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Short communication

Invasive European wasps alter scavenging dynamics around carrion

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ABSTRACT

European wasps (*Vespula germanica*) have invaded parts of North and South America, Australia and New Zealand. They are opportunistic predators and scavengers that can disrupt food webs and species interactions, but their role in food webs associated with carrion is poorly understood. In this study we examined wasp abundance at 20 vertebrate carcasses in south-eastern Australia. We also collected data on the abundance of blowflies and the occurrence and behavior of vertebrate scavengers at the same carcasses. Wasps arrived within minutes of deploying fresh carcasses and were approximately 4.3 times more abundant in forest compared with grassland habitats. Wasps killed and mutilated native blowflies and may have prevented them from ovipositing on carcasses, as we subsequently found that these carcasses were devoid of fly larvae. European wasps also appeared to interfere with dingoes (*Canis dingo*) feeding on carcasses, based on observations from cameras showing dingoes snapping their heads in the air and then retreating from the carcasses suddenly. The other major vertebrate scavenger in the system, feral pigs (*Sus scrofa*), did not show similar behavioral responses. Although we observed European wasps feeding on carcasses, carcass mass loss was slow. This could be a direct result of European wasps suppressing flies and potentially excluding dingoes from accessing carcasses. We conclude that European wasps may alter the way energy flows through scavenging food webs, which could have cascading impacts on ecosystem dynamics and services, although manipulative experiments would help to further evaluate these possibilities.

Invasive species have the capacity to cause severe environmental degradation by altering species dynamics and ecosystem processes (Salo et al., 2007). Such effects are well documented among invasive vertebrates, with hundreds of extinction events now recognized (Doherty et al., 2016). Less well known are the effects of invasive insects, with research efforts historically focusing on a select few areas and taxa (Kenis et al., 2009). Invasive insects have the capacity to alter ecosystems via their effects on food webs and species interactions. This might occur through similar mechanisms as invasive vertebrates, such as through changes to herbivory (Jenkins, 2003), predation or parasitism (Boettner et al., 2000; Snyder and Evans, 2006), or through more complex mechanisms such as competition, disease transmission or pollination disruption (Council, 2002; Desurmont et al., 2014). However, invasive insects have very different biology (e.g. seasonal life cycles) to most invasive vertebrates, and they might be causing damage in ways we do not easily see or fully appreciate. This may especially be true if the invasive insects are also alien species that have unique adaptations that give them an advantage over native species.

A highly successful invasive alien insect in Australia is the European wasp (or German wasp; *Vespula germanica*). The European wasp is native to Europe, Northern Africa and parts of Asia, but has been introduced to other countries including North and South America, Australia and New Zealand (Akre et al., 1989; Edwards, 1978). It is a social wasp, and an opportunistic generalist that utilizes both visual and olfactory cues to detect prey, and often returns to patches that have previously yielded high foraging success (Moreyra et al., 2007). Worker adult European wasps can specialize on different foraging tasks (Hurd et al., 2007), and therefore have different trophic positions in food webs. One distinct role of mature workers is foraging for protein, and can include directly preying on other insects, or scavenging meat from dead animals (Richter, 2000). Although there is recognition of the ecological impacts of wasps in areas they have invaded (e.g. Beggs, 2001; Cook, 2019; Haupt, 2015; Kasper et al., 2004), very little is known about the role of wasps in scavenging and carrion food webs (e.g. Archer and Elgar, 2003; Wilson et al., 2010).

European wasps could disrupt food webs around carrion in their invaded range by consuming co-occurring insects directly, or by competing with both vertebrate and insect scavengers for the carcass resources. Similar impacts have been observed with their successful invasion of beech (*Nothofagus*) forests in New Zealand, and the wasps' monopoly

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of honeydew resources. Not only has their dominance of this resource lead to substantial negative impacts on vulnerable insect and bird species that rely on honeydew, it also supports high wasp densities, which drastically increases wasp predation of insect species in the area (Beggs, 2001). Like New Zealand, European wasps in Australia lack any natural predators, and, due to their comparatively broad diet, they may also outcompete other native predators such as the common paper wasp (*Polistes humilis*; Kasper et al., 2004). The distinct behavior and foraging ecology of European wasps and their status as an "apex" insect in Australia, therefore, means they have the potential to monopolize carrion and outcompete other scavengers around this focal food resource.

