of urbanization, while the larger area overlaid for the avian scavengers encompassed some remnant natural vegetation, resulting in lower percentages of urban land cover. On the contrary, the two most non-urban study sites on North Stradbroke island encompassed only natural vegetation (0% urban) in the smaller fox home ranges (4.6 km²), whereas the larger raptor home ranges (169.3 km²) tended to overlap with some developed areas further inland from the beach, resulting in a small increase (4–8%) in urban land cover. Overall, the selected study sites showed large and interspersed variability of land use, emphasizing the suitability of this geographic region for quantifying the effects of coastal urbanization on scavenger dynamics.

Experimental set-up

Scavenger guild composition and scavenging rates were measured by placing a fish carcass in front of a motion-triggered camera at the beach-dune boundary. Six replicate cameras were deployed at each site during two separate 24-h trials, one starting in the morning and the other just before sunset. This was carried out to capture both diurnal and nocturnal scavengers. Previous experiments showed that scavengers are able to locate and utilize carrion within 24 h (Huijbers *et al.*, 2013), ensuring that this time period was appropriate to monitor scavenging dynamics. Additionally, urban beaches are regularly groomed and longer exposures would increase the risk of interference by beach cleaners. All results are reported against this standard exposure time of 24 h. There was no significant relationship between the duration camera traps were recording in the field at a particular site and the percentage of urban land cover at that site ($r = 0.08$ for daytime hours and $r = 0.11$ for night-time hours), meaning that small variations in deployment time were not systematically associated with land use and hence could not bias our results. Daytime and night-time trials at the same site were on average 11 days apart, and the entire experiment lasted over a period of 5 weeks in November–December 2012. We deployed 168 cameras in total, but retrieved data from only 136 successful deployments due to theft and vandalism.

Although there was a weak correlation ($r_s = 0.26$) between the number of successful camera deployments per beach and ordinations of species assemblages, there was no significant correlation between the number of successful deployments and the percentage of urban land cover ($P = 0.251$), ensuring that measured differences in scavenger assemblages were not confounded by variations in sampling effort between sites.

For each deployment, one flathead mullet, *Mugil cephalus*, weighing 258.2 ± 85.6 g (SD), was placed on the beach, 5–10 m away from the camera which was placed in the frontal dune. Mullet was chosen as carrion source because this species has a widespread distribution, is commonly found in the surf zone of beaches and is consumed by a wide variety of scavenger species (Schlacher *et al.*, 2013a). Digital passive infrared (PIR) motion-triggered cameras (ScoutGuard SG560Z-8M) were used to monitor the presence of scavengers at the fish carcasses. Each camera was set to take three consecutive pictures upon detection of movement, with a reset period of 7 s between trigger events. All cameras within a site were deployed approximately 200 m apart and positioned on the edge of the dunes. Pictures taken by the cameras provided information on the time and date of carrion detection and removal, the number and species of scavengers observed during a deployment, and the scavenger species that removed a carcass. Animals in the images were recorded as scavengers when they were detected with the fish in their mouth, with their mouth touching the fish, or when they appeared next to the fish in an image (i.e. they 'photobombed' the experiment) and the fish was gone in the next image.

Data analysis

Differences in the species composition of scavenger guilds among study sites were visualized using nonmetric multidimensional scaling (nMDS) in R (R Development Core Team, 2010) using the R package *vegan* (Oksanen *et al.*, 2013). The ordination was based on Bray–Curtis resemblance matrices calculated from aggregated species incidence per site. The influence of the percentage of urban land cover on the scavenger guild ordination was analysed by the *envfit* function in the *vegan* package. Binomial generalized additive models (GAMs) were used to model the relationship between percentage urban land cover and the proportion of carrion removed across beaches, because we had no *a priori* expectation about the shape of the curve. This relationship was modelled for total removal of carrion from study sites and separately for the two dominant scavenger groups, raptors and foxes/dogs. Carrion removal was calculated as the proportion of total number of fish carcasses removed (i.e. the fish was not present around the camera site upon retrieval of the camera after 24 h) for the total number of fish carcasses deployed. For removal by either raptors or foxes and dogs, the total number of carrion items deployed was based on availability during the time period when these scavengers are mostly actively foraging. Thus, for species that mainly search

for carcasses during the day, the number of available carcasses consisted of the number of fish deployed in the morning + the number of fish deployed before sunset that were still present after sunrise the next day. For scavengers that forage mainly at night, the number of available carcasses consisted of the number of fish deployed before sunset + the number of fish deployed in the morning that were still present at sunset. All GAM analyses were executed in R using the mgcv package (Wood, 2012).

