



Key Ecological Function Peaks at the Land–Ocean Transition Zone When Vertebrate Scavengers Concentrate on Ocean Beaches

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ABSTRACT

Ecotones can form hot spots of biodiversity by containing species from multiple ecosystems. Because biodiversity is often linked to ecological function, we posit that rates of key ecological functions are highest at ecotones and decline away from them. Here we test this hypothesis by measuring spatial decays in the function of carrion scavenging on a gradient ranging from ocean beaches upland into abutting coastal dunes. A large field experiment in Eastern Australia, at the ecotone formed by ocean beaches, employed multiple carrion placements and motion-triggered cameras to identify the animals consuming

carcasses and the removal rates of necromass. Significantly more carrion was consumed by vertebrate scavengers at the beach interface (50–80% of total necromass removed) and declined significantly with distance (max. 350 m) into the abutting coastal dunes (20–25%). This marked cline was due to the consumption of carrion by both dune-dwelling and beach-dwelling animals at the beach–dune interface and a decline in scavenging activity by both groups farther upland. These spatial effects were consistent between sites, but the lower carrion removal away from the beach became less pronounced as the carcasses putrefied, suggesting that microbial actions can modify carrion suitability for vertebrate scavengers and hence change spatial patterns in ecological function. Our findings provide quantitative support for the widespread notion that ecological transition zones are hot spots of ecological functions and highlight the importance of managing functionally important species at ecotones.

Key words: Carrion scavenging; Coastal dunes; Ocean beaches; Raptors; Functional spatial ecology.

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INTRODUCTION

*Even as poor birds, deceived with painted grapes,
Do surfeit by the eye and pine the maw,
Even so she languisheth in her mishaps,
As those poor birds that helpless berries saw.*
William Shakespeare, *Venus and Adonis*

Ecosystems that are functionally linked via transition zones between adjacent systems (that is, meta-ecosystems) exchange energy, matter, and organisms across boundaries (Loreau and others 2003a, b; Leibold and others 2004). Such transition zones, or ecotones, can be hot spots for biodiversity because they draw species from adjoining ecosystems, thereby forming spatial concentrations of biodiversity in many settings (Araujo 2002). Because biodiversity can correlate with the rates of ecological function (Risser 1995a, b; Loreau and others 2003a, b; Micheli and Halpern 2005), it is plausible that species-rich ecotones have higher rates of ecological functions than adjacent areas. For example, shorelines support greater rates of predation than adjacent aquatic or terrestrial areas in both freshwater (for example, bears consuming salmon, fish feeding on insects) and estuarine settings (for example, crocodiles feeding on terrestrial vertebrates, shorebirds feeding on smaller invertebrates and fishes intertidally), partly because species from both abutting domains feed at the interface (Bocher and others 2014; Andersson and Reynolds 2017; Somaweera and others 2018). Whilst ecological functions are widely assumed to peak at, or near, many types of interface, there may be exceptions. For example, if interfaces correspond with the physiological limits of species (Risser 1995a, b; Van Rensburg and others 2009), functions might be lower at interfaces (Hoffmann and Blows 1994) (see, however, Sexton and others 2009). Environmental conditions at interfaces might also be inimical to some species, even when the interface encompasses the core range of a species (Lidicker 1999; Harris and Reed 2002). Finally, if functions are dominated by a single species, or a few species, higher biodiversity at interfaces may not be linked to functions (Clavel and others 2011; Inger and others 2016).

Globally, ocean beaches are regarded as prominent interfaces between the sea and the land (Schlacher and others 2015a, b; Borland and others

