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Review

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Review

The Little Fire Ant (Hymenoptera: Formicidae): A Global Perspective

M. P. Montgomery,[1,2,4] C. Vanderwoude,[2] M. Lintermans,[1] and A. J. Jasmyn Lynch[1,3]

[1]Institute for Applied Ecology, University of Canberra, ACT 2601, Australia,[2]Hawai`i Ant Lab, Pacific Cooperative Studies Unit, University of Hawai`i, Hilo, HI 96720, USA,[3]Conservation and Water Planning Policy Branch, Environment, Planning, and Sustainable Development, ACT Government, Australia, and [4]Corresponding author, e-mail: michelle.montgomery@littlefireants.com

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Abstract

Wasmannia auropunctata (Roger) is an invasive tramp ant species that has been transported globally since [at least] the early twentieth century. It is often claimed that despite the negative impacts associated with this species and its listing among the world's worst invasive species, very little research attention has been paid to *W. auropuntata*. Although the need for future research exists, there is currently a considerable body of research from around the world and spanning back to the 1920's on this species. Here we synthesize over 200 peer reviewed research manuscripts, book chapters, conference presentations, and media reports of new distributions spanning 1929–2022 culminating in a comprehensive literature review on *W. auropunctata*. This review covers all current knowledge on this species and is intended to serve as a quick reference for future research and provide the reference resources for those seeking more in-depth information on specific topics. Topics included in this review include taxonomic identification, current global distribution and pathways, life history, impacts, detection, and control. We discuss where consensus and ambiguity currently lie within the research community, identify contextual considerations for future researchers when interpreting data, and suggest where we believe more research or clarifications are needed.

Key words: little fire ant, distribution, biology, impact, control

Invasive alien species (IAS) are species that have been introduced beyond their native range and negatively impacts those new areas. The negative impacts associated with IAS range from human health risks to reduced species diversity, plant and animal disease transmission, and altered ecosystem processes (Resnik 2018, Liang 2019). Insects are particularly easy to transport inadvertently from one place to another (Meurisse et al. 2019) and eusocial insects are predisposed to be successful invaders wherever they are introduced (Bertelsmeier 2021, Eyer and Vargo 2021) Specifically, invasive Hymenoptera are well known for causing multitiered negative impacts wherever they are introduced.

Ants (Hymenoptera: Formicidae) are among the most species-rich taxa in the animal kingdom with over 12,000 described species (Ward 2007). They are important for healthy ecological functioning (Andersen 1988, Abbott 1989, Folgarait 1998, Del Toro et al. 2012) but some cause negative ecological and human health impacts. The worst invasive ant species are also notable 'tramp' species due to the ease at which they are transported by anthropogenic means and their ability to thrive in areas disturbed by humans (Wilson and Taylor 1967, McGlynn 1999, Loope and Krushelnycky 2007). Other factors attributed to the success of some invasive ants include a combination of biological and behavioral traits such as polygyny, unicoloniality and low intraspecific aggression, high interspecific aggression, reproduction within the nest, and colony founding via budding instead of nuptial flights (Hölldobler and Wilson 1977, Brandao and Paiva 1994, Passera 1994, Jourdan 1997a, Helms and Vinson 2002, Holway et al. 2002).

The Little fire ant, *Wasmannia auropunctata* (Roger) (Hymenoptera: Formicidae) is an invasive tramp ant listed as one of the world's worst 100 IAS (Lowe et al. 2000), and has an alarming rate of spread globally with 43% of known new introductions occurring since the year 2000 (Wetterer 2013, Gruber et al. 2016, Espadaler et al. 2018, GBIF.org 2021, Vanderwoude et al. 2021, Chen et al. 2022). Consequently, research interest in this species has increased over the past 20 yr. Previous literature reviews on *W. auropunctata* to date have either focused on its global or local distribution, with life history, control, and impacts being minor components (Wetterer and Porter 2003, Herrera and Causon 2008, Wetterer 2013, Vanderwoude et al. 2015) or have focused on the latter three topics while omitting distribution information (Bousseyroux et al. 2019). More recently there has been considerable research into life history, control, and impacts and reports of new distribution data that has yet to be synthesized.

Here, we provide the first comprehensive literature review synthesizing all research on this species before June, 2022. The review is timely given the ongoing spread of this serious global pest and the need for research into cost-effective control methods. We review literature spanning the past 90 yr detailing its taxonomy, life history, distribution, range expansion, impacts, detection, and control of *W. auropunctata*. We provide an overview of its significance as an invasive species and identify priority areas for further research to fill knowledge gaps. Literature included in the review met two primary criteria: 1) it was published in a peer-reviewed journal, book section, government report or document, university scientific research, or extension report; and 2) *W. auropunctata* was either the primary focus or one of the primary foci of the study. Exceptions to these criteria were when the information obtained was novel in context and not reported elsewhere, such as new research presented during a conference or media report detailing a first detection for a locality.

Table 1. Past taxonomic synonyms for *Wasmannia auropunctata* previously described as separate species (Longino and Fernández 2007)

Taxonomic synonyms	
Wasmannia atomum	(Santschi 1914)
W. australis	Emery 1894
W. glabra	Santschi 1894
W. laevifrons	Emery 1894
W. obscura	Forel 1912
W. panamana	(Enzmann 1947)
W. pulla	Santschi 1931
W. nigricans	Emery 1906
W. rugosa	(Forel 1886)

Taxonomy and Systematics

Commonly referred to as little fire ant, *W. auropunctata* was first described by Roger in 1863 and originally included as a species of *Tetramorium* (Smith 1929, Nickerson 1983). After the genus *Wasmannia* was described by Forel in 1893, some arguments persisted around whether the species belonged within *Wasmannia* or the previously described genus *Ochetomyrmex* Mayr (Nickerson 1983, Longino and Fernández 2007). However, Longino and Fernández (2007) conducted a taxonomic review of *Wasmannia*, clearly distinguishing it from *Ochetomyrmex*, and provided a revised key for *Wasmannia*, including *W. auropunctata*.

Currently, ten *Wasmannia* species have been described, with *W. auropunctata* being the most common and widely distributed (Longino and Fernández 2007, Cuezzo et al. 2015). Although 21 *Wasmannia* species have been described historically, over half of these species were subsequently determined to be synonyms of other species and nine are currently considered to be synonymous with *W. auropunctata* (Table 1) (Longino and Fernández 2007).

Generalized ant taxonomy diagrams are presented in Fig. 1 for those unfamiliar with ant taxonomy or taxonomic terminology. Detailed morphological descriptions of *W. auropunctata* may be found in Ulloa-Chacon and Cherix (1990), Wetterer and Porter (2003), and Longino and Fernández (2007), but each description includes different morphological characteristics. Summarizing across all three descriptions, *W. auropunctata* may be identified by the following morphological characteristics:

Workers (Fig. 2) are tiny (~1.2–1.5 mm), monomorphic, rust-colored to pale yellow-brown myrmicine ants with two pedicle segments (petiole and post petiole) and long propodeal spines. The petiole node is roughly quadrate, approximately as high as it is wide. The hind margin of the node is slightly shorter than the fore margin when viewed in profile and meets the peduncle at nearly a 90-degree angle. The head and body are heavily sculptured with transverse

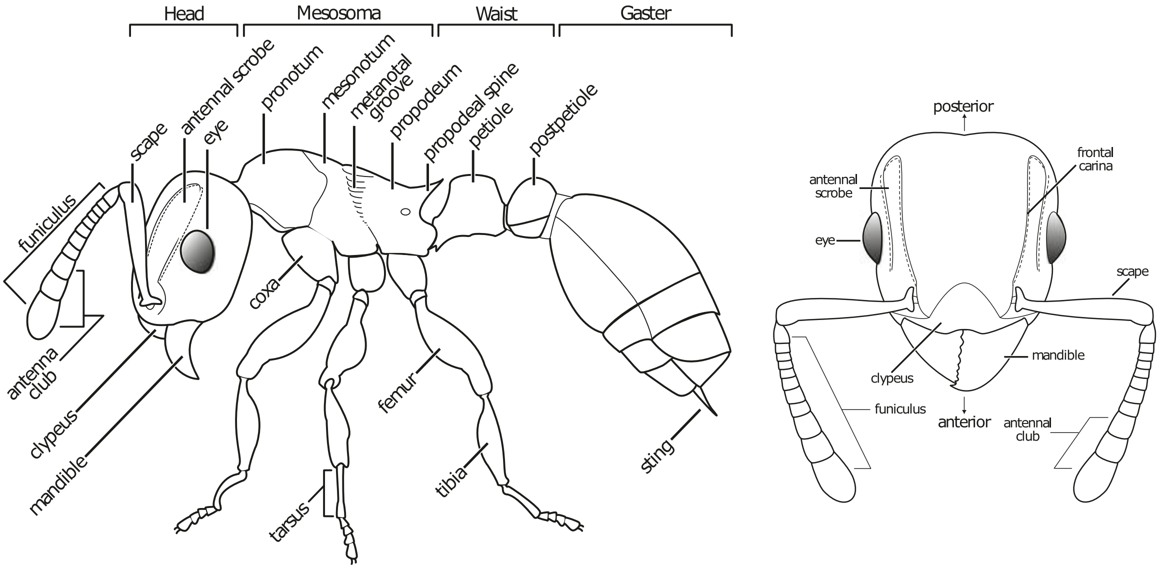

Fig. 1. General ant taxonomy diagrams of the whole body as viewed in profile (left) and the head as viewed from the front (right). Diagrams created by Eli Sarnat and used with permission.

rugules and reticulations, and sparse erect setae. The antenna consists of 11 segments. Funicular segments of the antenna gradually enlarge with the apical 2 segments distinctly larger than the rest and forming a club. Antennal scrobes are present, although shallow, and distinguishable by the presence of two prominent frontal carinae. Although generally considered 'monomorphic', aberrant worker morphs are common in large sample collections.

Reproductives (Figs. 3 and 4) are approximately three to four times larger than the workers (queens: 4.5–5.0 mm, males 4.2–4.5 mm). Two sympatric queen morphs have been documented, large- and small-headed queens. The antenna, sculpturing, and pubescence of the queens are similar to that of the workers. Queen coloration is uniformly dark brown but younger queens may be light brown and darken with age. Propodeal spines are present but shorter than those of workers. The node of the petiole gradually tapers upward but with distinct anterior and posterior angles along the dorsal margin. Wings may or may not be present. When present, the medial and SM1 cells are enclosed and the discoidal cell is absent on the fore wing (Fig. 3c). When not present, the sutures where the wings were detached are clearly visible.

Males (Fig. 4) are dark brown with yellowish antenna, legs, and genitalia. Antenna are long, 13-segmented, and without an apical club. Propodeal spines are absent, but the propodium angles sharply downward at a 90-degree angle. The petiolar node is large and dorsally rounded rather than angular. The parameres of the genital valve are long, curved intero-ventrally, and apically rounded (Fig. 4c.).

