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Ecosystem services provided by aculeate wasps

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ABSTRACT

The aculeate wasps are one of the most diverse and speciose insect taxa; they are omnipresent across ecosystems and exhibit diverse co-evolutionary and exploitative associations with other organisms. There is widespread conjecture that aculeate wasps are likely to perform essential ecological and economic services of importance to the health, well-being and nutritional needs of our planet. However, the scope and nature of the ecosystem services they provide are not well understood relative to other insect groups (e.g. bees, butterflies, beetles); an appreciation of their value is further tarnished by their public reputation as pointless pests. Here, we conduct the first comprehensive review of how aculeate wasps contribute to the four main areas of ecosystem services: regulatory, provisioning, supporting and cultural services. Uniting data from a large but previously disconnected literature on solitary and social aculeate wasps, we provide a synthesis on how these insects perform important ecosystem services as parasites, predators, biological indicators, pollinators, decomposers and seed dispersers; and their additional services as a sustainable alternative to meat for human consumption, and medicinal potential as sources of research leads for anti-microbials and cancer treatments. We highlight how aculeate wasps offer substantial, but largely overlooked, economic benefits through their roles in natural pest management and biological control programs. Accordingly, we provide data-driven arguments for reasons to consider the ecosystem service value of aculeate wasps on a par with other 'useful' insects (e.g. bees). Finally, we provide a research roadmap identifying the key areas of research required to capitalise better on the services provided by these important insects.

Key words: stinging wasps, economic value, biological control, predation, pollination

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> "*It really is unfortunate that one relatively small group of wasps should taint not only their own good work as predators, but also the work of thousands of solitary wasp species around the world.*"
> (Grissell, 2010)

I. INTRODUCTION

The natural world (from organisms to ecosystems) provides functions and goods – known as ecosystem services (ESs) – that are of value to society by supporting either directly or indirectly the quality of human life (Harrington *et al.*, 2010). These processes are broadly categorised into four types of services: (*i*) regulating services – i.e. regulation of ecosystems and ecosystem processes; (*ii*) provisioning services – i.e. material or energy outputs which can be gained directly from ecosystems; (*iii*) supporting services – i.e. helping maintain other ESs; and (*iv*) cultural services – i.e. where ecosystems play important roles in education, recreation or conservation (MEA, 2005). Insects represent one of the largest and most biodiverse groups in the animal kingdom and are renowned for their contributions to all four categories of ESs (Losey & Vaughan, 2006; Noriega *et al.*, 2018); for instance, 88% of angiosperm plants are pollinated by insects (Ollerton, Winfree & Tarrant, 2011), and the pollination services provided by insects are estimated to be worth over \$250billion/year worldwide (IPBES, 2016). Recently, these services have been linked directly to the Sustainable Development Goals (Dangles & Casas, 2019), reaffirming their importance for human welfare, health and provision.

Despite this, there is a severe taxon bias in research efforts to understand insect ESs (Donaldson *et al.*, 2017): for example, almost 30% of all publications on insect ESs over the last 50 years have been on the Hymenoptera (bees, wasps, ants, and sawflies) (Noriega *et al.*, 2018). This is unsurprising since the Hymenoptera are one of the most species-rich insect orders on earth, with over 150000 described species (Aguiar *et al.*, 2013). At a finer taxonomic level within this group, however, further taxon biases are apparent: the majority of studies focus on ESs provided by bees (Noriega *et al.*, 2018) and their role as pollinators (Klein *et al.*, 2007; Klatt *et al.*, 2014). Focussing on a specific ES overlooks taxonomic groups with more generalist life histories; e.g. insects that are both nectarivorous (thus providing pollination) and carnivorous (thus providing pest regulation). We lack an understanding of the functional roles for many of the other insects within ecosystems, how they contribute to ESs, and how anthropogenically driven changes in their populations will impact the services they provide (Noriega *et al.*, 2018).

Here we provide the first comprehensive review on the scope and nature of ESs provided by one such understudied insect group – the stinging (aculeate) wasps (Sumner, Law & Cini, 2018); this includes the non-social (solitary) aculeate wasps (excluding the relatively well-studied parasitoid wasps (non-aculeate) - previously known as the paraphyletic order Parasitica, and the fig wasps) as well as the social wasps. The potential ESs provided by this group remain only loosely defined (Elizalde *et al.*, 2020), despite accounting for ~20% of described hymenopteran species (Aguiar *et al.*, 2013). A recent review of the ESs of social insects explained the importance of the services provided by social insects but highlighted the paucity of data for specific taxonomic groups, including social wasps (Elizalde *et al.*, 2020). Consequently, the natural capital of aculeate wasps and their ESs are currently unclear and potentially under-valued. Further, assessing the ES contributions of understudied insects like aculeate wasps is especially important at a time of apparent global insect declines (Ollerton *et al.*, 2014; Outhwaite *et al.*, 2020; van Klink *et al.*, 2020).

Wasps are a paraphyletic group (Branstetter *et al.*, 2017) that account for approximately 103000 extant described species in the Hymenoptera; of these, 70% are parasitoid wasps (Aguiar *et al.*, 2013), whose roles in the regulation of agricultural pests are well recognised and reviewed extensively elsewhere (e.g. Quicke, 2015; Wang *et al.*, 2019). Here we focus on the other 33000 species of wasp – the aculeate wasps (henceforth referred to as 'wasps' for simplicity) (Fig. 1); around 1000 of these species are social (belonging to the vespid subfamilies Polistinae, Stenogastrinae and Vespinae), meaning they live in colonies. These insects suffer from poor

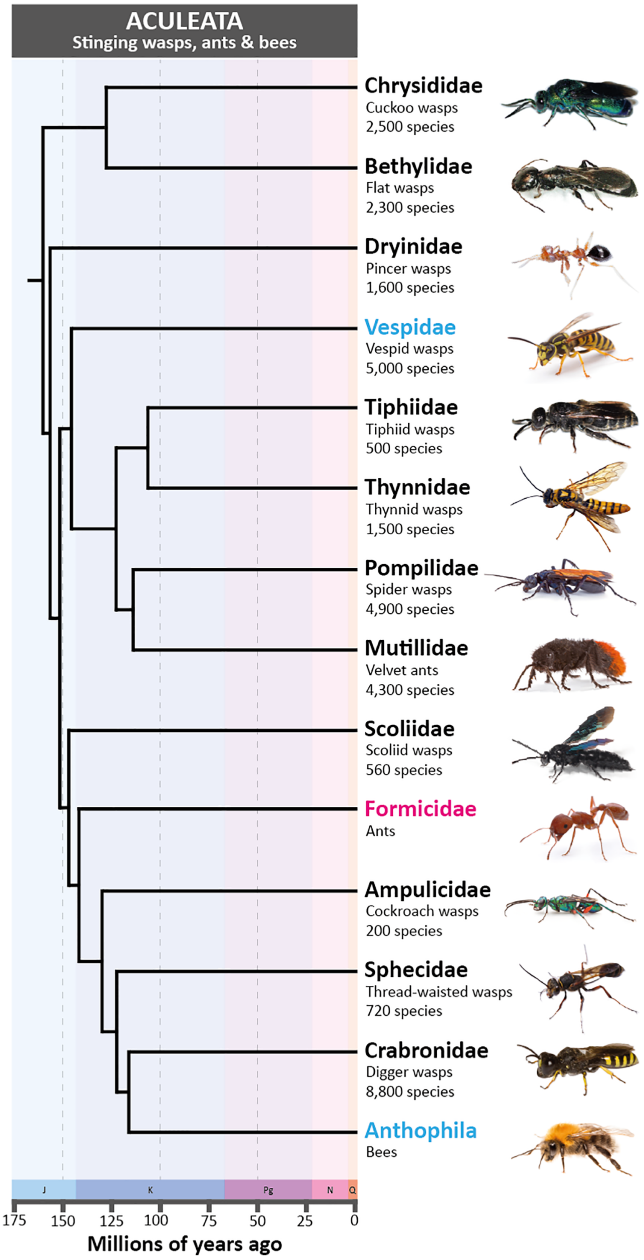

Fig. 1. Aculeate wasp diversity and their phylogenetic relationships. The aculeate wasps are a diverse, paraphyletic grouping of at least 33000 species across 22 families (Aguiar *et al.*, 2013; Branstetter *et al.*, 2017). For simplicity, this figure only includes 12 major aculeate wasp families (defined as those containing 200+ species); note that Formicidae and Anthophila are not aculeate wasps. Branch labels indicate the family name, common names (where available, taken from www.inaturalist.org), and the approximate number of species within each family. Colour of branch labels indicates the levels of social organisation found within each taxon: black, all species are solitary; blue, family includes both solitary and social species; pink, all species are social. Phylogenetic relationships are simplified from Branstetter *et al.* (2017). Photograph credits (all under CC license or used with prior permission): Chrysididae – Owen

(Figure legend continues on next column.)

public image, and even scientists are reluctant to invest research effort in them (Lester, 2018; Sumner *et al.*, 2018). As a result, their ES value remains poorly understood.

There are several reasons why it is important to review the provision of ESs by aculeate wasps. First, aculeate wasps are globally widespread, and exhibit high species richness (Fig. 1), exceeding that of other well-studied ecosystem servicing insects such as the bees and ants combined (Aguiar *et al.*, 2013). Second, the predatory value of aculeate wasps in regulating arthropod populations is largely anecdotal, lacking a synthesis of the empirical literature; and thus, the impact of aculeate wasps on natural and farmed ecosystems is currently unclear. This information is essential to motivate conservation programmes and for harnessing the ESs of these insects, as has been done very successfully for bees. Third, the ES provided by aculeate wasps through pollination of a variety of ecologically and economically important plants is almost entirely overlooked (Gess & Gess, 2010; Mello *et al.*, 2011; Akhter, Khanday & Ahmad, 2016). Fourth, to date it is the disservices – as opposed to the beneficial services – that predominate the ecological literature on aculeate wasps: they are an aggressive and destructive taxa outside of their native range, and serious pests as invasive species (Beggs *et al.*, 2011; Lester, 2018). Further, culturally, humans have an antagonistic relationship with aculeate wasps due to their propensity to sting (Sumner *et al.*, 2018; Jones, 2019). Finally, aculeate wasp populations are being affected by anthropogenic pressures in a similar way to bees (e.g. agricultural practices, habitat loss, climate change) (Dejean *et al.*, 2011; Archer, 2015; Outhwaite *et al.*, 2020).

In this review we adopt the broad-sense definition of ESs, namely, those services that support directly or indirectly the quality of human life (MEA, 2005). These include the provision of regulating services (e.g. pest control, pollination), provisioning services (e.g. human consumption, biomedical or pharmaceutical value); supporting services (e.g. decomposition, seed dispersal) and cultural services (e.g. bioindicators, recreation) (MEA, 2005; Noriega *et al.*, 2018). One review of ESs by insects identified 42 specific roles (Noriega *et al.*, 2018); another recent review of the ESs of social insects identified 10 roles (Elizalde *et al.*, 2020). Here we use the same approach to identify 10 ways through which aculeate wasps (solitary and social) provide ESs (Fig. 2; Table 1); we discuss the available evidence from extensive literature searches and provide a publicly available referenced database documenting this evidence (see online Supporting Information, Supplementary data sets S1–S6).

(Figure legend continued from previous column.)

Strickland (inaturalist); Bethylidae – B. Schoenmakers (Wikimedia commons); Dryinidae, Vespidae, Pompilidae, Mutillidae, and Formicidae – Insects Unlocked (Flickr); Tiphiidae wasp – Riley Walsh (inaturalist); Thynnidae – Ellura Sanctuary (inaturalist); Scoliidae – BenjaminT444 (Wikimedia commons); Ampulicidae – Steven Wang (inaturalist); Sphecidae – Robert Zimmermann; Crabronidae – David Evans (Flikr); Anthophila – Martin Taylor.

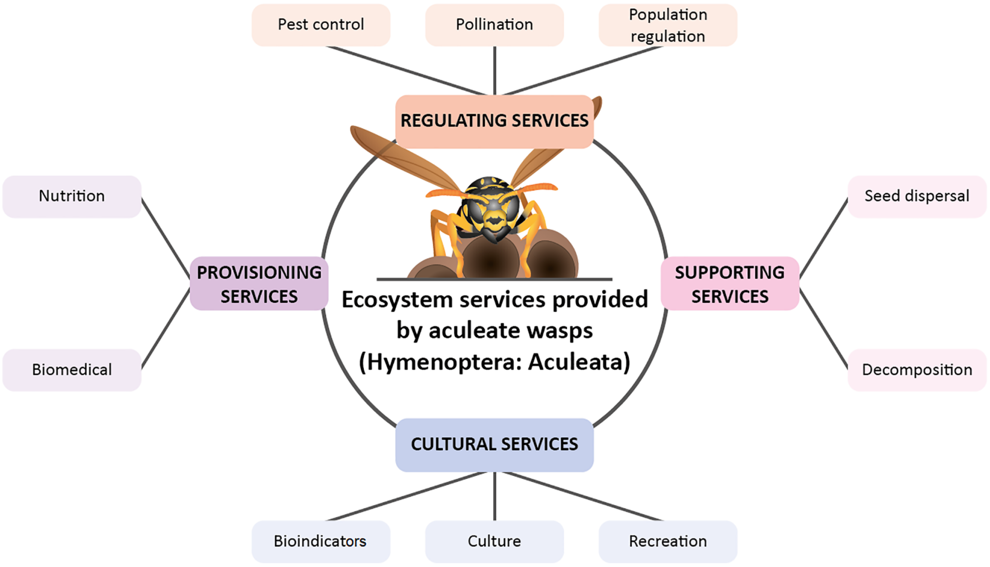

Fig. 2. Schematic overview of the ecosystem services provided by aculeate wasps. Aculeate wasps provide at least 10 ecosystem services across the four key areas of regulating, supporting, provisioning and cultural services. Evidence for each of these services is collated and synthesised in this review.

II. REGULATING SERVICES

(1) Regulation of natural arthropod populations

At least 30000 species of aculeate wasps are known to hunt a wide range of arthropods as predators or parasites (Goulet & Huber, 1993; Grissell, 2010), with impacts on arthropod populations in natural and farmed ecosystems. By regulating both carnivorous and phytophagous arthropod populations, wasps also indirectly deliver protection to invertebrate taxa and various plants lower down in food-chain networks. Limiting arthropod population growth is an essential function as arthropods can reproduce rapidly, reaching population sizes that can have detrimental effects on plant and other invertebrate taxa (Gaston & Lawton, 1988). The predatory impact of wasps is likely to be equal to or more effective than that of insectivorous birds, mammals and amphibians, as their short generation time allows them to match fluctuations in prey populations closely (Archer, 1985). Moreover, since wasps are central place foragers (delivering forage to one or more static nesting sites), they are likely to have considerable impact locally.

It is timely and important to understand the predator–prey interactions of the solitary and social wasps. Until recently, the prey of social wasps were poorly studied; recent molecular analyses of the prey captured by social wasps returning to the nest are providing new insights into the range of insect populations they help regulate (see below). Conversely, there is a vast (but largely forgotten) literature on the prey of some solitary wasp subfamilies from the early 20th century when studying wasp hunting behaviour was a popular pastime of natural historians. However, in recent years solitary wasps have received little research attention, probably because the economic, ecological or societal importance of such research is regarded as low. Here we unite these disconnected data to generate extensive data sets on the predator–prey relationships of solitary and social aculeate wasps. Importantly, our data synthesis provides an evidence base for how solitary and social wasps occupy a mix of discrete and overlapping niches in their impact on arthropod populations, and highlights the ecological diversity of aculeate wasps. Our data sets, especially for the solitary wasps, are unlikely to be exhaustive as we limited our searches to the peer-reviewed literature; we acknowledge that there are likely to be many personal observations of wasp-prey interactions by researchers and amateur naturalists in the grey literature.

(*a*) Predatory solitary wasps as regulators of arthropods

Solitary wasps represent the vast majority (~97%) of aculeate wasp diversity (Fig. 1), and, with the exception of the Masarinae subfamily (pollen provisioners), all represent predators and parasites of insect and arachnid species, many of which are phytophagous (Goulet & Huber, 1993). Typically, a female wasp will capture a prey item in her mandibles, paralyse it with her sting and transport it to her nest where an egg is laid *on* the prey item (as opposed to *inside* the prey, as in parasitoid wasps); when the egg hatches, the larva feeds off the paralysed prey. Further prey may be added as the larva develops (progressive provisioning), or more typically, the brood is provisioned with several prey items soon after the egg is laid, providing sufficient food for the brood to develop fully to pupation (mass provisioning).

We surveyed the peer-reviewed literature to generate a database on the identity of prey captured by solitary

Table 1. Summary (with examples) of the 10 ecosystem services provided by aculeate wasps.

Services		Function	Example wasp species	Life history	Example service	Reference
Regulating services	Pest control	Predation of arthropod pests of agricultural crops	*Polistes satan*	Social	Wasps observed directly feeding on fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae) and sugarcane borers, *Diatraea sacharalis* (Lepidoptera: Crambidae). Fall armyworm-infected maize plants exposed to wasps showed significantly reduced levels of pest populations and pest damage, relative to plants not exposed to wasps.	Southon *et al.* (2019)
			Polybia species	Social	Main predator of diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae) in cabbage crops in the absence of pesticides. Biocontrol by *Polybia* species produced equivalent yields and higher profit margins compared to crops in which wasp populations were reduced by pesticide usage.	Bommarco *et al.* (2011)
	Population regulation	Predation of arthropod populations in natural ecosystems	*Symmorphus cristatus*	Solitary	Main cause of mortality for the leaf beetle, *Chrysomela aeneicollis* (Coleoptera: Chrysomelidae), with each female wasp predating an average of 25 larvae for nest provision, equating to roughly 423 mg of prey biomass per nest.	Sears *et al.* (2001)
			Vespula vulgaris	Social	Social wasps exhibit highly generalist prey diets. Invasive populations in New Zealand can capture up to 4.8 million prey loads per season, equating to 8.1 kg of prey biomass per season, per hectare. This biomass intake across summer and autumn is equivalent to that of birds across the entire year.	Present study; Harris (1991)
	Pollination	Transfer of pollen between conspecific plants	Thynnidae species	Solitary	Male thynnid wasps are the sole pollinators of many orchid species, with pollination achieved through sexual deception of the male wasp.	Mant *et al.* (2002, 2005)
			Vespid species	Social	Yellow-jacket and paper wasps form widespread, adaptive and generalist pollination networks with plants.	Corlett (2001); Fateryga (2010); Mello *et al.* (2011)
			Polistes species	Social	Wasps can act as back-up pollinators when the primary pollinators of plants are not present. Visitation and pollination rates from *Polistes* species on the milkweed, *Asclepias verticillata* (Gentianales: Apocynaceae) increased significantly upon exclusion of their primary pollinators (bumblebees).	Hallett *et al.* (2017)
Supporting services	Decomposition	Breakdown and recycling of organic matter	*Vespula pensylvannica*	Social	Workers were found to scavenge on protein from dead birds, rodents and lizards, suggesting a role in decomposition and recycling.	Wilson *et al.* (2009)
	Seed dispersal	Movement of seeds away from parent plant to favourable conditions for germination	*Vespa velutina*	Social	Workers acted as the primary seed disperser of *Stemona tuberosa* (Pandanales: Stemonaceae), dispersing seeds an average of 110 m from the parent plant.	Chen *et al.* (2017)

Table 1. *(Cont.)*

Services		Function	Example wasp species	Life history	Example service	Reference
Provisioning services	Nutrition	Source of nutrition for human consumption	Vespinae and Polistinae species	Social	Larvae and pupae of social wasps are an important source of nutrition across at least 19 countries. Wasp nests sell for up to US$100 per kilogram at markets, and wasp-rearing represents a livelihood and income source for farmers.	Present study; Nonaka (2010)
	Biomedical	Production of compounds with medicinal potential	*Polybia dimorpha*	Social	Venom component Polydim-I, has anti-microbial activity against the human pathogen *Mycobacterium abscessus* (Actinomycetales: Mycobacteriaceae).	Das Neves *et al.* (2016)
			Vespinae species	Social	Mastoparan, a peptide isolated from the venom of yellow-jacket wasps, shows promise for combatting cancer.	Yamada *et al.* (2005); Moreno *et al.* (2014)
Cultural services	Bioindicators	Organism's presence used to indicate ecosystem quality	Sphecidae species	Solitary	Genus-level diversity of sphecid wasps is greater in mixed wood habitats than fallow/plantations.	Vieira *et al.* (2011)
			Polistes dominula	Social	Lead concentration in the faeces of larvae corresponded to levels of lead pollution across natural and urban habitats.	Urbini *et al.* (2006)
	Recreation: literature & arts	Depiction in the arts	Mostly *Vespula* and *Polistes* species	Social	Literature (e.g. The Bible; EF Russell's *Wasp*); Films (e.g. *The Wasp Woman*; *Dragon Wasp*; *Antman and the Wasp*); Art (e.g. during Qing dynasty)	Jones (2019)
	Culture & attitudes	Public perceptions	Vespinae species	Social	Wasps are generally perceived negatively by the public, mainly due to their ability to sting, sensationalist media coverage ('murder hornets') and the idea that wasps have no inherent value.	Sumner *et al.* (2018)

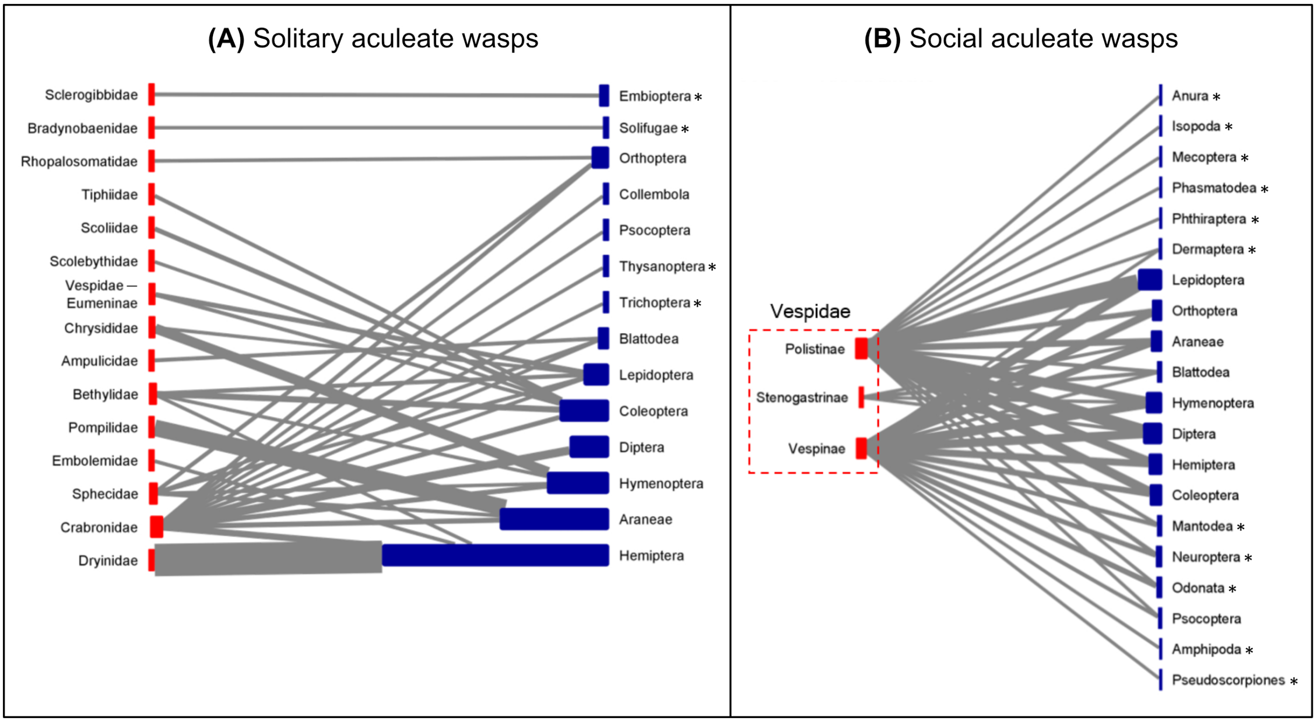

Fig. 3. Predation networks for (A) solitary and (B) social aculeate wasps. Red nodes indicate wasp taxa at family (A) or subfamily (B) level; the node size represents the number of prey orders hunted by that specific wasp taxon, i.e. the extent to which each wasp taxon is a generalist or specialist. Blue nodes indicate the arthropod (prey) orders; the node size indicates the total number of wasp species (across all families/subfamilies) recorded predating on that order. Tie strength (grey lines) indicate the total number of wasp species recorded as predators on each specific prey order. * highlights prey orders that have been recorded as prey of only solitary (A) or only social (B) wasps to illustrate how life history (solitary/social) influences the ecosystem services provided. Nodes are ordered to maximise clarity of visualisation rather than any ecological or evolutionary trait/relationship. Networks constructed using Cytoscape (Shannon *et al.*, 2003).

predatory wasps, including, where possible, representative members of each of the 22 families containing solitary aculeate wasps (see Fig. 1 for the major families). Using the Boolean terms "family name" AND "prey" OR "predat*" OR "parasit*" in *Web of Knowledge* (core databases; from 1900) and secondary searches using the paper-mining online tool, ConnectedPapers.com, we identified 2529 prey records for solitary wasp species from 15 families (Fig. 3A; Supplementary data set S1). No records could be found for the families Bradynobaenidae, Chyphotidae, Mutillidae, Myrmosidae, Plumariidae, Sierolomorphidae or Thynnidae.

Determining whether species are generalist (opportunistic) hunters or prey specialists is difficult to assess from the available data, as many studies sampled prey in nests but did not relate prey diversity to local prey availability (Federici *et al.*, 2007; Polidori *et al.*, 2010). As a functional group, however, solitary wasps are collectively generalists, implicating their importance in the maintenance of balanced ecosystems. Across the 15 families for which data could be collected (Fig. 3A), prey were hunted from across 14 different orders.

Solitary wasps are typically considered to be prey specialists; for example, the Ammophilinae (Sphecidae) and Eumeninae (Vespidae) mostly hunt Lepidoptera, with a minority hunting the larvae of beetles and sawflies; the Euparagiinae (Vespidae) hunt exclusively for weevil larvae (O'Neill, 2001) and the Pompilidae prey entirely on spiders. We found support for specialist hunting behaviours in our data set for 10 of the 15 families, each recorded hunting prey only from within a single order (see Fig. 3A). Analysis at a finer scale is beyond the scope of this review, but there is evidence that prey fidelity is not necessarily even a genus-level trait: some species of *Cerceris* appear to hunt just one family of beetle, whilst other species are generalist beetle hunters (Evans & Hook, 1986). Prey specialism may be due to taxon fidelity of the hunter, local prey ecology, and/or body size (Polidori *et al.*, 2010). For example, the hunting habits of *Sphex ichneumoneus* on grasshoppers are thought to be dictated by prey size, as females appear to shift to new prey species when the species hunted earlier in the season becomes too large (Brockmann, 1985). We also identified families with significant levels of generalist hunting behaviour: the Crabronidae is a highly speciose assemblage of predatory species with massively diverse diets (O'Neill, 2001; Polidori *et al.*, 2010, 2011) that include prey from at least 12 arthropod orders Fig. 3A; Supplementary data set S1). Females may be hunting the most abundant arthropod species in the environment irrespective of ecology, size or other prey traits (Stubblefield *et al.*, 1993).