2017; Olds and others 2017). This paradigm largely stems from observations of intense carbon processing when large masses of algal material accumulate along strandlines, providing a marine-derived resource subsidy to terrestrial food webs (Schlacher and others 2017; Baring and others 2018). The transfer of marine organic carbon from the surf zones to beaches is largely unimpeded by physical barriers (that is, beaches are 'open'); in contrast, transfers from the beach to coastal dunes are often restricted by landforms (for example, beach scarps) and vegetation, potentially creating steep gradients in function across this interfaces (Mellbrand and others 2011). Ocean beaches are hot spots for the ecological function of carrion scavenging because animal carcasses are regularly deposited on beaches from the ocean (for example, fish, turtle, bird, and marine mammal strandings) (Schlacher and others 2013) and are consumed by a diversity of scavenging animals that originate from the ocean (for example, seabirds), the beach (for example, waders), and adjacent landwards habitats (for example, mammals, reptiles, raptors) (Meager and others 2012; Bingham and others 2018a, b). When carrion is not consumed rapidly, it is colonised by bacteria which produce toxins that can repel vertebrate scavengers (Blandford and others 2019). Consequently, it is plausible that the functional composition of vertebrate scavengers changes with carrion putrefaction. Neither the spatial gradient of the scavenging function across the beach–dune transition zones nor the temporal change in scavenger species and consumption as carcasses age are currently known.

The paradigm of ecotones being comparatively species-rich, functional hot spots, and sites of steep ecological gradients is widespread, including beach–dune ecosystems. Yet, it has not been examined at the land–ocean transition zones of sandy shorelines. Here we test the paradigm by quantifying spatial gradients in the rates of carrion consumption at ocean-exposed sandy shores and in the coastal dunes backing them. We predict that the combination of distinct geomorphological (dune–beach) and ecological (terrestrial–marine) boundaries creates a distinct spatial peak of enhanced function.

METHODS

Study Sites

We tested for interface effects on carrion consumption in two areas in Eastern Australia: the southern end of Noosa North Shore beach

(26.21°S, 153.03°E) and the northern end of Main Beach at North Stradbroke Island (27.30°S, 153.30°E; Figure 1). Both locations have similar geomorphic terrain and vegetation, are of the same

morphodynamic beach state, and are subject to similar levels and types of human activities (Huijbers and others 2013; Brown and others 2015). Plant assemblages on foredunes are dominated by