As part of a study investigating vertebrate and insect scavenging on carrion across Australia, we observed carcass visitation by European wasps and recorded some of the impacts that they were having on co-occurring scavenger species. Specifically, we examined the relationship between European wasps and blowflies (family: Calliphoridae) and determined whether vertebrate scavengers were being influenced by wasp presence. Blowflies are an important scavenger that encourages rapid decomposition of carcasses via the larvae (i.e. maggots) they produce on decaying flesh (Benbow et al., 2019; Payne, 1965; Putman, 1978). Similarly, many vertebrates are considered efficient scavengers (DeVault et al., 2003) and as such, carcass decomposition may be delayed if these animals are deterred from feeding. Evidence of deterrence effects of wasps on scavenging flies and vertebrates may indicate potential cascading effects on food web dynamics around carrion. We predicted that blowflies would avoid wasps, appearing in lower numbers at carcasses where wasps were abundant (prediction 1). We also predicted that there would be more signs of blowfly predation where wasps were present in higher numbers (prediction 2). Finally, we predicted that the scavenging behavior of both the dingo and the pig would be disrupted by wasps (prediction 3).

Direct observations while monitoring 20 experimentally positioned eastern grey kangaroo (*Macropus giganteus*) carcasses (30.6 ± 1.2 kg) in Kosciuszko National Park, south-eastern NSW (Fig. 1), in March and April 2018, indicated that European wasps were congregating in large numbers around the animal carcasses. The carcasses were placed 1 km apart in forested ($n = 10$) and grassland ($n = 10$) habitats, and European wasps were present at all carcass sites. In some cases, individual carcasses attracted wasp swarms that we visually estimated to be in the thousands. Elevated wasp activity following carcass placement was also noticeable in the surrounding landscape. At ~80% of carcasses, wasps appeared rapidly, typically within the first 1 to 3 min of carcass placement. Wasps were observed feeding off the carcass meat (collecting and carrying it off for larvae in their nests), but even after 30 days of monitoring, some carcasses remained quite intact (e.g. 8 out of 20 carcasses had >90% biomass remaining).

We estimated wasp and fly activity on each carcass using two pitfall traps (i.e. 120 mL jars filled half-way with a preservative fluid, ethylene glycol, and buried flush with the ground). This method was utilized to form part of the larger study comparing general insect (i.e. beetle, fly and ant) activity and has been used successfully to compare insect succession on animal carcasses in previous Australian studies (e.g. Barton and Evans, 2017). Two of these traps were set approximately 20 cm from the top (i.e. mouth) and bottom (i.e. anus) of the carcass for 3 days at a time, directly after the carcass was positioned (days 1–3) and also two weeks after the carcass was laid (days 15–17). We counted and compared the number of European wasps and blowflies captured in traps using a linear regression (prediction 1). To test prediction 2 we counted the number of blowflies with any obvious signs of predation and compared these numbers with the number of wasps captured in traps using a linear regression. Obvious signs of predation included mutilation or removal of part or all of their abdomen and thorax, or decapitation. We used these more extreme signs of predation as we couldn't definitively identify flies that had been stung but not fed upon or mutilated by wasps, and because flies may have lost limbs or wings while trying to escape from the pitfall traps. As such, it is likely that we underestimated the cases of predation events on flies.

