Functional replacement across species pools of vertebrate scavengers separated at a continental scale maintains an ecosystem function

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Summary

1. The composition of species pools can vary in space and time. While many studies are focused on understanding which factors influence the make-up of species pools, the question to which degree biogeographic variation in species composition propagates to biogeographic variation in ecological function is rarely examined. If different local species assemblages operate in ways that maintain specific ecological processes across continents, they can be regarded as functionally equivalent. Alternatively, variation in species assemblages might result in the loss of ecological function if different species fulfil different functions, and thereby fail to maintain the ecological process.

2. Here, we test whether ecological function is affected by differences in the composition of species pools across a continental scale, comparing a tropical with a temperate pool. The model systems are assemblages of vertebrates foraging on ocean beaches, and the ecological function of interest is the consumption of wave-cast carrion, a pivotal process in sandy shore ecosystems.

3. We placed fish carcasses ($n = 179$) at the beach–dune interface, monitored by motion-triggered cameras to record scavengers and quantify the detection and removal of carrion. Scavenging function was measured on sandy beaches in two distinct biogeographic regions of Australia: tropical north Queensland and temperate Victoria.

4. The composition of scavenging assemblages on sandy beaches varied significantly across the study domain. Raptors dominated in the tropics, while invasive red foxes were prominent in temperate assemblages. Notwithstanding the significant biogeographic change in species composition, ecological function – as indexed by carcass detection and removal – was maintained, suggesting strong functional replacement at the continental scale.

5. Species pools of vertebrate scavengers that are assembled from taxonomically distinct groups (birds vs. mammals) and located in distinct climatic regions (temperate vs. tropical) can maintain an ecological process via replacement of species with comparable functional traits.

Key-words: biogeography, carrion, foxes, macroecology, raptors, sandy beaches

Introduction

Because most species have bounded ranges and discontinuous distributions, species pools vary geographically in all biomes (Ricklefs 2004; Cornell & Harrison 2014). It is this variation in the composition of species pools, complemented by local environmental conditions, that is pivotal in determining the structural and functional attributes of many ecosystems (Lessard *et al.* 2012). Understanding whether biogeographic variation in ecological structure

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and functions can reveal general ecological principles and theories, requires us to replicate studies at widely separated locations – a central approach of macroecology (Fraser *et al.* 2013).

Macroecological studies investigate ecological patterns at large spatial or temporal scales (Keith *et al.* 2012). These studies focus predominantly on patterns in species diversity and distribution that result from ecological and evolutionary processes along environmental gradients (Beck *et al.* 2012). Examples of environmentally induced patterns include changes in species richness along elevation gradients driven by temperature constraints (Lessard *et al.* 2011; Wu *et al.* 2014), as well as shifts in interspecific interactions as a result of changing climatic conditions (Harley 2011) or stress (He, Bertness & Altieri 2013). While these patterns are often deduced from prevailing conditions, evolutionary processes, such as speciation and adaptation, are regarded as the main drivers for phylogenetic diversity within and among species pools (Wiens & Donoghue 2004; Emerson & Gillespie 2008).

In recent years, there has been a shift towards incorporating functional aspects in analysing species distribution patterns (Carstensen *et al.* 2013; Lamanna *et al.* 2014) and community assembly processes (McGill *et al.* 2006; Kraft, Valencia & Ackerly 2008; Jaillard *et al.* 2014). A focus on functional traits rather than the presence or absence of individual species enhances our ability to identify general ecological patterns and predict responses of multispecies communities to environmental changes (Violle *et al.* 2014). Analyses of spatial variation in ecological function have, however, largely relied on documenting variation in functional traits of species rather than measuring directly how ecological functions vary geographically. Thus, a fundamental question remains unanswered: do biogeographic differences in the species composition of assemblages propagate to differences in functional properties?

