



Functional plasticity in vertebrate scavenger assemblages in the presence of introduced competitors

Ellen L. Bingham¹ · Ben L. Gilby^{1,2} · Andrew D. Olds^{1,2} · Michael A. Weston³ · Rod M. Connolly⁴ · Christopher J. Henderson^{1,2} · Brooke Maslo⁵ · Charles F. Peterson⁶ · Christine M. Voss⁶ · Thomas A. Schlacher^{1,2}

Received: 11 March 2018 / Accepted: 2 July 2018 / Published online: 6 July 2018
© Springer-Verlag GmbH Germany, part of Springer Nature 2018

Abstract

Introduced species may suppress or enhance ecological functions, or they may have neutral effects in ecosystems where they replace or complement native species. Few studies, however, have explicitly tested for these trajectories, and for the effect these might have for native species. In this study, we experimentally test the trajectory and scale of change in the function of ‘carriion removal’ at different carriion loads along ocean beaches in Eastern Australia that have different numbers of introduced red foxes (*Vulpes vulpes*) and several species of native raptors. We hypothesized that the ‘positive’ effect of foxes on carriion removal would be greatest at high carriion loads, because competition for resources between native and introduced species is lower. Scavenger abundance, fox occurrences, and carriion consumption by these species differed widely between locations and times. Despite distinct spatial differences in the structure of vertebrate scavenger assemblages, total carriion consumption was not significantly different between locations at any carriion load. This lack of variation in functional rates indicates potential functional plasticity in the scavenger assemblage and possible functional accommodation of red foxes. Neutral fox effects on ecological functions or the ecosystem more broadly are, however, very unlikely to extend beyond carriion consumption.

Keywords Beach · Carriion · Ecological functioning · Fox · Introduced species

Communicated by Janne Sundell.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00442-018-4217-0>) contains supplementary material, which is available to authorized users.

✉ Ben L. Gilby
bgilby@usc.edu.au

¹ School of Science and Engineering, University of the Sunshine Coast, Maroochydore, QLD 4558, Australia

² The ANIMAL Research Centre: Health + Ecology + Conservation, University of the Sunshine Coast, Maroochydore, QLD 4558, Australia

³ Centre for Integrative Ecology, School of Life and Environmental Sciences, Deakin University, Burwood, VIC 3125, Australia

⁴ Australian Rivers Institute, Coasts and Estuaries, Griffith University, Gold Coast 4222, QLD, Australia

⁵ Department of Ecology, Evolution and Natural Resources, The State University of New Jersey, Rutgers 08901, USA

⁶ Institute of Marine Sciences, University of North Carolina at Chapel Hill, Morehead City, NC 28557, USA

Introduction

Introduced species are now pervasive in many ecosystems (Crowl et al. 2008). Introduced species modify ecological functions by competing with native populations for space and food, or by directly preying upon native species that perform critical ecosystem functions (Buechley and Sekercioglu 2016; Finke and Denno 2005; Gurevitch and Padilla 2004). For example, introduction of European rabbits (*Oryctolagus cuniculus*) can alter ecosystem function by modifying plant community structure and rates of primary production via overgrazing (Keane and Crawley 2002). Globally, research into the effects of introduced species on ecological functions has uncovered mostly negative effects on ecological processes (Pyšek et al. 2012; Tumolo and Flinn 2017; Van Kleunen et al. 2015; Vilà et al. 2011). However, introduced species may not cause a decline in functions in all cases; they can either replace or augment functions (Didham et al. 2005; Schlaepfer et al. 2011). For example, introduced species can enhance ecological function by supplementing the role of native species, resulting in increased efficiency of

ecological processes (e.g., pollination performed by the European honey bee, *Apis mellifera*) (Bergstrom et al. 2009; Schmitz 2008). Alternatively, introduced species could simply replace the functional capacity of native species as introduced populations increase and native populations decrease (i.e. maintain functional equivalence) (Chapin et al. 2000; Crowl et al. 2008).

Evolutionary and ecological processes can alter the abundance and population structure of species that occupy similar environments and perform similar functional roles (Broadbent et al. 2018; Leibold and McPeck 2006; Losos 2011). This allows ecological functions to be maintained while assemblages undergo change following species introductions (Loreau 2004; M’Gonigle et al. 2012). Functional equivalency is often established in species-rich communities (Hubbell 2005), and is sometimes also observed when introduced species directly supplant native species and their functional roles (Glen and Dickman 2005; Hubbell 2005). Whilst it is hypothesized that three potential relationships between introduced species expansion and ecological functions are possible (functional augmentation, reduction, or equivalency), a few studies have explicitly tested the functional trajectories that introduced species may take when they invade (e.g., Lyons and Schwartz 2001).

Sandy beaches are important habitats for a diversity of species, and provide an array of important and valuable ecosystem services (Schlacher et al. 2015b). Wave-cast carrion can provide a major food source to a diverse range of scavengers on beaches (Schlacher et al. 2013; Wilson and Wolkovich 2011). Wave-cast carrion is, however, a resource that varies in both quantity and location across time and space (Huijbers et al. 2015; Schlacher and Connolly 2009). This variability alters resource availability for scavengers and can modify food-web structure (Moreno-Opo et al. 2012; Schlacher et al. 2013). Whilst previous studies have established how the intensity and distribution of scavenging varies with different ecological factors (urbanisation, presence of people, introduced species, etc.), the majority of published research has focused on small carrion loads (i.e., one fish) (Brown et al. 2015; Huijbers et al. 2015, 2016b; Schlacher et al. 2013). In reality, carrion occurs on sandy shores in varying amounts, from single seabird carcasses, to large fish kills, or whale strandings (Chan et al. 2017). Therefore, the potential ‘positive’ effects of the introduced scavengers on functioning might be less at low carrion loads, because native and introduced species compete for available carrion, and higher as carrion loads increase, because the amount of carrion available eventually becomes greater than the amount consumed by any one animal group per unit time (Fig. 1). Conversely, if introduced species have suppressed