RESULTS

Urbanization significantly altered the species composition of the vertebrate scavenger guild foraging at the land–sea interface (Fig. 3, nMDS with envfit analysis for urban land cover, $P = 0.041$). Raptors (brahminky kite, *Haliastur indus*; whistling kite, *Haliastur sphenurus*; white-bellied sea eagle, *Haliaeetus leucogaster*) dominated the scavenger guilds on largely undeveloped beaches that had < 10% of the upland vegetation converted to urban land (Figs 2 & 3). While raptors were recorded occasionally in our camera deployments on beaches with intermediate levels of urbanized land (10–40%), no raptors were observed scavenging on the highly urbanized beaches (i.e. Main Beach and Tugun). Scavenging at semi-urban beaches (20–50% urban land cover) was dominated either by domestic dogs (*Canis familiaris*) or by red foxes (*Vulpes vulpes*); the occurrence of these mammalian scavengers was, however, unrelated to the intensity of urbanization behind the beaches: both carnivores occurred across study sites with varying levels of urbanization. At beaches with > 60% urban land cover, half of the camera deployments recorded no scavengers at all. Overall scavenger richness was similar across the urbanization gradient (Fig. 2) and relatively high on urban beaches, chiefly because of the presence of rats (*Rattus* spp.), domestic cats (*Felis catus*), Torresian crows (*Corvus orru*)

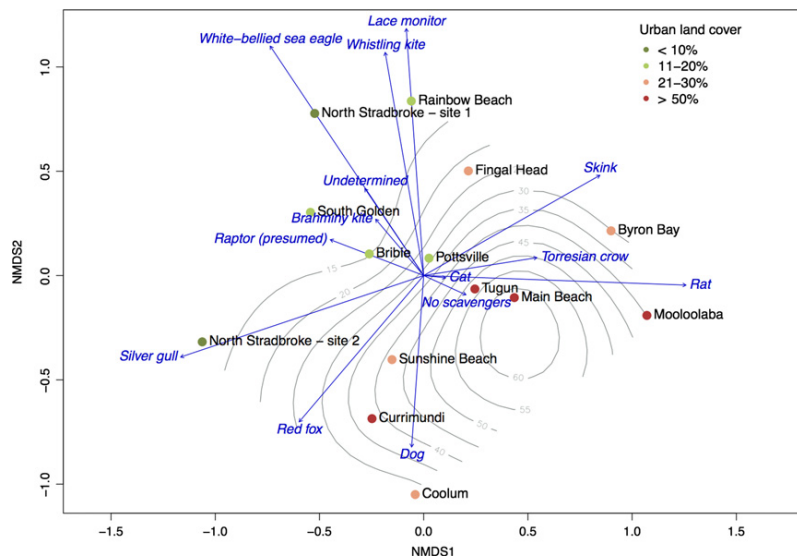
and silver gulls (*Chroicocephalus novaehollandiae*) that complemented domestic dogs and foxes.