Unfortunately, quantitative data on the extent of arthropod regulation by solitary aculeate wasps is sorely lacking; but life-history, provisioning behaviour, and environment are likely to influence the impact that solitary wasps can have on prey populations. The biomass of prey taken will depend on the predator's brood size, the number of generations per year and the climate. In temperate zones, solitary wasps tend to be univoltine (one generation per year), with the pupae undergoing diapause through autumn and winter before completing development and emerging as an adult in late spring (Spradbery, 1973). In more tropical regions, solitary wasps may have several generations within a year and thus likely consume a larger amount of biomass per individual than solitary wasps with a univoltine life cycle (Spradbery, 1973).

In the absence of any quantitative measures of how much prey wasps consume, it is reasonable to make extrapolations based on the assumption that the total mass of prey provided for each larva must be (at least) approximately equal to the final size the wasp will attain upon completing development (Grissell, 2010). The life history of the wasp species will influence the number of individual prey items, and size of prey taken. For example, parasitic aculeate wasps often provide each of their larvae with a single large prey item [e.g. in the tarantula hawk wasps (Pompilidae)] whilst predatory species may provide each larva with several smaller items, such as in the Crabronidae and the Ammophilinae (subfamily: Sphecidae) (Polidori, 2011*a*). Within a Californian population of *Symmorphus cristatus* (Eumeninae; Vespidae), nests were found to contain a mean (SD) of 5 (1.5) occupied cells, each provisioned with 4.8 (1.5) larvae [equivalent to 84.6 (27.8) mg of prey biomass] of the beetle *Chrysomela aeneicollis* per cell, equating to approximately 423 mg of prey biomass per nest (Sears *et al.*, 2001). Further, Smiley & Rank (1986) found *Symmorphus* to be a major cause of mortality of the leaf beetle *C. aeneicollis* in a willow forest in America. Among the Crabronidae, a single nest of *Cerceris fumipennis*, which hunts exclusively for wood-boring beetles (Buprestidae), may contain up to 83 prey beetles, representing approximately 4.8 g of prey biomass (Kurczewski & Miller, 1984).

The predator–prey relationships of solitary aculeate wasps are understudied relative to social wasps, given they outnumber social wasps by approximately 100:1. Our database provides an overview of how, collectively, solitary wasps are likely to contribute to regulating populations of Lepidoptera, Coleoptera, Diptera, Hymenoptera, Hemiptera and Araneae (Fig. 3A). Given their diversity, numerousness, and cosmopolitan distribution, the ES provided by solitary wasps as natural pest controllers has thus far been undervalued (Sumner *et al.*, 2018).

(*b*) Predatory social wasps as regulators of arthropods

Although the social wasps account for less than 3% of all wasp species (Aguiar *et al.*, 2013; Bell & Sumner, 2013), their ecological impact as predators is likely to be highly significant because of their large colony sizes, with hundreds to thousands of workers and brood accounting for a large amount of biomass in ecosystems (Thomas *et al.*, 1990; Wilson, 1990; Elizalde *et al.*, 2020). Adult wasps forage for water, wood pulp, nectar and, most importantly, protein (Spradbery, 1973; Richter, 2000). Unlike solitary prey-hunting wasps, the larvae of all social wasps develop in an uncapped cell and are provisioned progressively with protein obtained from predation on various arthropod species (Spradbery, 1973).

There has been much more research interest (and success) in determining what social wasps hunt than for solitary wasps. Social wasps are easily located and observed due to their large numbers and central place foraging: by sitting at the nest, observers can collect prey from returning foragers. However, since foragers masticate prey items extensively before returning to the nest, it can be difficult to identify prey using morphology: success varies from 30% (Gambino, 1986), 39% (Sackmann *et al.*, 2000), to 70% (Harris, 1991) and 95% (Harris & Oliver, 1993). These methods may not capture the range of species predated by aculeate wasps. More recently, molecular techniques have been used to identify masticated prey items to the family, genus, or species level (Kasper *et al.*, 2004; Wilson, Mullen & Holway, 2009) and, given the cheaper sequencing technology available due to the genomics revolution (Schuster, 2008) and higher accuracy, these methods are likely to become the norm for prey identification in the future. Another approach is to sequence the gut contents of the larvae using the metabarcoding methods made possible by advances in the resolution of molecular technology and expanding online databases of species-level DNA barcodes (Ward & Ramón-Laca, 2013).

Here we collate data from across these different types of studies to compile a database of the prey of social wasps. The literature search was performed in the same way as for solitary wasps, searching for subfamilies within the family Vespidae that contain social species (i.e. Polistinae, Stenogastrinae and Vespinae). We identified 198 prey records across the three subfamilies of social wasps (Supplementary data set S2). Despite the vastly smaller data set compared to the solitary wasps, the data clearly indicate that social wasps (even at the subfamily level) collectively prey on a huge variety of arthropods; but moreover, in contrast to the solitary wasps, all three subfamilies of the social wasps appear to be highly opportunistic (and thus generalist) foragers (Fig. 3B). By far the largest proportion of data comes from the Polistinae [e.g. *Agelaia vicina* in Brazil was observed capturing at least 10 orders of insects: Lepidoptera, Coleoptera, Dermaptera, Hymenoptera, Heteroptera, Mantodea, Diptera, Neuroptera, Blattodae and Hemiptera (Oliveira, Noll & Wenzel, 2010); *Mischocyttarus flavitarsis* was observed predating on flies and caterpillars (Snelling, 1953); and *Mischocyttarus drewseni* reportedly preys on small spiders, ants and a hemipteran nymph (Jeanne, 1972)], and the Vespinae [e.g. *Vespula sulphurea* in California are reported foraging on flies, caterpillars and grasshoppers (Akre & Myhre, 1994); see Supplementary data set S2)]. Evidence from the Vespinae suggest that prey choice varies depending on habitat and season: the prey of both *Vespula vulgaris* and *Vespula germanica* differ depending on the abundance of arthropod families throughout the season, as well as the location of the nest (Harris & Oliver, 1993). Reports on prey types hunted by the third subfamily of social wasps – Stenogastrinae – are more scarce: *Parischnogaster nigricans serrei* have been reported returning to nests with Araneae, Blatttodea and Diptera, *P. mellyi* was observed capturing tiny midges in sunny patches of forest or plucking prey from spider webs, whilst *Liostenogaster vechtii* were observed predating on Blattodea and Hymenoptera (Turillazzi, 1983, 2012).

The opportunistic foraging of social wasps is apparent from the reported variation in diet composition; for example, the diet of *V. germanica* varied dramatically with location and season (Harris, 1991; Sackmann *et al.*, 2000); likewise, the diet of *Vespa velutina* in its invasive French range varied depending on habitat (Villemant *et al.*, 2011). The success of the social wasps beyond their native ranges (Wilson *et al.*, 2009; MacIntyre & Hellstrom, 2015), where prey are novel, is likely due to their ability to prey opportunistically upon a huge range of arthropods. Irrespective of where social wasps live, there is a predominance of Lepidoptera, Diptera, Hymenoptera, Hemiptera and Coleoptera in their diets (Fig. 3B; Supplementary data set S2); these orders include many economically and ecologically important species. Finally, it is important to note that although arthropod prey makes up the majority of social wasp diets, many also scavenge vertebrate and invertebrate carrion [suggesting further ecological roles as ecosystem recyclers – see Section IV.2 (Wilson *et al.*, 2009; Wilson & Wolkovich, 2011)] and are even known to prey on live vertebrates, such as frog tadpoles (Warkentin, 2000) and hummingbird chicks (Grant, 1959).

Quantitative estimates of the ecological impact of social wasp predation can be extrapolated from their colony sizes and productivity. Over the course of the colony cycle, nests of the yellowjacket wasp *V. vulgaris* are estimated to produce an average of 9601 adult wasps, including 7274 workers, 1438 males and 889 queens (Archer, 2003). Assuming a 1:1 larva: prey mass ratio, and an average adult mass of ~23, ~163 and ~85 mg for worker, queen, and male respectively (Archer, 1998), a single *V. vulgaris* nest may therefore require 0.43 kg of prey biomass during the colony cycle.

Ecological impact can also be measured by counting prey loads collected by foragers on arrival at their colony; such data are available for a few species, but heavily skewed to the ecologically dominant *Vespula* species in invasive regions like New Zealand. For example, Harris (1991) reported that *V. vulgaris* can capture up to 4.8 million prey loads per hectare in one season, and Thomas *et al.* (1990) estimated them to be responsible for the capture of 8.1 kg of prey per season/hectare. This biomass intake by wasps/hectare over just the summer and autumn months is comparable to that of the local insectivorous bird population throughout the whole year (Harris, 1991). In their native range, *Vespula* typically have an annual colony cycle. In warmer latitudes such as California (Gambino, 1986) and New Zealand (Plunkett, Moller & Hamilton, 1989), colonies can over-winter and as a result be up to 10 times larger than colonies in temperate regions, containing up to 3–4 million cells and producing over 115000 adults in some cases (Spradbery, 1973; Archer, 2003).

Nest density strongly influences the prey biomass removed from an ecosystem: in high-density areas (as found in invasive zones; Lester & Beggs, 2019), *V. vulgaris* and *V. germanica* are estimated to remove up to 11.28 kg of prey biomass/hectare/season, whilst in low-density areas, it could be as low as 0.01 kg (Harris & Oliver, 1993). In New Zealand, where *V. vulgaris* has become a problematic invasive species (MacIntyre & Hellstrom, 2015), Thomas *et al.* (1990) found a mean of 11.9 nests per hectare. Using the above estimation of 0.43 kg of prey biomass collected per colony, this amounts to at least 5.1 kg of prey biomass consumed per hectare by *V. vulgaris* alone. Two nests of *V. germanica* in New Zealand were estimated to have consumed 26.6 and 99 kg of prey biomass respectively over their two-year life cycles (Harris, 1996). However, in their native range overwintering colonies are very rare (accounting for just 4% of nests) and thus their overall predatory contribution was estimated to be 0.16 kg of prey per colony, per season, per hectare (Harris, 1996).

Few data are available on prey biomass taken by species other than *Vespula* species. Data exist for another invasive species, the Asian paper wasp *Polistes chinensis* (Polistinae) which has become established in New Zealand (Clapperton, Tilley & Pierce, 1996). Although nests of *P. chinensis* are far smaller than those of *Vespula* species, the number of *P. chinensis* nests was far higher per hectare, resulting in estimates of 0.96 kg of prey biomass/season/hectare (Clapperton, 1999), a similar value to that of the two invasive vespine wasps (Harris & Oliver, 1993). Thus, nest size alone is not indicative of impact on insect populations. Therefore, estimates of nest density as well as prey consumption and colony productivity are required for an estimate of quantitative impact. Further estimates exist for other *Polistes* species: single colonies of *Polistes versicolor* are estimated to capture around 4015 prey in a year (Prezoto *et al.*, 2006).

The generalist, adaptable and opportunistic nature of predation by social wasps, together with their capacity to remove many kilograms of insect biomass from habitats each year suggest that the social wasps have a very important role in maintaining balanced phytophagous arthropod populations in natural ecosystems. Accurate quantification of their ecological impact on native and invasive arthropod populations (e.g. Losey & Vaughan, 2006) is essential to fully understand the extent to which they provide this ES, the economic and ecological value of this service and the consequences of changing populations of social wasps in natural ecosystems.

(2) Regulation of agricultural arthropod pests

As well as their role as regulators of insect populations in natural ecosystems, aculeate wasps are also likely to be important as bio-control agents. Biological control of pests is likely to play an integral role in meeting the ever-growing demand for food production in future decades (Carvalho, 2006). Unlike chemical control methods (e.g. pesticides), biological control is based on pre-existing predator–prey relationships, meaning that pest resistance is unlikely. The ES provided by biological control has an estimated value of US $417 billion per year (Costanza *et al.*, 1998). In North America alone, the value of natural control provided by insects was estimated at US$4.5 billion annually (Losey & Vaughan, 2006). Most successful examples of biological control using invertebrates have involved parasitoid wasps (Greathead & Greathead, 1992) and their economic value in such programmes is well documented (e.g. Dean *et al.*, 1979; Zeddies *et al.*, 2001; Bokonon-Ganta, De Groote & Neuenschwander, 2002). The reputation of wasps as effective agents of biocontrol entirely refers to the non-aculeate parasitoids, which make up 48.7% of the 230 invertebrate species commercially available for augmentative biological control (van Lenteren, 2012). The potential roles of aculeate wasps in such programmes have largely been ignored, with only a few notable successes; this is surprising given their ecosystem contributions as predators and parasites.

As specialist predators and parasites, the solitary aculeate wasps offer potential for biocontrol programs. Despite this, only four species of aculeate wasps are commercially available for augmentative biological control practices, all of which are solitary (van Lenteren, 2012): *Cephalonomia stephanoderis* and *Prorops nasuta* (both Bethylidae) are used to control coffee berry borer beetle (*Hypothenemus hampei*); *Goniozus legneri* (Bethylidae) is used to control lower naval orangeworm (*Amyelois transitella*) and *Ampulex compressa* (Ampulicidae) is used to control domestic cockroaches (see Supplementary data set S1). Unfortunately, the number of unsuccessful introductions of aculeate wasps for biological control far outweighs the number of successful introductions (e.g. Krombein, 1948; O'Neill, 2001). This is likely due to a lack of knowledge on life histories and poor management strategies. For example, whilst the introduction of *Campsomeris marginella* to Hawaii was a success, its introduction to Taiwan to control other sugarcane pests was unsuccessful (Cheng, 1991). Our review of solitary wasp predation (see Section II.2*a*) highlights that some of these wasp families have more generalist prey choice than commonly assumed, with many species attacking either multiple species within a genus or, in some cases, multiple genera; such lack of prey specificity would preclude their release into novel habitats (Supplementary data set S1). Ultimately, if the success rate of future solitary aculeate biological control programmes is to match that of the parasitoid wasps, then more effort is needed to understand wasp life history fully, prior to introductions.

Social wasps hold untapped promise as biocontrol agents (Prezoto *et al.*, 2019; Elizalde *et al.*, 2020). Firstly, they are generalist predators. In a meta-analysis of (non-wasp) generalist arthropod predators, significant reductions in pest numbers were reported in 75% of studies (Symondson, Sunderland & Greenstone, 2002). The generalist predatory nature of social wasps (Fig. 3B) along with their high demand for arthropod protein makes them a potentially effective agent of pest control across agricultural ecosystems. Ironically, it is exactly because of the social wasps' generalist diet that they been largely ignored as a means of biological control: effective biocontrol agents are typically specialist predators or parasites. Secondly, social wasps hold great potential for biocontrol because Lepidoptera and Diptera make up a large part of their preferred diet (Fig. 3B); many lepidopterans and dipterans are significant crop pests. Predatory wasps are common in a range of agricultural environments, suggesting that such crops provide rewarding forage patches (Bommarco *et al.*, 2011; Rodriguez *et al.*, 2012; Souza *et al.*, 2013; Jacques *et al.*, 2015, 2018; Tomazella *et al.*, 2018). Moreover, observational studies report social predatory wasps as one of the main natural predators of lepidopteran pests in agricultural settings (Rabb & Lawson, 1957; Picanço *et al.*, 2006, 2010; Bommarco *et al.*, 2011; Picanço, 2012; Pereira *et al.*, 2018; Lourido *et al.*, 2019) and that they can successfully locate such prey using olfactory cues (Pietrantuono, Moreyra & Lozada, 2018; Southon *et al.*, 2019). A third reason why social wasps are promising biocontrol agents is due to the sheer numbers of hunters provided by each colony; a single *V. vulgaris* colony has up to 10000 workers and produces thousands of larvae; *Vespula* has been suggested as a viable candidate for development as a manageable pest controller (Donovan, 2003). Finally, social wasps are well equipped to deal with pest species outbreaks effectively. Many social wasp species appear to lack the efficient forager recruitment traits found in other social insects [e.g. Jeanne, Hunt & Keeping, 1995; although see Overmyer & Jeanne (1998) and Wilson Rankin (2014)]. However, wasp foragers in some species (e.g. *Polistes*) are known to return to sites where they have previously had success in hunting and to 'fixate' on a particular prey type (Richter, 2000) whilst others are known to be capable of learning from nest-mate workers how to extract caterpillar prey from silk retreats spun on host plants (Weiss, Wilson & Castellanos, 2004). Given the tendency for caterpillars to feed in aggregations (Greeney, Dyer & Smilanich, 2012), such hunting behaviour would cause workers to focus their hunting in areas where caterpillars aggregate. Therefore, social wasps have the potential to control lepidopterous pests directly through predation, and indirectly by breaking-up beneficial feeding aggregations, exposing caterpillars to less-optimal feeding conditions (Nakasuji, Yamanaka & Kiritani, 1976; Stamp & Bowers, 1988).

Despite these compelling traits of social wasps that make them promising biocontrol agents, the experimental research base for their efficacy is sparse, even though their potential was recognised over a century ago; e.g. *Polistes* were cited as the most important predatory enemies of cotton worm (*Alabama argillacea*) in several West Indian islands 90 years ago (Myers, 1931; Rabb & Lawson, 1957); Ballou (1915) attributed 10 successful crop years of pesticide-free cotton production on the island of St Vincent to the predatory impact of *Polistes annularis*, nesting in sheds erected in the fields by planters (Ballou, 1909). More recently, there have been observations of a diverse range of social wasp species predating on pest species in agricultural environments; e.g. Prezoto & Braga (2013) observed *Synoeca cyanea* predating the fig fly *Zaprinus indianus*, a pest to many fruit crops in Brazil; seven species of polistine wasps were observed naturally predating on the key tomato crop pest *Tuta absoluta* in Brazil (Picanço *et al.*, 2011). Observational studies like these clearly show that Vespidae wasps preferentially predate the larger 2nd–5th instar larvae (Gonring *et al.*, 2003; Picanço *et al.*, 2010; Picanço, 2012), without quantifying the impact of this on the prey population. These studies are only illustrative of foraging behaviour, not the foraging capacity of the wasp species, and so do not help estimate of the value of wasps as biological control agents. More recently, an experimental study on the Brazilian species *Polistes satan* showed that their presence has a significant effect in reducing the population sizes and impact of the globally important Lepidopteran pest, the fall army worm (*Spodoptera frugiperda*) maize plants (Southon *et al.*, 2019). This study, however, was performed under semi-controlled conditions in a screen house. Field-realistic data on the impact of social wasps as biocontrol agents are lacking.

Social wasps are unlikely to replace other forms of biocontrol (e.g. parasitoids), but the evidence suggests they hold a great deal of promise as part of an integrated pest management programme, especially in developing countries in tropical/sub-tropical climates where social wasps are abundant and relatively tolerant of anthropogenic landscapes, and where farming is small scale (Barbosa *et al.*, 2018; Prezoto *et al.*, 2019). Augmentative control using artificially inflated populations of social wasps to control pest outbreaks shows great promise. The generalist nature of social wasp diets would theoretically keep most pest populations under control, and thus unlike species-specific biological control agents (like parasitoids) they are unlikely to enable other pest species to become prominent (Pearson & Callaway, 2003).

(3) Pollination services

Over 75% of human-cultivated crops worldwide depend directly on (or show increased fruit or seed set as a result of) insect pollination (Klein *et al.*, 2007). Insect pollination is estimated to be worth over \$250billion/year worldwide (IPBES, 2016), amounting to at least 9.5% of the value of world agricultural production (Gallai *et al.*, 2009). We collated records of plants that were visited by aculeate wasps using the Boolean terms "family name" AND "pollinat*" OR "flower" NOT "ficus" (to exclude the fig wasps, reviewed elsewhere) in *Web of Knowledge*. We identified 2288 unique flower–wasp visitation records for aculeate wasp species from seven families (Fig. 4; Supplementary data sets S3 and S4). We categorised these records into those for plants that are known to rely solely on aculeate wasps for pollination (obligate pollination; Supplementary data set S3), and those where wasps have a non-specialist relationship with plants, visiting them for nectar opportunistically and thus having the potential to contribute to their pollination (facultative pollination; Supplementary data set S4). Our survey reveals relationships of 960 plant species with aculeate wasp pollinators.

(*a*) Obligate pollination – where plants rely solely on aculeate wasps for pollination

We identified 164 plant species across six plant families and four orders that are reported to depend solely on aculeate wasps for pollination (Fig. 4A; Supplementary data set S3). Wasp pollination of orchids is an example of co-evolution between the plant and the wasps. Pollination by chemical deception is primarily restricted to the Orchidaceae (Gaskett, 2011), although such deception has been reported outside of this group (Ellis & Johnson, 2010; Vereecken *et al.*, 2012). Within the orchids, sexual deception is one of the most specialised forms of chemical deception used to achieve pollination, with the Scoliidae and Thynnidae wasp families especially important in this relationship (Supplementary data set S3). Such deception involves the attraction of male wasps to the orchid through species-specific mimicry of the appearance and sex pheromones released by females (Mant *et al.*, 2002; Ayasse *et al.*, 2003). Upon attempting to copulate with the flower, pollinaria are attached to the male and are then transferred to the next flower the male attempts to copulate with, completing the pollination process (Stoutamire, 1975) (Fig. 4B). Such interactions tend to be highly species specific, ensuring that hybrids are not formed through cross-species pollination (Mant *et al.*, 2002). Furthermore, due to orchid chemical profile changes after pseudocopulation, males tend not to revisit the same plant, enhancing the reproductive success of the orchid and ensuring that self-pollination does not occur (Schiestl & Ayasse, 2001).

Orchids also deceive wasps by falsely advertising the presence of food. At least two species of orchid, *Epipactis helleborine* and *E. purpurata*, employ food deception to achieve specialist pollination from the social wasps *V. germanica* and *V. vulgaris* (Brodmann *et al.*, 2008). The orchids advertise the presence of caterpillar prey (a protein reward) through the floral release of green-leaf volatiles, mimicking the chemical profiles of plants under attack from phytophagous insects, to attract their social wasp pollinators (Brodmann *et al.*, 2008). Other orchids release honey bee alarm pheromone to attract hornets for pollination (Brodmann *et al.*, 2009). Given the location in which these orchids grow (dark forest understorey) and that their green-leaf volatiles fail to attract other potential pollinators, it is thought that both species are solely reliant on social wasps for pollination (Brodmann *et al.*, 2008).

Besides orchids, plants that are solely reliant on wasps for pollination include representatives of the Apocynaceae, Asparagaceae, Euphorbiaceae and Iridaceae families, most of which are pollinated by spider wasps (Pompilidae) in the genera *Hemipepsis* and *Pepsis* (Supplementary data set S3). This guild of plants demonstrates highly convergent traits to attract their spider wasp pollinators, such as cryptic floral colouring and synchronised blooming periods when the wasps are at their most active (Shuttleworth & Johnson, 2012). Furthermore, to deter other non-pollinating insect species, certain plants within the guild produce bitter, unpalatable nectar which is preferentially

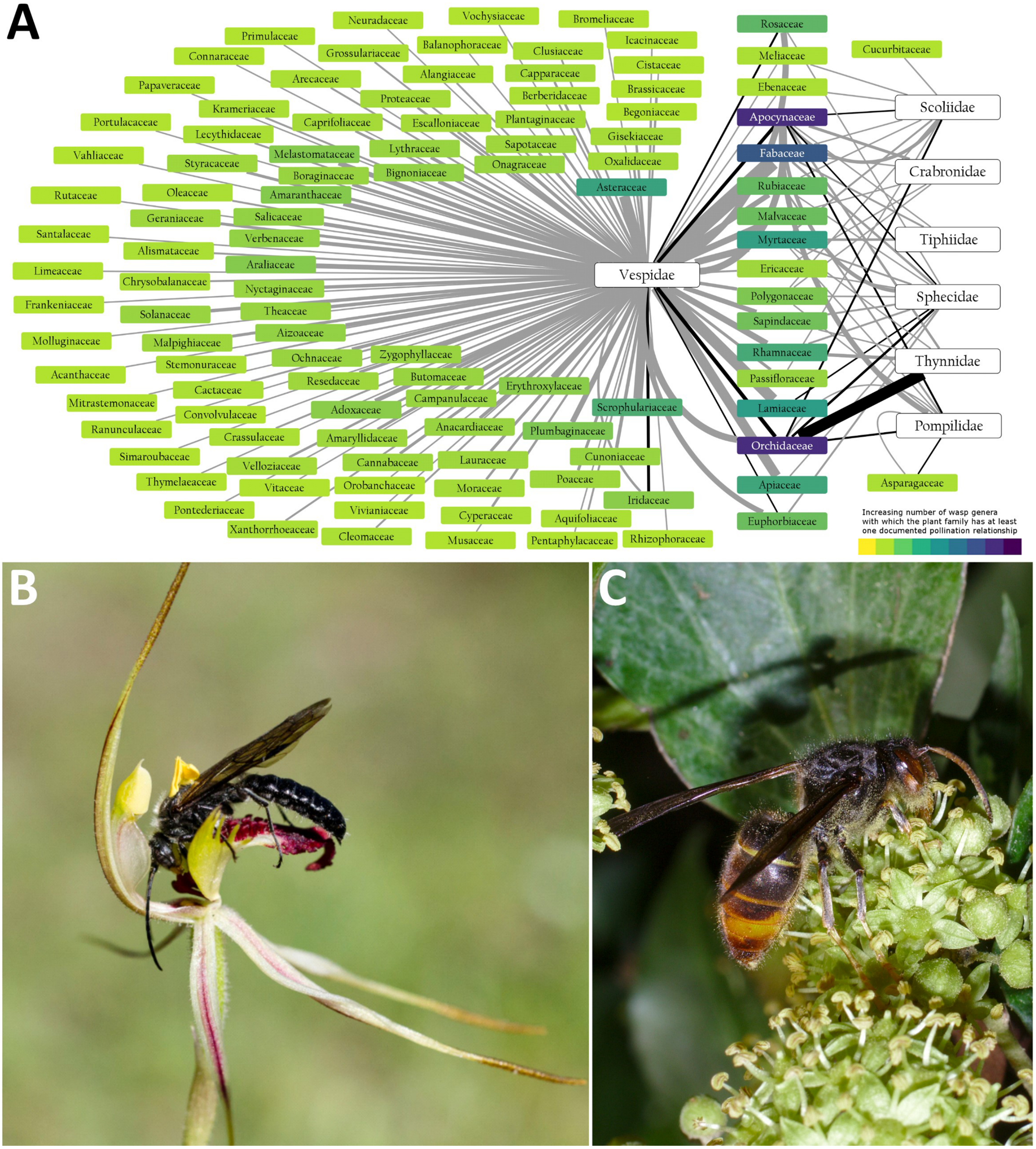

Fig. 4. (A) Pollination networks of the aculeate wasps. Records of wasps from the different aculeate families (white nodes) visiting different plant families (coloured nodes). Plant node colour indicates the number of wasp genera recorded visiting (scale indicated in figure is qualitative not quantitative). Tie strength (grey/black lines) indicate the number of documented relationships between each pair of wasp–plant families: the thicker the line, the more species pairs reported. Black ties indicate obligate relationships, where plants are known to rely on wasps for pollination; grey ties indicate putative facultative relationships, where plants may benefit from wasp visitations through pollination. Node size contains no information. Network constructed using Cytoscape (Shannon *et al.*, 2003). (B) Example of obligate wasp pollination as a male *Lophocheilus anilitatus* (Thynnidae) attempts to copulate with the sexually deceptive spider orchid *Caladenia phaeoclavia* (Orchidaceae), during which pollinia are attached to the wasp thorax. Photograph used with permission from Tobias Hayashi. (C) Example of facultative pollination as a pollen-covered Asian hornet (Vespidae: *Vespa velutina*) visits common ivy (Araliaceae: *Hedera helix*). Photograph by Stanze (Flickr) and used under CC License.

consumed by spider wasps (Shuttleworth & Johnson, 2006, 2009*b*,*c*, 2012).

