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Silver gull carcasses host unique carrion insect communities on a nearshore island

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Abstract

Island ecosystems offer unique opportunities to study the dynamics of species that rely on ephemeral resources such as carrion. This study investigated the necrophagous insect communities associated with carrion of silver gulls (*Chroicocephalus novaehollandiae*) on a small nearshore island off the east coast of Australia, to assess how necrophagous insect communities on islands compare with the mainland community, and the degree to which these communities varied over time. Over three breeding seasons, we analysed what insect species were colonising gull carcasses and, using baited traps, compared total adult community composition and richness of carrion-associated insect species on the island with the adjacent mainland. Our findings reveal that an island separated by less than 500 m from the mainland can harbour distinct carrion-breeding fly assemblages. These assemblages vary between years but are notably dominated by a potential seabird-carrion specialist fly—the littoral species *Calliphora maritima*. These results underscore the importance of seabird carrion as a critical resource for necrophagous insects on islands and contribute to our understanding of how island environments influence insect community dynamics and specialisation.

KEYWORDS

Australia, avian, coastal, decomposition, Diptera, island biogeography, necrobiome

INTRODUCTION

Islands serve as unique habitats with distinct ecological characteristics. Island Biogeography Theory (IBT) predicts that species richness is generally lower on islands compared to mainland areas due to barriers to dispersal and colonisation (MacArthur & Wilson 1967). Limited resources, including food and space, exert additional selective pressure on island populations, potentially leading to specialised adaptations, constrained population sizes, or ultimately local extinctions (Kadmon & Allouche 2007; Whitcomb et al. 1976). These effects are thought to be stronger for smaller islands, and for islands more distant from mainlands (MacArthur & Wilson 1967). Island environments also often lack equilibrium, as characterised by fluctuating populations and resource availability (Gillespie & Roderick 2002; Kadmon & Allouche 2007; MacArthur & Wilson 1967). For instance, seasonal and migratory seabird colonies can dramatically alter resource availability through provision of guano, carrion, and discarded food (Bauer & Hoye 2014). These seasonal breeding events dramatically increase population densities for short periods, which can subsidise consumer populations, thereby impacting species diversity and community dynamics on islands (Obrist et al. 2022; Polis, Anderson, & Holt 1997; Polis & Hurd 1995, 1996).

Necrophagous insects have been documented on almost every habitat on Earth, and are common inhabitants of islands including the seemingly inhospitable Sub-Antarctic islands, such as Campbell Is and the Antipodes

Is (Dear 1985). Necrophagous insects typically have high dispersal capabilities as they often travel great distances to locate carrion to use as food resource and breeding substrate (Evans, Wallman, & Barton 2020; Norris 1965). Several species of *Chrysomya*, *Lucilia* and *Phormia* can disperse >15 km in less than 48 h (Norris 1965). The population dynamics of necrophagous insects across island habitats has attracted interest, particularly due to the potential applications of these community data in forensic entomology. However, the results of these studies are somewhat contradictory, with a study in Australia showing very little structural difference between main-land and island populations (Rottnest Is.; Essarras et al. 2021), in contrast to a similar study of community structure along an island gradient in the Baltic Sea that showed that smaller islands display lower carrion-breeding fly species richness (Kuusela & Kuusela 1983). Both of these studies utilised introduced vertebrate carrion baits (pig and fish, respectively) and as such natural carrion sources on islands and their associated insect communities remain poorly understood.