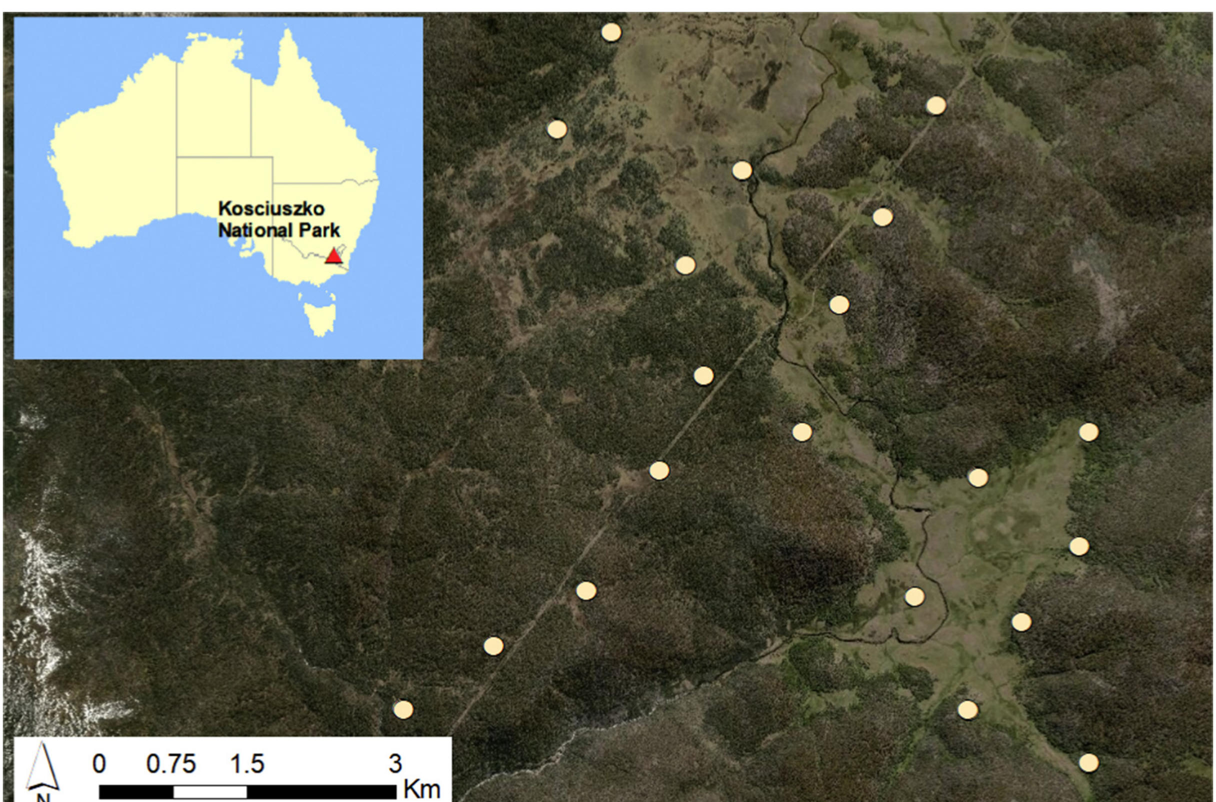

Fig. 1. Map of the study area in Kosciuszko National Park, Australia, with positioning of eastern grey kangaroo carcasses displayed (yellow circles).

Our comparison of European wasp and blowfly captures across the different habitats (forested and grassland) and time periods (days 1–3 and days 15–17) revealed differences between blowfly and European wasp activity on the carcasses (Fig. 2), with more wasps compared to flies captured in the later time period (total wasp: fly ratio = 819:19) compared to the earlier period (total wasp: fly ratio = 247:164; PERMANOVA: $F_{1,36} = 22.200$, $p \leq 0.001$, using 999 random permutations). For the blowfly, a difference between time periods was detected, with more flies captured in the earlier period compared to the later period (GLM: $Z = -4.273$, $p = 0.018$). For the wasp, a difference between both habitat and time period was found, with more wasps captured in the forest habitat compared to the grassland habitat (GLM: $Z = -3.708$, $p \leq 0.001$) and with more wasps captured in the later time period compared to the earlier period (GLM: $Z = 3.217$, $p = 0.001$; for further information on the statistical methods and results see Table S1). The eastern golden-haired blowfly (*Calliphora stygia*) was the most commonly identified blowfly species in our traps, comprising 91% of blowflies (Diptera: Calliphoridae) trapped.

When we examined whether reduced blowfly numbers were associated with higher wasp presence, against prediction 1 we did not find a relationship between the number of blowflies and the number of European wasps captured in traps ($F_{1,38} = 2.771$, $p = 0.104$; Fig. 3A). However, when sorting through traps we identified many blowflies with evidence of mutilation by the wasps (Figs. 3, 4). In total, 18 (11%) blowflies were mutilated and only blowflies of the species *C. stygia* were mutilated. Fly mutilation was also only present at sites where wasps appeared in traps, and there was a significant positive linear relationship between wasp presence and the proportion of mutilated blowflies in line with prediction 2 ($F_{1,23} = 10.07$, $p = 0.004$). Direct observations of predation were also made in the field; when blowflies and wasps were present, flies attempting to reach the carcass were rapidly attacked and subdued by wasps in all observed instances (~35 instances). We also didn't find any fly larvae (i.e. maggots) in, under or on top of the carcass for up to one month following carcass placements, despite checking the orifices and lifting the carcasses on multiple occasions to check the soil underneath.

