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Scavenging with invasive species

Thomas Newsome[1,*], Rhys Cairncross[1], Calum X. Cunningham[2], Emma E. Spencer[1], Philip S. Barton[3], William J. Ripple[4] and Aaron J. Wirsing[2]

[1]*School of Life and Environmental Science, University of Sydney, Sydney, New South Wales 2006, Australia*
[2]*School of Environmental and Forest Sciences, University of Washington, College of the Environment, Box 352100, Seattle, WA 98195-2100, USA*
[3]*School of Life and Environmental Science, Deakin University, Geelong, Victoria 3216, Australia*
[4]*Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA*

ABSTRACT

Carrion acts as a hotspot of animal activity within many ecosystems globally, attracting scavengers that rely on this food source. However, many scavengers are invasive species whose impacts on scavenging food webs and ecosystem processes linked to decomposition are poorly understood. Here, we use Australia as a case study to review the extent of scavenging by invasive species that have colonised the continent since European settlement, identify the factors that influence their use of carcasses, and highlight the lesser-known ecological effects of invasive scavengers. From 44 published studies we identified six invasive species from 48 vertebrates and four main groups of arthropods (beetles, flies, ants and wasps) that scavenge. Invasive red foxes (*Vulpes vulpes*), domestic dogs (*Canis familiaris*), feral pigs (*Sus scrofa*), black rats (*Rattus rattus*) and feral cats (*Felis catus*) were ranked as highly common vertebrate scavengers. Invasive European wasps (*Vespula germanica*) are also common scavengers where they occur. We found that the diversity of native vertebrate scavengers is lower when the proportion of invasive scavengers is higher. We highlight that the presence of large (apex) native vertebrate scavengers can decrease rates of scavenging by invasive species, but that invasive scavengers can monopolise carcass resources, outcompete native scavengers, predate other species around carcass resources and even facilitate invasion meltdowns that affect other species and ecological processes including altered decomposition rates and nutrient cycling. Such effects are likely to be widespread where invasive scavengers occur and suggest a need to determine whether excessive or readily available carcass loads are facilitating or exacerbating the impacts of invasive species on ecosystems globally.

Key words: scavenging, invasive species, decomposition, apex scavenger, invasion meltdown.

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* Author for correspondence (Tel.: +61 2 9351 4473; E-mail: thomas.newsome@sydney.edu.au).

I. INTRODUCTION

(1) Scavenging in ecosystems

Recent interest in the role of scavenging in ecosystems reflects a shift away from focusing predominantly on animals acquiring food *via* predation (Wilson & Wolkovich, 2011). This trend also reflects growing recognition that carcasses function as more than just a focal location for vertebrate and arthropod scavenging activity (Wirsing & Newsome, 2021; Newsome *et al.*, 2021). Indeed, the ecological effects of carrion extend to influencing soil properties (Barton *et al.*, 2019), below-ground microbes (Cobaugh, Schaeffer & DeBruyn, 2015), vegetation growth (Barton *et al.*, 2016), predation rates in the vicinity of the carcass (Cortés-Avizanda *et al.*, 2009) and pollination services (Cusser, Pechal & Haddad, 2020). Thus, in addition to understanding the use of carrion by scavengers, there is a need to ascertain the role of carrion in food webs more broadly.

Of the biotic and abiotic factors known to modulate both the persistence of a carcass and the scavengers that use it, research has demonstrated the influence of apex (Wikenros *et al.*, 2013) and obligate (Ogada *et al.*, 2012) scavengers, and how their presence is a key indicator of a well-functioning scavenging community (Newsome *et al.*, 2021). Carcass size (Moleón *et al.*, 2015), type (Munoz-Lozano *et al.*, 2019) and condition (Selva *et al.*, 2005; Munro, Mondor & Lampert, 2019) can influence how long a carcass persists and the scavengers it attracts. Time of day can influence the initial use of the carcass by scavengers (Williams *et al.*, 2017; Carrasco-Garcia *et al.*, 2018), and carcass age (days since death) can affect the quality of the tissues (e.g. moisture content) and thus successional stage of the associated arthropod and microbial community (Barton *et al.*, 2019; Pechal *et al.*, 2019).

Other factors known to influence rates of scavenging relate to the characteristics of the site itself. For example, the specific habitat in which a carcass is located (e.g. open or closed canopy) can influence scavenger presence and detection times (Carrasco-Garcia *et al.*, 2018; Pardo-Barquin, Mateo-Tomas & Olea, 2019). Season, along with daily temperatures, humidity and moisture levels greatly impact carcass persistence rates *via* the effects they have on regulating microbial and insect activity (Matuszewski *et al.*, 2010; Turner *et al.*, 2017; Barton & Bump, 2019). Snow cover may also increase or change scavenging rates by certain vertebrate species (Selva *et al.*, 2005).

(2) Scavenger assemblages: what roles for invasives?

At a broad spatial scale, different biomes/landscapes host different scavenger guilds, and guild characteristics will ultimately influence rates of scavenging, species interactions around carrion, and the broader role of carrion in ecosystems (Pardo-Barquin *et al.*, 2019). In anthropogenically altered landscapes, for instance, vertebrate scavenger species richness has been shown to be lower compared to more remote wilderness areas, and that could result in carrion persisting for longer with implications for disease transmission and nutrient cycling (Sebastián-González *et al.*, 2019). But many landscapes around the world also contain invasive vertebrate or insect species that scavenge, such as domestic dogs (*Canis familiaris*) (Butler & du Toit, 2002), feral pigs (*Sus scrofa*) (DeVault & Rhodes, 2002), and fire ants (*Solenopsis invicta*) (Holway & Cameron, 2021). Invasive species threaten biodiversity globally, and have the potential to disrupt ecosystem dynamics (Courchamp, Chapuis & Pascal, 2003). Yet, the extent of carcass use by invasive species and their role in scavenging food webs is not well described, including in countries that have experienced high rates of invasion success. Many invasive species have flexible feeding strategies (Chapple, Simmonds & Wong, 2012) and most invasive vertebrate predators readily scavenge so carrion resources could aid their spread and subsequent establishment. Invasive species could also dominate carrion resources under some circumstances. Indeed, use of carrion by invasive vertebrate scavengers has been assessed on a small island ecosystem in Hawaii, where 55% of carcasses monitored were removed by mongoose (*Herpestes javanicus*), rodents, domestic cats (*Felis catus*), feral pigs, and common myna (*Acridotheres tristis*), all invasive species (Abernethy *et al.*, 2016).

(3) Australia as an ideal case study to understand invasive scavengers

Australia is an island continent with a well-documented history of invasions. Yet knowledge of the role of these invasive species in carrion consumption and scavenging is only just emerging. Estimates or direct measurements of carrion availability to invasive species in Australia do not yet exist for most ecosystems. However, changes in fauna assemblages over time provides some insights into what was historically available compared to nowadays. For example, Australia is one of the driest continents on Earth and has nutrient-poor soils (Orians & Milewski, 2007). This low productivity, coupled with isolation, likely limited the species richness and the body mass of large mammalian herbivores, and in turn, the diversity of large mammalian predators (which may have scavenged) (Lee & Cockburn, 1985; Flannery, 1994; Wroe, Argot & Dickman, 2004). During the late Pleistocene [100–10 thousand years ago (ka)], for instance, Australia exhibited a predominance of browsing mesoherbivores (10–100 kg body mass) and only had one megaherbivore (>1000 kg); this pattern contrasts with South America (which has higher overall annual rainfall than Australia), which was dominated by herbivores with body masses exceeding 100 kg, including 16 megaherbivores (Owen-Smith, 2013). During this same period, the species richness of mammalian carnivores of 2.5 kg or more body mass was 2.9 times higher in South America compared to Australia (Wroe *et al.*, 2004). Historically, therefore, Australia likely had lower carrion input rates compared to continents with more diverse herbivore populations. This likely influenced the diversity of vertebrates that relied solely on carrion as a source of food. Indeed, only one Old World vulture species has been identified from the Australian Pleistocene fossil record to date (Mather, Lee & Worthy, 2022).

Nowadays, Australia experiences periods where carrion is produced in relatively high densities, such that it is potentially available in large quantities to scavengers. There are several reasons for this pattern. First, despite widespread extinctions of small-to-medium-sized marsupials across Australia since European settlement (Woinarski, Burbidge & Harrison, 2015), some large native marsupial herbivores including the red kangaroo (*Osphranter rufus*) and eastern grey kangaroo (*Macropus giganteus*) have prospered owing to increased food and water supplies (Newsome, 1975; Coulson, 2007) coupled with the removal or persecution of Australia's apex predator, the dingo (*Canis dingo*) (Letnic, Ritchie & Dickman, 2012). These kangaroo populations can experience large population increases following good rains (Corbett & Newsome, 1987), but mass mortalities during droughts (see Robertson, 1986) can result in influxes of carcasses (Rees, Kingsford & Letnic, 2019). Second, Australia hosts a plethora of invasive herbivores including feral pigs, deer (six species), rabbits (*Oryctolagus cuniculus*), horses (*Equus ferus*), camels (*Camelus dromedarius*), goats (*Capra hircus*), and buffalo (*Bubalis bubalis*). The presence of these invasive species has altered the types and quantities of carrion available. Third, some native and most invasive wild herbivores are culled each year to control their numbers, with carcasses typically left to lie *in situ*, totalling millions of carcasses annually. These carcasses add to the necromass in the ecosystem along with other major anthropogenic contributions to carrion biomass from vehicle collisions (Hobday & Minstrell, 2008; Nguyen *et al.*, 2019) or mass mortalities following climate-change-induced weather events such as bush fires (van Eeden *et al.*, 2020).

