Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Insect Science

The importance of scavenging in ant invasions

David A Holway[1] and Erin K Cameron[2]

Recent work underscores that ants are highly proficient and ubiquitous scavengers. These tendencies extend to numerically and behaviorally dominant introduced ants, which exhibit a suite of traits that allow them to exploit and monopolize carrion to a greater extent than is widely appreciated. We thus contend that an understanding of how introduced ants fit into food webs remains incomplete. Monopolization of carrion resources by introduced ants could increase worker production, enhance the ability of these species to compete with and prey upon other organisms, and alter the strength of direct and indirect interactions within food webs. Future work should consider how ant invasions influence energy transfer within and between green and brown food webs.

Addresses
[1] Division of Biological Sciences, University of California at San Diego, MC 0116, 9500 Gilman Drive, La Jolla, CA 92093, United States
[2] Department of Environmental Science, Saint Mary's University, 923 Robie Street, Halifax, Nova Scotia B3H 3C3, Canada

Corresponding author: Holway, David A (dholway@ucsd.edu)

Current Opinion in Insect Science 2021, **46**:39–42

This review comes from a themed issue on **Social insects**

Edited by **Michael Goodisman** and **Brendan Hunt**

https://doi.org/10.1016/j.cois.2021.01.007

Invasions by non-native species can disrupt trophic interactions and ecosystem functioning. Many studies on invasion impacts focus on the roles of competition and predation [1], while the effects of scavenging are less well known [2]. This limitation reflects a general inadequacy in food web ecology. The importance of scavenging, the consumption of non-living, animal matter [2], appears underappreciated in terms of how it influences energy flow and the strength of biotic interactions within food webs [2–5,6••]. This lack of understanding reflects difficulties in observing trophic interactions and the fact that scavenging, unlike predation, has no direct demographic effect on populations of organisms that are consumed [2]. In this review we focus on the importance of scavenging in ant invasions. Although previous reviews address the ecological effects associated with these invasions in detail [7–11], we argue here that an understanding of ant invasions is incomplete given that introduced ants, which typically act both as scavengers and predators, link together green food webs (primary producers, herbivores, and their consumers) and brown food webs (detritus, decomposers, and their consumers).

Why is scavenging important to ants?

Ants as a whole exhibit considerable trophic diversity and include species that are specialized predators of other arthropods [12]. Many ant species, however, act as scavenging predators that opportunistically consume living (prey) and dead (carrion) animal matter [12,13]. Although general features of the diets of such species seem obvious, quantifying exactly what these ants eat and how they obtain their food presents a greater challenge. A colony's workers can simultaneously forage in multiple locations, remain active day and night, feed extensively on liquids, and exchange food with brood and other workers inside concealed nests. Recent work, however, indicates that scavenging by ants may be more common than previously recognized and that these insects are highly proficient scavengers. In a recent literature review, for example, Eubanks *et al.* [14••] found that scavenging of vertebrate carrion by ants was exhibited by species in all major subfamilies and by all of the most geographically widespread, behaviorally dominant introduced species. Carrol and Janzen [13] also emphasized the importance of scavenging by ants, especially for species that produce small workers, use pheromone-based recruitment, and display aggressive behavior against competitors. Introduced ant species that are behaviorally dominant (i.e. species that consistently exhibit aggressive behavior towards individuals from other colonies), exemplify these traits and, coupled with their tendency to form decentralized colonies made up of multiple, interconnected nests [7], seem well suited to both exploit and monopolize carrion resources.

Carrion represents a valuable resource to ants because of its nutritional composition and its availability. Carrion is efficiently assimilated (i.e. it has a high consumption efficiency) because of its stoichiometric similarity not only to prey but to scavengers themselves [2]. Although the removal of carrion from the environment will expose scavenging ants to competitors, enemies and stressful physical conditions, obtaining carrion does not entail costs associated with killing prey [2], which for ants would include worker injury and mortality. Moreover, the abundance of invertebrates in most terrestrial ecosystems and the high turnover rate of these populations would suggest that invertebrate carrion inputs alone would constitute a highly valuable resource in terms of biomass. In addition, some types of invertebrates (e.g. large bodied species, insects that are strong fliers) and most vertebrates would be impossible for ants to capture as prey but would be available for consumption by ants as carrion.

