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Invasive carnivores alter ecological function and enhance complementarity in scavenger assemblages on ocean beaches

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Abstract. Species composition is expected to alter ecological function in assemblages if species traits differ strongly. Such effects are often large and persistent for nonnative carnivores invading islands. Alternatively, high similarity in traits within assemblages creates a degree of functional redundancy in ecosystems. Here we tested whether species turnover results in functional ecological equivalence or complementarity, and whether invasive carnivores on islands significantly alter such ecological function. The model system consisted of vertebrate scavengers (dominated by raptors) foraging on animal carcasses on ocean beaches on two Australian islands, one with and one without invasive red foxes (*Vulpes vulpes*). Partitioning of scavenging events among species, carcass removal rates, and detection speeds were quantified using camera traps baited with fish carcasses at the dune–beach interface. Complete segregation of temporal foraging niches between mammals (nocturnal) and birds (diurnal) reflects complementarity in carrion utilization. Conversely, functional redundancy exists within the bird guild where several species of raptors dominate carrion removal in a broadly similar way. As predicted, effects of red foxes were large. They substantially changed the nature and rate of the scavenging process in the system: (1) foxes consumed over half (55%) of all carrion available at night, compared with negligible mammalian foraging at night on the fox-free island, and (2) significant shifts in the composition of the scavenger assemblages consuming beach-cast carrion are the consequence of fox invasion at one island. Arguably, in the absence of other mammalian apex predators, the addition of red foxes creates a new dimension of functional complementarity in beach food webs. However, this functional complementarity added by foxes is neither benign nor neutral, as marine carrion subsidies to coastal red fox populations are likely to facilitate their persistence as exotic carnivores.

Key words: birds of prey; food webs; foxes; functional traits; invasive species; raptors; sandy beaches; scavengers.

Introduction

"*Many foxes grow gray but few grow good*"
—Benjamin Franklin

Animal carcasses are fundamental resources in many food webs, supporting a diverse and abundant suite of scavengers in multiple environmental settings, including sandy beaches (Kruuk 1972, DeVault et al. 2003, Wilson and Wolkovich 2011, Beasley et al. 2012, Barton et al. 2013, Schlacher et al. 2013*b*). In fact, carcasses of marine animals washing up on sandy beaches are a critical input for scavengers feeding at the sea–land interface (Rose and Polis 1998). Consumption of beach-cast marine carrion is also rapid and often complete on sandy shorelines, suggesting evolutionary pathways resulting in a pivotal role of carrion in beach food webs (Huijbers et al. 2013, 2015, Schlacher et al. 2013*b*). This makes beach ecosystems good model systems to examine broader questions in food-web ecology, particularly those involving carrion–scavenger pathways.

Theoretically, the taxonomic and functional composition of the scavenger assemblage is important in setting scavenging efficiency and modes of carcass detection (Barton et al. 2013, Pereira et al. 2014). For example, because bird scavengers generally differ from mammals in the mode of carcass detection (Houston 1979, Cortés-Avizanda et al. 2014), expectations are that variations in the taxonomic make-up of the vertebrate scavenger guild propagate to variations in carcass detection and removal rates in different habitats (Sebastián-González et al. 2013). Similarly, because of behavioral dominance patterns among species feeding on carcasses (Lopez-Lopez et al. 2014), changes in the composition of scavenger assemblages are predicted to result in changes

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to carcass removal rates and patterns (Ogada et al. 2012). Finally, addition of scavengers to food webs via species invasion, extirpation of apex predators that feed as facultative scavengers, and introductions of mesopredators are all predicted to alter the dynamics and structure of carrion-based food webs (DeVault et al. 2011, Moleón et al. 2014).

In situations where different species fulfill similar roles in ecosystems, functional equivalence may be present to varying degrees (Leibold and McPeek 2006, Losos 2011, M'Gonigle et al. 2012). Under conditions where functional roles are not strongly differentiated among species, and hence theoretically replaceable, functional redundancy is predicted to occur; conversely, ecological and evolutionary processes that differentiate functions in species assemblages lead to functional complementarity (Loreau 2004). Thus, functional complementarity requires clear differences in functional attributes, whereas functional redundancy results from close similarities in species attributes.

When the concepts of redundancy and complementarity are applied to carrion-based food webs, the fundamental question arises to which degree multiple scavenger species overlap in functional niche space, either partitioning common carrion resources (complementarity) or functionally converging in their necromass removal (redundancy). Thus, in this study, we define ecological function as the rate of biological carrion processing, and ask to what extent biological partitioning of scavenging events among species and higher taxa reflects ecological equivalence and redundancy reflecting similar functional traits of species in the scavenger assemblages. We also ask whether complementarity in functional niche space is altered or enhanced in the presence of additional top-level consumers in food webs supported by carrion.

Scavenging by canids and felines on marine shores is not uncommon globally (Moore 2002, Carlton and Hodder 2003). Examples of mammalian beach scavengers include coyotes in California (Rose and Polis 1998), hyenas and lions in Namibia (Skinner et al. 1995), and foxes in Canada, Norway, and Italy (Ricci et al. 1998, Roth 2002, 2003, Killengreen et al. 2011, Tarroux et al. 2012), In Australia, dingos or Tasmanian devils *Sarcophilus harrisii* are the only native mammal likely to be an important scavenger on ocean beaches. Most other native Australian mammals that regularly scavenge have either small geographic ranges, occur at low densities, or are small (body mass <1.6 kg), and are thus unlikely to be significant in carrion-based food webs on sandy shores. In contrast to the low incidence of scavenging by native mammals on Australian ocean shores, invasive red foxes are widespread, abundant, and significant consumers of beach-cast carrion (Saunders et al. 2010, Schlacher et al. 2013*a*).