Colonial breeding seabirds represent a common source of carrion on islands. Yet this resource is highly patchy in both space and time due to the site specificity and seasonal nature of seabird colonies. Additionally, seabird carrion differs to that of vertebrate carrion in terms of anatomy (e.g., feathers vs. fur, airsacs vs. lungs, muscle structures), diet (marine vs. terrestrial) and physiology (e.g., drinking and excreting salt water vs. freshwater). Seabird carrion is also smaller than that of terrestrial vertebrates typically included in entomological studies and will likely support a smaller and unique carrion community (Butterworth, Benbow, & Barton 2022; Moleón et al. 2015). It should be noted that most seabird species have breeding colonies restricted to islands, and seabird carrion is not widely available outside of these environments (Croxall et al. 2012; Spatz et al. 2014). Therefore, to survive on islands, necrophagous insect species may need to adapt and specialise to feed and breed in seabird carrion. Currently, little is known about the necrophagous insect communities that colonise seabird carrion, or how necrophagous insect communities are impacted by fluctuating carrion sources.

Here we investigated the necrophagous insect species colonising silver gull [*Chroicocephalus novaehollandiae*, (Stephens, 1826)] carrion on a small nearshore island, 500 m off the east coast of Australia to assess how necrophagous insect communities on islands compare with the mainland community, and the degree to which these communities varied over time. To address these questions, we examined insects colonising seabird carrion over three breeding seasons. We also compared adult necrophagous insect communities on the island with those on the adjacent mainland to determine whether nearshore islands might exert filtering effects on the carrion insect community composition. We discuss our results in light of potential island biogeography factors and evolutionary specialisation of some insect species to seabird carrion, and highlight the unique entomofauna exploiting coastal environments compared with those in the more frequently studied urban or inland rural habitats.

METHODS

Study site

We conducted our study on Big Island (traditionally Booirodoong, Dharawal custodians), Five Islands Group, NSW, Australia, which is located approximately 500 m offshore from the mainland (34°29′24″S 150°55′42″E). Big Island is the largest of the Five Islands Group, with an area of 19.8 ha, of which 10.7 ha is vegetated (Carlile et al. 2017). Since 1960, the island has been designated a nature reserve and is closed to the public. Several species of seabirds use the island as a seasonal breeding colony including silver gulls, crested terns [*Thalasseus bergii* (Lichtenstein, MHC, 1823)], Australian pelicans (*Pelecanus conspicillatus* Temminck, 1824), Australian white ibis [*Threskiornis Molucca* (Cuvier, 1829)], little penguins [*Eudyptula minor* (Forster, 1781)], wedge-tailed shearwaters [*Ardenna pacifica* (Gmelin, JF, 1789)], short-tailed shearwaters [*Ardenna tenuirostris* (Temminck, 1836)], white-faced storm petrels [*Pelagodroma marina* (Latham, 1790)], and sooty oystercatchers (*Haematopus fuliginosus* Gould, 1845) (Carlile et al. 2017). The only other vertebrate inhabiting the island is the resident eastern water skink [*Eulamprus quoyii* (A.M.C. Duméril & Bibron, 1839)], with no mammals reported (Carlile et al. 2017). The most abundant species is the silver gull, with an estimated 3000 breeding pairs during the breeding season (Carlile et al. 2017). Silver gulls lay eggs in August and rear chicks between September and February, with adult and chick mortalities largely related to intraspecific aggression observed throughout chick rearing (Hoye unpublished data).

Sampling

Sampling of gull carcasses occurred on the island over three consecutive breeding seasons (2020, 2021 and 2022). Each breeding season, the gull colony was visited every 7–10 days from August through December to search for carcasses. Carcasses of gulls of any age (adult, fledging, and chick) with visible maggot masses were collected when observed [$n = 12$ (2020); 26 (2021); 16 (2022)]. Whole carcasses, individually double sealed in zip lock bags, were transported to the University of Wollongong. Carcasses were then placed in sealed rearing cages with a single mesh panel for ventilation, in a temperature-controlled room (24 ± 1°C) with a 12:12 h light/dark cycle to allow larvae to complete their

