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Short communication

Crowdsourced online images provide insights into predator-prey interactions of putative natural enemies

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ABSTRACT

Most megadiverse clades of insects are herbivores, but several large radiations consist almost entirely of predators. Their species numbers make comprehensive direct observations of predator-prey interactions difficult to obtain. Citizen science approaches are increasingly utilized to harvest ecological data for organisms including insects. We use crowdsourced images documenting predator-prey interactions of assassin bugs (Hemiptera: Reduviidae), a speciose clade of predatory insects, to (1) determine the breakdown of assembled online images by geographic region and reduviid subfamily; (2) evaluate if the accumulated images provide new insights into prey diversity; and (3) assess evidence for taxa that feed on pest species, pollinators, and engage in intraguild predation. Photographs were assembled (n = 832) and resulted in an image database that included representatives of 11 subfamilies; most records belonged to diurnal Harpactorinae and Phymatinae, but some subfamilies with poorly understood prey diversity were also documented. Taxa with substantial image representation of prey (21–242 predation events) showed significant overlap with prey reported in the literature. A high percentage of images for *Apiomerus* Hahn and *Phymata* Latreille documented predation events on native and non-native bees; percentages varied widely among species of *Zelus* Fabricius. *Arilus cristatus* (Linnaeus) was documented to prey on several pest species, with little evidence for pollinator predation. Potential effects of these natural enemies on pollinators and intraguild predators should be further investigated, providing important insights into mechanisms influencing community structure and ecosystems processes.

Insects are megadiverse and ubiquitous in terrestrial ecosystems (Stork et al., 2015). They engage in diverse feeding strategies including herbivory, carnivory, parasitism, and parasitoidism, and serve diverse roles including as plant pests, disease vectors, beneficial biological control agents, and pollinators (DeBach and Rosen, 1991; Vanbergen et al., 2013; Mayer et al., 2017). Although the majority of insect species are herbivores (Mitter et al., 1988), several radiations have given rise to speciose clades of parasitoids and predators (Wiegmann et al., 1993; Maddison et al., 2009). Given their overwhelming species richness, small body size, and often cryptic habits, much remains to be discovered about inter-specific interactions. While a large body of literature focuses on pests of agricultural crops and specialist parasitoid species that may be used to control them (Stiling and Cornelissen, 2005; Heraty, 2009; Derocles et al., 2016), generalist predatory insects are recognized as important natural enemies, but are less intensively studied (Bosco et al., 2008; Tan et al., 2016; Batista et al., 2017). Predatory insects that feed on many prey species may have limitations for biological control applications because of prey-switching, weak interaction strengths, and intraguild predation (Symondson et al., 2002). Certain generalist natural enemy taxa have been studied in field and lab settings, both to evaluate their effectiveness as natural enemies and their impact on other beneficial insects (Shackelford et al., 2013; Bray and Nieh, 2014; Frago, 2016; Katsanis et al., 2017), and some are now utilized as biocontrol agents (de Oliveira et al., 2016; Gomez-Polo et al., 2016; Riddick, 2017). However, prey diversity for most predatory insect species is unknown, among them species belonging to some of the most diverse lineages of terrestrial predators, e.g., carabid beetles (>40,000 spp.; Lovei and Sunderland, 1996), asilid flies (>8000 spp.; Dikow, 2009), and assassin bugs (~7000 spp.; Maldonado, 1990; Weirauch et al., 2014). This lack of natural history data impedes our understanding of predator-prey communities in natural and agricultural systems.

Field observations, predator exclusion experiments, prey bait trials, molecular analyses of gut contents, stable isotope techniques, and analysis of fatty acids – all have started to accelerate the collection of predator-prey interaction data in arthropod systems (Birkhofer et al., 2017). Although the onset of molecular diagnostics has revolutionized the study of trophic interactions (Symondson and Harwood, 2014) and is increasingly applied to predator-prey networks in insects (Lundgren and Fergen, 2014; Rondoni et al., 2015; Unruh et al., 2016; Masonick et al., 2019), live observations or video surveillance (Grieshop et al., 2012; Chisholm et al., 2014; Zou et al., 2017) in the

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field remain important. However, their quantitative study is limited to systems where observation does not disrupt predatory behaviors and that allow for sight identification of predators and prey (Sunderland, 1988). Many direct observation studies, therefore, are confined to particular prey or predator species (Choate and Lundgren, 2015; Michalek et al., 2017).

A number of recent initiatives have promoted crowdsourcing of nature observations, e.g., iSpot Nature https://www.ispotnature.org/ or iNaturalist https://www.inaturalist.org/. In addition to raising interest in the natural world, these platforms also provide data for ecological investigations (Silvertown et al., 2015). The potential, and limitations, of citizen science-generated data have been discussed in the context of conservation issues. Studies have largely focused on vertebrates and plants (Swanson et al., 2016; Turnhout et al., 2016; Ellwood et al., 2017), while projects involving insects have been devoted primarily to butterflies (Howard and Davis, 2009; Schmeller et al., 2009). We propose that crowdsourced, expert-curated, photographs can be valuable for generating natural history data on predator-prey interactions in certain groups of predatory insects with poorly documented ecologies. This type of data is likely most readily available for predatory arthropods that are large-bodied, charismatic due to their morphology, coloration, or behavior, and found in habitats easily accessed by humans. We pose that assassin bugs (Insecta: Hemiptera: Reduviidae) are one of these groups of predatory arthropods and here examine the potential, and limitations, of crowdsourced predatory-prey interaction data for this species-rich taxon.