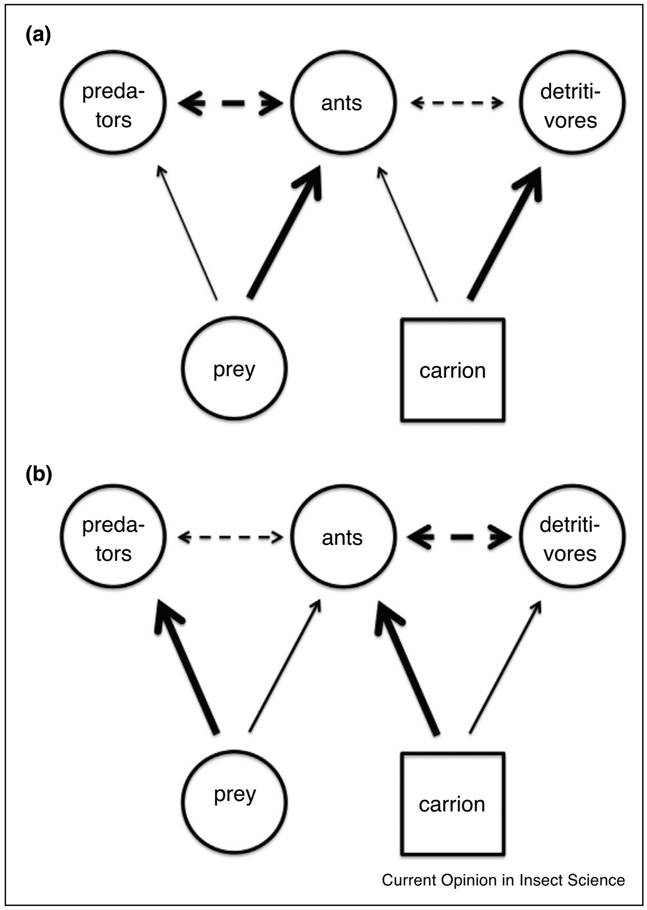
Why is scavenging by ants important?

Ants readily scavenge carrion. The implicit value of insect carrion in particular is reflected in the common use of dead insects as a means to study ant foraging behavior. Insect carrion, for example, has been used to examine how the size of insect carcasses influences the likelihood of carrion removal [15,16] and which species prevail in the face of interspecific competition [17]. Small-scale field studies that track removal of insect carcasses consistently find that ants discover and retrieve this type of resource more quickly and to a greater extent compared to other scavengers [18–21]. Young [15] and Seastedt *et al.* [22] reached similar conclusions but did not explicitly quantify the relative importance of ants versus other types of consumers. The broadly consistent findings of these studies, combined with the span of latitudes and environments considered, suggest that ants remove (and presumably consume) most insect carrion from terrestrial environments. Although quantitative estimates of carrion inputs are in general lacking [6••], arthropod carrion likely makes up a major fraction of animal carrion in most terrestrial ecosystems [4,6••,23].

Consumption of vertebrate carrion by ants must also be important [14••], but ants compete for this type of resource with scavenging vertebrates and with carrion-feeding insects. Rapid recruitment of nestmates to vertebrate carcasses may give ants an early advantage over competitors (Eubanks *et al.* [14••]), and colony satiation may occur at large carcasses. The relative importance of ants as scavengers was dramatically illustrated by Griffiths *et al.* [24••], who combined large-scale, ant removal experiments with vertebrate exclosures to estimate the scavenging ability of ants, non-ant arthropods, and vertebrates in Malaysian rainforests. Using baits (dried fish, biscuits, and sunflower seeds) to estimate scavenging ability, Griffiths *et al.* [24••] found that ants removed more than half of all baits and reduced the abundance of most other scavenging arthropods present. While baits may not perfectly emulate carrion, the results of this study clearly demonstrate the potential capacity of ants to exploit and monopolize carrion resources.