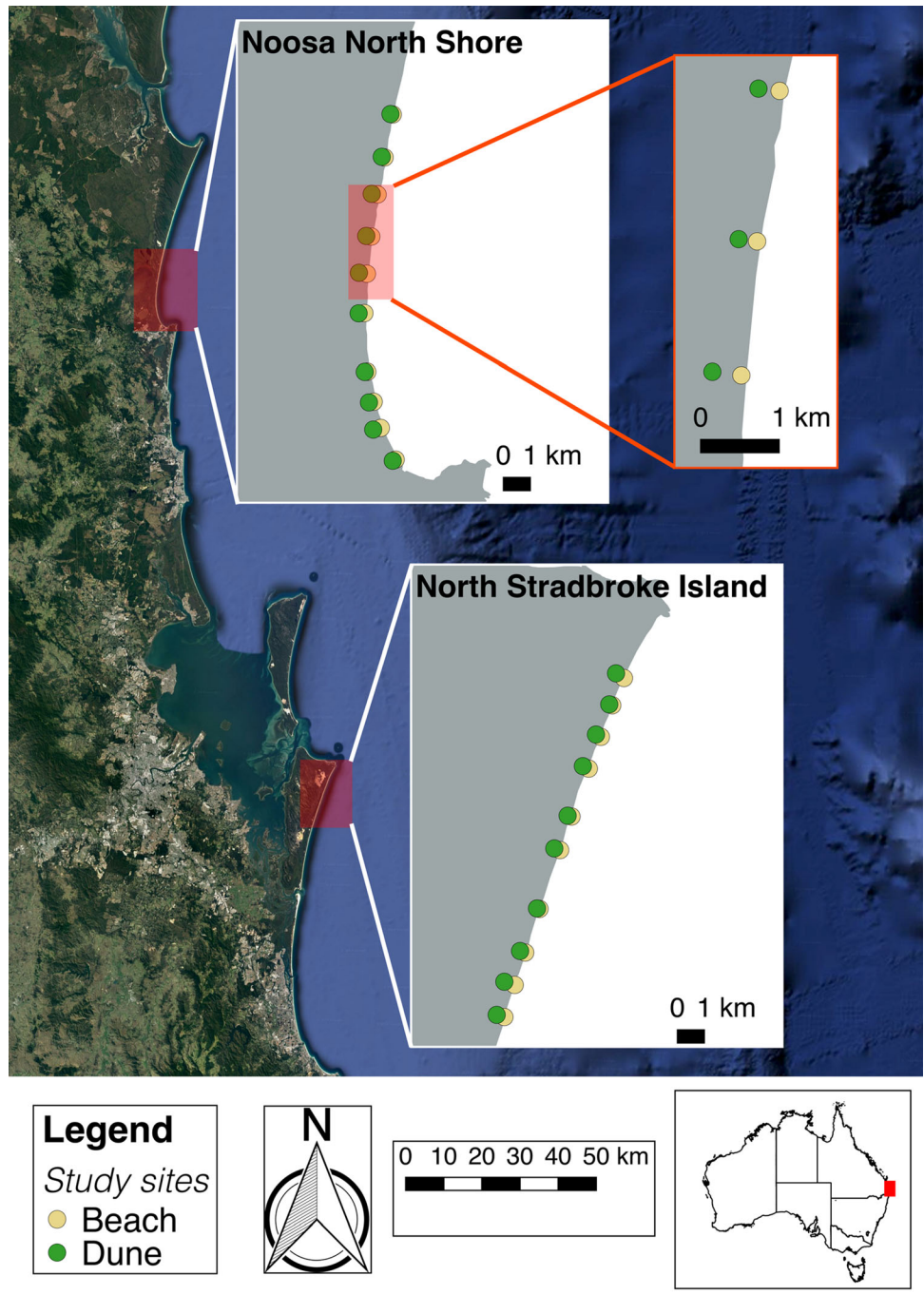


Figure 1. The location of study sites in Eastern Australia (SE-Queensland). We experimentally deployed fish carcasses and wildlife camera traps in two areas (Noosa North Shore and North Stradbroke Island), with 20 sites dispersed over 13.5 km of shoreline in each study area location (large inserts). To examine spatial patterns in carrion removal with reference to the beach–dune ecotone, we deployed half of all experimental camera stations at the beach–dune interface (that is, base of the foredune) and the other half landwards from the beach (at approximately right angles) in the vegetated dunes at distances of 89–362 m upland from the sea (see small insert for illustration).

beach spinifex (*Spinifex longifolius*), whilst the secondary dunes are a mixed forest dominated by melaleucas, casuarinas, eucalypt trees (up to 20 m in height), and understory scrubs (for example, invasive *Lantana camara* and several native species).

Ten experimental sites were established in each study area, dispersed along 13.5 km of beach (Figure 1). At each site, carrion and camera traps were deployed at two locations, one on the non-vegetated part of the beach (typically at the base of the foredune or up to 1 m upland in the foredune depending on site characteristics) and a matched location perpendicular upland in the dunes. The upland distance of each dune site was determined randomly, with the average distance from the seaward-facing base of the foredune being 220 m (± 94 m s; range 89–364 m; Figure 1).

Assemblages of vertebrate scavengers differ between these two locations (Bingham and others 2018a, b). North Stradbroke Island typically supports high densities of native raptors (white-bellied sea eagles, *Haliaeetus leucogaster*; brahminy kites, *Haliastur indus*; and whistling kites, *Haliastur sphenurus*) and few invasive red foxes (*Vulpes vulpes*). Conversely, fewer raptors and more red foxes are found at Noosa North Shore (Bingham and others 2018a, b).

Carrion Consumption Experiments

We used experimentally deployed carcasses of sea mullet (*Mugil cephalus*) and motion-activated trail cameras to determine the composition and activity levels of scavenger species across the beach–dune interface. Sea mullet are common in the surf zones of beaches in the region (Borland and others 2017), and it is readily consumed by scavengers (Brown and others 2015; Huijbers and others 2016a; b).

Carrion deployments consisted of 50 pre-weighted and individually tagged fish (equalling a necromass of 26.1–26.7 kg) placed at each camera station. All experiments were performed during the austral summer: 12 Feb. 2017 to 17 Feb. 2017 at North Stradbroke Island, and 25 Feb. 2017 to 30 Feb. 2017 at Noosa North Shore. We deployed all fish carcasses ($n = 1000$ per study area) and camera traps (40 per study area) during the afternoon of the first day at each site (Time = '0') and checked all deployments during the afternoons of five subsequent days. We initially attempted to weight all fish carcasses over the full course of the experiment to determine time courses of necromass loss. This was logistically not feasible due to the large scale of the experiment and the need to access all sites on foot. Instead, during checks we recorded all

remaining fish carcasses and visually gauged the percentage of remaining flesh for partially consumed carcasses; this allowed us to calculate daily necromass consumption. At most sites, the fish carcasses were in an advanced stage of putrefaction (for example, replete with maggots, repulsively odoriferous) from day three to four onwards.