Australia's scavenging guild has also changed dramatically over the last 3500 years. The arrival of the dingo on the mainland at least 3300 years ago (Balme, O'Connor & Fallon, 2018), and subsequent extinction of the Tasmanian devil (*Sarcophilus harrisii*) and thylacine (*Thylacinus cynocephalus*), represented a major shift in the mainland carnivore assemblage (Letnic, Fillios & Crowther, 2014). The loss of the Tasmanian devil, in particular, would have altered scavenging dynamics as it is a specialised scavenger (Pollock *et al.*, 2022) and has jaw morphology adapted for scavenging, including a strong bite (Wroe, McHenry & Thomason, 2005). The next major shift occurred following European settlement in 1788 with the arrival and subsequent spread of invasive species, including some that are known to scavenge such as the red fox (*Vulpes vulpes*) (Jedrzejewska & Jedrzejewska, 1992; Helldin & Danielsson, 2007), feral pig (Selva *et al.*, 2005) and feral cat (Schwartz *et al.*, 2018). Of the invertebrates/arthropods that have been introduced into Australia post European settlement, the European wasp (*Vespula germanica*) is a known scavenger; mature workers forage for protein, directly preying on other insects, or by scavenging dead animals for meat (Richter, 2000). This situation of having invasive species that scavenge, in combination with the potential for abundant carcass loads, highlights the need to understand scavenging dynamics in Australian landscapes. Indeed, no other continent on Earth has experienced the devastating impacts of invasive species to the extent that Australia has. Predation by the feral cat and red fox in particular has contributed to Australia's native mammal extinction crisis (Woinarski *et al.*, 2015). Bringing together knowledge about the role of biotic and abiotic processes in shaping Australian scavenging food webs will therefore help inform the main factors that regulate carrion availability to invasive species more broadly.

(4) Overview of review

Herein, we review Australian studies that characterised either the presence of vertebrate or arthropod scavengers at carcass sites, or those that focused on the broader effects of carcasses on other components of the ecosystem including soils and plants. We use the results to characterise the state of knowledge, then extract available data on scavenging rates to assess the relative use of carcasses by invasive species, and whether invasive vertebrate scavengers have any biological traits that differentiate them from native scavengers. A series of case studies are then presented to demonstrate how apex scavengers can influence scavenging by invasive species, and to highlight some less well-known ecological effects of invasive scavengers. We end with a section on the broader implications of the findings to help shape the future of carrion ecology research anywhere where invasive scavengers occur.

For context, we adopted the following definition for an invasive species, which combines the description for an 'introduced population' and 'invasive population' by Simberloff *et al.* (2013), i.e. a population that arrives at a site with intentional or accidental human assistance and then spreads and maintains itself without human assistance. However, we only considered invasive species as a population that arrived in Australia post-European settlement in 1788.

II. SCAVENGING IN AUSTRALIA

(1) State of knowledge

An initial review of literature identified that Fuller (1934) and Bornemissza (1957) were among the first to publish an Australian carrion ecology study, focusing on the succession of carrion-frequenting arthropods (Fuller, 1934) and the influence of carrion on soil fauna (Bornemissza, 1957) (see online Supporting Information, Table S1, for details of search terms and included studies). Both Fuller (1934) and Bornemissza (1957) found that decay stages correlated with arthropod succession and Bornemissza (1957) also reported that the decomposition of small guinea pig carcasses had a marked effect on soil fauna to a depth of 14 cm. Despite the broader ecological implications of this work, it was not until 47 years later that scavenger use of carcasses in Australia was examined in the field (see Read & Wilson, 2004), although some taphonomic and forensic studies took place (e.g. Reed, 2001; Archer & Elgar, 2003) and observations of scavenging by larger species such as the dingo were noted (Newsome *et al.*, 1983).

There are now at least 44 studies in Australia that contain information about vertebrate or arthropod scavenging, carrion persistence rates or changes to soil properties following decomposition (Table S1). The majority focused on vertebrate scavenging ($N = 32$), with fewer addressing arthropod scavenging ($N = 12$; predominantly insects, with one study including mites) and changes to soil properties ($N = 6$). Only three studies simultaneously focused on insects and soils or vegetation responses. No studies have considered explicitly the effects of vertebrate scavenging on soils and vegetation. The 44 studies span a range of environments, having been carried out across arid, coastal, alpine and temperate environments, and on both the mainland of Australia and in Tasmania. Carcasses monitored included small fish, guinea pigs, wallabies, brushtail possums (*Trichosurus vulpecula*), rabbits, red and eastern grey kangaroos, deer, dingoes, sheep, feral goats, cattle, whales, dugongs, turtles and stingrays.

(2) Vertebrate scavenging patterns

Forty-eight vertebrate scavengers have been recorded in Australian studies, including 16 mammals, 28 birds and four reptiles (Table S2). Common vertebrate scavengers include Tasmanian devils, corvids, red foxes (invasive), raptors, feral pigs (invasive), domestic dogs (invasive), brushtail possums and dingoes (Fig. 1). Several factors have been shown to influence vertebrate scavengers' use of carcasses (Fig. 2). Season, habitat and a flooding event have been shown to influence the use of carcasses by corvids in the arid Simpson Desert, such that they discovered carcasses faster in open- compared to closed-canopy habitats, in winter compared to spring, and in post-flood compared with pre-flood periods (Bragato *et al.*, 2022). In the same arid site and over the same time period, overall vertebrate scavenging activity increased post-flood but only in warm seasons (Krige, 2020). By contrast, Brown, Field & Letnic (2006) found that scavenging activity by vertebrates generally increased during below- average rainfall periods in a different arid site, suggesting that vertebrate scavenger responses to background environmental conditions are context specific. Season has been shown to influence patterns of scavenging by dingoes, with quicker carcass discovery or increased time spent feeding on carcasses documented in warmer seasons compared to cool seasons (Spencer & Newsome, 2021). Feral pigs, on the other hand, increased scavenging during cooler periods and in open habitats in the alpine area of south-eastern Australia (Kane, 2020). In another study, corvids were found to be the dominant users of kangaroo offcuts (leftover body parts, such as viscera, discarded after the carcass is harvested by humans for meat) in summer, whereas wedge-tailed eagles (*Aquila audax*) and red foxes were the dominant users in spring (Read & Wilson, 2004).

The influence of the 2019/2020 Australian megafires on scavenging rates has been assessed, with results indicating no overall decline in scavenger species richness following the fire event, but avian scavengers detected carcasses quicker and increased their feeding time post-fire (Newsome & Spencer, 2021). Despite the increase in avian scavenging post-fire, carcasses persisted for longer post-fire compared to pre-fire suggesting that other factors in addition to fire affected carcass persistence (Newsome & Spencer, 2021). The influence of urbanisation on scavenging has been assessed in multiple studies along the eastern coastline of Australia. Huijbers *et al.* (2013) found that large raptors were abundant scavengers on rural beaches, but much less so on urban beaches where scavenging was dominated by red foxes, feral cats and domestic dogs (all invasive). The decline of raptors in urban areas can lead to carcasses persisting for longer, suggesting limited functional redundancy in scavenger communities that have been subject to anthropogenic changes (Schlacher, Strydom & Connolly, 2013*a*; Schlacher *et al.*, 2015; Huijbers *et al.*, 2015). Functional redundancy among vertebrate scavenger guilds has also been assessed at a continental scale, by comparing scavenging dynamics between tropical and temperate Australian ecosystems (Huijbers *et al.*, 2016). Although the composition of the scavenger guild varied between these two ecosystems, carcass detection and removal were similar, suggesting functional replacement can occur (Huijbers *et al.*, 2016).

Several studies have assessed the scavenging behaviours of larger apex scavengers in Australia, focusing on the Tasmanian devil and dingo. Specifically, studies have noted

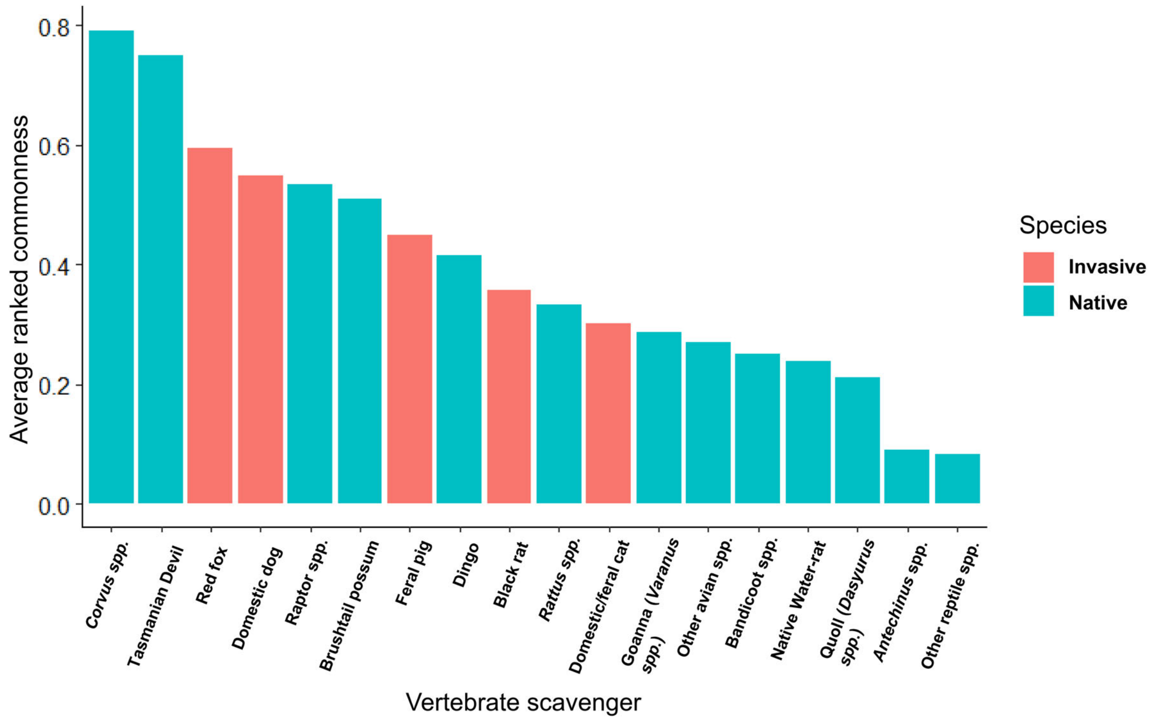

Fig. 1. Average ranked commonness of the main vertebrate scavengers documented visiting carcass sites in Australian studies (see Table S1 for list of included studies). For ranked commonness, each scavenger was given a weighted score based on rank: 1/rank of each scavenger in that study. For example, in one study of four different scavenger species the most common animal was ranked first and given a score of 1/1 = 1, the second most common 1/2 = 0.5 and so on. The values plotted here represent the average ranked scavenger commonness values across the number of studies that observed each scavenger species. Note this includes studies where only the presence or absence of scavenger species was recorded.