Reduviidae are a diverse family of true bugs (Hemiptera: Heteroptera), with 24 subfamilies and about 7000 described species (Maldonado, 1990; Weirauch et al., 2014; Forthman and Weirauch, 2017). Certain lineages of reduviids are stenophagous, including the termite specialist Salyavatinae (McMahan, 1982; Gordon and Weirauch, 2016), millipede assassin bugs in the subfamily Ectrichodiinae (Haridass, 1985; Forthman and Weirauch, 2012), ant-luring Holoptilinae (Weirauch and Cassis, 2006), or vertebrate blood-feeding Triatominae (Lent and Wygodzinsky, 1979). While most of the evidence for the stenophagous feeding habits in these groups is derived from sparse direct observations (Jacobson, 1911; McMahan, 1983), recent studies have started to embrace molecular diagnostics for Salyavatinae, Triatominae, and Phymatinae (Gordon and Weirauch, 2016; Georgieva et al., 2017; Masonick et al., 2019), and have crowdsourced online images for Ectrichodiinae and Salyavatinae (Forthman and Weirauch, 2012; Gordon and Weirauch, 2016). The largely diurnal and vegetation-associated Harpactorinae and Phymatinae are thought to be generalist predators of flower- and vegetation-associated insects (Readio, 1927; Haviland, 1931; Balduf, 1939; Balduf, 1964), consistent with a recent gut metabarcoding study of one Phymatinae species (Masonick et al., 2019). Although prey ranges for the majority of assassin bug species are unknown, several species of Harpactorinae have been investigated as potential natural enemies of insect pest species. Among these are *Pristhesancus plagipennis* Walker that was implemented in integrated pest management approaches in Australia (Grundy and Maelzer, 2003; Grundy, 2007), *Cosmolestes picticeps* (Stål) that has potential for the control of bagworms in oil palm plantations (Jamian et al., 2017), and *Zelus longipes* (Linné) that could assist in controlling picture-winged flies in corn fields (Kalsi et al., 2014), among other species. Although potentially beneficial as natural enemies, the possible impacts on pollinators (Marques et al., 2003), and their tendency for intraguild predation (Rosenheim et al., 1993; Cisneros and Rosenheim, 1997), have only been experimentally investigated for few species of Harpactorinae. Feeding habits for other assassin bug lineages are virtually unknown, e.g., for the primarily nocturnal Stenopodainae or the bark-associated Hammacerinae (Readio, 1927). Overall, prey diversity for Reduviidae species is poorly documented.

We here use image crowdsourcing to investigate if online citizen scientist-contributed data can be used to gain a better understanding of prey diversity in assassin bugs. Specifically, we set out to determine the representation of different assassin bug families in our assembled image database; the geographic origin of images; evaluate if this image database provides new insights into prey diversity; and assess evidence for these taxa to feed on pest species or beneficial insects or to engage in intraguild predation.

A database of images documenting interactions of Reduviidae with putative prey organisms was assembled from searches of the photographic websites Flickr (https://www.flickr.com/), iSpot Nature (https://www.ispotnature.org/), BugGuide (http://bugguide.net/node/view/15740), NatureWatch (https://www.naturewatch.ca/), and Google. The search terms used were "Reduviidae", "True Bugs"/"Heteroptera" or subfamily names (e.g., "Harpactorinae"). Searches were conducted June–November 2016 (260 search hours). We did not exclusively use the term "prey" because photographers may not be aware that they document a predation event. The terms "True Bugs"/"Heteroptera" were used because assassin bugs may be misidentified as other heteropteran families. This study focuses on predatory Reduviidae, so we excluded Triatominae; Ectrichodiinae and Salyavatinae were not searched comprehensively, because photo-based prey data for both groups are published (Forthman and Weirauch, 2012; Gordon and Weirauch, 2016). A photograph was classified as documenting a predation event if (1) the tip of the assassin bug labium was in contact with the prey organism (interpreted as probing, feeding, or scavenging); or (2) if the photographer stated that the assassin bug was feeding. Scavenging occurs in certain Harpactorinae (Zhang et al., 2016) but has not been reported for other assassin bugs. Some images may document probing rather than feeding; because of the longer duration, we argue that the probability of photographing feeding rather than probing is high (Edwards, 1966; Cohen and Tang, 1997; Weirauch et al., 2012). To assess if our image searches were exhaustive, or if a new search conducted one year later (July 2017) would result in additional images, two lab members assembled 100 predation event photos; only 40% of the images were identical.

A total of 832 photographs were assembled (Supplemental Table 1), derived from 37 countries, in six biogeographic regions with the majority (86%) from North America (Fig. 1). This bias is likely due to the search sites used and the fact that searches were carried out using key words in English. All assassin bugs were classified to subfamily; 24 individuals were not identified to genus, and 98 not to species. Identification of prey was more challenging; 56, 373, and 569 individuals were not identified to order, family, or genus, respectively. Eleven of the 24 assassin bug subfamilies are represented (Fig. 1), with the majority documenting predation events of Harpactorinae (602 events; 73%), followed by Phymatinae (168; 20%) and Emesinae (22; 3%). These results are likely explained by the fact that Harpactorinae (>2800 spp. worldwide; (Maldonado, 1990; Weirauch et al., 2014)) and Phymatinae (~300 spp.) are speciose in North America and are frequently encountered by humans due to their diurnal, flower-visiting, or vegetation-dwelling habits. Feeding observations for the typically nocturnal Emesinae, Hammacerinae, Peiratinae, and Stenopodainae are sparse and only provide limited insights into prey diversity. About one third of the images documented Emesinae preying on Araneae, while Lepidoptera, Diptera, Hemiptera, and Psocodea were other identifiable prey groups (Supplemental Table 1). The most comprehensive synopsis of Emesinae feeding habits lists all of the above orders (Wygodzinsky, 1966), while recent publications focused on arachnophilous habits of certain Emesinae (Soley et al., 2011; Pape, 2013; Soley and Taylor, 2013). Hammacerinae have been observed to feed on bark scorpions (Stevenson and Stohlgren, 2015) and blattellid cockroaches (Horn and Hanula, 2002) and, consistent with the subcorticulous habits of species in this group, the single predation event derived from the image database involved a cerambycid beetle (Suppl. Table 1). Readio (1927) reported a preference of the peiratine *Melanolestes picipes* (Herrich-Schaeffer) for melolonthine beetles under experimental conditions; the three assembled images for this species show predatory interactions with beetles in different families. The biology of Stenopodainae,

including their feeding habits, are unknown; the two predation events documented in our image database show species feeding on Gryllidae (Supplemental Table 1).

We assembled image collections for several North American assassin bug taxa, including harpactorine *Arilus cristatus* (71 events), *Apiomerus* Hahn (109 events), and *Zelus* Fabricius (213 events), and the phymatine species *Phymata americana* Melin (93 events) and *Phymata pacifica* Evans (20 events). We discuss our findings for these data in the context of previously reported prey and highlight taxa that were repeatedly documented to prey on pollinators, intraguild predators and parasitoids, or herbivores with plant pest potential.

Published prey records for *Apiomerus* spp., the bee killer assassin bugs, comprise a wide range of flower pollinators (Weaver et al., 1975; Alcock, 1998; Marques et al., 2003; da Silva and Gil-Santana, 2004; Meira Marques et al., 2006; Ruiz-Sanchez et al., 2017), Coleoptera including Buprestidae, Curculionidae, Scarabaeidae, and Tenebrionidae (Morgan, 1907; Deloya, 1987; Gil-Santana, 2002), and also ants (Cade et al., 1978). Our survey (Fig. 2) is consistent with these reports, as Hymenoptera accounted for 63% of prey photographs and 58% of these were bees (Apoidea). *Apis mellifera* Linnaeus, the European honey bee, contributed 72% of bee prey records, with 80% of bees overall classified as Apidae. Coleoptera accounted for 32% of prey photographs; Scarabaeidae (17%) and Coccinellidae (11%) were the two most common families; we were unable to classify to family 54% of Coleoptera records.