Functional changes in ecosystems can be particularly large, widespread, and persistent when they are induced by invasive species (Simberloff et al. 2013). Such invasive species effects are often most severe on islands invaded by nonnative carnivores (Courchamp et al. 2003). Here we test whether functional changes are attributable to invasive carnivores by contrasting vertebrate scavenger food webs and carrion consumption rates on two Australian islands, one with and one without the nonnative red fox (*Vulpes vulpes*).

Methods

Study sites

Scavengers and carrion consumption were measured on the exposed ocean beaches of two sand barrier islands in eastern Australia: Moreton and North Stradbroke Island (Fig. 1). A feature of particular relevance for this paper is the similarity in habitats juxtaposed with faunal differences between the islands. Both islands are geographically close (separated by less than 10 km), have the same habitat types, are of comparable size (35–39 km long, 8–11 km wide), share the same geological history and the same climate (Fig. 1). They differ markedly, however, in terms of vertebrate beach scavengers present: Moreton Island harbors no large native marsupials (e.g., kangaroos, wallabies). In 1865, pigs and goats were deliberately introduced to Moreton Island from Naval vessels as a food source for shipwrecked sailors; a small population of feral pigs remains today. In contrast, large marsupials are common on North Stradbroke Island, which also contains a sizeable population of red foxes that forage regularly on the island's beaches (Schlacher et al. 2013*a*, *b*, Huijbers et al. 2015). Dogs are allowed on North Stradbroke Island, but are banned from Moreton Island.

Conservation areas have been established on both islands, with all of Moreton Island declared a National Park. About half of North Stradbroke Island was gazetted as Naree Budjong Dara National Park in 2011. Dune camping, surf fishing, and sand driving are popular activities on the eastern beaches of both islands (Schlacher and Morrison 2008, Meager et al. 2012, Schlacher et al. 2013*c*, Weston et al. 2014).

The chief objective of our study was to test how invasive red foxes alter carcass removal from beaches. Only one location on the east coast of Australia, Moreton Island, has the condition of having no red foxes: all other parts of the subtropical coastline have foxes present. Therefore our spatial study design was constrained by the availability of fox-free locations. However, we have matched the fox-free island (Moreton Island) with a fox island (North Stradbroke Island), which is geographically very close, and is highly similar in all other aspects that could potentially influence our comparisons (i.e., high similarity in geomorphology, dimensions, vegetation types, exposure to wave-cast carrion, etc.). Other potentially useful locations with foxes (which would have allowed an asymmetrical design) were ruled out because of differences in habitats and particularly because of the