Each carrion deployment was monitored with two trail cameras (ScoutGuard Zero Glow) over the full duration of the experiment: one camera was set to take bursts of three photographs (8 mp), and the other set to take 10 s videos (1280 \times 720 pixels) when activated by motion. All cameras were set to the highest sensitivity levels and the longest flash range (8 m) possible. Cameras were positioned at all sites 2–3 m above the carcasses and angled so that all remaining carrion remained within the field of view. At the beach sites, cameras were placed on stakes in the frontal dune above the carrion deployment, whilst in the more upland dune sites, they were set in a similar position on a nearby tree or on nearby ridges. Placement of carrion with regards to canopy cover was randomised within 20 m of a GPS site.

Videos and photographs retrieved from camera traps allowed us to identify the species consuming carrion and to measure the number of fish carcasses physically removed from each site by each species. A fish was considered removed by a scavenger when a scavenger was either observed with the fish in its mouth or beak or when the scavenger and the fish were present in one frame, and then were both gone in the next frame. Because we checked sites every day and therefore knew precisely how many fish were removed from each site each day, we are confident that our two-camera set up gave us reliable data on carrion consumption and the composition of the scavenger assemblages consuming the carrion.

Data Analyses

We used a generalised linear model (GLM) in R to test how total carrion consumption (percentage of total deployment weight consumed) varied with distance of a site from the beach into the dunes (that is, distance from beach; fixed scale variable) at each location. We then examined whether the age of carcasses interacted with the spatial factors of study area (larger scale) and positions across the beach–dune interface (smaller scale) to determine patterns of carrion removal. This second analysis was done with a GLM comprising the factors study area (fixed factor, two levels; Noosa North Shore and North Stradbroke Island), time since carrion

deployment (fixed factor, five levels; days 1–5), and position (fixed factor, two levels; beach site or dune site). We used *lsmeans* and *multcomp* packages in R to identify differences in means that were responsible for significant treatment effects.

RESULTS

Total carrion consumption declined significantly ($p < 0.001$) with distance upland from the beach, decreasing from 50 to 80% of total necromass being removed at the beach–dune interface to 20–25% at sites furthest (> 300 m) upland; the steepest decline in carrion consumption was observed over the first 150 m upland from the beach–dune interface (Figure 2B). Significantly more carrion was consumed at North Stradbroke Island than at Noosa North Shore ($p < 0.001$), but there was no interaction between area and distance from beach ($p = 0.91$).

We identified six vertebrate species consuming carrion: white-bellied sea eagles, brahminy kites, whistling kites, Torresian crows, red foxes, and lace monitors (Table 1; Figure 2A). Overall, red foxes were the main scavenger, consuming 40% of all deployed carcasses at a mean removal rate of two carcasses per day per camera station (± 1.04 ; Table 1). Foxes consumed 6 times more fish carcasses from the beach (removal rate 3.45 ± 1.36 carcasses per day) than from the vegetated dunes further upland (removal rate 0.55 ± 0.37 carcasses per day; Table 1). Collectively, birds consumed 45% of all carcasses (30% by white-bellied sea eagles, 7% by crows, 4.5% by brahminy kites, and 3.5% by whistling kites) at an average rate of 2.25 carcasses per day per camera station (± 0.64). Removal of fresh carcasses by birds was only detected on the beach in our experiment (Table 1). Lace monitors consumed 15% of carrion at an average rate of 0.75 carcasses per camera station per day (± 0.37); this rate was lower than that red foxes and white-bellied sea eagles, but at least twice that of the other smaller bird scavengers (Table 1). Carcass removal by lace monitors was roughly the same at the beach and in the dunes (Table 1).