We used remotely-triggered Reconyx PC800 Hyperfire™ camera traps (Professional Reconyx Inc., Holmen, WI, USA) to monitor large vertebrate scavenger activity on carcasses over a 30 day period, which included the period of time when we sampled flies and wasps. Camera traps were set to take continuous photographs each time the camera was triggered (i.e. rapid fire, no wait period). After tagging all the images to species level, we focused on the responses by dingoes (*Canis dingo*) and feral pigs (*Sus scrofa*) as they are the largest vertebrate scavengers present in the area. We noted where there was any evidence of feeding or scavenging behaviors being disrupted by counting when a dingo or pig snapped their jaws or swung their heads in the air and then retreated from the carcass suddenly.

Our camera traps captured 221,078 photos of vertebrate animals visiting the carcasses. Dingoes were captured visiting 25% of the carcasses and were identified in 1890 photos, while pigs visited 60% of carcasses and appeared in 139,323 photos. Of these images, in support of prediction 3, we counted 20 instances where dingoes were clearly disturbed or interrupted by wasps around carcasses. For the dingo, two individuals were recorded snapping at the air and then rapidly backing off from carcasses during 4 separate feeding bouts (i.e. separated by >4 h.; e.g. Fig. 5). In all cases, the individuals were solitary, and they each appeared on different carcasses. The first individual fed on 3 separate occasions on a carcass in the grassland habitat, while the second fed on a carcass in the forest habitat, on one occasion. These feeding bouts all occurred during the day (between 8 am and 6 pm) when high wasp activity was obvious in the sequence of camera images, although dingoes did visit and feed on carcasses at night. Feral pigs scavenged heavily during both the day and night and appeared on carcasses where high wasp activity was obvious. Against prediction 3, however, pigs did not appear to be affected by wasps, and they only displayed head swinging and jaw snapping behaviors in response to other visiting pigs (e.g. Fig. 5).

Our study shows that European wasps can be abundant scavengers that detect carcasses with a high efficiency. Wasps visited all 20 carcasses, appearing at carcasses rapidly and swarming in large numbers. We did not, however, find a relationship between the number of flies and wasps in pitfall traps, which suggests that flies were not avoiding carcasses where wasps were more abundant. Instead, variation in blowfly numbers among carcasses is likely due to differences in odor cues, which can be moderated by prevailing winds and vegetation or other barriers (Verheggen et al., 2017). This is probably also the case for wasps, although they may select carcasses based on their nest location, as workers rarely travel >200 m from their nests when foraging (Perrott, 1975). While flies did not avoid carcasses where wasps were abundant, our findings did show that there is a potential for fly populations to incur sizable localized impacts where they co-occur in high numbers with wasps. Wasps excluded flies from carcasses through direct predation, attacking flies before they landed on the resource. Wasps also seemed to prevent flies from ovipositing, evident by the absence of blowfly larvae observed during carcass inspections. These observations may explain why many carcasses displayed little to no decomposition after 30 days.

The cool autumn weather experienced in March (max: 20 °C, min: −3 °C) might have also suppressed blowfly reproduction and microbial growth during our study, which in-turn slowed carcass decomposition. Indeed, blowflies and microbes both show greatest activity on carcasses in warmer temperatures and rapid carcass decomposition is strongly associated with high insect and microbial activity (Putman, 1978).