(*b*) Facultative pollination – where plants are opportunistically pollinated by aculeate wasps

Whilst the diet of wasp larvae is heavily reliant on protein obtained from arthropods, adult diets consist largely of carbohydrates, most of which are obtained by feeding on nectar from flowers (Spradbery, 1973). During these visits to flowers, wasps may inadvertently transfer pollen between flowers (Fig. 4C). The efficacy of this putative facultative pollination is almost completely unstudied. The data we present here, therefore, are of plant–wasp relationships that could potentially constitute pollination services. We identified 798 plant species across 106 families and 35 orders which fit this category (Supplementary data set S4; Fig. 4A). Due to sparse reporting, the number of plant species we report is likely to be a vast underestimate of the true number that have the potential to benefit from wasps. One exception are the well-studied wasp–plant interactions reported for Southern Africa (Gess & Gess, 2010). Elsewhere, partial pollination networks have been reported for the paper wasps (Polistinae) of South America (Santos, Aguiar & Mello, 2010; Mello *et al.*, 2011; Clemente *et al.*, 2012), and the vespid wasps of the Crimea (Fateryga, 2010) and various localities across Asia (Kato, 2000; Corlett, 2001).

The Vespidae family are the most dominant generalist pollinators (Fig. 4A; Supplementary data set S4): variability of flower species visited is extremely high, with wasps such as *Brachygastra lecheguana* pollinating at least 76 plant species across 29 families, whilst other wasps such as *Celonites pulcher* (which pollinates two species both belonging to the Scrophulariaceae) and *Ceramius cerceriformis* (which pollinates two species both belonging to the Aizoceae) seem restricted to the pollination of very few species (Supplementary data set S4). Across temperate to arid zones, the vespid subfamily Masarinae (pollen wasps) seem to be the most important wasps for generalist pollination (Gess & Gess, 2010; Supplementary data set S4). These wasps have reverted to a phytophagous lifestyle and exclusively provision their larvae with pollen instead of insect prey (Gess & Gess, 2010). It has been suggested that pollen wasps should be considered to perform the same functional pollination roles as bees in some ecosystems (Gess & Gess, 2004).

Social wasps (Polistinae and Vespinae) are likely to be especially important as facultative pollinators, across both temperate and tropical regions (Supplementary data set S4). Within plant–pollinator networks, social wasps show high degrees of connectivity; and are generalists in terms of the plants they visit (Santos *et al.*, 2010). This is likely a result of their social nature, with multiple foraging workers utilising the most abundant species of plants within the foraging range of their nest for nectar collection (Santos *et al.*, 2010). Thus, there are high levels of overlap between plants and their wasp pollinators, producing a plant–pollinator network that is highly robust to extinction on either side of the mutualism (Mello *et al.*, 2011). Because of their lack of preference for specific plants, social wasps may be more abundant than bees in degraded or fragmented habitats and thus play an important role as 'backup' pollinators (Mello *et al.*, 2011).

From an economic perspective, wasps have also been found to pollinate a number of important crops, providing similar 'Pollination Importance Values' to the key greenhouse pollinator, the bumble bee (*Bombus* spp.), in the pollination of mustard, apples, and pumpkins (Akhter *et al.*, 2016). In some cases, wasps are considered to be more important for generalist pollination than bees. For example, the increased mobility of the sphecid wasps *Bembix borrei* and *Sphex* spp. allowed high levels of movement between patches of the shrub *Allophylus serratus*, ensuring rapid and efficient cross-pollination when compared to various bees, which tended to focus on a single plant (Aluri, Reddi & Das, 1998). Remarkably, a recent experiment showed that *Polistes* wasps were able to completely replace the pollination services of bumble bees in greenhouses, proving as efficient in pollen transfer as bumble bees (Hallett *et al.*, 2017). This study alone brings into focus the extent to which the pollinating services of social wasps have been overlooked.

The paucity of data on wasps as pollinators, in both natural and farmed environments currently precludes putting a value on their services as pollinators. Given the importance of natural pollinators to human health, welfare and food security (Klein *et al.*, 2007; Gallai *et al.*, 2009; Potts *et al.*, 2016), and current concerns over declining populations of well-recognised pollinators such as bees (Potts *et al.*, 2010; Senapathi *et al.*, 2015), it is timely to investigate in more detail the pollinating value of aculeate wasps. Their generalist interactions with plants, their potential for pollinating in degraded habitats, and the apparent resilience of some species to anthropogenic change (Jonsson *et al.*, 2021) warrant more research effort to quantify their potential.

III. PROVISIONING SERVICES

(1) Aculeate wasps as nutrition for humans

Insects are a viable healthy alternative to eating meat, being high in protein and essential amino acids. Insect farming offers many advantages over traditional meat production, using less space and water, emitting fewer greenhouse gases and ammonia, and generating a much higher food-conversion efficiency than livestock (van Huis, 2013). At least two billion people across the globe consume insect protein (entomophagy) as part of their diet: this includes over 2000 insect species, with the orders Coleoptera (31%), Lepidoptera (18%) and Hymenoptera (15%) being the most prominent (Jongema, 2017). Wasp larvae have an exceptional dry protein mass (ranging from 46% in *Polistes sagittarius* up to 81% in *Polybia* spp.), typically contain around 70% of required amino acids and have an extremely low fat content Ramos-Elorduy, 1997; Chen, Feng & Chen, 2009; Ying *et al.*, 2010). We searched the literature to gather information on the range of aculeate wasp species eaten around the world using the search terms: "Entomophagy" OR "edible" OR "human food" as topics, and "Insect" OR "wasp" OR "Aculeata" as titles, across all years available in *Web of Knowledge*. Wasps account for 4.8% of the insect species consumed: we detected 109 wasp species reported as being eaten across 19 countries (Supplementary data set S5). This is likely to be an underestimate since many wasps sold for human consumption can only be identified to genus level and data are only known for a small number of countries.

Typically, wasps are eaten in their larval or pupal stages and thus mainly social species are utilised, since the nests of solitary species are rarely large enough to merit the efforts of collection (Ruddle, 1973; Supplementary data set S5). During the autumn harvest in Japan, wasp nests typically sell for US$100 per kg and demand is often so high that markets must be supplemented by the importation of further nests from China, New Zealand, and the Republic of Korea (Nonaka, 2010). Wasps are a popular street food in East Asia, Africa, and South America (Ramos-Elorduy, 2009). In rural China, wasps are the most common edible insects for sale; 18 species have been recorded at market (although many more remain unidentified) (Chen *et al.*, 2009). Furthermore, in tropical climates, the perennial colony cycles of wasps means they are reliable food source which can be collected year-round (Acuña *et al.*, 2011).

Several wasp genera produce honey (e.g. *Brachygastra*, *Parachartergus*, *Polybia*, *Mischocyttarus* and *Polistes*) (Sugden & McAllen, 1994; Hunt *et al.*, 1998; Guimarães, De Castro & Prezoto, 2008), which is a valued food source across Latin America (Onore, 1997; Bentley & Rodriguez, 2001): *Brachygastra mellifica* hoards excess nectar collected from floral visitation, and steals high-energy honey of various honeybee species (Sugden & McAllen, 1994). Honey stored by *Brachygastra*, *Polistes* and *Polybia* contains high levels of fructose and a diverse array of amino acids, suggesting that wasp honey is a nutritious source of energy (Sugden & McAllen, 1994; Hunt *et al.*, 1998). However, wasp honey production is unlikely to be commercially viable because the honey output of a typical wasp hive tends to be far smaller than the 0.45 kg of honey produced per colony per day by the European honey bee (Rinderer, Collins & Tucker, 1985; Sugden & McAllen, 1994).

Finally, social wasps provide safe overwintering havens for wine-producer's yeast *Saccharomyces cerevisiae*. Yeast cells survive in the intestines of overwintering queens of *Vespa crabro* and *Polistes dominula*; the yeast is transferred to workers and future foundress queens through trophallaxis, and finally distributed to vineyards (Stefanini *et al.*, 2012). The intestines of social wasps provide the appropriate conditions for yeast reproduction, with multiple strains mating with one another whilst inside their vector, maintaining local phenotypic variability of yeast strains (Dapporto *et al.*, 2016) and suggesting an important role of wasps in the evolution and genetic diversity of *S. cerevisiae* (Stefanini *et al.*, 2012, 2016).

(2) The medicinal properties of aculeate wasps and their products

The venom of aculeate wasps is a complex mixture of toxins, allergens, enzymes, and amines (de Graaf *et al.*, 2009) which are utilised in a wide range of biological functions, such as self-defence (or colony defence in the case of social vespids), prey capture and host manipulation. Given their compositional complexity, it is unsurprising that wasp venoms contain many biologically active molecules which are of significant pharmacological interest. Of recent interest is the potential of wasp venom in the treatment of cancer (Heinen & Gorini da Veiga, 2011). The most extensively studied of these molecules is mastoparan, a family of amphipathic peptides found in the venom of social wasps (Hirai *et al.*, 1979; Argiolas & Pisano, 1984; Wang *et al.*, 2008*b*) which show considerable promise for the treatment of cancer (Yamada *et al.*, 2005; Moreno, Zurita & Giralt, 2014; Leite *et al.*, 2015).

The antibiotic properties of wasp venom, larval secretions (e.g. Turillazzi *et al.*, 2004; Herzner *et al.*, 2013; Moreau, 2013) and nest materials have long been recognised, with use in historic and contemporary folk medicine (Wang *et al.*, 2008*a*). The venom of solitary and social wasps has anti-microbial properties. Solitary wasps use antibiotics to keep their paralysed prey healthy for the developing offspring to feed off. Anoplin, a peptide isolated from the venom of *Anoplius samariensis* (Pompilidae), and Eumenitin, isolated from the venom of *Eumenes rubronotatus* (Vespidae), show strong inhibitory activity against both Gram-positive and Gram-negative bacteria (Konno *et al.*, 2001, 2006). Furthermore, larvae of the emerald cockroach wasp, *Ampulex compressa* secrete large amounts of oral antimicrobials whilst inside their cockroach hosts, providing defence against the bacterium *Serratia marcescens* (Herzner *et al.*, 2013), an opportunistic human pathogen.

The life-history challenges facing social wasps have driven the evolution of anti-microbial defence systems. Like all social insects, social wasps are vulnerable to pathogens due to the reduced genetic diversity within colonies and high chances of pathogen transmission among colony members (Cremer, Armitage & Schmid-Hempel, 2007). Social wasps combat this using anti-microbials in the venom and in the larval secretions with which workers coat themselves, the brood, and the nest (Turillazzi *et al.*, 2004, 2006). Many of these anti-microbials may be of direct benefit to human health. For instance, Polydim-I, a peptide isolated from the venom of *Polybia dimorpha*, exhibited promising anti-microbial activity against *Mycobacterium abscessus* both *in vitro* and *in vivo* (Das Neves *et al.*, 2016), a mycobacterium which commonly causes soft tissue and skin infections after invasive surgery (Lee *et al.*, 2015). Further examples include Dominulin A and B, peptides isolated from the venom of *Polistes dominula*, which were effective against Gram-negative and Gram-positive bacteria (Turillazzi *et al.*, 2006) and the larval secretions of *P. dominula*, which showed anti-microbial activity against *Bacillus subtilis* and *Escherichia coli* (Turillazzi *et al.*, 2004).

Finally, wasp products have a history of use in traditional medicine. For instance, quinone 7,8-*seco-para*-ferruginone isolated from the nests of *Vespa simillima* exhibits potent inhibition of rat hepatoma cells (Fujiwara *et al.*, 2008); the peptide Nidus Vespa Protein 1 found in nest comb collected from a variety of social wasps including *Polistes olivaceous*, *P. japonicus* and *Parapolybia varia* promotes apoptosis and inhibits the proliferation of hepatoma cells, implicating its potential as a future treatment for liver cancer (Wang *et al.*, 2008*a*). Nest comb components also show potential as a novel oral anti-microbial, reducing the biofilm capabilities of *Streptococcus mutans* (a bacterium heavily associated with dental plaque and decay) (Xiao *et al.*, 2007; Guan *et al.*, 2012). Furthermore, the flavonoids quercetin and kaempferol isolated from nest comb were shown to considerably inhibit the growth of various *Streptococcus*, *Actinomyces* and *Lactobacillus* species (Guan *et al.*, 2012). Amongst the solitary wasps, nests of the mud-daubers (e.g. *Sceliphron* and *Synagris)* are a popular source of essential minerals, such as magnesium, calcium, manganese, iron and zinc for pregnant women and children in parts of rural Africa as a form of insect earths (geophagy) (Fairhead, 2017). The effectiveness and active ingredients of other wasp products (e.g. 'hornet juice', which contains amino acids found in the trophollaxis fluid produced by *V. mandariania* hornets and is marketed for 'boosting endurance') remain undetermined.

Determining the extent of provisioning services offered by the medicinal properties of wasp products requires a more comprehensive research base, along with clinical trials. The evidence so far, however, suggests that wasp nests and wasp venom exhibit high medicinal potential, especially as anti-microbials and possibly for cancer treatment.

IV. SUPPORTING SERVICES

(1) Vespicochory – wasp-mediated seed dispersal

Insects are important for seed dispersal; for example, myrmecochory (ant-mediated seed dispersal) is a common and widespread method, occurring in at least 11532 angiosperm species across 334 genera and 77 families (Lengyel *et al.*, 2009). The presence of a lipid-rich appendage (known as the elaiosome) on the seed causes ants to transport it to the nest, feed the elaiosome to their brood, and discard the intact seed, aiding in the seed's dispersal (Beattie & Hughes, 2002). A similar behaviour (known as 'vespicochory') has been reported in *Vespula* species (Pellmyr, 1985), suggesting that, along with ants, social wasps may also play a role in seed dispersal. We searched the literature for reports of vespicochory using the search terms "seed dispersal" OR "vespicochory" AND "wasp" OR "Vespidae" as topics, across all years available in *Web of Knowledge*. The search returned vespicochorous interactions occurring between 10 plant species and 12 social wasp species (either in the subfamily Vespinae or Polistinae) in Asia, Europe, and North America (Supplementary data set S6).

These vespicochorous interactions involve the direct dispersal of seeds by worker wasps (e.g. Zettler, Spira & Allen, 2001; Chen *et al.*, 2017; Burge & Beck, 2019) or the theft and subsequent dispersal of seeds from foraging myrmecochorous ants (Bale *et al.*, 2003). The degree of reliance on wasps for seed dispersal appears to differ among plant species. For instance, *Vespa velutina* represents the primary disperser of *Stemona tuberosa* seeds, with wasps dispersing 100% of available seeds from parent plants (Chen *et al.*, 2017), whilst *Vespa affinis* dispersed 33% of *Aquilaria malaccensis* seeds, with parent plants relying on the action of wind and gravity for dispersal of the remaining seeds (Manohara, 2013). Interestingly, *Vespula* species were found to remove more *Trillium discolor* seeds than the ant species *Aphaenogaster texana*, *Formica schaufussi* and *Solenopsis invicta*, suggesting their importance for seed dispersal (Bale *et al.*, 2003). Furthermore, the presence of *Vespula* in this myrmecochorous system seemingly increased the foraging efficiency of the ants, suggesting that *Vespula* may also indirectly impact seed dispersal (Bale *et al.*, 2003).

The large foraging range of wasps suggests that the process of vespicochory may disperse seeds further afield than ants (average dispersal: 1.99 m; Gómez & Espadaler, 2013), thus influencing population genetic structure, density-dependent mortality, and range expansion of plant species (Jules, 1996; Zettler *et al.*, 2001). Unfortunately, data on seed dispersal distance and seed fate from vespicochory are lacking and, thus, we are unable to verify the importance of this supporting service. Three studies have investigated dispersal distances from vespicochory to date, with distances ranging from 1.4 m (range = 0.1–2.6 m, $N = 41$) in vespicochorous interactions between *Vespula* and *Trillium* species (Zettler *et al.*, 2001) to 80 m ($N = 40$) and 110 m (range = 5–150 m, $N = 2138$) in interactions between *Vespa* species and *Aquilaria sinensis* and *Stemona tuberosa* respectively (Chen, Liu & Sun, 2016; Chen *et al.*, 2017).

We suggest that vespicochorous interactions between plants and social wasps may be more common than the literature currently suggests, with vespicochory representing an underappreciated service in ecosystems for social wasps, especially given the large dispersal distances of which they are capable (Chen *et al.*, 2016, 2017). The true value of this wasp ES is currently obscured due to the lack of data on seed dispersal efficiency, seed dispersal distance, and seed fate.

(2) Decomposition and nutrient cycling

The role of wasps in decomposition and nutrient cycling is almost entirely unstudied. Wasps primarily predate live prey. Social wasps, however, have been reported engaging in necrophagy (the eating of dead or decaying animals); carcasses are a source of amino acids, lipids, protein, carbohydrates, vitamins and minerals, although the quality of these resources depend on the taxon and stage of decomposition (Roubik, 1989). Reports of wasp necrophagy appear in the early literature (Ducke, 1910; Richards & Richards, 1951; Cornaby, 1974); e.g. Bertoni (1912) describes how bird carcasses can be stripped clean of flesh within hours by the actions of social wasps; anecdotal accounts of meat-eating by *Agelaia* wasps in South American countries abound, where these wasps have been given the local (Spanish) name of 'carniceras' (meaning 'butchers') (O'Donnell, 1995). Mammalian protein has also been detected in molecular analyses of wasp gut contents (Kasper *et al.*, 2004). This raises the possibility that wasps may contribute to the decomposition of waste products and to the recycling of nutrients.

Previous evidence suggests necrophagy by polistine wasps in Central and South America, with the swarm-founding genera *Polybia*, *Agelaia*, *Angiopolybia*, *Brachygastra*, *Parachartergus*, *Protonectarina* and *Synoeca* feeding on a wide range of wild 'carrion' from large insects to birds, reptiles, and mammals, to agricultural waste such as poultry, pigs and rats, and tuna fish baits laid out for ants (O'Donnell, 1995; Gomes *et al.*, 2007; Somavilla, Linard & Rafael, 2019). More recently, *Apoica* and *Polybia* have been reported scavenging on fresh and decaying pig carcasses under natural conditions in Brazil (Simões *et al.*, 2013); six species of *Epiponines* in Brazilian rainforest were detected using carrion traps (Silveira *et al.*, 2005) and 10 species were collected from carcasses of rats in similar environments (Somavilla *et al.*, 2019), with different species compositions on fresh and decaying cadavers; interestingly, wasps visiting the heavily decomposed cadavers were also observed preying on the fly eggs and larvae of Sarcophagidae and Calliphoridae (typically the first flies to colonise such carcasses) that were present. Finally, *Vespula* species are reported to scavenge on honey bee corpses (Pusceddu *et al.*, 2018).

It has been suggested that wasps are most likely to visit carcasses that are in an advanced stage of decay and thus may contribute little to the decomposition process itself. Reports of wasps attempting to extract tissue from live vertebrates, and also freshly killed carcasses suggest that this is not always the case and that the cues used to find the prey are not directly linked to the decay process itself. Wasps may additionally prey on the larvae laid by flies on carcasses, thus contributing a regulatory service by reducing fly populations (Gomes *et al.*, 2007), but also a cultural service through forensic analyses (see Section V.1). The possible effects of social wasps as consumers of fresh and decaying flesh may be substantial, but further research into the extent to which their presence speeds up decomposition is required.

V. CULTURAL SERVICES

(1) Aculeate wasps as biological indicators

Biological indicators are taxa that reflect the state of an environment, the effect of environmental change on a habitat or ecosystem, or the diversity of a subset of taxa within an area (Duelli & Obrist, 2003). Due to their important ESs, ubiquity and abundance, insects make excellent biological indicators (McGeoch, 1998). Theoretically, the predatory and parasitic aculeate wasps should be particularly useful in indicating the health of an ecosystem: by ranking highly in food webs, their presence in a habitat indicates the presence of an abundant and diverse community of prey arthropods (Gayubo *et al.*, 2005). Moreover, unlike vertebrate keystone predators, sampling wasp populations and measuring their abundance is relatively cheap and easy (Gayubo *et al.*, 2005).

Both solitary and social aculeate wasps appear to be useful bioindicators. For example, solitary apoid wasp diversity correlated well with habitat quality in a natural park in Portugal (Vieira, Oliveira & Gayubo, 2011): wasp diversity was highest in mixed juniper woodland, a well-protected native habitat, and lowest in eucalyptus plantation and fallow land, habitats that have been ecologically damaged by human intervention. Similarly, social wasp diversity correlated significantly with vegetative diversity in three contrasting Brazilian ecosystems – mangrove swamp, Atlantic rain forest and lowland sandy regions (Santos *et al.*, 2007). A further study in Brazil also found the social species *Pseudopolybia vespiceps* and *Polybia fastidiosuscula* to be excellent indicators of healthy forest ecosystems with high conservation value, whilst *Mischocyttarus drewsenii* was an indicator of the most disturbed habitats (de Souza *et al.*, 2010). Social wasps are also useful indicators of environmental contamination: analysis of larval faecal matter of both *Dolichovespula saxonica* and *Polistes dominula* reveals levels of lead and other heavy metals in the environment (Kowalczyk & Watała, 1989; Urbini, Sparvoli & Turillazzi, 2006); there is some evidence that the degree of melanisation in the facial marking of *Vespula* wasps is influenced by the level of heavy metals (Skaldina *et al.*, 2020). Such studies imply potential uses of solitary and social wasps for assessing ecosystem health, including the success of rewilding projects (Henson, Craze & Memmott, 2009).

Wasp larvae guts are promising units for arthropod biodiversity monitoring. Their generalist diets, and the sessile nature of wasp nests means sampling is likely to be holistic and geographically consistent. Metagenomic sequencing of the gut contents of parasitoid wasp larvae has revealed the identity of the larval host species of parasitoid wasps (Rougerie *et al.*, 2011). Sampling larval guts of aculeate wasps throughout the season could potentially provide data on seasonal variation in insect abundance and diversity. Furthermore, wasps may be used as a method of 'biosurveillance' across ecosystems. For instance, the prey range of *Cerceris fumipennis* (Crabronidae) includes the emerald ash borer (*Agrilus planipennis*), a highly invasive and damaging pest species of ash trees (*Fraxinus* spp.) across northern Europe and North America, and this wasp has been used to detect the presence of emerald ash borer, a method which far surpasses comparable human technology (Careless *et al.*, 2009).

The association of wasps with animal carcasses (see Section IV.2) also raises the possibility that wasps could be indicators of decay and thus of use in entomological forensics.

Different species of wasps have been reported at the same carcasses in the early and late stages of decay, raising the possibility that the type of wasp species could indicate, albeit qualitatively, the time since death. Unfortunately, wasp necrophagy may also add confusion to forensic investigations: the insects tend to remove lumps of tissue from cavities such as noses, mouth, ears and anus, altering the skin texture, size of cavities, and apparent injuries that may confuse *post-mortem* results, leading to errors in forensic investigations regarding the cause or mode of death (Moretti *et al.*, 2008; Simões *et al.*, 2013; Somavilla *et al.*, 2019).

(2) Wasps in culture and recreation

Wasps have a historically rocky relationship with humans, and this is apparent in cultures through the ages (Jones, 2019). The first published entomologist, Aristole, wrote: "Hornets and wasps…are devoid of the extraordinary features which characterize bees; this we should expect, for they have nothing divine about them as the bees have." God sends hornets as punishment to sinners in three books of the Bible (Deuteronomy 7:20; Exodus 23:28; Joshua 24:12). The novelist E.M. Forster (1924) in *A Passage to India* describes how his lead character on a discussion about which animals might be invited into heaven was able to accept that perhaps monkeys and jackals were welcome, but was uneasy with the idea that there may be a place in heaven for wasps. Science fiction writer Eric Frank Russell (1957) gave his 'terrorists' handbook' novel the title *Wasp* to depict the secretive, persistent and pernicious nature of the protagonist. The dislikeable nature of wasps perpetuates through film: the mistreated female star of the thriller, *The Wasp Woman*, becomes an evil, man-devouring 'wasp' by night (Corman, 1959); while over-sized fire-breathing wasps star as the antagonists in *Dragon Wasps*, an action movie set in the jungles of Belize. More positive media interpretations include that of the Marvel superhero 'The Wasp' (Reed, 2018). Wasps have also inspired art; e.g. wasps feature on ornaments and artwork from Asia, especially Japan, where evidence of appreciation of the beauty of wasps is apparent in pottery depicting the nest structures of social wasps, and as predators in scrolls dating back to the Qing dynasty (17th–18th century) (Jones, 2019).

Sadly, these few favourable depictions of wasps in art and culture are far out-numbered by the anger, hatred and general negativity expressed towards them from ancient to modern times. There are two reasons why people feel negatively towards wasps. The first is that they sting: in a survey of 750 members of the public, the word 'sting' was used overwhelmingly to describe wasps, but not bees (which also sting); the same study revealed that people believe that there is nothing useful about wasps, whereas the same group of people recognised the importance of bees as pollinators (Sumner *et al.*, 2018). Facets of nature that are uncharismatic *and* of no perceived value to humans receive the least attention by conservation initiatives (Daily *et al.*, 2000). Determining the ESs offered by a particular facet of nature has become the currency by which nature is valued and liked by humans (Redford & Adams, 2009).

The many and important ESs provided by stinging wasps (Table 1; Fig. 2) may provide the currency for humans to shift their perceptions of wasps to a more positive and tolerant one. Effective marketing of the benefits of wasps as a valuable, natural commodity that contributes to our health, food security and health (Hart & Sumner, 2020) may help elevate wasps towards a more valued status, alongside other beneficial insects.

VI. A RESEARCH ROADMAP FOR VALUING THE ECOSYSTEM SERVICES OF ACULEATE WASPS

We have collated from a vast, disconnected literature, a holistic evidence-base that aculeate wasps provide a wide array of important ESs (Table 1; Fig. 2). To date, these services have largely gone unappreciated. One of the reasons for this is that aculeate wasps are poorly studied relative to other insects whose ESs are well recognised; e.g. bees, hoverflies, beetles and even their close relatives the parasitoid wasps. We lack the necessary comprehensive information on aculeate wasp life histories and the experimental data to make quantitative and qualitative assessments of the magnitude of their impact. Here we outline some of the key questions that would help address these knowledge gaps and put the ESs of wasps on the map, alongside their relatives.

(1) Quantifying the impact of wasps as regulators of arthropod populations

The most important service provided by aculeate wasps is undoubtedly their role as nature's pest controllers in both natural and agricultural landscapes. In almost all cases, we lack direct quantification and experimentation. Outstanding questions include:

(*a*) In which natural ecological networks are social wasps key predators, and how will these networks be affected by changing populations of wasps?

We have shown qualitatively the diversity of arthropod orders that are preyed upon by social and solitary wasps (Fig. 3); but we have few quantitative data on of the quantity of prey items removed by wasps in a life cycle. Exclusion experiments (e.g. see Gould & Jeanne, 1984) are required to quantify the extent to which arthropod populations are regulated by different wasp species; such data will also provide insights into the potential ecological consequences of declining wasp populations (Archer, 2015; Bueno, Souza & Clemente, 2019; Outhwaite *et al.*, 2020) and the impacts of introduced wasp species across their invasive ranges (Beggs *et al.*, 2011; Lester & Beggs, 2019).

(*b*) What is the economic value of aculeate wasps as agents of biocontrol in agricultural landscapes?

Our review of wasp predation suggests that wasps hold great potential in controlling crop pests and we highlight the ways in which social wasps in particular may be especially effective biocontrol agents. Data are still sorely lacking on the extent to which wasps are effective in regulating pests in field-realistic situations, in the company of other predators and in complex ecological interactions. Moreover, the methods by which the predatory services of aculeate wasps can be harnessed and applied safely remain almost entirely unexplored. Vespiaries (wasp 'hives', akin to apiaries for bees) have been trialled only rarely (Gould & Jeanne, 1984; Donovan, 2003), and may only suit certain wasp species whose nests can be easily relocated; furthermore, managing wasps for biocontrol also demands sociological research in order to successfully implement strategies to surmount the negative cultural attitudes that people have towards wasps (Sumner *et al.*, 2018). Addressing the logistical, sociological and husbandry issues may be a greater challenge than answering the biological questions.