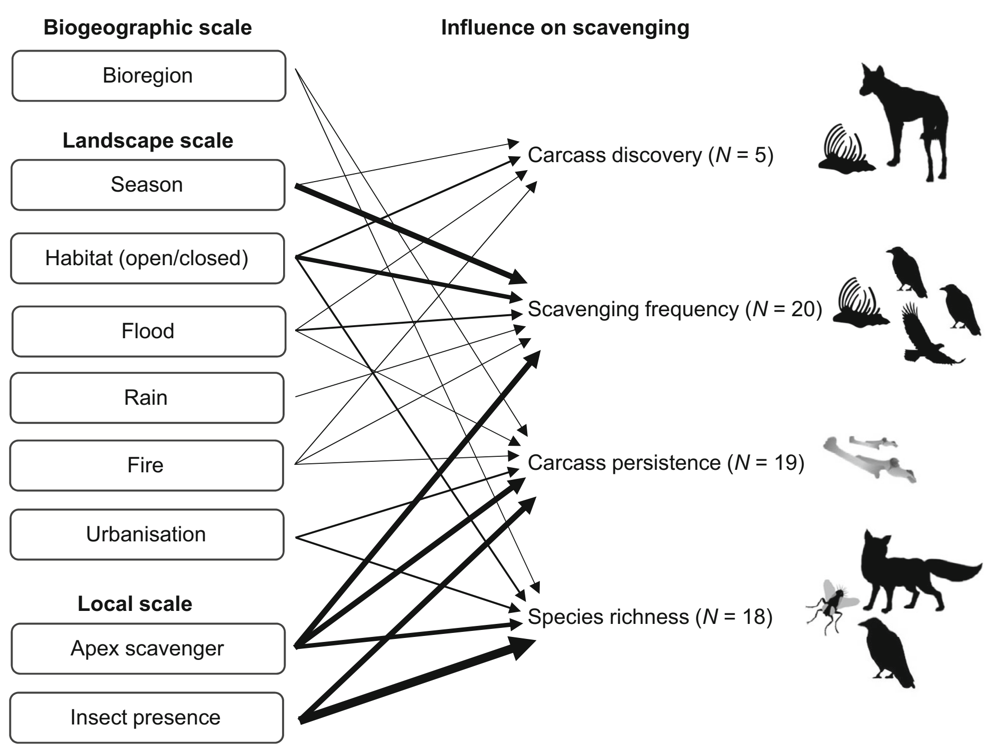

Fig. 2. Factors known to influence scavenging patterns based on studies included in this review. The total number of studies assessing each pathway is shown (*N*), with thicker lines also indicating a higher number of studies (range 1–9).

and/or directly assessed the efficiency of scavenging by Tasmanian devils in terms of their ability to remove carcass biomass (Cunningham *et al*., 2018; Fielding *et al*., 2021, 2022). The presence of Tasmanian devils at carcass sites can influence the use of carcasses by smaller vertebrate scavengers (Cunningham *et al*., 2018; Fielding *et al*., 2022). Dingoes have similarly been shown to accelerate carcass biomass removal but only in winter when insects were not common (Spencer & Newsome, 2021). More broadly, the loss of dingoes from landscapes can increase numbers of their herbivorous prey due to a reduction in top-down effects (Letnic *et al*., 2012). This can, in turn, increase the availability of carrion in the landscape, potentially benefiting other facultative scavengers (Rees *et al*., 2019, 2020). Conversely, the presence of dingoes at carcass sites has been shown to deter the use of carcasses by smaller vertebrate scavengers (Forsyth *et al*., 2014). The ability of Tasmanian devils and dingoes to influence carcass biomass on the landscape scale and the use of carcasses by other species suggests they may play a role in regulating carcass use by invasive species, as discussed in Section V.

(3) Arthropod scavenging patterns

Compared to vertebrates, there has been far less research into the ecological role of Australian arthropod scavengers. Twelve studies have incorporated arthropod scavengers within their scope, with seven focussing solely on insect groups and one study also including mites (Table S1). This relatively low number of publications is despite Australia's often-warm climate providing optimal conditions for many necrophagous insects. Common families recorded at carrion in Australia (Fig. 3) reflect global patterns and include flesh flies (Diptera: Sarcophagidae), house flies (Diptera: Muscidae) and blowflies (Diptera: Calliphoridae) (Archer & Elgar, 2003; Voss, Spafford & Dadour, 2009). Also following global patterns, beetles tend to form the most diverse communities of insects that associate with carrion in Australia. For example, 88 beetle species from 28 different families were collected from 18 eastern grey kangaroo carcasses in one study (Barton, Weaver & Manning, 2014). Ants have also been recognised as potentially important members of carrion necrobiome communities in Australia. Large numbers of meat ants (*Iridomyrmex purpureus*) have been observed on carcasses from rabbits to kangaroos and may either inhibit carrion decomposition *via* predation on fly larvae or could enhance it by feeding directly on the carrion resource (Read & Wilson, 2004; Barton & Evans, 2017). Ant species diversity associated with carcasses can be high and comparable to beetle species diversity in some areas. For example, 34 different ant species (compared to 15 fly and 35 beetle species) were collected on 18 rabbit carcasses in a woodland area outside of Canberra, south-eastern Australia (Barton & Evans, 2017).

Insect scavengers can play a vital role in releasing nutrients derived from carrion into ecosystems (Barton *et al*., 2019; Woelber-Kastner *et al*., 2021) and rapidly depleting carcass biomass in suitable conditions (Matuszewski *et al*., 2010; Pechal *et al*., 2014). This role is reflected in the existing Australian literature. For example, Barton & Evans (2017) quantified carcass mass loss in different habitats and in the absence of different insect assemblages, and found that insect presence led to a doubling in mass loss irrespective of habitat (grassland or forested), even though habitat type affected the composition of ant and beetle assemblages. The composition of insects at carcass sites can also change over time. Barton *et al*. (2014) found that the abundance and richness patterns of mites and beetles at carcass sites were very different, with mites reaching peak abundance and richness at

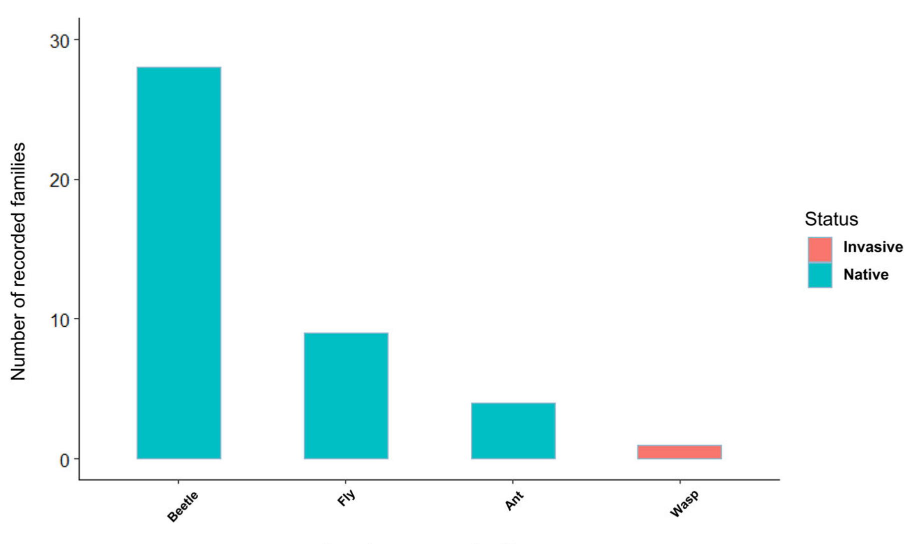

Fig. 3. Total number of scavenger insect families (or ant subfamilies) collected from carcasses based on Australian scavenging studies ($N = 12$ have an arthropod focus). Note that each individual carcass can host thousands of individual insects and a great diversity of genera and species.

weeks 6 and 12 (post death/placement), and beetles at weeks 1 and 6, possibly owing to differences in their dispersal and reproductive traits. The functional traits of some scavenging insects likely enable them to exploit carrion as a food source. For example, beetles at carcass sites in Australia have been shown to be twice as large as beetles at sites with no carcasses, and they had higher wing loadings (Barton *et al*., 2013*b*). Larger sized beetles and flies were also more common in earlier stages of decomposition as they can locate and utilise carcasses efficiently (Evans, Wallman & Barton, 2020). The combination of insect assemblages changing over time at carcass sites and the fact that carcasses attract insects with certain traits highlights the role of carrion as a driver of diversity and heterogeneity in ecosystems (Barton *et al*., 2013*a*), and as a selection force driving adaptation and evolution (Butterworth, Benbow & Barton, 2022).