During the first 24 h of the experiment, we observed scavenger species, and carrion removal, at all but two of the 20 camera stations established on the beach. By contrast, no scavengers were detected during the same time at half of all stations located further upland into the dunes. At both locations, scavengers removed significantly more necromass from the beach than from the upland dunes (Table 2; Figure 3). At North Stradbroke Island, 9 times more carrion was consumed per hour

on the beach than in the dunes, and at the Noosa North Shore beach scavenging was 5.3 times higher (Figure 3; Table S1). Whilst carrion consumption on the beach decreased over time as the fish carcasses putrefied (becoming replete with maggots at many sites from day three or four onwards), the reverse temporal pattern was observed in the dunes; here more of the putrefied carcasses were consumed during the last two days of the experiment, mainly by lace monitors (Figure 3).

DISCUSSION

Ecotones are considered important hot spots for biodiversity, and this biodiversity is often hypothesised to lead to enhanced ecological function (Smith and others 1997; Spector and Ayzama 2003), but this is rarely tested with empirical data. In this study, we found a strong negative spatial cline in the function of carrion consumption with increasing distance from a beach–coastal dune ecotone, which reflected the concentration of scavenging species at the interface of beaches and dunes. We also identified that differences in consumption rates between the beach and dunes were highest when carrion deployed was ‘fresh’ (that is, in the first 2 days of the experiment), narrowing over time to the point that consumption did not differ between the beach and dunes at one of our study areas. Our findings support the hypothesis that beaches are hot spots of ecological function and that this is predominantly due to meta-populations crossing the ecotone boundary. From the perspective of the function of carrion consumption, beaches and coastal dunes can therefore be considered meta-ecosystems whereby matter, populations, and energy are readily exchanged, but mostly from the beach to the coastal dunes, and very rarely vice versa. Quantifying the magnitude and direction of these transfer effects across other ecotones, especially those where the transition across the ecotone is not as stark as on beaches relative to upland dunes, is, arguably, a rewarding future study that can encompass a true global footprint.

In this study, we adopted conceptually, and operationally with respect to study design, the frequently cited definition of ‘ecotone’ as being a zone of transition between adjacent ecological systems (that is, beach vs. dune), characterised by steep gradients in environmental characteristics and species compositions of the biota (Clements 1907; Gosz 1993; Risser 1995a, b; Ries and others 2004). We note that because ecotonal phenomena occur over a range of spatial scales (Gosz 1993) there is no ‘fixed’ demarcation or extent that un-