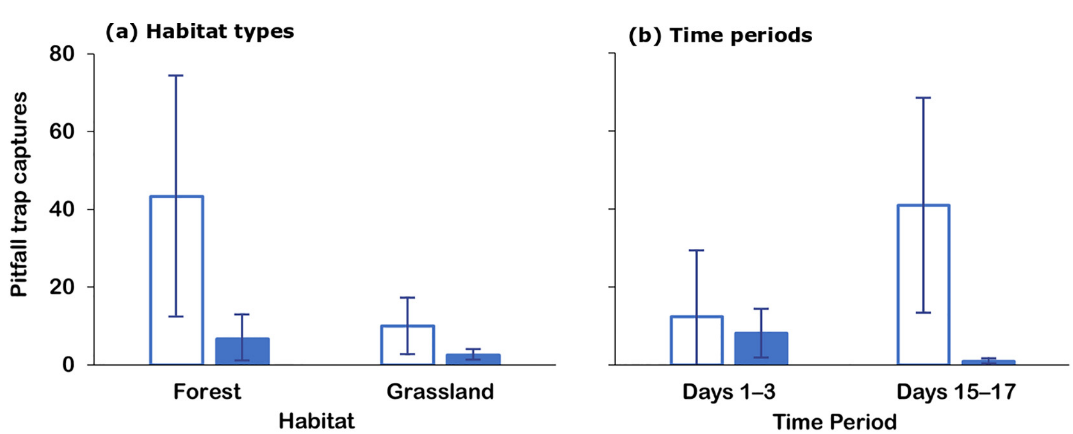

Fig. 2. The average number of European wasps (open bars; ±95% CI) and blowflies (closed bars; ±95% CI) caught in traps set (a) in forest and grassland habitat types and (b) in earlier (days 1–3) and later (days 15–17) sampling periods, in Kosciuszko National Park, Australia.