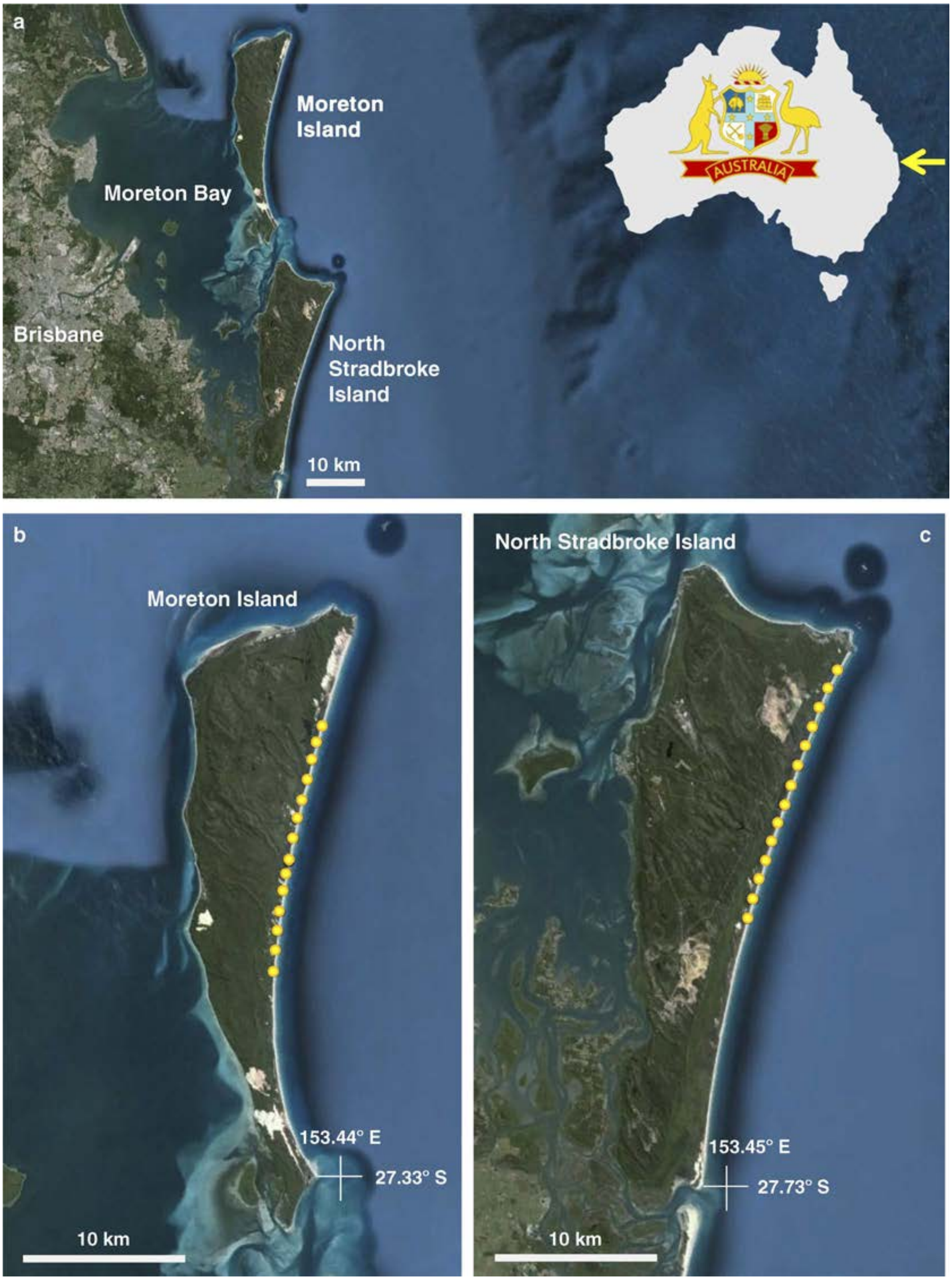

FIG. 1. (a) Location of the study sites at Moreton Island and North Stradbroke Island in eastern Australia and (b, c) positions of sampling sites on the ocean beaches of each island where beach scavengers were recorded with camera traps.

extent of urbanization, a factor known to strongly alter the composition of scavenger guilds and the rate of scavenging in this region (Huijbers et al. 2013, 2015). We acknowledge that, whenever feasible, statistically robust tests call for replication of treatments at all levels, but contend that alternative designs can be validly employed in science to support an a priori hypothesis. Here, we use a design with limited replication to assess compliance of natural process with a priori hypotheses. While the lack of replication precludes strong attribution, as well as generalization, results can provide evidence in support of, or against, the stated hypotheses.

Field data collection: scavenger species and carrion consumption rates

Scavenging rates (i.e., time to carcass detection and removal) and the species compositions of the scavenger assemblage were quantified with camera traps baited with fish carcasses; techniques followed procedures developed and refined for scavenging studies on ocean beaches in the region (Huijbers et al. 2013, 2015, Schlacher et al. 2014, 2015).

Camera traps were deployed at 14 sites on each island, dispersed over 16 km of ocean shore (Fig. 1). Distance between sites (1.2 ± 0.14 km [mean ± SD]) was a compromise between maximizing spatial dispersion (i.e., distance between sites) and achieving adequate replication (i.e., number of sites per island), while avoiding setting cameras in camping zones (e.g., the southern part of North Stradbroke Island). It is possible that individual scavengers visit more than one camera during an experiment, potentially leading to non-independence of adjacent camera deployments. We tested for lack of independence with Moran's I, a standard metric of univariate spatial correlation. Calculations were done with the R package spdep (Bivand et al. 2013, Bivand and Piras 2015). Moran's I was computed for two univariate responses, time to detection and time to removal of carcasses, and its significance tested using 999 Monte Carlo permutations after Crawley (2013). There is no evidence of spatial correlation for either metric for any deployment period (day/night) at any island (maximum $I = -0.0203$, $P = 0.19$). In addition, for either response variable, spatial correlations (Moran's I) were very close to zero ($P > 0.37$ in all cases) when calculated for neighboring cameras with lags of 1 and 2. This confirms that our observations of detection and removal rates were not pseudo-replicated (non-independent).

All sites were surveyed at monthly intervals from February to May 2014. To measure scavenging by nocturnal consumers, fish carcasses were placed as close as possible after End Evening Civil Twilight or last light, as gazetted by Geoscience Australia for each camera site. Similarly, to record diurnal scavenging, fish were deployed within 1 h of Begin Morning Civil Twilight (first light). Cameras deployed at first light were collected at the next last light after sunset; cameras deployed at last light were collected at the next first light before sunrise. Three deployments were made per site during each survey, resulting in a total sampling effort of 336 replicate camera trap sessions over the course of the study. Our main intent was to test whether the presence of red foxes in the beach food webs alters the *patterns* of carcass removal in terms of the partitioning of carrion removal between diurnal and nocturnal scavengers and between native birds and invasive mammals. Hence our experimental carcass deployments were designed to encompass full day and full night exposures, lasting 12.03 hours on average (day, 721 ± 39 minutes; night, 725 ± 55 minutes [mean ± SD]). The experiments were not designed to measure the total rate of carrion processing in the food web, which would require whole-ecosystem experiments of much longer duration.

Two motion-activated passive infrared trailcams (ScoutGuard Zero Glow SG560Z-8M; BOLY Media, Santa Clara, California, USA) were deployed at each trap site. The cameras were set in the seaward face, or near the crest, of the primary dune, typically 5–10 m landward of the strandline (i.e., the band of beach-cast material marking the uppermost reach of the swash and tides on sandy beaches). Cameras were positioned to give approximately orthogonal and overlapping fields of view of a fish carcass placed at the dune–beach boundary where marine carrion normally accumulates on sandy beaches. One freshly thawed sea mullet (*Mugil cephalus*), a common and widespread fish in the surf zone of Australian beaches, was used per camera deployment; all fish (mass = 359 ± 11 g [mean ± SE]) used in the experiment were sourced from a local fishing company. Animals in the images and videos captured with the camera traps were recorded as scavengers when they were seen to actively feed on the carcass (e.g., mouth, beak, or talons 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 (see also Huijbers et al. 2015).

Data analysis

The probabilities of carcass detection (i.e., a scavenger locating a fish) and removal (i.e., complete consumption in situ or removal/translocation from the beach site) by a scavenger were modelled using a generalized linear mixed model (GLM) with a binomial link function (Zuur et al. 2009). The full model included island (Moreton vs. Stradbroke Island) and time (day vs. night) as fixed factors, and trial as a random factor (i.e., there was no specific hypothesis associated with replicate trials in February, March, and late April/early May). Carcass persistence in relation to location and time of day was examined using survival analysis (Liu 2012). Differences in species composition of the scavenger guild between islands were tested with permuational analysis of variance (Anderson 2001), based on Bray-Curtis resemblance coefficients derived from summed occurrences of species per site. Contributions of individual species to dissimilarities in assemblage composition between islands were calculated using SIMPER (similarity percentages; Clarke and Gorley 2006).