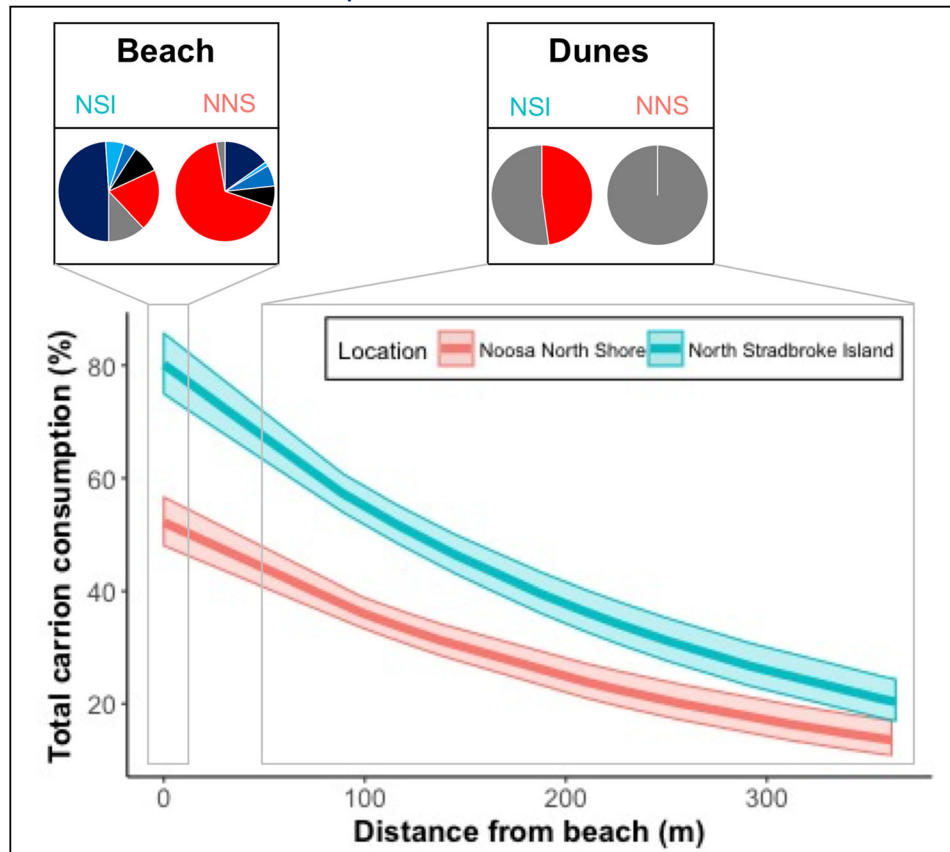
A Consumers**B Necromass consumption**

Figure 2. **A** carrion was consumed by (i) red foxes, (ii) white-bellied sea eagles, (iii) brahminy kites, (iv) whistling kites, (v) Torresian crows, and (vi) lace monitors at ocean beaches and in the abutting vegetated dunes. **B** Decline in carrion consumption with distance inland from the beach (the seaward-facing base/toe of the frontal dunes). Lines are a generalised linear model output of total carrion removal over the five-day experiment in two areas (Noosa North Shore and North Stradbroke Island, compare Figure 1)). Pie charts illustrate the proportion of fresh carcasses removed by each species (with the colours corresponding to the borders in **A**, contrasting assemblages at the beach–dune interface with those further upland in the dunes). The error bars are 95% confidence intervals.

Table 1. List of Vertebrate Scavengers Observed and the Number of Carcasses Removed per Day at Two Locations (North Stradbroke Island and Noosa North Shore) and Positions (Beach or Dunes)

Species	North Stradbroke Island						Noosa North Shore						North Stradbroke Island and Noosa North Shore					
	Beach		Dune		Total		Beach		Dune		Total		Beach		Dune		Total	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Red fox (<i>Vulpes vulpes</i>)	2.0	1.0	1.1	0.7	1.55	0.9	4.9	2.5	-	-	2.5	1.9	3.5	1.4	0.6	0.4	2.0	1.0
White-bellied sea eagle (<i>Haliaeetus leucogaster</i>)	4.9	1.5	-	-	2.45	1.3	1.1	0.7	-	-	0.6	0.5	3.0	0.9	-	-	1.5	0.7
Lace monitor (<i>Varanus varius</i>)	1.2	0.9	1.2	0.5	1.2	0.7	0.2	0.1	-	0.3	0.3	0.2	0.7	0.5	0.8	0.3	0.8	0.4
Torresian crow (<i>Corvus orru</i>)	0.9	0.7	-	-	0.45	0.5	0.5	0.3	-	-	0.3	0.2	0.7	0.4	-	-	0.4	0.3
Brahminy kite (<i>Haliastur indus</i>)	0.4	0.2	-	-	0.2	0.2	0.5	0.3	-	-	0.3	0.2	0.5	0.2	-	-	0.2	0.1
Whistling kite (<i>Haliastur sphenurus</i>)	0.6	0.5	-	-	0.3	0.4	0.1	0.1	-	-	0.1	0.1	0.4	0.3	-	-	0.2	0.2