Life History

Genetics

Cytogenetics and molecular genetics provide insights on evolutionary and biological processes as well as population dynamics and species identification. To date, the mitochondrial genome has been mapped and macrosatellite markers have been identified for *W. auropunctata* which provided the tools necessary to conduct important foundational research (Fournier et al. 2005b, Souza et al. 2009, de Souza et al. 2011, Duan et al. 2016, Silva et al. 2018). The use of various genetic analyses have allowed researchers to trace the evolutionary history of this species (Chifflet et al. 2016), trace and track historical and current population expansions (Foucaud et al. 2010b, Chifflet et al. 2016, Coulin et al. 2019), distinguish native from exotic populations (Foucaud et al. 2010b), trace the origins of exotic populations (Foucaud et al. 2010b, Coulin et al. 2019), and identify certain biological and behavioral traits linked to invasive potential (Fournier et al. 2005b; Foucaud et al. 2006, 2010b; Mikheyev et al. 2009; Souza et al. 2009; Vonshak et al. 2009; Rey et al. 2011; Tindo et al. 2012). Additionally, genetics can help to identify when and where evolutionary adaptations occurred that has led to *W. auropunctata* being able to invade such a wide range of ecosystems and climates (Rey et al. 2012, Foucaud et al. 2013, Chifflet et al. 2016, Coulin et al. 2019).

The field of genetics is rapidly expanding with new technologies for phylogenetics, species identification, detection, and even pest control. Two technologies with especially promising applications are the use of environmental DNA (eDNA) for detection and RNA interference (RNAi) for control of pest ants. Trace amounts of genetic material are now able to be detected. That, with the advent of metabarcoding, has led to the growing practice of using eDNA to detect species presence from water or substrate samples without direct observation or collection of the target species (Kudoh et al. 2020, Uchida et al. 2020). Proof of concept for using eDNA as an ant detection tool has been reported for *Linepithema humile* Mayr (Yasashimoto et al. 2021). However, eDNA technology requires further development and testing before it can be deemed as a reliable tool for the detection of other species and under different scenarios. Development of RNAi technology for ant control appears to be promising as a future alternative to conventional pesticides. This is the process by which double-stranded RNA (dsRNA) or DNA (dsDNA) is used to stop the normal functioning of messenger RNA (Allen 2021). A construct of dsRNA or dsDNA may be delivered to the target pest via genetically modified crops, sprays, and bait delivery systems (Cagliari et al. 2019) and, when integrated into cells, interferes with gene transcription and effectively activates or silences gene expression. However, efficacy varies depending on target species and delivery system (Allen 2021). Functionality of RNAi on ants has been demonstrated (Allen 2021, List et al. 2022), but considerably more work is needed before the technology can be considered a viable control method (Allen 2021, List et al. 2022). Species-specific target genes must be identified and corresponding dsRNA or dsDNA constructs need to be developed. Degradation of dsRNA and dsDNA due to exposure of digestive enzymes, through trophallaxis, and under field conditions for various delivery systems is currently unknown and needs further investigation (Allen 2021). Finally, standardized testing and evaluation procedures need to be agreed upon

Fig. 2. *Wasmannia auropunctata* worker profile (a) and detail or head (b.). Photographs by: E. M. Sarnet, specimen CASENT 0171093. From www.antweb.org

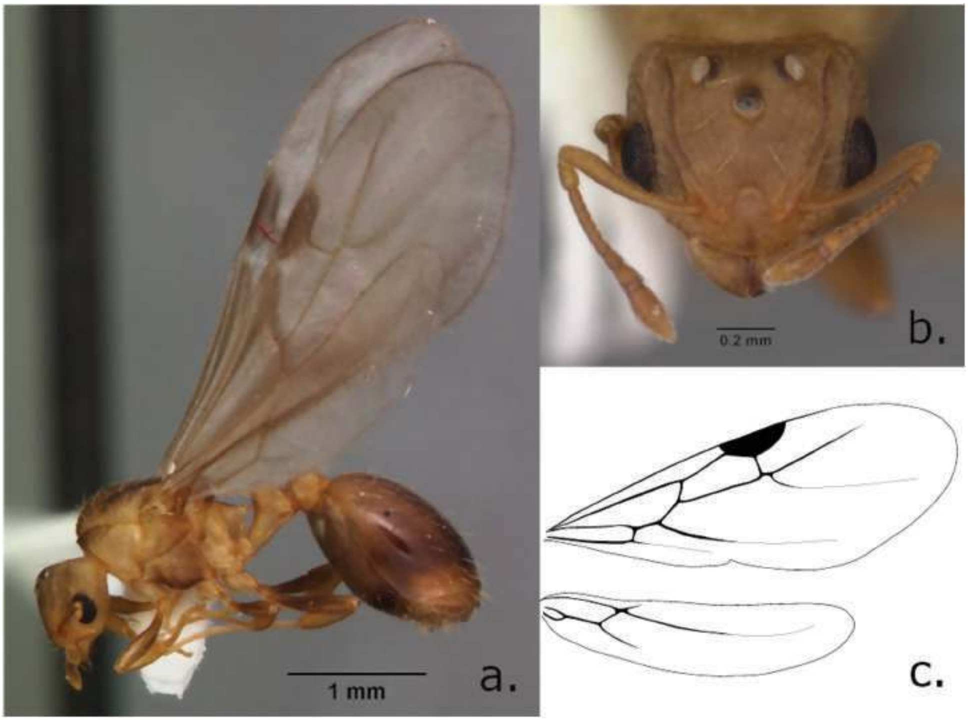

Fig. 3. *Wasmannia auropunctata* queen profile (a), detail of head (b), and wing diagram (c). Photographs by: A. Nobile, specimen CASENT 0102747. From www.antweb.org

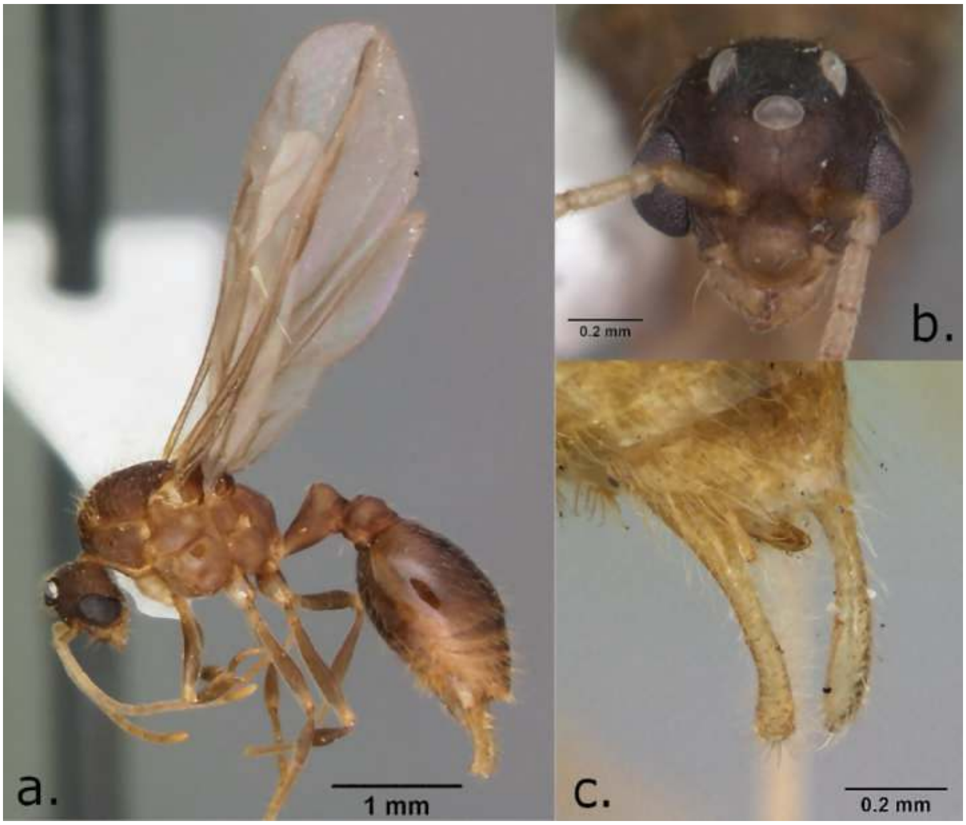

Fig. 4. *Wasmannia auropunctata* male profile (a), detail of head (b), and parameres (c). Profile and head photographs by: A. Nobile, specimen CASENT0102748. Parameres photograph by: A. Nobile, specimen CASENT 0173250. From www.antweb.org.

by the scientific community as it is with conventional pesticides to establish baseline expectancies for field efficacy trials (Allen 2021, List et al. 2022).

Reproduction and Development

Rudimentary aspects of *W. auropunctata* reproduction and development were first described by Ulloa-Chacon and Cherix (1990). Only queens lay eggs and fecundity fluctuates over a queen's lifespan, suggesting that fecundity is influenced by age and colony composition (Ulloa-Chacon and Cherix 1990). While worker brood is produced regularly to maintain nest population, reproductives are produced when high worker:brood ratios occur in the nest or when queen fecundity is low (Ulloa-Chacon and Cherix 1990).

Wasmannia auropunctata reproduction is unique and complex. They are not a typical haplodiploid species as with most social Hymenoptera (Fournier et al. 2005a). In typical haplodiploid reproduction systems, diploid females (queens and workers) are the progeny of sexual reproduction and haploid males are produced through arrhenotokous parthenogenesis, males developing from unfertilized eggs (Normark 2003). However, *W. auropunctata* exhibit a complex reproduction system, where the reproductive mode varies between different populations (Foucaud et al. 2007, 2009, 2010a).

Reproductive castes are produced in several ways. Haploid males are produced either via arrhenotokous parthenogenesis (arrhenotoky), males developing from unfertilized eggs, or via androgenesis, males developing from fertilized eggs through the elimination of the entire maternal genome. The latter process is rare in the animal kingdom and results in male clones that are genetically identical to their fathers. Diploid queens are produced through normal sexual reproduction or via automictic thelytokous parthenogenesis with central fusion (Rey et al. 2011). Automictic thelytokous parthenogenesis occurs from the fusion of two meiotic oocytes. Unusually low recombination rates during the meiotic division process result in clonal diploid queen lineages (Rey et al. 2011).

The occurrence of one reproductive mode or another is linked to *W. auropunctata* ecological dominance (Foucaud et al. 2009). Typical haplodiploid reproduction (sexually produced queens and arrhenotokous males) occurs primarily among nondominant variegate populations whereas clonal reproduction (automictic parthenogenesis and androgenesis) occurs primarily among dominant variegate populations (Foucaud et al. 2009, 2010a). Even though there is a trend linking dominance and reproductive mode, this is not a strict rule. Occasionally dominant sexual population, clonal nondominant populations, and rare occurrences of sexual reproduction within clonal populations have been detected (Foucaud et al. 2006, 2009, 2010b; Tindo et al. 2012). Interestingly, whether males are produced via arrhenotoky or androgenesis is maternally determined (Rey et al. 2013a). Queens from typical haplodiploid nests never produce male clones. They only produce arrhenotokous males whereas clonal queens produce androgen male clones, regardless of insemination or genetic lineage of the fathers (Foucaud et al. 2010a, Rey et al. 2013a). While it is possible for parthenogenic queens to produce arrhenotokous males, this phenomenon has only been documented during a single laboratory experiment (Tindo et al. 2012) and has not been detected among wild populations. It is possible this occurs at such low rates that research to date has failed to detect it.