Results

Carcasses located and removed, necromass consumed

Scavenging rates differed significantly between the two islands, driven by significantly higher nocturnal carcass detection and removal from beach sites

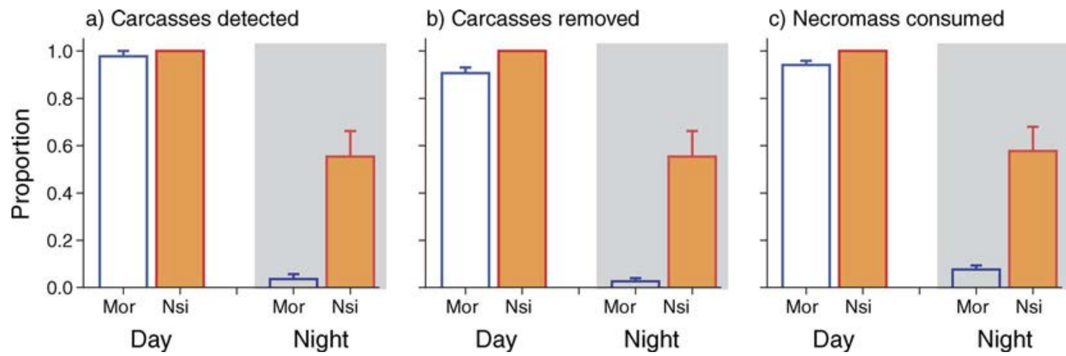

FIG. 2. Comparison of (a) carcass detection rates, (b) carcass removal rates, and (c) the proportion of fish necromass consumed by scavengers in 12 h between Moreton Island (Mor, open bars) and North Stradbroke Island (Nsi, solid bars) for experimental carrion deployment during the day and night (shaded areas).

frequented by red foxes on North Stradbroke Island (Fig. 2). On Moreton Island, only 3 of the 82 carcasses deployed (4%) were detected by scavengers at night, compared with North Stradbroke Island where 45 of 82 carcasses (55%) were located by red foxes at night ($P < 0.001$, Fig. 2a). In contrast to the substantially higher detection rate at night on North Stradbroke Island, the proportion of carcasses detected during the day was not significantly different ($P = 0.99$) between islands.

Carcass removal during the day was near complete on both islands ($P = 0.99$). Diurnal scavengers consumed entirely, or translocated, 39 out of the 43 fish carcasses deployed on Moreton Island (91%), and all 44 carcasses deployed on North Stradbroke Island (Fig. 2a). By contrast, at night only 2 carcasses were removed from the beaches of Moreton Island, while on North Stradbroke Island 45 of 82 carcasses (55%) were removed by scavengers ($P < 0.001$; Fig. 2b).

Of the 90 kg of fish necromass that was added to the beaches over the course of this experiment, more than 48 kg was consumed by scavengers during the experimental deployments. Patterns of consumption were spatially and temporally highly unbalanced: on North Stradbroke Island total biomass consumption (31.6 kg) was nearly double that of Moreton Island (16.6 kg). This was mostly due to a large difference in necromass consumed by nocturnal scavengers: 14.5 kg on North Stradbroke, compared with only 2.3 kg on Moreton Island. Diurnal scavengers removed similar quantities on both islands, 17.1 kg on North Stradbroke and 16.6 kg on Moreton Island. Thus, the proportion of necromass consumed showed a large island effect for nocturnal scavenging events ($P < 0.001$), while no significant island effect could be detected for diurnal consumption rates ($P = 0.99$; Fig. 2c).

Time to detection and removal, carcass persistence

Diurnal scavengers were slightly, but not significantly ($P = 0.698$), faster at detecting fish carcasses on North Stradbroke Island (126 ± 23 minutes [mean ± SD]) than on Moreton Island (139 ± 25 minutes). Inter-island differences in the rate of carrion processing were more pronounced ($P = 0.182$) for carcass removal: diurnal scavengers took almost one hour longer to remove carcasses from beaches at North Stradbroke Island (198 ± 25 minutes) than at Moreton Island (139 ± 23 minutes). At night, the average time to carcass detection and removal on North Stradbroke Island was identical, since all carcasses were removed by red foxes once detected ($n = 43$; time to detection and removal, 226 ± 29 minutes). There were too few scavenging events at night on Moreton island ($n = 3$) to enable a meaningful comparison between islands.

Carcass persistence (i.e., survival rates) did not differ significantly between islands during the day (Fig. 3a). Median carcass survival time was 85 minutes on Moreton Island and 124 minutes on North Stradbroke Island, resulting in a survival ratio (Moreton : North Stradbroke) of 0.69 and a log-rank hazard ratio of 1.11 (Mantel-Cox $\chi^2 = 0.3198$, $P = 0.57$). By contrast, carcass survival between the islands' beaches was fundamentally different for fish carcasses deployed at night (Mantel-Cox $P < 0.001$; Fig. 3b). Calculated median survival time on Moreton during the night was undefined due to the scarcity of mortality events, whereas on North Stradbroke, median survival time for all night-deployed carcasses was 609 minutes (log-rank hazard ratio Moreton : North Stradbroke was 0.35).