Changes in community composition can affect ecosystem functioning through the replacement of species that fulfil specific functions (Hooper *et al.* 2005; Tilman, Isbell & Cowles 2014). It is generally believed that greater species diversity leads to more potential species fulfilling a function, which may increase the likelihood that ecosystem function is maintained both in undisturbed and stressed situations (Díaz & Cabido 2001; Elmqvist *et al.* 2003; Naeem, Duffy & Zavaleta 2012). Comparative studies across continents have shown that patterns of species diversity can affect ecological processes such as producer–consumer relationships and predator–prey interactions (Jetz *et al.* 2009; Sandom *et al.* 2013). This regional effect of diversity on ecological processes indicates that different species assemblages may affect ecosystem functioning, but empirical data to test this relationship are still scarce.

Sandy beach ecosystems dominate, geographically, the coastlines of the world. Beach systems harbour a diversity of species, contributing to multiple ecosystem functions that range from the breakdown of beach wrack to supporting fisheries via complex food web connections (Schlacher *et al.* 2008, 2015a). Marine carrion regularly washes up on beaches where it is readily consumed by terrestrial scavengers, forming an important flow of nutrients across habitat boundaries (Polis & Hurd 1996; Beasley, Olson & DeVault 2012). Scavengers are abundant on beaches, including invertebrates such as ghost crabs as well as apex consumers such as raptors and foxes that respond rapidly to carcass falls (Schlacher, Strydom & Connolly 2013; Huijbers *et al.* 2015a). Thus, scavenging is a key function of ecosystems at the land–ocean interface (Schlacher *et al.* 2015a). Here, we focus on carrion consumption, an ecological function that, energetically, constitutes a strong link in most food webs in most ecosystems (Wilson & Wolkovich 2011). Differences in scavenger assemblages on sandy beaches across a continental scale naturally emerge from the biogeographic distribution of potential scavenger species. Consequently, sandy beaches are an ideal natural laboratory to test how differences in the composition of species pools affect ecosystem functioning.

In this study, we test how variations in regional species pools shape ecological functioning. As a result of natural variability in species assemblages across latitudinal gradients (Willig, Kaufman & Stevens 2003), we expect distinct differences in the composition of the scavenger assemblage in different regions at a continental scale. Differences in species composition among regions might significantly alter ecosystem function, here measured as the probability of carrion detection and removal. Alternatively, if species are functionally replaced, macroecological differences in species pools will result in similar rates of ecological functioning. To distinguish between these alternatives, we first measured differences in the species composition of vertebrate beach scavengers between two widely separated biogeographic regions and then tested whether these differences affect carrion detection and removal.

Materials and methods

STUDY SITES

Experiments for this study were conducted in sandy beach ecosystems located in two distinct biogeographic regions, separated by >2000 km, in the northern and southern part of Australia – tropical North Queensland and temperate Victoria (Fig. 1). We selected 12 beaches in North Queensland and 13 beaches in Victoria along a stretch of 250 km of coast in each region. Individual beaches within a region were *c.* 15–20 km apart.