III. CARCASS USE BY INVASIVE SCAVENGERS

Invasive species identified as scavenging or visiting carcasses in Australian studies include red foxes, domestic dogs, feral pigs, feral cats, black rats (*Rattus rattus*) and European wasps. Scavenging by red foxes in Australia is unsurprising given that they are known to consume carrion in their native range and have a highly flexible and opportunistic diet (Castañeda *et al*., 2022). Red foxes ranked as the third most commonly recorded vertebrate scavenger in Australian studies reviewed herein, and the most commonly recorded invasive scavenger (Fig. 1). The use of carcasses by red foxes can influence the nature and rate of scavenging. For example, Brown *et al*. (2015) found that red foxes dominated the consumption of fish carcasses along a beach–dune interface on North Stradbroke Island in Queensland, but on a nearby island without red foxes there was a significant shift in the scavenger guild, with brahminy kites (*Haliastur indus*) scavenging more in the absence of foxes.

Dominant use of carrion by red foxes is important to consider because they occupy most of non-tropical Australia and may increase competition for a food resource that would otherwise be available for native species. Many species switch between hunting and scavenging modes to meet their energetic requirements (DeVault, Rhodes, Jr. & Shivik, 2003), but a decline of carrion (due to red fox scavenging) could have negative demographic impacts on species that would otherwise rely on that food source. Concurrently, the availability of carcasses in Australian landscapes could be bolstering red fox populations and exacerbating their impacts on native prey. Such impacts could occur in the vicinity of carcasses, as demonstrated by Spencer *et al*. (2021) who found that red foxes were the most common mammal that depredated artificial bird nests located within 50 m of carcasses (discussed in Section V). By implication, there is a need to consider the role of red foxes as an invasive scavenger, and the relationship between their scavenging rates and predation rates.

Domestic dogs are well known scavengers globally, often concentrating around garbage and livestock carcass dumps (Doherty *et al*., 2017). Dogs were recorded scavenging in seven published studies, although in the study by Forsyth *et al*. (2014) they were likely dingoes. In the studies by Huijbers *et al*. (2013), Huijbers *et al*. (2016) and Schlacher *et al*. (2015), domestic dogs scavenged on fish carcasses, potentially outcompeting birds of prey. By supplanting birds of prey as a primary consumer of carrion, domestic dogs are fulfilling an ecological function by scavenging. But domestic dogs are also well known globally to cause detrimental impacts on ecosystems *via* predation, disturbance, disease transmission, competition and hybridisation (Doherty *et al*., 2017). Although there are no known free-roaming domestic dog populations persisting far from human settlements in Australia, there is little known about the ecology and impacts of free-roaming domestic dogs where they do occur. In addition, the extent of scavenging by domestic dogs is unclear, although a study from central Australia indicated that up to 38% of their dietary intake is from scavenging on different forms of human-provided rubbish/food scraps (Newsome *et al*., 2014).

Feral pigs ranked as the third most common invasive vertebrate scavenger (Fig. 1). In the study by Brown *et al*. (2006), feral pigs contributed to carcass removal; they attended every monitored carcass that was completely removed. Relatively high use of carcasses by feral pigs has also been documented in the Australian Alps, ranking third in terms of scavenging events recorded on 40 eastern grey kangaroo carcasses monitored, behind corvids and brushtail possums (Kane, 2020). Notably, feral pigs in the Australian Alps were recorded scavenging in groups of up to 10 individuals, their presence at carcasses accelerated carcass biomass loss, and red foxes and brushtail possums were more likely to scavenge on carcasses visited by feral pigs compared to carcasses scavenged by native/long-established dingoes (Kane, 2020). These results suggest that feral pigs can influence carcass persistence rates, but also potentially the composition of the scavenger community at carcass sites. However, such effects may depend on the extent of scavenging by feral pigs, which are omnivores and thus feed on a wide variety of foods (Wishart *et al*., 2015).

Feral cats were the least common invasive vertebrate scavenger recorded (Fig. 1), potentially reflecting a preference for live prey. However, they were recorded visiting nine out of 40 red kangaroo carcasses monitored in the arid zone of Australia, with a single feral cat consuming a 30 kg carcass over several days (Spencer *et al*., 2021). Feral cat use of carcasses may be influenced by the presence or absence of larger scavengers. For example, feral cats increased their consumption of carrion following a red fox control program in south-eastern Australia (Molsher *et al*., 2017). Feral cats also increased the proportion of carcasses they scavenged in areas where populations of the larger Tasmanian devil had reduced due to disease (Cunningham *et al*., 2018). Seasons may play a role in influencing rates of scavenging by feral cats. For example, carrion appeared in the diet of feral cats in central Australia during dry winters only, suggesting a potential switch to carrion when prey numbers are low (Paltridge, Gibson & Edwards, 1997). A study on Macquarie Island also found that feral cats scavenged on dead elephant seals (*Mirounga leonine*) and penguins (multiple species) on beaches, especially during winter (Jones, 1977).

No studies focused specifically on scavenging by black rats, but they were recorded visiting carcasses in five studies. It is possible that scavenging rates by black rats are higher than recorded in studies to date, as their small body size makes them harder to detect using motion- and heat-sensing cameras (Cunningham *et al.*, 2018). This possibility is important to investigate as the availability of carcasses as an additional food source could increase the abundance of invasive rodents and exacerbate their impacts on other species (Imber, Harrison & Harrison, 2000). This is also the case for the European wasp, which was the only invasive insect recorded scavenging in Australian studies (Fig. 3). Observations of European wasps killing flies has been noted in forensic studies (Archer & Elgar, 2003), and more recent work confirmed this interaction around carcasses monitored in the Australian Alps (Spencer *et al.*, 2020; Cairncross *et al.*, 2022). Predation on flies by wasps has the potential to influence food-web dynamics around carcasses more broadly, as discussed in Section V.

IV. TRAITS ANALYSIS

(1) Traits as a determinant of scavenging efficiency

The traits that scavengers possess may be important determinants of scavenging efficacy and can influence the functioning of scavenger communities (Kane *et al.*, 2017; Sebastián-González *et al.*, 2021). These functional traits may not only predict the ability of species to utilise carrion but also how species assemblages respond to changing environmental conditions (Violle *et al.*, 2014; Huijbers *et al.*, 2016). This extends to invasive species and their intrusion into native scavenger communities, which can cause cascading changes within ecosystems (Brown *et al.*, 2015; Pettit, Ward-Fear & Shine, 2021). Given the extent to which invasive species have spread throughout all of Australia's bioregions, understanding the traits that scavengers possess, both native and invasive, will facilitate a greater awareness of the dynamics of scavenger communities that contain both groups. Some work has been conducted to assess what traits Australian insect scavengers possess (Barton *et al.*, 2013*b*; Evans *et al.*, 2020), with larger body size and greater dispersal ability linked to early colonisation of carrion resources, but no study on vertebrate scavenger traits has yet been conducted in Australia.

(2) How traits influence species commonness

Using available data from studies reviewed herein that included vertebrate scavengers, we analysed how traits influence species commonness (see Table S3, Appendix S1, and Table S4 for list of traits included, methodology, model output and limitations). We focused on vertebrate species as these were the most widely studied group and had the most available data of the collated studies. Initial analysis was conducted on all vertebrate scavengers, irrespective of life history or habitat. The results suggest that there is wide variation in the traits that influence vertebrate scavenger commonness. When considering all scavenger species, statistically significant effects on commonness were found for species that were noisier and had a tendency to form familial or social groups (Table S4, Fig. 4). There were also trends in commonness towards species that had high visual acuity and omnivorous diets, despite these traits not showing a statistical effect at alpha = 0.05 (Table S4, Fig. 4). Minimal effects were evident for species that are invasive, have larger body masses and home ranges, have the ability to fly or are considered to be either apex scavengers or apex predators (Fig. 4).

A second analysis using the same method to assess how the traits of terrestrial-only vertebrate scavengers influence their commonness was also carried out (Fig. 5). None of these traits had a statistically significant effect on commonness from the respective models that were constructed, however there was a trend for species with higher visual acuity to be more common (Table S4, Fig. 5). Weak effects were found for invasive species, apex predators and apex scavengers, species with larger home ranges and body masses and omnivorous diets. A statistical analysis of how olfaction and noisiness influenced terrestrial scavenger commonness was not possible due to limited sample size since no terrestrial scavengers in the available data were categorised as having low olfactory abilities (observations: $N = 78$ high olfactory, $N = 0$ low olfactory abilities) or to be 'noisy' feeders, apart from Tasmanian devils, which are well known to produce loud vocalisations particularly when feeding and defending food items like carrion ($N = 2$ noisy, $N = 72$ quiet feeders) (Buchmann & Guiler, 1977). Similarly, an analysis of the trait 'sociality' was not possible for terrestrial scavengers due to unequal sample sizes. Nevertheless, despite solitary scavengers being recorded far more frequently, there appears to be no difference in commonness between solitary terrestrial scavenger species (mean ± SD commonness = 0.261 ± 0.179, $N = 65$ observations) and those forming social or familial groups (mean ± SD commonness = 0.283 ± 0.206, $N = 13$ observations).