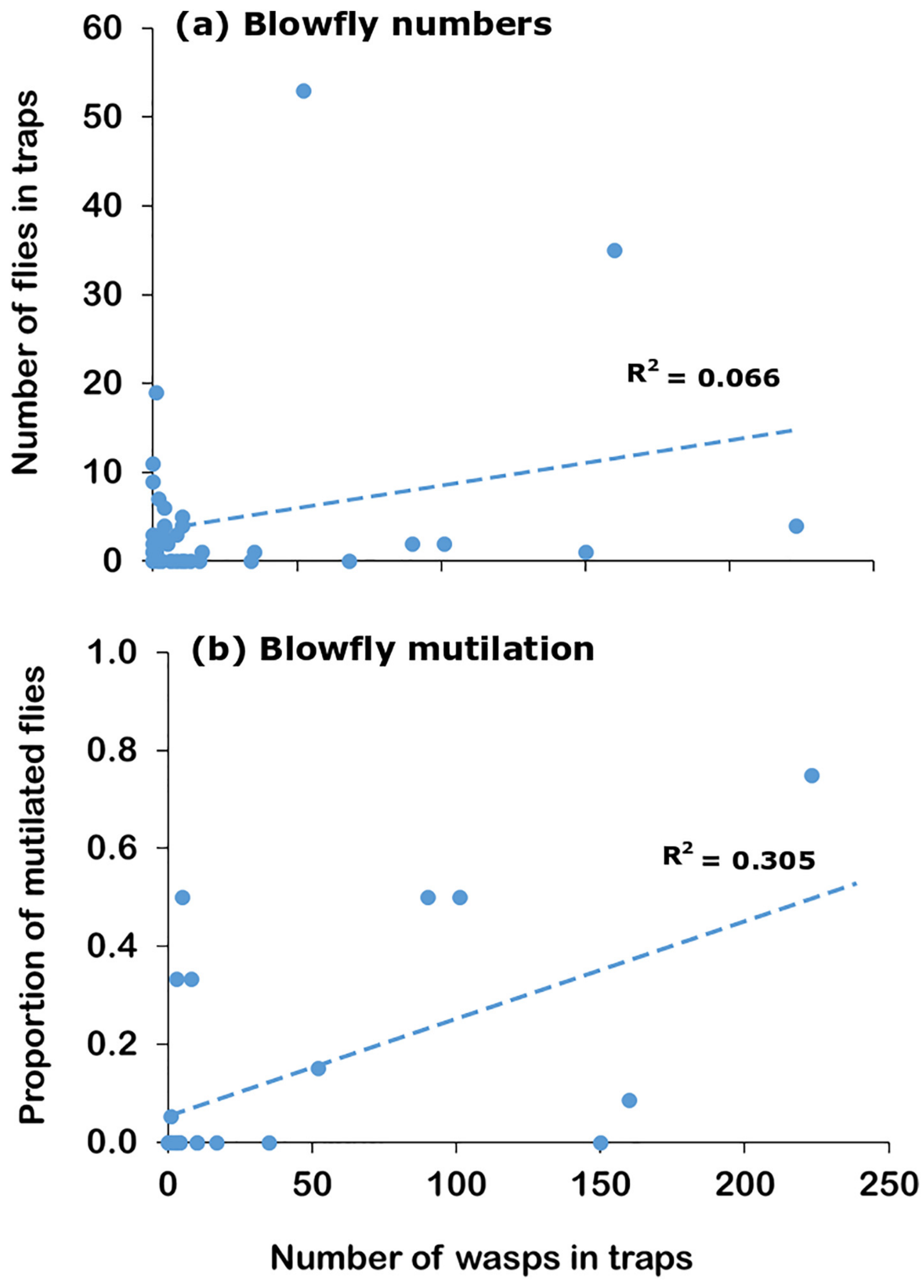

Fig. 3. Plots showing the relationship between the number of European wasps caught in traps and (a) the number of blowflies and (b) the proportion of mutilated blowflies caught in traps in Kosciuszko National Park, Australia.

Without the wasp, however, we would have likely detected at least some larvae on the carcasses, as the dominant blowfly species observed (i.e. *C. stygia*) is well adapted to Australian subalpine and alpine regions and actively reproduces at low temperatures (Salter, 1946). Along with the effects of temperature on fly activity, blowflies also prefer fresher carcasses as oviposition sites (Putman, 1978). This explanation for the decrease in fly numbers later in the sampling period also fits with general carrion insect succession theory (Benbow et al., 2019). On the other hand, the increase in wasp numbers during this later period probably reflects the wasps' sociality. Social wasps, including the European wasp, may recruit nestmates to food sources over time through processes such as local enhancement (D'Adamo et al., 2000; Parrish and Fowler, 1983; Reid et al., 1994).

The behaviors displayed by dingoes when wasps were present at carcass sites suggest that wasps might also be influencing their scavenging activity. Interference with vertebrate feeding behaviors has been documented when certain species of invasive fire ants (e.g. *Solenopsis invicta*) are present on carcasses (e.g. Antworth et al., 2005), although these behaviors were inferred by comparing biomass loss on carcasses where ants were present or absent. That pigs did not display similar behaviors (perhaps due to their thickened hides; Frädrich, 1974) is worth noting because pigs are a recent (~230 years) invasive animal in Australia and they cause considerable environmental damage through grazing and when they root up the ground (Hone, 1995). Dingoes, on the other hand, are longer established (>4000 years) and are considered Australia's apex predator, helping to regulate the numbers of smaller pests and overabundant herbivores (Letnic et al., 2012). While dingoes predate on pigs (Newsome et al., 1983; Saunders, 1993) and pigs likely avoid dingoes, the presence of European wasps on carcasses could counter some of these effects, as scavenging pigs are provided a competitive advantage over dingoes. This advantage lends support to the invasional meltdown theory, which suggests that some invasive species will

Fig. 4. Two eastern golden-haired blowflies (*Calliphora stygia*) captured in pitfall traps with mutilation evident in the form of decapitation (i.e. removal of their heads).

facilitate the success and spread of other invasive species in certain systems (Simberloff and Von Holle, 1999). Prior studies have already established that invasive scavengers may be facilitated by the carcasses of other invasive species (e.g. Abernethy et al., 2016), but virtually nothing is known on whether invasive scavenging insects facilitate other scavengers. Further, the prospect of an invasive scavenging insect facilitating an invasive scavenging vertebrate is intriguing.

The local interactions we observed could also trigger broader cascading interactions in the surrounding system (see Fig. 6 for a summary of potential cascading interactions). For the blowfly, their ability to reproduce and their survival may be impeded by wasp presence on carcasses as a result of direct predation. Apart from influencing carcass decomposition rates and nutrient dispersal throughout the landscape, this could lead to cascading effects on other important ecological functions and processes such as pollination. Indeed, in our study region, the blowfly is considered a major pollinator of flowers in alpine areas (Inouye and Pyke, 1988). If wasp numbers are supported by prevalent carcass resources, then pollination in the region may be negatively impacted. Similarly, native vegetation could also be impacted by cascading interactions between wasps, dingoes and pigs. If wasps deter dingoes but not pigs, this might concentrate the activity of pigs in certain areas (i.e. where carcasses are present) and exacerbate environmental degradation via processes such as grazing and ground rooting. Social wasps such as the European wasp also provide pollination services (Shuttleworth and Johnson, 2009) and contribute to carcass scavenging. When exploring potential cascading interactions around carrion, therefore, it is also important that we consider the potential ecosystem services that the wasp may provide, along with any negative impacts.