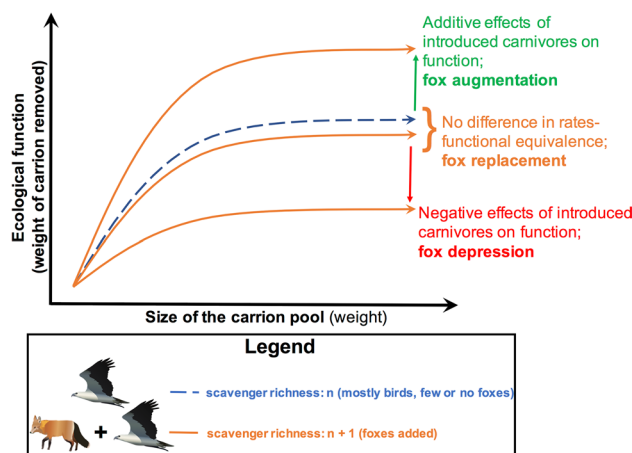


Fig. 1 Conceptual diagram illustrating how total carrion removal by vertebrate scavengers is predicted to change with the type of scavengers, particularly the presence of introduced red foxes on Australian beaches. Native scavengers, depicted by the white-bellied sea eagle, includes all native vertebrate scavengers mainly encompassing raptors and other birds, monitor lizards, and native mammalian carnivores (e.g., dingoes, Tasmanian devils, quolls, and thylacine). The orange lines illustrate three possible outcomes when exotic red foxes invade scavenger guilds: (i) red arrow: foxes suppress overall carrion consumption; (ii) green arrow: foxes increase consumption; or (iii) the middle orange line: no significant change to overall function or rates in the presence of foxes. Note that the model predicts stronger effects of introduced carnivores at greater carcass levels

native scavengers, and the function not fully replaced by the introduced species, the maximum amount of carrion consumed per unit time could be lowered across all carrion load levels, meaning a greater ‘negative’ effect on function at high carrion loads (Fig. 1).

This study examined how the presence of an introduced carnivore (the European red fox *Vulpes vulpes*) in carrion-based food webs alters the consumption rates of carcasses at different resource levels (i.e., carrion amounts). In this sense, our focus is on determining differences in scavenging rates between broader locations (10 s of km scale) as a result of different levels of fox abundance, as opposed to site-specific influences of foxes at small scales (100 s m). We specifically tested three predictive hypotheses:

- (1) ‘Fox augmentation’: consumption rates of beach-cast carrion are predicted to be significantly higher in food webs invaded by foxes. This ‘augmentation effect’ operates by foxes adding to carrion processing normally performed by birds (crows and raptors), and is predicted to be strongest when the number of available carcasses exceeds the capacity of native scavengers to eat them (Fig. 1);

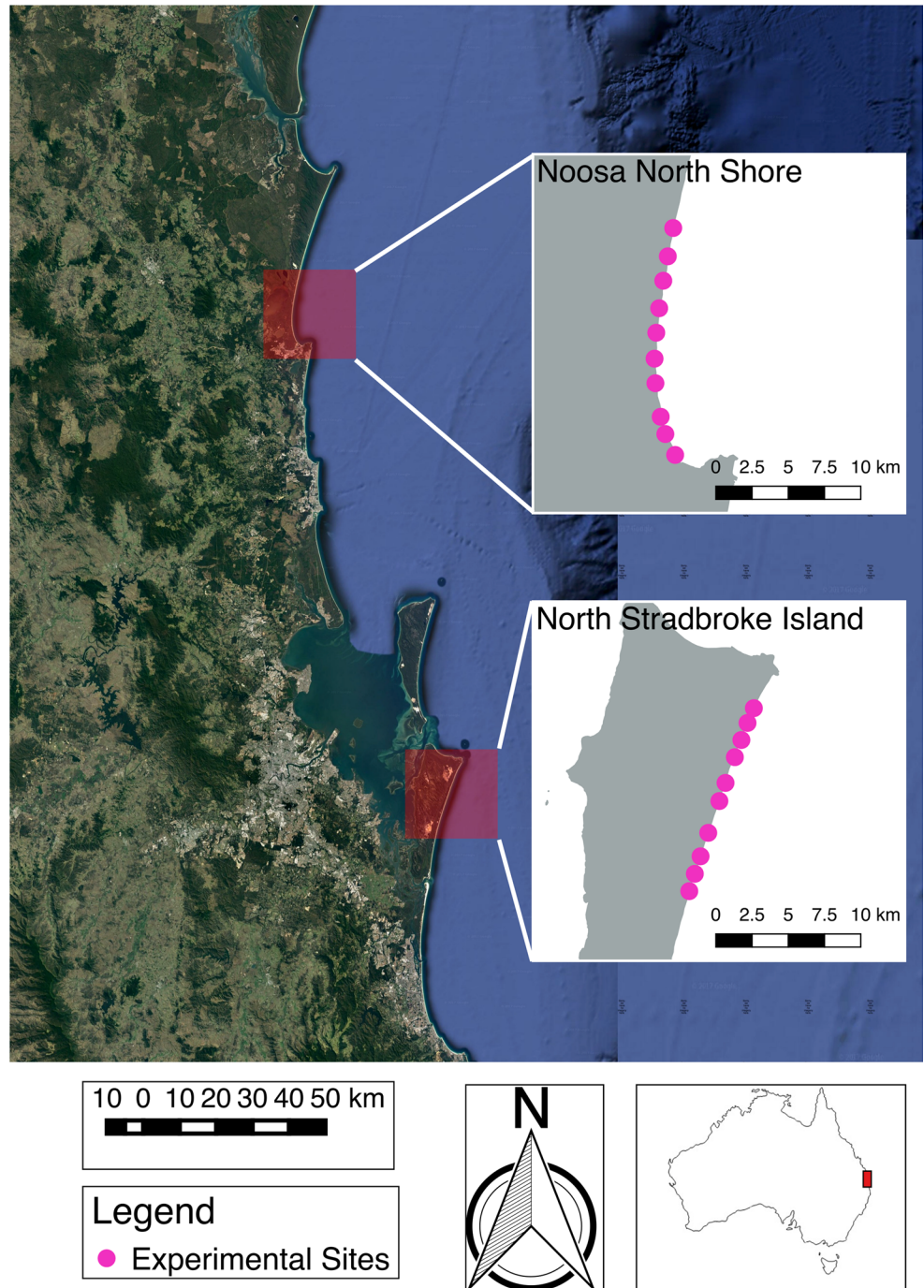
- (2) ‘Fox depression’: carcass removal rates are lower in the presence of introduced foxes, because they suppress the activity and/or population size of native scavenger species and this native species suppression is not replaced by their own scavenging (Fig. 1);
- (3) ‘Fox replacement’: no significant changes occur to carcass removal rates in food webs invaded by foxes, because foxes replace the role of native scavengers at equal rates (i.e., functional equivalency; Fig. 1).