(*c*) Can life history and taxonomy be used to predict the quality and scope of biocontrol services provided by aculeate wasps?

Our databases on prey types of solitary and social aculeate wasps (Supplementary data sets S1 and S2; Fig. 3) identify life history (solitary *versus* social) as a primary indicator of the type of biocontrol services that wasps can provide, but also highlight how taxonomy (at the family or subfamily level) can also indicate specialist prey choice. It is clear that social wasps are, without exception, generalists in their prey choice (Fig. 3B). Although there are a great deal more data available on the prey of solitary aculeate wasps than social wasps, we lack a comprehensive understanding of the life histories of the vast majority of subfamilies, and as a consequence an understanding of their ecological impacts are taxonomically biased and poor in breadth and depth, especially when compared to the parasitoid wasps (Hawkins, Cornell & Hochberg, 1997). This lack of knowledge may account for the low utilisation of aculeate wasps in biological control programmes when compared to the parasitoid wasps (Greathead & Greathead, 1992; O'Neill, 2001) and their lack of commercial availability in augmentative biological control programmes (van Lenteren, 2012).

(2) Determining the contributions of aculeate wasps as pollinators in natural and agricultural landscapes

We identified 962 plant species, of diverse taxonomy, which depend either solely or partially on wasps for their pollination (Fig. 4). These include a number of orchids and shrubs which are solely reliant on wasps for pollination, without which they would go extinct; there is also evidence to suggest that wasps sometimes are at least as effective crop pollinators as bees. Extensive plant–pollinator networks for aculeate wasps only exist for southern Africa and partial pollination networks exist for areas in South America, Asia, and the Crimea (e.g. Kato, 2000; Corlett, 2001; Fateryga, 2010; Clemente *et al.*, 2012); such data are lacking for other locations where wasps are abundant. The plant–pollinator reports for aculeate wasps are largely limited to flower visitation records and rarely quantify the effectiveness of pollen transfer between flowers by wasps. Thus, we lack knowledge on the extent to which wasps contribute to the reproductive success of the plants they visit, and how wasps compare as pollinators to other well-studied species. It remains to be seen whether wasps may be effective back-up pollinators in poor-quality habitats where specialist pollinators such as bees and hoverflies may struggle to maintain populations.

(3) Developing social wasps as biological indicators

Aculeate wasps offer potential as bioindicators of habitat quality, biodiversity, and pollution from the species abundance, larval gut contents and potentially their body markings, respectively. However, the evidence for all these utilities is nascent and each requires substantial experimental research before wasps can be exploited for these services in any meaningful way.

(4) Harnessing the provisioning services of aculeate wasps

Societal benefits to humans offered by aculeate wasps include their role as a food source (Supplementary data set S5), providing a source of highly nutritious protein with low fat content in the diets of over 2 billion people worldwide. Their potential contribution to sustainable food production is underappreciated in most parts of the world; however, harvesting wasp colonies for nutrition is practiced by diverse communities in remote locations from rural India to Japan and Latin America, providing evidence that the logistical challenges of working with stinging insects can be surmounted if the prize is valued. At a time when sustainable food security for a growing human population is of global concern, alternative sources of protein are likely to become of critical economic and ecological importance. Along with other insect protein sources (e.g. soldier flies), social wasp larvae hold great potential due to the large quantity of brood to be harvested from a single colony. Finally, from a biomedical perspective, there is a growing research field exploiting the biochemical components of social wasp venom for antimicrobial properties and use in the treatment of cancer and other diseases.

(5) Documenting drivers of change for wasp populations

The impact of 'insectageddon' (Thomas, Jones & Hartley, 2019) is as relevant to the lesser loved insects, such as wasps, as it is to more beloved insects like bees and butterflies (Sumner *et al.*, 2018). We herein provide an evidence-base on 'the point of wasps', encouraging scientists, policymakers, conservationists and members of the public to *care* about aculeate wasp populations and how they may be affected by changing environments. Occurrence records for aculeate wasps suffer the same paucity of attention as other aspects of wasp biology (Sumner *et al.*, 2019). Recent analyses of 100 years of records on UK species highlight how some species appear to be relatively resilient to anthropogenic change (e.g. *Vespula vulgaris*), whilst others are declining rapidly (e.g. *Vespula rufa*) (Jonsson *et al.*, 2021; Outhwaite *et al.*, 2019); this pattern is typical of most insect groups (Outhwaite *et al.*, 2020) and calls for more tolerant approaches to dealing with wasps in human living spaces and in their conservation management. Given the potential contributions of aculeate wasps through the ESs they provide, tackling declines in wasp populations (e.g. Outhwaite *et al.*, 2019) could prove as important as ameliorating the decline of other 'high value' insects, such as bees.

VII. CONCLUSIONS

(1) We have collated data from a broad and disparate literature on how the varied life-histories of aculeate wasps impact the ecosystems they inhabit through pest control and pollination, and their broad-reaching potential for economic impacts on agriculture and human health. Our synthesis of these data provides the evidence base to show that aculeate wasps offer significant value to natural and agricultural ecosystems, the global economy, human health and society.

(2) Aculeate wasps offer important ESs as predators of arthropods. The hunting behaviour of both parasitic and predatory aculeate wasps is likely to play important roles in regulating arthropod communities across habitats worldwide. This suggests they are a fundamental part of the wider functioning of ecosystems, with a key role in the maintenance of biodiversity. Our synthesis of the data affords the identification of key differences in the ecological roles of aculeate wasps that may be due to their life histories. Solitary wasps are renowned for being prey specialists (Grissell, 2010); our data analysis indicates that some families are in fact more holistic in their hunting habits than previously thought. Further analyses of these groups are required to determine the extent to which prey choice is specialised at the genus, subfamily or species level. Taxonomy, therefore, may be a key predictor of the type and extent of regulatory services that solitary wasps provide. Social wasps are, without exception, generalist predators; their large colony sizes, and opportunistic predatory nature may mean that their ecological impact is significant in any habitat where they are present, natural or farmed.

(3) Anecdotal evidence has previously pointed to the roles of wasps as pollinators. Our data analysis reveals that wasps are involved in almost 1000 plant–pollinator relationships across a range of plants and habitats. Through obligate plant–pollinator relationships (where plants are solely reliant on wasps for pollination), wasps are vital to the survival and pollination of at least 164 plant species, perhaps most important of which are interactions between orchids and thyniid wasps, without which the orchids would almost certainly go extinct. Wasps also play roles in facultative plant–pollinator relationships (where plants are reliant on a range of insects, including wasps for pollination), potentially pollinating at least 798 plant species. Importantly, wasps appear to form highly generalist pollination networks and can function effectively as 'back-up' pollinators, ensuring that pollination can continue even when plants lose their primary pollinators (Hallett *et al.*, 2017).

(4) Wasp and wasp-derived products directly support human welfare. The larvae and pupae of social wasp species provide a nutritious dietary component for humans in at least 19 countries (although this is likely to be an underestimate), and the rearing of wasp nests as a marketable food source represents an important source of income for farmers in countries such as China and Japan, with nests selling for up to US$100 per kg in wet markets (Nonaka, 2010). Besides food, wasp-derived products such as venom, saliva and nest materials appear to present medicinal potential in the prevention of bacterial infections and in the treatment of cancer and other diseases.

(5) Wasps indirectly support the functioning of ecosystems through roles in seed dispersal and carrion decomposition. We identified at least 10 plant species in Asia, Europe and North America that have formed vespicochorous interactions with social wasps, and as a result are reliant upon them for efficient seed dispersal. Further, as scavengers, wasps also play roles in the decomposition and recycling of nutrients from vertebrate carrion.

(6) The cultural services provided by wasps include their use as biological indicators, along with their (largely negative) inspiration of the arts and appearance in the media. Given their predatory nature, both social and solitary wasp species diversity within an ecosystem can provide accurate measures of overall arthropod diversity, while some social wasp species have been shown to be accurate indicators of heavy metal contamination. Culturally, wasps have historically suffered from a negative relationship with humans, ranging from their delivery of punishment by God in the Bible, through to yearly tabloid coverage branding them with terms such as 'murder hornets'. Such coverage is unfortunate given the ESs provided by wasps, and we hope that public awareness of such services may lead to wasps being seen in a different light.

(7) The aculeate wasps are a highly speciose group of insects (Fig. 1) which display huge ecological and

evolutionary diversity. Unfortunately, it is one group of only 53 species that tarnishes our impression of wasps: the social wasps (which includes the genera *Vespa*, *Vespula* and *Dolichovespula*) account for just over 3% of aculeate wasps (Aguiar *et al.*, 2013). Their sometimes aggressive, annoying nature and the dominance of research into their success as invasive species (Lester & Beggs, 2019), has led to a focus on the economic and ecological *costs* associated with wasps, largely overlooking any benefits (e.g. Clapperton *et al.*, 1989; MacIntyre & Hellstrom, 2015). As a result, there is a general paucity of research on aculeate wasp life history, evolution and ecology, preventing an accurate quantitative and economic assessment of these roles. This is of pressing concern given recent evidence that wasp populations are declining at similar rates to other key insect ES providers (Outhwaite *et al.*, 2019). Quantitative and qualitative data on wasp life-history evolution and biotic interactions are required to assess their overall importance at ecological and economic scales. We have highlighted key areas of promise for understanding and harnessing better the ESs of wasps.

(8) A definition of ESs that includes 'both the benefits people perceive, and those they do not' (Costanza, 2016) is apt for the aculeate wasps. We look forward to a future where wasps are not viewed as 'pointless', but where their critical roles in multiple facets of human health and wellbeing are recognised, quantified and conserved. Wasps are most certainly a flagship group for illustrating the broader impacts of ESs, and in expanding our awareness of the range of values conferred by nature.

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IX. REFERENCES

Abbate, A., Campbell, J., Bremer, J. & Kern, W. H. (2018). The introduction and establishment of *Campsomeris dorsata* (Hymenoptera: Scoliidae) in Florida. *Florida Entomologist* **101**, 543–545.

Acuña, A. M., Caso, L., Aliphat, M. M. & Vergara, C. H. (2011). Edible insects as part of the traditional food system of the Popoloca town of los Reyes Metzontla, Mexico. *Journal of Ethnobiology* **31**, 150–169.

Aguiar, A. P., Deans, A. R., Engel, M. S., Forshage, M., Huber, J. T., Jennings, J. T., Johnson, N. F., Lelej, A. S., Longino, J. T., Lohrmann, V., Miko, I., Ohl, M., Rasmussen, C., Taeger, A. & Yu, D. S. K. (2013). Order Hymenoptera. *Zootaxa* **3703**, 51–62.

Akhter, F., Khanday, A. L. & Ahmad, S. T. (2016). Pollination potential: a comparative study of various hymenopteran insects pollinating some economically important crops in Kashmir. *International Journal of Advanced Research in Biological Sciences* **3**, 50–59.

Akre, R. D. & Myhre, E. A. (1994). The nesting biology and behavior of the California yellowjacket, *Vespula sulfurea* (Hymenoptera, Vespidae). *Entomological News* **105**, 141–148.

Alcock, J. (2000). Interactions between the sexually deceptive orchid *Spiculaea ciliata* and its wasp pollinator *Thynnoturneria* sp. (Hymenoptera: Thynninae). *Journal of Natural History* **34**, 629–636.

Ali, T. (1994). Pollination ecology of some Asclepiads (Asclepiadaceae) from Pakistan. PhD Thesis, University of Karachi, Pakistan.

Almeida, A. L. S., Albuquerque, U. P. & Castro, C. C. (2011). Reproductive biology of *Spondias tuberosa* Arruda (Anacardiaceae), an endemic fructiferous species of the caatinga (dry forest), under different management conditions in northeastern Brazil. *Journal of Arid Environments* **75**, 330–337.

Aluri, J. S. R., Reddi, C. S. & Das, K. R. (1998). Temporal dioecism and pollination by wasps and bees in *Allophylus serratus* (Roxb.) Radlk. (Sapindaceae). *Plant Species Biology* **13**, 1–5.

Alves-Silva, E., Barônio, G. J., Torezan-Silingardi, H. M. & Del-Claro, K. (2013). Foraging behavior of *Brachygastra lecheguana* (Hymenoptera: Vespidae) on *Banisteriopsis malifolia* (Malpighiaceae): Extrafloral nectar consumption and herbivore predation in a tending ant system. *Entomological Science* **16**, 162–169.

Amante, M., Schöller, M., Suma, P. & Russo, A. (2017). Bethylids attacking stored-product pests: an overview. *Entomologia Experimentalis et Applicata* **163**, 251–264.

Araújo, M. S. & Gonzaga, M. O. (2007). Individual specialization in the hunting wasp *Trypoxylon (Trypargilum) albonigrum* (Hymenoptera, Crabronidae). *Behavioral Ecology and Sociobiology* **61**, 1855–1863.

Araujo, Y. & Beserra, P. (2007). Diversidad de invertebrados consumidos por las etnias Yanomami y Yekuana del alto Orinoco, Venezuela. *Interciencia* **32**, 318–323.

Archer, M. E. (1985). Population dynamics of the social wasps *Vespula vulgaris* and *Vespula germanica* in England. *Journal of Animal Ecology* **54**, 473–485.

Archer, M. E. (1998). Worker versus sexual, and sex ratio investments in the social wasp *Vespula vulgaris* (L) (Hymenoptera: Vespinae) in England. *Journal of Hymenoptera Research* **7**, 257–267.

Archer, M. E. (2003). A numerical account of the development of colonies of the social wasp *Paravespula vulgaris* (L.) (Hym., Vespinae) in England and overseas. *Entomologist's Monthly Magazine* **139**, 139–160.

Archer, M. E. (2015). Population dynamics of a suburban garden's social wasps (Hymenoptera: Vespidae) over 30 years in Leicester, England. *Entomologist's Monthly Magazine* **151**, 189–195.

Argiolas, A. & Pisano, J. J. (1984). Isolation and characterization of two new peptides, mastoparan C and crabrolin, from the venom of the European hornet, *Vespa crabro*. *Journal of Biological Chemistry* **259**, 10106–10111.

Asanov, K. (1980). Predators and parasites of the lesser grain borer. *Zashchita Rastenii* **5**, 23.

Ashmead, W. H. (1894). The habits of the aculeate Hymenoptera—II. *Psyche* **7**, 39–46.

Auko, T. H., Silvestre, R. & Pitts, J. P. (2013). Nest camouflage in the spider wasp *Priochilus captivum* (Fabricius, 1804) (Hymenoptera: Pompilidae), with notes on the biology. *Tropical Zoology* **26**, 140–144.

Ayasse, M., Schiestl, F. P., Paulus, H. F., Ibarra, F. & Francke, W. (2003). Pollinator attraction in a sexually deceptive orchid by means of unconventional chemicals. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **270**, 517–522.

Baldock, J. W. (1934). The status of *Tiphia vernalis* Rohwer, an imported parasite of the Japanese beetle, at the close of 1933. *Journal of Economic Entomology* **27**, 491–496.

Bale, M. T., Zettler, J. A., Robinson, B. A., Spira, T. P. & Allen, C. R. (2003). Yellow jackets may be an underestimated component of an ant-seed mutualism. *Southeastern Naturalist* **2**, 609–614.

Ballou, H. A. (1909). Treatment of cotton pests in the West Indies in 1907. *West Indian Bulletin* **9**, 235–241.

Ballou, H. A. (1915). West Indian wasps. *Agricultural News (Barbados)* **14**, 298.

Barbosa, B. C., Silva, N. J. J., Zanuncio, J. C. & Prezoto, F. (2018). Occurrence of social wasps (Hymenoptera: Vespidae) in a sugarcane culture. *Sociobiology* **65**, 320–324.

Beattie, A. J. & Hughes, L. (2002). Ant-plant interactions. In *Plant Animal Interactions: An Evolutionary Approach* (eds C. M. Herrerea and O. Pellmyr), pp. 211–236. John Wiley & Sons, Hoboken.

Beggs, J. R., Brockerhoff, E. G., Corley, J. C., Kenis, M., Masciocchi, M., Muller, F., Rome, Q. & Villemant, C. (2011). Ecological effects and management of invasive alien Vespidae. *BioControl* **56**, 505–526.

Bell, E. & Sumner, S. (2013). Ecology and social organisation of wasps. In *eLS*. John Wiley & Sons, Ltd, Chichester.

Benamú, M., García, L. F., Viera, C., Lacava, M. & Korenko, S. (2020). Koinobiont life style of the spider wasp *Minagenia* (Hymenoptera, Pompilidae) and its consequences for host selection and sex allocation. *Zoology* **140**, 125797.

Bentley, J. W. & Rodriguez, G. (2001). Honduran folk entomology. *Current Anthropology* **42**, 285–300.

Berberet, R. C. & Helms, T. J. (1970). Notes on the biology of *Tiphia berbereti* (Hymenoptera: Tiphiidae), a parasite of larval *Phyllophaga anxia*. *Annals of the Entomological Society of America* **63**, 471–473.

Berchtold, E. (1981). Contribuição ao estudo da germinação e da biologia floral de *Asclepias curassavica* L. (Asclepiadaceae). Dissertação de mestrado, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brasil.

Bertoni, A. W. (1912). Contribucion a la biologia de las avispas y abejas del Paraguay (Hymenoptera). *Anales del Museo Nacional de Historia Natural de Buenos Aires* **15**, 97–146.

Betz, R. F., Struven, R. D., Wall, J. E. & Heitler, F. B. (1994). Insect pollinators of 12 milkweed (*Asclepias*) species. In *Proceedings of the Thirteenth North American Prairie Conference: Spirit of the Land, our Prairie Legacy* (eds R. G. Wickett, P. D. Lewis, A. Woodliffe and P. Pratt), pp. 45–60. Department of Parks & Recreation, Windsor.

Bhatnagar, S. (1986). On insect adaptations for pollination in some asclepiads in Central India. In *Pollination Biology - An Analysis* (ed. R. P. Kapil), pp. 37–57. Inter-India Publications, New Delhi.

Bhowmik, P. C. & Bandeen, J. D. (1976). The biology of Canadian weeds 19: *Asclepias syrinca* L. *Canadian Journal of Plant Species* **56**, 579–586.

Bohart, R. M., Bohart, R. M. & Menke, A. S. (1976). *Sphecid Wasps of the World: A Generic Revision*. University of California Press, Berkley.

Bohman, B., Phillips, R. D., Flematti, G. R., Barrow, R. A. & Peakall, R. (2017). The spider orchid *Caladenia crebra* produces sulfurous pheromone mimics to attract its male wasp pollinator. *Angewandte Chemie International Edition* **56**, 8455–8458.

Bokonon-Ganta, A. H., de Groote, H. & Neuenschwander, P. (2002). Socio-economic impact of biological control of mango mealybug in Benin. *Agriculture, Ecosystems & Environment* **93**, 367–378.

Bommarco, R., Miranda, F., Bylund, H. & Björkman, C. (2011). Insecticides suppress natural enemies and increase pest damage in cabbage. *Journal of Economic Entomology* **104**, 782–791.

Borowiec, M. L. & Kimsey, L. S. (2015). The first host record for the wasp subfamily Brachycistidinae (Hymenoptera: Tiphiidae). *Proceedings of the Entomological Society of Washington* **117**, 62–64.

Boulidam, S. (2010). Edible insects in a Lao market economy. In *Forest Insects as Food: Humans Bite Back* (eds P. B. Durst, D. V. Johnson, R. N. Leslie and K. Shono), pp. 131–141. Food and Agriculture Organisation of the United Nations, Bangkok.

Bower, C. C. (1996). Demonstration of pollinator-mediated reproductive isolation in sexually deceptive species of *Chiloglottis* (Orchidaceae: Caladeniinae). *Australian Journal of Botany* **44**, 15–33.

Bower, C. C. (2001a). *Arthrochilus* pollination. In *Genera Orchidacearum* (Volume **2**, eds A. Pridgeon, P. Cribb, M. Chase and F. Rasmussen), pp. 138–139. Oxford University Press, Oxford.

Bower, C. C. (2001b). *Caladenia* pollination. In *Genera Orchidacearum* (Volume **2**, eds A. Pridgeon, P. Cribb, M. Chase and F. Rasmussen), pp. 93–97. Oxford University Press, Oxford.

Bower, C. C. (2001c). *Caleana* pollination. In *Genera Orchidacearum* (Volume **2**, eds A. Pridgeon, P. Cribb, M. Chase and F. Rasmussen), pp. 141–143. Oxford University Press, Oxford.

Bower, C. C. & Branwhite, P. (1993). Observations on the pollination of *Calochilus campestris*. *The Orchadian* **11**, 68–71.

Bower, C. C. & Brown, G. R. (2009). Pollinator specificity, cryptic species and geographical patterns in pollinator responses to sexually deceptive orchids in the genus *Chiloglottis*: the *Chiloglottis gunnii* complex. *Australian Journal of Botany* **57**, 37–55.

Branstetter, M. G., Danforth, B. N., Pitts, J. P., Faircloth, B. C., Ward, P. S., Buffington, M. L., Gates, M. W., Kula, R. R. & Brady, S. G. (2017). Phylogenomic insights into the evolution of stinging wasps and the origins of ants and bees. *Current Biology* **27**, 1019–1025.

Brian, M. V. & Brian, A. D. (1952). The wasp, *Vespula sylvestris* Scopoli: feeding, foraging and colony development. *Transactions of the Royal Entomological Society of London* **103**, 1–26.

Bridwell, J. C. (1920). Some notes on Hawaiian and other Bethylidae (Hymenoptera) with the description of a new genus and species. 2nd paper. *Proceedings of the Hawaiian Entomological Society* **4**, 291–314.

Bristowe, W. S. (1948). Notes on the habits and prey of twenty species of British hunting wasps. *Proceedings of the Linnean Society of London* **160**, 12–37.

Brockmann, H. J. (1985). Provisioning behavior of the great golden digger wasp, *Sphex ichneumoneus* (L.) (Sphecidae). *Journal of the Kansas Entomological Society* **58**, 631–655.

Brodmann, J., Twele, R., Francke, W., Hölzler, G., Zhang, Q. H. & Ayasse, M. (2008). Orchids mimic green-leaf volatiles to attract prey-hunting wasps for pollination. *Current Biology* **18**, 740–744.

Brodmann, J., Twele, R., Francke, W., Yi-Bo, L., Xi-Qiang, S. & Ayasse, M. (2009). Orchid mimics honey bee alarm pheromone in order to attract hornets for pollination. *Current Biology* **19**, 1368–1372.

Brothers, D. J. (1981). Note on the biology of *Ycaploca evansi* (Hymenoptera: Scolebythidae). *Journal of the Entomological Society of Southern Africa* **44**, 107–108.

Brothers, D. J. & Finnamore, A. T. (1993). Superfamily Vespoidea. In *Hymenoptera of the World: An Identification Guide to Families* (eds H. Goulet and J. T. Huber), pp. 161–278. Canada Communication Group-Publishing, Ottawa.

Brown, E. M., Burbidge, A. H., Dell, J., Edinger, D., Hopper, S. D. & Wills, R. T. (1997). *Pollination in Western Australia: A Database of Animals Visiting Flowers*. Western Australia Naturalist's Club, Perth.

Brügger, B. P., La Cruz, R. A. D., de Carvalho, A. G., Soares, M. A., Prezoto, F. & Zanuncio, J. C. (2019). *Polybia fasticiosuscula* (Hymenoptera: Vespidae) foraging activity patterns. *Florida Entomologist* **102**, 264–265.

Budrienė, A. (2003). Prey of *Symmorphus* wasps (Hymenoptera: Eumeninae) in Lithuania. *Acta Zoologica Lituanica* **13**, 306–310.

Bueno, E. T., Carvalho, B. A. P. & Souza, M. M. (2020). Marimbondos (Hymenoptera, Vespidae) como fonte de alimentação humana no Brasil: Uma revisão de literatura. *Ethnoscientia* **5**, 1–8.

Bueno, E. T., Souza, M. M. & Clemente, M. A. (2019). The effect of forest fragmentation on Polistinae. *Sociobiology* **66**, 508–514.

Burge, D. O. & Beck, J. J. (2019). Dispersal of spicebush (*Calycanthus occidentalis*) by yellow jackets (genus *Vespula*; Hymenoptera: Vespidae). *Madrono* **66**, 41–46.

Buschini, M. L. T., Borba, N. A. & Brescovit, A. D. (2008). Patterns of prey selection of *Trypoxylon (Trypargilum) lactitarse* Saussure (Hymenoptera: Crabronidae) in southern Brazil. *Brazilian Journal of Biology* **68**, 519–528.

Buschini, M. L. T., Borba, N. A. & Brescovit, A. D. (2010a). Prey selection in the trap-nesting wasp *Trypoxylon (Trypargilum) opacum* Brèthes (Hymenprtera; Crabronidae). *Brazilian Journal of Biology* **70**, 529–536.

Buschini, M. L. T., Caldas, T. R., Borba, N. A. & Brescovit, A. D. (2010b). Spiders used as prey by the hunting wasp *Trypoxylon (Trypargilum) agamemnon* Richards (Hymenoptera: Crabronidae). *Zoological Studies* **49**, 169–175.

Buzatto, C. R., Davies, K. L., Singer, R. B., Pires Dos Santos, R. & van den Berg, C. (2012). A comparative survey of floral characters in *Capanemia* barb. Rodr. (Orchidaceae: Oncidiinae). *Annals of Botany* **109**, 135–144.

Cacayorin, N. D., Solsoloy, A. D., Damo, M. C. & Solsoloy, T. S. (1993). Beneficial arthropods regulating population of insect pest on cotton. *Cotton Research Journal* **6**, 1–8.

Cai, Y., Zhao, Y., Shih, C. & Ren, D. (2012). A new genus of Scolebythidae (Hymenoptera: Chrysidoidea) from the early cretaceous of China. *Zootaxa* **3504**, 56–66.

Callan, E. M. (1952). Embioptera of Trinidad with notes on their parasites. *Transactions of the Ninth International Congress of Entomology* **1**, 483–489.

Cambra, T. R., Quintero, A. D. & Miranda, R. (2004). Presas, comportamiento de anidación y nuevos registros de distribución en pompílidos neotropicales (Hymenoptera: Pompilidae). *Tecnociencia* **6**, 95–109.

Camillo, E. & Brescovit, A. D. (2000). Spider prey (Araneae) of *Trypoxylon (Trypargilum) rogenhoferi* (Hymenoptera: Sphecidae) in southeastern Brazil. *Revista de Biologia Tropical* **48**, 647–656.

Campbell, J. W., Stanley-Stahr, C., Bammer, M., Daniels, J. C. & Ellis, J. D. (2019). Contribution of bees and other pollinators to watermelon (*Citrullus lanatus* Thunb.) pollination. *Journal of Apicultural Research* **58**, 597–603.

Campos-Farinha, A. E. C. & Pinto, N. P. O. (1996). Natural enemies of *Chlosyne lacinia saundersii* Doubl. & hew. (Lepidoptera: Nymphalidae) in the state of São Paulo. *Anais da Sociedade Entomológica do Brasil* **25**, 165–168.

Careless, P. D., Marshall, S. A., Gill, B. D., Appleton, E., Favrin, R. & Kimoto, T. (2009). *Cerceris Fumipennis - A Biosurveillance Tool for Emerald Ash Borer*. Canadian Food Inspection Agency, Guelph.

Carvalho, F. P. (2006). Agriculture, pesticides, food security and food safety. *Environmental Science and Policy* **9**, 685–692.