Speculation around what leads to the expression of one reproductive mode over another is ongoing. An early hypothesis was that endosymbiotic bacteria, such as *Wolbachia,* could be responsible for the shift from typical haplodiploid reproduction to clonal reproduction (Rey et al. 2013b). *Wolbachia* is a widespread arthropod endosymbiont that is maternally inherited and influences sex determination during reproduction, including through the initiation of thelytokous parthenogenesis (Werren et al. 2008). *Wolbachia* is a known endosymbiont of *W. auropunctata*, but *Wolbachia* is less prevalent in clonal populations than in typical haplodiploid populations suggesting that it was not likely responsible for the reproductive difference (Rey et al. 2013b). The current hypothesis surrounding the expression of one reproductive mode over another involves the influence of ecological factors. Some sources suggest *W. auropunctata* are typically found amid floodplains (i.e., creek beds) within primary forests and clonal reproduction may have arisen as an evolutionary response to the repeated disturbance experienced in such habitats (Rey et al. 2012, Chifflet et al. 2018). Nests in floodplains would likely be under pressures such as fragmentation, transportation, and colony founding with every flooding event. Studies on the emergence of clonal reproduction in plants have suggested this reproduction mode may have evolved as an alternative lifecycle loop allowing populations to persist despite the absence of the necessaries sustaining the species normal lifecycle, such as a mate (Honnay and Bossuyt 2005). It is possible that the reproductive plasticity of *W. auropunctata* evolved in a similar way. Repeated flooding events likely increased the frequency of population fragmentation and a need to establish and persist for a short period of time without males. If this is the case, this phenotypic plasticity or adaptation to ecological pressures of floodplain habitats has undoubtedly become a leading factor contributing to their success as an invading species.

The unusual reproductive system of *Wasmannia auropunctata* has been implicated as an important factor contributing to the successful establishment of small founder colonies (Mikheyev et al. 2009). For newly introduced species, the establishment phase is particularly difficult (Foucaud et al. 2009, Mikheyev et al. 2009). In general, founding populations of an introduced species frequently fail to establish as a consequence of the principal cost of sex; the need to find a mate (Smith 1978). For those that do establish, the genetic diversity of the population is low due to few individuals surviving and reproducing. Such a genetic bottleneck leads to inbreeding and loss of heterozygosity over time within sexually reproducing populations and, theoretically, loss of fitness. However, reproductive plasticity in *W. auropunctata* allows for the preservation of heterozygosity when genetic diversity is low and avoids the consequences of inbreeding (Foucaud et al. 2010a, Rey et al. 2013a). It is likely that clonal reproduction via thelytokous parthenogenesis allows for the persistence of genetic adaptations responsible for *W. auropunctata* being able to successfully invade a wide variety of human modified habitats. Indeed, introductions of single female and male genotypes can give rise to area-wide infestations as seen in New Caledonia (Foucaud et al. 2006), Hawai`i (Mikheyev et al. 2009), Cameroon (Mbenoun Masse et al. 2011) and Israel (Vonshak et al. 2009). Rarely, recombination, mutation, and sexually produced queens within clonal populations have been observed which would add small amounts of genetic diversity within otherwise clonal populations (Foucaud et al. 2006, Vonshak et al. 2009, Tindo et al. 2012).

Although insemination does not contribute to *W. auropunctata* genetic diversity and is not strictly required for a queen to lay viable eggs, insemination is necessary to maintain egg development and hatching success (Miyakawa and Mikheyev 2015). Despite the possibility of virgin queens producing viable brood, the rate of successful hatching, pupation, and emergence among uninseminated brood is too low for colony maintenance (Miyakawa and Mikheyev 2015). Sex is therefore an essential part of both reproductive modes.

Nesting and Population Dynamics

Rather than building subterranean nests and mounds like many other ants, *W. auropunctata* prefer to nest opportunistically in warm, moist, and shaded areas (Ulloa-Chacon and Cherix 1990, Wetterer and Porter 2003). They can exploit ecological or man-made features on the ground, in tree canopies, and in other vegetation (Clark et al. 1982, Wetterer and Porter 2003, Le Breton et al. 2005, Mikissa et al. 2013, Álvarez et al. 2018, Santos et al. 2019, Wisniewski et al. 2019). Ideal nesting locations include leaf litter, under rocks and logs, loose bark, clusters of moss, epiphytes, and plant petioles (Wetterer and Porter 2003), but the species also frequently nests in electrical sockets, vehicles, machinery, pallets, metal pipes, furniture, garbage piles, and anywhere that provides shade, moisture, and refuge.

Individual nests are small and often difficult to identify (Clark et al. 1982). Nests are comprised of brood (eggs, larvae, and pupae), sterile workers, multiple queens, and occasionally males. A single nest may be divided into separate aggregations, of which three types have been described; workers + brood + queens, workers + brood, and workers only (Ulloa-Chacon and Cherix 1990). The purpose of separate aggregations and caste segregation has not been identified but could be due to capacity limits at the nest location, protection and defense of brood and queens, or other reasons. Such nesting habits allow *W. auropunctata* to utilize all available nesting sites in an area and support extremely high population densities (Hölldobler and Wilson 1995, Souza et al. 2008).

Typical queen:worker ratios for a *W. auropunctata* nest have been described as ranging between 1:250 and 1:500 with up to 16 queens per nest (Ulloa-Chacon and Cherix 1990). However, one cannot ignore the question of what defines an individual nest within a supercolony and when a 'single' nest may be comprised of separate aggregations. Indeed, many more queens have been observed within proximity to each other amid large infestations (personal observation) but it is uncertain how common this is or what factors influence the number of queens per nest. As with other eusocial insects, older workers forage outside of the nest while younger workers remain within the confines of the nest and care for queens and brood, a process referred to as temporal polytheism (Robinson et al. 1994, Ortiz-Alvarado et al. 2021). Queens are typically relegated to laying eggs but will forage and care for brood when worker populations are low (Ortiz-Alvarado and Rivera-Marchand 2020). This behavior likely contributes to *W. auropunctata* surviving the colony founding period when introduced to new locations and during the budding process.

Two *W. auropunctata* ecological variegates are known throughout their native range: nondominant and dominant (Levings and Franks 1982, Tennant 1994, Foucaud et al. 2009, Orivel et al. 2009). The nondominant variegate typically reproduces sexually and is restricted to natural, primary forests throughout its native range. Although common, nests are diffusely dispersed throughout the forests and these *W. auropunctata* do not display the same level of interspecific aggression as the dominant variegate (Tennant 1994, Salguero Rivera et al. 2011). The dominant variegate typically reproduces clonally and is widely distributed in human modified habitats through its native and introduced ranges (Foucaud et al. 2009, Orivel et al. 2009, Chifflet et al. 2018). The dominant variegate displays high levels of interspecific aggression and other behavioral traits that allow *W. auropunctata* to successfully dominate other ant species. Interestingly, before the 1980s, the nondominant variegate was unknown (Levings and Franks 1982) despite the current hypothesis that the dominant variegate arose from nearby nondominant populations (Foucaud et al. 2007). The behavioral and physiological plasticity of *W. auropunctata* and correlation between human disturbance and dominance has led researchers to label *W. auropunctata* as a 'disturbance specialist' (Majer 1999, Solomon and Mikheyev 2005, Foucaud et al. 2009, Orivel et al. 2009, Chifflet et al. 2018, Achury et al. 2020). Despite this designation, it is still unclear whether certain types and intensity of disturbances create unsuitable habitat (Rojas et al. 2021). For example; although *W. auropunctata* is a well-known agricultural pest, they may not be able to invade annual cropping systems as well as perennial crops and orchards due to annual cropping systems undergoing frequent harvesting, tillage, and replanting (Rojas et al. 2021). Additionally, development of rural areas and increased urbanization dramatically alters landscapes in a way that may reduce suitable habitat for *W. auropunctata* while becoming more suitable to other ant species (Mbenoun Masse et al. 2021). It is likely the effects of disturbance on *W. auropunctata* invasion vary from one location to another and this should be looked into further. Low intraspecific aggression allows workers to freely move between nest aggregates and share food resources, thus forming three dimensional 'supercolonies' (Foucaud et al. 2009). While both the nondominant and dominant variegates build supercolonies, those of the nondominant variegates are smaller and multiple, genetically distinct, supercolonies are present throughout a given landscape (Foucaud et al. 2009). Alternately, the dominant variegate is often unicolonial, building a single expansive supercolony with undefined nest boundaries and extending over hundreds of kilometers (Hölldobler and Wilson 1977, Le Breton et al. 2004, Errard et al. 2005). This unicolonial social organization differs from most ant species (Hölldobler and Wilson 1990) but is common among invasive ants (Holway et al. 2002). Such cooperative networks are conducive to exponential population growth, easily supporting densities of 20,000 workers and 37–52 queens per square meter (200 million workers and 370,000–520,000 queens per ha) (Ulloa-Chacon and Cherix 1990, Souza et al. 2008). This population estimate is over five times that of the estimate for polygynous *Solenopsis invicta* Buren by Macom and Porter (1996) and may be among the highest of all ant species in the world. Hölldobler and Wilson (1990, p. 63) described *W. auropunctata* as '*creating a living blanket of ants that kill and eat nearly all other ants in their path*'.

The underlying cause for the shift towards ecological dominance is not well understood. Foucaud et al. (2009) suggested that human disturbance, rather than unicolonality, is likely responsible for triggering ecological dominance. This hypothesis is supported when the history of invasive populations and the impact of *W. auropunctata* on the local fauna are considered. The alteration of natural ecosystems into agricultural and urban environments results in shifts of biotic and abiotic pressures. Reduced biodiversity in altered ecosystems often creates open niches ready for exploitation. Open niches and the inability of local species to successfully defend against *W. auropunctata* likely allow for the exhibition of dominant behaviors early on in the invasion process and before the formation of large supercolonies. Over time, an invading supercolony is able to expand its boundaries because *W. auropunctata* is able to dominate, outcompete, and displace other species. The degree of impact on local arthropod fauna is not universal since some species are able to successfully defend against *W. auropunctata* (Le Breton et al. 2007a, b; Mbenoun Masse et al. 2019b, 2021; Perfecto and Vandermeer 2020b). Could the presence of highly competitive local arthropod fauna also play a role in regulating ecological dominance of native and exotic *W. auropunctata* populations? It is interesting that the global distribution of other well known invasive ant species overlaps that of *W. aurpounctata* yet their competitive strength against *W. auropunctata* seems to vary from one location to another (Kirschenbaum and Grace 2007a, Mbenoun Masse et al. 2019b).

Future research on the driving factors of ecological dominance, and subsequent ecological impacts should consider the roles different types of human disturbance and multispecies interrelationships have on the degree of ecological dominance (Perfecto and Vandermeer 2020b). Future research should also investigate possible links between *W. auropunctata* genetics and ecological dominance. It is possible that certain haplogroups or haplotypes are more likely to show greater levels of ecological dominance than others.

Social Behaviors

The complex intra- and inter-specific behaviors of *W. auropunctata* provide insight into how this species quickly establishes and eventually dominates in some areas while accounting for a mere fraction of the biodiversity elsewhere. Variation in intra- and interspecific behavior between the dominant and nondominant variegates highlights a behavioral plasticity that is not well understood (Le Breton et al. 2004, 2007a). Since dominant and nondominant variegates exist throughout the native range, it is important to consider behavioral studies in the context of this variation rather than simply as native and nonnative populations. However, most studies focusing on intraspecific aggression were conducted before Foucaud (2009) describing the dominant and nondominant variegates and so intraspecific aggression has typically been reported in the context of native versus nonnative populations rather than according to variegate (Le Breton et al. 2004, Errard et al. 2005). The consensus among these studies is that invasive populations display much lower intraspecific aggression than native populations but it is likely that the native populations studied were of the nondominant variegate since the study sites in question were typically within primary forests rather than disturbed habitats. To date, no studies have examined intraspecific aggression in the context of native and nonnative dominant versus nondominant populations.