Methods

Study sites

We tested the functional effects of the presence of different numbers of foxes in carrion-based food webs at two locations in southeast Queensland, 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

Fig. 2 Locations of study sites in Southeast Queensland, Australia



(27.30°S, 153.30°E; Fig. 2). These locations exhibit similar geomorphological characteristics; both are ocean-exposed shores of an intermediate morphodynamic type (intertidal 50–80 m wide, sand grain size 300–500 microns, and modal wave height 1–2 m), backed by vegetated dunes comprising relatively low levels of anthropogenic development (Huijbers et al. 2013). Ten experimental sites were established at each location and dispersed evenly along 13.5 km of beach, an average distance of 1.5 km between each site (Fig. 2).

Field methods—ambient avian scavengers

Bird surveys were conducted using area search surveys at each location during each study period to estimate the abundance of bird scavengers along beaches (i.e., independent of camera trapping activities). Bird surveys were done by driving the length of each beach in a four-wheel drive vehicle at a maximum speed of 40 km/h just after sunrise the mornings before, during, and after each carrion deployment for a total of three beach-wide bird counts per treatment. Two observers identified, counted, and recorded positions of birds observed between the outer boundary of the surf zone and the tree line at the back of the fore dune during surveys (Meager et al. 2012).

Field methods—scavengers and carrion consumption

The principal technique to identify the species of vertebrate scavengers (i.e., consumer assemblages) and the rate of carcass removal by scavengers (i.e., function) was to monitor experimentally deployed fish carcasses with camera traps (Brown et al. 2015). Sea mullet (*Mugil cephalus*) were chosen as the carrion source, because this species is widely distributed, commonly found in the surf zone of ocean beaches within the study area (Borland et al. 2017), and consumed by several scavenger species (Schlacher et al. 2013).

Carrion addition treatments consisted of one fish per site (i.e., a total of 10 fish at each location across our 10 sites) (0.29–0.43 kg), 25 fish per site (6–6.5 kg), 32 fish per site (13.83–14.54 kg), and 50 fish per site (26.12–26.7 kg; Table S1A). All fish were randomly placed (i.e., in no particular orientation or arrangement) within a 1 m² area in the foredune at each site. These treatment levels were chosen based on our predictive hypotheses (Fig. 1): (a) low carcass level (1 fish carcass) at which no clear introduced species effects were predicted to occur, (b) two intermediate carcass levels (medium and high levels; approximately 25 and 32 fish per site, respectively) at which introduced species effects were predicted to be variable or indistinct, and (c) very high carcass levels (50 fish per site) at which introduced species effects were predicted to be strongest. This design enabled us to determine the approximate threshold above which no

more carrion can be consumed per day (i.e., a carrion consumption ‘threshold’), and whether these relationships differ for sites with and without foxes. High treatment levels were designed a priori to exceed the likely total consumption rates of native scavengers based on scavenging rates determined in the previous experiments in the region (Brown et al. 2015; Huijbers et al. 2015).

Four sets of field experiments occurred approximately 1 month apart (i.e., deployment periods) to minimize the risk of scavengers developing learned behaviour to repeatedly visit the experimental sites. All deployments were conducted during the austral summer. Deployments were usually conducted at low tide due to accessibility issues at high tide. All ten sites at each beach received the same treatment (i.e., carrion load) during each deployment period. All fish used for all treatments were weighed individually before deployment, placed in the field at sunset, and then weighed individually again at sunrise (after approximately 12 h), and at sunset the next day (after 24 h) (per Brown et al. 2015; Huijbers et al. 2015). This design resulted in a total of 80 deployments overall (2 locations × 10 sites × 4 treatments). The previous studies in the region using this deployment method have shown no significant reduction in unconsumed carcass weights during the 24 h deployment period (Brown et al. 2015).

Each carcass deployment was monitored using two camera traps (ScoutGuard Zero Glow) to record carcass detection, removal, and consumption of carrion by scavenger species. Fish were placed at the seaward edge of the dunes near the strandline, with the two camera traps positioned on the dune face at an angle of 30°–45° in a slightly elevated position 5–8 m from the carcasses. One camera was set to record videos (1280 × 720 pixels; 10 s duration per detected event), the other set to take still images (8 MP) in three photo bursts per detection, at the highest possible sensitivity setting with a maximum flash range of 8 m.

Image analysis

Still images and videos obtained by camera traps provided data on the timing of carrion detection and removal events during deployments, and the species to which carcass removal events can be attributed. Animals were recorded as being a scavenger when seen with a fish in their mouth/beak, or when both the fish and the scavenger were present in one image, and the fish and scavenger were absent in the next image (Brown et al. 2015; Huijbers et al. 2015). Where carcass loss could not be attributed to any specific species, we attributed the loss using the proportion of carcasses removed by each scavenging species during that particular location/treatment combination (i.e., a value between 0 and 1 per non-attributed for each potential scavenging species). Importantly, because we checked baits

in the mornings, we could readily attribute differences in night scavenger (all foxes) versus day scavengers (mostly raptors) (Brown et al. 2015).

The number and type of animals consuming carrion were also quantified from the video and still image footage using the *MaxN* metric; *MaxN* is the maximum number of individuals of a species recorded by cameras per 24 h experimental deployment (Gilby et al. 2017; Ogada et al. 2012). *MaxN* is a conservative measure of relative species abundance, because it accounts for individuals repeatedly entering and leaving the camera's field of view. The *MaxN* of a species on camera trapping was always higher than the number of fish carcasses consumed by that species, because not all individuals took bait from our sites.

Data analysis

Data analysis overview

Our analytical approach incorporated three key steps. We first used the ambient avian scavenger data for bird scavengers, and *MaxN* data from the camera trapping for foxes and other land-based scavengers to show how the potential scavenger communities, especially the abundance of foxes, differed between our locations (a central assumption in our hypotheses). Second, we used multivariate analyses to quantify differences in the number of carcasses consumed by each species between our treatments and locations. Finally, we used regression analyses to show how the total amount of carrion consumed differed between treatments and locations.

Ambient scavengers

Differences in ambient scavenger densities (i.e., from 4WD bird surveys and *MaxN* values for foxes and monitors) between locations (fixed factor, two levels; NSI and NSS) and treatment periods (fixed factor, four levels per location) were tested using generalised linear models (GLMs) in R (R Core Team 2014). These data could not be analysed using multivariate methods, because the level of replication differed between camera trapping ($n = 10$ per treatment) and bird surveys ($n = 3$ per treatment), and because the two methods are fundamentally different in their approach. GLM analyses were run with Poisson distributions on the total number of birds of each species identified during each survey for bird surveys, and with binomial distributions on the number of foxes and monitors (because fox and monitor *MaxN* were always 0 or 1). Significant differences from GLM analyses were further examined using Tukey's post hoc tests.