Species effects: biological partitioning of scavenging events and guild composition

Of the 134 fish carcasses that were detected by scavengers during the experiment, 86 were located by birds and 47 by mammals. Taxonomic partitioning of total scavenging activity differed between time of the day and island (Fig. 4). All carcasses located during the day were scavenged by birds. Within the bird guild, raptors were functionally dominant, both in terms of carcass detection (i.e., first species at carrion in 75 cases), and in terms of carcass removal (complete consumption or translocation of 79 fish). Torresian Crows detected 10 carcasses first and removed 3, while a beach stone-

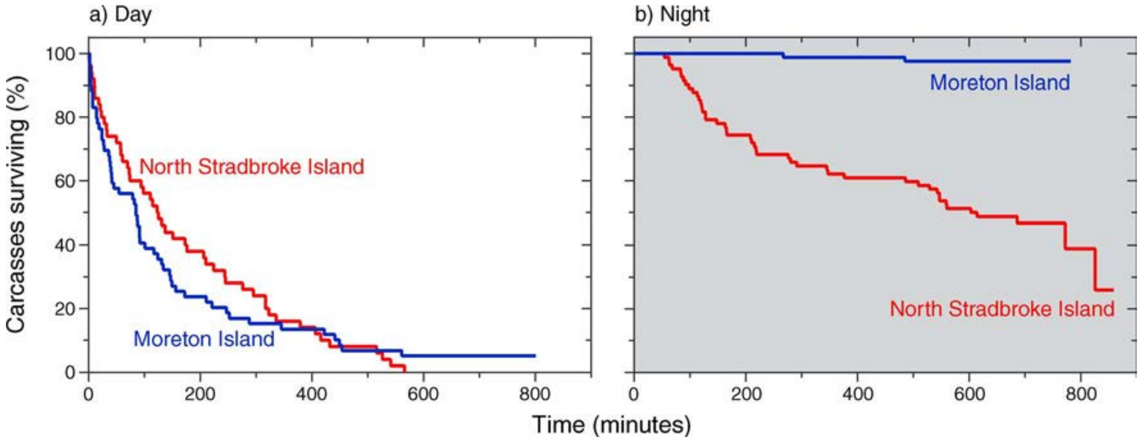

FIG. 3. Comparison between islands of survival curves for fish carcasses during the (a) day and (b) night.

curlew located one fish. Mammals detected all carcasses during the night, save for a single case of a beach stone curlew on Moreton Island. On North Stradbroke Island, red foxes accounted for all carrion detections and removals by mammals at night (n = 45). Nocturnal scavenging activity was extremely low on Moreton Island (Fig. 2), only two fish carcasses having been removed by mammals, one by a feral pig, the other by a (native) water rat.

Scavenging events also differed between islands with respect to the first species arriving at a carcass and the species removing a carcass (Fig. 4). During the day, Brahminy Kites arrived first at 52% of all scavenged carcasses on Moreton Island, whereas on North

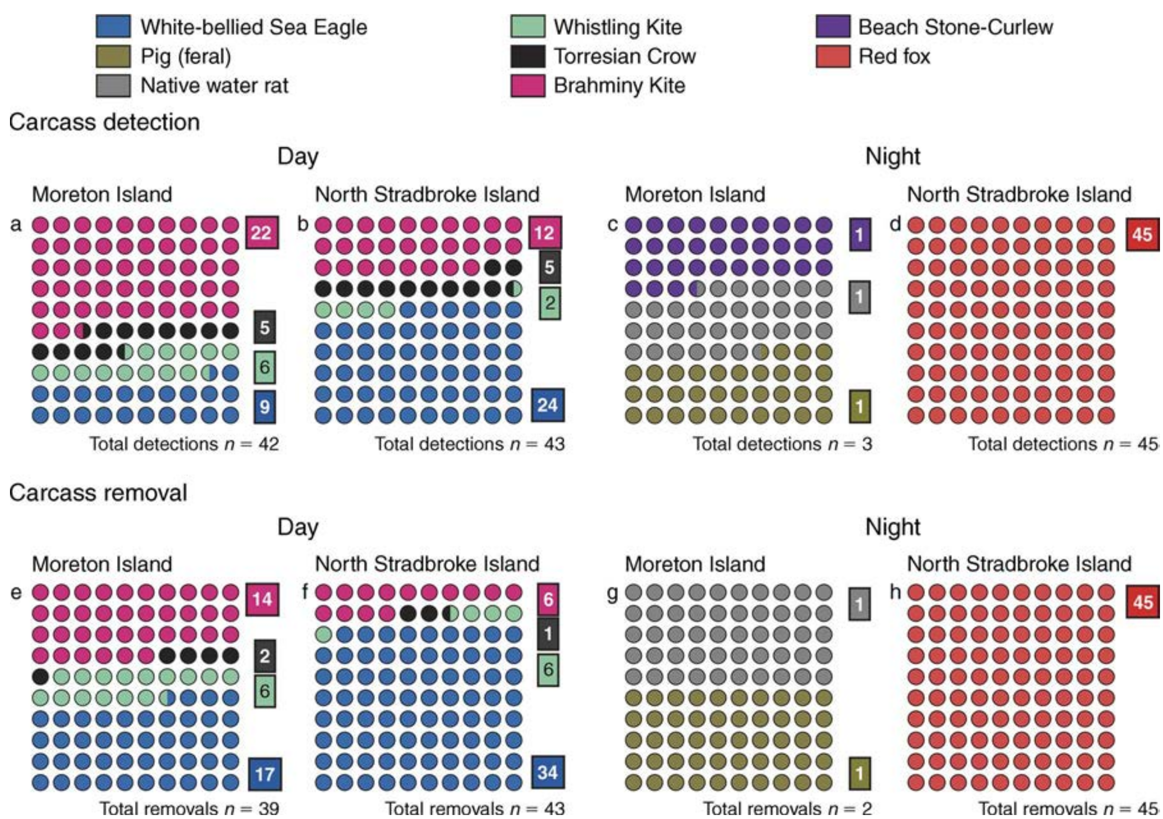

FIG. 4. Partitioning of scavenging events among scavenger species for (a, b, e, f) diurnal events and (c, d, g, h) nocturnal events in terms of carcass detections attributable to a species (a–d) and carcass removals (e–h). Panels show the fraction of all events attributed to a species; the actual number of carcasses detected or removed is given for each species to the right of the main panels. Note that very few carcasses were scavenged at Moreton Island at night.