Generalist natural enemies in the genus *Zelus* have been studied, in the context of biological control and integrated pest management, more than any other group of Nearctic assassin bugs (Cisneros and Rosenheim, 1998; Lanham, 1998; Hagler, 2016). *Zelus renardii* Kolenati, the leaf hopper assassin bug, is currently also the only commercially available assassin bug species (http://www.arbico-organics.com/) in the United States. Prey ranges of *Zelus* spp. include a range of Hemiptera, Lepidoptera, and Diptera, including Pentatomoidea (Greenstone et al., 2014; Tillman et al., 2015); Lygus bugs (Asiimwe et al., 2014) and other true bugs (Law and Rosenheim, 2011), Gelechiidae (Speranza et al., 2014; Luna et al., 2015), Geometridae (Barreto and Mojena, 2014), Ulidiidae (Kalsi et al., 2014); and the whitefly pest *Bemisia tabaci* (Gennadius) (Hagler et al., 1993). Our image database comprises 213 predation events for individuals of *Zelus* spp., involving a number of plant pests such as *Fieberiella florii* Stål, the Privet leafhopper [*Zelus longipes* (Linnaeus)], *Diabrotica undecimpunctata* Mannerheim, the Spotted cucumber beetle (*Z. renardii* and *Zelus tetracanthus* Stål), the sharpshooter *Graphocephala versuta* Say (*Zelus luridus* Stål) and *Lygus lineolaris* de Beauvois (*Z. luridus*). The majority of interactions (Fig. 2) involved Hymenoptera (36%; mostly small native bees and wasps, only six events with *A. mellifera*) and Diptera (32%; several families including Calliphoridae, Muscidae, Syrphidae, and Sarcophagidae), indicating that pollinator predation should be a consideration when assessing the potential of *Zelus* assassin bugs as natural enemies. Interestingly, 28 photographs of *Zelus* showed these assassin bugs with their rostrum inserted in flowers (mainly Asteraceae) either documenting nectaring or predation on small insects hidden in flowers; otherwise, only ambush bugs were documented nectaring in the image dataset (three events in *P. americana*, one in *P. pacifica*).

Prior predation records derived from cage experiments and field observations show the wheel bug *A. cristatus* (Fig. 3) to feed on a wide range of Coleoptera, Lepidoptera, and Hemiptera, including several plant pests such as *Epilachna varivestis* Mulsant, the Mexican bean beetle, and *Halyomorpha halys* Stål, the brown marmorated stink bug (Moul, 1945; Richman et al., 1980; Dowd and Kok, 1981; McCauley and Lawson, 1986; Eisner and Aneshansley, 2000; Barringer and Smyers, 2016; McCoshum et al., 2016; Mead, 2017). Among the 71 images analyzed here, Coleoptera accounted for the largest proportion of observations (47%) and included predation events on *Leptinotarsa decemlineata* Say, the Colorado potato beetle, and *Popillia japonica* Newman, the Japanese beetle. Multiple individuals preyed on *H. halys*, making up almost half (44%) of the photographed hemipteran prey. About one fifth of the observations involved Lepidoptera, including pest species such as *Manduca sexta* (Linnaeus), the tobacco hornworm. Hymenoptera accounted for only 14% of photographed prey insects including native honey bees and wasps.

Among ambush bugs, more than half of the images for *P. americana* (Fig. 3) involved predation on Hymenoptera (65%), with Apidae accounting for 41% of the hymenopteran predation events. None of the photographed prey species were pests, but rather pollinators or other flower-visiting insects (e.g., adult Lepidoptera where 54% of observations were of Hesperiidae). Despite the smaller number of images available (20), we included *P. pacifica* because a gut metabarcoding-based prey dataset for this species was recently published (Masonick et al., 2019). Images documented predation mostly on Hymenoptera (35%), Lepidoptera (25%), Coleoptera (25%), and Diptera (15%), with events in Hymenoptera predominantly involving bees (Apidae: 72%; Halictidae: 14%). Gut metabarcoding at one locality in Southern California detected phytophagous insects including Lepidoptera, Hemiptera, and Coleoptera (33%), a surprisingly small proportion of native and non-native bees (20%), but an abundance of entomophagous arthropods (35%) (Masonick et al., 2019).

Among the Reduviidae discussed above, *A. cristatus* may have the greatest potential as a managed natural enemy, as it was documented consuming a diversity of plant pest species while rarely attacking bees. In contrast, the large number of predation events on native and non-native pollinators by species of *Apiomerus* and *Phymata americana*, and substantial intraguild predation by *Phymata pacifica* (Masonick et al., 2019), suggest that these species may have negative effects on pollinators and other natural enemies. Prey type percentages varied between species of *Zelus* (e.g., *Z. longipes*: 20% Hymenoptera, 4% Coleoptera, 64% Diptera; *Z. luridus*: 34% Hymenoptera, 8% Coleoptera, 27% Diptera), suggesting that some species may have more promise as

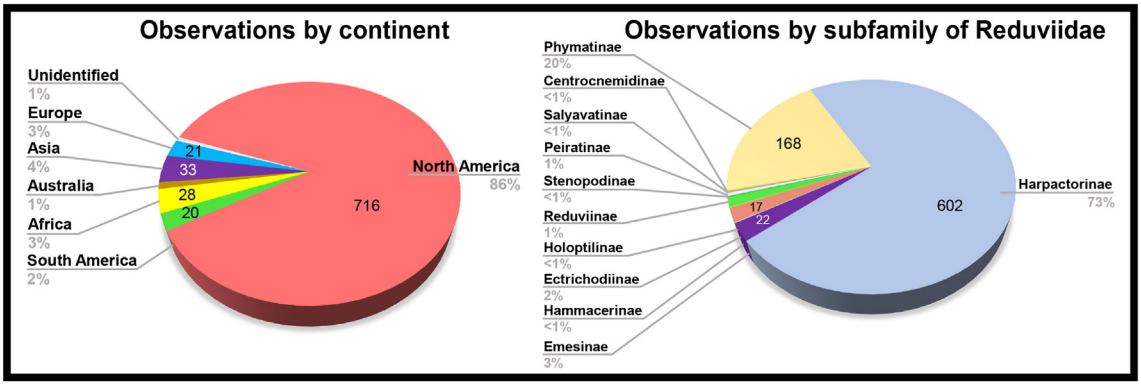

Fig. 1. Online images of predatory interactions (n = 832) between Reduviidae (assassin bugs) and arthropod prey organisms by continent (left) and assassin bug subfamily (right).