Scavenging assemblage and scavenging rates

Differences in the number of carcasses removed by each species during camera trapping surveys between locations and treatments were tested using permutational multivariate analysis of variance (PERMANOVA) on square root transformed Bray–Curtis measures in the multivariate statistical program PrimerE (Anderson et al. 2008).

Finally, we used generalised additive models (GAMs) in the *mgcv* package (Wood 2012) of R to test for the effects of location and initial deployment weight (i.e., 'treatment'; continuous variable) on the amount of carrion consumed at each site.

Results

Ambient scavenger densities vary widely in space and time

Numbers of bird scavenger species were highly variable with no clear and consistent patterns with respect to location, experimental period, or both (Table 1, Fig. 3). Brahminy kite, *Haliastur indus*, abundance differed

Table 1 Generalised linear model results for differences in potential scavenging species during scavenger occurrence surveys (i.e., birds using 4WD-based avifaunal surveys, and foxes and monitors using *MaxN* from camera trapping)

Source	df	χ^2	P
4WD Bird counts			
Brahminy kite			
Location	1	153.1	<0.001
Treatment	3	113.7	<0.001
Location × treatment	3	50.6	<0.001
Whistling kite			
Location	1	124.5	0.02
Treatment	3	120.7	0.27
Location × treatment	3	84.7	<0.001
White-bellied sea eagle			
Location	1	67.4	<0.001
Treatment	3	39.1	<0.001
Location × treatment	3	38.5	0.9
Camera trapping <i>MaxN</i>			
European red fox			
Location	1	106	<0.001
Treatment	3	103.5	0.46
Location × treatment	3	101.5	0.58
Lace monitor			
Location	1	60.4	0.73
Treatment	3	49.5	0.01
Location × treatment	3	44.4	0.16

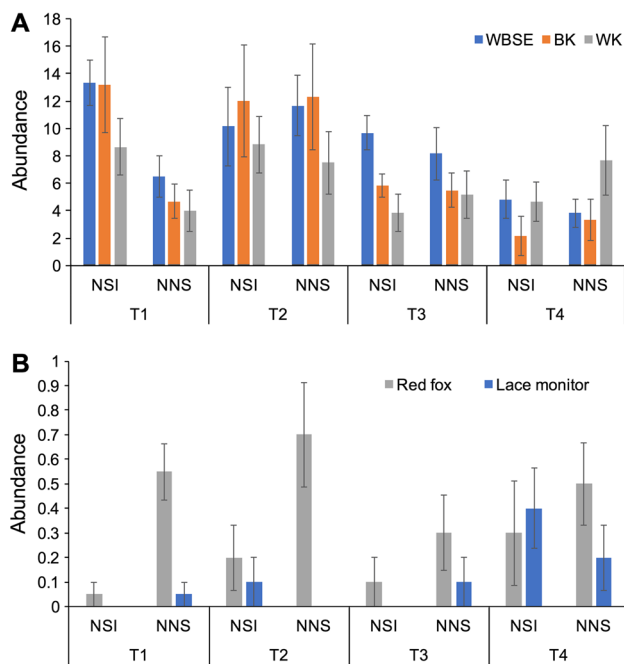


Fig. 3 Abundance of identified scavenging species (mean, SE) during scavenger occurrence surveys using **a** beach bird 4WD-based counts, and **b** occurrence during camera trapping surveys. Associated tests are provided in Table 1. *WBSE* white-bellied sea eagle, *BK* brahminy kite, *WK* whistling kite, *NSI* North Stradbroke Island, *NNS* Noosa North Shore

significantly between locations and treatment periods, with counts highest during medium carrion treatments (Table 1, Fig. 3). Counts of whistling kites, *Haliastur sphenurus*, varied significantly between locations during different treatments, with prominent abundance spikes during the low and medium carrion deployments at North Stradbroke Island and during the very high carrion treatment at the Noosa North Shore (Table 1, Fig. 3). White-bellied sea eagles, *Haliaeetus leucogaster*, were more abundant at North Stradbroke Island and decreased in abundance over time (Table 1, Fig. 3).

Our predictive hypotheses called for variable presence and frequencies of foxes among locations and treatments. This was, indeed, the case with foxes. The index of fox abundance from camera trapping surveys was significantly higher at the Noosa North Shore (Table 1, Fig. 3). Whilst there was no significant difference in fox abundance between experimental sets, there was a general trend for foxes to be more abundant during low carrion treatment at the Noosa North Shore, whilst more foxes were recorded during high carrion additions at North Stradbroke Island (Fig. 3). There were no significant differences in the abundance of lace monitors between locations or treatment periods (Table 1, Fig. 3).

Scavenging rates by individual species differ between locations

Whilst the same guild of vertebrate scavengers was observed at both locations, carcass removal rates by individual species differed significantly between locations (Fig. 4a). At Noosa North Shore, foxes dominated carcass removal except for during the highest experimental carcass additions, when white-bellied sea eagles removed more carcasses (Table S1B). At this location, foxes consumed on average 2.4 mullet carcasses per day, corresponding to an average weight of carrion consumed of 953 g day⁻¹ and 129 carcasses consumed in total throughout the study. Raptors consumed significantly less carrion at the Noosa North Shore, with white-bellied sea eagles consuming 0.96 carcasses and 345.46 g of carrion per day, and 48 carcasses throughout the duration of the study. The remaining raptors remove fewer than 0.41 carcasses and less than 44.45 g per day on average for a total of 36 carcasses throughout the study (Table S1B). At North Stradbroke Island, raptors dominated carcass removal, with white-bellied sea eagles consuming the most (average of 3.24 carcasses and 159.26 g of carrion per day, and a total of 162 carcasses throughout the study (Table S1B). By contrast, foxes removed significantly fewer carcasses than raptors, averaging 1.64 carcasses and 590.11 g of carrion per day, and a total of 74 carcasses throughout the study (Table S1B).

Distinct scavenger assemblages consume the same total carcass weight

At the assemblage level, the functional structure (i.e., the number of fish removed by each scavenging species) of the scavenger guild differed significantly (PERMANOVA $P < 0.05$) between locations during all but the highest experimental carcass additions. Despite these significant differences in scavenger assemblages between locations, there were no significant differences in total carrion consumption between locations ($df = 1$, $F = 0.077$, $P = 0.78$) (Fig. 4b). Unsurprisingly, there was a significant effect of the initial deployment weight (i.e., treatment) on the amount of total carrion consumed ($df = 2.4$, $F = 2.7$, $P \leq 0.001$), with consumption increasing to an asymptote of approximately 15 kg fish carrion consumed day⁻¹ at individual sites (Fig. 4b, Table S1B).