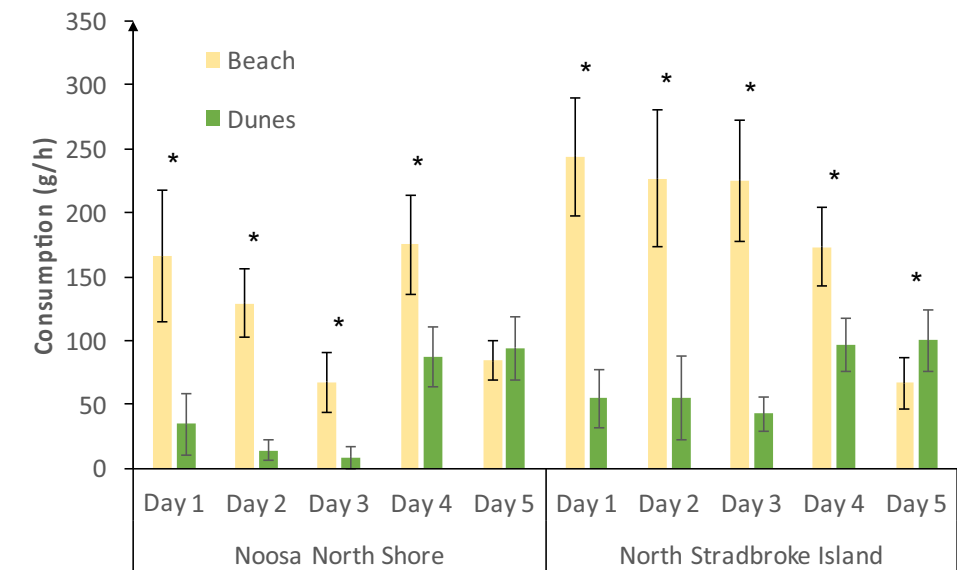
iquely defines the transition between sandy beaches and upland systems. Rather, it is likely to be a dynamic gradient contingent upon landscape and oceanographic settings that define exchange processes across boundaries and species pools performing ecological functions. Future studies in these systems are challenged to measure spatial properties of these gradients in more nuanced ways at both broader and finer grains (see also McClain and Schlacher 2015; Schlacher and others 2015a, b).

We found significantly higher rates of carrion consumption on the beach and a significant decrease in carrion scavenging with increasing distance upland into the dunes. These results provide strong evidence for the hypothesis that beaches are hot spots for the function of carrion scavenging. This pattern was, however, not associated with marked spatial contrasts in the diversity of vertebrate scavengers, with the same suite of consumers occurring in both habitat types. Whilst the link between biodiversity and function has been demonstrated in many settings, it is not universal (Micheli and Halpern 2005; Bellwood and others 2006; Ripple and Beschta 2007; Hoey and Bellwood 2009; Gamfeldt and Roger 2017). Furthermore, some recent studies suggest that the function of carrion consumption might be only weakly linked to biodiversity on land and in the sea (Inger and others 2016; Olds and others 2018a, b). In this study, rates of carrion consumption were significantly higher on the beach due to consumption by a broad suite of animals typically foraging at the beach–dune interface, dominated by several raptors. All of the upland sites in our study had some canopy cover. Thus, it is possible that detection of carcasses by raptors in the vegetated dunes might have been impeded by plants. We have, however, observed raptors feeding on carcasses under trees, but the exact role of canopy cover needs further clarification. The functional role of monitor lizards and foxes, species typically considered to be of terrestrial provenance, was lower near the beach–dune interface at several sites, possibly due to competitive displacement by larger raptors.

Whilst the overall patterns in the distribution of the function of carrion scavenging were ‘positive’ in terms of proximity to ecotones, there were several important patterns that we identified that might temper this effect. In this system, we identified relatively low functional redundancy among carrion scavengers (sensu Bingham and others 2018a, b; Olds and others 2018a, b), whereby the majority of consumption was performed by two species—red foxes and white-bellied sea eagles.

Table 2. Generalised Linear Model Results Testing the Effects of Study Area, Day, and Position on the Amount of Carrion Consumed at Each Site per Hour

Source	d.f.	<i>F</i>	<i>p</i>
Area (North Stradbroke Island, Noosa North Shore)	1	846	< 0.001
Day of experiment (1,2,3,4,5)	4	173	< 0.001
Position (beach, dune)	1	4553	< 0.001
Area × day	4	237	< 0.001
Area × position	1	0.9	0.34
Day × position	4	573	< 0.001
Day × position × area	4	45.2	< 0.001

**Figure 3.** Patterns in carrion consumption rates (mean \pm se) between two study areas (Noosa North Shore vs. North Stradbroke Island, compare Figure 1), at the beach–dune interface (yellow = ‘beach’) and in the vegetated dunes upland from the interface (green—‘dunes’) on each of the five days of the experiment (stars indicate significant ($p < 0.05$) pairwise differences in carrion consumption between the beach and dunes at each area/day combination).