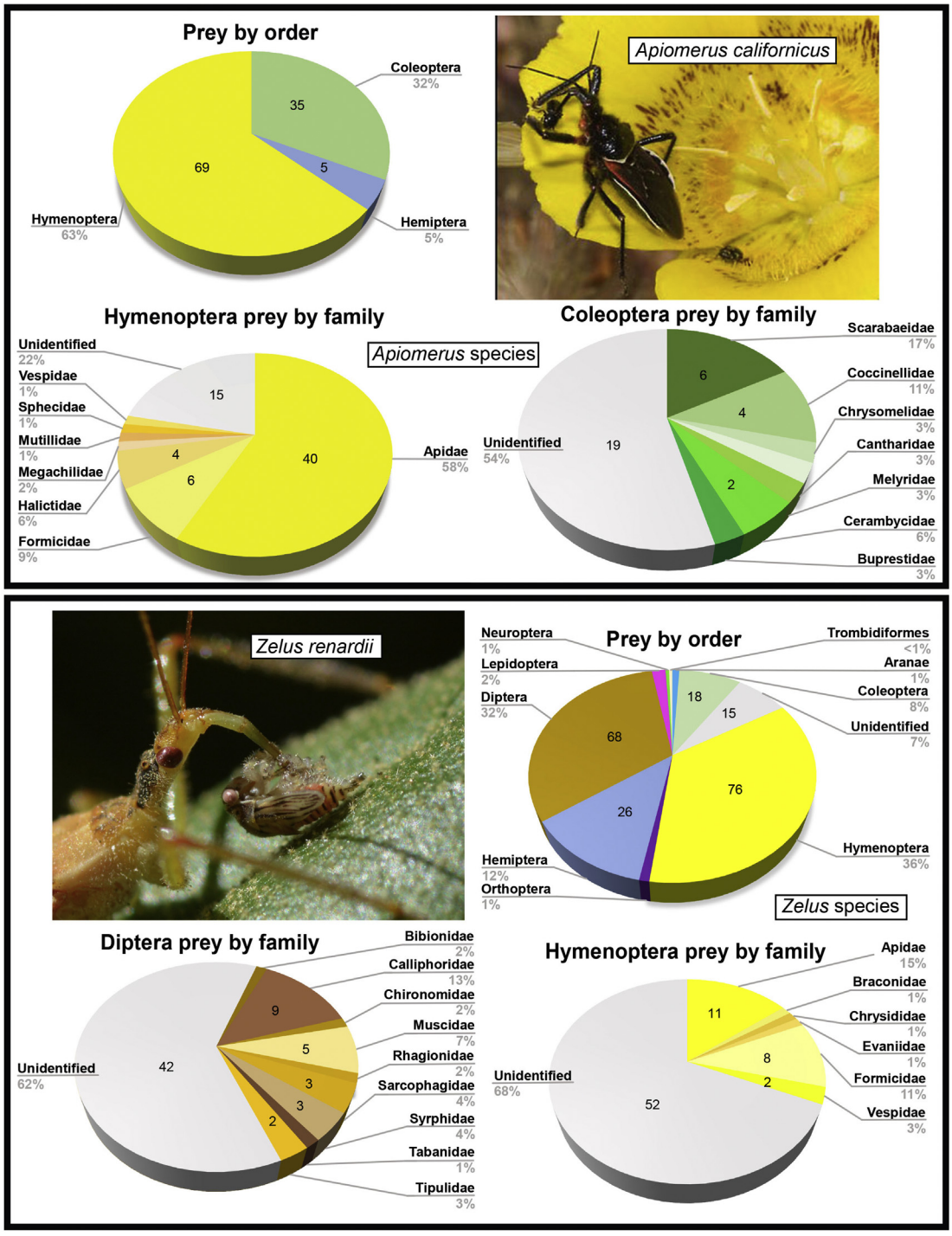

Fig. 2. Prey distribution for species of *Apiomerus*, the bee killer assassin bugs (top panel), and *Zelus*, the leafhopper assassin bugs (bottom panel), based on the image survey. In addition to prey order, classification by prey family is shown for selected orders. Photographs of *Apiomerus californicus* and *Zelus renardii* made available by Jack Owicki and Marc Kummel, respectively.

managed natural enemies than others and emphasizing the need for additional research.

While the presented data may not comprehensively represent diet diversity of assassin bugs, the analysis of online photographs assembled by citizen scientists is clearly valuable. Our study on this speciose group of predatory arthropods suggests that data collection via citizen science is biased by factors including key word search language, geographic region, and frequency of encounters with humans, among others. Nevertheless, this image collection has provided new insights into prey diversity of this group of predatory insects that includes natural enemies of pest species, but also pollinator and intraguild predators. These images have lent support to previously reported prey preferences for obscure reduviid taxa rarely observed in the field. Large image collections can be assembled fairly straightforwardly for large-bodied diurnal flower-visiting predatory insects. These data then allow for a preliminary assessment of the prevalence of predation events involving pollinators or intraguild predators for a given species and can assist in selecting the most promising taxa for biological control and integrated management applications. Beyond these applied aspects, citizen science generated databases contribute new insights into predator-prey