Discussion

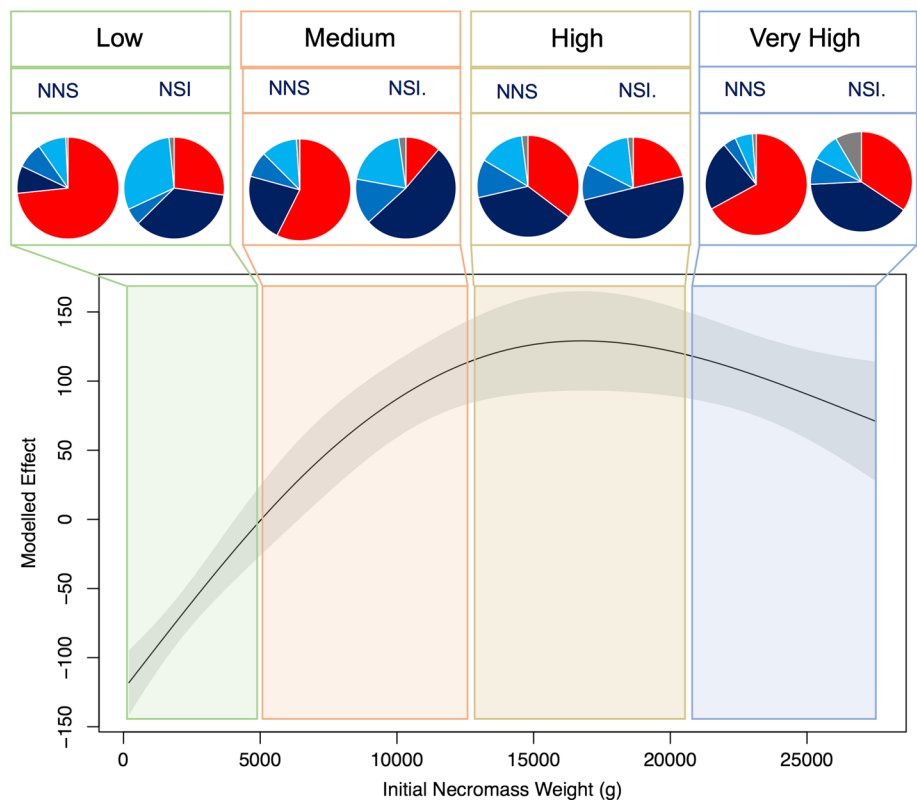
Theoretically, introduced species can have neutral effects where they functionally replace native species. We found that the presence of introduced red foxes did not significantly alter a particular ecological function—the rate of

Fig. 4 a Carrion is consumed by (i) red foxes, (ii) white-bellied sea eagles, (iii) brahminy kites, (iv) whistling kites, and (v) lace monitors on ocean-exposed sandy beaches in Queensland, Australia. **b** Generalised additive model output showing the relationship between the amount of carrion consumed and the biomass of carrion experimentally deployed. Experiments were run at two locations with ten replicate carcass deployment sites per location (cf. Fig. 1). Because there was no significant difference ($P=0.78$) in total consumption rates between locations, these are not plotted separately. Pie charts represent the proportion of carrion removed at each location by individual species during four experimental sets of different carrion addition treatments ('low', 'medium', 'high', and 'very high'). *NSI* North Stradbroke Island, *NNS* Noosa North Shore. Y-axis values denote the estimated degrees of freedom of the term being plotted

A Consumers



B Necromass consumption



carrion consumption by vertebrate scavengers on ocean beaches. Carrion consumption rates were also unaffected by large variations in the composition of the scavenger guild, suggesting functional plasticity in these assemblages. Furthermore, we demonstrate an upper limit to the capacity of scavenger assemblages to remove carcasses; this asymptote (i.e., saturation point) is again independent of assemblage composition. Although the majority of studies focusing on

species invasions demonstrate significant negative effects on key ecological functions (Short and Smith 1994; Tilman et al. 2014), our findings suggest that red fox populations exert a net neutral influence on the ecological function of carrion consumption where native scavenger populations are reduced.

Functional equivalency occurs when different species, or groups of species, perform an ecological function at

comparable rates (Gitay et al. 1996; Hubbell 2005; Walker 1995). Functional replacement is evident for the scavenger assemblages in this system. As a key mechanism, we posit temporal niche segregation between foxes that forage mainly nocturnally, and raptors search for washed-up carcasses during the day (Brown et al. 2015). It follows that, at low resource levels (likely at necromass levels below the asymptote in Fig. 4), removal of carcasses by foxes may reduce food resources available to native raptor populations. This is crucial, as carrion is likely to comprise a significant proportion of coastal raptor diets (Schlacher et al. 2013; Smith 2016), and they perform a number of other critical ecosystem services, especially predation to control populations of small vertebrates (Olsen et al. 2006; Smith 2016). Foxes may further lower carcass availability by caching large numbers of carcasses when these occur as a pulse (Macdonald 1976; Wagon and Serfass 2017). This temporal niche segregation also likely allows day-time, land-based scavengers, like the lace monitors observed here, an opportunity to forage where the scavenging pressure from raptors is lower. There was, however, no evidence of this relationship in this study, likely because the abundance of monitors was relatively low (Fig. 3).

Historically, several species of native marsupial mammals occurred in coastal dunes of Australia (e.g., Tasmanian devils, quolls, and thylacines) that scavenged animal carcasses on the beach; this still occurs on Tasmanian beaches where these carnivores exist. In many other parts of the Australian coastline, native carnivores are, however, very sparse or functionally extirpated (Glen and Dickman 2005). Arguably, red foxes may have functionally replaced carrion removal by native scavenging species in these situations.

Possible functional replacement of a single function by red foxes, however, does not imply benign effects of red foxes more broadly. On the contrary, a large body of evidence conclusively demonstrates widespread and severe negative ecological effects of foxes in Australia (Kinnear et al. 2002; Tilman et al. 2014). Foxes cause lethal impacts on native Australian species and represent key threatening processes for many endangered animals (Calver et al. 1998; Dickman 1996; Glen and Dickman 2005). For example, in eastern Victoria, Australia, foxes suppress long-nosed potoroos, a small mammal, which spread fungi essential to plants in sandy soils. This results in reduced plant community condition and overall ecosystem health (Fleming et al. 2014). These negative effects of foxes are reported broadly across areas where they are invasive (Dickman 1996; Saunders et al. 2010).