Overall, this analysis indicates varying trends among different traits, with some influencing the commonness of all vertebrate species differently compared to the analysis across terrestrial-only vertebrates. For the analysis of all vertebrate scavengers, the traits associated with higher levels of commonness are similar to those identified in studies of scavenger traits from other continents (Sebastián-González *et al.*, 2021). Interestingly, there was minimal difference between invasive and native scavengers (trait 'status' in Fig. 4), suggesting that within vertebrate scavenger communities in Australia, invasive species do not consistently outcompete native scavengers. However, for terrestrial-only vertebrates, we found a stronger, nonetheless statistically insignificant, positive effect on commonness for invasive species (Figs 4 and 5,

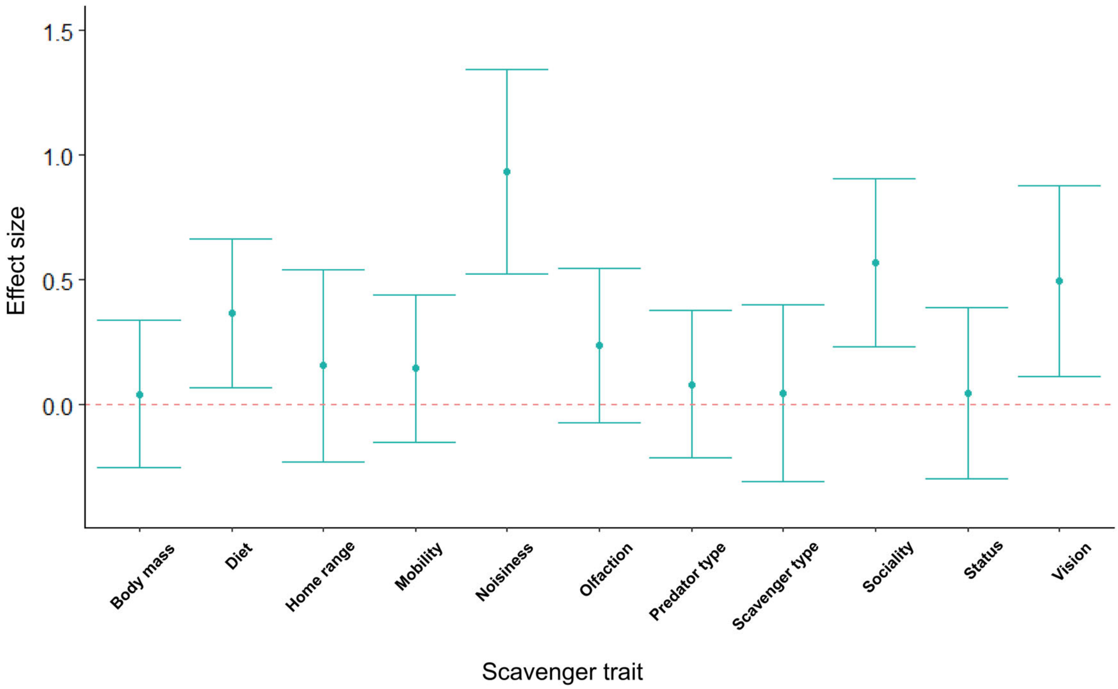

Fig. 4. Effect sizes derived from the vertebrate scavenger traits analysis. Effect sizes were derived from linear mixed models assessing variation in the natural logarithm of the ranked abundance of each scavenger species modelled against trait type. Traits were fitted as a fixed factor and study identifier and species as random effects. All effect sizes are Hedges' *g* apart from the Body mass and Home range variables, which are Cohen's *d*. See Table S3 for details of scavenger trait variables and Table S4 for full model results. Error bars indicate 95% confidence intervals.

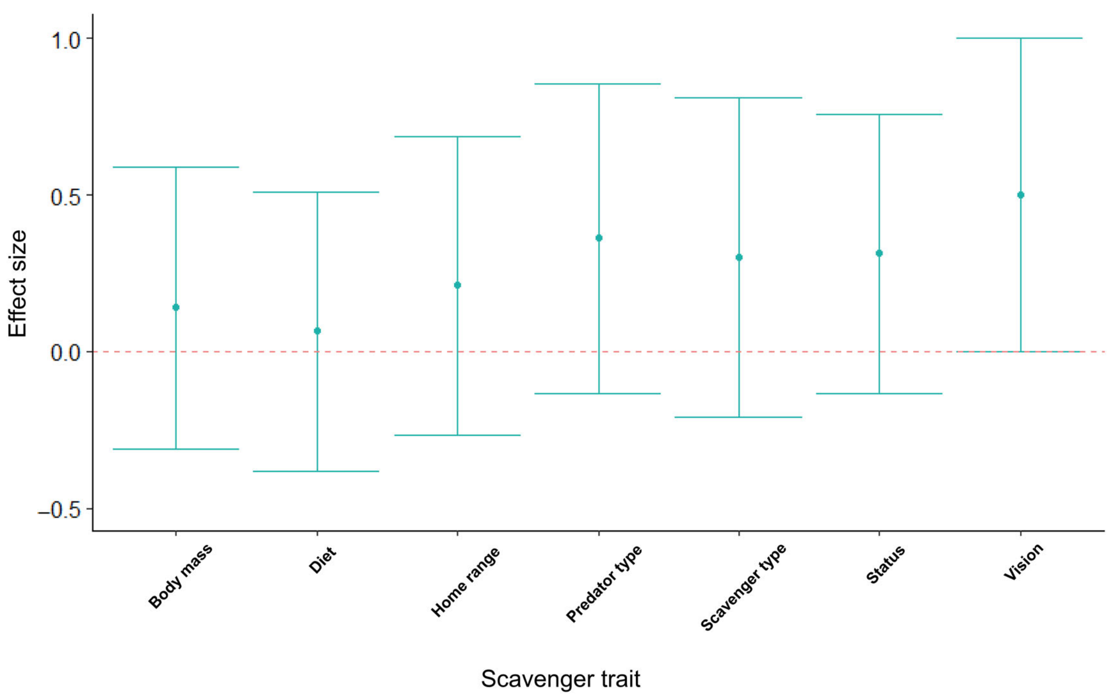

Fig. 5. Effect sizes derived from the terrestrial-only vertebrate scavenger traits analysis. Effect sizes were derived from linear mixed models assessing variation in the natural logarithm of the ranked abundance of each scavenger species modelled against trait type. Traits were fitted as a fixed factor and study identifier and species as random effects. All effect sizes are Hedges' *g* apart from the Body mass and Home range variables, which are Cohen's *d*. See Table S3 for details of scavenger trait variables and Table S4 for full model results. Error bars indicate 95% confidence intervals.

Table S4). This finding perhaps reflects the prevalence of invasive species within communities of terrestrial fauna (Doherty *et al*., 2015). With the decline and extinction of native apex predators across the Australian mainland and in Tasmania, this would be unsurprising. Accordingly, invasive fauna may have continual, cascading impacts on terrestrial scavengers in Australia, and by extension on biodiversity more broadly. Additionally, the results also suggest that, when present, apex predators and apex scavengers are more prevalent within communities of Australian terrestrial scavengers. However, the lower number of observations of apex predators ($N = 21$) and apex scavengers ($N = 21$) compared to mesopredators ($N = 57$) and mesoscavengers ($N = 52$) within the reviewed literature underscores the generally scarce nature of these fauna at carcass sites.

V. CASE STUDIES

(1) Apex scavenger effects on invasive species

Interactions between carnivores range from intra-guild killing and competition to facilitation through carrion provisioning (Palomares & Caro, 1999; Prugh & Sivy, 2020). This interplay results in a risk–reward trade-off that differs according to the predatory and scavenging characteristics of large-bodied apex scavengers and smaller mesoscavengers (O'Bryan, Holden & Watson, 2019; Prugh & Sivy, 2020). Apex scavengers are typically functionally dominant during scavenging, allowing them to locate/consume carcasses more efficiently than other scavengers (Sebastián-González *et al*., 2016). They can be obligate or facultative scavengers, relying either entirely on carrion (obligate scavengers such as vultures) or only partially whilst also functioning as predators (Ogada *et al*., 2012). There is growing global interest in the relationships between apex scavengers and co-occurring mesoscavengers, especially as some of these smaller, less-dominant scavengers may have detrimental ecosystem impacts. Exploring these interactions is important as apex scavengers are declining globally (O'Bryan *et al*., 2019) and this phenomenon could influence carcass use by invasive species.

There are several ways in which apex scavengers might influence invasive species. Apex scavengers might remove carcass biomass more efficiently, and thus reduce the amount available to other scavengers. Apex scavengers may also influence invasive scavenger use of carcasses *via* direct predation or fear effects (e.g. risk-induced changes to behaviour), which may reduce their use of the food resource. Collectively, this competition and deterrence may limit the benefits that invasive scavengers can derive from the resource, which could in turn influence their fitness in the environment, and their population sizes. On the other hand, some apex scavengers may benefit invasive species. Apex scavengers can open up tough-skinned animals to allow increased access for other scavengers. Apex scavengers that are also predators can supply carcasses. For example, the remains of kills by grey wolves (*Canis lupus*) in North America are an important source of carrion for coyotes (*Canis latrans*) and avian scavengers (e.g. corvids), especially during winter (Wilmers *et al*., 2003; Wilmers & Getz, 2005; Wilmers & Post, 2006). Conversely, by supressing overall numbers of their primary prey such as herbivores, apex predators that are also scavengers may reduce carcass loads resulting from natural deaths, or following mass die-offs during periods of poor environmental conditions such as droughts (Rees *et al*., 2019).

Australia's largest mammalian scavengers, dingoes (~15 kg) and Tasmanian devils (6–13 kg) have very different characteristics, including different adaptations for scavenging and hunting. Whereas Tasmanian devils do kill prey directly, this is relatively rare and their reliance on scavenging is high (Andersen *et al*., 2020). Tasmanian devils can reach very high densities (3/km^2; Cunningham *et al*., 2021) and possess morphological adaptations such as robust teeth and massive jaw musculature that enable them to consume all parts of a carcass, including the bones (Jones, 2003). Dingoes will also scavenge animal remains (Newsome *et al*., 1983; Brook & Kutt, 2011; Davis *et al*., 2015), but they also predate a wide variety of animals to meet their energetic needs (Doherty *et al*., 2019). Thus, Tasmanian devils may have a stronger limiting effect on carrion supply compared to dingoes. Both dingoes and Tasmanian devils have suffered substantial range contractions since European settlement in Australia (Letnic *et al*., 2012; Cunningham *et al*., 2021), which could have cascading effects on scavenging food webs.