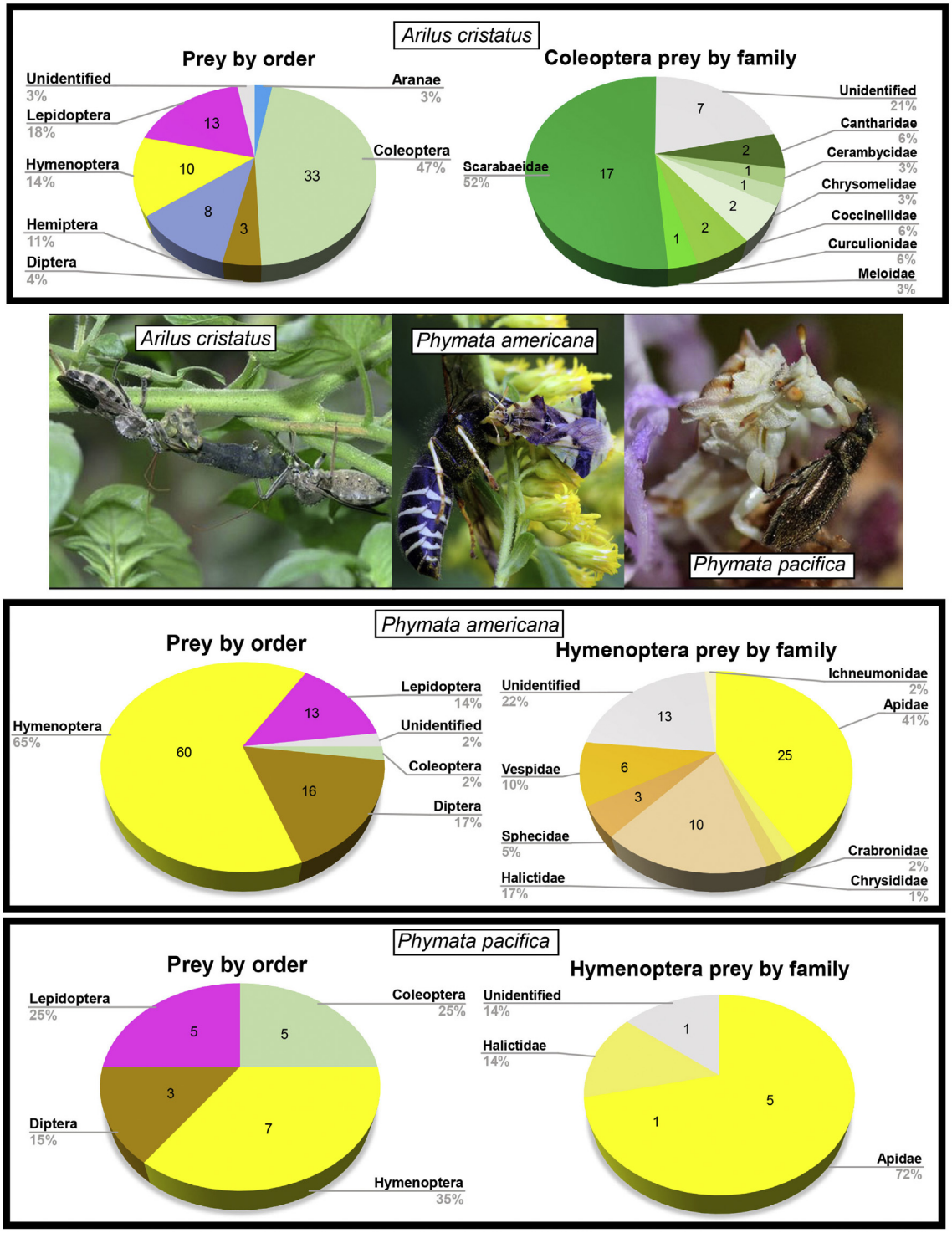

Fig. 3. Prey distribution for *Arilus cristatus*, *Phymata americana*, and *Phymata pacifica*, by prey order and family for selected orders. Photographs were provided by Marvin Smith (*A. cristatus*), Roxanne Bernard (*P. americana*), and Marc Kummel (*P. pacifica*).

networks and have the potential to encourage future research with focus on mechanisms that shape community structure and ecosystems processes. Our analysis shows that additional photographs depicting predator-prey interactions become available at a fast pace; we therefore predict that the contribution of these growing databases to scientific discovery will continue to increase.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.fooweb.2019.e00126.

Declaration of competing interest

None.

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References

Alcock, J., 1998. Sleeping aggregations of the bee *Idiomelissodes duplocincta* (Cockerell) (Hymenoptera: Anthophorini) and their possible function. J. Kansas Entomol. Soc. 71, 74–84.

Asiimwe, P., Naranjo, S.E., Ellsworth, P.C., 2014. Effects of irrigation levels on interactions among *Lygus hesperus* (Hemiptera: Miridae), insecticides, and predators in cotton. Environ. Entomol. 43, 263–273.

Balduf, W.V., 1939. Food habits of *Phymata pennsylvanica americana* Melin (Hemip.). The Canadian Entomologist. 71, 66–74.

Balduf, W.V., 1964. Numbers of ovarioles in the Heteroptera (Insecta). Proc. Entomol. Soc. Wash. 66, 2–5.

Barreto, M.R., Mojena, P.A., 2014. Registration of *Thyrinteina arnobia arnobia* (Stoll) (Lepidoptera: Geometridae) in *Eucalyptus* sp (Myrtaceae) in Sorriso, Mato Grosso and its predation by *Zelus armillatus* (Lepeletier & Serville) (Hemiptera: Reduviidae: Harpactorinae). EntomoBrasilis. 7, 69–71.

Barringer, L.E., Smyers, E., 2016. Predation of the spotted lanternfly, *Lycorma delicatula* (White) (Hemiptera: Fulgoridae) by two native Hemiptera. Entomological News. 126, 71–73.

Batista, M.C., Marques Fonseca, M.C., Teodoro, A.V., Martins, E.F., Pallini, A., Venzon, M., 2017. Basil (*Ocimum basilicum* L.) attracts and benefits the green lacewing *Ceraeochrysa cubana* Hagen. Biol. Control 110, 98–106.

Birkhofer, K., Bylund, H., Dalin, P., Ferlian, O., Gagic, V., Hambäck, P.A., et al., 2017. Methods to identify the prey of invertebrate predators in terrestrial field studies. Ecol Evol. 7, 1942–1953.

Bosco, L., Giacometto, E., Tavella, L., 2008. Colonization and predation of thrips (Thysanoptera: Thripidae) by *Orius* spp. (Heteroptera: Anthocoridae) in sweet pepper greenhouses in Northwest Italy. Biol. Control 44, 331–340.

Bray, A., Nieh, J., 2014. Non-consumptive predator effects shape honey bee foraging and recruitment dancing. PLoS One 9, e87459.

Cade, W.H., Simpson, P.H., Breland, O.P., 1978. *Apiomerus spissipes* (Hemiptera: Reduviidae): a predator of harvester ants in Texas. Southwestern Entomologist. 3, 195–197.

Chisholm, P.J., Gardiner, M.M., Moon, E.G., Crowder, D.W., 2014. Tools and techniques for investigating impacts of habitat complexity on biological control. Biol. Control 75, 48–57.

Choate, B.A., Lundgren, J.G., 2015. Invertebrate communities in spring wheat and the identification of cereal aphid predators through molecular gut content analysis. Crop Prot. 77, 110–118.

Cisneros, J., Rosenheim, J., 1997. Ontogenetic change of prey preference in the generalist predator *Zelus renardii* and its influence on predator–predator interactions. Ecological Entomology. 22, 399–407.

Cisneros, J.J., Rosenheim, J.A., 1998. Changes in the foraging behavior, within-plant vertical distribution, and microhabitat selection of a generalist insect predator: an age analysis. Environ. Entomol. 27, 949–957.

Cohen, A.C., Tang, R., 1997. Relative prey weight influences handling time and biomass extraction in *Sinea confusa* and *Zelus renardii* (Heteroptera: Reduviidae). Environ. Entomol. 26, 559–565.