Variation in intraspecific aggression and nest-mate recognition is linked to the chemical composition of cuticular hydrocarbons (CHCs) (Errard et al. 2005, Martin and Drijfhout 2009, Vonshak et al. 2009). Errard et al. (2005) reported a correlation between intraspecific aggression and variation of CHC's among native and nonnative *W. auropunctata* populations. Likewise, there is high genetic variability among the nondominant variegate and low genetic variability among the dominant variegate due to their different reproductive modes (Foucaud et al. 2007). This supports the hypothesis that the native population studied by Errard et al. was of the nondominant variate rather than the dominant variegate; however, research is needed to confirm this. Moreover, CHC production and variability are not only governed by genetic factors but are also influenced by environmental factors such as diet, habitat, and season (Vonshak et al. 2009). Studies have shown that CHC production and intraspecific aggression shift when *W. auropunctata* are taken from their natural environment and placed into laboratory culture (Vonshak et al. 2009).

Wasmannia auropunctata has a reputation for being highly agonistic toward other species, with direct aggression being primarily responsible for its success (de la Vega 1994; Kirschenbaum and Grace 2007a, b, 2008; Vonshak et al. 2012). However, although interspecific aggression in *W. auropunctata* is well documented, many factors contribute to its success as an invader. *Wasmannia auropunctata* population densities appear to be an underlying factor influencing interspecific aggression. At low densities or when not numerically dominant, *W. auropunctata* workers are pliant in the presence of other, more dominant species, and act as an insinuator species (Achury et al. 2008, Vonshak et al. 2012, Yitbarek et al. 2017). Its small size may allow *W. auropunctata* to select what type of interaction is most appropriate and beneficial for a given situation (Tennant 1994, Le Breton et al. 2007a, Achury et al. 2008, Vonshak et al. 2012, Yitbarek et al. 2017). Low population densities occur within populations of the nondominate variegate and early in the invasion process, after colony establishment for the dominant variegate. For new introductions, low interspecific aggression may enable *W. auropunctata* to coexist with other species and exploit resources necessary for colony growth (Vonshak et al. 2012, Yitbarek et al. 2017). Once numerically dominant, a behavioral shift occurs and *W. auropunctata* workers become highly agonistic toward other species, excluding them from resources and destroying their nests (Vonshak et al. 2012). The low worker:queen ratio, high fecundity rates, and low intraspecific aggression typical of the dominant variegate allow for quick colony growth and numerical dominance (Clark et al. 1982, Ulloa-Chacon and Cherix 1990, Brandao and Paiva 1994, de la Vega 1994, Way and Bolton 1997, Delsinne 2001, Kirschenbaum and Grace 2008).

The ability of competitor species to fend off *W. auropunctata* attacks and defend resources also plays a role in regulating *W. auropunctata* population dynamics (Le Breton et al. 2007a, Perfecto and Vandermeer 2020a). Controlled behavioral experiments have shown that the presence of *W. auropunctata* elicits reactive responses from some competitor ant species (e.g., immediate recruitment of larger castes able to attack and kill *W. auropunctata*) but not from other species (Kirschenbaum and Grace 2007a, Le Breton et al. 2007a, Kirschenbaum and Grace 2008, Perfecto and Vandermeer 2020b). It's not yet known if successful defense against *W. auropunctata* within its native range is dependent on which ecological variegate is encountered and habitat type (i.e., disturbed or natural). Only the most aggressive competitor ant species seem able to fend off *W. auropunctata* in its native range and these are typically other well-known invasive ant species (Le Breton et al. 2007a, b; Mbenoun Masse et al. 2019b, 2021; Perfecto and Vandermeer 2020b). Interestingly, *Pheidole megacephala* Fabricus has been documented as a displaced species throughout much of *W. auropunctata's* introduced range while also being implicated as a potential cause of a rare invasion contraction event in Cameroon (Mbenoun Masse et al. 2019b, 2021). Additionally, *W. auropunctata* have been documented nesting near and tolerating other species when not competing for food resources (Way and Bolton 1997). This highlights the complexity of interspecific competition and that it is often oversimplified. It is likely that successful competition and resilience against *W. auropunctata* rely on both biotic and abiotic factors (Jourdan et al. 2006, Vandermeer and Perfecto 2020).

Diet

Wasmannia auropunctata is a true generalist, feeding on whatever is available including nectar (floral and extrafloral) (Schemske 1980, Horvitz 1990, Deyrup 2000, Apple 2001), plant parts (Clemente and Whitehead 2020), other invertebrates (Smith 1942, Feinsinger and Swarm 1978, Clark et al. 1982, Way and Bolton 1997), animal feces (Rosumek 2017), and honeydew-producing phytophagous insects (Spencer 1941, Smith 1942, Fabres and Brown 1978, Delabie and Cazorla 1991, Delabie et al. 1994, Naumann 1994, de Souza et al. 1998, Fasi et al. 2013). Few nutrient allocation or dietary studies have been conducted on *W. auropunctata*, but studies on other ant species indicate that dietary preferences and needs may vary seasonally (Stein et al. 1990) and between arboreal and ground-dwelling conspecific ants (Hahn and Wheeler 2002, Bluthgen et al. 2003). Additionally, *W. auropunctata* raised under laboratory conditions can display differences in food-lure preferences when compared to wild conspecifics (Montgomery et al. 2020).

It is common for laboratory-raised insects to behave differently to wild conspecifics and this likely influences observations during laboratory experiments (Herard et al. 1988, Propkopy et al. 1989, Ennis et al. 2015). Since laboratory experiments are valuable components of the research and experimentation process, differences in foraging behaviors should be accounted for when conducting dietary, palatability, and bait efficacy assessments (Montgomery et al. 2020).

Global Distribution

The global distribution and spread of *W. auropunctata* were first outlined in 2003 and has been tracked since (Wetterer and Porter 2003, Wetterer 2013). Currently, *W. auropunctata* is more widespread globally than *S. invicta* (Buren), although the latter receives considerably more attention as a research and legislative priority. *Wasmannia auropunctata* is native to the Neotropics of Central and South America (Wheeler 1929). Its southerly range extends to central Argentina (Chifflet et al. 2016), east of the Andes, and it was recently postulated that *W. auropunctata* may be native as far north as the United States—Mexico border (Mikheyev and Mueller 2007, Wetterer 2013).

Genetic analysis on specimens collected throughout this region has identified two phylogenetic clades (Clad A and Clad B) with numerous haplogroups based on cytochrome c oxidase 1 partial mitochondrial genome analysis (Chifflet et al. 2016). Even though this research has provided empirical evidence for determining places *W. auropunctata* is likely native, there is still uncertainty as to how far the native range extends and where this species has been introduced. For example, *W. auropunctata* is native to northern Argentina, as evidenced by the presence of genetically diverse sexual and clonal populations (Chifflet et al. 2016, 2018). However, the occurrence of only clonal populations of and little genetic variation in central Argentina has been suggested as evidence of range expansion within the past 60 yr and may be indicative of anthropogenic introductions (Chifflet et al. 2016, 2018). Currently, there is a noticeable lack of records from central and western Mexico and no genetic analysis has been done on any *W. auropunctata* collected in Mexico. To tease out the northern limitations of *W. auropuntata's* native range, future research should focus on documenting the ant biodiversity of this area and genetic analysis of *W. auropunctata* populations throughout Mexico should be conducted. Despite the uncertainty surrounding the northern limitations of its native range and the need for additional work, the Mexican populations are presumed part of *W. auropunctata*'s native range in this review due to its contiguous distribution where it is known to occur throughout Central America. We acknowledge that this matter requires further investigation before it is fully reconciled.

Historically, there has been uncertainty surrounding the status of *W. auropunctata* in the Caribbean due to its pervasiveness throughout the region with records dating back to the mid-1800s (Wetterer and Porter 2003, Mikheyev and Mueller 2007, Wetterer 2013). However, molecular genetics and analysis of eco-evolutionary pathways identified the presence of the same clonal lineages being present on multiple islands and in parts of South America (Mikheyev and Mueller 2007, Foucaud et al. 2010b). While this does not preclude the idea of the Caribbean being part of *W. auropunctata*'s native range, it does indicate that numerous introduction events have occurred throughout the region (Mikheyev and Mueller 2007, Foucaud et al. 2010b). The lack of evidence of sexually reproducing populations in the Caribbean is another indication that *W. auropunctata* is not likely native to the region (Mikheyev and Mueller 2007, Foucaud et al. 2010b). It is possible that the Caribbean distribution contains a mix of native and introduced populations (Wetterer 2013) but, no genetic evidence has been presented that suggests this is the case.

The earliest confirmed record of *W. auropunctata* outside of its presumed native range was from Gabon in 1894 by Emery who recognized it as having the potential to become a serious invasive tramp ant (Wetterer 2013). Indeed, since then, *W. auropunctata* has been introduced and established in 23 countries and island groups beyond its presumed native range (Wetterer and Porter 2003, Wetterer 2013, Espadaler et al. 2018, Mayron 2019, Vanderwoude et al. 2021). To date, the nondominant variegate has not been documented outside of *W. auropunctata*'s native range. Since the latest global distribution list (Wetterer 2013) there have been five new detections of established *W. auropunctata* populations in the world. Three new detections were made in Oceania: Wanyaan, Yap, Federated States of Micronesia in 2017 (GBIF.org 2021); Tutuila, American Samoa in 2018 (Gruber et al. 2016); and Suva, Fiji in 2019 (Vanderwoude et al. 2021). A detection in Malaga, Spain in 2018 was confirmed to be the northernmost outdoor population recorded to date (Espadaler et al. 2018). The populations in Israel and Spain represent the only outdoor infestations in Palearctic and Nearctic biogeographical regions. All other infestations in these biogeographical regions were documented in greenhouses and indoor nursery settings (Wetterer and Porter 2003). The most recent detection was confirmed in 2022 from Shantou, Guangdong Province in south-eastern China (Chen et al. 2022). This is the first official record of *W. auropunctata* in the Indomalayan biogeographical region.

The global distribution presented in this review is conservative (Fig. 5), with only confirmed, established populations of *W. auropunctata* as of June of 2021 being included. Not included on the map are *W. auropunctata* occurrences of unconfirmed detections of possible wild populations, which are included on other distribution lists, specifically, detections from California (USA), southern Texas (USA), Lisca Bianca Island (Italy) (Jucker et al. 2008, Wetterer 2013), and Dhaka, Bangladesh (GBIF.org 2022). Unconfirmed detections are either unsubstantiated reports of establishment or instances in which a single specimen was collected or photographed in the wild and presumably positively identified yet no verification, further record, or knowledge exists. It is possible that established *W. auropunctata* populations exist in these locales yet no follow-up sampling was ever conducted to verify their existence. Follow-up surveys and sampling should be a priority for all unconfirmed records of *W. auropunctata* as this information will be invaluable for the understanding of this species presumed native range and potential global distribution. Notably, *W. auropunctata* is regularly intercepted in California by Department of Agriculture quarantine inspectors, but no wild populations have been confirmed in (G. Arakelian, Los Angeles County Entomologist, personal communication) despitean early claim that it was established in Los Angeles County (Keifer 1937) and repeated citing of this claim in numerous distribution lists. Regulatory and responding agencies around the world should be hyper-vigilant, especially in areas where *W. aurounctata* is frequently intercepted but not believed to be established. It is important to acknowledge that *W. auropunctata* are likely established beyond the locations indicated here and have yet to be officially detected due to the ease at which they are distributed and the probability of going unnoticed.