Carvalho-Filho, F. D. S., Auko, T. H. & Waichert, C. (2015). Observations on the nesting behaviour of the spider wasp *Eragenia congrua* (Hymenoptera: Pompilidae), with the first record of the host. *Journal of Natural History* **49**, 2035–2044.

Cazier, M. A. & Mortenson, M. A. (1964). Bionomical observations on tarantula-hawks and their prey (Hymenoptera: Pompilidae: Pepsis). *Annals of the Entomological Society of America* **57**, 533–541.

Cesário, L. F. & Gaglianone, M. C. (2013). Polinizadores de *Schinus terebinthifolius* Raddi (Anacardiaceae) em formações vegetacionais de restinga no norte do estado do Rio de Janeiro. *Bioscience Journal* **29**, 458–467.

Chase, M. W. (1986). Pollination ecology of two sympatric synchronously flowering species of *Leochilus* in Costa Rica. *Lindleyana* **1**, 141–147.

Chaturvedi, S. K. (1986). Pollination and pollen germination in *Cynanchum canescens* (Willd.) Schum. *Asklepios* **40**, 93–96.

Chaturvedi, S. K. & Pant, D. D. (1986). Further studies in the pollination of some Indian asclepiads. *Bulletin of the Botanical Survey of India* **28**, 23–30.

Chauhan, S., Chauhan, S. V. S. & Galetto, L. (2017). Floral and pollination biology, breeding system and nectar traits of *Callistemon citrinus* (Myrtaceae) cultivated in India. *South African Journal of Botany* **111**, 319–325.

Chen, G., Liu, C. & Sun, W. (2016). Pollination and seed dispersal of *Aquilaria sinensis* (Lour.) Gilg (Thymelaeaceae): an economic plant species with extremely small populations in China. *Plant Diversity* **38**, 227–232.

Chen, G., Wang, Z. W., Qin, Y. & Sun, W. B. (2017). Seed dispersal by hornets: an unusual insect-plant mutualism. *Journal of Integrative Plant Biology* **59**, 792–796.

Chen, X., Feng, Y. & Chen, Z. (2009). Common edible insects and their utilization in China. *Entomological Research* **39**, 299–303.

Cheng, J., Shi, J., Shangguan, F. Z., Dafni, A., Deng, Z. H. & Luo, Y. B. (2009). The pollination of a self-incompatible, food-mimic orchid, *Coelogyne fimbriata* (Orchidaceae), by female *Vespula* wasps. *Annals of Botany* **104**, 565–571.

Cheng, W. Y. (1991). Importation of natural enemies for the control of sugarcane insect pests in Taiwan in 1955 to 1989. *Taiwan Sugar* **38**, 11–17.

Chung, A. Y. C. (2010). Edible insects and entomophagy in Borneo. In *Forest Insects as Food: Humans Bite Back* (eds P. B. Durst, D. V. Johnson, R. N. Leslie and K. Shono), pp. 141–150. Food and Agriculture Organisation of the United Nations, Bangkok.

Ciotek, L., Giorgis, P., Benitez-Vieyra, S. & Cocucci, A. A. (2006). First confirmed case of pseudocopulation in terrestrial orchids of South America: pollination of *Geoblasta pennicillata* (Orchidaceae) by *Campsomeris bistrimacula* (Hymenoptera, Scoliidae). *Flora: Morphology, Distribution, Functional Ecology of Plants* **201**, 365–369.

Clapperton, B. K. (1999). Abundance of wasps and prey consumption of paper wasps (Hymenoptera, Vespidae: Polistinae) in northland, New Zealand. *New Zealand Journal of Ecology* **23**, 11–19.

Clapperton, B. K., Alspach, P. A., Moller, H. & Matheson, A. G. (1989). The impact of common and German wasps (Hymenoptera: Vespidae) on the New Zealand beekeeping industry. *New Zealand Journal of Zoology* **16**, 325–332.

Clapperton, B. K., Tilley, J. A. V. & Pierce, R. J. (1996). Distribution and abundance of the Asian paper wasp *Polistes chinensis antennalis* Pérez and the Australian paper wasp *P. humilis* (fab.) (Hymenoptera: Vespidae) in New Zealand. *New Zealand Journal of Zoology* **23**, 19–25.

Clemente, M. A., Campos, N. R., Vieira, K. M., Del-Claro, K. & Prezoto, F. (2017). Social wasp guild (Hymenoptera: Vespidae) visiting flowers in two of the phytophysiognomic formations: riparian forest and Campos rupestres. *Sociobiology* **64**, 217–224.

Clemente, M. A., Lange, D., Del-Claro, K., Prezoto, F., Campos, N. R. & Barbosa, B. C. (2012). Flower-visiting social wasps and plants interaction: network pattern and environmental complexity. *Psyche (London)* **2012**, 1–10.

Clements, F. E. & Long, F. L. (1923). *Experimental Pollination; An Outline of the Ecology of Flowers and Insects*. Carnegie Institution of Washington, Washington, DC.

Clinebell, R. R. & Bernhardt, P. (1998). The pollination ecology of five species of *Penstemon* (Scrophulariaceae) in the tallgrass prairie. *Annals of the Missouri Botanical Garden* **85**, 126–136.

Coombs, G. (2010). *Ecology and Degree of Specialization of South African Milkweeds with Diverse Pollination Systems*, p. 312. Rhodes University, Grahamstown.

Coombs, G., Peter, C. & Johnson, S. (2009). A test for allee effects in the self-incompatible wasp-pollinated milkweed *Gomphocarpus physocarpus*. *Austral Ecology* **34**, 688–697.

Cooper, K. W. (1953). Biology of eumenine wasps I. the ecology, predation, nesting and competition of *Ancistrocerus antilope*. *Transactions of the American Entomological Society* **79**, 13–35.

Corlett, R. T. (2001). Pollination in a degraded tropical landscape: a Hong Kong case study. *Journal of Tropical Ecology* **17**, 155–161.

Corman, R. (1959). *The Wasp Woman*. Allied Artists Pictures Corporation, Glendale.

Cornaby, B. W. (1974). Carrion reduction by animals in contrasting tropical habitats. *Biotropica* **6**, 51–63.

Costa, F. G., Pérez-Miles, F. & Mignone, A. (2004). Pompilid wasp interactions with burrowing tarantulas: *Pepsis cupripennis* versus *Eupalaestrus weijenberghi* and *Acanthoscurria suina* (Araneae, Theraphosidae). *Studies on Neotropical Fauna and Environment* **39**, 37–43.

Costanza, R. (2016). Ecosystem services in theory and practice. In *Routledge Handbook of Ecosystem Services* (eds M. Potschin, R. Haines-Young, R. Fish and R. K. Turner), pp. 15–24. Routledge, London.

Costanza, R., D'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R. V., Paruelo, J., Raskin, R. G., Sutton, P. & van den Belt, M. (1998). The value of the world's ecosystem services and natural capital. *Nature* **387**, 253–260.

Cotton, R. T. & Good, N. E. (1937). *Annotated List of the Insects and Mites Associated with Stored Grain and Cereal Products, and of their Arthropod Parasites and Predators (No. 258)*. United States Department of Agriculture, Washington, DC.

Coville, R. E. & Griswold, C. (1983). Nesting biology of *Trypoxylon xanthandrum* in Costa Rica with observations on its spider prey (Hymenoptera: Sphecidae; Araneae: Senoculidae). *Journal of the Kansas Entomological Society* **56**, 205–216.

Cremer, S., Armitage, S. A. O. & Schmid-Hempel, P. (2007). Social immunity. *Current Biology* **17**, R693–R702.

Das, K. R., Reddi, C. S., Aluri, R. J. S. & Atluri, J. B. (1997). Sexual system and pollination ecology of *Cardiospermum halicacabum* L.(Sapindaceae). *Bombay Natural History Society* **94**, 333–341.

Daily, G. C., Söderqvist, T., Aniyar, S., Arrow, K., Dasgupta, P., Ehrlich, P. R., Folke, C., Jansson, A., Jansson, B.-O., Kautsky, N., Levin, S., Lubchenco, J., Mäler, K.-G., Simpson, D., Starrett, D., et al. (2000). The value of nature and the nature of value. *Science* **289**, 395–396.

Dang, H. T. & Nguyen, L. T. P. (2019). Nesting biology of the potter wasp *Rhynchium brunneum brunneum* (Fabricius, 1793) (Hymenoptera: Vespidae: Eumeninae) in North Vietnam. *Journal of Asia-Pacific Entomology* **22**, 427–436.

Dangles, O. & Casas, J. (2019). Ecosystem services provided by insects for achieving sustainable development goals. *Ecosystem Services* **35**, 109–115.

Danthanarayana, W. (1980). Parasitism of the light brown apple moth, *Epiphyas Postvittana* (Walker), by its larval ectoparasite, *Goniozus jicintae farrugia* (Hymenoptera: Bethylidae), in natural populations in Victoria. *Australian Journal of Zoology* **28**, 685–692.

Dapporto, L., Stefanini, I., Rivero, D., Polsinelli, M., Capretti, P., de Marchi, P., Viola, R., Turillazzi, S. & Cavalieri, D. (2016). Social wasp intestines host the local phenotypic variability of *Saccharomyces cerevisiae* strains. *Yeast* **33**, 277–287.

Das Neves, R. C., Trentini, M. M., de Castro E Silva, J., Simon, K. S., Bocca, A. L., Silva, L. P., Mortari, M. R., Kipnis, A. & Junqueira-Kipnis, A. P. (2016). Antimycobacterial activity of a new peptide polydim-i isolated from neotropical social wasp *Polybia dimorpha*. *PLoS One* **11**, e0149729.

Dean, H., Schuster, M., Boling, J. & PT, R. (1979). Complete biological control of *Antonina graminis* in Texas with *Neodusmetia sangwani* (a classic example). *Bulletin of the Entomological Society of America* **25**, 262–267.

de Brito, V. L. G., Rech, A. R., Ollerton, J. & Sazima, M. (2017). Nectar production, reproductive success and the evolution of generalised pollination within a specialised pollen-rewarding plant family: a case study using *Miconia theizans*. *Plant Systematics and Evolution* **303**, 709–718.

de Charmoy, D. D. (1917). Notes relative to the importation of *Tiphia parallela*, Smith, from Barbados to Mauritius for the control of *Phytalus smithi* Arrow. *Bulletin of Entomological Research* **8**, 93–102.

DeFoliart, G.R. (2002). The human use of insects as a food resource: a bibliographic account in progress. http://labs.russell.wisc.edu/insectsasfood/the-human-use-of-insects-as-a-food-resource/

de Graaf, D. C., Aerts, M., Danneels, E. & Devreese, B. (2009). Bee, wasp and ant venomics pave the way for a component-resolved diagnosis of sting allergy. *Journal of Proteomics* **72**, 145–154.

Dejean, A., Céréghino, R., Carpenter, J. M., Corbara, B., Hérault, B., Rossi, V., Leponce, M., Orivel, J. & Bonal, D. (2011). Climate change impact on Neotropical social wasps. *PLoS One* **6**, e27004.

Dejean, A., Rodríguez-Pérez, H., Carpenter, J. M., Azémar, F. & Corbara, B. (2017). The predatory behavior of the Neotropical social wasp *Polybia rejecta*. *Behavioural Processes* **140**, 161–168.

de Melo, G. A. R. & Evans, H. E. (1993). Two new microstigmus species (Hymenoptera: Sphecidae) with the description of their parasite *Goniozus microstigmi* new-species (Hymenoptera: Bethylidae). *Proceedings of the Entomological Society of Washington* **95**, 258–263.

de Souza, M. M., Louzada, J., Serrão, J. E. & Zanuncio, J. C. (2010). Social wasps (Hymenoptera: Vespidae) as indicators of conservation degree of riparian forests in Southeast Brazil. *Sociobiology* **56**, 387–396.

Devi, K. R., Atluri, J. B. & Reddi, C. S. (1989). Pollination ecology of *Zizyphus mauritiana* (Rhamnaceae). *Proceedings: Plant Sciences* **99**, 223–239.

Dickson, C. R. & Petit, S. (2006). Effect of individual height and labellum colour on the pollination of *Caladenia* (syn. *Arachnorchis*) *behrii* (Orchidaceae) in the northern Adelaide region, South Australia. *Plant Systematics and Evolution* **262**, 65–74.

Dodson, C. H. (1990). Brassia. In *Native Colombian Orchids, vol. I* (eds R. Escobar and J. M. Munera), pp. 52–53. Editorial Colina, Compañía Litografica Nacional, Medellín.

Domínguez, K. & Jiménez, M. L. (2008). Composition of spider prey captured by the wasp *Trypoxylon (Trypargilum) tridentatum tridentatum* in two habitats in an oasis in Baja California Sur, Mexico. *The Canadian Entomologist* **140**, 388–392.

Donaldson, M. R., Burnett, N. J., Braun, D. C., Suski, C. D., Hinch, S. G., Cooke, S. J. & Kerr, J. T. (2017). Taxonomic bias and international biodiversity conservation research. *FACETS* **1**, 105–113.

Donovan, B. (2003). Potential manageable exploitation of social wasps, *Vespula* spp. (Hymenoptera: Vespidae), as generalist predators of insect pests. *International Journal of Pest Management* **49**, 281–285.

dos Santos, E. F., Waichert, C. & Scott dos Santos, C. P. (2017). Behavioural notes on the Neotropical parasocial spider wasp *Ageniella* (*Lissagenia*) *flavipennis* (banks) (Hymenoptera: Pompilidae), with host association. *Ecological Entomology* **42**, 96–99.

Ducke, A. (1910). Révision des guêpes sociales polygames d'Amérique. *Annales Museu Nationalis Hungarici* **8**, 449–544.

Duelli, P. & Obrist, M. K. (2003). Biodiversity indicators: the choice of values and measures. *Agriculture, Ecosystems and Environment* **98**, 87–98.

Dufour, D. L. (1987). Insects as food: a case study from the Northwest Amazon. *American Anthropologist* **89**, 383–397.

Dupont, Y. L. & Olesen, J. M. (2009). Ecological modules and roles of species in heathland plant-insect flower visitor networks. *Journal of Animal Ecology* **78**, 346–353.

Elizalde, L., Arbetman, M., Arnan, X., Eggleton, P., Leal, I. R., Lescano, M. N., Saez, A., Werenkraut, V. & Pirk, G. I. (2020). The ecosystem services provided by social insects: traits, management tools and knowledge gaps. *Biological Reviews* **95**, 1418–1441.

Ellis, A. G. & Johnson, S. D. (2010). Floral mimicry enhances pollen export: the evolution of pollination by sexual deceit outside of the orchidaceae. *The American Naturalist* **176**, E143–E151.

Endo, T. & Endo, A. (1994). Prey selection by a spider wasp, *Batozonellus lacerticida* (Hymenoptera: Pompilidae): effects of seasonal variation in prey species, size and density. *Ecological Research* **9**, 225–235.

Evans, H. E. (1987). Observations on natural enemies of western spruce budworm (*Choristoneura occidentalis* freeman) (Lepidoptera, Tortricidae) in the Rocky Mountain area. *Great Basin Naturalist* **47**, 319–321.

Evans, H. E. & Hook, A. W. (1986). Prey selection by Australian wasps of the genus *Cerceris* (Hymenoptera, Sphecidae). *Journal of Natural History* **20**, 1297–1307.

Evans, H. E. & O'Neill, K. M. (2007). *The Sand Wasps*. Harvard University Press, Cambridge.

Evans, H. E. & Rubinka, W. L. (1979). Notes on the nesting behavior of the Bethylid wasp, *Epyris eriogoni* Kieffer, in southern Texas. *Psyche* **86**, 313–319.

Evans, H. E. & West-Eberhard, M. J. (1970). *The Wasps*. University of Michigan Press, Ann Arbor.

Fabre, J. H. (1920). *More Hunting Wasps*. Hodder & Stoughton, London.

Fairhead, J. R. (2017). Termites, mud daubers and their earths: a multispecies approach to fertility and power in West Africa. *Conservation and Society* **14**, 359–367.

Fateryga, A. (2010). Trophic relations between vespid wasps (Hymenoptera, Vespidae) and flowering plants in the Crimea. *Entomological Review* **90**, 698–705.

Fateryga, A. V. & Ivanov, S. P. (2013). Nesting biology of *Paravespa rex* (von Schulthess 1924) (Hymenoptera: Vespidae: Eumeninae) in the Crimea, Ukraine. *Zootaxa* **3721**, 589–600.

Federici, M., Polidori, C., Pesarini, C. & Andrietti, F. (2007). Factors affecting spider prey selection by *Sceliphron* mud-dauber wasps (Hymenoptera: Sphecidae) in northern Italy. *Animal Biology* **57**, 11–28.

Fernandes, F. L., de Fernandes, M. E. S., Picanço, M. C., Geraldo, G. C., Demuner, A. J. & Da Silva, R. S. (2010). Coffee volatiles and predatory wasps (Hymenoptera: Vespidae) of the coffee leaf miner *Leucoptera coffeella*. *Sociobiology* **56**, 455–464.

Field, J. (1992). Intraspecific parasitism and nest defence in the solitary pompilid wasp *Anoplius viaticus* (Hymenoptera: Pompilidae). *Journal of Zoology* **228**, 341–350.

Filho, C. C. B., Santos, G. M. D. M., dos Santos Filho, A. B., Santana-Reis, V. P., da Cruz, J. D. & Gobbi, N. (2010). Foraging behavior of the swarm-founding wasp *Polybia (Trichothorax) sericea* (Hymenoptera, Vespidae): Daily resource collection activity and flight capacity. *Sociobiology* **55**, 899–907.

Filho, G.M.T. (2008). Fenologia, biologia reprodutiva e ecologia da polinização de *Calotropis procera* Ait. R. Br. (Apocynaceae-Asclepiadoideae). Dissertação (Mestrado), Universidade Federal de Pernambuco, Brasil.

Fishbein, M. & Venable, D. L. (1996). Diversity and temporal change in the effective pollinators of *Asclepias tuberosa*. *Ecology* **77**, 1061–1073.

Fleming, P. A., Hofmeyr, S. D. & Nicolson, S. W. (2007). Role of insects in the pollination of *Acacia nigrescens* (Fabaceae). *South African Journal of Botany* **73**, 49–55.

Forster, E. M. (1924). *A Passage to India*. Edward Arnold Publishers Ltd, London.

Freitas, L., Bernardello, G., Galetto, L. & Paoli, A. A. S. (2001). Nectaries and reproductive biology of *Croton sarcopetalus* (Euphorbiaceae). *Botanical Journal of the Linnean Society* **136**, 267–277.

Freitas, L. & Sazima, M. (2006). Pollination biology in a tropical high-altitude grassland in Brazil: interactions at the community level. *Annals of the Missouri Botanical Garden* **93**, 465–516.

Fujiwara, Y., Mangetsu, M., Yang, P., Kofujita, H., Suzuki, K., Ohfune, Y. & Shinada, T. (2008). A quinone isolated from the nest of *Vespa simillima* and its growth-inhibitory effect on rat liver cancer cells. *Biological and Pharmaceutical Bulletin* **31**, 722–725.

Galetto, L. (2006). Morfología y anatomía floral en especies de Asclepiadoideae (Apocynaceae). *Kurtziana* **32**, 1–18.

Gallai, N., Salles, J. M., Settele, J. & Vaissière, B. E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics* **68**, 810–821.

Gambino, P. (1986). Winter prey collection at a perennial Colony of *Paravespula vulgaris* (l.) (Hymenoptera: Vespidae). *Psyche* **93**, 331–340.

Gambino, P., Medeiros, A. C. & Loope, L. L. (1987). Introduced vespids *Paravespula pensylvanica* prey on Maui's endemic arthropod fauna. *Journal of Tropical Ecology* **3**, 169–170.

Garcete-Barrett, B. R. & Dück, C. H. K. (2010). Biological observations on the genus *Ceramiopsis zavattari* (Insecta: Hymenoptera: Vespidae: Masarinae). *Boletín del Museo Nacional de Historia Natural del Paraguay* **16**, 8–17.

Gaskett, A. C. (2011). Orchid pollination by sexual deception: pollinator perspectives. *Biological Reviews* **86**, 33–75.

Gaston, K. J. & Lawton, J. H. (1988). Patterns in the distribution and abundance of insect populations. *Nature* **331**, 709–712.

Gayubo, S. F., González, J. A., Asís, J. D. & Tormos, J. (2005). Conservation of European environments: the Spheciformes wasps as biodiversity indicators (Hymenoptera: Apoidea: Ampulicidae, Sphecidae and Crabronidae). *Journal of Natural History* **39**, 2705–2714.

Genaro, J. A. & Alayón, G. (1994). Las presas (Araneae) de *Trypoxylon (Trypargilum) subimpressum* (Hymenoptera: Sphecidae) en Cuba. *Revista de Biologia Tropical* **42**, 353–356.

Genaro, J. A. & Sanchez, C. S. (1993). Conducta de nidificacion de *Cerceris cerverae*, *C. cubensis* y *C. festiva* en Cuba (Hymenoptera: Sphecidae). *Caribbean Journal of Science* **29**, 39–43.

Gess, F. W. (2009). The genus *Quartinia* Ed. André, 1884 (Hymenoptera, Vespidae, Masarinae) in southern Africa. Part III. New and little known species with incomplete venation. *Journal of Hymenoptera Research* **18**, 244–281.

Gess, F. (2011a). The genus Quartinia Ed. André, 1884 (Hymenoptera, Vespidae, Masarinae) in southern Africa. Part IV. New and little known species with complete venation. *Journal of Hymenoptera Research* **21**, 1–39.

Gess, F. (2011b). The genus Quartinia Ed. André, 1884 (Hymenoptera, Vespidae, Masarinae) in southern Africa. Part V. new and little known species with complete venation. *Journal of Hymenoptera Research* **21**, 1–39.

Gess, F. (2012). The genus Quartinia Ed. Andre, 1884 (Hymenoptera, Vespidae, Masarinae) in southern Africa. Part VI. New and little known species both with complete and incomplete venation. *Journal of Hymenoptera Research* **24**, 95–115.

Gess, S. K. & Gess, F. W. (2004). Distributions of flower associations of pollen wasps (Vespidae: Masarinae) in southern Africa. *Journal of Arid Environments* **57**, 17–44.

Gess, S. K. & Gess, F. W. (2010). *Pollen Wasps and Flowers in Southern AfricaSANBI Biodiversity Series 18*. South African National Biodiversity Institute, Pretoria.

Giannotti, E., Prezoto, F. & Machado, V. L. L. (1995). Foraging activity of *Polistes lanio lanio* (Fabr.) (Hymenoptera: Vespidae). *Anais da Sociedade Entomológica do Brasil* **24**, 455–463.

Gobbi, N. & Machado, V. L. L. (1985). Material capturado e utilizado na alimentação de *Polybia (Myrapetra) paulista* Ihering, 1896 (Hymenoptera, Vespidae). *Anais da Sociedade Entomológica do Brasil* **14**, 189–195.

Gobbi, N. & Machado, V. L. L. (1986). Material capturado e utilizado na alimentação de *Polybia (Trichothorax) ignobilis* (Haliday, 1836) (Hymenoptera, Vespidae). *Anais da Sociedade Entomológica do Brasil* **15**, 117–124.

Gobbi, N., Machado, V. L. L. & Tavares Filho, J. A. (1984). Sazonalidade das presas utilizadas na alimentação de *Polybia occidentalis occidentalis* (Oliver, 1791) (Hym., Vespidae). *Anais da Sociedade Entomológica do Brasil* **13**, 63–69.

Goldblatt, P., Bernhardt, P. & Manning, J. C. (2009). Adaptive radiation of the putrid perianth: *Ferraria* (Iridaceae: Irideae) and its unusual pollinators. *Plant Systematics and Evolution* **278**, 53–65.

Gomes, L., Gomes, G., Oliveira, H. G., Morlin, J. J., Desuó, I. C., Da Silva, I. M., Shima, S. N. & Von Zuben, C. J. (2007). Foraging by *Polybia* (*Trichothorax*) *ignobilis* (Hymenoptera, Vespidae) on flies at animal carcasses. *Revista Brasileira de Entomologia* **51**, 389–393.

Gómez, C. & Espadaler, X. (2013). An update of the world survey of myrmecochorous dispersal distances. *Ecography* **36**, 1193–1201.

Gonring, A. H. R., Picanço, M. C., Guedes, R. N. C. & Silva, E. M. (2003). Natural biological control and key mortality factors of *Diaphania hyalinata* (Lepidoptera: Pyralidae) in cucumber. *Biocontrol Science and Technology* **13**, 361–366.

Gonzaga, M. O. & Vasconcellos-Neto, J. (2006). Nesting characteristics and spiders (Arachnida: Araneae) captured by *Auplopus argutus* (Hymenoptera: Pompilidae) in an area of Atlantic Forest in southeastern Brazil. *Entomological News* **117**, 281–287.

Gould, W. P. & Jeanne, R. L. (1984). *Polistes* wasps (Hymenoptera: Vespidae) as control agents for lepidopterous cabbage pests. *Environmental Entomology* **13**, 150–156.

Goulet, H. & Huber, J. T. (1993). *Hymenoptera of the World: An Identification Guide to Families*. Canada Communication Group-Publishing, Ottawa.

Grant, J. (1959). Hummingbirds attacked by wasps. *Canadian Field-Naturalist* **73**, 174.

Greathead, D. J. & Greathead, A. H. (1992). Biological control of insect pests by parasitoids and predators: the BIOCAT database. *Biocontrol News and Information* **13**, 61–68.

Greeney, H. F., Dyer, L. A. & Smilanich, A. M. (2012). Feeding by lepidopteran larvae is dangerous: a review of caterpillars' chemical, physiological, morphological, and behavioral defenses against natural enemies. *Invertebrate Survival Journal* **9**, 7–34.

Griffin, A. R., Hingston, A. B. & Ohmart, C. P. (2009). Pollinators of *Eucalyptus regnans* (Myrtaceae), the world's tallest flowering plant species. *Australian Journal of Botany* **57**, 18–25.

Grissell, E. (2010). *Bees, Wasps, and Ants: The Indispensable Role of Hymenoptera in Gardens*. Timber Press, Portland.

Guan, X., Zhou, Y., Liang, X., Xiao, J., He, L. & Li, J. (2012). Effects of compounds found in Nidus Vespae on the growth and cariogenic virulence factors of *Streptococcus mutans*. *Microbiological Research* **167**, 61–68.

Guglielmino, A., Olmi, M. & Buckle, C. (2013). An updated host-parasite catalogue of world Dryinidae (Hymenoptera: Chrysidoidea). *Zootaxa* **3740**, 1–113.

Guimarães, D. L., de Castro, M. M. & Prezoto, F. (2008). Patterns of honey storage in colonies of the social wasp *Mischocyttarus cassununga* (Hymenoptera, Vespidae). *Sociobiology* **51**, 655–660.

Gurney, A. B. (1953). Notes on the biology and immature stages of a cricket parasite of the genus *Rhopalosoma*. *Proceedings of the United States National Museum* **103**, 19–34.

Gutiérrez-Chacón, C., Fornoff, F., Ospina-Torres, R. & Klein, A. M. (2018). Pollination of granadilla (*Passiflora ligularis*) benefits from large wild insects. *Journal of Economic Entomology* **111**, 1526–1534.

Hallett, A. C., Mitchell, R. J., Chamberlain, E. R. & Karron, J. D. (2017). Pollination success following loss of a frequent pollinator: the role of compensatory visitation by other effective pollinators. *AoB PLANTS* **9**, plx020.

Hamm, A. H. & Richards, O. W. (1926). The biology of the British Crabronidae. *Transactions of the Royal Entomological Society of London* **2**, 297–331.