Sandy beaches are hotspots for the function of carrion scavenging, because carrion is regularly delivered to beaches from the ocean, and accumulates along exposed strandlines (Spiller et al. 2010). There are numerous invertebrate (Morton and Jones 2003), and vertebrate scavengers who rely

almost exclusively on this key subsidy as a food source along exposed coastlines, including some who are threatened by extinction (Schlacher et al. 2013). Foxes have exceptional trophic and behavioural plasticity, and hence flourish in beach and dune habitats (Schlacher et al. 2013, 2015a). For example, foxes also prey on the eggs and chicks of ground-nesting birds such as red-capped plovers *Charadrius ruficapillus* in the coastal dunes of the study area (Maslo et al. 2016). This potentially alters the efficiency and distribution of other ecological functions native species perform within ecosystems (Brown et al. 2015; Huijbers et al. 2016b; Schlaepfer et al. 2011). For example, the birds upon which foxes prey might also be important for functions like plant seed dispersal (Ellis 2005), or as prey for native carnivores (Behrendorff et al. 2016; Dunlop et al. 2017). Whilst few studies globally have directly assessed the effects that foxes have on coastal scavenging outside of this study area (Brown et al. 2015; Huijbers et al. 2015), it is likely that these negative effects of foxes on coastal scavenging assemblages would continue in other areas where they are not native (Huijbers et al. 2016a).

Given these negative effects of foxes across multiple ecosystems, foxes are culled in numerous predator control schemes (Saunders et al. 2010). The ethics of lethal methods is, however, increasingly challenged (Calver et al. 1998; Saunders et al. 2010). Fox control is also very costly and very rarely successful (Bomford and O'Brien 1995; Ebbert and Byrd 2002), except for large-scale efforts that are sustained over many years (Dexter and Murray 2009). Because foxes regularly visit carcass locations, this repeated behaviour offers an opportunity to selectively catch foxes and euthanize them humanely; it also offers the option to apply alternative control measures (e.g., contraceptive implants), should these approaches develop to a point at which they represent useful tools to suppress populations (Bomford and O'Brien 1995; Macdonald and Baker 2004). Further research, however, is required to determine how, and by which species, the niche opened by the removal of foxes locally is filled, and how long this effect takes to occur. Foxes may also modify the impact of other feral species. For example, foxes suppress cats, *Felis catus*, a notorious predator of small and medium-sized native species in Australia. Conversely, dingoes, *Canis lupus dingo*, have been shown to suppress red fox populations (Glen et al. 2007; Johnson and VanDerWal 2009). This suggests that trophic cascades may exist in beach ecosystems where dingoes suppress foxes as mesopredators consuming carrion. Alternatively, dingoes may directly outcompete foxes for animal carcasses on beaches where both species occur.

Our results suggest that the amount of carrion consumed asymptotes at approximately 15 kg of carrion per day in eastern Australia. The reason for the asymptote occurring at 15 kg is likely related to the number of scavengers that

can be naturally supported along these beaches by ambient carrion loads, or ambient prey sources (i.e., total carrying capacity given natural carrion loads and available prey). This hypothesis, however, requires further study in this region. The asymptote may, however, suggest a point upon which these carcasses, if not consumed, become toxic or unpalatable and will, therefore, only undergo microbial degradation and/or provide energy to mostly insect scavengers (Janzen 1977). Whilst factors such as the composition and size of the of scavenger guild, the consumption capacity of individual animals, and quality and extent of adjacent natural habitat (e.g., breeding and nesting sites) may influence overall consumption (Schlacher et al. 2013), this study suggests that individual systems have a threshold upon which this function might not be able to maintain ecosystem condition.

Maintaining ecological functioning is an important goal of many ecosystem management plans (DeFries et al. 2004, 2007). Invasive species can alter the scale and geographic extent of key ecological functions (Brown et al. 2015; Huijbers et al. 2016b); therefore, making good management decisions requires a better understanding of how these changes occur, and the degree to which management interventions might alter these ecological functions (Cortes-Avizanda et al. 2010). In this study, we show that assemblages of vertebrate scavengers on ocean beaches of Australia have remarkable functional plasticity that appears to be able to accommodate an introduced carnivore. Because this functional accommodation is in sharp contrast to the vulnerability of native species populations to red foxes, management interventions to maintain functions need to be nuanced. It also emphasizes that functional losses may be masked by exotic carnivores invading niches of locally extirpated native fauna.

Acknowledgements The authors acknowledge the spending help of Andreas Fischer, Hayden Borland, Tom Brook, Makeely Blanford, Cassandra Duncan, Sarah Thackway, and Rachel Bycroft for their commitment to the deployment of copious kilograms of pungent mullet. Financial support for this study was provided by the University of the Sunshine Coast in the form of a Vice Chancellor's bursary to ELB, SeaWorld Research and Rescue Foundation, Sekisui House, and Water Sciences Collaborative Research Network (CRN).

Author contribution statement EB, TS, BG, and AO conceived the idea and designed the experiments; EB, BG, TS, AO, CH, CP, and CV conducted the experiments; EB, BG, and TS analysed the data; all authors contributed equally to the interpretation of results, and editing the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare they have no conflict of interest.

Ethics approval All procedures performed in studies involving human participants were in accordance with the ethical standards of the insti-

tutional and/or national research committee and with the 1964 Helsinki declaration and its later amendments or comparable ethical standards. All applicable institutional and/or national guidelines for the care and use of animals were followed.

Data availability The data sets generated during and/or analysed during the current study are available in the Zenodo repository; <https://zenodo.org/record/1195793#.WqXRZJNuZTY>.