Tasmanian devils became extinct on the Australian mainland several thousand years ago, coinciding with a period of human population growth and the arrival of dingoes (Prowse *et al*., 2014; Morris *et al*., 2022). More recently, they have undergone severe declines in their island refuge of Tasmania, caused by a novel transmissible cancer. In areas where Tasmanian devils have declined, macropod carcasses now persist 2.6-fold longer (Cunningham *et al*., 2018). Consequently, feral cats were three times more likely to scavenge in areas with suppressed Tasmanian devil densities (Cunningham *et al*., 2018), and seven times more likely to scavenge on environmentally similar offshore islands that lack native predators altogether (Fielding *et al*., 2021). This increase in scavenging by feral cats challenges a widespread misconception that feral cats do not scavenge, and has been proposed as a potential explanation for the observed mesopredator release of cats following Tasmanian devil declines (Hollings *et al*., 2014, 2016; Cunningham, Johnson & Jones, 2020). Similarly, invasive black rats commonly scavenge in Tasmania (Cunningham *et al*., 2018), where they are now the most common small mammal (Cunningham *et al*., 2020), especially in areas with declining Tasmanian devil populations (Hollings *et al*., 2016). The disease-caused Tasmanian devil population decline highlights that native carnivores can limit resource acquisition by problematic invasive species, suggesting that recovery of native carnivore populations could help to combat the negative effects of some invasive species (Doherty *et al*., 2016).

Range contractions by dingoes on the mainland of Australia primarily have been linked to lethal control programs and the erection of dingo-proof fences (Newsome *et al.*, 2015). Although dingoes may subsidise smaller mesopredators such as feral cats and red foxes by killing large herbivores and thus providing carrion, it is the removal of dingoes from landscapes that is more likely to influence carrion loads. Specifically, it is well established that some large herbivore populations in Australia are much more abundant in the absence of dingoes due to a reduction in top-down effects (Letnic *et al.*, 2012). These uncontrolled herbivore populations can experience population crashes during droughts or following control by humans (culling) that can temporarily increase the availability of carcasses to scavengers. The provision of such carcasses in the absence of dingoes has been shown to increase the local abundances of scavenging corvids, but to decrease detection rates of small passerine birds, indicating that dingo removal, and the subsequent availability of herbivore carcasses, could subsidise facultative scavengers but indirectly affect co-occurring species (Rees *et al.*, 2020).

Where dingoes persist, there is evidence that they can influence the use of carcasses by invasive species. Forsyth *et al.* (2014) report spatial and temporal separation in carcass use by red foxes and dingoes, consistent with the hypothesis that red foxes avoid dingoes. Although feral cats are not frequently recorded scavenging in mainland studies, incidental observations in the Simpson Desert suggested that feral cats visited carcasses when dingoes were not present (Spencer, 2023). In some cases, high rates of dingo scavenging may help to accelerate carcass biomass loss. For example, in south-east Australia, dingoes visited 32 out of 40 carcasses in groups of up to 13 individuals (Spencer & Newsome, 2021). These visits were linked to lower carcass persistence times during the cool season. In the warm season, dingo scavenging did not influence rates of carcass persistence, likely reflecting a period when insects are common and also accelerate carcass biomass loss (Spencer & Newsome, 2021).

(2) Lesser-known effects of invasive species

The presence of carrion in ecosystems has been linked previously to vertebrate predator survival and, as a result, indirectly increasing their predatory impacts in ecosystems. For instance, carcass resources are critical for the survival of native red foxes in Scandinavia and Norway during winter, when alternative food sources are scarce (Needham *et al.*, 2014; Gomo *et al.*, 2021). A greater abundance of foxes, as well as other predatory species, in the vicinity of carcasses has been correlated with significant population declines for their prey in the same area, due to both direct predation and fear effects (Cortés-Avizanda *et al.*, 2009; Frank *et al.*, 2020). In areas invaded by exotic scavengers, similar trends have been identified. For example, Norway rats (*Rattus norvegicus*), by eating eggs and nestlings, reduced the reproductive rates of grey-faced petrels (*Pterodroma macroptera gouldii*) on Whale Island, New Zealand to negligible levels after the introduction of rabbits. Rats scavenged on overabundant rabbit carcasses as a supplementary food source. As a result, their abundance increased, strengthening their existing predatory impacts on these birds (Imber *et al.*, 2000). The impact of native predators subsidised by carrion on ground-nesting birds has also been shown to be strong (Cortés-Avizanda *et al.*, 2009; Rees *et al.*, 2015). However, the detrimental effects on native bird species of invasive predators that also scavenge is likely to be even greater (Salo *et al.*, 2007), as suggested by Imber *et al.* (2000).

In Australia, there has been little focus on the impacts of invasive species regarding carrion resources. However, Spencer *et al.* (2021) found that both native corvids and invasive red foxes accounted for the majority of depredation events on artificial nests of two different ground-nesting bird species, the little button quail (*Turnix velox*) and the critically endangered night parrot (*Pezoporus occidentalis*). Corvids were responsible for most raids on quail nests, whilst foxes accounted for the most depredation of night parrot nests. The frequency of predation for both nest types increased significantly closer to carcasses, although nest predation by foxes was most strongly influenced by carrion. Foxes preyed on the artificial quail nests approximately equally to their predation rates at parrot nests but were able to access parrot nests more than corvids as these are typically located in thicker scrub habitats. These results highlight how carrion used by invasive vertebrates can facilitate increased predation pressure on nearby species.

The effects of invasive invertebrates subsidised by scavenging on native ecosystems may also be significant but have received little attention in Australia. Invasive insects can outcompete native invertebrate scavengers for carrion (McNatty, Abbott & Lester, 2009; Angulo, Caut & Cerdá, 2011; Carmo *et al.*, 2018), potentially destabilising ecosystems (Porter & Savignano, 1990). Such insects are typically generalist predators and facultative scavengers, with their sociality supporting rapid recruitment from colonies and efficient monopolisation of high-value resources like carcasses (Crowder & Snyder, 2010; Eyer & Vargo, 2021).

Social wasps of the family Vespidae are an example of a highly successful invader that has infiltrated scavenger communities globally. In Australia, the European wasp is widespread (Spradbery & Maywald, 1992) but research into their impacts on scavenging dynamics is sparse. Wasps were first reported to attack and kill native necrophilous flies by Archer & Elgar (2003). This study observed that both wasps and flies were attracted to carrion for foraging opportunities. Fly predation was an indirect result of the arrival of European wasps at carrion, with many families of fly commonly associated with scavenging (e.g. Calliphoridae, Muscidae and Sarcophagidae) forming a large part of the wasp's polyphagous diet (Madden, 1981).

Spencer *et al.* (2020) explored the scavenging dynamics of European wasps in a sub-alpine ecosystem in Australia, finding that wasps not only actively preyed on flies at carcasses but also mutilated them, leaving the dead flies where they were killed or flying off with their headless bodies. This behaviour prevented flies from accessing the carrion, whilst wasps were recorded utilising carcasses for food, cutting out portions of flesh and taking these back to their nests. This is typical behaviour of other vespid wasps that scavenge in their native habitats (Merrit *et al.*, 2015). However, with no native wasps in Australia using carrion in this way, native insects are potentially naïve and susceptible to attack. Additionally, by feeding their broods on tissues and flies gathered from carrion, these sources of abundant protein may help to sustain European wasp nests over winter (Potter-Craven *et al.*, 2018; Cairncross *et al.*, 2022), leading to population explosions in spring and, by extension, the possible worsening of their impacts (Harris, 1996; Fearn, Dowde & Maynard, 2015). Spencer *et al.* (2020) also showed that wasps deterred native vertebrate scavengers such as dingoes by stinging them, as fire ants do elsewhere (Turner, Conner & Beasley, 2021). In comparison, invasive vertebrates like feral pigs were not affected by wasp presence, perhaps because their hides were too thick for the stings to penetrate.

Cairncross *et al.* (2022) provided more detail on the impact of wasps on flies and carcass decomposition. In this study, carcasses were split open to simulate the scavenging activity of large vertebrates on fresh carrion, which has been shown to increase fly abundance (Meehan, Seminet-Reneau & Quinn, 2005; Munro *et al.*, 2019). Although no difference in fly or wasp abundance was found between open and intact carrion in their investigation, numbers of observed wasp predation and mutilation events were higher at open carcasses, ultimately suggesting that the predatory and competitive effects of wasps can shift irrespective of wasp numbers. Interestingly, the wing-buzzing defensive strategy of scavenging blowflies like *Calliphoria stygia* was ineffective when attacked by wasps, in contrast to other studies highlighting this as an effective measure against invasive ants (e.g. Sawyer *et al.*, 2021). As the impact of wasp predation on insect populations can be extreme (Burne *et al.*, 2017), and given that blowflies are often important pollinators, carcass provisioning throughout landscapes invaded by European wasps may additionally impact scavenging fly pollination services (Spencer *et al.*, 2020). Similar conclusions have been drawn in Hawaii, where a species of yellowjacket (*Vespula pensylvanica*) has infiltrated scavenger and pollinator communities, with deleterious effects on native bee species (Wilson & Holway, 2010; Wilson & Wolkovich, 2011).

VI. GLOBAL IMPLICATIONS AND FUTURE DIRECTIONS

Australia is in the midst of an extinction crisis, partly driven by invasive species (Woinarski *et al.*, 2015). Knowledge of the factors that facilitate invasive species impacts and spread can help to prevent or slow down future invasions or impacts by these pest species. We reviewed and quantitatively synthesised Australian studies exploring the use of carrion by vertebrate and arthropod scavengers, including invasive species. Our analysis highlights several key interactions between invasive scavengers and native taxa at carcasses while also showcasing the potential for invasive scavengers to affect ecosystems more broadly and pointing out directions for future research.

