OXFORD

Non-native and Invasive *Nylanderia* Crazy Ants (Hymenoptera: Formicidae) of the World: Integrating Genomics to Enhance Taxonomic Preparedness

Jason L. Williams and Andrea Lucky[1]

Entomology and Nematology Department, University of Florida, 1881 Natural Area Drive, Gainesville, FL 32611-0620 and [1]Corresponding author, e-mail: alucky@ufl.edu

Abstract

Invasive species have devastating economic and ecological impacts worldwide, but proactive monitoring programs are rare on the global stage. By definition, tramp ants are associated with disturbance and human-mediated dispersal, making them especially concerning invasive threats. A proactive—rather than reactive—approach to monitoring for, preventing, and managing invasive species depends on taxonomic preparedness, which enables rapid and accurate identification. Emerging tools and technologies, including genomic barcoding and interactive online keys, can aid in species delimitation and diagnosis. However, resolving tramp species' identities remains the fundamental first step in invasive species management because diagnostic tools cannot be developed and disseminated until species names are stable. Diagnosis of morphologically difficult species requires basic knowledge of species boundaries, biogeography, and phylogenetic relationships. This review comprehensively synthesizes information available for 15 known and five potential tramp ant species in *Nylanderia* (Emery) (Hymenoptera: Formicidae): a globally distributed genus of over 130 described species, many of which are only diagnosable by subtle morphological characters. *Nylanderia* records were drawn from published literature, specimen databases, and museum collections to compile known distributions, biology, natural history, and taxonomy for each species. We review existing resources for visualizing known geographic ranges and high-resolution images of ants globally and encourage the use of these types of tools in support of invasive species diagnosis and distribution tracking. Finally, we discuss how taxonomic and life history information can be used synergistically with genomic and digital technology to develop tools for identification of these, and other emerging invasive insect species.

Key words: invasive species, tramp ant, taxonomy, management, misidentification

Invasive species are non-native organisms that threaten human health and safety, cause economic damage, and upset natural ecosystems. Executive Order No. 13751 (2016 defines invasive species as follows: 'With regard to a particular ecosystem, a non-native organism whose introduction causes or is likely to cause economic or environmental harm, or harm to human, animal, or plant health'. Importantly, the movement of most invasive species to areas where they are not native is the result of accidental or deliberate human transportation (Lowe et al. 2000, Pimentel et al. 2005). Proactive monitoring programs are the most cost-effective way to manage invasive species because they prevent invasion from occurring in the first place (Myers et al. 2000). These measures rely on strong foundational taxonomy because timely and accurate diagnosis of invasive species must happen before it is too late for containment and eradication. Taxonomic preparedness facilitates rapid invasive

species identification during the early stages of invasion, modeling the spread of invasive species, and the implementation of integrative pest management strategies such as the use of biological control agents (Buffington et al. 2018). Predictive models of invasive species spread rely on the ability to match species to their distributions, interactions with biotic and abiotic factors, and behavioral dominance over native species (Bertelsmeier et al. 2015).

Of the more than 16,000 described ant (Hymenoptera: Formicidae) species and subspecies worldwide (AntWeb 2019), more than 240 have been reported outside of their native ranges, having been dispersed along global trade routes in recent human history (Bertelsmeier et al. 2017). Invasive ants are known to disrupt native ant and invertebrate communities (Holway 1999, Holway et al. 2002, Le Breton et al. 2003, Abbott 2005, Hoffmann and Parr 2008), mutualisms between seed-dispersing ants and plants (Ness and

Bronstein 2004, Rodriguez-Cabal et al. 2012), and native mammal, bird, amphibian, and reptile populations (Allen et al. 2004, Abbott 2005, Meyers and Gold 2008), including endemic tortoises in the Galapagos (Wauters et al. 2018). The dearth of information about many invasive ant species' taxonomy, distribution, biology, and natural history makes it challenging to recognize these species in areas where they have become newly established, and complicates assessment of their economic and ecological threat, all of which are necessary to curtail further spread. The challenge of recognizing invasive ant species can be attributed to factors including the high number and ubiquity of ant species distributed worldwide, the tendency for adventive species to be dispersed by humans, and unresolved taxonomic boundaries between closely related species that have few to no morphological characters useful for identification.