Given compelling evidence that ants are important consumers of carrion, their role as detritivores (*sensu* [6••]) should be more widely acknowledged [14••,24••]. Although quantifying the amount of resources that ants consume through predation versus scavenging is difficult, energy flow to ants from detrital resources appears common and could lead to overestimates of the energy obtained by these insects through predation (Figure 1). The effects of scavenging and predation on ant colonies may also interact; increased worker production resulting from carrion consumption could enhance the ability of ants to prey upon other species. Wilson & Wolkovich [2] argue that such interactions can be considered a form of apparent competition in which carrion and populations of prey are linked through a shared consumer (Figure 1). A possible example of this type of interaction comes from observations of ants not only feeding on carrion but also preying upon carrion-feeding insects at the same time, sometimes to such a degree that ants slow the rate of decomposition [6••,14••]. In cases where carrion

Figure 1



Alternative views of the importance of scavenging by ants. **(a)** Ants primarily act as predators and occasionally scavenge carrion. In this first scenario, ants compete strongly with predators but weakly with detritivores, which consume the majority of carrion resources. **(b)** Ants primarily act as scavengers and only occasionally prey on living organisms. In this second scenario, ants and detritivores strongly compete for carrion. In both (a) and (b), prey and carrion are linked to one another through a shared consumer (ants). Introduced ants that act as scavenging predators and that attain high densities could simultaneously compete strongly with both predators and detritivores. One-way arrows indicate interactions between resources and consumers; two-way dashed arrows indicate competitive interactions. Arrow width indicates interaction strength. Modified from Wilson and Wolkovich [2] and Moleón *et al.* [5].

availability exceeds that of prey, the redistribution of dead animal matter by ants and its subsequent concentration in and around their nests could represent a key component of nutrient cycling [20].

Why is scavenging by introduced ants important to an understanding of ant invasions?

The importance of scavenging by introduced ant species has received surprisingly little attention. Small-scale studies have found that introduced ants can discover, recruit to and remove dead insects more quickly and to a greater extent compared to native ant assemblages as a whole [25–27]. These studies further reveal that introduced ants monopolize insect carrion in invaded areas but that multiple native ant species divide this resource among themselves in uninvaded areas. If introduced ants differentially acquire carrion resources in general, carrion consumption might increase invader abundance, enhance competitive ability, and magnify the ecological effects of invasions in unexpected ways. A better understanding of scavenging by introduced ant species could thus lead to a reassessment of their role in food webs.

In accordance with the evidence summarized in this review, numerically and behaviorally dominant introduced ants likely assimilate far more carrion than widely acknowledged. Unqualified assertions that introduced ants primarily act as predators may implicitly exaggerate the strength of the interaction between these ants and their prey and underestimate the amount of energy transferred to these ants via carrion (Figure 1). Wilson and Wolkovich [2] and Moleón *et al.* [5] argue further that access to carrion resources in general can lead to a variety of unexpected bottom-up and top-down feedbacks within food webs; such effects seem especially plausible for introduced ants considering that these abundant insects interact with a diversity of other species including competitors, predators, prey, and mutualists.

Monopolization of carrion resources by introduced ants could increase worker production and in turn enhance the ability of these species to compete with and prey upon other taxa. Given that ants can reduce the abundance of scavenging arthropods at baits [24••], behaviorally and numerically dominant introduced ants would seem well positioned to compete with non-ant detritivores for carrion (Figure 1). Although a handful of studies on ant invasions explicitly consider detritivory [27–30], we are aware of no study that specifically investigates competitive interactions between introduced ants and non-ant arthropod consumers of carrion. Documenting elevated predation by introduced ants as a result of their ability to monopolize carrion would likely require experimental manipulation of resources in a controlled setting but seems likely to occur in the context of ant invasions. To our knowledge, such interactions have not been documented for ant invasions but may occur as a result of yellowjacket wasp invasions in Hawaii [31]. Lastly, insofar as carrion resources elevate worker production, colony growth would itself eventually increase carrion availability in the in the form of ant carcasses. Such inputs of carrion might be especially pronounced during periods of the annual colony cycle when worker numbers naturally decline or in situations where whole infestations die off for other reasons [32]. This form of carrion recycling might reduce the value of carrion as a resource given that ant carcasses are small and rich in chitin.

How do introduced ants fit into food webs?

Despite considerable attention devoted to the study of ant invasions, we submit that an ecological understanding of these invasions remains hindered by a lack of information about the relative importance of predation versus scavenging. Moreover, stable isotope analysis, molecular analysis of gut contents, and buffet experiments, while providing valuable information about diet composition and nutrient preferences, don't — in and of themselves — differentiate between resources obtained through predation versus scavenging [2]. Results of stable isotope analyses, in particular, have a high potential for misinterpretation given that trophic positions of known herbivores and predators are often quantitatively compared to those of focal ant species that can act in part as predators but that also acquire considerable energy from carrion (e.g. Figure 1) of unknown and variable origin. Experimental studies that address the form and magnitude of trophic interactions involving introduced ants are thus clearly needed to resolve these uncertainties.