We assessed several environmental characteristics of each beach to test whether environmental variations among beaches affect differences in vertebrate scavenger assemblages and scavenging rates. These characteristics included both natural metrics that might affect vertebrate scavengers living at the terrestrial fringe of the beach, such as dune width and distance to nearest rocky headland, as well as metrics related to human interference with the natural environment, such as distance to nearest road, buildings and caravan parks, and percentage of urban land cover abutting the beach (see Appendix S1, Supporting information for an overview of all beaches with measurements of these characteristics). Dune width and distance to nearby features were measured as a straight line in Google Earth from the position of the most central camera within
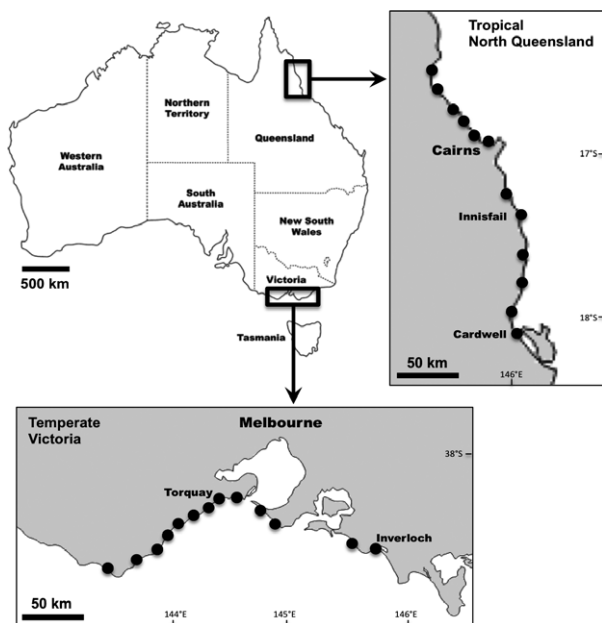
Fig. 1. Overview of the two study regions in Australia, with locations of each beach site in the tropical North Queensland region (right panel) and the temperate Victoria region (bottom panel).

the array (see Experimental set-up). The intensity of urbanisation at each beach was calculated using a random-point count methodology in Coral Point Count with Excel extensions (CPCe) (Kohler & Gill 2006). This was done for an area around each beach that matched the daily home range of potential scavenger species. The average daily home range of the red fox *Vulpes vulpes* [1·6 km linear distance (Meek & Saunders 2000; Dekker, Stein & Heitkönig 2001)] was used as a proxy for daily movement ranges of all mammals, while the average daily home range of the white-bellied sea eagle *Haliaeetus leucogaster* [9·2 km linear distance (Wiersma & Richardson 2009)] was used for all birds. An extensive literature review indicated that the daily home ranges of other potential scavengers would fall within these two ranges (see Huijbers *et al.* 2015a for details).

EXPERIMENTAL DESIGN

Fish carcasses, monitored by motion-triggered cameras, were deployed on each beach to determine the species composition of scavenger assemblages and to measure rates of carrion detection and removal. Four cameras, separated by 200 m, were placed at each beach. Each camera was baited twice with a fish carcass, first in the morning (daytime deployment), and then revisited and reset just before sunset (night-time deployment). This resulted in eight deployments per beach, consisting of 4-day and four-night placements of carcasses. The total carcass deployment time per camera was *c.* 24 h, split approximately equally between day and night exposures. This design ensured an equal chance of capturing both diurnal and nocturnal scavengers. Previous surveys with similar equipment in southeast Queensland showed that scavengers are able to locate, consume or remove carrion within 24 h (Huijbers *et al.* 2015a). Experiments in both regions were conducted over a period of 3 weeks in March–April 2013. We aimed for 200 deployments (25 beaches*4 cameras*2 deployments) and were able to retrieve data from 179 deployments (*n* = 75 in North Queensland, *n* = 104 in Victoria) due to vandalism and theft of equipment.

Carcasses of flathead mullet, *Mugil cephalus,* weighing 840 ± 227 g (SD), were placed at the beach–dune boundary, 5–

10 m seawards from the cameras. Mullet was chosen as carrion source because this species has a widespread distribution and was locally available in both regions. These fish are commonly found in the surf zone of beaches and consumed by a wide range of scavenger species when washed ashore (Schlacher, Strydom & Connolly 2013). Digital passive infrared (PIR) motion-triggered cameras 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. Fish carcasses that were still present when cameras were revisited between daytime and night-time deployments were replaced with a fresh carcass. Images captured by the cameras provided information on the timing of carrion detection and removal, the number and species identity of scavengers observed during a deployment, and the scavenger species responsible for removal of the 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 one image and the fish was absent in the next image. When a fish was removed so rapidly that the camera took an image that did not capture the species taking the fish, which is sometimes the case with raptors that lift the fish from the beach without landing, we recorded this as a 'presumed raptor'.