Hanboonsong, Y. (2010). Edible insects and associated food habits in Thailand. In *Forest Insects as Food: Humans Bite Back* (eds P. B. Durst, D. V. Johnson, R. N. Leslie and K. Shono), pp. 173–182. Food and Agriculture Organisation of the United Nations, Bangkok.

Hanboonsong, Y. & Durst, P. B. (2014). *Edible Insects in Lao PDR: Building on Tradition to Enhance Food Security*. Food and Agriculture Organisation of the United Nations, Regional Office for Asia and the Pacific, Bangkok.

Harrington, R., Anton, C., Dawson, T. P., de Bello, F., Feld, C. K., Haslett, J. R., Kluvánkova-Oravská, T., Kontogianni, A., Lavorel, S., Luck, G. W., Rounsevell, M. D. A., Samways, M. J., Settele, J., Skourtos, M., Spangenberg, J. H., Vandewalle, M., Zobel, M. & Harrison, P. A. (2010). Ecosystem services and biodiversity conservation: concepts and a glossary. *Biodiversity and Conservation* **19**, 2773–2790.

Harris, R. J. (1991). Diet of the wasps *Vespula vulgaris* and *V. germanica* in honeydew beech forest of the South Island, New Zealand. *New Zealand Journal of Zoology* **18**, 159–169.

Harris, R. J. (1996). Frequency of overwintered *Vespula germanica* (Hymenoptera: Vespidae) colonies in scrubland-pasture habitat and their impact on prey. *New Zealand Journal of Zoology* **23**, 11–17.

Harris, R. J. & Oliver, E. H. (1993). Prey diets and population densities of the wasps *Vespula vulgaris* and *V. germanica* in scrubland-pasture. *New Zealand Journal of Ecology* **17**, 5–12.

Hart, A. G. & Sumner, S. (2020). Marketing insects: can exploiting a commercial framework help promote undervalued insect species? *Insect Conservation and Diversity* **13**, 214–218.

Hawkins, B. A., Cornell, H. V. & Hochberg, M. E. (1997). Predators, parasitoids, and pathogens as mortality agents in phytophagous insect populations. *Ecology* **78**, 2145–2152.

Hazarika, L. K., Puzari, K. C. & Wahab, S. (2001). Biological control of tea pests. In *Biocontrol Potential and Its Exploitation in Sustainable Agriculture* (eds R. K. Upadhyay, K. G. Mukerji and B. P. Chamola), pp. 159–180. Springer US, New York.

Heinen, T. E. & Gorini da Veiga, A. B. (2011). Arthropod venoms and cancer. *Toxicon* **57**, 497–511.

Henson, K. S. E., Craze, P. G. & Memmott, J. (2009). The restoration of parasites, parasitoids, and pathogens to heathland communities. *Ecology* **90**, 1840–1851.

Herdina, A. S., Bitencourt, G. S. S., di Mare, R. A. & Barbosa, B. C. (2016). *Polybia (Myrapetra) scutellaris* (Hymenoptera: Vespidae) foraging on flies at carcasses of *Rattus norvegicus* (Rodentia: Muridae). *Sociobiology* **63**, 728–730.

Herzner, G., Schlecht, A., Dollhofer, V., Parzefall, C., Harrar, K., Kreuzer, A., Pilsl, L. & Ruther, J. (2013). Larvae of the parasitoid wasp *Ampulex compressa* sanitize their host, the American cockroach, with a blend of antimicrobials. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 1369–1374.

Hirai, Y., Yasuhara, T., Yoshida, H., Nakajima, T., Fujino, M. & Kitada, C. (1979). A new mast cell degranulating peptide 'mastoparan' in the venom of *Vespula lewisii*. *Chemical and Pharmaceutical Bulletin* **27**, 1942–1944.

Hokche, O. & Ramirez, N. (1990). Pollination ecology of seven species of *Bauhinia* L. (Leguminosae: Caesalpinioideae). *Annals of the Missouri Botanical Garden* **77**, 559–572.

Hood, J. D. (1913). Notes on the life history of *Rhopalosoma poeyi* Cresson. *Proceedings of the Entomological Society of Washington* **15**, 145–147.

Hopper, S. D. & Brown, A. P. (2006). Australia's wasp-pollinated flying duck orchids revised (*Paracaleana*: Orchidaceae). *Australian Systematic Botany* **19**, 211–244.

Hopper, S. D. & Brown, A. P. (2007). A revision of Australia's hammer orchids (*Drakaea*: Orchidaceae), with some field data on species-specific sexually deceived wasp pollinators. *Australian Systematic Botany* **20**, 252–285.

Houston, T. F. (1995). Notes on the ethology of *Rolandia maculata* (Hymenoptera: Vespidae: Masarinae), a pollen wasp with a psammophore. *Records-Western Australia Museum* **17**, 343–349.

Howard, R. W. (1992). Comparative analysis of cuticular hydrocarbons from the ectoparasitoids *Cephalonomia waterstoni* and *Laelius utilis* (Hymenoptera: Bethylidae) and their respective hosts, *Cryptolestes ferrugineus* (Coleoptera: Cucujidae) and *Trogoderma variabile* (Coleptera: Dermestidae). *Annals of the Entomological Society of America* **85**, 317–325.

Hunt, J. H., Jeanne, R. L. & Keeping, M. G. (1995). Observations on *Apoica pallens*, a nocturnal neotropical social wasp (Hymenoptera: Vespidae, Polistinae, Epiponini). *Insectes Sociaux* **42**, 223–236.

Hunt, J. H., Rossi, A. M., Holmberg, N. J., Smith, S. R. & Sherman, W. R. (1998). Nutrients in social wasp (Hymenoptera: Vespidae, Polistinae) honey. *Annals of the Entomological Society of America* **91**, 466–472.

Indsto, J. O., Weston, P. H., Clements, M. A., Dyer, A. G., Batley, M. & Whelan, R. J. (2007). Generalised pollination of *Diuris alba* (Orchidaceae) by small bees and wasps. *Australian Journal of Botany* **55**, 628–634.

Infante, F., Mumford, J. & García-Ballinas, A. (2003). Predation by native arthropods on the African parasitoid *Prorops nasuta* (Hymenoptera: Bethylidae) in coffee plantations of Mexico. *Florida Entomologist* **86**, 86–88.

Inoue, M. & Endo, T. (2008). Below-ground host location by *Campsomeriella annulata* (Hymenoptera: Scoliidae), a parasitoid of scarabaeid grubs. *Journal of Ethology* **26**, 43–50.

IPBES (2016). *The Assessment Report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on Pollinators, Pollination and Food Production*. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn.

Ishay, I., Bytinski-Salz, H. & Shulov, A. (1967). Contributions to the bionomics of the oriental hornet *Vespa orientalis*. *Israel Journal of Entomology* **2**, 46–106.

Ivey, C. T., Martinez, P. & Wyatt, R. (2003). Variation in pollinator effectiveness in swamp milkweed, *Asclepias incarnata* (Apocynaceae). *American Journal of Botany* **90**, 214–225.

Jacobs, J. H., Clark, S. J., Denholm, I., Goulson, D., Stoate, C. & Osborne, J. L. (2010). Pollinator effectiveness and fruit set in common ivy, *Hedera helix* (Araliaceae). *Arthropod-Plant Interactions* **4**, 19–28.

Jacquemyn, H., Brys, R. & Hutchings, M. J. (2014). Biological flora of the British Isles: *Epipactis palustris*. *Journal of Ecology* **102**, 1341–1355.

Jacques, G. C., Pires, E. P., Hermes, M. G., Faria, L. D. B., Souza, M. M. & Silveira, L. C. P. (2018). Evaluating the efficiency of different sampling methods to survey social wasps (Vespidae: Polistinae) in an anthropized environment. *Sociobiology* **65**, 515–523.

Jacques, G. C., Souza, M. M., Coelho, H. J., Vicente, L. O. & Silveira, L. C. P. (2015). Diversity of social wasps (Hymenoptera: Vespidae: Polistinae) in an agricultural environment in Bambuí, Minas Gerais, Brazil. *Sociobiology* **62**, 439–445.

Jeanne, R. L. (1972). Social biology of the neotropical wasp, *Mischocyttarus drewseni*. *Bulletin of the Museum of Comparative Zoology of Harvard University* **144**, 63–150.

Jeanne, R. L., Hunt, J. H. & Keeping, M. G. (1995). Foraging in social wasps: *Agelaia* lacks recruitment to food (Hymenoptera: Vespidae). *Journal of the Kansas Entomological Society* **68**, 279–289.

Jennings, D. T. & Parker, F. D. (1987). Habitats and spider prey of habitats and spider prey of *Dipogon sayi* Sayi (Hymenoptera: Pompilidae) in Washington County, Maine. *The Great Lakes Entomologist* **20**, 5.

Jeon, M. G., Kim, T. G., Jung, J. C. & Choi, M. B. (2019). Prey diversity of *Polistes rothneyi koreanus* in different landscapes using DNA barcoding. *Journal of Applied Entomology* **143**, 1052–1063.

Johnson, S. D. (2005). Specialized pollination by spider-hunting wasps in the African orchid *Disa sankeyi*. *Plant Systematics and Evolution* **251**, 153–160.

Johnson, S. D., Ellis, A. & Dötterl, S. (2007). Specialization for pollination by beetles and wasps: the role of lollipop hairs and fragrance in *Satyrium microrrhynchum* (Orchidaceae). *American Journal of Botany* **94**, 47–55.

Johnson, S. D., Harris, L. F. & Procheş, Ş. (2009). Pollination and breeding systems of selected wildflowers in a southern African grassland community. *South African Journal of Botany* **75**, 630–645.

Jones, D. L. & Gray, B. (1974). The pollination of *Calochilus holtzei* F. Muell. *American Orchid Society Bulletin* **43**, 604–606.

Jones, R. (2019). *Wasp*. Reaktion Books Ltd, London.

Jongema, Y. (2017). *List of Edible Insects of the World (April 1, 2017)*. Wageningen University & Research, Wageningen.

Jonsson, G. M., Broad, G. R., Sumner, S., Isaac, N. J. B. (2021). A century of social wasp occupancy trends from natural history collections: spatiotemporal resolutions have little effect on model performance. *Insect Conservation and Diversity* (doi:10.1111/icad.12494)

José, L., Carrillo, S. & Caltagirone, L. E. (1970). Observations on the biology of *Solierella peckhami*, *S. blaisdelli* (Sphecidae), and two species of Chrysididae (Hymenoptera). *Annals of the Entomological Society of America* **63**, 672–681.

Jules, E. S. (1996). Yellow jackets (*Vespula vulgaris*) as a second seed disperser for the myrmecochorous plant, *Trillium ovatum*. *American Midland Naturalist* **135**, 367–369.

Kaiser-Bunbury, C. N., Mougal, J., Whittington, A. E., Valentin, T., Gabriel, R., Olesen, J. M. & Blüthgen, N. (2017). Ecosystem restoration strengthens pollination network resilience and function. *Nature* **542**, 223–227.

Kakutani, T., Inoue, T. & Kato, M. (1989). Nectar secretion pattern of the dish-shaped flower, *Cayratia japonica* (Vitaceae), and nectar utilization patterns by insect visitors. *Researches on Population Ecology* **31**, 381–400.

Kasper, M. L., Reeson, A. F., Cooper, S. J. B., Perry, K. D. & Austin, A. D. (2004). Assessment of prey overlap between a native (*Polistes humilis*) and an introduced (*Vespula germanica*) social wasp using morphology and phylogenetic analyses of 16S rDNA. *Molecular Ecology* **13**, 2037–2048.

Kato, M. (1996). Plant-pollinator interactions in the understory of a lowland mixed dipterocarp forest in Sarawak. *American Journal of Botany* **83**, 732–743.

Kato, M. (2000). Anthophilous insect community and plant-pollinator interactions on Amami Islands in the Ryukyu archipelago, Japan. *Contributions from the Biological Laboratory Kyoto University* **29**, 157–252.

Kelemu, S., Niassy, S., Torto, B., Fiaboe, K., Affognon, H., Tonnang, H., Maniania, N. K. & Ekesi, S. (2015). African edible insects for food and feed: inventory, diversity, commonalities and contribution to food security. *Journal of Insects as Food and Feed* **1**, 103–119.

Keller, S. & Armbruster, S. (1989). Pollination of *Hyptis capitata* by eumenid wasps in Panama. *Biotropica* **21**, 190–192.

Kephart, S. R. (1980). The floral ecology and reproductive isolation of three sympatric species of *Asclepias*. *Evolution* **34**, 738–746.

Kimsey, L. S. (2006). *California Cuckoo Wasps in the Family Chrysididae (Hymenoptera)*. University of California Press, Berkeley and Los Angeles.

Kimsey, L. S. & Bohart, R. M. (1990). *The Chrysidid Wasps of the World*. Oxford University Press, Oxford.

Kitamura, K. (1986). Comparative studies on the biology of dryinid wasps in Japan (4). Longevity, oviposition and host-feeding of adult females of *Haplogonatopus atratus* Esaki et Hashimoto (Hymenoptera: Dryinidae). *Bulletin of the Faculty of Agriculture, Shimane University* **20**, 191–195.

Klatt, B. K., Holzschuh, A., Westphal, C., Clough, Y., Smit, I., Pawelzik, E. & Tscharntke, T. (2014). Bee pollination improves crop quality, shelf life and commercial value. *Proceedings of the Royal Society B: Biological Sciences* **281**, 20132440.

Klein, A., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C. & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* **274**, 303–313.

Klein, J. A. & Beckage, N. E. (1990). Comparative suitability of *Trogoderma variabile* and *T. glabrum* (Coleoptera: Dermestidae) as hosts for the ectoparasite *Laelius pedatus* (Hymenoptera: Bethylidae). *Annals of the Entomological Society of America* **83**, 809–816.

Knisley, C. B., Reeves, D. L. & Stephens, G. T. (1989). Behavior and development of the wasp *Pterombrus rufiventris hyalinatus* Krombein (Hymenoptera, Tiphiidae), a parasite of larval tiger beetles. *Proceedings of the Entomological Society of Washington* **91**, 179–184.

Konno, K., Hisada, M., Fontana, R., Lorenzi, C. C. B., Naoki, H., Itagaki, Y., Miwa, A., Kawai, N., Nakata, Y., Yasuhara, T., Ruggiero Neto, J., de Azevedo, W. F., Palma, M. S. & Nakajima, T. (2001). Anoplin, a novel antimicrobial peptide from the venom of the solitary wasp *Anoplius samariensis*. *Biochimica et Biophysica Acta - Protein Structure and Molecular Enzymology* **1550**, 70–80.

Konno, K., Hisada, M., Naoki, H., Itagaki, Y., Fontana, R., Rangel, M., Oliveira, J. S., dos Cabrera, M. P. S., Neto, J. R., Hide, I., Nakata, Y., Yasuhara, T. & Nakajima, T. (2006). Eumenitin, a novel antimicrobial peptide from the venom of the solitary eumenine wasp *Eumenes rubronotatus*. *Peptides* **27**, 2624–2631.

Koschnitze, C. (2015). Polinizadores e visitantes florais de três táxons de Asclepiadoideae (Apocynaceae) na restinga de Maricá, Rio de Janeiro, Brasil. *Nature* **13**, 165–176.

Koschnitzke, C. & Sazima, M. (1997). Biologia floral de cinco espécies de *Passiflora* L. (Passifloraceae) em mata semidecídua. *Brazilian Journal of Botany* **20**, 119–126.

Kowalczyk, J. K. & Watała, C. (1989). Content of some heavy metal ions in various developmental stages of the social wasp, *Dolichovespula saxonica* (Fabr.) (Hymenoptera, Vespidae). *Bulletin of Environmental Contamination and Toxicology* **43**, 415–420.

Krombein, K. V. (1948). Liberation of oriental scolioid wasps in the United States from 1920 to 1946 (Hymenoptera: Scoliidae, Tiphiidae). *Annals of the Entomological Society of America* **41**, 58–62.

Krombein, K. V., Hurd, P. D., Smith, D. R. & Burks, B. D. (1979). *Catalog of Hymenoptera in America North of Mexico*. Smithsonian Institution Press, Washington, DC.

Kugler, H. (1980). Zur bestäubung von *Lantana camara* L. *Flora* **169**, 524–529.

Kurczewski, F. E. (2010). Prey and nesting behavior of some north American spider wasps (Hymenoptera: Pompilidae). *Northeastern Naturalist* **17**, 115–124.

Kurczewski, F. E., Coville, R. E. & Schal, C. (2010). Observations on the nesting and prey of the solitary wasp, *Tachysphex inconspicuus*, with a review of nesting behavior in the *T. obscuripennis* species group. *Journal of Insect Science* **10**, 183.

Kurczewski, F. E., Edwards, G. B. & Pitts, J. P. (2017). Hosts, nesting behavior, and ecology of some north American spider wasps (Hymenoptera: Pompilidae), II. *Southeastern Naturalist* **16**, 1–82.

Kurczewski, F. E. & Kiernan, D. H. (2015). Analysis of spider wasp host selection in the eastern Great Lakes region (Hymenoptera: Pompilidae). *Northeastern Naturalist* **22**, 1–88.

Kurczewski, F. E., Kurczewski, E. J. & Norton, R. A. (1987). New prey records for species of Nearctic Pompilidae (Hymenoptera). *Journal of the Kansas Entomological Society* **60**, 467–475.

Kurczewski, F. E. & Miller, R. C. (1984). Observations on the nesting of three species of *Cerceris* (Hymenoptera: Sphecidae). *Florida Entomologist* **67**, 146–155.

Kurczewski, F. E. & Spofford, M. G. (1986). Observations on the behaviors of some Scoliidae and Pompilidae (Hymenoptera) in Florida. *The Florida Entomologist* **69**, 636–644.

Latif, A., Malik, S. A., Saeed, S., Iqbal, N., Saeed, Q., Khan, K. A., Ting, C. & Ghramh, H. A. (2019). Diversity of pollinators and their role in the pollination biology of chickpea, *Cicer arietinum* L. (Fabaceae). *Journal of Asia-Pacific Entomology* **22**, 597–601.

Lau, C. P. Y., Saunders, R. M. K. & Ramsden, L. (2009). Floral biology, breeding systems and population genetic structure of three climbing *Bauhinia* species (Leguminosae: Caesalpinioideae) in Hong Kong, China. *Journal of Tropical Ecology* **25**, 147–159.

Lebeck, L. M. (1991). A review of the hymenopterous natural enemies of cockroaches with emphasis on biological control. *Entomophaga* **36**, 335–352.

Lee, M. R., Sheng, W. H., Hung, C. C., Yu, C. J., Lee, L. N. & Hsueh, P. R. (2015). *Mycobacterium abscessus* complex infections in humans. *Emerging Infectious Diseases* **21**, 1638–1646.

Leeuwenberg, A. M. L. (1994). Taxa of the Apocynaceae above the genus level, series of Apocynaceae XXXVIII. *Wageningen Agricultural University Papers* **94**, 45–60.

Legner, E. F. & Gordh, G. (1992). Lower navel orange worm (Lepidoptera: Phycitidae) population densities following establishment of *Goniozus legneri* (Hymenoptera: Bethylidae) in California. *Journal of Economic Entomology* **85**, 2153–2160.

Leite, N. B., Aufderhorst-Roberts, A., Palma, M. S., Connell, S. D., Neto, J. R. & Beales, P. A. (2015). PE and PS lipids synergistically enhance membrane poration by a peptide with anticancer properties. *Biophysical Journal* **109**, 936–947.

Lengyel, S., Gove, A. D., Latimer, A. M., Majer, J. D. & Dunn, R. R. (2009). Ants sow the seeds of global diversification in flowering plants. *PLoS One* **4**, e5480.

Lester, P. J. (2018). *The Vulgar Wasp: The Story of a Ruthless Invader and Ingenious Predator*. Victoria University Press, Wellington.

Lester, P. J. & Beggs, J. R. (2019). Invasion success and management strategies for social *Vespula* wasps. *Annual Review of Entomology* **64**, 1–21.

Liede, S. & Whitehead, V. (1991). Studies in the pollination biology of *Sarcostemma viminale* R. BR. *sensu lato*. *South African Journal of Botany* **57**, 115–122.

Lim, J., Oh, M., Lee, J. & Lee, S. (2007). *Cephalonomia gallicola* (Hymenoptera: Bethylidae), new to Korea, an ectoparasitoid of the cigarette beetle, *Lasioderma serricorne* (Coleoptera: Anobiidae). *Journal of Asia-Pacific Entomology* **10**, 335–338.

Lin, S. & Bernardello, G. (1999). Flower structure and reproductive biology in *Aspidosperma quebracho-blanco* (Apocynaceae), a tree pollinated by deceit. *International Journal of Plant Sciences* **160**, 869–878.

Logan, D. P. (2019). Rearing indicates life cycles of 2–5 years for coastal sand scarab beetles *Pericoptus punctatus* and *P. truncatus* (Coleoptera: Scarabaeidae). *New Zealand Journal of Zoology* **46**, 236–252.

Lohrmann, V., Falin, Z. H., Bennett, D. J. & Engel, M. S. (2014). Recent findings of *Olixon banksii* in the Nearctic with notes on its biology (Hymenoptera: Rhopalosomatidae). *Journal of the Kansas Entomological Society* **87**, 258–260.

Lopez, G. Y., Hernandez, D. J. & Caraballo, P. (2013). Actividad de forrajeo de la avispa social *Polybia emaciata* (Hymenoptera: Vespidae: Polistinae). *Revista Colombiana de Entomología* **39**, 250–255.

Losey, J. E. & Vaughan, M. (2006). The economic value of ecological services provided by insects. *Bioscience* **56**, 311–323.

Lourido, G. M., Lopes, T. M. V., Somavilla, A. & Guerra, K. F. G. (2019). Social wasps as biological control agents against *Diaphania hyalinata* (Linnaeus, 1767) (Lepidoptera, Crambidae), a cucumber pest in Amazonas, Brazil. *Sociobiology* **66**, 610–613.

Lukáš, J., Šambergerová, V. & Stejskal, V. (2007). Influence of deltamethrin on *Cephalonomia tarsalis* (Ashmead)(Hymenoptera: Bethylidae). *Compte Rendu de la Réunion* **30**, 287–290.

MacDonald, J. F., Akre, R. D. & Hill, W. B. (1974). Comparative biology and behavior of *Vespula atropilosa* and *V. pensylvanica* (Hymenoptera: Vespidae). *Melanderia* **18**, 1–66.

Machado, V. L. L., Gobbi, N. & Alves Junior, V. V. (1988). Material capturado e utilizado na alimentação de *Polybia (Trichothorax) sericea* (Olivier, 1791) (Hymenoptera, Vespidae). *Revista Brasileira de Zoologia* **5**, 261–266.

Machado, V. L. L., Gobbi, N. & Simões, D. (1987). Material capturado e utilizado na alimentação de *Stelopolybia pallipes* (Olivier, 1791) (Hymenoptera, Vespidae). *Anais da Sociedade Entomológica do Brasil* **16**, 73–79.

MacIntyre, P. & Hellstrom, J. (2015). *An Evaluation of the Costs of Pest Wasps (Vespula Species) in New Zealand*. Department of Conservation and Ministry for Primary Industries, Wellington.

Macior, L. W. (1965). Insect adaptation and behavior in *Asclepias* pollination. *Bulletin of the Torrey Botanical Club* **92**, 114–126.

MacLellan, C. R. (1973). Natural enemies of the light brown apple moth, *Epiphyas postvittana*, in the Australian capital territory. *The Canadian Entomologist* **105**, 681–700.

Manohara, T. N. (2013). Wasp-mediated seed dispersal in agarwood plant (*Aquilaria malaccensis*), a critically endangered and overexploited species of north East India. *Current Science* **105**, 298–299.

Mant, J., Brown, G. R. & Weston, P. H. (2005). Opportunistic pollinator shifts among sexually deceptive orchids indicated by a phylogeny of pollinating and non-pollinating thynnine wasps (Tiphiidae). *Biological Journal of the Linnean Society* **86**, 381–395.

Mant, J. G., Schiestl, F. P., Peakall, R. & Weston, P. H. (2002). A phylogenetic study of pollinator conservatism among sexually deceptive orchids. *Evolution* **56**, 888–898.

Martins, R. P. (1991). Nesting behavior and prey of *Poecilopompilus algidus fervidus* and *Tachypompilus xanthopterus* (Hymenoptera: Pompilidae). *Journal of the Kansas Entomological Society* **64**, 231–236.

Martynova, K. V. (2017). *Hedychridium monochroum* and *Chrysis lanceolata* (Hymenoptera: Chrysididae)– two species of cuckoo wasps reared from nests of *Solierella compedita* (Hymenoptera: Crabronidae) in southeastern Ukraine. *Turkish Journal of Zoology* **41**, 397–407.

Matsuura, M. (1984). Comparative biology of the five Japanese species of the genus *Vespa* (Hymenoptera, Vespidae). *Bulletin of the Faculty of Agriculture, Nïigata University* **69**, 1–131.

Matsuura, M. & Yamane, S. (1990). *Biology of the Vespine Wasps*. Springer Verlag, Berlin.

Mauss, V. (1996). Contribution to the bionomics of *Ceramius tuberculifer* Saussure (Hymenoptera, Vespidae, Masarinae). *Journal of Hymenoptera Research* **5**, 22–37.

Mauss, V., Fateryga, A. & Prosi, R. (2016). Taxonomy, distribution and bionomics of *Celonites tauricus* Kostylev, 1935, stat. n. (Hymenoptera, Vespidae, Masarinae). *Journal of Hymenoptera Research* **48**, 33–66.

Mauss, V., Müller, A. & Yildirim, E. (2003). Nesting and flower associations of the pollen wasp *Ceramius fonscolombei* Latreille, 1810 (Hymenoptera: Vespidae: Masarinae) in Spain. *Journal of the Kansas Entomological Society* **76**, 1–15.

Mauss, V., Müller, A. & Yildirim, E. (2005). First contribution to the bionomics of the pollen wasp *Ceramius caucasicus* André 1884 (Hymenoptera: Vespidae: Masarinae) in Turkey. *Journal of the Kansas Entomological Society* **78**, 201–220.

Mauss, V., Müller, A. & Yildirim, E. (2010). First contribution to the bionomics of the pollen wasp *Ceramius palaestinensis* (Giordani Soika, 1957) (Hymenoptera: Vespidae: Masarinae) in Turkey. *Journal of the Kansas Entomological Society* **13**, 42–59.

Mayhew, P. J. & Heitmans, W. R. B. (2000). Life history correlates and reproductive biology of *Laelius pedatus* (Hymenoptera: Bethylidae) in The Netherlands. *European Journal of Entomology* **97**, 313–322.

Mazzon, L., Visentini, A. & Girolami, V. (2000). Sex ratio of European natural populations of *Neodryinus typhlocybae* (Ashmead)(Hymenoptera: Dryinidae), predator-parasitoid of *Metcalfa pruinosa* (say)(Homoptera: Flatidae). *Frustula Entomologica* **23**, 30–36.

McGeoch, M. A. (1998). The selection, testing and application of terrestrial insects as bioindicators. *Biological Reviews* **73**, 181–201.

MEA (2005). *Ecosystems and Human Well-Being: Synthesis*. Island Press, Washington, DC.

Mello, M. A. R., de Santos, G. M. M., Mechi, M. R. & Hermes, M. G. (2011). High generalization in flower-visiting networks of social wasps. *Acta Oecologica* **37**, 37–42.

Menz, M. H. M., Phillips, R. D., Dixon, K. W., Peakall, R. & Didham, R. K. (2013). Mate-searching behaviour of common and rare wasps and the implications for pollen movement of the sexually deceptive orchids they pollinate. *PLoS One* **8**, e59111.