Given the patterns observed in the distribution of beach- and dune-associated animals, it follows that functional redundancy in the vegetated dunes is lower. Red foxes are an invasive species, and so their abundance is managed under control programs at our study locations. Significant reductions in red fox abundance might therefore have consequences for this function. Previous studies have indicated that the effect of red foxes on the function of carrion scavenging is significant and that red foxes might have functionally replaced the role of native carnivores that have been extirpated (Bingham and others 2018a, b). Conversely, the functional role of white-bellied sea eagles might be replaced by the other five identified species under a scenario where the sea eagle abundance is reduced, thereby indicating a positive effect of the ecotone boundary on redundancy along the beach. These

hypothetical scenarios regarding redundancy should be tested further by examining other sites where the influence of foxes or white-bellied sea eagles is lower.

Identifying consistency of patterns in ecological functions over time, or at changing resource availability, is an increasing focus in the literature. This is particularly the case for carrion consumption because the ‘freshness’ of carrion is a likely a significant determinant of its availability, and detectability, for carrion consumers (Blandford 2016). Our data show that carcasses that are badly rotten and infested with large numbers of dipteran larvae were rarely consumed by most vertebrate scavengers. Similarly, it is well established that microbes have an important role in the decay and turnover of rotting flesh in all ecosystems and that microbes can ‘outcompete’ vertebrate scavengers

by producing toxins that make carcasses unpalatable (Howard and others 2012; Blandford 2016; Oliveira and others 2016). These processes likely had a role in shaping the patterns found in this study with carcasses reaching a putrid state after three to four days corresponding with changes in the consumption rates of carrion at both sites. Given these patterns over time, it was somewhat unexpected to see so little consumption of fresh carcasses in the dunes, even when carrion was relatively 'fresh.' This could mean that dunes are simply not attractive habitats for vertebrate scavengers or that foraging behaviours or modes on the beach are energetically more profitable because they are easier to detect either visually or through olfactory cues due to lack of complex forest or grassland cover. Under either scenario, the consistency in effects between dunes across time and between study locations is additional strong evidence to support the function hot spot thesis for ocean beaches.

Ecotones are hot spots for biodiversity, and there is increasing evidence, including from this study, that they are also hot spots of ecological functions. Ecotones are, however, particularly sensitive to environmental changes because many species occurring at them may be at their ecological or physiological limits (Fortin and others 2000), and the negative consequences of edge effects on some species can be stronger (Batary and Baldi 2004; Peyras and others 2013). Consequently, ecotones are often important targets for conservation (Reid 1998). For example, it has been well established that conserving the interface between several ecosystems in reserves assist species migrations, persistence, and ecosystem resilience (Olds and others 2012). By contrast, in this study we discovered 'unidirectional connectivity' across an ecotone boundary via the spillover of terrestrial animals onto the beach. Understanding how animals use different types of ecotones throughout their life-cycle (Sheaves and others 2014; Maxwell and others 2015), the degree to which these patterns in use by animals are reflected in the patterns in ecological functions and the health or impact levels within ecosystems (Olds and others 2012), and testing consistencies for different types of ecotones is therefore an important future task for ecologists and managers alike (Gaston and others 2001).

CONCLUSIONS

Ecological functions maintain the condition, resilience, and persistence of ecosystems in the face of disturbances. Identifying patterns in ecological

functioning and anticipating how they might vary with impacts and management interventions is therefore important. Ecotones might be considered hot spots of ecological functions because they are often characterised by high biodiversity, but this is rarely tested empirically. In this study, we show a significant spatial cline in the function of carrion scavenging with increasing distance from a beach-coastal dune interface. The species driving these patterns originated from both beach and terrestrial ecosystems, thereby highlighting the importance of cross-ecosystem management in the maintenance of ecological function across ecotones. We also show also that the rates of this function change over time, likely due to the effects of carrion decomposition on the palatability of carcasses. Our findings have implications for models of beaches as hot spots of ecological function and represent the first quantitative investigation of these effects for this particular interface type. Future studies should test whether these clines in function: (1) are persistent in other ecosystems, especially where the boundary between the two ecosystems is more porous (that is, materials can be more easily exchanged, or the movement of animals is not restricted by forest structure as it was in this study) and (2) are associated with corresponding spatial clines in biodiversity in diverse types of ecosystems. Improving our knowledge more broadly regarding the patterns of ecological functioning across ecosystems, and testing paradigms in ecology about the relative importance of ecotones for both biodiversity and ecological function more generally, is a critical step to better predict how ecosystems respond to disturbance and how to manage these responses.

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