DeBach, P., Rosen, D., 1991. Biological Control by Natural Enemies. CUP Archive.

Deloya, C., 1987. Observaciones acerca de la depradacion de *Apiomerus venosus* y *A. pictipes* (Hemiptera: Reduviidae) sobre coleopteros lamelicornios adultos. Folia Entomologica Mexicana 73, 65–66.

Derocles, S.A.P., Plantegenest, M., Rasplus, J.-Y., Marie, A., Evans, D.M., Lunt, D.H., et al., 2016. Are generalist Aphidiinae (Hym. Braconidae) mostly cryptic species complexes? Syst. Entomol. 41, 379–391.

Dikow, T., 2009. Phylogeny of Asilidae inferred from morphological characters of imagines (Insecta: Diptera: Brachycera: Asiloidea). Bull. Am. Mus. Nat. Hist. 319, 1–175.

Dowd, P.F., Kok, L.T., 1981. Predators of *Rhinocyllus conicus* (Coleoptera: Curculionidae) in Virginia. Environ. Entomol. 10, 136–138.

Edwards, J.S., 1966. Observations on the life history and predatory behaviour of *Zelus exsanguis* (Stål) (Heteroptera: Reduviidae). Proceedings of the Royal Entomological Society of London Series A, General. Entomology. 41, 21–24.

Eisner, T., Aneshansley, D.J., 2000. Defense by foot adhesion in a beetle (*Hemisphaerota cyanea*). Proc. Natl. Acad. Sci. U. S. A. 97, 6568–6573.

Ellwood, E.R., Crimmins, T.M., Miller-Rushing, A.J., 2017. Citizen science and conservation: recommendations for a rapidly moving field. Biol. Conserv. 208, 1–4.

Forthman, M., Weirauch, C., 2012. Toxic associations: a review of the predatory behaviors of millipede assassin bugs (Hemiptera: Reduviidae: Ectrichodiinae). European Journal of Entomology. 109, 147–153.

Forthman, M., Weirauch, C., 2017. Millipede assassins and allies (Heteroptera: Reduviidae: Ectrichodiinae, Tribelocephalinae): total evidence phylogeny, revised classification and evolution of sexual dimorphism. Syst. Entomol. 42, 575–595.

Frago, E., 2016. Interactions between parasitoids and higher order natural enemies: intraguild predation and hyperparasitoids. Curr Opin Insect Sci. 14, 81–86.

Georgieva, A.Y., Gordon, E.R.L., Weirauch, C., 2017. Sylvatic host associations of Triatominae and implications for Chagas disease reservoirs: a comprehensive review and new host records based on archival specimens. PeerJ Preprints https://doi.org/10.7287/peerj.preprints.3006v1.

Gil-Santana, H.R., 2002. Predaçao de *Lagria villosa* Fabricius, 1783 (Coleoptera: Lagriidae) por *Apiomerus nigrilobus* Stål, 1872 (Hemiptera: Reduviidae: Apiomerinae) em Cabo Frio, estado do Rio de Janeiro, Brasil. Entomologia y Vectores 9, 201–208.

Gomez-Polo, P., Alomar, O., Castane, C., Aznar-Fernandez, T., Lundgren, J.G., Pinol, J., et al., 2016. Understanding trophic interactions of *Orius* spp. (Hemiptera: Anthocoridae) in lettuce crops by molecular methods. Pest Manag. Sci. 72, 272–279.

Gordon, E.R.L., Weirauch, C., 2016. Efficient capture of natural history data reveals prey conservatism of cryptic termite predators. Mol Phylogenet Evol. 94, 65–73.

Greenstone, M.H., Tillman, P.G., Hu, J.S., 2014. Predation of the newly invasive pest *Megacopta cribraria* (Hemiptera: Plataspidae) in soybean habitats adjacent to cotton by a complex of predators. J. Econ. Entomol. 107, 947–954.

Grieshop, M.J., Werling, B., Buehrer, K., Perrone, J., Isaacs, R., Landis, D., 2012. Big brother is watching: studying insect predation in the age of digital surveillance. Am. Entomol. 58, 172–182.

Grundy, P.R., 2007. Utilizing the assassin bug, *Pristhesancus plagipennis* (Hemiptera: Reduviidae), as a biological control agent within an integrated pest management programme for *Helicoverpa* spp. (Lepidoptera: Noctuidae) and *Creontiades* spp. (Hemiptera: Miridae) in cotton. Bull. Entomol. Res. 97, 281–290.

Grundy, P.R., Maelzer, D.A., 2003. Towards the on-farm conservation of the assassin bug *Pristhesancus plagipennis* (Walker) (Hemiptera: Reduviidae) during winter using crop plants as refuges. Aust. J. Entomol. 42, 153–158.

Hagler, J.R., 2016. A false-positive food chain error associated with a generic predator gut content ELISA. Entomologia Experimentalis et Applicata. 161, 187–192.

Hagler, J.R., Naranjo, S.E., Machtley, S., Durand, C., Figuli, P.J., Henneberry, T.J., 1993. Identifying key predators of sweetpotato whitefly and pink bollworm using pest-specific monoclonal antibodies. Proceedings Beltwide Cotton Conferences. 2, 983–985.

Haridass, E.T., 1985. Feeding and ovipositional behaviour in some reduviids (Insecta-Heteroptera). Proceedings of the Indian Academy of Sciences, Animal Sciences. 94, 239–247.

Haviland, M.D., 1931. The reduviidae of Kartabo Bartica district. British Guiana. Zoologica. 7, 129–154.

Heraty J. Parasitoid biodiversity and insect pest management. In: Foottit RG, Adler PH, editors. Insect Biodiversity. Wiley-Blackwell; 2009. p. 445–62. http://onlinelibrary.wiley.com/doi/10.1002/9781444308211.ch19/summary. Accessed 7 Jan 2016.

Horn, S., Hanula, J.L., 2002. Life history and habitat associations of the broad wood cockroach, *Parcoblatta lata* (Blattaria: Blattellidae) and other native cockroaches in the coastal plain of South Carolina. Ann. Entomol. Soc. Am. 95, 665–671.

Howard, E., Davis, A.K., 2009. The fall migration flyways of monarch butterflies in eastern North America revealed by citizen scientists. J. Insect Conserv. 13, 279–286.

Jacobson, E., 1911. Biological notes on the hemipteron Ptilocerus ochraceus. Tijdschrift voor Entomologie. 54, 175–179.

Jamian, S., Norhisham, A., Ghazali, A., Zakaria, A., Azhar, B., 2017. Impacts of 2 species of predatory Reduviidae on bagworms in oil palm plantations. Insect Science. 24, 285–294.