DATA ANALYSIS

Differences in the composition of the scavenger assemblage between regions were tested using an additive permutational multivariate analysis of variance (PERMANOVA), and visualized using non-metric multidimensional scaling (nMDS) with the package 'VEGAN' (Oksanen *et al.* 2012) in R (R Development Core Team 2010). The analyses were based on the Bray–Curtis resemblance measure calculated from aggregated species incidence data per beach. Beaches where no scavengers were observed (1 beach in each region) were excluded from the analyses, as we were only interested in differences in observed scavenger assemblages. The influence of environmental characteristics of each beach on the scavenger assembly ordination was analysed by the 'envfit' function in the VEGAN package. This function models each environmental predictor separately as a simple regression of MDS scores for each ordination axis and performs a permutation test to assess statistical significance.

The probability of a fish carcass being detected and removed by scavengers within either a day or night deployment was modelled using a generalized linear mixed-effects model (GLMM) with binomial error structure. The model included two fixed factors having two levels each (Region: tropical and temperate; Time: day and night) and their interaction; it also had Beach and Camera as random effects. GLMM is powerful because it acknowledges the nested structure of the experimental design and accommodates missing values for deployments where cameras could not be retrieved (Zuur, Ieno & Smith 2007).

New Atlas of Australian Birds data supplied by BirdLife Australia were used to calculate the occurrence and abundance of potential bird scavengers in both regions. We used data from the survey type 'area search <500 m', which means that all birds observed within 500 m around a central point are recorded. We generated shapefiles in ArcGIS with a buffer of 9·2 km around our study sites, which corresponds to the proxy for daily movement ranges for birds that was used to calculate the percentage of urban land cover. These shapefiles were used to extract data on the occurrence of bird species known to scavenge fish from beach, expressed as the number of bird sightings per survey (BSPS). Because there was some overlap in bird survey locations among beaches within each region, we analysed differences in bird occurrence between the two regions as a whole. Each region was divided into 5 blocks of 50 km coastline to generate a mean and
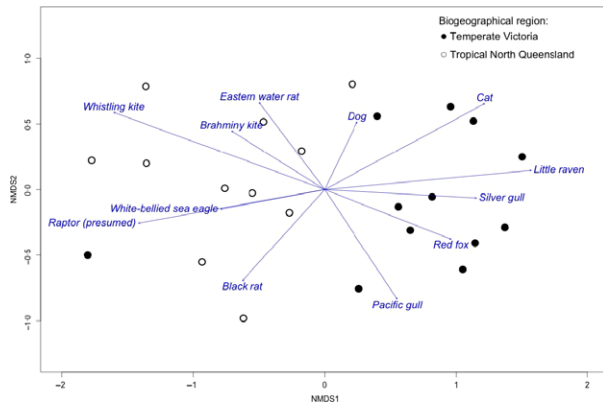
Fig. 2. Ordination (nonmetric multidimensional scaling, nMDS biplot) based on Bray–Curtis resemblance matrix calculated from aggregated species incidence per beach (2D stress value = 0·10). Study sites are colour-coded according to region. The position of species names reflects their associations across the nMDS ordination.

variance of bird counts per region. Differences in BSPS between regions were tested with independent-samples *t*-tests for bird species with non-significant differences in variances, while Wilcoxon tests were used for species with significantly different variances. Due to a lack of abundance data for potential mammalian scavenger species, these could not be compared between regions. It is, however, known that red foxes (*V. vulpes*) are abundant in coastal areas of the temperate region, but do not occur in the tropical region surveyed in this study (www.ala.org.au, C.M. Huijbers, M.B. Brown, T.A. Schlacher, pers. obs.).