(1) Interactions of invasive species at carcass sites

Studies in systems outside of Australia have raised the concern that invasive species can exclude access to carcass resources by native scavengers (e.g. Hawaii, USA; Abernethy *et al.*, 2016). Accordingly, multiple Australian scavenging studies reviewed herein found or suggested that invasive species can monopolise carrion resources. Such competition appears likely to arise if invasive species can locate and consume carrion more quickly than native species, or because the presence of invasive species simply increases competition for the food resource. Moreover, the studies we reviewed offer partial support for the idea that use of carcasses by invasives negatively affects native scavengers. Although species commonness within overall scavenger communities in Australia did not differ as a function of invasive *versus* native status, invasive terrestrial scavengers were more common at carcasses than their native counterparts. Furthermore, although ecosystems with invasive species may be degraded to some degree and have fewer native species, we also found evidence that the diversity of native scavengers visiting carcass sites decreases in studies that had a higher proportion of invasive vertebrate scavengers (Fig. 6, Table S5). Collectively, these trends underscore the potential for invasions to reshape scavenging dynamics, suggest that some native scavengers, and especially vertebrates, may be excluded from carcass resources by invasives, and emphasise the need for studies that assess the causes and consequences of interspecific competition for carcasses among native and invasive species directly (Fig. 7).

Many invasive species are generalists that may scavenge facultatively or act as predators (DeVault *et al.*, 2003). Thus, scavenging by these species has the potential also to shape patterns of predation at and around carcasses (Fig. 7). Our review found studies documenting this phenomenon, for example with elevated nest depredation rates by invasive red foxes near carcasses (Spencer *et al.*, 2021). Such carcass-related predation by invasives may be especially ecologically important given that predation pressure exerted by these unfamiliar species can be acute (Sih *et al.*, 2010). Furthermore, it suggests that factors that modify carcass availability in the landscape such as livestock production may concomitantly drive changes to predation regimes and thus jeopardise vulnerable prey populations (Doherty *et al.*, 2016). Although there is growing recognition that invasive species can facilitate native species through such mechanisms as habitat modification, trophic subsidy, and competitive and predatory release (Rodriguez, 2006), any benefits from invasive species as scavengers have yet to be explored as a general phenomenon. While they are often overlooked, our review suggests that benefits from scavenging invasives could be pervasive and substantial, for example in the form of carcass removal (i.e. ecosystem cleaning). However, the ability of some species effectively to replace carrion removal by obligate or apex scavengers may be limited. For example, a 4 year study

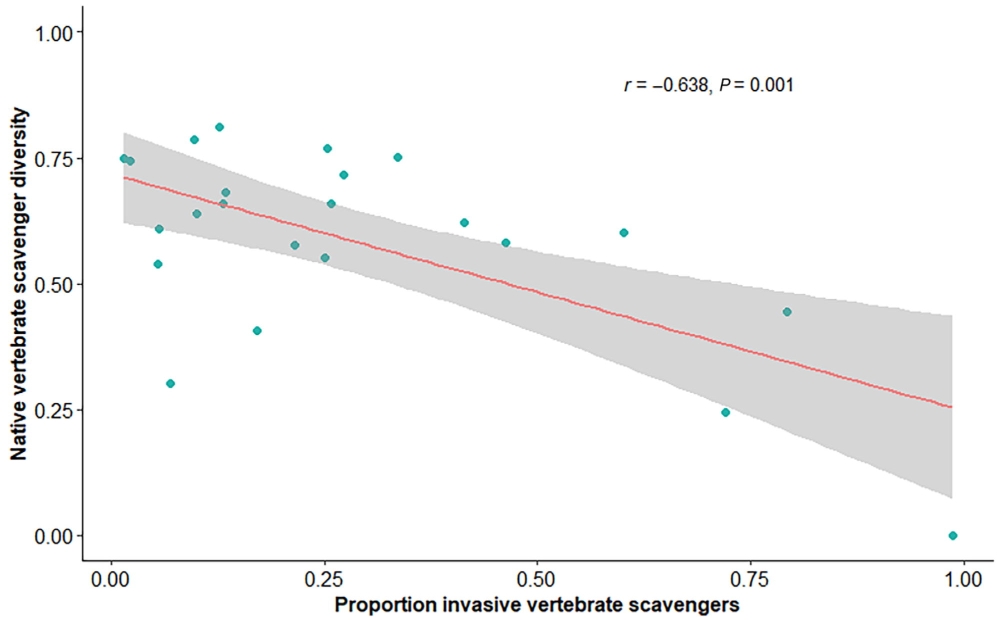

Fig. 6. Relationship between native vertebrate scavenger diversity across all scavenger species and the proportion of invasive vertebrate scavengers recorded in Australian studies ($N = 23$) (Table S5). Simpson's Diversity index was calculated for all native vertebrate species recorded in each study. The proportion of invasive vertebrate scavengers reflects their relative commonness based on scavenging rates across all species recorded in each study. r is Pearson's correlation coefficient. Grey shaded areas indicated standard error.

in Ethiopia found that domestic dog visits to abattoirs increased as visits by other scavengers, including vultures (*Gyps* spp.), declined but there was a concurrent 12% decrease in carrion removal (Buechley *et al.*, 2022). Similarly, in New Jersey, USA, the presence of domestic dogs resulted in carcasses taking longer to be detected and the proportion of carrion consumed decreased (Maslo *et al.*, 2022).

Our review further underlines the importance of invasive scavenger suppression by apex scavengers like dingoes and Tasmanian devils. This suppression can occur when apex scavengers remove carrion from the landscape, as when dingoes reduce large herbivore numbers (Letnic *et al.*, 2012) and thus carcass availability, and when they kill or induce avoidance of carcasses by mesoscavengers like red foxes and feral cats (Forsyth *et al.*, 2014; Cunningham *et al.*, 2018). Accordingly, apex scavenger declines have broad implications for the activity of invasive scavengers. In a notable case of apparent mesoscavenger release (O'Bryan *et al.*, 2019), the disease-caused decline of Tasmanian devils led not only to markedly increased carcass persistence in the landscape but also to a functional switch to greater scavenging by a species better known as a predator – the feral cat – along with black rats (Cunningham *et al.*, 2018). By implication, recovery of apex scavengers in Australia and elsewhere may offer a passive means to control invasive scavenger populations and thus restore pre-invasion ecosystem dynamics.

Finally, this review highlights the ecological influence of invasive invertebrate scavengers in Australian ecosystems. In particular, European wasps appear to exert strong effects on other scavenger populations, both as predators of and competitors with other invertebrates (e.g. native flies) and as deterrents to vertebrate scavengers like dingoes (Spencer *et al.*, 2020; Cairncross *et al.*, 2022) (Fig. 7). These impacts raise concern about factors that promote the success of invasive invertebrates, such as anthropogenic landscape modification (Schmack *et al.*, 2020) and climate change (Chown *et al.*, 2007).

(2) Broader ecosystem impacts

Much of the available research on scavenging, including in Australia, has focused on interactions and localised impacts around carcass sites, although there is increasing awareness that the ecological effects of scavenging can extend well beyond sites where carrion is available (Wirsing & Newsome, 2021; Newsome *et al.*, 2021). Several of the studies we reviewed point to mechanisms by which these broader effects can occur. For example, the absence of dingoes as an apex scavenger may not only facilitate invasive scavengers but also appears to subsidise smaller avian scavengers (corvids) while reducing detections of small passerines (Rees *et al.*, 2020), perhaps because the increased presence of corvids induces avoidance by the latter group, although the degree to which smaller invasive scavengers, rather than native corvids, might similarly transmit this putative indirect effect has yet to be determined.

Three additional pathways are also highlighted by our review of the Australian arthropod literature and from

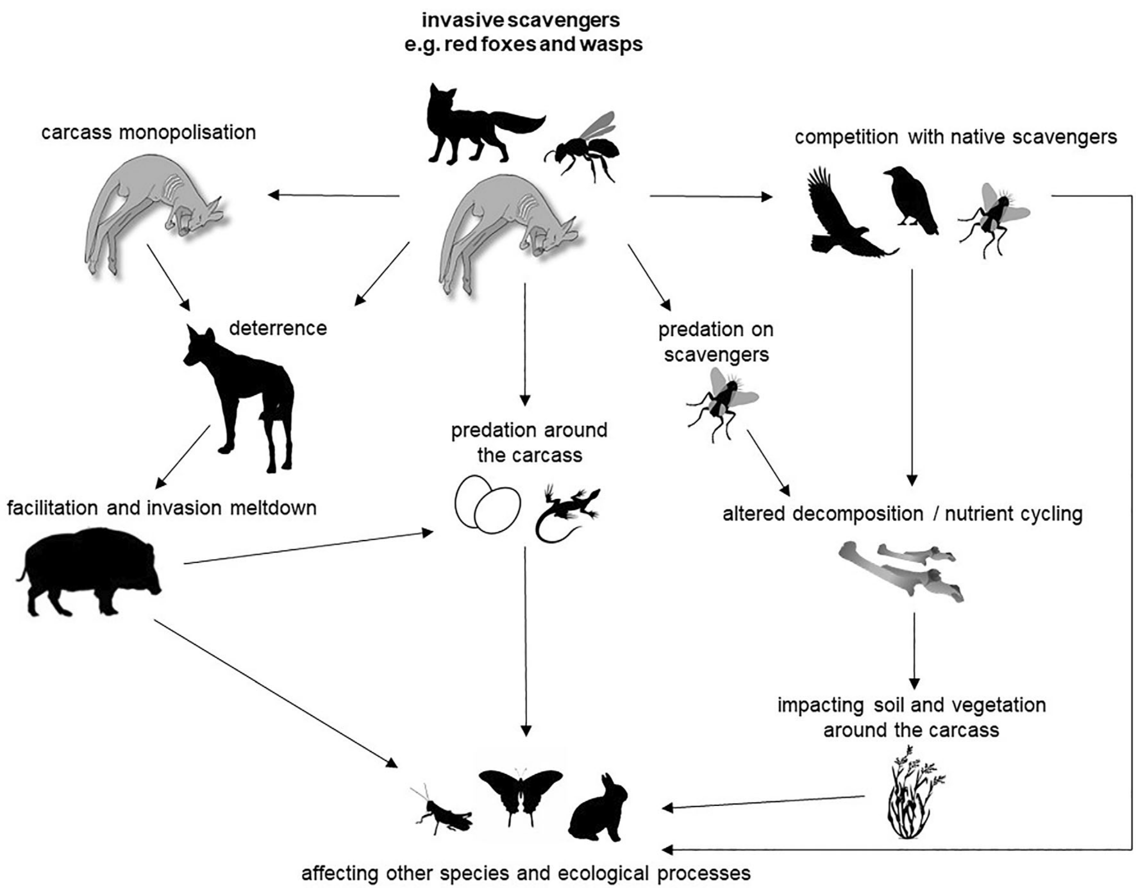

Fig. 7. Conceptual model showing documented interactions and ecological effects arising from monopolisation of carcasses by invasive scavengers, and the possible cascading effects on ecosystems.