Kalsi, M., Seal, D.R., Nuessly, G.S., Capinera, J.L., Martin, C.G., 2014. Distribution of *Zelus longipes* (Hemiptera: Reduviidae) in South Florida corn fields and its functional response to corn-infesting picture-winged flies (Diptera: Ulidiidae). Environ. Entomol. 43, 1223–1234.

Katsanis, A., Magro, A., Ramon-Portugal, F., Kenis, M., Babendreier, D., 2017. Chemical defences of native European coccinellid eggs against intraguild predation by the invasive Asian coccinellid, *Harmonia axyridis* (Pallas). Biocontrol. 62, 385–396.

Lanham, M.D., 1998. Predatory Heteroptera: Their Ecology and Use in Biological Control. In: Coll, M., Ruberson, J. (Eds.), Thomas Say Publications in Entomology, Entomological Society of America. USA, pp. 170–197.

Law, Y.-H., Rosenheim, J.A., 2011. Effects of combining an intraguild predator with a cannibalistic intermediate predator on a species-level trophic cascade. Ecology (Washington D C). 92, 333–341.

Lent, H., Wygodzinsky, P., 1979. Revision of the Triatominae (Hemiptera, Reduviidae), and their significance as vectors of Chagas' disease. Bull. Am. Mus. Nat. Hist. 163, 125–520.

Lovei, G.L., Sunderland, K.D., 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). Annu. Rev. Entomol. 41, 231–256.

Luna, M.G., Pereyra, P.C., Coviella, C.E., Nieves, E., Savino, V., Salas Gervassio, N.G., et al., 2015. Potential of biological control agents against *Tuta absoluta* (Lepidoptera: Gelechiidae): current knowledge in Argentina. Fla. Entomol. 98, 489–494.

Lundgren, J.G., Fergen, J.K., 2014. Predator community structure and trophic linkage strength to a focal prey. Mol. Ecol. 23, 3790–3798.

Maddison, D.R., Moore, W., Baker, M.D., Ellis, T.M., Ober, K.A., Cannone, J.J., et al., 2009. Monophyly of terrestrial adephagan beetles as indicated by three nuclear genes (Coleoptera: Carabidae and Trachypachidae). Zool. Scr. 38, 43–62.

Maldonado, J., 1990. Systematic catalogue of the Reduviidae of the World. Mayagüez: Caribbean Journal of Science, Special publication No. 1. University of Puerto Rico.

Marques, O.M., Gil-Santana, H.R., Magalhaes, A.C.A., de Carvalho, C.A.L., 2003. Predation of *Apiomerus lanipes* (Fabricius, 1803) (Hemiptera: Reduviidae) over *Apis mellifera* (Linnaeus, 1758) (Hymenoptera: Apidae), in the State of Bahia, Brazil. Entomologia y Vectores 10, 419–429.

Masonick, P., Hernandez, M., Weirauch, C., 2019. No guts, no glory: gut content metabarcoding unveils the diet of a flower-associated coastal sage scrub predator. Ecosphere. 10, e02712.

Mayer, S.V., Tesh, R.B., Vasilakis, N., 2017. The emergence of arthropod-borne viral diseases: a global prospective on dengue, chikungunya and zika fevers. Acta Trop. 166, 155–163.

McCauley, D.E., Lawson, E.C., 1986. Mating reduces predation on male milkweed beetles. Am. Nat. 127, 112–117.

McCoshum, S.M., Andreoli, S.L., Stenoien, C.M., Oberhauser, K.S., Baum, K.A., 2016. Species distribution models for natural enemies of monarch butterfly (*Danaus plexippus*) larvae and pupae: distribution patterns and implications for conservation. J. Insect Conserv. 20, 223–237.