References

- Anderson MJ, Gorley RN, Clarke RK (2008) Permanova+ for primer: guide to software and statistical methods. Primer-E Limited, Plymouth, UK
- Behrendorff L et al (2016) Insects for breakfast and whales for dinner: the diet and body condition of dingoes on Fraser Island (K'gari). *Sci Rep*. <https://doi.org/10.1038/srep23469>
- Bergstrom DM et al (2009) Indirect effects of invasive species removal devastate World Heritage Island. *J Appl Ecol* 46:73–81. <https://doi.org/10.1111/j.1365-2664.2008.01601.x>
- Bomford M, O'Brien P (1995) Eradication or control for vertebrate pests? *Wildl Soc Bull* 1973–2006(23):249–255
- Borland HP, Schlacher TA, Gilby BL, Connolly RM, Yabsley NA, Olds AD (2017) Habitat type and beach exposure shape fish assemblages in the surf zones of ocean beaches. *Mar Ecol Prog Ser* 570:203–211. <https://doi.org/10.3354/meps12115>
- Broadbent A, Stevens CJ, Peltzer DA, Ostle NJ, Orwin KH (2018) Belowground competition drives invasive plant impact on native species regardless of nitrogen availability. *Oecologia* 186:577–587. <https://doi.org/10.1007/s00442-017-4039-5>
- Brown MB et al (2015) Invasive carnivores alter ecological function and enhance complementarity in scavenger assemblages on ocean beaches. *Ecology* 96:2715–2725
- Buechley ER, Sekercioglu CH (2016) The avian scavenger crisis: looming extinctions, trophic cascades, and loss of critical ecosystem functions. *Biol Conserv* 198:220–228. <https://doi.org/10.1016/j.biocon.2016.04.001>
- Calver M, King D, Short J (1998) Ecological blunders and conservation: the impact of introduced foxes and cats on Australian native fauna. *J Biol Educ* 32:67–72
- Chan DK, Tsui HC, Kot BC (2017) Database documentation of marine mammal stranding and mortality: current status review and future prospects. *Dis Aquat Org* 126:247–256
- Chapin FS et al (2000) Consequences of changing biodiversity. *Nature* 405:234–242. <https://doi.org/10.1038/35012241>
- Core Team R (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Cortes-Avizanda A, Carrete M, Donazar JA (2010) Managing supplementary feeding for avian scavengers: guidelines for optimal design using ecological criteria. *Biol Conserv* 143:1707–1715. <https://doi.org/10.1016/j.biocon.2010.04.016>
- Crowl TA, Crist TO, Parmenter RR, Belovsky G, Lugo AE (2008) The spread of invasive species and infectious disease as drivers of ecosystem change. *Front Ecol Environ* 6:238–246. <https://doi.org/10.1890/070151>
- DeFries RS, Foley JA, Asner GP (2004) Land-use choices: balancing human needs and ecosystem function. *Front Ecol Environ* 2:249–257. [https://doi.org/10.1890/1540-9295\(2004\)002\[0249:Lcbhna\]2.0.Co;2](https://doi.org/10.1890/1540-9295(2004)002[0249:Lcbhna]2.0.Co;2)
- DeFries R, Hansen A, Turner BL, Reid R, Liu J (2007) Land use change around protected areas: management to balance human needs and ecological function. *Ecol Appl* 17:1031–1038

- Dexter N, Murray A (2009) The impact of fox control on the relative abundance of forest mammals in East Gippsland, Victoria. *Wildl Res* 36:252–261
- Dickman CR (1996) Impact of exotic generalist predators on the native fauna of Australia. *Wildl Biol* 2:185–195
- Didham RK, Tylianakis JM, Hutchison MA, Ewers RM, Gemmell NJ (2005) Are invasive species the drivers of ecological change? *Trends Ecol Evol* 20:470–474. <https://doi.org/10.1016/j.tree.2005.07.006>
- Dunlop JA, Rayner K, Doherty TS (2017) Dietary flexibility in small carnivores: a case study on the endangered northern quoll, *Dasyurus hallucatus*. *J Mammal* 98:858–866. <https://doi.org/10.1093/jmammal/gyx015>
- Ebbert S, Byrd G (2002) Eradications of invasive species to restore natural biological diversity on Alaska Maritime National Wildlife Refuge. Turning the tide: the eradication of invasive species (CR Veitch and MN Clout, Editors). IUCN Invasive Species Specialist Group, Gland, Switzerland and Cambridge, United Kingdom: pp 102–109
- Ellis JC (2005) Marine birds on land: a review of plant biomass, species richness, and community composition in seabird colonies. *Plant Ecol* 181:227–241. <https://doi.org/10.1007/s11258-005-7147-y>
- Finke DL, Denno RF (2005) Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecol Lett* 8:1299–1306. <https://doi.org/10.1111/j.1461-0248.2005.00832.x>
- Fleming PA, Anderson H, Prendergast AS, Bretz MR, Valentine LE, Hardy GES (2014) Is the loss of Australian digging mammals contributing to a deterioration in ecosystem function? *Mammal Rev* 44:94–108. <https://doi.org/10.1111/mam.12014>
- Gilby BL, Olds AD, Yabsley NA, Connolly RM, Maxwell PS, Schlacher TA (2017) Enhancing the performance of marine reserves in estuaries: just add water. *Biol Cons* 210:1–7. <https://doi.org/10.1016/j.biocon.2017.03.027>
- Gitay H, Wilson JB, Lee WG (1996) Species redundancy: a redundant concept? *J Ecol* 84:121–124
- Glen AS, Dickman CR (2005) Complex interactions among mammalian carnivores in Australia, and their implications for wildlife management. *Biol Rev* 80:387–401. <https://doi.org/10.1017/S1464793105006718>
- Glen AS, Dickman CR, Soule ME, Mackey B (2007) Evaluating the role of the dingo as a trophic regulator in Australian ecosystems. *Austral Ecol* 32:492–501
- Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends Ecol Evol* 19:470–474. <https://doi.org/10.1016/j.tree.2004.07.005>
- Hubbell SP (2005) Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct Ecol* 19:166–172. <https://doi.org/10.1111/j.0269-8463.2005.00965.x>
- Huijbers CM, Schlacher TA, Schoeman DS, Weston MA, Connolly RM (2013) Urbanisation alters processing of marine carrion on sandy beaches. *Landsc Urban Plan* 119:1–8. <https://doi.org/10.1016/j.landurbplan.2013.06.004>
- Huijbers CM, Schlacher TA, Schoeman DS, Olds AD, Weston MA, Connolly RM (2015) Limited functional redundancy in vertebrate scavenger guilds fails to compensate for the loss of raptors from urbanized sandy beaches. *Divers Distrib* 21:55–63. <https://doi.org/10.1111/ddi.12282>
- Huijbers CM et al (2016a) Functional replacement across species pools of vertebrate scavengers separated at a continental scale maintains an ecosystem function. *Funct Ecol* 30:998–1005. <https://doi.org/10.1111/1365-2435.12577>
- Huijbers CM et al (2016b) Functional replacement across species pools of vertebrate scavengers separated at a continental scale maintains an ecosystem function. *Funct Ecol* 30:998–1005. <https://doi.org/10.1111/1365-2435.12577>
- Janzen DH (1977) Why fruits rot, seeds mold, and meat spoils. *Am Nat* 111:691–713
- Johnson CN, VanDerWal J (2009) Evidence that dingoes limit abundance of a mesopredator in eastern Australian forests. *J Appl Ecol* 46:641–646
- Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends Ecol Evol* 17:164–170. [https://doi.org/10.1016/S0169-5347\(02\)02499-0](https://doi.org/10.1016/S0169-5347(02)02499-0)
- Kinnear JE, Sumner NR, Onus ML (2002) The red fox in Australia—an exotic predator turned biocontrol agent. *Biol Conserv* 108:335–359. [https://doi.org/10.1016/S0006-3207\(02\)00116-7](https://doi.org/10.1016/S0006-3207(02)00116-7)
- Leibold MA, McPeck MA (2006) Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87:1399–1410
- Loreau M (2004) Does functional redundancy exist? *Oikos* 104:606–611
- Losos JB (2011) Convergence, adaptation, and constraint. *Evolution* 65:1827–1840. <https://doi.org/10.1111/j.1558-5646.2011.01289.x>
- Lyons KG, Schwartz MW (2001) Rare species loss alters ecosystem function \pm invasion resistance. *Ecol Lett* 4:358–365
- Macdonald DW (1976) Food caching by red foxes and some other carnivores. *Ethology* 42:170–185. <https://doi.org/10.1111/j.1439-0310.1976.tb00963.x>
- Macdonald D, Baker S (2004) Non-lethal control of fox predation: the potential of generalised aversion. *Anim Welf* 13:77–86
- Maslo B et al (2016) Regional drivers of clutch loss reveal important trade-offs for beach-nesting birds. *PeerJ* 4:e2460
- Meager JJ, Schlacher TA, Nielsen T (2012) Humans alter habitat selection of birds on ocean-exposed sandy beaches. *Divers Distrib* 18:294–306. <https://doi.org/10.1111/j.1472-4642.2011.00873.x>
- M'Gonigle LK, Mazzucco R, Otto SP, Dieckmann U (2012) Sexual selection enables long-term coexistence despite ecological equivalence. *Nature* 484:506–509. <https://doi.org/10.1038/nature10971>
- Moreno-Opo R, Margalida A, García F, Arredondo Á, Rodríguez C, González LM (2012) Linking sanitary and ecological requirements in the management of avian scavengers: effectiveness of fencing against mammals in supplementary feeding sites. *Biodivers Conserv* 21:1673–1685. <https://doi.org/10.1007/s10531-012-0270-x>
- Morton B, Jones DS (2003) The dietary preferences of a suite of carrion-scavenging gastropods (Nassariidae, Buccinidae) in Princess Royal Harbour, Albany, Western Australia. *J Mollus Stud* 69:151–156. <https://doi.org/10.1093/mollus/69.2.151>
- Ogada DL, Torchin ME, Kinnaird MF, Ezenwa VO (2012) Effects of vulture declines on facultative scavengers and potential implications for mammalian disease transmission. *Conserv Biol* 26:453–460
- Olsen J, Fuentes E, Rose AB (2006) Trophic relationships between neighbouring White-bellied Sea-Eagles (*Haliaeetus leucogaster*) and Wedge-tailed Eagles (*Aquila audax*) breeding on rivers and dams near Canberra. *Emu* 106:193–201. <https://doi.org/10.1071/mu05046>
- Pyšek P et al (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Glob Change Biol* 18:1725–1737
- Saunders GR, Gentle MN, Dickman CR (2010) The impacts and management of foxes *Vulpes vulpes* in Australia. *Mamm Rev* 40:181–211. <https://doi.org/10.1111/j.1365-2907.2010.00159.x>
- Schlacher TA, Connolly RM (2009) Land–ocean coupling of carbon and nitrogen fluxes on sandy beaches. *Ecosystems* 12:311–321
- Schlacher TA, Strydom S, Connolly RM (2013) Multiple scavengers respond rapidly to pulsed carrion resources at the land–ocean interface. *Acta Oecol* 48:7–12. <https://doi.org/10.1016/j.actao.2013.01.007>