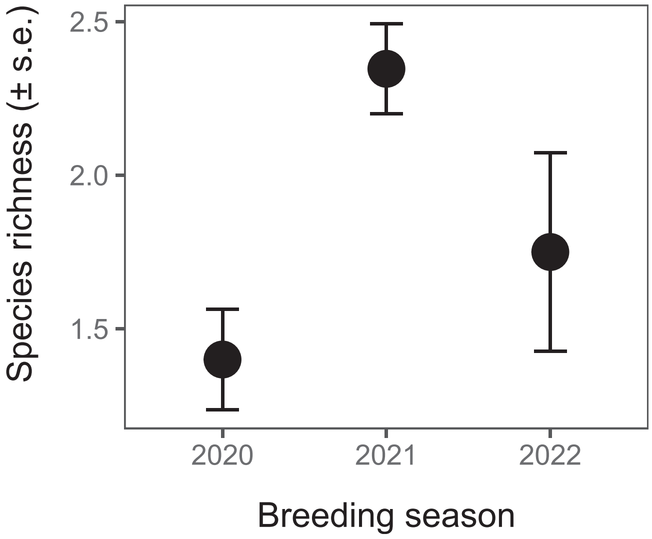

FIGURE 1 Mean larval species richness within individual gull carcasses across three breeding seasons. Error bars represent standard error.

development and pupate into adults. Adult insects were collected and identified to species level where possible using taxonomic keys (Johnston et al. 2025a; Norris 1994; Wallman 2001a, 2001b), such that a complete list of species was recorded for each carcass.

To determine the assemblage of adult carrion breeding species present during the gull breeding season on the island and adjacent mainland we used baited West Australian blowfly traps (Vogt & Havenstein 1974) to sample adult insects. A pair of traps (one on the mainland, and the other on the island) were placed on the 9th September 2021, 2nd December 2021, and 8th November 2022. The mainland traps were placed at Hill 60 (34°29′31″S 150°55′00″E), located approximately 1 km from the Big Island traps (200 m inland). All traps were baited with 500 g of kangaroo mince mixed with 50 ml of water and 5 g of sodium sulfide. This combination is known to successfully attract necrophagous flies (Kavazos & Wallman 2012). Traps were left on site for 1 week and all captured flies were identified to species level where possible using the taxonomic resources described above.

Data analysis

Species richness of insect larvae collected from gull carcasses was compared between breeding seasons using a linear model from the R base package version 4.2.3 (R Core Team 2021; Available from: https://www.R-project.org/) and model performance was assessed using the performance package version 0.11.0 (Lüdecke et al. 2021). A pairwise comparison was conducted to compare the different breeding seasons using the multcomp package version 1.4.23 (Hothorn, Bretz, & Westfall 2008). Composition of the insect species colonising gull carrion was compared across the three breeding seasons by plotting the proportion of carrion on which each insect species was present. Adult community composition collected in the traps was visualised as average abundance of each species across all sampling periods using heatmaps. All plots were created using the ggplot2 package version 3.5.0 (Wickham 2016) and all analyses and plotting were conducted in R.

RESULTS

The larvae of 12 carrion breeding insect species were detected in gull carrion over the study period, with each gull carcass found to host the larvae of between one and five species. Average species richness within a carcass differed between breeding seasons ($F_{[2,\ 54]} = 5.61$, $p = 0.006$) (Figure 1), with significantly more species observed on individual carrion in 2021 (2.35 mean ± 0.15 s.e.) compared with 2020 (1.4 mean ± 0.16 s.e.; $p < 0.01$). There was no significant difference in species richness on individual carrion between 2020 and 2022 (1.75 mean ± 0.32 s.e.; $p = 0.53$), or between 2021 and 2022 ($p = 0.12$).