Results

The structure of scavenger assemblages differed significantly between beaches located in the tropical and temperate regions (PERMANOVA, *P* < 0·001, Fig. 2). The tropical scavenger assemblage consisted mainly of raptors (brahminy kite, *Haliastur indus*, whistling kite, *Haliastur sphenurus*, white-bellied sea eagle, *H. leucogaster*), in contrast to temperate beaches, where red foxes and gulls (Pacific gull, *Larus pacificus*; silver gull, *Chroicocephalus novaehollandiae*) were the most abundant scavengers. With the exception of latitude, none of the other beach characteristics analysed had a significant influence on this difference in scavenger assemblage structure (Table 1).

Notwithstanding significant geographic variation in the composition of the scavenger assemblages, rates of ecological function, as indexed by scavenging, were similar between regions. Across all beaches, scavengers detected approximately 50% of all fish carcasses, and total carcass removal was approximately 25% within *c.* 12 h. In modelling the probability of carcass detection, inclusion of the interaction between Region and Time did not significantly enhance model fit (log-likelihood ratio test: χ^2 = 1·1393, d.f. = 1, *P* = 0·286). Further model simplification indicated that the main effects for Region (log-likelihood ratio test: χ^2 = 0·2857, d.f. = 1, *P* = 0·593) and Time (log-likelihood ratio test: χ^2 = 0·9816, d.f. = 1, *P* = 0·322) also failed to

**Table 1.** Influence of beach characteristics on scavenger assemblage structure, as analysed with an envfit analysis

Environmental factor	R^2	*P*-value
Latitude	0·53	**0·002**
Distance to major rocky headland	0·25	0·057
Dune width	0·12	0·266
Distance to nearest caravan park	0·12	0·266
Percentage urban land cover in birds' home range	0·09	0·401
Percentage urban land cover in mammals' home range	0·08	0·484
Distance to nearest road	0·06	0·566
Distance to nearest buildings	0·06	0·563
Number of successful deployments per beach	0·05	0·566
Distance to nearest beach access point	0·02	0·806

Bold *P*-values indicate a significant influence of the environmental factor on scavenger assemblages.
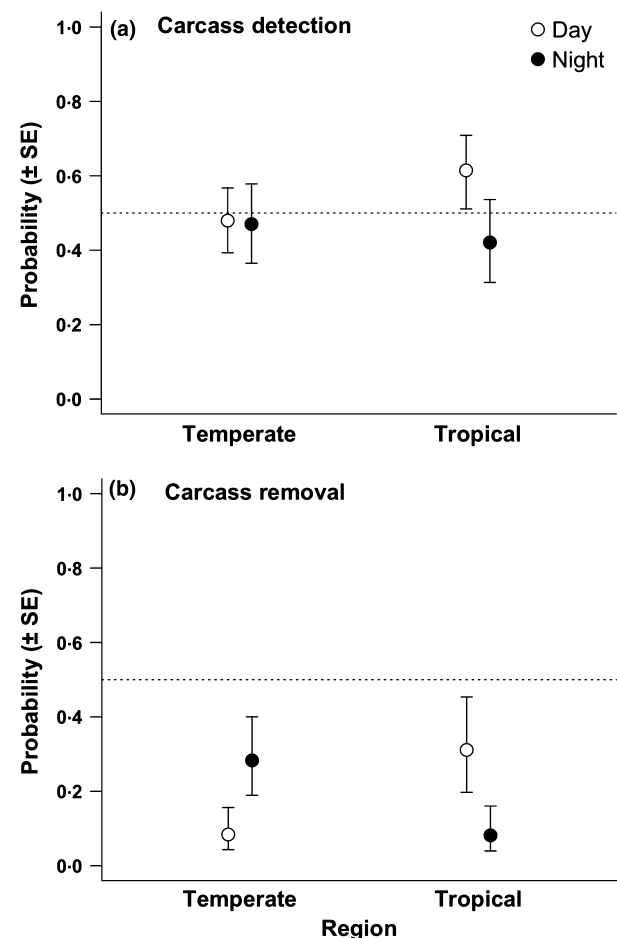
Fig. 3. Probability (calculated from a logistic mixed-effects model with binomial error structure) that a fish carcass would be (a) detected or (b) removed during day or night deployments from beaches in temperate Victoria and tropical north Queensland. The dashed line represents the 50 : 50 chance that a carcass was detected or removed.
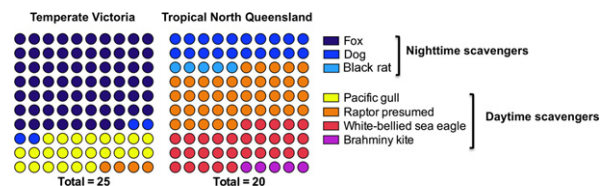
Fig. 4. Percentage contribution of different scavenger species to the removal of fish carcasses from sandy beaches in temperate Victoria and tropical north Queensland.