- Schlacher TA et al (2015a) Conservation gone to the dogs: when canids rule the beach in small coastal reserves. *Biodivers Conserv* 24:493–509. <https://doi.org/10.1007/s10531-014-0830-3>
- Schlacher TA, Weston MA, Schoeman DS, Olds AD, Huijbers CM, Connolly RM (2015b) Golden opportunities: a horizon scan to expand sandy beach ecology. *Estuar Coast Shelf S* 157:1–6. <https://doi.org/10.1016/j.ecss.2015.02.002>
- Schlaepfer MA, Sax DF, Olden JD (2011) The potential conservation value of non-native species. *Conserv Biol* 25:428–437. <https://doi.org/10.1111/j.1523-1739.2010.01646.x>
- Schmitz OJ (2008) Effects of predator hunting mode on grassland ecosystem function. *Science* 319:952–954. <https://doi.org/10.1126/science.1152355>
- Short J, Smith A (1994) Mammal decline and recovery in Australia. *J Mamm* 75:288–297
- Smith GC (2016) An analysis of prey remnants from osprey *Pandion haliaetus* and white-bellied sea-eagle *Haliaetus leucogaster* feeding roosts. *Emu* 85:198–200. <https://doi.org/10.1071/mu9850198>
- Spiller DA et al (2010) Marine subsidies have multiple effects on coastal food webs. *Ecology* 91:1424–1434
- Tilman D, Isbell F, Cowles JM (2014) Biodiversity and ecosystem functioning. *Annu Rev Ecol Evol Syst* 45:93–112
- Tumolo BB, Flinn MB (2017) Top-down effects of an invasive omnivore: detection in long-term monitoring of large-river reservoir chlorophyll-a. *Oecologia* 185:293–303. <https://doi.org/10.1007/s00442-017-3937-x>
- Van Kleunen M et al (2015) Global exchange and accumulation of non-native plants. *Nature* 525:100–103
- Vilà M et al (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett* 14:702–708
- Wagnon CJ, Serfass TL (2017) Use of camera traps provides insight into the feeding ecology of red foxes *Vulpes vulpes*. *Can Field-Nat* 131:19. <https://doi.org/10.22621/cfn.v131i1.1950>
- Walker B (1995) Conserving biological diversity through ecosystem resilience. *Conserv Biol* 9:747–752
- Wilson EE, Wolkovich EM (2011) Scavenging: how carnivores and carrion structure communities. *Trends Ecol Evol* 26:129–135. <https://doi.org/10.1016/j.tree.2010.12.011>
- Wood S (2012) mgcv: Mixed GAM Computation Vehicle with GCV/AIC/REML smoothness estimation