Across all carcasses, *Calliphora maritima* Norris 1994 was the most frequently collected larvae with the larvae of this species being present in 80–96% of carcasses collected in all three breeding seasons (Figure 2). The second most common species differed between breeding seasons: *Sarcophaga impatiens* Walker, 1849 in 2020 (33% of carcasses), and *Calliphora augur* (Fabricus, 1775) in 2021 (85% of carcasses) and 2022 (25% of carcasses). Interestingly *Calliphora augur* was not observed in any carcasses in 2020 (Figure 2). Cumulative species richness across all carcasses within a season, and the composition of these species, also differed between breeding seasons (Figure 2). Only four of the 12 species (*Australophyra rostrata* [Robineau-Desvoidy 1830], *Calliphora maritima*, *Sarcophaga impatiens*, and the beetle *Dermestes* sp.) were observed in in all three breeding seasons. Seven of the 12 species were only observed in a single breeding season, often in a single carcass (Figure 2). In line with species richness, there were fewer total species observed within individual carrion specimens in 2020 ($n = 5$) compared with 2021 and 2022 ($n = 8$) (Figure 2).

Twenty-four species were trapped as adults across the six trapping periods. Adult fly diversity was higher in the mainland traps (Table 1), with all 24 species observed, eight of which were represented by a single individual (Figure 3). In contrast, only six species were collected from the nearshore island trap (< 1 km away). These island-trapped adults represented five of the 11 species observed breeding in gull carcasses. Surprisingly, *C. maritima* was only the third most abundant species in island traps, despite being the most common species collected from gull carcasses. In general, species trapped on

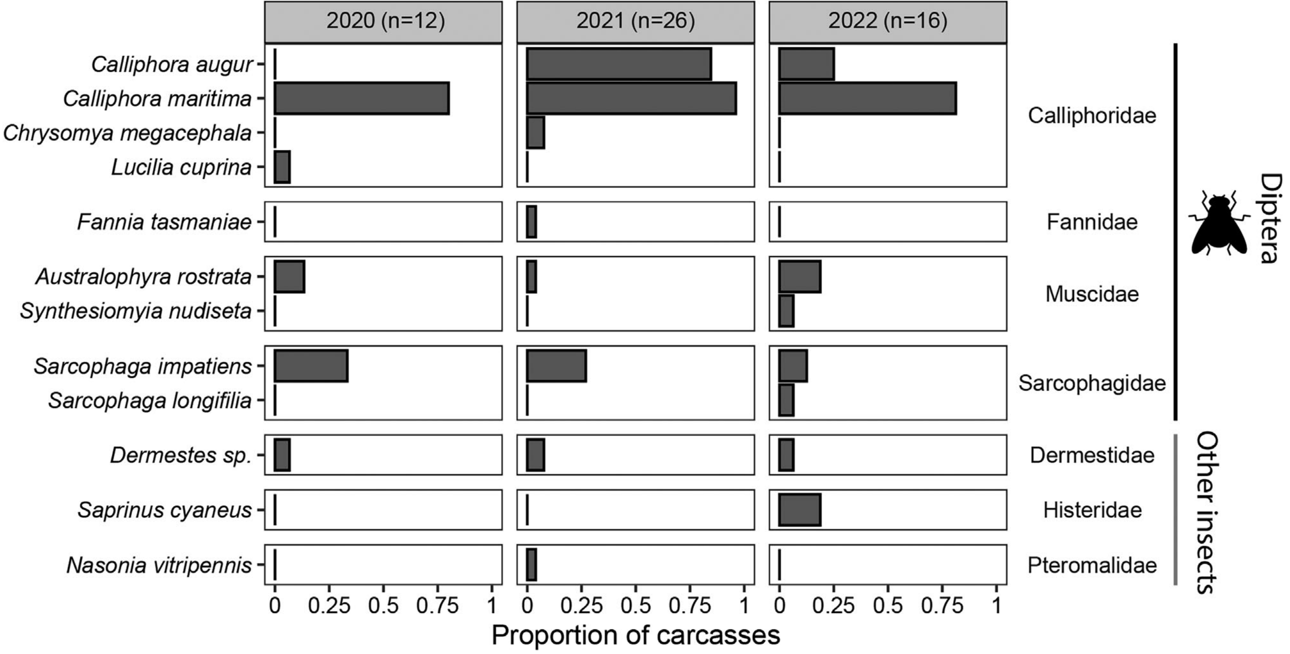

FIGURE 2 Proportion of gull carcasses in which each carrion breeding insect species was present as larvae over the three breeding seasons of sampling.