As with the study of detrital resources generally [2,6••], the amount of carrion available to ants and the proportion that ants assimilate remain largely unknown. The evidence summarized in this review, however, suggests that the role of behaviorally dominant, introduced ant species in food webs should be re-evaluated in light of their use of carrion resources. Studies that attempt to estimate carrion inputs and the role of ants in the removal and consumption of this type of resource thus seem warranted. Future work could also focus on species interactions among detritivores and in particular focus on how the presence of numerically and behaviorally dominant introduced ants influences the rate and degree of energy transfer within and between green and brown food webs. Moreover, studies that consider how the importance of scavenging differs among introduced ant species or changes with latitude (e.g. Ref. [33]) could be used to forecast the effects of ant invasions in terms of the use of carrion resources. Clarifying these issues seems important given that carrion resources [34] and ant invasions [35,36] can each have surprising and far-reaching effects on ecosystem structure and function. Moreover, ant invasions as a whole will continue to increase in geographical extent given expansions in global commerce and increasing human modifications to the environment.

Conflict of interest statement

Nothing declared.

Acknowledgements

Funding for this research was provided by the National Science Foundation Long-term Research in Environmental Biology 1654525 (DAH). M.D. Eubanks and E.G. LeBrun provided helpful comments on the manuscript.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

•• of outstanding interest

1. Blackburn TM *et al.*: **A unified classification of alien species based on the magnitude of their environmental impacts**. *PLoS Biol* 2014, **12**:e1001850.

2. Wilson EE, Wolkovich EM: **Scavenging: how carnivores and carrion structure communities**. *Trends Ecol Evol* 2011, **26**:129-135.

3. DeVault TL, Rhodes OE, Shivik JA: **Scavenging by vertebrates: behavioural, ecological, and evolutionary perspectives on an important energy transfer pathway in terrestrial ecosystems**. *Oikos* 2003, **102**:225-234.

4. Barton PS, Cunningham SA, Lindenmayer DB, Manning AD: **The role of carrion in maintaining biodiversity and ecological processes in terrestrial ecosystems**. *Oecologia* 2013, **171**:761-772.

5. Moleón M, Sanchez-Zapata JA, Selva N, Donazar JA, Owen-Smith N: **Inter-specific interactions linking predation and scavenging in terrestrial vertebrate assemblages**. *Biol Rev* 2014, **89**:1042-1054.

6. •• Benbow ME, Barton PS, Ulyshen MD, Beasley JC, DeVault TL, Strickland MS, Tomberlin JK, Jordan HR, Pechal JL: **Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter**. *Ecol Monogr* 2019, **89**:e01331.

This comprehensive review synthesizes current knowledge about the ecological importance of decomposition. The authors make an appeal for bridging disciplines that relate to decomposition ecology so that its central importance is more widely acknowledged.

7. Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ: **The causes and consequences of ant invasions**. *Annu Rev Ecol Syst* 2002, **33**:181-233.

8. Lach L: **Invasive ants: unwanted partners in ant-plant interactions?** *Ann Missouri Bot Garden* 2003, **90**:91-108.

9. Ness JH, Bronstein J: **The effects of invasive ants on prospective ant mutualists**. *Biol Invasions* 2004, **6**:445-461.

10. Lach L, Hooper-Bui LM: **Consequences of ant invasions**. In *Ant Ecology*. Edited by Lach L, Parr CL, Abbott KL. Oxford University Press; 2010:261-286.

11. Cameron EK, Vilà M, Cabeza M: **Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems**. *Glob Ecol Biogeogr* 2016, **25**:596-606.

12. Ward PS: **Ants: a primer**. *Curr Biol* 2006, **16**:R152-R155.

13. Carroll CR, Janzen DH: **Ecology of foraging by ants**. *Annu Rev Ecol Syst* 1973, **4**:231-257.

14. •• Eubanks MD, Lin C, Tarone AM: **The role of ants in vertebrate carrion decomposition**. *Food Webs* 2019, **18**:e00109.

This literature review summarizes what is known about the importance of scavenging by ants on vertebrate carrion. The authors make a compelling case for this form of detritivory being phylogenetically widespread among ants and ecologically important.