Urbanization significantly depressed ecological function as measured by carrion consumption rates via vertebrate scavengers. GAMs showed a significant nonlinear decline in the total amount of carrion removed ($P = 0.023$) and removal by raptors ($P = 0.039$) from beaches within 24 h with an increase in urban land cover. While the probability of carcass removal was > 70% for study sites with < 15% urban land cover, this probability rapidly declined to < 30% for sites with > 60% urban land cover (Fig. 4a). Raptors were responsible for the majority of carrion removed from sandy beaches in non-urban areas (Fig. 4b). Within the standardized period of 24 h, raptors consumed 70–100% of the carrion in areas with < 8% urban land cover in their daily home range. Beyond this threshold, carrion removal by raptors dropped significantly and was absent on the most urban beach (Main Beach). Two semi-urban beaches (Sunshine Beach and Coolum) with 30–40% urban land cover showed relatively high carcass removal rates (65–72%), attributable to foxes and dogs. Although this shows a partial replacement of the scavenging function, and thus contributes to arresting the decline in total carrion removal at intermediate urbanization levels, it does not fully replace scavenging rates by raptors. On beaches with > 50% urban land cover, no other scavenger species, including foxes and dogs, compensated for the lack of carrion removal by raptors (Fig. 4c). In this system, fundamental human changes of the landscape resulted in species loss and replacement with significant consequences for net ecosystem function, indicating a lack of functional redundancy in the scavenger guild.

DISCUSSION

Mitigating the ecological consequences of accelerated environmental change requires understanding how changes in

Figure 3 Ordination (nonmetric multidimensional scaling, nMDS biplot) based on Bray–Curtis resemblance matrix calculated from aggregated species incidence per site (2D stress value = 0.16). Study sites are colour-coded according to average percentage of urban land cover, and the smoothed gradient of urbanization, fitted using thin-plate generalized additive models (GAM) splines, is projected onto the ordination as grey isopleths. The position of species names reflects their associations across the nMDS ordination.



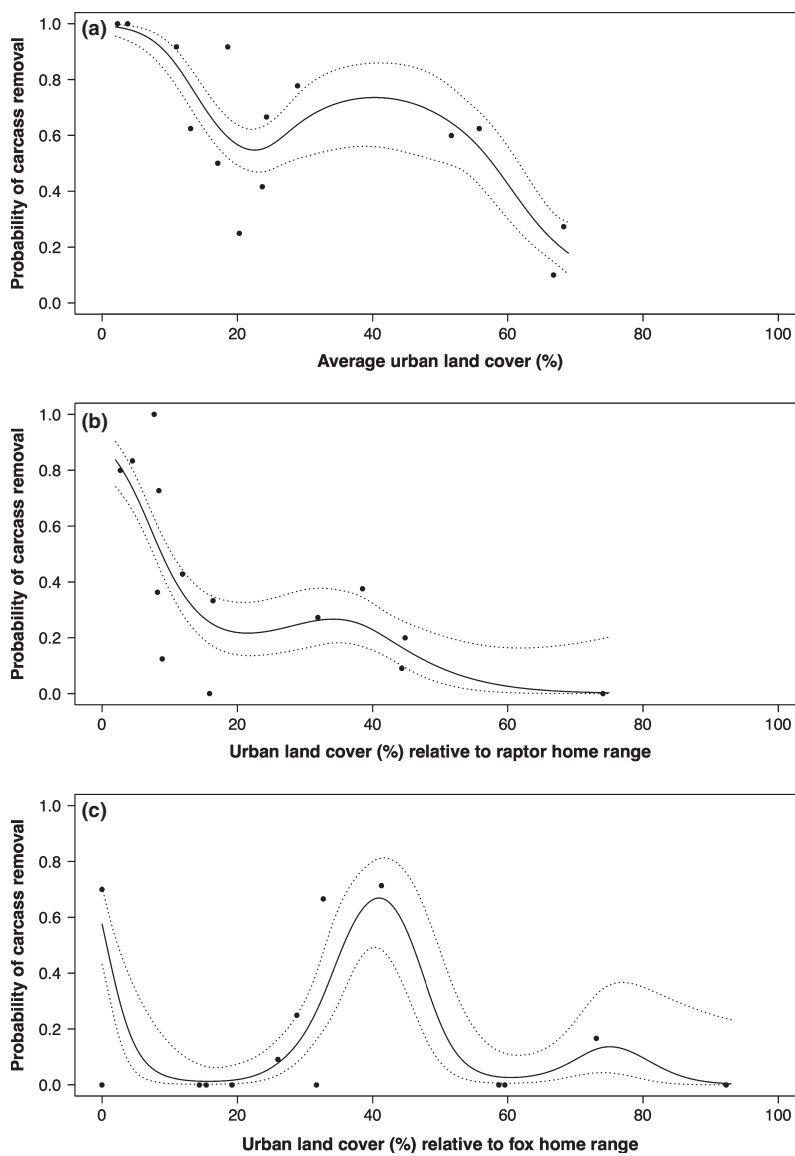


Figure 4 Results of general additive modelling of the probability of carrion removed as a function of the percentage urban land cover across a gradient of beaches (fitted relationships as solid lines; standard errors as stippled lines) for (a) total carrion removal, (b) carrion removal by raptors and (c) carrion removal by foxes and domestic dogs.