Mertins, J. W. (1985). *Laelius utilis* [Hym.: Bethylidae], a parasitoid of *Anthrenus fuscus* [Col.: Dermestidae] in Iowa. *Entomophaga* **30**, 65–68.

Meyer-Rochow, V. B. (2005). Traditional food insects and spiders in several ethnic groups of Northeast India, Papua New Guinea, Australia and New Zealand. In *Ecological Implications of Minilivestock: Potential of Insects, Rodents, Frogs and Snails* (ed. M. G. Paoletti), pp. 389–414. Science Publishers, Inc., Plymouth.

Misra, R. M. (1996). Some observations on the life history and behaviour of *Scolia (Discolia) affinis* Guerin (Hymenoptera: Scoliidae) a parasite of *Holotrichia consanguinea* blanch (Coleoptera: Scarabaeidae). *Indian Forester* **122**, 1174–1178.

Mita, T., Matsumoto, Y., Sanada-Morimura, S. & Matsumur, M. (2012). Passive long-distance migration of apterous dryinid wasps parasitizing rice planthoppers. In *Global Advances in Biogeography* (ed. L. Stevens), pp. 49–60. InTech Open, Rijeka.

Mora-Kepfer, F., Espinoza, A. M. & Rica, C. (2009). Parasitism and predation of the planthopper *Tagosodes orizicolus* (Homoptera: Delphacidae) by a dryinid parasitoid in Costa Rica. *Revista de Biologia Tropical* **57**, 2003–2011.

Moreau, S. J. M. (2013). "It stings a bit but it cleans well": venoms of Hymenoptera and their antimicrobial potential. *Journal of Insect Physiology* **59**, 186–204.

Moreno, M., Zurita, E. & Giralt, E. (2014). Delivering wasp venom for cancer therapy. *Journal of Controlled Release* **182**, 13–21.

Moretti, T. C., Thyssen, P. J., Godoy, W. A. C. & Solis, D. R. (2008). Necrophagy by the social wasp *Agelaia pallipes* (Hymenoptera: Vespidae, Epiponini): possible forensic implications. *Sociobiology* **51**, 393–398.

Myers, J. G. (1931). A preliminary report on an investigation into the biological control of West Indian insect pests. *Empire Marketing Board* **42**, 172.

Nakase, Y. & Kato, M. (2012). A nocturnal *Provespa* wasp species as the probable pollinator of epiphytic orchid *Coelogyne fimbriata*. *Entomological Science* **15**, 253–256.

Nakasuji, F., Yamanaka, H. & Kiritani, K. (1976). Predation of larvae of the tobacco cutworm *Spodoptera litura* (Lepidoptera, Noctuidae) by *Polistes* wasps. *Kontyû* **44**, 205–213.

Nannoni, A., Cervo, R. & Turillazzi, S. (2001). Foraging activity in European *Polistes* wasps (Hymenoptera Vespidae). *Bollettino della Società Entomologica Italiana* **133**, 67–78.

Narbona, E. & Dirzo, R. (2010). A reassessment of the function of floral nectar in *Croton suberosus* (Euphorbiaceae): a reward for plant defenders and pollinators. *American Journal of Botany* **97**, 672–679.

Nayak, K. G. & Davidar, P. (2010). Pollination and breeding systems of woody plant species in tropical dry evergreen forests, southern India. *Flora* **205**, 745–753.

Nazarov, V. V. (1995). Pollination of *Steveniella satyrioides* (Orchidaceae) by wasps (Hymenoptera, Vespoidea) in the Crimea. *Lindleyana* **10**, 109–114.

Neto, E. C. & Ramos-Elorduy, J. (2006). Los insectos comestibles de Brasil: etnicidad, diversidad e importancia en la alimentación. *Boletín Sociedad Entomológica Aragonesa* **38**, 423–442.

Nilsson, L. A., Jonsson, L., Rason, L. & Randrianjohany, E. (1986). The pollination of *Cymbidiella flabellata* (Orchidaceae) in Madagascar: a system operated by sphecid wasps. *Nordic Journal of Botany* **6**, 411–422.

Nonaka, K. (2009). Feasting on insects. *Entomological Research* **39**, 304–312.

Nonaka, K. (2010). Cultural and commercial roles of edible wasps in Japan. In *Forest Insects as Food: Humans Bite Back* (eds P. B. Durst, D. V. Johnson, R. N. Leslie and K. Shono), pp. 123–130. Food and Agriculture Organisation of the United Nations, Bangkok.

Noriega, J. A., Hortal, J., Azcárate, F. M., Berg, M. P., Bonada, N., Briones, M. J. I., del Toro, I., Goulson, D., Ibanez, S., Landis, D. A., Moretti, M., Potts, S. G., Slade, E. M., Stout, J. C., Ulyshen, M. D., et al. (2018). Research trends in ecosystem services provided by insects. *Basic and Applied Ecology* **26**, 8–23.

O'Donnell, S. (1995). Necrophagy by Neotropical swarm-founding wasps (Hymenoptera: Vespidae, Epiponini). *Biotropica* **27**, 133–136.

O'Neill, K. M. (2001). *Solitary Wasps: Behavior and Natural History*. Cornell University Press, Ithaca.

Obeysekara, P. T., Legrand, A. & Lavigne, G. (2014). Use of herbivore-induced plant volatiles as search cues by *Tiphia vernalis* and *Tiphia popilliavora* to locate their below-ground scarabaeid hosts. *Entomologia Experimentalis et Applicata* **150**, 74–85.

Oliveira, M. M., Gomes, F. B., Somavilla, A. & Krug, C. (2017). *Polistes canadensis* (Linnaeus, 1758) (Vespidae: Polistinae) in the Western Amazon: a potential biological control agent. *Sociobiology* **64**, 477–483.

de Oliveira, O. A. L., Noll, F. B. & Wenzel, J. W. (2010). Foraging behavior and colony cycle of *Agelaia vicina* (Hymenoptera: Vespidae; Epiponini). *Journal of Hymenoptera Research* **19**, 4–11.

Ollerton, J., Erenler, H., Edwards, M. & Crockett, R. (2014). Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science* **346**, 1360–1362.

Ollerton, J., Johnson, S. D., Cranmer, L. & Kellie, S. (2003). The pollination ecology of an assemblage of grassland asclepiads in South Africa. *Annals of Botany* **92**, 807–834.

Ollerton, J., Liede-Schumann, S., Endress, M. E., Meve, U., Rech, A. R., Shuttleworth, A., Keller, H. A., Fishbein, M., Alvarado-Cárdenas, L. O., Amorim, F. W., Bernhardt, P., Celep, F., Chirango, Y., Chiriboga-Arroyo, F., Civeyrel, L., et al. (2019). The diversity and evolution of pollination systems in large plant clades: Apocynaceae as a case study. *Annals of Botany* **123**, 311–325.

Ollerton, J., Winfree, R. & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos* **120**, 321–326.

Olmi, M., Belokobylskij, S. A. & Guglielmino, A. (2014). Revision of the family Embolemidae of Russia and Ukraine (Hymenoptera: Chrysidoidea), with description of a new species. *Annales Zoologici* **64**, 97–108.

Olmi, M. & Copeland, R. S. (2011). A catalogue of Dryinidae, Embolemidae and Sclerogibbidae of Kenya and Burundi, with descriptions of new species (Hymenoptera: Chrysidoidea). *African Invertebrates* **52**, 177–206.

Olmi, M., Copeland, R. S. & Guglielmino, A. (2015). An updated checklist of Dryinidae, Embolemidae and Sclerogibbidae (Hymenoptera) of Kenya and Burundi, with descriptions of thirteen new species. *Acta Entomologica Musei Nationalis Pragae* **55**, 333–380.

Olmi, M. & van Harten, A. (2000). Notes on Dryinidae, Embolemidae and Sclerogibbidae (Hymenoptera: Chrysidoidea) of Yemen, with keys to the species of the Arabian peninsula. *Fauna of Arabia* **18**, 253–272.

Olmi, M. & van Harten, A. (2006). Dryinidae, Embolemidae and Sclerogibbidae (Hymenoptera: Chrysidoidea) of Yemen, with revised keys to the species of the Arabian peninsula. *Fauna of Arabia* **21**, 307–337.

Onore, G. (1997). A brief note on edible insects in Ecuador. *Ecology of Food and Nutrition* **36**, 277–285.

Onore, G. (2005). Edible insects in Ecuador. In *Ecological Implications of Minilivestock: Potential of Insects, Rodents, Frogs and Snails* (ed. M. G. Paoletti), pp. 343–352. Science Publishers, Inc., Plymouth.

Ortega-Olivencia, A., Rodríguez-Riaño, T., Pérez-Bote, J. L., López, J., Mayo, C., Valtueña, F. J. & Navarro-Pérez, M. (2012). Insects, birds and lizards as pollinators of the largest-flowered *Scrophularia* of Europe and Macaronesia. *Annals of Botany* **109**, 153–167.

Ospina-Calderón, N., Diazgranados-Cadelo, M. & Viveros-Bedoya, P. (2007). Observaciones de la polinización y fenología reproductiva de *Brassia cf. antherotes* Rchb.f. (Orchidaceae) en un relicto de selva subandina en la reserva natural La Montaña del Ocaso en Quimbaya, Quindío (Colombia). *Universitas Scientiarum* **12**, 83–95.

Outhwaite, C. L., Gregory, R. D., Chandler, R. E., Collen, B. & Isaac, N. J. B. (2020). Complex long-term biodiversity change among invertebrates, bryophytes and lichens. *Nature Ecology & Evolution* **4**, 384–392.

Outhwaite, C. L., Powney, G. D., August, T. A., Chandler, R. E., Rorke, S., Pescott, O. L., Harvey, M., Roy, H. E., Fox, R., Roy, D. B., Alexander, K., Ball, S., Bantock, T., Barber, T., Beckmann, B. C., et al. (2019). Annual estimates of occupancy for bryophytes, lichens and invertebrates in the UK, 1970-2015. *Scientific Data* **6**, 1–12.

Overmyer, S. L. & Jeanne, R. L. (1998). Recruitment to food by the German yellowjacket, *Vespula germanica*. *Behavioral Ecology and Sociobiology* **42**, 17–21.

Pant, D. D., Nautiyal, D. D. & Chaturvedi, S. K. (1982). Pollination ecology of some Indian asclepiads. *Phytomorphology* **32**, 302–313.

Paoletti, M. G., Buscardo, E. & Dufour, D. L. (2000). Edible insects among Amazonian indians: a critical review of disappearing knowledge. *Environment, Development and Sustainability* **2**, 195–225.

Parker, D. E. (1935). *Chrysis shanghaiensis* Smith, a parasite of the oriental moth. *Journal of Agricultural Research* **52**, 449–458.

Paulus, H. F. & Gack, C. (1990). Pollinators as prepollinating isolation factors: evolution and speciation in *Ophrys* (Orchidaceae). *Israel Journal of Botany* **39**, 43–79.

Peakall, R. (1990). Responses of male *Zaspilothynnus trilobatus* Turner wasps to females and the sexually deceptive orchid it pollinates. *Functional Ecology* **4**, 159–167.

Pearson, D. E. & Callaway, R. M. (2003). Indirect effects of host-specific biological control agents. *Trends in Ecology and Evolution* **18**, 456–461.

Pellmyr, O. (1985). Yellow jackets disperse *Vancouveria* seeds (Berberidaceae). *Madrono* **32**, 56.

Pereira, R. R., Neves, D. V. C., Campos, J. N., Santana Júnior, P. A., Hunt, T. E. & Picanço, M. C. (2018). Natural biological control of *Chrysodeixis includens*. *Bulletin of Entomological Research* **108**, 831–842.

Pérez-Lachaud, G., Hardy, I. C. W. & Lachaud, J. P. (2002). Insect gladiators: competitive interactions between three species of bethylid wasps attacking the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). *Biological Control* **25**, 231–238.

Perrard, A., Haxaire, J., Rortais, A. & Villemant, C. (2009). Observations on the colony activity of the Asian hornet *Vespa velutina* Lepeletier 1836 (Hymenoptera: Vespidae: Vespinae) in France. *Annales de la Société Entomologique de France* **45**, 119–127.

Phillips, R. D., Bohman, B., Brown, G. R., Tomlinson, S. & Peakall, R. (2020). A specialised pollination system using nectar-seeking thynnine wasps in *Caladenia nobilis* (Orchidaceae). *Plant Biology* **22**, 157–166.

Phillips, R. D., Brown, G. R., Dixon, K. W., Hayes, C., Linde, C. C. & Peakall, R. (2017). Evolutionary relationships among pollinators and repeated pollinator sharing in sexually deceptive orchids. *Journal of Evolutionary Biology* **30**, 1674–1691.

Phillips, R. D., Faast, R., Bower, C. C., Brown, G. R. & Peakall, R. (2009). Implications of pollination by food and sexual deception for pollinator specificity, fruit set, population genetics and conservation of *Caladenia* (Orchidaceae). *Australian Journal of Botany* **57**, 287–306.

Phillips, R. D. & Peakall, R. (2018). Breaking the rules: discovery of sexual deception in *Caladenia abbreviata* (Orchidaceae), a species with brightly coloured flowers and a non-insectiform labellum. *Australian Journal of Botany* **66**, 95–100.

Phillips, R. D., Peakall, R., Hutchinson, M. F., Linde, C. C., Xu, T., Dixon, K. W. & Hopper, S. D. (2014). Specialized ecological interactions and plant species rarity: the role of pollinators and mycorrhizal fungi across multiple spatial scales. *Biological Conservation* **169**, 285–295.

Picanço, M. C. (2012). Natural biological control of *Diaphania* spp. (Lepidoptera: Crambidae) by social wasps. *Sociobiology* **59**, 561–572.

Picanço, M. C., Bacci, L., Queiroz, R. B., Silva, G. A., Miranda, M. M. M., Leite, G. L. D. & Suinaga, F. A. (2011). Social wasp predators of *Tuta absoluta*. *Sociobiology* **58**, 621–633.

Picanço, M. C., de Oliveira, I. R., Rosado, J. F., da Silva, F. M., Gontijo, P. C. & da Silva, R. S. (2010). Natural biological control of *Ascia monuste* by the social wasp *Polybia ignobilis* (Hymenoptera: Vespidae). *Sociobiology* **56**, 67–76.

Picanço, M. C., Ribeiro, L. J., Leite, G. L. D. & Gusmão, M. R. (2006). Seletividade de inseticidas a *Polybia ignobilis* (Haliday) (Hymenoptera: Vespidae) predador de *Ascia monuste orseis* (Godart) (Lepidoptera: Pieridae). *Anais da Sociedade Entomológica do Brasil* **27**, 85–90.

Pietrantuono, A. L., Moreyra, S. & Lozada, M. (2018). Foraging behaviour of the exotic wasp *Vespula germanica* (Hymenoptera: Vespidae) on a native caterpillar defoliator. *Bulletin of Entomological Research* **108**, 406–412.

Piji, L. & Dodson, C. H. (1966). *Orchid Flowers: Their Pollination and Evolution.* University of Miami Press, Miami.

Plunkett, G. M., Moller, H. & Hamilton, C. (1989). Overwintering colonies of German (*Vespula germanica*) and common wasps (*Vespula vulgaris*) (Hymenoptera: Vespidae) in New Zealand. *New Zealand Journal of Zoology* **16**, 345–353.

Polidori, C. (2011a). *Predation in the Hymenoptera: An Evolutionary Perspective.* Transworld Research Network, Trivandrum.

Polidori, C. (2011b). The role of increased prey spectrum and reduced prey size in the evolution of sociality in *Cerceris* wasps. In *Predation in the Hymenoptera: An Evolutionary Perspective* (ed. C. Polidori), pp. 199–216. Transworld Research Network, Trivandrum.

Polidori, C., Gobbi, M., Chatenoud, L., Santoro, D., Montani, O. & Andrietti, F. (2010). Taxon-biased diet preference in the 'generalist' beetle-hunting wasp *Cerceris rubida* provides insights on the evolution of prey specialization in apoid wasps. *Biological Journal of the Linnean Society* **99**, 544–558.

Polidori, C., Mendiola, P., Asís, J. D., Tormos, J., García, M. D. & Selfa, J. (2009). Predatory habits of the grasshopper-hunting wasp *Stizus continuus* (Hymenoptera: Crabronidae): diet preference, predator-prey size relationships and foraging capacity. *Journal of Natural History* **43**, 2985–3000.

Polidori, C., Santoro, D., Asís, J. D. & Tormos, J. (2011). Individual prey specialization in wasps: predator size is a weak predictor of taxonomic niche width and niche overlap. In *Predation in the Hymenoptera: An Evolutionary Perspective* (ed. C. Polidori), pp. 101–121. Transworld Research Network, Trivandrum.

Pollard, S. D. (1982). *Epipompius insularis* (Hymenoptera: Pompilidae), a parasitoid of hunting spiders. *New Zealand Journal of Zoology* **9**, 37–39.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* **25**, 345–353.

Powell, E. C. & Taylor, L. A. (2017). Specialists and generalists coexist within a population of spider-hunting mud dauber wasps. *Behavioral Ecology* **28**, 890–898.

Prezoto, F. & Braga, N. (2013). Predation of *Zaprinus indianus* (Diptera: Drosophilidae) by the social wasp *Synoeca cyanea* (Hymenoptera: Vespidae). *Florida Entomologist* **96**, 670–672.

Prezoto, F., Giannotti, E. & Machado, V. L. L. (1994). Atividade forrageadora e material coletado pela vespa social *Polistes simillimus* Zikán, 1951 (Hymenoptera, Vespidae). *Insecta* **3**, 11–19.

Prezoto, F., Lima, M. A. P. & Machado, V. L. L. (2005). Survey of preys captured and used by *Polybia platycephala* (Richards) (Hymenoptera: Vespidae, Epiponini). *Neotropical Entomology* **34**, 849–851.

Prezoto, F., Santos-Prezoto, H. H., Machado, V. L. L. & Zanuncio, J. C. (2006). Prey captured and used in *Polistes versicolor* (Olivier) (Hymenoptera: Vespidae) nourishment. *Neotropical Entomology* **35**, 707–709.

Prezoto, F., Maciel, T. T., Detoni, M., Mayorquin, A. Z. & Barbosa, B. C. (2019). Pest control potential of social wasps in small farms and urban gardens. *Insects* **10**, 192.

Punzo, F. (1994). The biology of the spider wasp, *Pepsis thisbe* (Hymenoptera: Pompilidae) from trans Pecos, Texas. I. Adult morphometrics, larval development and the ontogeny of larval feeding patterns. *Psyche* **101**, 229–241.

Punzo, F. (2005). Studies on the natural history, ecology, and behavior of *Pepsis cerberus* and *P. mexicana* (Hymenoptera: Pompilidae) from big bend National Park, Texas. *Entomologica Americana* **113**, 84–95.

Pusceddu, M., Mura, A., Floris, I. & Satta, A. (2018). Feeding strategies and intraspecific competition in German yellowjacket (*Vespula germanica*). *PLoS One* **13**, e0206301.

Quicke, D. L. J. (2015). *The Braconid and Ichneumonid Parasitoid Wasps: Biology, Systematics, Evolution and Ecology*. Wiley-Blackwell Publishing Ltd, Hoboken.

Rabb, R. L. & Lawson, F. R. (1957). Some factors influencing the predation of *Polistes* wasps on the tobacco hornworm. *Journal of Economic Entomology* **50**, 778–784.

Rafferty, N. E. & Ives, A. R. (2012). Pollinator effectiveness varies with experimental shifts in flowering time. *Ecology* **93**, 803–814.

Raine, N. E., Pierson, A. S. & Stone, G. N. (2007). Plant-pollinator interactions in a Mexican *Acacia* community. *Arthropod-Plant Interactions* **1**, 101–117.

Raju, A. J. S., Jonathan, K. H. & Lakshmi, A. V. (2006). Pollination biology of *Ceriops decandra* (Griff.) ding Hou (Rhizophoraceae), an important true viviparous mangrove tree species. *Current Science* **91**, 1235–1238.

Raju, A. J. S. & Rani, D. S. (2017). Pollination ecology of *Triumfetta rhomboidea* (Tiliaceae). *Annali di Botanica* **7**, 33–41.

Raju, A. J. S., Zafar, R. & Rao, S. P. (2005). Floral device for obligate selfing by remote insect activity and anemochory in *Wrightia tinctoria* (Roxb.) R. Br. (Apocynaceae). *Current Science* **88**, 1378–1380.

Ramirez, M., Rivera, E. & Ereu, C. (1999). Fifteen cases of atropine poisoning after honey ingestion. *Veterinary and Human Toxicology* **41**, 19.

Ramos, F. N. & Santos, F. A. M. (2006). Floral visitors and pollination of *Psychotria tenuinervis* (Rubiaceae): distance from the anthropogenic and natural edges of an Atlantic Forest fragment. *Biotropica* **38**, 383–389.

Ramos-Elorduy, J. (1997). The importance of edible insects in the nutrition and economy of people of the rural areas of Mexico. *Ecology of Food and Nutrition* **36**, 347–366.

Ramos-Elorduy, J. (2009). Anthropo-entomophagy: cultures, evolution and sustainability. *Entomological Research* **39**, 271–288.

Ramos-Elorduy, J., Pino Moreno, J. M. & Morales de León, J. (2002). Análisis químico proximal, vitaminas y nutrimentos inorgánicos de insectos consumidos en el Estado de Hidalgo, México. *Folia Entomológica Mexicana* **41**, 15–29.

Rayor, L. S. (1996). Attack strategies of predatory wasps (Hymenoptera: Pompilidae; Sphecidae) on colonial orb web-building spiders (Araneidae: *Metepeira incrassata*). *Journal of the Kansas Entomological Society* **69**, 67–75.

Reddy, T. B. & Aruna, C. (1990). Pollination ecology of *Alangium lamarkii* (Alangiaceae). *Proceedings: Plant Sciences* **100**, 195–204.

Redford, K. H. & Adams, W. M. (2009). Payment for ecosystem services and the challenge of saving nature. *Conservation Biology* **23**, 785–787.

Reding, M. E. & Klein, M. G. (2001). *Tiphia vernalis* (Hymenoptera: Tiphiidae) parasitizing oriental beetle, *Anomala orientalis* (Coleoptera: Scarabaeidae) in a nursery. *The Great Lakes Entomologist* **34**, 8.

Reed, P. (2018). *Ant-Man and the Wasp*. Walt Disney Studios Motion Pictures, Burbank.

Rego, F. N. A. A., Rheims, C. A. & Venticinque, E. M. (2004). Notes on the predation of an aviculariine spider (Araneae: Theraphosidae, *Avicularia* sp.) by *Pepsis frivaldszkyi* (Hymenoptera: Pompilidae) in Brazilian Amazonia. *Journal of the British Tarantula Society* **20**, 18–25.

Rehnberg, B. G. (1987). Selection of spider prey by *Trypoxylon politum* (say) (Hymenoptera: Sphecidae). *The Canadian Entomologist* **119**, 189–194.

Reiter, N., Bohman, B., Flematti, G. R. & Phillips, R. D. (2018). Pollination by nectar-foraging thynnine wasps: evidence of a new specialized pollination system for Australian orchids. *Botanical Journal of the Linnean Society* **188**, 327–337.

Reiter, N., Bohman, B., Freestone, M., Brown, G. R. & Phillips, R. D. (2019). Pollination by nectar-foraging thynnine wasps in the endangered *Caladenia arenaria* and *Caladenia concolor* (Orchidaceae). *Australian Journal of Botany* **67**, 490–500.

Richards, O. W. & Richards, M. J. (1951). Observations on the social wasps of South America (Hymenoptera: Vespidae). *Transactions of the Royal Entomological Society of London* **102**, 1–169.

Richter, M. R. (2000). Social wasp (Hymenoptera: Vespidae) foraging behavior. *Annual Review of Entomology* **45**, 121–150.

Rinderer, T. E., Collins, A. M. & Tucker, K. W. (1985). Honey production and underlying nectar harvesting activities of Africanized and European honeybees. *Journal of Apicultural Research* **24**, 161–167.

Robertson, C. (1928). *Flowers and Insects; Lists of Visitors of 453 Flowers*. The Science Press Printing Company, Lancaster, Philadelphia, USA.

Rodríguez-Riaño, T., Ortega-Olivencia, A., López, J., Pérez-Bote, J. L. & Navarro-Pérez, M. L. (2014). Main sugar composition of floral nectar in three species groups of *Scrophularia* (Scrophulariaceae) with different principal pollinators. *Plant Biology* **16**, 1075–1086.

Rodriguez, F. A., Barros, L. C., Caroline, P., Souza, M. M., Serrao, J. E. & Zanuncio, J. C. (2012). Nidification of *Polybia platycephala* and *Polistes versicolor* (Hymenoptera: Vespidae) on plants of *Musa* spp. in Minas Gerais state, Brazil. *Sociobiology* **59**, 457–461.

Rogers, M. E. & Potter, D. A. (2004). Biology of *Tiphia pygidialis* (Hymenoptera: Tiphiidae), a parasitoid of masked chafer (Coleoptera: Scarabaeidae) grubs, with notes on the seasonal occurrence of *Tiphia vernalis* in Kentucky. *Environmental Entomology* **33**, 520–527.

Roubik, D. W. (1989). *Ecology and Natural History of Tropical Bees*. Cambridge University Press, Cambridge.

Rougerie, R., Smith, M. A., Fernandez-Triana, J., Lopez-Vaamonde, C., Ratnasingham, S. & Hebert, P. D. N. (2011). Molecular analysis of parasitoid linkages (MAPL): gut contents of adult parasitoid wasps reveal larval host. *Molecular Ecology* **20**, 179–186.

Rovira, A. M. L., Bosch, M., Molero, J. & Blanché, C. (2002). Pollination ecology and breeding system of the very narrow coastal endemic *Seseli farrenyi* (Apiaceae). Effects of population fragmentation. *Nordic Journal of Botany* **22**, 727–740.

Ruddle, K. (1973). The human use of insects: examples from the Yukpa. *Biotropica* **5**, 94–101.

Russell, E. F. (1957). *Wasp*. Perseus Books Group, New York.

Rutledge, C. E., Hellman, W., Teerling, C. & Fierke, M. K. (2011). Two novel prey families for the buprestid-hunting wasp *Cerceris fumipennis* say (Hymenoptera: Crabronidae). *The Coleopterists Bulletin* **65**, 194–196.

Sá, T., Furtado, M. T., Ferrero, V., Pérez-Barrales, R., Rodrigues, E. B., Dos Santos, I. G. & Consolaro, H. (2016). Floral biology, reciprocal herkogamy and breeding system in four *Psychotria* species (Rubiaceae) in Brazil. *Botanical Journal of the Linnean Society* **182**, 689–707.

Sackmann, P., D'Adamo, P., Rabinovich, M. & Corley, J. C. (2000). Arthropod prey foraged by the German wasp (*Vespula germanica*) in NW Patagonia, Argentina. *New Zealand Entomologist* **23**, 55–59.

Sahagún-Godínez, E. & Lomelí-Sención, J. A. (1997). *Pedilanthus diazlunanus* (Euphorbiaceae): pollination by hymenopterans in a bird-pollinated genus. *American Journal of Botany* **84**, 1584–1587.

Santos, G. M. D. M., Aguiar, C. M. L. & Mello, M. A. R. (2010). Flower-visiting guild associated with the Caatinga flora: trophic interaction networks formed by social bees and social wasps with plants. *Apidologie* **41**, 466–475.

Santos, G. M. D. M., Bichara Filho, C. C., Resende, J. J., da Cruz, J. D. & Marques, O. M. (2007). Diversity and community structure of social wasps (Hymenoptera: Vespidae) in three ecosystems in Itaparica Island, Bahia state, Brazil. *Neotropical Entomology* **36**, 180–185.