similar studies globally. First, Barton *et al.* (2013*b*) found that carcasses attracted different insects over time and insects with particular traits, revealing that both the presence and persistence of carrion in the landscape can shape community composition by providing niche space for a variety of scavengers. Conversely, carcass removal, including by invasive species, could reduce resource availability and therefore limit its ability to support species diversity in ecosystems. Second, work in multiple Australian studies (Spencer *et al.*, 2020; Cairncross *et al.*, 2022), together with findings from Burne *et al.* (2017), suggest that invasive wasp predation on pollinating blowflies that rely on carcasses for reproduction, and by extension other invasive scavengers that prey on pollinators, could have far-reaching consequences for plant communities in areas being invaded by wasps where carcasses are also abundant. Third, in a process analogous to climate warming allowing tree pests (e.g. mountain pine beetles, *Dendroctonus ponderosae*) to persist during cold intervals and thus expand their ranges and drive higher levels of tree mortality (e.g. Cudmore *et al.*, 2010), carrion and prey gathered at carcass sites may allow invasive European wasps to survive the winter (Potter-Craven *et al.*, 2018; Cairncross *et al.*, 2022) and thereby exacerbate their population and ecosystem effects (Harris, 1996; Fearn *et al.*, 2015) (Fig. 7). More work is clearly needed, but this process could represent a general mechanism whereby carrion acts as a buffer against control agents that would normally impede ecological invasions by scavengers.

(3) Knowledge gaps and research outlook

Carrion ecology in Australia began as natural history case studies and has been shifting towards a greater quantitative and comparative focus over the last 20 years. The growing literature on scavenging in Australia now reveals carcasses to be the centre of complex interactions among species and their environment that combine to shape population demography, species assemblages, ecosystem dynamics, and notably, invasions. Regarding invasions, however, there remains much to be learned, in large part because most studies of scavenging by invasive species and its broader effects have been observational and localised around carcass sites. Looking ahead, our understanding of the interactions and impacts of invasive scavengers in Australia and beyond would benefit from further experimental work, with manipulations targeting both tissue utilisation patterns and the consequences of their interactions in the immediate vicinity of carcasses and, perhaps more importantly, their effects on other species and ecosystem processes (e.g. broader community assembly, nutrient cycling) on a landscape scale. These experiments should be guided by a clear research agenda focusing on the following topics as fruitful avenues for enquiry: (*i*) the extent to which invasive predators that facultatively scavenge are also responsible for the full suite of 'scavenging effects' (*sensu* Wirsing & Newsome, 2021); (*ii*) when and how invasive scavengers benefit one another, potentially precipitating invasion meltdowns; (*iii*) the role of invasive scavengers in ecosystems that have been modified by humans; (*iv*) the possible impacts of carcass provisioning to reduce predation by invasive species that facultatively scavenge but may lead to population increases in these species and associated negative effects; and (*v*) the factors that limit invasive species access to carrion, especially the presence of apex scavengers.

When predators scavenge facultatively, they have the potential to exert numerous impacts including reducing carcass availability and detectability, killing or displacing other species, accidentally ingesting other species, altering how decomposition influences soil biogeochemistry and local vegetation, reducing the attractiveness of carcass sites to herbivores and pollinators by constraining local plant and soil enrichment, affecting patterns of microbe and parasite transmission through communities, and inducing trait changes in other species by acting as kleptoparasites (Wirsing & Newsome, 2021). To date, research has typically addressed only the first two of these pathways (i.e. competition and predation). Accordingly, studies examining all potential effects will be crucial to a full understanding of the ecological and economic impacts of facultative scavenging around carcasses, whether by native or invasive predators. For instance, invasive feral pigs and foxes are key consumers of carrion in Australia and elsewhere (Fig. 1) (Forsyth *et al*., 2014; Wenting, Rinzema & van Langevelde, 2022), and may functionally replace absent native apex scavengers by removing carcasses. For example, introduced raccoon dogs (*Nyctereutes procyonoides*) on a small island in Japan replaced the scavenging role vacated by native scavengers in a process of functional compensation (Sugiura & Hayashi, 2018).

Exotic species may form positive interactions that promote the proliferation of at least one invader in a process termed 'invasion meltdown' (Simberloff & Holle, 1999), as in the case of non-native crazy ants (*Anoplolepis gracilipes*) facilitating population increases of the exotic coffee green scale (*Coccus celatus*) within the forest canopies of Christmas Island (O'Dowd, Green & Lake, 2003). Empirical support for invasion meltdown is growing (Braga *et al*., 2018), but evidence from vertebrate systems remains scant and this process has not been explored rigorously in scavenger communities. Notably, our review included a study showing what might be a similar phenomenon, but centred around carcasses, whereby invasive wasps deter scavenging by native species like dingoes by stinging them, potentially reducing competition experienced by non-native feral pigs, which are more resistant to wasp attacks (Spencer *et al*., 2020). This scenario will need to be confirmed, but even as a hypothesis it provides impetus for a new research direction given that carcasses represent a pervasive resource around which invasive scavengers might benefit one another (Fig. 7).

Conversely, a trade-off may also exist in some ecosystems where a supply of abundant carrion provides a larger proportion of the diet for invasive species than predation (Mellard *et al*., 2021), thereby potentially alleviating pressure on native species that are prey items of invasive predators which also scavenge. Where invasive species occur, research determining rates of predation and scavenging and the mechanisms that determine when animals switch between these are key to a better understanding of the potential for this process to occur. Indeed, if carcass resources are found to increase the abundance and associated negative impacts of invasive scavengers, then carcass removal could mitigate this problem. The rate at which carcasses are removed, however, may be key to the success of such a management approach. For example, in an analogous scenario where endangered woodland caribou (*Rangifer tarandus caribou*) were subject to apparent competition with other ungulates through their shared grey wolf predators, a sudden deer (*Odocoileus* spp.) decline led to increased predation by cougars (*Puma concolor*), which had to prey switch, and a 40% caribou population decline. However, a gradual moose (*Alces alces*) reduction *via* a management experiment led to a wolf population decline without a corresponding shift to consumption of caribou, allowing the caribou population to stabilise (Serrouya *et al*., 2015). In these scenarios, rapid depletion of the primary resource for the predator triggered a transient increase in risk for caribou before the eventual wolf numerical response manifested. Similarly, there is need for research examining the possibility that rapid carcass removal could lead facultative invasive scavengers to switch to predation, potentially imperilling other species before resource reduction causes them to decline. By implication, calculation of the net impacts of invasive species that scavenge should account for these positives alongside the expected negative impacts.

VII. CONCLUSIONS

(1) Invasive scavengers are common in Australia and the diversity of native vertebrate scavengers at carcass sites appears to be lower when the proportion of invasive vertebrate scavengers is higher. Future research may resolve the mechanisms behind this relationship, which may stem from the loss of apex scavengers, which in turn allows invasive scavengers to flourish. Alternatively, or in conjunction with the loss of apex scavengers, invasive species may facilitate an invasional meltdown that results in some degraded scavenger communities being dominated by invasive species.

(2) Terrestrial vertebrate scavenger commonness at carcass sites is also positively linked to whether a species is classed as invasive. This pattern reiterates findings of individual studies showing that invasive vertebrate species can monopolise carcass resources. There is also evidence that invasive insects can monopolise carcasses in the same way, particularly social

hymenopterans that display aggressive behaviour and occur in large numbers.

(3) Other documented effects of invasive species around carrion resources include deterrence, competition, and predation that can in turn have cascading effects on other species and ecosystem processes through altered rates of decomposition and nutrient cycling.

(4) The use of carcasses as a food source by invasive scavengers is likely to be widespread globally, and such use could act as a buffer against effective invasive species control. However, our review also highlights the potential role that large apex scavengers can play in either rapidly removing carcass biomass from the landscape or deterring smaller scavengers, including invasive species, from utilising carrion. The protection and restoration of large apex scavengers may therefore provide one pathway to reduce use of carrion by invasive species.

(5) There remain several knowledge gaps globally with respect to the role carrion plays in facilitating the impacts of invasive species, and the extent to which invasive species alter decomposition and nutrient cycling. We suggest that future research should focus broadly on understanding the extent of scavenging by invasive species, their interactions and ecological effects at and around carrion sites in different landscapes, and the factors that limit their access to carrion resources.

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Overview of Australian scavenging studies based on a *Web of Science* search.

Table S2. Vertebrate scavengers documented visiting carcass sites in the Australian studies listed in Table S1.

Table S3. Scavenger traits that were assessed as fixed factors, and their respective levels, along with justification for inclusion.
Appendix S1. Methodology for analysis of traits, relationship between native scavenger diversity and the presence of invasive scavengers.
Table S4. Model output for the linear mixed models assessing $\ln(x + 1)$-transformed commonness against species traits across all vertebrate scavenger species and terrestrial-only species.
Table S5. Model output for the linear model assessing the proportion of invasive species commonness against the Simpson's diversity index for native vertebrate scavengers in studies with available data ($N = 23$).

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