biodiversity affect ecosystem functioning (Loreau & Mazancourt, 2013). The results of this study show that urbanization led to a significant change in the composition of scavenger guilds of sandy beach ecosystems and a reduction in scavenging efficiency. In non-urban areas, raptors dominated the scavenger guild, removing the majority of fish carcasses. On beaches where the abutting land had been largely cleared for urban development carrion removal by raptors declined precipitously, being effectively lost as an ecosystem function. This loss of function was not fully compensated by other scavenger species, indicating that there is limited functional redundancy in these ecosystems to mitigate detrimental landscape transformation.

Land use change has been identified as a dominant driver for future global biodiversity loss (Pereira *et al.*, 2010). A decline in species richness as a result of modification of the

natural environment – for example by agriculture, logging or urban development – can potentially lead to the loss of essential ecosystem functions (Zavaleta & Hulvey, 2004; Flynn *et al.*, 2009; Mori *et al.*, 2013). Here, we found that overall species richness of the scavenger community of beaches did not decline in areas with greater levels of urbanization but that the composition of the scavenger assemblage changed significantly. This could not have resulted from other factors, such as geographical limits or seasonal changes in species occurrence, as all recorded scavenger species were observed along the entire coastline included in this study and throughout the study period. Urban beaches also had a significantly lower number of fish carcasses removed in comparison to less-developed areas. This leads to the conclusion that it was the loss of the functionally most important group of scavengers – raptors – from urbanized beaches that drove

the steep decrease in the rate of carrion removal. Carrion consumption by scavengers is an important process in stabilizing and structuring food webs and is thus a key component of ecosystem functioning (Barton *et al.*, 2013). It remains to be tested whether other ecosystem functions, such as predation, breeding success or nutrient cycling rates, respond in a similar way, and whether similar results can be found on sandy beaches in other parts of the world (Schlachter *et al.*, 2014). Yet, our study shows a detrimental effect of urbanization on one key process, indicating a loss of function driven by the decline of one particular group.

The vulnerability of species to land use changes depends on species-specific traits and habitat preferences (Knapp *et al.*, 2009; Evans *et al.*, 2011) and the spatial pattern of urban growth (Sushinsky *et al.*, 2013). Within the avian community, corvids and small raptors are generally less sensitive to habitat loss or fragmentation compared with raptors with large home ranges such as the white-bellied sea eagle (Chace & Walsh, 2006). Indeed, we observed scavenging corvids at the majority of our study sites (9 of 14), regardless of whether these sites were highly urbanized or not. Raptors were observed at sites with intermediate levels of urbanization, such as Sunshine Beach and Fingal Head, but in much lower numbers compared with largely non-urbanized sites. This indicates that some function can be retained in areas with intact green spaces in the vicinity of urban development. This finding corresponds with an earlier study that showed that locally intense, but spatially constrained, urbanization has less severe impacts on distributions of urban-sensitive bird species compared with areas with lower residential densities spread across a larger spatial scale (Sushinsky *et al.*, 2013). Other species that appeared to be less sensitive to urbanization included non-native and feral animals, such as red foxes, dogs and cats. It is a common observation that urbanization benefits non-native species (McKinney, 2006), yet in our study system, they only partially offset the loss of raptors at intermediate levels of urbanization where their activities were most intense. The concentration of dogs on semi-urban beaches likely results from dog restrictions on highly urban beaches due to health-related issues (Wright *et al.*, 2009) and on non-urban beaches because of conservation concerns. Even where partial functional replacement was observed, it is highly questionable whether replacement by non-native, feral species is qualitatively equivalent. Moreover, while these species might elevate the species count in urban areas, the decrease of local native species can lead to a global loss of biodiversity (Simberloff *et al.*, 2013).