Schiestl, F. P. & Ayasse, M. (2001). Post-pollination emission of a repellent compound in a sexually deceptive orchid: a new mechanism for maximising reproductive success? *Oecologia* **126**, 531–534.

Schiestl, F. P., Peakall, R., Mant, J. G., Ibarra, F., Schulz, C., Franke, S. & Francke, W. (2003). The chemistry of sexual deception in an orchid-wasp pollination system. *Science* **302**, 437–438.

Schimitschek, E. (1968). Insekten als nahrung, in brauchtum, kult und kultur. *Anzeiger für Schädlingskunde* **43**, 44–45.

Schlumpberger, B. O. & Badano, E. I. (2005). Diversity of floral visitors to *Echinopsis atacamensis subsp. pasacana* (Cactaceae). *Haseltonia* **11**, 18–26.

Schuster, S. C. (2008). Next-generation sequencing transforms today's biology. *Nature Methods* **5**, 16–18.

Sears, A. L. W., Smiley, J. T., Hilker, M., Muller, F. & Rank, N. E. (2001). Nesting behavior and prey use in two geographically separated populations of the specialist wasp *Symmorphus cristatus* (Vespidae: Eumeninae). *American Midland Naturalist* **145**, 233–246.

Senapathi, D., Carvalheiro, L. G., Biesmeijer, J. C., Dodson, C. A., Evans, R. L., McKerchar, M., Morton, D. R., Moss, E. D., Roberts, S. P. M., Kunin, W. E. & Potts, S. G. (2015). The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. *Proceedings of the Royal Society B: Biological Sciences* **282**, 20150294.

Shannon, P., Markiel, A., Ozier, O., Baliga, N. S., Wang, J. T., Ramage, D., Amin, N., Schwikowski, B. & Ideker, T. (2003). Cytoscape: a software environment for integrated models of biomolecular interaction networks. *Genome Research* **13**, 2498–2504.

Shimizu, A. (1992). Nesting behavior of the semi-aquatic spider wasp, *Anoplius eous*, which transports its prey on the surface film of water (Hymenoptera, Pompilidae). *Journal of Ethology* **10**, 85–102.

Shuttleworth, A. & Johnson, S. D. (2006). Specialized pollination by large spider -hunting wasps and self-incompatibility in the African milkweed *Pachycarpus aperifolius*. *International Journal of Plant Science* **167**, 1177–1186.

Shuttleworth, A. & Johnson, S. D. (2009a). New records of insect pollinators for south African asclepiads (Apocynaceae: Asclepiadoideae). *South African Journal of Botany* **75**, 689–698.

Shuttleworth, A. & Johnson, S. D. (2009b). Palp-faction: an African milkweed dismembers its wasp pollinators. *Environmental Entomology* **38**, 741–747.

Shuttleworth, A. & Johnson, S. D. (2009c). Specialized pollination in the African milkweed *Xysmalobium orbiculare*: a key role for floral scent in the attraction of spider-hunting wasps. *Plant Systematics and Evolution* **280**, 37–44.

Shuttleworth, A. & Johnson, S. D. (2009d). The importance of scent and nectar filters in a specialized wasp-pollination system. *Functional Ecology* **23**, 931–940.

Shuttleworth, A. & Johnson, S. D. (2012). The *Hemipepsis* wasp-pollination system in South Africa: a comparative analysis of trait convergence in a highly specialized plant guild. *Botanical Journal of the Linnean Society* **168**, 278–299.

Silveira, O. T., Esposito, M. C., dos Santos, J. N. & Gemaque, F. E. (2005). Social wasps and bees captured in carrion traps in a rainforest in Brazil. *Entomological Science* **8**, 33–39.

Simões, M. H., Guedes, A. O., Thyssen, P. J. & Silva, M. S. (2013). Ecological and forensic implications of social wasps on pig carcass degradation in Brazilian savannah. *Brazilian Journal of Forensic Sciences, Medical Law and Bioethics* **2**, 286–293.

Singh, O. T., Nabam, S. & Chakravorty, J. (2007). Edible insects of Nishi tribe of Arunachal Pradesh. *Hexapoda* **14**, 56–60.

Skaldina, O., Ciszek, R., Peräniemi, S., Kolehmainen, M. & Sorvari, J. (2020). Facing the threat: common yellowjacket wasps as indicators of heavy metal pollution. *Environmental Science and Pollution Research* **27**, 29031–29042.

Smiley, J. T. & Rank, N. E. (1986). Predator protection versus rapid growth in a montane leaf beetle. *Oecologia* **70**, 106–112.

Smith, A. (1979). Life strategy and mortality factors of *Sceliphron laetum* (Smith) (Hymenoptera: Sphecidae) in Australia. *Australian Journal of Ecology* **4**, 181–186.

Snelling, R. R. (1953). Notes on the hibernation and nesting of the wasp *Mischocyttarus flavitarsis* (De Saussure) (Hymenoptera, Vespidae). *Journal of the Kansas Entomological Society* **26**, 143–145.

Somavilla, A. & Köhler, A. (2012). Preferência floral de vespas (Hymenoptera, Vespidae) no Rio Grande do Sul, Brasil. *Entomobrasilis* **5**, 21–28.

Somavilla, A., Linard, V. & Rafael, J. A. (2019). Social wasps (Vespidae: Polistinae) on carcasses of *Rattus norvegicus* (Mammalia: Muridae) in the Central Amazonia, Brazil: possible forensic implications. *Revista Brasileira de Entomologia* **63**, 18–21.

Southon, R. J., Fernandes, O. A., Nascimento, F. S. & Sumner, S. (2019). Social wasps are effective biocontrol agents of key lepidopteran crop pests. *Proceedings of the Royal Society B: Biological Sciences* **286**, 20191676.

de Souza, A. R., Venâncio, D. D. F. A., Prezoto, F. & Zanuncio, J. C. (2013). Social wasps (Hymenoptera: Vespidae) nesting in eucalyptus plantations in Minas Gerais, Brazil. *Florida Entomologist* **95**, 1000–1002.

Spradbery, J. P. (1973). *Wasps: An Account of the Biology and Natural History of Solitary and Social Wasps*. University of Washington Press, Seattle.

Srimuang, K., Bänziger, H. & Watthana, S. (2018). Pollination-system diversity in *Epipactis* (Orchidaceae): new insights from studies of *E. flava* in Thailand. *Plant Systematics and Evolution* **304**, 895–909.

Stamp, N. E. & Bowers, M. D. (1988). Direct and indirect effects of predatory wasps (*Polistes* sp.: Vespidae) on gregarious caterpillars (*Hemileuca lucina*: Saturniidae). *Oecologia* **75**, 619–624.

Stanley, E., Toscano-Gadea, C. & Aisenberg, A. (2013). Spider hawk in sand dunes: *Anoplius bicinctus* (Hymenoptera: Pompilidae), a parasitoid wasp of the sex-role reversed spider *Allocosa brasiliensis* (Araneae: Lycosidae). *Journal of Insect Behavior* **26**, 514–524.

Stefani, R. (1956). Descrizione e osservazioni sulla biologia e sulla larva di un nuovo Sclerogibbino della Sardegna. *Bollettino della Società Entomologica Italiana* **86**, 130–137.

Stefanini, I., Dapporto, L., Berná, L., Polsinelli, M., Turillazzi, S. & Cavalieri, D. (2016). Social wasps are a *Saccharomyces* mating nest. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 2247–2251.

Stefanini, I., Dapporto, L., Legras, J.-L., Calabretta, A., di Paola, M., de Filippo, C., Viola, R., Capretti, P., Polsinelli, M., Turillazzi, S. & Cavalieri, D. (2012). Role of social wasps in *Saccharomyces cerevisiae* ecology and evolution. *Proceedings of the National Academy of Sciences of the United States of America* **109**, 13398–13403.

Steiner, K. E., Whitehead, V. B. & Johnson, S. D. (1994). Floral and pollinator divergence in two sexually deceptive South-African orchids. *American Journal of Botany* **81**, 185–194.

Stoutamire, W. P. (1975). Pseudocopulation in Australian terrestrial orchids. *American Orchid Society Bulletin* **44**, 226–233.

Stoutamire, W. P. (1983). Wasp pollination species of *Caladenia* (Orchidacea) in South-Western Australia. *Australian Journal of Botany* **31**, 383–394.

Struck, M. (1994). Flowers and their insect visitors in the arid winter rainfall region of southern Africa: observations on permanent plots. Insect visitation behaviour. *Journal of Arid Environments* **28**, 51–74.

Stubblefield, J. W., Seger, J., Wenzel, J. W. & Heisler, M. M. (1993). Temporal, spatial, sex-ratio and body-size heterogeneity of prey species taken by the beewolf Philanthus sanbornii (Hymenoptera: Sphecidae). *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **339**, 397–423.

Suetsugu, K. (2019). Social wasps, crickets and cockroaches contribute to pollination of the holoparasitic plant *Mitrastemon yamamotoi* (Mitrastemonaceae) in southern Japan. *Plant Biology* **21**, 176–182.

Sugden, E. A. & McAllen, R. L. (1994). Observations on foraging, population and nest biology of the Mexican honey wasp, *Brachygastra mellifica* (say) in Texas [Vespidae: Polybiinae]. *Journal of the Kansas Entomological Society* **67**, 141–155.

Suma, P., Amante, M., Bella, S., la Pergola, A. & Russo, A. (2014). Stored-product insect natural enemies in wheat industry in Sicily. *IOBC/WPRS Bulletin* **98**, 227–233.

Sumner, S., Bevan, P., Hart, A. G. & Isaac, N. J. B. (2019). Mapping species distributions in 2 weeks using citizen science. *Insect Conservation and Diversity* **12**, 382–388.

Sumner, S., Law, G. & Cini, A. (2018). Why we love bees and hate wasps. *Ecological Entomology* **43**, 836–845.

Sundaramurthy, V. T. & Santhanakrishnan, K. (1979). The effect of population density of parasite *Perisierola nephantidis*[Hym.: Bethylidae] on the mortality of coconut caterpillar *Nephantis serinopa* [Lep.: Cryptophagidae]. *Entomophaga* **24**, 115–117.

Symondson, W. O. C., Sunderland, K. D. & Greenstone, M. H. (2002). Can generalist predators be effective biocontrol agents? *Annual Review of Entomology* **47**, 561–594.

Taki, H., Okabe, K., Makino, S., Yamaura, Y. & Sueyoshi, M. (2009). Contribution of small insects to pollination of common buckwheat, a distylous crop. *Annals of Applied Biology* **155**, 121–129.

Tanaka, H., Hatano, T., Kaneko, N., Kawachino, S., Kitamura, O., Suzuki, Y., Tada, T. & Yaoi, Y. (2006). Andromonoecious sex expression of flowers and pollinia delivery by insects in a Japanese milkweed *Metaplexis japonica* (Asclepiadaceae), with special reference to its floral morphology. *Plant Species Biology* **21**, 193–199.

Tepedino, V. J., Bowlin, W. R. & Griswold, T. L. (2011). Diversity and pollination value of insects visiting the flowers of a rare buckwheat (*Eriogonum pelinophilum*: Polygonaceae) in disturbed and "natural" areas. *Journal of Pollination Ecology* **4**, 2011.

Tepedino, V. J., Toler, T. R., Bradley, B. A., Hawk, J. L. & Griswold, T. L. (2007). Pollination biology of a disjunct population of the endangered sandhills endemic *Penstemon haydenii* S. Wats. (Scrophulariaceae) in Wyoming, USA. *Plant Ecology* **193**, 59–69.

Theiss, K., Kephart, S. & Ivey, C. T. (2007). Pollinator effectiveness on co-occurring milkweeds (*Asclepias*; Apocynaceae, Asclepiadoideae) 1. *Annals of the Missouri Botanical Garden* **94**, 505–516.

Thomas, C. D., Moller, H., Plunkett, G. M. & Harris, R. J. (1990). The prevalence of introduced *Vespula vulgaris* wasps in a New Zealand beech forest community. *New Zealand Journal of Ecology* **13**, 63–72.

Thomson, D. M. (2019). Effects of long-term variation in pollinator abundance and diversity on reproduction of a generalist plant. *Journal of Ecology* **107**, 491–502.

Tomazella, V. B., Jacques, G. C., Lira, A. C. & Silveira, L. C. P. (2018). Visitation of social wasps in Arabica coffee crop (*Coffea arabica* L.) intercropped with different tree species. *Sociobiology* **65**, 299–304.

Tormos, J., Asís, J. D., Beneitez, A. & Gayubo, S. F. (2009). Description of the mature larva of the sand wasp *Bembix bidentata* and its parasitoids (Hymenoptera: Crabronidae, Chrysididae, Mutillidae). *Florida Entomologist* **92**, 43–53.

Tormos, J., Asís, J. D., Gayubo, S. F., Calvo, J. & Martín, M. A. (2005). Ecology of crabronid wasps found in trap nests from Spain (Hymenoptera: Spheciformes). *Florida Entomologist* **88**, 278–284.

Townes, H. K. (1977). A revision of the Rhopalosomatidae (Hymenoptera). *Contributions of the American Entomological Institute* **15**, 1–34.

Trad, B. M., Silvestre, R., Auko, T. H., Lopez, V. M. & Santos, E. F. D. (2018). First host record of *Epipompilus* (Hymenoptera: Pompilidae) from Brazil and discussion of prey carriage mechanism. *Revista Brasileira de Entomologia* **62**, 253–256.

Traveset, A. & Sáez, E. (1997). Pollination of *Euphorbia dendroides* by lizards and insects: spatio-temporal variation in patterns of flower visitation. *Oecologia* **111**, 241–248.

Turillazzi, S. (1983). Extranidal behaviour of *Parischnogaster nigricans serrei* (Du Buysson) (Hymenoptera, Stenogastrinae). *Zeitschrift für Tierpsychologie* **63**, 27–36.

Turillazzi, S. (2012). *The Biology of Hover Wasps*. Springer, Berlin.

Turillazzi, S., Mastrobuoni, G., Dani, F. R., Moneti, G., Pieraccini, G., la Marca, G., Bartolucci, G., Perito, B., Lambardi, D., Cavallini, V. & Dapporto, L. (2006). Dominulin A and B: two new antibacterial peptides identified on the cuticle and in the venom of the social paper wasp *Polistes dominulus* using MALDI-TOF, MALDI-TOF/TOF, and ESI-ion trap. *Journal of the American Society for Mass Spectrometry* **17**, 376–383.

Turillazzi, S., Perito, B., Pazzagli, L., Pantera, B., Gorfer, S. & Tancredi, M. (2004). Antibacterial activity of larval saliva of the European paper wasp P*olistes dominulus* (Hymenoptera, Vespidae). *Insectes Sociaux* **51**, 339–341.

Ueno, T. (2015). The paper wasp *Polistes olivaceus* (Hymenoptera: Vespidae) as an important predator of beet armyworm in Vietnam. *Journal of Agriculture and Environmental Sciences* **4**, 54–57.

Urbini, A., Sparvoli, E. & Turillazzi, S. (2006). Social paper wasps as bioindicators: a preliminary research with *Polistes dominulus* (Hymenoptera Vespidae) as a trace metal accumulator. *Chemosphere* **64**, 697–703.

Vadivelu, S., Mohanasundaram, M. & Rao, P. V. S. (1975). Record of parasites and predators on some south Indian crop pests. *Indian Journal of Entomology* **37**, 100–101.

van der Meer Mohr, J. (1965). Insects eaten by the Karo-Batak people (a contribution to entomo-bromatology). *Entomologische Berichten, Amsterdam* **25**, 101–107.

van Helsdingen, P. J. (2011). Spiders in a hostile world (Arachnoidea, Araneae). *Arachnologische Mitteilungen* **40**, 55–64.

van Huis, A. (2013). Potential of insects as food and feed in assuring food security. *Annual Review of Entomology* **58**, 563–583.

van Huis, A., van Itterbeeck, J., Klunder, H., Mertens, E., Halloran, A., Muir, G. & Vantomme, P. (2013). *Edible Insects: Future Prospects for Food and Feed Security*. Food and Agriculture Organisation of the United Nations, Rome.

Vargas, H. A., Vargas-Ortiz, M., Huanca-Mamani, W. & Hausmann, A. (2014). Prey identification in nests of the potter wasp *Hypodynerus andeus* (Packard) (Hymenoptera, Vespidae, Eumeninae) using DNA barcodes. *Revista Brasileira de Entomologia* **58**, 157–160.

Varrone, R. & Olmi, M. (2010). First record of host of *Embolemus ruddii* Westwood (Hymenoptera Embolemidae). *Frustula Entomologica* **33**, 91–95.

van der Vecht, J. (1957). The Vespinae of the indo-Malayan and Papuan areas (Hymenoptera, Vespidae). *Zoologische Verhandelingen* **34**, 1–83.

van Klink, R., Bowler, D. E., Gongalsky, K. B., Swengel, A. B., Gentile, A. & Chase, J. M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* **368**, 417–420.

van Lenteren, J. C. (2012). The state of commercial augmentative biological control: plenty of natural enemies, but a frustrating lack of uptake. *BioControl* **57**, 1–20.

Vereecken, N. & Carriere, J. (2003). Contribution à l'étude éthologique de la grande Scolie à front jaune *Megascolia maculata flavifrons* (F., 1775) (Hymenoptera, Scoliidae) en France méditerranéenne. *Notes Fauniques de Gembloux* **53**, 71–80.

Vereecken, N. J., Wilson, C. A., Hotling, S., Schulz, S., Banketov, S. A. & Mardulyn, P. (2012). Pre-adaptations and the evolution of pollination by sexual deception: Cope's rule of specialization revisited. *Proceedings of the Royal Society B: Biological Sciences* **279**, 4786–4794.

Vieira, L. C., Oliveira, N. G. & Gayubo, S. F. (2011). On the use of Apiformes and Spheciformes (Insecta: Hymenoptera) populations as a management tool. *Biodiversity and Conservation* **20**, 519–530.

Vieira, M. F. & Shepherd, G. J. (1999). Pollinators of *Oxypetalum* (Asclepiadaceae) in southeastern Brazil. *Revista Brasileira de Biologia* **59**, 693–704.

Vikberg, V. & Koponen, M. (2005). Contribution to the taxonomy of the Palaearctic species of the genus *Laelius* Ashmead, mainly from Finland and Sweden (Hymenoptera: Chrysidoidea: Bethylidae). *Entomologica Fennica* **16**, 23–50.

Villanueva-Bonilla, G. A., Brescovit, A. D., dos Santos, E. & Vasconcellos-Neto, J. (2018). First record of *Epipompilus excelsus* (Bradley, 1944) (Hymenoptera, Pompilidae) as a koinobiont ectoparasitoid of *Ariadna mollis* (Holmberg, 1876)(Araneae, Segestriidae). *Journal of Hymenoptera Research* **66**, 15–21.

Villemant, C., Muller, F. Haubois, S., Perrard, A., Darrouzet, E. & Rome, Q. (2011). Bilan des travaux (MNHN et IRBI) sur l'invasion en France de Vespa velutina, le frelon asiatique prédateur d'abeilles. In: Barbancon, J. M. & L'Hostis, M. (eds), *Proceedings of the Journée Scientifique Apicole - 11* February 2011, pp. 3–12. Oniris-fnosad, Nantes, France.

Vislobokov, N. A. & Galinskaya, T. V. (2018). Pollination ecology of two co-occurring species of *Balanophora*: differences in range of visitors and pollinators. *International Journal of Plant Sciences* **179**, 341–349.

Waloff, N. (1974). Biology and behaviour of some species of Dryinidae (Hymenoptera). *Journal of Entomology Series A, General Entomology* **49**, 97–109.

Wang, C., Chen, P., Jin, H., Yan, X., Gan, L., Li, Y., Zhou, S., Chang, J., Wang, Y., Yang, G. & He, G. (2008a). Nidus vespae protein inhibiting proliferation of HepG2 hepatoma cells through extracellular signal-regulated kinase signaling pathways and inducing G1 cell cycle arrest. *Acta Biochimica et Biophysica Sinica* **40**, 970–978.

Wang, K., Zhang, B., Zhang, W., Yan, J., Li, J. & Wang, R. (2008b). Antitumor effects, cell selectivity and structure-activity relationship of a novel antimicrobial peptide *Polybia*-MPI. *Peptides* **29**, 963–968.

Wang, Z. Z., Liu, Y. Q., Shi, M., Huang, J. H. & Chen, X. X. (2019). Parasitoid wasps as effective biological control agents. *Journal of Integrative Agriculture* **18**, 705–715.

Ward, D. F. & Ramón-Laca, A. (2013). Molecular identification of the prey range of the invasive Asian paper wasp. *Ecology and Evolution* **3**, 4408–4414.

Ward, M., Johnson, S. D. & Zalucki, M. P. (2012). Modes of reproduction in three invasive milkweeds are consistent with Baker's rule. *Biological Invasions* **14**, 1237–1250.

Warkentin, K. M. (2000). Wasp predation and wasp-induced hatching of red-eyed treefrog eggs. *Animal Behaviour* **60**, 503–510.

Wcislo, W. T., West-Eberhard, M. J. & Eberhard, W. G. (1988). Natural history and behavior of a primitively social wasp, *Auplopus semialatus*, and its parasite, *Irenangelus eberhardi* (Hymenoptera: Pompilidae). *Journal of Insect Behavior* **1**, 247–260.

Wearing, C. H. & Harris, A. C. (1999). Evaluation of the predatory wasp, *Ancistrocerus gazella*, for biological control of leafrollers in Otago fruit crops: 1. Prey composition, nest structure and wasp productivity from artificial nests. *Biocontrol Science and Technology* **9**, 315–325.

Wearing, C. H. & Harris, A. C. (2005). Evaluation of the predatory wasp, *Ancistrocerus gazella*, for biological control of leafrollers in Otago fruit crops. II. Wasp phenology and seasonal changes in prey composition. *Biocontrol Science and Technology* **15**, 281–298.

Weiss, M. R., Wilson, E. E. & Castellanos, I. (2004). Predatory wasps learn to overcome the shelter defences of their larval prey. *Animal Behaviour* **68**, 45–54.

Wiemer, A. P., Sérsic, A. N., Marino, S., Simões, A. O. & Cocucci, A. A. (2012). Functional morphology and wasp pollination of two south American asclepiads (Asclepiadoideae-Apocynaceae). *Annals of Botany* **109**, 77–93.

Wiesenborn, W. D. (2018). Conspecific pollen on insects visiting female flowers of *Phoradendron juniperinum* (Viscaceae) in Western Arizona. *Western North American Naturalist* **77**, 478–486.

Williams, F. X. (1956). Life history studies of *Pepsis* and *Hemipepsis* wasps in California (Hymenoptera, Pompilidae). *Annals of the Entomological Society of America* **49**, 447–466.

Williams, G. & Adam, P. (1998). Pollination ecology of Australian subtropical rainforests–implications for the conservation of remnant lowland communities. In *Rainforest remnants, a decade of growth. Proceedings of a conference on rainforest remnants and regeneration at Southern Cross University Conference Centre, 21-23rd November*, pp. 47–59.

Wilson-Rankin, E. E. (2014). Social context influences cue-mediated recruitment in an invasive social wasp. *Behavioral Ecology and Sociobiology* **68**, 1151–1161.

Wilson, E. E., Mullen, L. M. & Holway, D. A. (2009). Life history plasticity magnifies the ecological effects of a social wasp invasion. *Proceedings of the National Academy of Sciences of the United States of America* **106**, 12809–12813.

Wilson, E. E. & Wolkovich, E. M. (2011). Scavenging: how carnivores and carrion structure communities. *Trends in Ecology and Evolution* **26**, 129–135.

Wilson, E. O. (1990). *Success and Dominance in Ecosystems: The Case of the Social Insects*. Ecology Institute, Oldendorf/Luhe.

Wolff, D., Meve, U. & Liede-Schumann, S. (2008). Pollination ecology of Ecuadorian Asclepiadoideae (Apocynaceae): how generalized are morphologically specialized flowers? *Basic and Applied Ecology* **9**, 24–34.

Xiao, J., Zuo, Y. L., Liu, Y., Li, J. Y., Hao, Y. Q. & Zhou, X. D. (2007). Effects of Nidus Vespae extract and chemical fractions on glucosyltransferases, adherence and biofilm formation of *Streptococcus mutans*. *Archives of Oral Biology* **52**, 869–875.

Xu, H., Bohman, B., Wong, D. C., Rodriguez-Delgado, C., Scaffidi, A., Flematti, G. R., Phillips, R. D., Pichersky, E. & Peakall, R. (2017). Complex sexual deception in an orchid is achieved by co-opting two independent biosynthetic pathways for pollinator attraction. *Current Biology* **27**, 1867–1877.

Yamada, Y., Shinohara, Y., Kakudo, T., Chaki, S., Futaki, S., Kamiya, H. & Harashima, H. (2005). Mitochondrial delivery of mastoparan with transferrin liposomes equipped with a pH-sensitive fusogenic peptide for selective cancer therapy. *International Journal of Pharmaceutics* **303**, 1–7.

Yamashiro, T., Yamashiro, A., Yokoyama, J. & Maki, M. (2008). Morphological aspects and phylogenetic analyses of pollination systems in the *Tylophora–Vincetoxicum* complex (Apocynaceae-Asclepiadoideae) in Japan. *Biological Journal of the Linnean Society* **93**, 325–341.

Yhoung-Aree, J. & Viwatpanich, K. (2005). Edible insects in the Laos PDR, Myanmar, Thailand, and Vietnam. In *Ecological Implications of Minilivestock: Potential of Insects, Rodents, Frogs and Snails* (ed. M. G. Paoletti), pp. 415–440. Science Publishers, Inc., Plymouth.

Yildirim, E. (2003). A new cleptoparasitoid of *Gymnomerus laevipes* (Hymenoptera, Vespidae, Eumeninae) and a description of its nest. *Deutsche Entomologische Zeitschrift* **50**, 111–112.

Yin, W., Liu, J., Liu, H. & Lv, B. (2017). Nutritional value, food ingredients, chemical and species composition of edible insects in China. In *Future Foods* (ed. H. Mikkola), pp. 27–53. InTech Open, Rijeka.

Ying, F., Xiaoming, C., Long, S. & Zhiyong, C. (2010). Common edible wasps in Yunnan Province, China and their nutritional value. In *Forest Insects as Food: Humans Bite Back* (eds P. B. Durst, D. V. Johnson, R. N. Leslie and K. Shono), pp. 93–98. Food and Agriculture Organisation of the United Nations, Bangkok.

Yong, S. & Breto, D. (2015). Nuevos reportes de bupréstidos (Coleoptera: Buprestidae) como presas de la avispa *Cerceris cerverae* (Hymenoptera: Crabronidae). *Boletín Sociedad Entomológica Aragonesa* **56**, 370–372.

Zeddies, J., Schaab, R. P., Neuenschwander, P. & Herren, H. R. (2001). Economics of biological control of cassava mealybug in Africa. *Agricultural Economics* **24**, 209–219.

Zettler, J. A., Spira, T. P. & Allen, C. R. (2001). Yellow jackets (*Vespula* spp.) disperse *Trillium* (spp.) seeds in eastern North America. *American Midland Naturalist* **146**, 444–446.

X. Supporting information

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

Supplementary data set S1. Existing prey records for solitary aculeate wasps.

Supplementary data set S2. Existing prey records for social aculeate wasps.

Supplementary data set S3. Obligate plant-pollination services provided by aculeate wasps.

Supplementary data set S4. Facultative plant-pollination services provided by aculeate wasps.

Supplementary data set S5. Existing records of aculeate wasp species used as a source of human nutrition and the countries in which they are consumed.

Supplementary data set S6. Existing records of seed dispersal services (vespicochory) provided by aculeate wasps.

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