contribute significantly to explaining variability in the response. Thus, the probability of carcass detection was unaffected by either Region or Time. For carrion removal, there was a significant interaction between Region and Time (log-likelihood ratio test: $\chi^2 = 12{\cdot}507$, d.f. = 1, $P < 0{\cdot}001$), indicating that the probability that a fish carcass would be removed in either region was dependent on whether it was available to scavengers during the day or the night (Fig. 3b). In temperate Victoria, the probability of carcass removal was significantly higher during the night compared to the day (Wald $Z = 2{\cdot}337$, $P = 0{\cdot}019$). This pattern was reversed in tropical North Queensland where significantly more carcasses were removed during the day (Wald $Z = 2{\cdot}280$, $P = 0{\cdot}023$). Between regions,

however, there were no significant differences in carcass removal either during daytime or night-time deployments (Day: Wald $Z = 1{\cdot}903$, $P = 0{\cdot}057$, Night: Wald $Z = 1{\cdot}709$, $P = 0{\cdot}088$), resulting in similar overall removal rates for the different scavenger assemblages.

The partitioning of scavenging events among day and night between regions was caused by the difference in dominant species that were responsible for the removal of carcasses. In tropical North Queensland, these were mainly diurnally active avian scavengers in contrast to predominantly nocturnally active mammalian scavengers in temperate Victoria (Fig. 4). Despite this taxonomic difference, the efficiency with which the scavengers removed carrion from the beaches was not significantly different between regions (Table 2). Time to detection did show some significant differences with faster detection by daytime scavengers in tropical North Queensland compared to night-time scavengers, and significantly faster detection during the night in temperate Victoria compared to tropical North Queensland (Table 2).

Bird survey data showed that the presence of potential avian scavengers was significantly different for most species between regions (Table 3). Brahminy kites and Torresian crows were only present in the tropical region, while Pacific gulls and little ravens were only found in the tem-

Table 2. Time it took scavengers to detect and remove fish carcasses from beaches in two distinct biogeographic regions of Australia: tropical North Queensland and temperate Victoria. Differences between day and night carcass deployments within and between regions were analysed using a linear mixed-effects model

Region	Deployment	Time (min)	Within region			Between regions		
			d.f.	*t*-Value	*P*-value	d.f.	*t*-Value	*P*-value
Carcass detection (Time to detection)								
Tropical	Day	245 ± 143	23	2·49	**0·020**	21	Day: 0·57	0·578
	Night	435 ± 389						
Temperate	Day	177 ± 167	23	0·65	0·52		Night: 2·65	**0·015**
	Night	225 ± 241						
Carcass removal (Time to removal)								
Tropical	Day	287 ± 164	4	2·34	0·080	13	Day: 0·65	0·525
	Night	567 ± 368						
Temperate	Day	213 ± 175	4	1·30	0·276		Night: 1·95	0·073
	Night	344 ± 213						

Bold *P*-values highlight significant ($P < 0{\cdot}05$) differences.