TABLE 1. Scavenger species recorded feeding on fish carcasses at the beach–dune interface during the experiment on Moreton Island (Mor) and North Stradbroke Island (Nsi).

Scavenger species	No. sites Mor	No. sites Nsi	No. carcasses Mor	No. carcasses Nsi	SIMPER dissimilarity Contribution (%)	SIMPER dissimilarity Cumulative (%)
Red fox (*Vulpes vulpes*)	0	**14**	0	**45**	30.2	30.2
Torresian Crow (*Corvus orru*)	8	8	15	**19**	24.5	54.6
White-bellied Sea-Eagle (*Haliaeetus leucogaster*)	11	**14**	16	**34**	13.5	68.1
Brahminy Kite (*Haliastur indus*)	**12**	10	**23**	15	13.3	81.4
Whistling Kite (*Haliastur sphenurus*)	**8**	4	**9**	7	8.6	90.0
Silver Gull (*Chroicocephalus novaehollandiae*)	0	**4**	0	**13**	6.8	96.8
Pig (feral) (*Sus scrofa*)	**1**	0	**1**	0	0.7	97.5
White-faced Heron (*Egretta novaehollandiae*)	0	**1**	0	**1**	0.7	98.2
Rat (*Rattus* sp.)	**1**	0	**1**	0	0.6	98.8
Water rat (*Hydromys chrysogaster*)	**1**	0	**1**	0	0.6	99.4
Beach Stone-Curlew (*Esacus magnirostris*)	**1**	0	**1**	0	0.6	100.0

Notes: Species are ordered by their contribution to community-wide differences in assemblage composition based on SIMPER (similarity percentage) analysis. Entries in boldface type denote higher values in comparisons between islands for the metrics of site occupancy and the number of carcasses at which a species was detected.

Stradbroke Island, White-bellied Sea-Eagle dominated first arrivals, detecting 55% of fish carcasses first (Fig. 4). White-bellied Sea-Eagles removed most fish carcasses on both islands (Moreton, 44%; North Stradbroke, 79%), while Brahminy Kites removed 36% of carcasses on Moreton Island, but only 14% on North Stradbroke Island (Fig. 4).

Based on all recorded feeding events across sites and deployments, the composition of the scavenger guild differed significantly (PERMANOVA, $P < 0.001$) between islands (Table 1; Figs. 5 and 6). A large part of inter-island differences in the scavenger guild is attributable to the dominance of red foxes as nocturnal scavengers at all sites on North Stradbroke Island, in

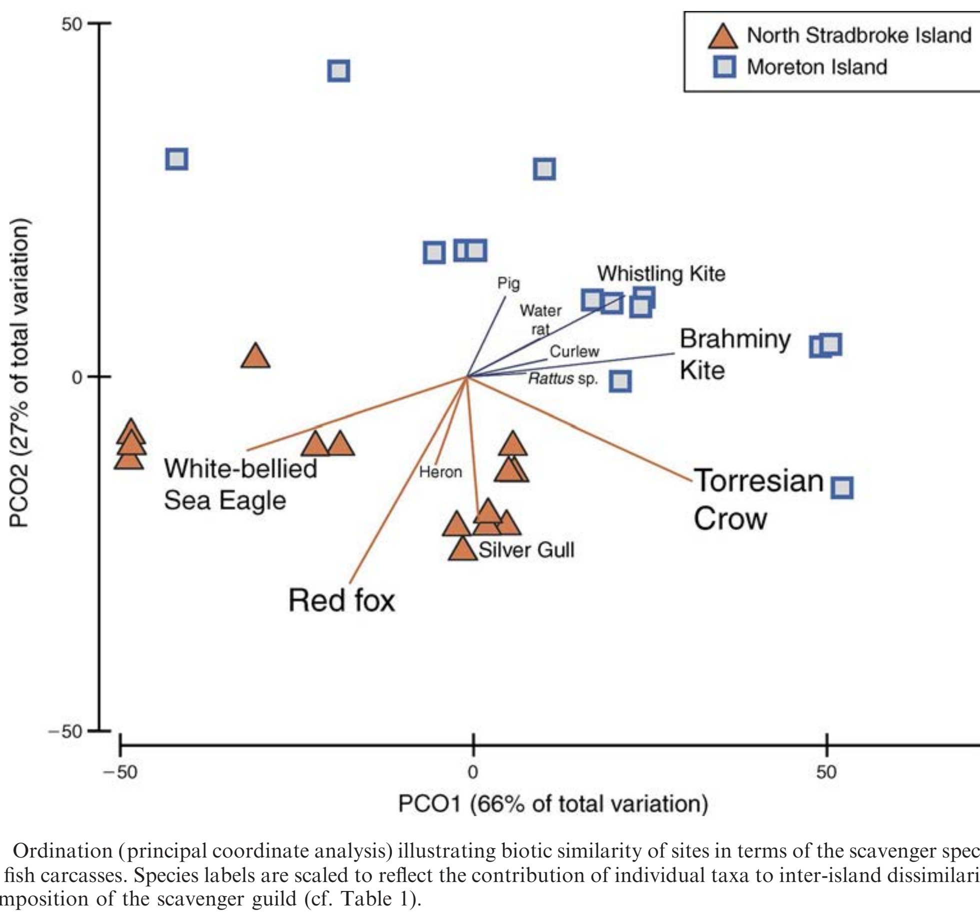

FIG. 5. Ordination (principal coordinate analysis) illustrating biotic similarity of sites in terms of the scavenger species recorded to feed on fish carcasses. Species labels are scaled to reflect the contribution of individual taxa to inter-island dissimilarity in overall species composition of the scavenger guild (cf. Table 1).