One key limitation of our study was that it lacked a negative control where carcasses had wasps excluded from feeding. This made it difficult

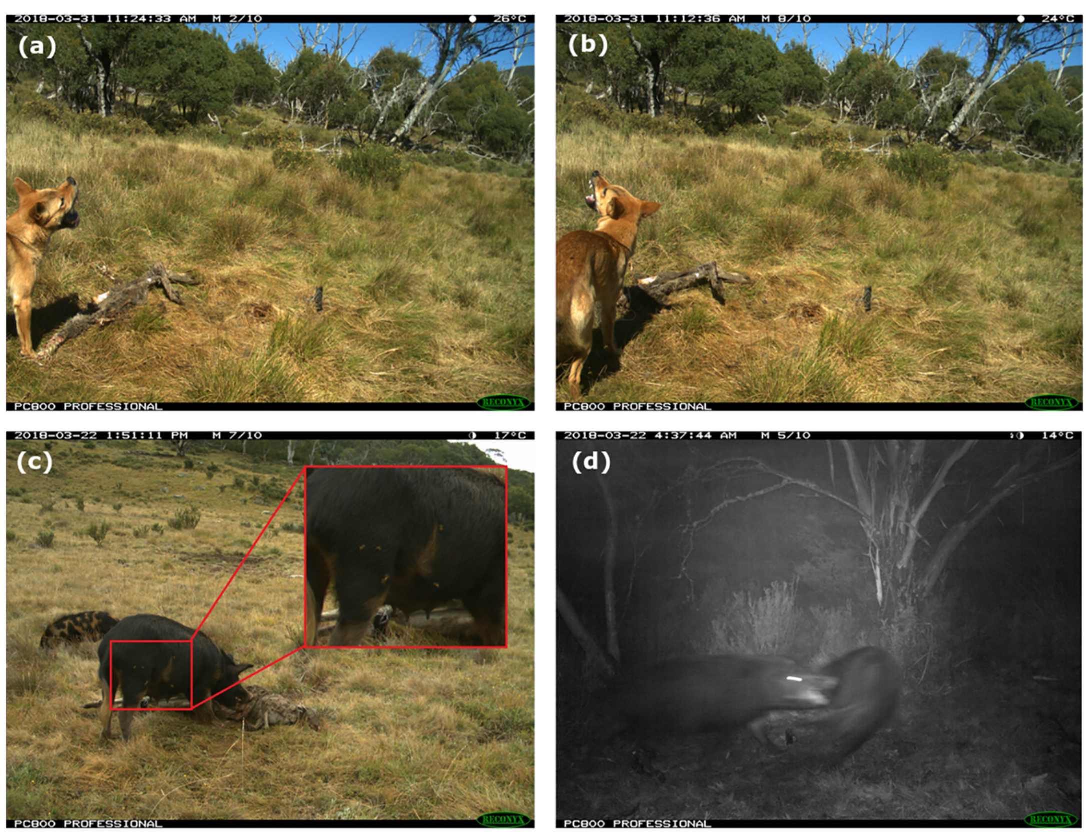

Fig. 5. A selection of camera trap images where (a–b) dingoes are displaying behaviors indicative of disturbance or interference by swarming European wasps (i.e. snapping at wasps around their heads), and where (c) European wasps are pictured landing on feral pigs and where (d) a pig is pictured snapping at and chasing another pig.