Distribution Pathways

Transportation and dispersion of *W. auropunctata* typically occur in three ways: natural active dispersion, natural passive dispersion, and human-mediated transport. Natural active dispersal occurs primarily via budding (Ulloa-Chacon and Cherix 1990). When a nest becomes

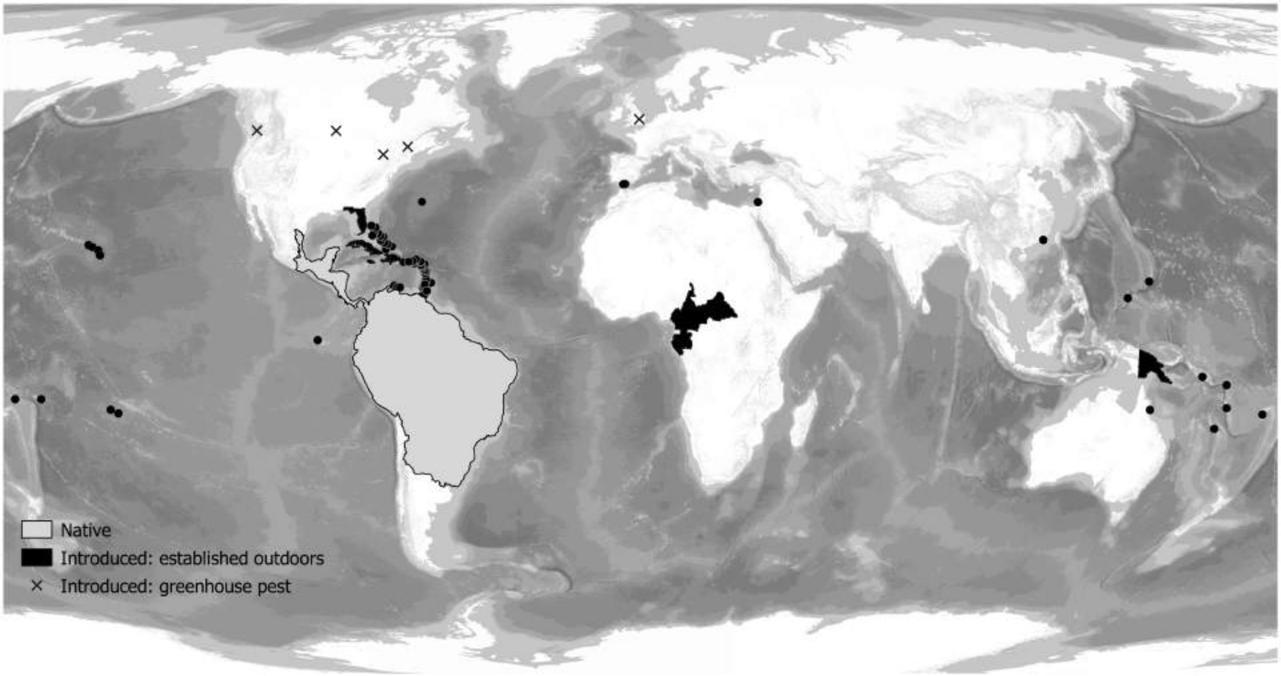

Fig. 5. Global distribution of *W. auropunctata* as of 2022. Gray shaded areas and points indicate the presumed native range. Black shaded areas and points indicate locations where exotic outdoor populations are established. Black x's indicate locations where *W. auropunctata* have been introduced and are documented as indoor greenhouse pests but no outdoor populations have been documented. The current distribution map includes data from J.K. Wetterer's 2013 distribution map and all subsequent records of confirmed established *W. auropunctata* populations detected since 2013.

crowded or the nest is disturbed, a queen will carry a small number of workers to a nearby location and establish a new nest aggregation (Feitosa 2007, Mbenoun Masse et al. 2011). Because of this, outward expansion of an infested area is slow, measured in the tens of meters per year, with dispersal propelled by the ant's direct effort (Walsh et al. 2004). However, the rate of outward expansion may also be influenced by population density and ecological factors (Mikheyev et al. 2008). *Wasmannia auropunctata*'s unicolonial colony structure, low intra-specific aggression, and generalist nesting preferences allow for population densities far beyond that of multicolonial ant species and species with specialized nesting preferences. Therefore, the rate of outward expansion may increase or decrease depending on site features such as nesting site availability and physical barriers between the current infested area and the closest suitable habitat. Invasion contraction events (i.e., reduction of previously invaded area) have been documented, but appear to be rare and warrant further investigation (Lester and Gruber 2016, Mbenoun Masse et al. 2019b).

Modes of natural passive dispersion occur by rafting downstream on waterways and flood water, landslides, and possibly from high winds and storm events (Lubin 1984, Walker 2006, Vanderwoude et al. 2014). Modes of natural passive dispersion enable dispersion along greater distances than through budding and act as pathways for new introductions with transport via moving water being the most frequently observed (Walker 2006, Vanderwoude et al. 2014).

Human-mediated transport is the most common mode of long-distance dispersal (Walsh et al. 2004, Mikheyev et al. 2008, Foucaud et al. 2010b) and both intentional and unintentional introductions have occurred world-wide. *Wasmannia auropunctata* is frequently transported locally, intra- and inter-nationally through human commerce including, but not limited to, the movement of infested nursery stock and planting media, construction materials, vehicle and machinery, stockyard supplies such as wooden pallets, and by the movement of other types of items held at infested sites to uninfested sites (e.g., furniture, portable toilets, salvaged materials, etc.) (Walsh et al. 2004). Phylogenetic analysis allows tracing of the place of origin for invasive populations and their spread (Mikheyev and Mueller 2007, Silva et al. 2018). Distinct genetic similarities have been found between invasive populations of *W. auropunctata* in countries with strong trade ties or sharing established shipping routes (Foucaud et al. 2010b).

Intentional human introduction and movement of *W. auropunctata* has occurred for biocontrol purposes (Bruneau de Miré 1969, Wetterer et al. 1999, Ndoutoume-Ndong and Mikissa 2007, Fasi 2009). Although it is well known that the costs associated with *W. auropunctata* invasion outweigh any potential benefit, it's possible such intentional introductions will continue due to this species being highlighted repeatedly as a natural enemy and potential biocontrol agent for coffee berry borer (Curculionidae: *Hypothenemus hampei* Ferrari) and Asian citrus psyllid (Liviidae: *Diaphorina citri* Kuwayama) (Morris and Perfecto 2016, Kondo et al. 2018, Morris et al. 2018, Jiménez-Carmona et al. 2019, Perfecto and Vandermeer 2020a) (Morris and Perfecto 2022).

Predicting Future Range Expansion

Wasmannia auropunctata has traditionally been considered a tropical and subtropical pest species. The outdoor infestations in Spain and Israel show this is a misleading conception and more attention should be given to the species' current potential range and future range expansion under climate change. 'Clade A' and 'Clade B' each display different range potential (Chifflet et al. 2016) with the former distributed primarily in the tropics and the latter having a much wider range into subtropical and Mediterranean climates (Chifflet et al. 2016).

Species distribution models (SDMs) are often used to predict the potential range expansion of a target species. However, SDMs are far from perfect and ecologists are still trying to determine which models and variables best describe limiting factors, potential range predictions, and eco-evolutionary scenarios (Elith et al. 2010, Rey et al. 2012, Federman et al. 2013, Coulin et al. 2019). To date, only two studies have modeled the potential distribution of *W. auropunctata* (Federman et al. 2013, Coulin et al. 2019). Temperature and precipitation were identified early on as limiting factors for its habitat suitability (Jourdan and Dumas 2004). Since then, minimum and maximum critical thermotolerances of the species have been identified through laboratory experiments and included in SDMs (Rey et al. 2012, Foucaud et al. 2013, Coulin et al. 2019). Some have speculated elevation as a limiting factor due to *W. auropunctata* not occurring above 700 m in New Caledonia (Jourdan et al. 2006), but infestations have been detected in Hawai`i at over 1,200 m (M. Montgomery personal observation). This suggests that elevation is not likely a limiting factor in and of itself, but as it relates to temperature and moisture thresholds. Additionally, although SDMs using climatic factors are undoubtedly useful, the spatial scale at which these models analyze climactic data may not identify localized microclimates and the models do not account for human disturbances that influence local microclimates which may aid in triggering natural adaptations within the species (Federman et al. 2013, Foucaud et al. 2013).

Because *W. auropunctata* is considered a disturbance specialist, human disturbances such as irrigation can transform naturally unsuitable habitats into suitable habitats that are unlikely to be detected by correlative SDMs when using naturally occurring precipitation data (Vonshak 2010, Federman et al. 2013). Federman et al. (2013) demonstrated that using a precipitation correction accounting for irrigation estimates increased the precision and accuracy of model predictions. Models based solely on data collected from the target species native range are also likely to fail to identify all suitable habitat and global distribution potential of highly adaptable species (Elith et al. 2010). Contrary to correlative SDMs that use climatic and known distribution data, mechanistic SDMs use functional attributes, niches, and spatial data to predict potential range expansion. Models combining mechanistic and correlative SDMs that account for human disturbances and incorporate data from the species' known global distribution should be investigated further for their potential to refine predictions of habitat suitability and potential global range expansion.

Impacts

Impacts and benefits associated with *W. auropunctata* are multitiered and may be characterized as direct or indirect. Direct impacts are those caused by *W. auropunctata* while indirect impacts are those caused by other organisms influenced by the presence of *W. auropunctata*. For example, the extirpation of a species due to predation or resource competition by *W. auropunctata* is a direct impact whereas an increase in plant disease due to higher populations of scale insects farmed by *W. auropunctata* would be considered an indirect impact. Humans, animals, and entire ecosystems are known to be affected by *W. auropunctata*. Numerous ecological studies and economic impact assessments have been conducted documenting the multitiered impacts of *W. auropunctata* and have determined that while some impacts may be considered positive (i. e. biological control of coffee berry borer), the vast majority are negative (Bousseyroux et al. 2019). Careful and thorough cost-benefit considerations should be made before the intentional movement or maintenance of *W. auropunctata* infestations.

Mechanisms for Displacement and Impacts on Natural Ecosystems

Displacement of ants and other invertebrates by *W. auropunctata* is well documented (Clark et al. 1982; Lubin 1984; Jourdan 1997a,b Armbrecht and Ulloa-Chacon 2003; Le Breton et al. 2003; Wetterer and Porter 2003; Walker 2006; Grangier et al. 2007; Ndoutoume-Ndong and Mikissa 2007; Kirschenbaum and Grace 2008; Fasi 2009; Vonshak et al. 2010; Gasc et al. 2018; Bousseyroux et al. 2019; Mbenoun Masse et al. 2019b). In fact, Silberglied (1972 p. 13) commented that its impact in the Galapagos was 'the most serious of any introduced animal'. Ecological studies on insect biodiversity between areas and plots with and without *W. auropunctata* (Clark et al. 1982; Lubin 1984; Jourdan 1997b; Roque-Albelo et al. 2000; Le Breton et al. 2003, 2005; Walker 2006; Grangier et al. 2007; Ndoutoume-Ndong and Mikissa 2007; Vonshak et al. 2010; Mbenoun Masse et al. 2017, 2019b; Gasc et al. 2018) along with data on resource interference and competition and interspecific aggression (Grangier et al. 2007, Vonshak et al. 2012, Yitbarek et al. 2017) provide evidence linking this species to the extirpation of other insects within invaded areas). Such studies have built a foundation upon which insect populations and diversity are used as proxies for the impacts of *W. auropunctata* in forests. Additionally, the correlation between biodiversity and *W. auropunctata* presence or absence has led to *W. auropunctata* being used as an indicator species for low insect community diversity (Armbrecht and Ulloa-Chacon 2003, Achury et al. 2008, Berman et al. 2013).