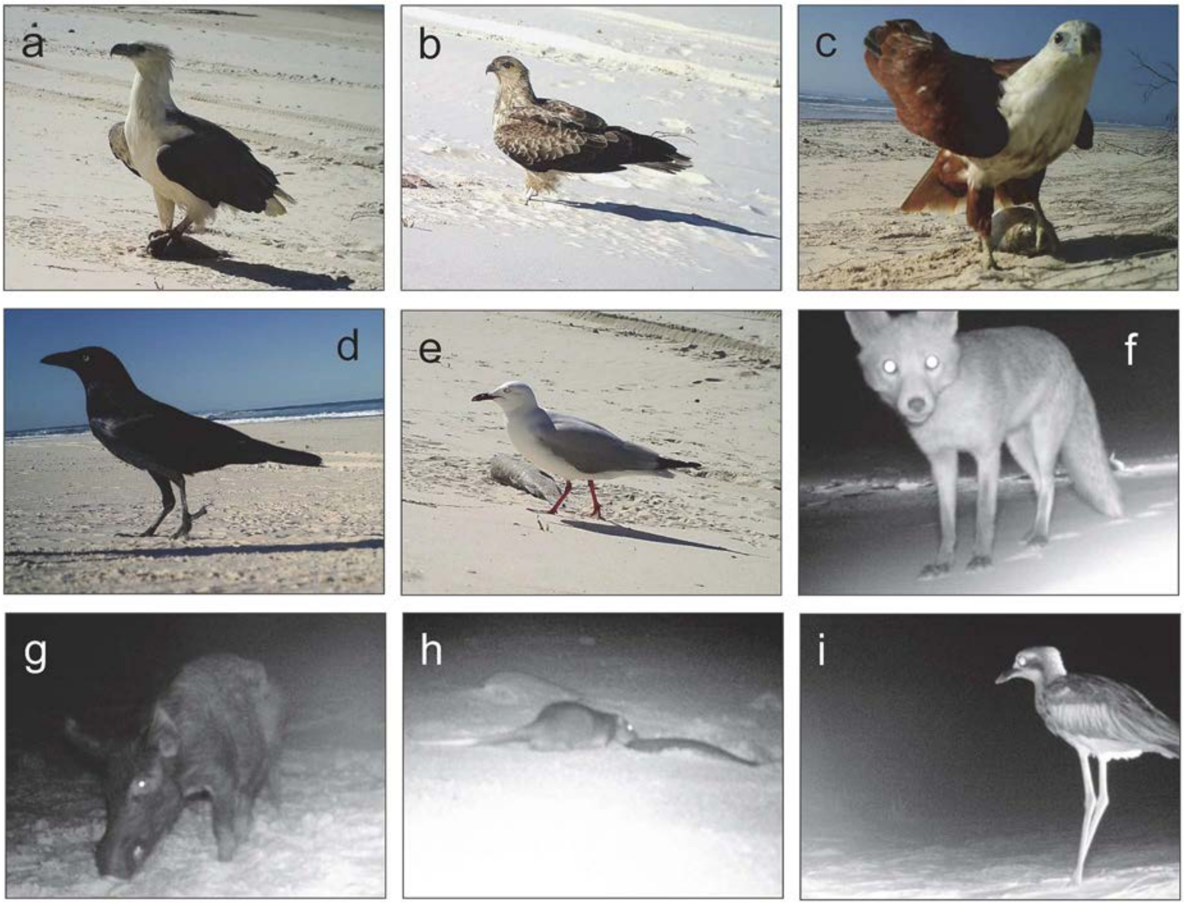

FIG. 6. Vertebrate scavengers recorded during the experiment at Moreton and North Stradbroke Islands: (a) White-bellied Sea-Eagle, (b) Whistling Kite, (c) Brahminy Kite, (d) Torresian Crow, (e) Silver Gull, (f) red fox, (g) feral pig, (h) water rat, and (i) Beach Stone-Curlew.

contrast to Moreton Island where no red fox activity was detected (Table 1). White-bellied Sea-Eagles were more widespread and active on North Stradbroke Island, while Brahminy Kites occurred at a higher frequency at fish carcasses on Moreton Island (Table 1; Figs. 5 and 6).

Discussion

Considering the ecological function of carrion removal, we found both clear partitioning of functional attributes (i.e., separation of temporal foraging niches between mammals and birds, suggesting complementarity) and similarity among taxa (i.e., rapid location and consumption of carrion during the day within the bird guild, suggesting redundancy). Combined, these findings are consistent with the presence of both functional complementarity and redundancy in the carrion food webs examined by us.

Red foxes (*Vulpes vulpes*) dominated beach carrion consumption on North Stradbroke Island, occurring at all experimental sites and removing more than half (55%) of carrion at night; such sizeable consumption of carrion by an invasive carnivore constitutes a significant functional change in the beach–dune food web. From a purely functional perspective, red fox consumption of marine carrion stranded on beaches has augmented the rate of carrion processing, a function fulfilled almost entirely by birds in the absence of foxes and dingos (as demonstrated on dingo- and fox-free Moreton Island). Elsewhere, marine carbon and nitrogen can form a substantial (>50%) part of the assimilated diet in coastal foxes (Roth 2002, 2003, Tarroux et al. 2012), and marine energy subsidies are thought to be instrumental in the establishment and persistence of the invasive red fox (Killengreen et al. 2011). Thus, marine carrion is also likely to subsidize coastal fox populations in the ecosystem studied by us; the fact that foxes fed regularly on fish carcasses supports this prediction empirically.