Species	Mean BSPS		Total BSPS		
	Tropical	Temperate	Tropical	Temperate	*P*-value
Brahminy kite	**0·13** ± 0·02	0 ± 0·07	0·12	0	0·007
White-bellied sea eagle	**0·10** ± 0·08	0·01 ± 0·05	0·07	0·005	0·008
Torresian crow	**0·05** ± 0·05	0 ± 0·02	0·03	0	0·007
Little raven	0 ± 0	**0·53** ± 0·6	0	1·01	0·007
Pacific gull	0 ± 0	**0·25** ± 0·12	0	0·24	0·007
Silver gull	0·94 ± 1·91	2·34 ± 3·73	3·21	6·27	0·444
Whistling kite	0·05 ± 0·06	0·04 ± 0·03	0·03	0·05	0·794

Table 3. Comparison of bird occurrence for species known to scavenge carrion from ocean beaches, contrasting coastal areas of tropical North Queensland with temperate Victoria in Australia. Data from BirdLife Australia were extracted using ArcGIS shapefiles with a buffer of 9·2 km around our study sites. We calculated the total of individual bird sightings per survey (BSPS) in each study region, as well as the mean (±SD) of 5 BSPS ratios by dividing each region into 5 blocks of 50 km coastline

Bold values highlight significantly ($P < 0{\cdot}05$) higher relative BSPS values for a region.

perate region. White-bellied sea eagles were present in both regions, but in significantly higher numbers in tropical North Queensland. Whistling kites and silver gulls were the only two species that did not differ in relative abundance between the two regions.

Discussion

Species pools change across large biogeographic scales, yet it is in most cases unknown how this affects ecosystem functioning (Cornell & Harrison 2014). Here, we show that two taxonomically different scavenger species assemblages in two distinct biogeographic regions are functionally equivalent with respect to the efficiency of carrion removal on sandy beaches. While fish carcasses deployed at tropical beaches were mostly scavenged by raptors, the temperate scavenger assemblage was dominated by invasive red foxes. The similarity in function was measured in multiple sites in two well-separated regions at the northern and southern end of a continent. While this does not represent a fully replicated test of either tropical or temperate species pools, our replication of a local study across a continental scale demonstrates the generality of functional replacement in the scavenging process at the land–ocean interface.

While overall scavenging function was similar, there were clear differences in the temporal scavenging patterns between regions, related to the behaviour of the predominant scavenger species. Avian scavengers accounted for most of the scavenging activity on tropical beaches in North Queensland, removing carrion during daytime hours. By contrast, nocturnally active foxes were the main consumers of beach carrion in temperate Victoria. Besides temporal variation in feeding activity of the consumers, the arrival of resource subsidies, such as marine carrion on beaches, can also be extremely variable in time, space and quantity (Yang *et al.* 2010). Although naturally occurring carrion supplies may differ between our study regions, large accumulations of animal carcasses stranded on the shore were not observed during this study. This suggests that substantial differences in marine carrion supply were not a major factor in driving the observed large-scale patterns in carcass removal. The unpredictability of resources subsidies has profound consequences for the structure of communities and population dynamics (Marczak, Thompson & Richardson 2007; Nowlin, Vanni & Yang 2008). It is also known to drive individuals to adopt a more generalist feeding strategy (Overington, Dubois & Lefebvre 2008). Most carrion consumers, including the raptors and foxes observed in our study, are opportunistic scavengers (Wilson & Wolkovich 2011). The rapid detection and removal times for carcasses deployed at our study sites illustrate that scavengers are adapted to utilize unpredictable resource subsidies efficiently.