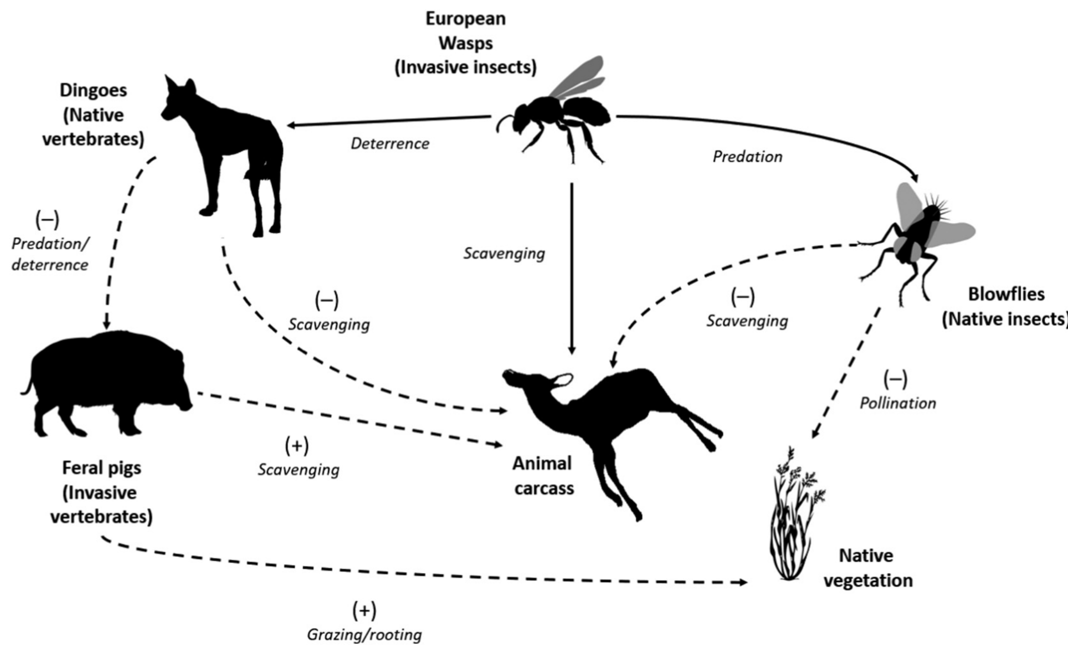

Fig. 6. Potential interactions between European wasps, blowflies and native and invasive vertebrate scavengers when European wasps are present in the system. The arrows show the direction of the interactions, and the (−) or (+) signs indicate whether the interaction decreases or increases, respectively, in the presence of wasps. Solid lines indicate direct interactions with the wasp, while dotted lines show the indirect (cascading) effects of wasp presence on other species.

to determine the degree to which European wasps influence insect and vertebrate scavenging and rates of carcass decomposition. Further manipulative experimentation, for example, by excluding wasps from half of the monitored carcasses using wasp-specific poison baits (e.g. Lester et al., 2013) would prove very useful. Pitfall traps can be highly effective at sampling blowflies at carcasses due to their habit of crawling over the carcass and nearby ground to find suitable oviposition sites (Barton et al., 2017). Nevertheless, they could be combined with other forms of collection such as sweep nets, sticky traps and hand collection (Schoenly et al., 2007). Our sampling methods were originally designed for a larger study investigating the general use of carcasses by different scavenger species across Australia. We did not exclude wasps from any carcasses and chose to use pitfall traps to sample insects, as we had intended to target a broad array of species and did not anticipate the presence of the invasive wasp on carcass resources.

Our findings have broader implications for managing carcass loads in Australian environments. For example, to mitigate the negative impacts of the European wasp, carcass removal could be focused in certain habitats. In our study, wasps showed preferences for carcasses in forest sites, potentially because these habitats provided more options for nesting (e.g. in rotted wood stumps). Managing carcasses may not be as important during seasons with low wasp activity. During these times, dingoes may scavenge more, competing with and repelling feral pigs and potentially other vertebrates such as the introduced red fox (*Vulpes vulpes*). Considering the numbers and sources of animal carcasses is also important when assessing wasp impacts and thus determining whether carcass removal will benefit a system. Mass mortality events resulting from weather extremes, natural disasters (e.g. bushfire and floods), disease or animal culls for pest control, for instance, could attract and support large populations of wasps over vast areas. These populations could then cause substantial impacts that are measurable on the landscape scale, for example, by decimating native pollinator populations or by facilitating pest scavengers such as the feral pig. To further disseminate these and other impacts, insights into the spatial and temporal use of carcasses by European wasps are required, as are more comprehensive experiments documenting their interactions with a greater range of insect and vertebrate species. Finally, when deciding whether and how to manage carcasses, it is important that the complexity of scavenging food webs is appreciated, especially if our observations of an invasive insect disrupting insect and vertebrate scavengers apply to other regions and scavenger guilds.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2020.e00144.

Ethics statement

A scientific license was obtained to use and relocate the kangaroo carcasses (SL 101901) and research was approved by the University of Sydney Animal Ethics Committee (Project number. 2017/1173). Kangaroos were sourced from preplanned animal culls in the local area, and as such were not killed for the purpose of this study.

Declaration of competing interest

None.

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