15. Young OP: **Utilization of dead insects on the soil surface in row crop situations**. *Environ Entomol* 1984, **13**:1346-1351.

16. Traniello JFA, Fujita MS, Bowen RV: **Ant foraging behavior: ambient temperature influences prey selection**. *Behav Ecol Sociobiol* 1984, **15**:65-68.

17. Cerda X, Retana J, Cros S: **Prey size reverses the outcome of interference interactions of scavenger ants**. *Oikos* 1998, **82**:99-110.

18. Fellers GM, Fellers JH: **Scavenging rates of invertebrates in an eastern deciduous forest**. *Am Midl Nat* 1982, **107**:389-392.

19. Retana J, Cerda X, Espadaler X: **Arthropod corpses in a temperate grassland: a limited supply?** *Holartic Ecol* 1991, **14**:63-67.

20. Bestelmeyer BT, Wiens JA: **Scavenging ant foraging behavior and variation in the scale of nutrient redistribution among semi-arid grasslands**. *J Arid Environ* 2003, **53**:373-386.

21. Tan CKW, Corlett RT: **Scavenging of dead invertebrates along an urbanization gradient in Singapore**. *Insect Conserv Divers* 2012, **5**:138-145.

22. Seastedt TR, Mameli L, Gridley K: **Arthropod use of invertebrate carrion**. *Am Midl Nat* 1981, **105**:124-129.

23. Lavelle P *et al.*: **Soil function in a changing world: the role of invertebrate ecosystem engineers**. *Eur J Soil Biol* 1997, **33**:159-193.

24. •• Griffiths HM, Ashton LA, Walker AE, Hasan F, Evans TA, Eggleton P, Parr CL: **Ants are the major agents of resource removal from tropical rainforests**. *J Anim Ecol* 2017, **87**:293-300.

These authors performed a novel and ingenious field experiment that combined large-scale ant removals with vertebrate exclosures to estimate the scavenging ability of ants, non-ant arthropods, and vertebrates in Malaysian rainforests. Their results clearly demonstrate the potential capacity of ants to exploit and monopolize carrion resources.

25. Porter SD, Savignano DA: **Invasion of polygyne fire ants decimates native ants and disrupts arthropod community**. *Ecology* 1990, **71**:2095-2106.

26. Baur ME, Kaya HK, Strong DR: **Foraging ants as scavengers on entomopathogenic nematode-killed insects**. *Biol Control* 1998, **12**:231-236.

27. Angulo E, Caut S, Cerda X: **Scavenging in Mediterranean ecosystems: effect of the invasive Argentine ant**. *Biol Invasions* 2011, **13**:1183-1194.

28. Dunham AE, Mikheyev AS: **Influence of an invasive ant on grazing and detrital communities and nutrient fluxes in a tropical forest**. *Divers Distrib* 2010, **16**:33-42.

29. LeBrun EG, Abbott J, Gilbert LE: **Imported crazy ant displaces imported fire ant, reduces and homogenizes grassland ant and arthropod assemblages**. *Biol Invasions* 2013, **15**:2429-2442.

30. Milligan PD, Prior KM, Palmer TM: **An invasive ant reduces diversity but does not disrupt a keyecosystem function in an African savanna**. *Ecosphere* 2016, **7**:e01502.

31. Wilson EE, Holway DA: **Multiple mechanisms underlie displacement of solitary Hawaiian Hymenoptera by an invasive social wasp**. *Ecology* 2010, **91**:3294-3302.

32. Lester PJ, Gruber MAM: **Booms, busts and population collapses in invasive ants**. *Biol Invasions* 2016, **18**:3091-3101.

33. Jeanne RL: **A latitudinal gradient in rates of ant predation**. *Ecology* 1979, **60**:1211-1224.

34. Yang LH: **Periodical cicadas as resource pulses in North American forests**. *Science* 2004, **306**:1565-1567.

35. O'Dowd D, Green P, Lake P: **Invasional "meltdown" on an oceanic island**. *Ecol Lett* 2003, **6**:812-817.

36. Riginos C, Karande MA, Rubenstein DI, Palmer TM: **Disruption of a protective ant-plant mutualism by an invasive ant increases elephant damage to savanna trees**. *Ecology* 2015, **96**:654-661.