TABLE 1 Summary of annual insect community characteristics of each trapping location.

Year	Location	Species richness	Total across carcass insect abundance	Mean (± s.e.) within carcass insect abundance
2021	Island	5	83	17 ± 10
2021	Island	3	18	6 ± 4
2022	Island	5	45	9 ± 5
2021	Mainland	5	159	32 ± 27
2021	Mainland	13	273	21 ± 12
2022	Mainland	16	200	13 ± 4

the island were also the most abundant species on the mainland, with the exception of *Chrysomya varipes* (Macquart, 1851)—the second most abundant species on the mainland, but not collected in traps on the island (Figure 3). Abundance of each species was considerably lower on the island (Table 1), with fewer individuals of each collected (Figure 3).

DISCUSSION

Entomofauna of silver gull carrion

We detected 12 species of necrophagous insects using gull carrion across the three breeding seasons. These species were predominantly flies ($n = 9$) but a small number of beetle species were also represented ($n = 3$). Across all three breeding seasons, the fly *Calliphora maritima* was the most common insect species collected from silver gull carrion, an unsurprising result given that it is confined to littoral environments in southern Australia (Norris 1994). This study is the first to identify the breeding habits of *C. maritima*, although it has been noted to be attracted to bird faeces in the past (Monzu 1977) and has also been trapped extensively at pig carrion in coastal regions of South Australia (J. F. Wallman, pers. comm.). The ubiquity of *Calliphora maritima*, present in >75% of carcasses in our study, might suggest this species is specialised on seabird carrion and potentially other coastal carrion. This hypothesis is somewhat strengthened by the presence of *C. maritima* larvae in additional carrion specimens collected during our study (one little penguin and one wedge-tailed shearwater). Our findings suggest that *C. maritima* may outcompete other locally abundant and widely effective carrion-breeding Diptera species (notably *C. augur*) for seabird carrion. It should also be noted that both *C. augur* and *C. maritima* employ an ovoviparous reproductive strategy (Johnston et al. 2025a) like many members of the *Calliphora stygia-group* sensu Johnston et al. (2025b), which would allow larvae to quickly colonise carcasses. Interestingly this study also demonstrated seabird carrion use in another fly species with previously unknown carrion-breeding behaviour—*Fannia tasmaniae* Pont, 1977 (collected only from a single carcass in 2021). Collectively, these observations highlight the unique entomofauna exploiting coastal environments and seabird carrion compared to the more frequently studied