Studies describing *W. auropunctata* impacts on insect communities throughout its native and nonnative ranges appear to make the important assumption that its inherent ability to dominate ecosystems remains constant and that differences in impact magnitude are due to the resilience of competing species. No consideration is given to whether the populations being studied are of the dominant or nondominant variegate described by Foucaud et al (2009). Since the two variegates differ biologically, physiologically, and behaviorally, results from studies that measure impacts between invasive populations and native populations without consideration of ecological variegate may be inherently flawed (Brandao and Silva 2008, Achury et al. 2012, Rojas and Fragoso 2021). Any future study comparing impacts of native versus nonnative populations should take care to ensure that populations being compared are of the same variegate.

Resource and interference competition have been indicated as the mechanisms by which *W. auropunctata* succeed as invaders and displace other insects. Multiple behaviors have been identified contributing to *W. auropunctata*'s competitive strength, including acting as an insinuator species when not numerically dominant (Le Breton et al. 2007a, Yitbarek et al. 2017). *Wasmannia auropunctata* workers frequently take significantly longer to discover and recruit to food resources compared with other ant species (Vonshak et al. 2012, Yitbarek et al. 2017). When first encountering food resources occupied by another species, their passivity toward the other species likely allows *W. auropunctata* to avoid aggressive interactions until enough nestmates can be recruited to successfully defend the resource (Vonshak et al. 2012, Yitbarek et al. 2017). Additionally, native ants often appear incapable of forming appropriate responses are unable to defend nesting and food resources creating niche opportunities that *W. auropunctata* effectively exploit (Le Breton et al. 2005, 2007a).

While the role of resource competition is widely suggested as a mechanism for competitive success, there is some debate as to the magnitude of its contribution. Observations during behavioral laboratory assays suggest that while *W. auropunctata* are aggressive toward some species, they are often unsuccessful defenders of food resources during general interspecific encounters (Kirschenbaum and Grace 2008, Vonshak et al. 2012). However, during one study, although *W. auropunctata* retreated from food resources when confronted by a competitor, they also invaded and completely destroyed the competitor's nests over the course of several days and weeks (Vonshak et al. 2012). Because they are generalist feeders and active 24 h per day, it's possible that the cost of aggressive encounters outweighs the benefit of immediate reward and it is better to wait or find an unoccupied resource. Also, laboratory studies don't often reflect what happens under natural circumstances. For example: in the wild, the dominant variegate is defined, in part, by its propensity to form expansive supercolonies. This allows for massive recruitment of resources. In contrast, laboratory colonies and experiments are highly structured and controlled and use only a single nest at a time. Field studies have suggested that *W. auropunctata* may share food resources when fewer than 500 foragers are present (Achury et al. 2008). If this is the case, it is unlikely that a single nest would provide high enough forager recruitment to a resource to successfully defend it during laboratory experiments and behavioral assays. The dichotomy between laboratory and wild conspecifics and the environmental conditions they are exposed to is an important consideration with interpreting results from such studies.

Although physical aggression, such as biting and stinging, appears to be the primary competitive mechanism by which *W. auropunctata* directly interferes with other species, chemical defenses may also play a role (Howard et al. 1982, Le Breton 2002, Showalter et al. 2010). Ants primarily communicate chemically and the use of pheromones is an important mode of communication for foraging, defense, and regulation of inner-nest functioning (Howard et al. 1982, Martin and Drijfhout 2009, Showalter et al. 2010, Cha et al. 2019). When distressed, *W. auropunctata* secrete an alarm pheromone from the mandibular gland which attracts nestmates and aids in mass recruitment for defensive action (Howard et al. 1982, Showalter et al. 2010). These mandibular gland secretions may also act as a repellant to competitor species (Howard et al. 1982), although this hypothesis has been challenged (Le Breton 2002). It is important to recognize that the two studies investigating repellant properties of the mandibular gland secretions employed very different methodologies and confounding factors may have influenced the results of one or both of the studies. One study tested the effects of extracts from the mandibular gland on the acceptability of mealworms to other ant species (Howard et al. 1982) whereas the other study exposed food lures to *W. auropunctata* in the field and later presented the exposed food lures to other species at different field locations without *W. auropunctata* (Le Breton 2002). Given their behavioral plasticity, it is possible that the mandibular gland excretions are secreted only during interspecific encounters, and thus may not have been present on the food lures during foraging when only *W. auropunctata* was present. Although the mandibular gland excretions are verified alarm pheromones used in mass recruitment and undoubtedly contribute to successful resource defense (Showalter et al. 2010), more research is needed to verify any potential repellant action of *W. auropunctata* mandibular gland secretions.

Wasmannia auropunctata has also been identified as a threat to vertebrates (Jourdan 2001, Walsh et al. 2004, Beavan et al. 2008). Tropical keratopathy (TK) is a condition in which the cornea of the eye becomes clouded over and appears superficially similar to cataracts. Mild cases of TK often appear as small, individual cloudy corneal spots whereas extreme cases appear as clouding over the entire cornea. *Wasmannia auropunctata* has been directly linked to occurrences of widespread TK in domestic animals and with occurrences of TK in humans (Theron 2007, Rosselli and Wetterer 2017, Patael et al. 2019). Although no studies have focused on documenting animal TK occurrences in invaded natural ecosystems, trail cameras in Gabon captured images of a leopard with severe TK (Walsh et al. 2004) and it is likely this is a problem not yet investigated. Agonistic interactions between *W. auropunctata* and several lizard (*Anolis*) species have been documented and it has been speculated that lower herpetofauna diversity may be found throughout infested areas (Jourdan 2001, Jourdan et al. 2001, Wetterer et al. 2007, Perfecto and Vandermeer 2020a). The effects of *W. auropunctata* on ground-nesting seabirds and forest birds has not been formally assessed, but other invasive ant species are known to reduce nesting and hatching success, foraging, and survival rates (Allen et al. 2004, Plentovich et al. 2008, Davis et al. 2009, Kropidlowski 2014). The diversity of suitable habitat for *W. auropunctata* likely increases the chances of ant-bird interactions, and the potential for negative impacts on avifaunal communities. Research is needed to identify possible impacts and the risk *W. auropunctata* poses to various avifaunal communities.

In some areas, *W. auropunctata* may directly and indirectly impact forest plant composition and regeneration through the assistance of or interference with seed production, dispersal, and ant-plant mutualisms (Horvitz 1990, Mikissa et al. 2013, Clemente and Whitehead 2020). *Wasmannia auropucunctata* have been observed harvesting fruits of *Piper sanctifelicis* Trel (Family: Piperaceae), a common South American shrub (Clemente and Whitehead 2020). Although it is not unusual for ants to harvest seeds of plants typically dispersed by vertebrates, it is the first and only record of *W. auropunctata* doing this. Additionally, *W. auropunctata* may aid in fruit set and seed production of some plants through predation on herbivorous insects (Horvitz and Schemske 1984). On the contrary, *W. auropunctata* have been observed interfering with ant-plant mutualisms and indirectly hindering forest regeneration by excluding ant mutualists from their obligate host plants (Mikissa et al. 2013). Other ant species, such as yellow crazy ant (*Anoplolepis gracilipes* [Smith]) have been implicated in 'invasional meltdowns' due to interference with natural ecosystem processes (O'Dowd et al. 2003, Green et al. 2011). For example, on Christmas Island in the Indian Ocean, *A. gracilipes*significantly reduced populations of endemic red land crabs (*Gecarcoidea natalis* Pocock), a keystone species, and is linked to population explosions of scale insect and sooty mold (O'Dowd et al. 2003, Green et al. 2011). These relationships have altered local litter decomposition rates, plant and insect species diversity, and forest structure, and led to secondary invasions within *A. gracilipes* invaded areas (O'Dowd et al. 2003, Green et al. 2011). Although *W. auropunctata* alters ecosystem processes, very little is understood on the ramifications of these relationships on floral communities and whether ecological variegation is a factor influencing the magnitude and direction of the impacts. It is possible that such relationships may also lead to 'invasional meltdowns', especially within insular island communities, but additional research is needed to assess this.

Agricultural Systems

Although ecological impacts of *W. auropunctata* are serious, they are often not enough to trigger concern and human intervention. Agriculture industries are the most affected by *W. auropunctata* according to past economic impact assessments (EIAs) (Lee et al. 2015, Angulo et al. 2021) and their multitiered impacts are perhaps most clearly documented within agriculture systems. Agricultural workers are frequently stung while maintaining and harvesting crops. Reports from Tahiti and Florida indicate that farm workers have been unable or unwilling to harvest crops and to perform other duties in heavily infested citrus orchards and coffee fields (Spencer 1941, Smith 1965, Fabres and Brown 1978, Delabie 1988, Perfecto and Vandermeer 2020b) resulting, in some cases, in the abandonment of family lands (Vanderwoude et al. 2015). A similar trend has been observed in Hawai`i, where farm workers routinely fail to come to work on days when infested fields are scheduled to be picked (M. Montgomery personal observation).

The mutualistic relationship between *W. auropunctata* and honeydew-producing phytophagous insects results in indirect impacts such as population explosions of economically important plant pests (Smith 1965, Fabres and Brown 1978, Delabie 1989, Fasi et al. 2013). In particular, population levels of Homopterans including aphids, scale insects, and mealybugs are positively correlated with *W. auropunctata* population levels and negatively correlated with plant health and crop productivity (Delabie and Cazorla 1991, de Souza et al. 1998, Fasi et al. 2013). These mutualisms are a consequence of the protection that *W. auropunctata* provides the insects against natural enemies and the ants feeding on the sugary exudates (honeydew) of these insects. Many of these plant pests are known vectors of diseases that reduce plant health leading to crop loss and excess honeydew also acts as a medium for sooty mold growth.

Despite the association with economically important plant pests and their direct impact on farm workers, *W. auropunctata* has been intentionally introduced and moved around as a biocontrol agent against significant crop pests in the Solomon Isands and Gabon (Wetterer et al. 1999, Fasi et al. 2013). Recently, research also confirmed *W. auropunctata* is potentially effective at reducing populations of coffee berry borer and Asian citrus psyllid (Kondo et al. 2018, Morris et al. 2018, Jiménez-Carmona et al. 2019, Perfecto and Vandermeer 2020a, Morris and Perfecto 2022). However, researchers of those studies noted that the benefits do not outweigh the costs. Conversely, *W. auropunctata* has been documented interfering with various biocontrol agents (Kondo et al. 2018, Kulikowski 2020, Perfecto and Vandermeer 2020a, Perfecto et al. 2021). Whether intentionally or unintentionally introduced, farmers face a variety of issues due to *W. auropunctata* infestations.

Residential and Urban Areas

Wasmannia auropunctata infestations in urban environments have garnered little attention despite its recognition as a house pest (Smith 1929, Fernald 1947, Delabie 1995, Espadaler et al. 2018, Mbenoun Masse et al. 2019a, Kidon et al. 2022, Mbenoun Masse et al. 2021). The Hawai`i infestation reported by Conan and Hirayama in 2000 represents the first record of *W. auropunctata* as a major residential pest in any western society (Conant and Hirayama 2000). Their small size, brownish-orange color, and cryptic nesting habits allow this species to go unnoticed for many years and it is common for Hawaiian residents to become impacted by *W. auropunctata* only after the infestation has spread throughout the entire property and the ants have begun encroaching into homes and other structures (M. Montgomery personal observation). This is not unique to Hawai`i. The recent detection in Malaga, Spain, was due to a resident reporting an infestation of stinging ants in their home to a pest control company (Espadaler et al. 2018). Follow-up surveys by authorities revealed a 5.8 ha infestation spanning 50 private residences with some ants nesting in electrical receptacles (Espadaler et al. 2018). It was estimated that *W. auropunctata* was introduced over five years before detection but residents reported first noticing them only about two to three years prior (Espadaler et al. 2018). Since the original detection in 2018, two other infestations within the Malaga province have been detected at 13 and 17 km away from the original infestation (Espadaler et al. 2020). At this time, these new detections have not yet been completely delimited and their size is unknown (Espadaler et al. 2020).