The prime 'function' of beaches in the public's eye is the provision of recreational opportunities and aesthetically pleasing landscapes (McLachlan *et al.*, 2013; Schlacher *et al.*, 2013c). Dunes are ecologically closely linked to beaches but are conventionally considered to function mainly as coastal defence units to protect human assets further inland (Schlachter *et al.*, 2008). For both beaches and dunes, conservation of wildlife is seldom explicitly included or efficiently

enforced in management plans (Weston *et al.*, 2014). By protecting intact dune and beach habitats, managers could achieve two goals simultaneously: carrion will be removed by natural scavengers, reducing the need for expensive beach grooming, and at the same time, this creates clean beaches and a landscape with iconic species such as raptors that together provide an aesthetic view and increase potential for ecotourism. However, despite their immense socio-economic importance and the severe threats from climate change impacts and coastal development, sandy beach ecosystems are still largely overlooked in conservation management plans (Schlachter *et al.*, 2007; Dugan *et al.*, 2010; Harris *et al.*, 2014).

In conclusion, our study shows that conversion of dunes to urban land is associated with severe declines in raptor populations in the coastal strip. These declines have substantial ecological repercussions for a key ecological function, removal of carcasses by scavengers. Theoretically, changes to species compositions do not necessarily result in corresponding shifts in ecological processes if other functionally equivalent species offset species losses. This was not the case in our experimental setting: we show that the loss, or reduction in number, of raptors from urban beaches is not matched by increases in other scavenger species, leading to a net functional loss of this ecosystem process. Our results imply that spatial conservation planning for coastal systems must extend to larger wildlife that maintain the delivery of critical ecosystem services. We cannot automatically assume that functional diversity and redundancy provide insurance against impacts on functional attributes of ecosystems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Detailed description of CPC methods that were used to quantify percentages of urban land cover around the study sites.

BIOSKETCH

All authors are part of the CRN (Collaborative Research Network) Water Sciences group. Their research is focused on key emerging issues in marine, estuarine and coastal ecology. An overview of our research is presented in the following YouTube video: <http://youtu.be/-1fea7mFpf8>.

Author contributions: All authors were involved in conceiving the idea, sampling, analysing the data and writing the paper.

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Supporting Information

The intensity of urban land cover around each sample location was quantified using Coral Point Count with Excel extensions (CPCe, Kohler and Gill 2006). Based on daily home ranges for foxes (1.6 km linear distance) and raptors (9.2 km), two rectangles were drawn in Google Earth around each site, measuring the linear daily home range vertically along the shoreline to the north and south, and horizontally landwards (see Figure S1). A still image was saved for each rectangle around each site and uploaded into CPCe.

In CPCe, we used a stratified random method of point specification. Each image was subdivided into four columns and eight rows (32 cells), and each cell was populated with random points. The number of random points assigned to each rectangle was weighted according to the relative size of each daily home range. Thus, the raptor home range was 5.75 times the size of the fox home range, and subsequently was assigned 5.75 times more points. This resulted in a total of 128 points for the fox rectangle, which comprised an area of 5.12 km², resulting in an average distance between points of 200m. The raptor rectangle consisted 736 points in an area of 169.3 km², resulting in an average distance of 480m between points.

A customisation option in CPCe allowed the specification of random points to user-defined land cover codes, which were divided into four main categories: natural vegetation, natural water, urban land (i.e., strongly modified impervious land), and urban water (i.e., strongly modified water such as canals and ponds). Raw and summarised data of each land cover type per rectangle per site could then be exported into Excel for further analysis. We excluded the data from the outermost western corner cells of each image to create a semi-circle around each study site.

The reported percentages of urban land cover in the manuscript refer to all points that were assigned in the urban land category, thus excluding areas that were assigned to urban water. Urban land included all bitumen roads, buildings,

industrial areas, public amenities, airports, strongly modified vegetation such as parks and golf clubs, cleared land and landfills.