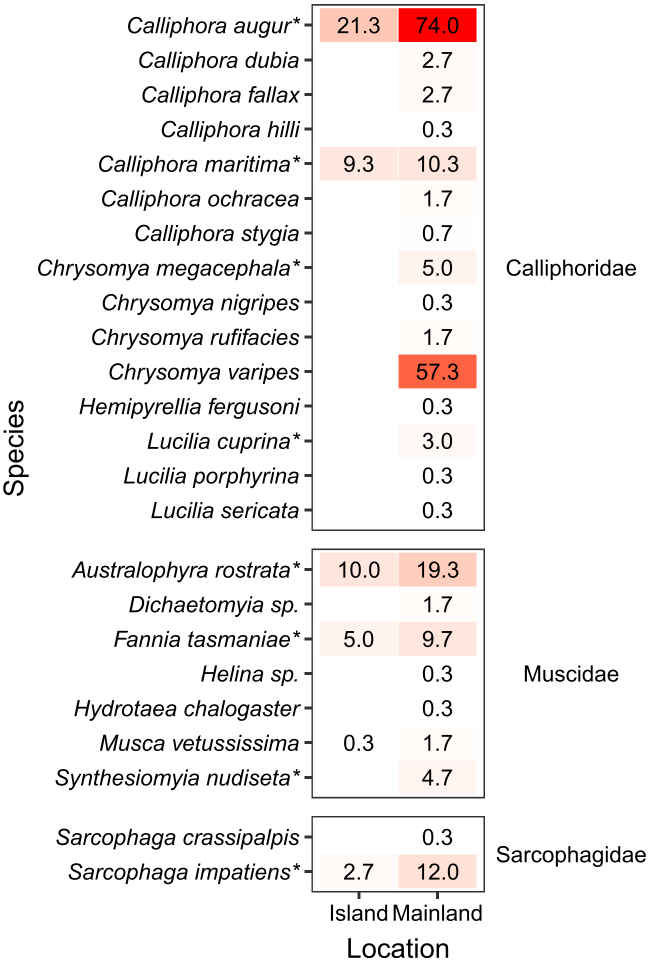

FIGURE 3 Average number of adult flies collected over three sampling periods for the island and mainland necrophagous fly traps. *Represents species that were also collected as larvae from gull carcasses.

urban or inland rural habitats. While other necrophagous species were able to successfully colonise the gull carrion on the island (e.g., the flies: *A. rostrata*, *Lucilia cuprina* [Wiedemann, 1830] and *S. impatiens*), their presence varied between seasons with some species being frequent colonisers in one or two breeding seasons and completely absent in others. Of the 12 species observed breeding in the gull carcasses, half were observed in only a single breeding season and in their respective seasons only in a small proportion of carcasses (<20%). Thus, while these species can breed in seabird carrion it appears far less common and thus these species might represent rare and transient visitors to the island. The other beetle and wasp species collected during this study (*Saprinus cyaneus* (Fabricius, 1775), *Nasonia vitripennis* (Walker, 1836) and *Dermestes* sp.) would not have been easily collected using our trapping method, so the colonisation of the island by these species remains untested.

Considerable variation in community composition was observed between breeding seasons in this study. This could potentially be attributed to factors such as rainfall or temperature which varied between years, with 2022 being particularly wet early in the breeding season (more than double the rainfall seen in 2020 and 2021 in September and October; supplementary material Table S1). Studies of the abundance of stable flies (Muscidae) in California, USA, have shown a positive correlation between rainfall and fly abundance (Mullens & Peterson 2005). However, similar studies of the effect of climate variation on fly abundance in New Zealand showed no strong effect of rainfall on species abundance instead showing that daily minimum temperature was the strongest predictor of abundance (Henning et al. 2005).

Variation between island and mainland carrion breeding fly communities

Despite using a common bait (kangaroo mince) and trap sites being separated by only ~1 km, the diversity and abundance of adult flies varied dramatically between the island and mainland. Only six of the 24 species detected in the mainland traps were collected on the island. Although the majority of the species detected in our mainland traps were similar to a study of blowfly community composition across an urban gradient completed in the Sydney region (~50 km north of the Illawarra region) in 2010, our mainland trap collected three species (*C. maritima*, *C. fallax* Hardy, 1930 or *C. dubia* [Macquart, 1855]) that were not seen in any of their trapping locations ($n = 12$), despite some of these sites being within 1–2 km of the ocean (Kavazos & Wallman 2012). We have also studied the local species composition of carrion breeding blowflies attracted to traps using a similar bait (sheep liver instead of kangaroo mince) at the University of Wollongong (approximately 2 km inland; 10 km from Big Is.), finding similar species composition to the mainland traps with very low occurrence of *C. maritima* and instead domination by *C. fallax* and *Calliphora ochracea* Schiner, 1868 (Figure S1).