Red foxes dominated the scavenger assemblage on temperate beaches, removing the majority of fish carcasses in this region. The paucity of scavenging raptors in this region

compared with North Queensland (this study) and South East Queensland (Brown *et al.* 2015; Huijbers *et al.* 2015a) raises the question of whether foxes, a non-native species in Australia, have suppressed raptors or are occupying an empty niche. The comparison of bird survey data between our study regions shows that raptors are significantly less abundant in Victoria compared with North Queensland (Table 3). This continental-scale difference in raptor abundance could suggest that foxes on temperate beaches may occupy a niche that is not completely filled by raptors. Scavenging by canids and felines on marine shores is not uncommon globally (Moore 2002; Carlton & Hodder 2003). Examples of mammalian beach scavengers include coyotes in California (Rose & Polis 1998), foxes in Canada, Norway and Italy (Ricci *et al.* 1998; Roth 2002, 2003; Killengreen *et al.* 2011; Tarroux *et al.* 2012), and hyenas and lions in Namibia (Skinner, Aarde & Goss 1995). Invasive red foxes are, however, known to compete with local, often endangered, coastal scavengers (Killengreen *et al.* 2012; Schlacher *et al.* 2015b), and in our study, raptors were abundant in the tropical region where foxes were absent. It is conceivable, but unproven, that competition with foxes for beach-cast carrion on temperate beaches may have contributed to the lower removal of carrion by raptors in this locations. Brown *et al.* (2015) showed that overall scavenging of fish carcasses on an island invaded by red foxes was significantly higher compared with a fox-free island nearby, which raises the possibility that carrion removal by red foxes is in direct competition with bird scavengers that dominate this niche and function in fox-free locations. Additionally, we noticed a lack of native mammalian scavengers in the temperate region, which could be due to recent invasion (and functional replacement) by red foxes or more historical extirpation of small- and medium-sized mammals such as quolls and Tasmanian devils from the Australian mainland (Glen & Dickman 2005). Thus, while foxes seem to maintain an important ecological process, which is equivalent to that provided by raptors in other biogeographic regions, the dominance of this non-native species on Victorian beaches might prevent native scavengers from utilizing nutrient-rich food sources at the land-ocean interface. While there are currently no empirical data on the consequences of putative competitive interactions between red foxes and native scavengers (raptors and smaller mammalian carnivores) on ocean beaches, our results emphasize that effects of invasive species are potentially multifaceted. Resolving questions about possible empty beach niches, competition and historical extirpation is important as the answers determine how we view the biological impacts of non-native species more widely.

Although rates of carrion removal by different scavenger assemblages in the tropical and temperate regions were similar, the maintenance of the scavenging process depends on the persistence of one particular scavenger group in each region. In north Queensland, this is a group (raptors) that is particularly sensitive to changes in land use (Huijbers *et al.* 2013, 2015a). In Victoria, it is a non-native

species that causes negative impacts on local fauna, and is subjected to attempted control through extensive baiting and culling programmes (McKenzie *et al.* 2007; Saunders, Gentle & Dickman 2010). This indicates that despite the functional equivalency of different scavenger species across the Australian continent, there is currently limited redundancy in these communities. Loss of a particular group of species might, therefore, result in loss of scavenging efficiency and thus compromised ecosystem functioning.

By replicating a local study across a continental scale, we determined that different assemblages of vertebrate beach scavengers are functionally equivalent in maintaining an important ecosystem process. This kind of approach can advance our understanding of how local biotic interactions, in our case competition for food, influence the biogeographic distribution of species, which is essential to improve species distribution models (Boulangeat, Gravel & Thuiller 2012). More importantly, this knowledge is crucial for establishing and testing general paradigms in ecology about ecosystem functioning, and for predicting responses of organisms and communities to environmental changes and management strategies (Violle *et al.* 2014).

Acknowledgements

Data accessibility

Data for this study are archived in the University of the Sunshine Coast Data Research Bank: http://dx.doi.org/10.4227/39/55f6533bef07d (Huijbers *et al.* 2015b).

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Supporting Information

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

Appendix S1. Overview of study sites and environmental characteristics measured for each of these sites (NQ = North Queensland; VIC = Victoria).