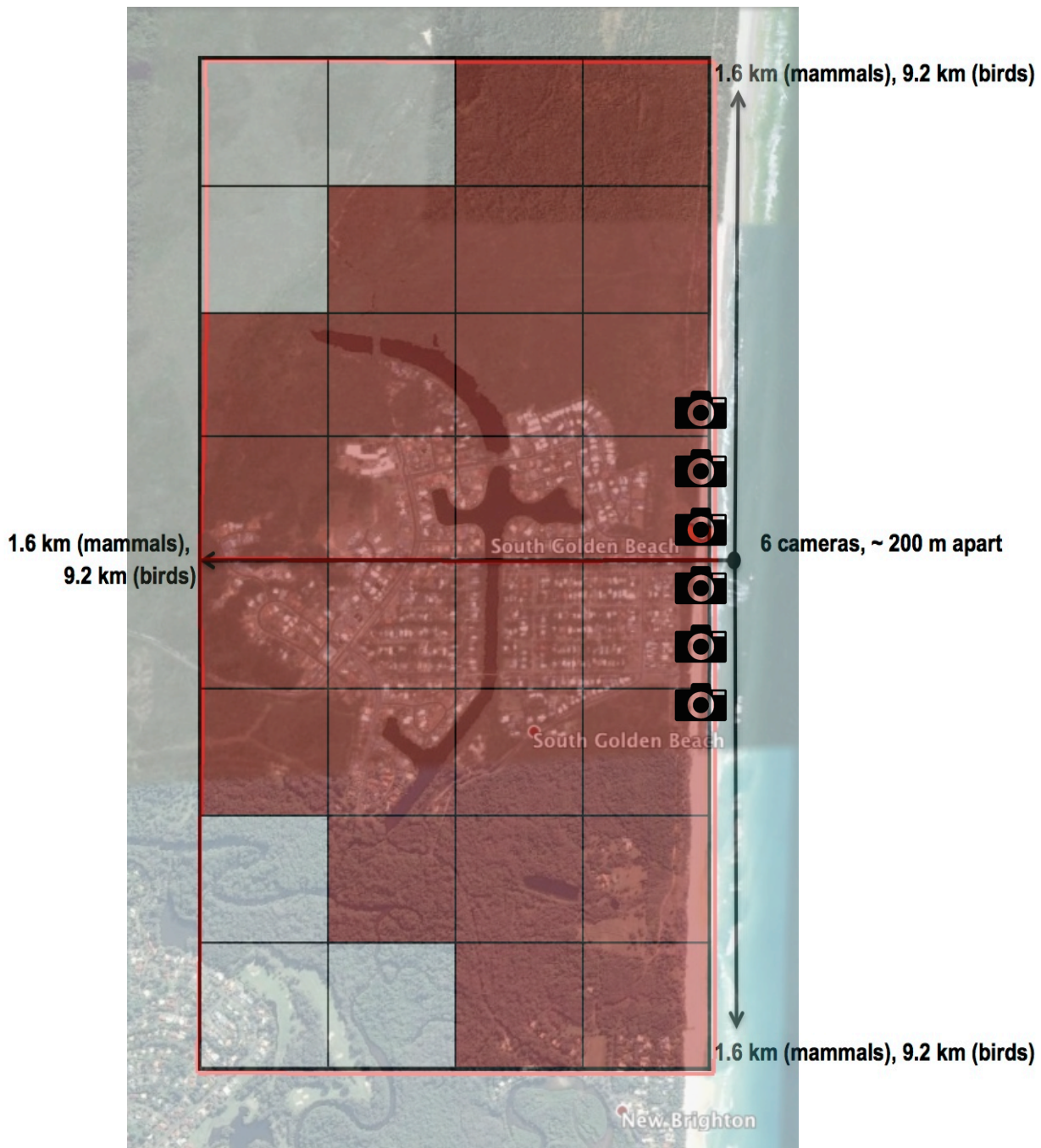


Figure S1. Image of study site from Google Earth overlaid with grid to assign random points in CPCe. Only the points in the red grid cells were used for analysis to create a semi-circle around the study site in which land cover was assessed.

Kohler, K. E. & S. M. Gill, 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences* 32: 1259-1269