Reduced diversity on the island may indicate the ocean could be acting as a dispersal barrier, preventing the flies from accessing the island. Because 1–5 km is considered well within the flight range of most species of flies (Evans, Wallman, & Barton 2020; Norris 1965), it may be that the ocean presents additional barriers beyond distance alone. Open water could be more difficult for some fly species to navigate, particularly as there is no shelter from environmental conditions such as high wind and few navigational cues. Similarly, with the presence of waves and mist, the ocean could also be obscuring the detection of volatile organic compounds (VOCs) produced by carrion resources and be masking the attractiveness of the island to the flies. The island itself also has much less shelter than the mainland, with no large structures, only small vegetation (less than 2 m maximum height) and no sources of fresh water. It is also worth noting that the small land mass of the island in combination with the abundance of gull carcasses would act to reduce the patchiness of carrion resources available to carrion-breeding flies. Low resource patchiness has been shown in previous studies to reduce species diversity in competitive carrion-breeding fly communities (Kouki & Hanski 1995).

Island-specialist blowflies

The most common species detected breeding in the gull carrion, *C. maritima*, represents only a small part of a diverse range of blowfly species that have experienced specialisation and radiation across island environments. The blowfly genus *Xenocalliphora*, is endemic to New Zealand where it is known from two littoral species present on the mainland, however, a further eight species are known from eight separate islands surrounding the New Zealand mainland (Dear 1986). A similar phenomenon has also been observed in some other *Calliphora* species in Australia, whereby islands such as Norfolk Is. and Lord Howe Is. each have their own unique endemic species (*Calliphora norfolka* Kurahashi, 1971 and *Calliphora lordhowensis* Kurahashi, 1987, respectively). These species all are likely to employ a necrophagous life history like mainland blowflies however, no comprehensive study has investigated their feeding biology.

It is possible that species that dominate island environments are restricted to bird carrion as a breeding substrate. No endemic New Zealand blowfly species have been able to establish a successful Australian population despite several introduction events (Dear 1985), but conversely several Australian blowflies (i.e., *Calliphora stygia* Fabricus, 1782 and *Calliphora hilli* Patton, 1925) have successfully invaded mainland New Zealand and are now widespread. This directionality in invasion success could be attributed to the specialisation of endemic fauna to the unique characteristics of the carrion resources available in these different countries. Unlike Australia, New Zealand was historically dominated by birds and has no native mammals or marsupials. As such, it might be expected that the New Zealand native carrion-breeding flies have evolved to be specialist necrophages in bird carrion. This specialisation would then limit their invasion success in Australia where carrion resources tend to be dominated by mammals and marsupials. From the other perspective, Australian endemic carrion breeding flies would have had a broader range of carrion resources and as such are more likely to be generalists and exploit the full range of carrion resources in New Zealand, particularly since agriculture and the introduction of game stock have changed the faunal landscape of this country since European colonisation.

CONSERVATION IMPLICATIONS AND CONCLUSION

This study shows the considerable variation in carrion-associated Diptera communities between mainland and island habitats. Our results suggest that flies exploiting seabird carrion may have developed specialisation to this resource as they do not mirror assemblages on mainland vertebrate carrion both in the Illawarra (Figure S1) and greater Sydney regions (Kavazos & Wallman 2012). Understanding the unique Diptera fauna inhabiting island communities is of critical importance to both identification and conservation. For example, some blowflies are significant agricultural pests, such as *C. stygia*, *C. augur* and *L. cuprina*, which cause myasis in sheep (Heath & Bishop 2006; Watts et al. 1976) and are actively targeted by eradication programmes. *Calliphora maritima* is difficult to distinguish from other *Calliphora* species (differing only in minor coloration differences and of the placement of setae on the thorax) and could be incorrectly targeted, wasting management resources and potentially eliminating a valuable specialist decomposer.

This study demonstrates that an island separated by less than 500 m from the mainland can harbour distinct carrion-breeding fly assemblages. These assemblages vary between years but are notably dominated by the littoral species *C. maritima*. Future research is needed to identify the environmental, biological and physical factors that shape the unique community structures on islands, as this would provide further insight into the barriers influencing the evolution, speciation, and specialisation of insects in these habitats.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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

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