Information gathered through public outreach communications in Hawai`i (M. Montgomery, unpublished data) has revealed that residents are frequently stung in their beds, while using the bathroom, or sitting on certain types of furniture (e.g., sofas, recliners). Despite this, individual sentiments toward *W. auropunctata* vary wildly. Some residents appear determined to manage *W. auropunctata* infestations and reduce the impacts themselves while others appear despondent and assume their situation is without a solution (M. Montgomery personal observation). For example, *W. auropunctata* was introduced to the Solomon Islands in the 1960s or early 1970s and continues to spread throughout the archipelago (Fasi et al. 2016). Public attitudes toward *W. auropunctata* appear to shift with communities having dealt with infestations for longer periods being more tolerant of the ant than communities with more recent invasions (Fasi et al. 2016). Once apathy toward *W. auropunctata* begins to take hold in a community, management practices likely decline. Similar attitudes are common in Hawai`i. In many Hawaiian communities, some residents are only persuaded to take management action against *W. auropunctata* when social pressure increases and they fear being stigmatized in their community (Niemiec et al. 2018, 2019).

Economic Impacts

There is no doubt that *W. auropunctata* negatively impacts ecosystem functions and quality of life but the reports are generally qualitative, difficult to quantify into monetary units, and rarely used to guide legislation aimed at biosecurity and prevention. Economic impact assessments (EIAs) and cost-benefit analyses (CBAs) attempt to place monetary values on damages incurred across various economic sectors and costs associated with postarrival management and prevention efforts. These cost factors are used in bioeconomic models to project how economic costs associated with a target species compound change over time under different management strategies. Unfortunately, quantification and reporting of costs associated with *W. auropunctata* are rare. Because EIAs rely on reported costs that can be quantified monetarily and largely ignore qualitative metrics, EIAs tend to grossly underestimate impacts (Angulo et al. 2021), especially in subsistence economies.

Three studies detailing the economic impacts of *W. auropunctata* have been compiled. Two focus on economic impacts in Hawai`i (Motoki et al. 2013, Lee et al. 2015). The other is a global assessment of the economic impact of invasive ants, including *W. auropunctata* (Angulo et al. 2021). In the global assessment, *Wasmannia auropunctata* was identified as one of the most economically impactful species in the world, second only to *S. invicta* with cumulative global costs since 1930 estimated at US$19.91 billion, predominantly incurring over the past ten years (Angulo et al. 2021). The greatest damage and highest costs of management are in the agriculture and public welfare sectors (Lee et al. 2015, Angulo et al. 2021). In Hawai`i, *W. auropunctata* was projected to cost the state US$6.1 billion over 35 yr if the current management efforts are sustained or US$12.9 billion if the management status quo is not maintained (Motoki et al. 2013, Lee et al. 2015). Conversely, economic costs can be greatly reduced with increased management, rapid response efforts to newly detected infestations, and enhanced prevention measures. Despite higher management cost than the status quo and reduced effort scenarios, overall costs (damages + direct costs of management and prevention efforts) of enhanced action plans were projected to reach only $US51 million over 35 yr (Motoki et al. 2013, Lee et al. 2015).

Most of these assessments focus on costs and damages without considering potential economic benefits of the target species. In Hawai`i, the invasion of *W. auropunctata* has spurred business development focusing on ant management in landscapes (M. Montgomery personal observation) and sales of ant baits generate revenues for local businesses. Additionally, the coffee berry borer is a major pest of coffee in Hawai`i with few effective management options. The recent identification of *W. auropunctata* as a potentially effective biological control (Kondo et al. 2018, Morris et al. 2018, Jiménez-Carmona et al. 2019) may provide a valuable nonchemical pest control option for Hawaiian coffee farmers. The reduction in costs associated with coffee berry borer control could be considered as a cost-saving economic benefit when viewed in isolation. However, *W. auropunctata* is also a major pest in coffee and creates costs associated with control efforts.

Detection and Control

Detection

Traditionally, nontoxic food lures have been the primary tool used for detecting *W. auropunctata*. Foods high in lipids and/or protein, such as peanut butter, hotdogs, or tuna fish, are typically used as lures during ecological studies to determine *W. auropunctata* presence with recruitment to the food lures frequently used as a surrogate for population size or density. Food lures are also used to delimit infestations and monitor the effectiveness of control programs. Few studies have investigated the attractiveness of pure lipids, proteins, and carbohydrates to *W. auropunctata* (Williams and Whelan 1992, Montgomery et al. 2020), but the consensus is that lipid-rich foods are the most attractive food lures (Williams and Whelan 1992, Meier 1994, Armbrecht and Ulloa-Chacon 2003, Montgomery et al. 2020). This is important because the use of a suboptimal or less attractive, food lure is likely to underestimate distribution, density, and confound results. Additionally, it is uncertain whether *W. auropunctata* would defend ideal food resources more than suboptimal resources which could influence the results of competition behavior studies.

Given their generalist diet, it is possible that food-lure preference may vary from one site to another or temporally within the same location depending on the season, available resources, nutrient deficiencies, and colony needs. For example, in Hawai`i, *W. auropunctata* recruitment rates to lipid-based food lures have been documented to be 6- —and 11-fold greater than carbohydrate and protein food lures, respectively among wild ants whereas laboratory colonies showed a preference for carbohydrate food lures (Vanderwoude et al. 2015). It is unknown whether fluctuations in dietary needs of wild populations and available resources influence their attraction to different food lures. To minimize possible confounding effects of food-lure selection, more information is needed elucidating food preference variability and the relationship between food preference and interspecific competition.

Despite detection via food lures being the norm, accuracy of area-wide surveys using food-lure detection protocols varies greatly depending on spacing between lures, foraging distance, and operator experience. Additionally, detection of arboreal colonies is difficult with traditional lure-based surveys and require special consideration (Cox et al. 2020). Early detection and control projects often must seek a compromise between feasibility and accuracy depending on personnel, time, and funding restrictions. Such compromises often manifest as wider spacing between lures and fewer survey efforts, and have resulted in false negative results and premature declarations of eradication (Montgomery unpublished data).

Food-lure detection methods are inexpensive and easy to use but these benefits come at a cost. Aside from variations in accuracy and precision, they are not species specific to *W. auropunctata* and ants collected during such surveys must be competently identified. This can be time consuming and further delay time-sensitive control actions. Species-specific detection methods are being developed that hold promise over conventional food-lure detection methods. The use of detector dogs is common for agriculture quarantine inspections and biosecurity programs around the world. Their use in invasive species monitoring programs has also grown in recent years (Lin et al. 2011, Wylie et al. 2016, Baker et al. 2017, Poland and Rassati 2019). Similarly, the development and marketing of lateral flow immunoassay rapid tests has revolutionized detection surveys targeting *S. invicta* by circumventing the need for time-consuming professional or laboratory diagnostics and allowing quick identification in the field (Valles et al. 2017, 2020). Should a comparable rapid test be developed for *W. auropunctata,* it would undoubtedly be an invaluable resource for biosecurity, rapid response and control efforts. The use of alarm pheromones for *W. auropunctata* management has shown to be ineffective, although they may hold potential as a species-specific detection tool in the near future and the development of pheromone lures is ongoing (Troyer et al. 2009, Derstine et al. 2012). Remote sensing has been used to identify *S. invicta* mounds by aerial searches (Vogt et al. 2008). Finally, advances in genetic research will likely lead to improved EDNA technology suitable for testing terrestrial substrates and may be useful for detecting nascent ant colonies. Although the future holds much promise for improved detection, currently, all but the conventional food lure-based and sniffer dog detection methods are still theoretical or unavailable for *W. auropunctata.*

Chemical Control

Ant control is more nuanced than control of most other insect pests. Historically, persistent and nonpersistent general use of contact insecticides, mound treatments, insecticidal ant baits (hereafter referred to as baits), and physical barriers have been used to control pest ants in various habitats (Osburn 1949, Delabie 1989, Williams 1994, Brooks and Nickerson 2008, Cabral et al. 2011). As the term implies, the general use of contact insecticides (hereafter referred to as contact insecticides) kill a wide variety of insects on contact through direct spray or when the insect comes into contact with a treated surface. Horizontal transfer, the acquisition of insecticide through physical contact with a treated individual, of active ingredients has been used to control some species of ants in residential and conservation areas (Soeprono and Rust 2004, Choe and Rust 2008, Klotz et al. 2009, Buczkowski 2019, Buczkowski and Wossler 2019, Zhang et al. 2022, Cabral et al. 2011), but few active ingredients are effective through horizontal transfer. Horizontal transfer, also, has not been tested as a possible control method for *W. auropunctata* and should be investigated further. Other contact insecticides may be used as a soil drench for potted plants or individual nests. While use pattern may be useful to treat infested nursery stock and potted plants at home, it is impractical to attempt control of *W. auropunctata* through drenching individual nests given its nesting behavior. Most contact insecticides are ineffective at producing lasting results for area-wide management because their effects are limited to killing foraging workers only while the rest of the colony within the nest remains unaffected. Baits hold significant advantages over other general use insecticide products in that they are typically lower in toxicity, have fewer nontarget impacts, and minimize insecticide use (Williams 1983, Klotz et al. 2003, Tollerup et al. 2004). Comprised of an attractant, carrier, and small amount of active ingredient, baits use the ant's natural foraging behavior to seek out, collect, and share the bait throughout the colony which affects reproductive, worker, and brood castes alike. To be effective, the active ingredient constituent in baits must be nonrepellant, lethal at very low doses and after dilution by trophallaxis, and also maintain delayed mortality effects (Levy et al. 1973, Williams 1983, Rust et al. 2000, Braness 2002, Tollerup et al. 2004).

Baits developed for 'fire ants' target lipid-responding ants and have been developed primarily for control of *S. invicta*. Although *W. auropunctata* is also a species that is attracted to lipids, there are substantial differences between the two species and the types of habitats they invade which render some baits more effective than others in various situations. For example, *S. invicta* build mounds in soil and prefer open, dry habitats whereas *W. auropunctata* nest opportunistically on the ground and in trees, preferring shady, moist habitats (Perfecto and Vandermeer 2020b). Chemical sensitivity differences between these two species is also apparent which influences efficacy of 'fire ant' baits against *W. auropunctata* (Hara et al. 2014, Montgomery et al. 2015). Site features, chemical sensitivities, and environmental degradation of baits and their active ingredients are the three main issues needing careful consideration when selecting a bait to control *W. auropunctata*. Management and eradication failures against this species have, in part, been attributed to a failure in addressing one or more of these issues during the eradication planning and implementation processes (Bossin and Padovani 2010).

Commercial baits used against *W. auropunctata* are available as granules, pastes and gels and may be used in bait stations, or broadcast treatments. Outdoor control using bait stations has been reported as inconsistent and less effective than broadcast bait applications (Ulloa-Chacón and Cherix 1994, Souza et al. 2008). *Wasmannia auropunctata* do not build mounds, therefore, baits are typically broadcast rather than applied to a mound or individual nests. Although broadcast applications are regarded as more effective than bait stations, there may be situations where bait stations are preferred. To date, no studies have attempted to determine foraging distances and effective bait station densities to control *W. auropunctata*. Such studies often rely on data from mark-capture and mark-release-recapture studies, and marking techniques for this species are under investigation (Montgomery et al. 2019).