McMahan, E.A., 1982. Bait-and-capture strategy of a termite-eating assassin bug. Insects Sociaux, Paris. 29, 346–351.
McMahan, E.A., 1983. Bugs angle for termites. Natural History 92, 40–47.
Mead, F.W., 2017. Wheel Bug, *Arilus cristatus* (Linnaeus) (Insecta: Hemiptera: Reduviidae). http://edis.ifas.ufl.edu/in243, Accessed date: 18 July 2017.
Meira Marques, O., Gil-Santana, H.R., Lopes Coutinho, M., da Silva Junior, D.D., 2006. Predatory bugs (Hemiptera, Reduviidae, Harpactorinae) in tobacco (*Nicotiana tabacum* L.) in the municipal district of Cruz das Almas, Bahia. Revista Brasileira de Zoociencias 8, 55–59.
Michalek, O., Petrakova, L., Pekar, S., 2017. Capture efficiency and trophic adaptations of a specialist and generalist predator: a comparison. Ecol Evol. 7, 2756–2766.
Mitter, C., Farrell, B., Wiegmann, B., 1988. The phylogenetic study of adaptive zones: has phytophagy promoted insect diversification? Am. Nat. 132, 107–128.
Morgan, A.C., 1907. Papers on the cotton boll weevil and related and associated insects. A predatory bug reported as an enemy of the cotton boll weevil. U S Department of Agriculture Bureau of Entomology Bulletin 63, 49–54.
Moul, E.T., 1945. Notes on *Arilus cristatus* (Linnaeus) in York County, Pennsylvania and on its prey (Heteroptera: Reduviidae). Entomological News Lancaster. 56, 57–59.
de Oliveira, R.L., Moscardini, V.F., Gontijo, P.C., Samia, R.R., Marucci, R.C., Budia, F., et al., 2016. Life history parameters and feeding preference of the green lacewing *Ceraeochrysa cubana* fed with virus-free and potato leafroll virus-infected *Myzus persicae*. Biocontrol. 61, 671–679.
Pape, R.B., 2013. Description and ecology of a new cavernicolous, arachnophilous thread-legged bug (Hemiptera: Reduviidae: Emesini) from Kartchner Caverns, Cochise County, Arizona. Zootaxa. 3670, 137–156.
Readio, P.A., 1927. Studies on the biology of the Reduviidae of America North of Mexico. University of Kansas Science Bulletin. 17, 5–291.
Richman, D.B., Hemenway, R.C., Whitcomb, W.H., 1980. Field cage evaluation of predators of the soybean looper, *Pseudoplusia includens* (Lepidoptera: Noctuidae). Environ. Entomol. 9, 315–317.
Riddick, E.W., 2017. Spotlight on the positive effects of the ladybird *Harmonia axyridis* on agriculture. Biocontrol. 62, 319–330.
Rondoni, G., Athey, K.J., Harwood, J.D., Conti, E., Ricci, C., Obrycki, J.J., 2015. Development and application of molecular gut-content analysis to detect aphid and coccinellid predation by *Harmonia axyridis* (Coleoptera: Coccinellidae) in Italy. Insect Science. 22, 719–730.
Rosenheim, J.A., Wilhoit, L.R., Armer, C.A., 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia. 96, 439–449.
Ruiz-Sanchez, E., Peredo, L.C., Santacruz, J.B., Ayala-Barajas, R., 2017. Bamboo flowers visited by insects: do insects play a role in the pollination of bamboo flowers? Plant Syst. Evol. 303, 51–59.
Schmeller, D.S., Henry, P.-Y., Julliard, R., Gruber, B., Clobert, J., Dziock, F., et al., 2009. Advantages of volunteer-based biodiversity monitoring in Europe. Conserv. Biol. 23, 307–316.
Shackelford, G., Steward, P.R., Benton, T.G., Kunin, W.E., Potts, S.G., Biesmeijer, J.C., et al., 2013. Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. Biol. Rev. 88, 1002–1021.
da Silva, A.C., Gil-Santana, H.R., 2004. Predation of *Apiomerus pilipes* (Fabricius) (Hemiptera, Reduviidae, Harpactorinae, Apiomerini) over Meliponinae bees (Hymenoptera, Apidae), in the State of Amazonas, Brazil. Revista Brasileira de Zoologia. 21, 769–774.
Silvertown, J., Harvey, M., Greenwood, R., Dodd, M., Rosewell, J., Rebelo, T., et al., 2015. Crowdsourcing the identification of organisms: a case-study of iSpot. Zookeys. 125–146.
Soley, F.G., Taylor, P.W., 2013. Ploys and counterploys of assassin bugs and their dangerous spider prey. Behaviour. 150, 397–425.
Soley, F., Jackson, R., Taylor, P., 2011. Biology of *Stenolemus giraffa* (Hemiptera: Reduviidae), a web invading, araneophagic assassin bug from Australia. New Zealand Journal of Zoology. 38, 297–316.
Speranza, S., Cecilia Melo, M., Gabriela Luna, M., Virla, E.G., 2014. First record of *Zelus obscuridorsis* (Hemiptera: Reduviidae) as a predator of the South American tomato leafminer, *Tuta absoluta* (Lepidoptera: Gelechiidae). Fla. Entomol. 97, 295–297.
Stevenson, D.J., Stohlgren, K.M., 2015. Predation on the scorpion *Centruroides hentzi* (Banks) (Scorpiones: Buthidae) by the assassin bug *Microtomus purcis* (Drury) (Insecta: Hemiptera: Reduviidae). Southeast. Nat. 14, N1–N4.
Stiling, P., Cornelissen, T., 2005. What makes a successful biocontrol agent? A meta-analysis of biological control agent performance. Biol. Control 34, 236–246.
Stork, N.E., McBroom, J., Gely, C., Hamilton, A.J., 2015. New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods. PNAS. 112, 7519–7523.
Sunderland, K.D., 1988. Quantitative methods for detecting invertebrate predation occurring in the field. Ann. Appl. Biol. 112, 201–224.
Swanson, A., Kosmala, M., Lintott, C., Packer, C., 2016. A generalized approach for producing, quantifying, and validating citizen science data from wildlife images. Conserv. Biol. 30, 520–531.
Symondson, W.O.C., Harwood, J.D., 2014. Special issue on molecular detection of trophic interactions: unpicking the tangled bank. Mol. Ecol. 23, 3601–3604.
Symondson, W.O.C., Sunderland, K.D., Greenstone, M.H., 2002. Can generalist predators be effective biocontrol agents? Annu. Rev. Entomol. 47, 561–594.
Tan, X., Hu, N., Zhang, F., Ramirez-Romero, R., Desneux, N., Wang, S., et al., 2016. Mixed release of two parasitoids and a polyphagous ladybird as a potential strategy to control the tobacco whitefly *Bemisia tabaci*. Sci. Rep. 6, 28245.
Tillman, P.G., Greenstone, M.H., Hu, J.S., 2015. Predation of stink bugs (Hemiptera: Pentatomidae) by a complex of predators in cotton and adjoining soybean habitats in Georgia, USA. Fla. Entomol. 98, 1114–1126.
Turnhout, E., Lawrence, A., Turnhout, S., 2016. Citizen science networks in natural history and the collective validation of biodiversity data. Conserv. Biol. 30, 532–539.
Unruh, T.R., Miliczky, E.R., Horton, D.R., Thomsen-Archer, K., Rehfield-Ray, L., Jones, V.P., 2016. Gut content analysis of arthropod predators of codling moth in Washington apple orchards. Biol. Control 102, 85–92.
Vanbergen, A.J., Baude, M., Biesmeijer, J.C., Britton, N.F., Brown, M.J.F., Brown, M., et al., 2013. Threats to an ecosystem service: pressures on pollinators. Front. Ecol. Environ. 11, 251–259.
Weaver, E.C., Clarke, E.T., Weaver, N., 1975. Attractiveness of an assassin bug to stingless bees. J. Kansas Entomol. Soc. 48, 17–18.
Weirauch, C., Cassis, G., 2006. Attracting ants: the trichome and novel glandular areas on the sternum of *Ptilocnemus lemur* (Heteroptera: Reduviidae: Holoptilinae). J New York Entomol Soc. 114, 28–37.
Weirauch, C., Alvarez, C., Zhang, G., 2012. *Zelus renardii* and *Z. tetracanthus* (Hemiptera: Reduviidae): biological attributes and the potential for dispersal in two assassin bug species. Fla. Entomol. 95, 641–649.
Weirauch, C., Bérenger, J.M., Berniker, L., Forero, D., Forthman, M., Frankenberg, S., et al., 2014. An illustrated identification key to assassin bug subfamilies and tribes (Hemiptera: Reduviidae). Canadian Journal of Arthropod Identifi cation. 26, 1–115.
Wiegmann, B.M., Mitter, C., Farrell, B., 1993. Diversification of carnivorous parasitic insects - extraordinary radiation or specialized dead-end. Am. Nat. 142, 737–754.
Wygodzinsky, P., 1966. A monograph of the Emesinae (Reduviidae, Hemiptera). Bull. Am. Mus. Nat. Hist. 133, 1–614.
Zhang, J., Weirauch, C., Zhang, G., Forero, D., 2016. Molecular phylogeny of Harpactorinae and Bactrodinae uncovers complex evolution of sticky trap predation in assassin bugs (Heteroptera: Reduviidae). Cladistics. 32, 538–554.
Zou, Y., de Kraker, J., Bianchi, F.J.J.A., van Telgen, M.D., Xiao, H., van der Werf, W., 2017. Video monitoring of brown planthopper predation in rice shows flaws of sentinel methods. Sci. Rep. 7. https://doi.org/10.1038/srep42210.