Since beach scavengers functionally couple marine with terrestrial ecosystems via the inland transfer of marine carbon (Stapp and Polis 2003, Spiller et al. 2010), foraging of foxes on beaches may also enhance this pathway. Multiple repeat visits by foxes to camera trap sites after an individual had removed a fish indicate that the potential rate of carcass removal could be higher than measured by us. The observed behavior may be related to the foxes' propensity to "surplus kill" and to cache food (Thomson and Kok 2002, Jackson et al. 2007). Translocation of marine organic matter inland and caching is thus a potentially significant pathway to energetically link marine with dune systems (sensu Bouchard and Bjorndal 2000). That nutrients from foxes become incorporated into coastal ecosystems is poignantly illustrated by Roth's (2003) observation that "fox dens in tundra areas are often very conspicuous because of the lush vegetation that results from soil enrichment and disturbance, and therefore are visible from long distances."

That marine carrion on beaches is likely to facilitate the persistence of an invasive carnivore species known to have severe negative ecological impacts in Australia is of conservation significance (Maguire et al. 2009, Maslo and Lockwood 2009, Saunders et al. 2010, Kurz et al. 2012). Plausible ecological consequences of foxes in the ecosystem may, inter alia, encompass (1) increased predation risks for turtles and birds resulting from larger fox populations and greater activity; (2) competition between foxes and raptors due to lower carrion availability following fox scavenging; (3) changed predator–prey interaction strengths in food webs for prey shared between foxes and raptors; and (4) the role of foxes as biological vectors linking marine and terrestrial carbon pools.

Foxes consumed one quarter of the fish necromass deployed on North Stradbroke Island during the experiments, making them efficient consumers of resources. Since wave- and tide-cast marine carrion is equally likely to become stranded during day and night, removal of large amounts of night-cast beach carrion by foxes effectively represents a form of direct exploitative competition between birds and mammals. By contrast, on beaches without foxes, marine carrion washed ashore at night remains available to diurnally foraging birds that start searching for carrion around sunrise. A salient finding of our study is that negative effects on coastal raptors by foxes are plausible, caused by foxes removing wave-cast carcasses that form an important part of raptor diets. We show that where foxes are present, they remove a large number of carcasses at night, and thus fewer are available for scavenging birds. This phenomenon potentially has implications both for the foxes and the birds: foxes could be subsidized by carrion and hence their impacts on other species may be amplified (e.g., predation on ground-nesting shorebirds and turtles), while birds could be "robbed" of carrion resources by the invasive foxes.

Active conservation management of scavenger populations, mainly large iconic birds of prey, can be in the form of enhancing the availability of carrion by placing animal carcasses in the consumers' habitat (Lopez-Lopez et al. 2014). This strategy is theoretically feasible for raptors on beaches. We have shown here and elsewhere that threatened birds of prey readily take fish carcasses placed on the beach or in the dunes (Huijbers et al. 2013, 2015, Schlacher et al. 2015). Thus, the option exists to mitigate negative effects of foxes on native wildlife by supplying coastal bird scavengers with fish carrion in a similar way as was done in this study.

External food inputs can drive consumer dynamics and biotic interactions in receiving systems, altering the trophic dynamics at several levels of food webs (Polis et al. 1997, Spiller et al. 2010, Tarroux et al. 2012, Moleón et al. 2014). In this context, marine carrion subsidies to coastal foxes could indirectly modify species interactions in beach-dune food webs where foxes and raptors share prey other than carrion (e.g., insects, small rodents, reptiles, birds). Two not mutually exclusive scenarios are hypothetically possible here: (1) hyper-predation, whereby foxes (by consuming carrion) could increase predation pressure on native prey species by raptors whose per capita access to carrion becomes more limited due to fox scavenging; and/or (2) hypo-predation, whereby foxes could depress predation pressures by raptors on live prey by having negative demographic impacts on raptor populations (e.g., fewer raptors at lower densities due to overall lower necromass in the system). Red foxes have an extraordinarily catholic diet that includes beach and dune invertebrates (Ricci et al. 1998) and many prey items usually taken by coastal raptors (Marchant and Higgins 1993) are also regularly consumed by foxes (Saunders et al. 2010). Moreover, prey switching and alternating between carrion scavenging and active hunting is common in foxes (Catling 1988). Given these biological attributes, higher-order interaction effects of foxes in local food webs could arise and these are amenable to testing at the study sites and beyond.

Conclusions

How co-occurring species partition functional niche space is a topic of fundamental importance in ecology, shaping our understanding of food-web architecture and dynamics. Convergence of roles is thought to promote functional redundancy, while niche divergence is predicted to enhance complementarity: the concepts of functional redundancy and complementarity form the theoretical backbone of our manuscript. Here we tested how changes in the species composition of consumer assemblages affect redundancy and complementarity using a unique model system of two islands that are highly similar in habitat types but differ in the suite of vertebrate scavengers they contain. This setting allowed us to test specifically for the effects of adding top consumers to food webs. We showed that adding red foxes (an invasive carnivore in Australia) significantly alters the degree of complementarity in scavenger food webs, against a backdrop of functional redundancy in the bird scavenger guild. Foxes were shown to be highly efficient nocturnal consumers of carcasses, competing with diurnal raptors that dominate consumption in fox-free habitats. Interest in how invasive species alter structural and functional attributes of ecosystems continues unabated. Thus, detecting functional changes in ecosystems caused by invasive carnivores offers opportunities to test fundamental ecological theses put forward to structure food webs.

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