Granular baits applied to the ground have been found to have little effect on arboreal ants in most situations. In Hawai`i, *W. auropunctata* nesting in tree canopies, palms, and tall foliage do not always forage on the ground and so some do not encounter the insecticidal bait (Souza et al. 2008, Taniguchi 2008, Montgomery et al. 2015). However, in Cairns, Australia, arboreal *W. auropunctata* appear to descend and forage on the ground at times depending on the availability of food resources in the canopy or foliage in which they reside (G. Morton personal communication). Additionally, the distance to the ground and weather are also factors likely to influence this. Therefore, the efficacy of bait applications on the ground may differ from one site to another. In areas where arboreal *W. auropunctata* do not forage on the ground, bait applications must be three-dimensional and include treatment of tree canopies and vegetation (Souza et al. 2008, Taniguchi 2008, Vanderwoude and Nadeau 2009, Vanderwoude et al. 2010) using a gel or paste bait. Gel bait formulations have the advantage over granules of adhering to vegetation and vertical surfaces, ensuring arboreal ants' access to the bait (Vanderwoude and Nadeau 2009, Vanderwoude et al. 2010).

Another issue is the weathering effects of sunlight, heat, and moisture on bait palatability and degradation. The corn grit carrier of granular baits quickly absorbs moisture from dew and rain making the bait soggy, reducing the oil content, and palatability becomes unpredictable (Banks et al. 1972, Hara et al. 2014, Oi et al. 2022). Oxidation of the soy oil food attractant resulting from heat, light, and humidity exposure also renders baits unpalatable (Markin and Hill 1971, Hara et al. 2014). This can occur from improper or prolonged storage of opened bait containers or after application in the field (M. Montgomery personal observation). Gel and paste baits are also susceptible to weathering. Although dew and light rain may help keep the bait moist and palatable, heavy rains wash the bait away and dry conditions result in desiccation. Additionally, some active ingredients, such as hydramethylnon, undergo rapid aqueous photolysis with a half-life of 42 min when exposed to light and water (Mallipudi 1986). In wet climates, such as windward Hawai`i where average annual rainfall may exceed 3,200 mm (Giambelluca et al. 2013, accessed 12 Oct 2021), there is a short window of opportunity for *W. auropunctata* to find, recruit to, feed on, and share the bait. Ensuring maximum attractiveness is maintained as long as possible and increasing chances for foragers to encounter the bait following broadcast applications is essential for achieving the highest treatment efficacy.

Finally, *W. auropunctata* appear to be more sensitive to certain active ingredients used in 'fire ant' baits. Insect growth regulators (IGRs), such as s-methoprene and pyriproxyfen, appear to be repellant to *W. auropunctata* (Hara et al. 2014, Montgomery et al. 2015). The inclusion of additional phagostimulants or adjuvants has been shown to effectively mask repellent substances, although this is likely only an option for homemade baits as commercial baits are ready-to-use products (Montgomery et al. 2015).

When site features, local climate, and chemical sensitivity are factored into the planning process for control operations, *W. auropunctata* can be effectively controlled using baits (Williams and Whelan 1992, Abedrabbo 1994, Ulloa-Chacón and Cherix 1994, Jourdan and Chazeau 2004, Causton et al. 2005, Vanderwoude et al. 2010, Cabral et al. 2012). Toxic (lethal) baits and IGR baits are equally effective for long-term control and management, but short-term results are drastically different. The use of toxic baits results in the rapid death of ants that ingest a lethal dose of the active ingredient, whereas IGRs are generally considered nonlethal and affect egg production, pupation, and development of reproductive and brood castes (Jourdan and Chazeau 2004; Cabral et al. 2012, 2017). Toxic bait usage results in rapid population knockdown immediately after application followed by a recovery period. Results from IGR bait applications do not show noticeable results immediately after application and instead a gradual population decline is observed over time and with repeated applications. When rapid population knockdown is desired, such as with preharvest treatments to protect harvesters, toxic baits are preferred. However, the nontoxic nature of IGR baits carry lower potential for ecological and nontarget impacts while not compromising long-term efficacy.

Nonchemical Control

When chemical control is either not effective or not desirable, such as for postharvest treatment of horticultural products including produce, cut flowers, and some nursery stock, nonchemical disinfestation methods are needed. Irradiation and hot water treatments have been tested against *W. auropunctata* and both are potentially effective phytosanitary procedures (Hara et al. 2011, Calcaterra et al. 2012). However, neither method is 100% effective and thus may not meet phytosanitary requirements (Hara et al. 2011, Calcaterra et al. 2012).

Biological Control

The parasitoid wasp *Orasema minutissima* is a common parasitoid of *W. auropunctata* throughout the Caribbean. Rather than seeking out *W. auropunctata*, *O. minutissima* oviposit in plant tissue, and emergent planidia (first instar larvae) are brought into the nest via phoretic attachment to a foraging worker or prey (Heraty 1994, Soto et al. 2010). Once inside the nest, they parasitize brood and produce cuticular hydrocarbons that mimic *W. auropunctata* brood leading to their acceptance within the nest. Although widespread and common throughout the Caribbean, parts of Central America, and northern South America, it is uncertain to what degree *O. minutissima* may aid in population control of *W. auropunctata* (Heraty 1994, Burks et al. 2018). The recent introduction and detection of *O. minutissima* on Hawai`i Island (Heraty et al. 2021), where *W. auropuncata* is widespread and a major pest, provides an opportunity to examine *O. minutssima* impacts on *W. auropunctata* over time.

Discussion

Wasmannia auropunctata is a truly fascinating species that has proven adaptable in the most surprising ways. From the unique reproductive systems (Fournier et al. 2005a) to their ability to invade a wide range of habitats and thermotolerance adaptability (Foucaud et al. 2013), *W. auropunctata*provides us with a glimpse of evolution in action. For example, clonality may have arisen to ensure successful establishment under the pressures of constant natural disturbances and the success of *W. auropunctata* in human modified habitats is a consequence of this adaptation. The specific type of clonal reproduction exhibited by *W. auropunctata* allows for the preservation of genotypes responsible for adaptations to specific ecological pressures, such as the expanded thermotolerance seen in Clad B (Chifflet et al. 2016, 2018; Coulin et al. 2019). What is not clear is whether other genetic adaptations are being preserved that influence the success of the different clades, haplogroups, or haplotypes.

The thermotolerance adaptations seen in 'Clade B' has allowed *W. auropunctata* to successfully invade Mediterranean climates previously believed to be unsuitable for the species (Rey et al. 2012; Chifflet et al. 2016, 2018; Coulin et al. 2019). Although rare, sexual reproduction has been documented in invasive clonal populations (Foucaud et al. 2006, Vonshak et al. 2009, Tindo et al. 2012). Could postinvasion sexual reproduction events lead to additional genetic adaptations? While this may be unlikely with the limited genetic diversity of invasive clonal populations, repeated introductions of different genotypes could lead to admixing and possibly the emergence of new adaptive phenotypes that may enhance its invasive potential. Alternately, genetic diversification might act as a regulating factor for invasive populations over time. The Caribbean invasion is believed to be the result of numerous introductions from Central and South America with evidence of genetic recombination and mutation events (Foucaud et al. 2010b). Given that *W. auropunctata* has been present in the region for over 100 yr, studying the Caribbean invasion could provide insight on the emergence of genetic adaptations of historical invasive *W. auropunctata* populations over time.

Wasmannia auropunctata is a serious pest ant throughout the world and is widely distributed, mostly in tropical and subtropical climates. Its ability to establish with low propagule pressure (Mikheyev et al. 2008) and to spread long-distances via human-mediated transport (Walsh et al. 2004, Mikheyev et al. 2008, Foucaud et al. 2010b) will undoubtedly allow this species to continue to spread at an alarming rate in the absence of strong biosecurity and prevention efforts. Once established, *W. auropunctata* is adept at avoiding conflict with competitor species while its population is low (Vonshak et al. 2012, Yitbarek et al. 2017). Infestations frequently go unnoticed for several years (Conant et al. 2007) and by the time a new infestation is detected, colony fragments have likely been inadvertently transported elsewhere. This is evident in Hawai`i, where new infestations on Hawai`i, Maui, Oahu, and Kaua`i islands continue to be detected despite over two decades of state-wide surveys, public outreach, and eradication attempts (Conant and Hirayama 2000, Null and Gundersen 2007, Vanderwoude et al. 2010, Vanderwoude et al. 2015).

Despite several studies investigating the relationship between *W. auropunctata* genetics, reproduction mode, and behavior (Foucaud et al. 2006, 2007, 2009, 2010a,b; Tindo et al. 2012; Rey et al. 2013b) our understanding is still limited and based on data collected from a select few locations. The biology and physiology associated with the ecological variegates and two clades highlight a plasticity rarely seen in nature. Could genetic adaptations be responsible for this plasticity be linked to specific haplogroups or haplotypes? It is possible that competitive, and thus invasion, potential may vary between clades, haplogroups, or haplotypes. It has been pointed out that exotic populations are unlikely to be traced back to their ancestral native population (Foucaud et al. 2010b). However, this may change with expanded sampling, phylogenetic analysis, and the pooling of genetic datasets. Understanding the driving forces, especially the relationships between ecological factors and genetic adaptations, behind biological and physiological shifts in *W. auropunctata* may elucidate how studying different populations could result in the occurrence of conflicting behavioral observations.

Understanding the driving forces behind biological and physiological shifts in *W. auropunctata* may also lead to the development of pesticide-free management tools and methods. For instance, if environmental factors can induce a physiological shift from nondominance to dominance, could the opposite also be true? Could RNAi target genes responsible for the physiological shift between nondominance/dominance? Additionally, rare occurrences of invasion contractions have been documented and it's unclear what led to the contractions (Lester and Gruber 2016; Mbenoun Masse et al. 2019b, 2021). Long term studies looking at expansion and contraction patterns may identify the circumstances necessary for a contraction to occur. If those circumstances were identified, would we be able to artificially induce an invasion contraction?

Interestingly, despite being a known invasive tramp ant and pest since the late 1800's, *W. auropunctata* garnered little attention from researchers and invasive species specialists until the early 2000s. In fact, the number of research publications focusing on *W. auropunctata* between 2000 and 2010 was almost double that published during the previous 80 yr. The importance of *W. auropunctata* as an invasive tramp ant was likely overshadowed by other pest ant species of importance such as *S. invicta* and *L. humile* and interest in it as a research subject was slow to develop. It is also possible that despite knowing the potential impacts of this species, researchers and invasive species specialists have underestimated its distribution potential and adaptability, thus assuming it to be a problem limited to the tropics and not relevant to cooler climates. Regardless, the delay in research focus has slowed the compilation of knowledge and understanding necessary to develop effective prevention and control methods. In this review, we have identified numerous knowledge gaps spanning distribution and status, life history, impacts, biosecurity, chemical ecology, and management. As our knowledge base on this species grows and with technological advancements, new questions arise. We encourage a greater research focus on this species in line with its global importance as an invasive species. The case of *W. auropunctata* not only highlights the importance of species-specific understanding for management and control, but also for effective biosecurity and prevention of accidental new species introductions.

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Data Availability

Data collected during and used for this project may be available upon reasonable request.

Author Contributions

Writing of the original draft was done by Michelle Montgomery and all other authors contributed to revising and editing all subsequent drafts. The final draft has been approved by all authors.

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