'Tramp' ants are defined as species closely associated with humans and which spread easily via human-mediated dispersal (Hölldobler and Wilson 1990, Passera 1994). Repeated arrivals of a non-native species increase genetic variability and exert propagule pressure, which facilitates the establishment of species that exhibit life history traits associated with invasion such as generalist omnivory, polygyny, large colony size, unicoloniality, and clonal reproduction (Suarez et al. 2005, Suarez and Tsutsui 2008). Most non-native ant arrivals are consequences of commercial activities such as importation and exportation of goods, movement of soil or plant material (e.g., ornamental, fruits, and vegetables), and the pet trade, all of which involve long-distance transportation of biological materials (Lowe et al. 2000). The range expansion of tramp and invasive ants, many of which thrive in warm and humid environments, is projected to increase as weather patterns change due to anthropogenic activity (Bertelsmeier et al. 2016). Furthermore, the increased frequency of unpredictable weather events such as hurricanes, flash floods, and wildfires may create environmental disturbances similar to those which invasive ant species have become adapted in their native ranges (Lee and Gelembiuk 2008).

Many invasive ants are well-adapted to environments characterized by regular disturbance. For example, non-native populations of the Argentine ant (*Linepithema humile*) (Mayr) (Hymenoptera: Formicidae) and the red imported fire ant (*Solenopsis invicta*) (Buren) originated in an area of northeastern Argentina subject to frequent large-scale floods (Lee and Gelembiuk 2008). These two species are among the most studied of the world's invasive ants and are notorious in part because their economic and ecological impacts are understood. The impacts of other, less well-characterized ant species may turn out to be equally important. For example, lesser-known and taxonomically challenging invasive species such as the Asian needle ant (*Brachyponera chinensis*) (Emery) and the tawny crazy ant (*Nylanderia fulva*) (Mayr) are only recently understood to have disastrous impacts on biodiversity in places where they have become established (Rodriguez-Cabal et al. 2012, Eyer et al. 2018, Guénard et al. 2018). Like the tawny crazy ant from central South America, several other *Nylanderia* species are also adapted to open, disturbed, and marginal habitats such as those found on Indo-Pacific islands (Matos-Maraví et al. 2018). Because *Nylanderia* is a large, taxonomically difficult genus with over a dozen tramp species that are frequently transported across the globe by humans, this is a group that merits serious attention.

The Ant Genus *Nylanderia* (Emery)

The subgenus *Nylanderia* was elevated to full genus status by LaPolla et al. (2010), but most accounts in the literature prior to 2010 refer to *Nylanderia* species as *Paratrechina*. This is important to keep in mind when seeking information in the older literature, as most *Nylanderia* species—especially those originally described more than a decade ago—were initially placed in closely related genera such as *Paratrechina* and *Prenolepis*, among others. *Nylanderia* is a major component of native ant communities worldwide. With more than 130 described species and subspecies (and likely hundreds more undescribed) on six continents, it is among the top five most frequently collected ant genera in leaf litter samples around the world (Ward 2000). Despite their ubiquity, the basic natural history of most species is undocumented. Among the better known species workers are small to medium-sized (1.0–4.0 mm) and monomorphic, and colonies make polydomous nests in soil, leaf litter, or rotting logs (Lapolla et al. 2011a). *Nylanderia* are typically generalist omnivores and foragers recruit very quickly to protein-rich (e.g., dead invertebrates) and sugary resources, including the honeydew secretions of plant-sucking hemipterans (i.e., scale insects, mealybugs, and aphids). Although they are quick to discover and efficient at exploiting resources, *Nylanderia* workers can be poor defenders of their spoils, losing them to other more dominant ant species (Lapolla et al. 2011a).

This review summarizes all publications about the 20 *Nylanderia* species that fulfill one or more of the following conditions: 1) established outside of its native range ('established, non-native'); (2) has been found outside of its native range, but have not become established in those recorded localities ('non-established'); (3) have records outside their native range, but those records are doubtful ('dubious'); and (4) have non-native records that await verification ('unverified'). We highlight insights, research questions, and gaps in knowledge that are roadblocks to stemming the spread of species with high economic and environmental destructive potential. This synthesis establishes the foundational information critical for addressing the impending threats posed by *Nylanderia* invasions and for improving taxonomy and identification tools. Finally, we discuss how high-throughput genomic data are important for invasive species delimitation, identification, and management, and outline how genomic tools are essential across disciplines—in integrative taxonomy and systematics as well as integrated pest management.

Materials and Methods

We conducted a comprehensive literature review to synthesize information about the distributions, biology, natural history, identification, and potentially destructive behavior of *Nylanderia* species that have become established, intercepted, misidentified, or have records that await verification outside of their native ranges. Our review began with an extensive search of distribution records for all 136 valid, extant *Nylanderia* species (109) and subspecies (27) (AntWeb 2019). Information available from AntMaps.org (Janicki et al. 2016) and the Global Ant Biodiversity Informatics Database (GABI) project (Guénard et al. 2017) was particularly useful, as the species distribution records are subdivided into five distinct categories: 'native', 'exotic', 'indoor introduced', 'needs verification', and 'dubious'. We compiled a list of every *Nylanderia* species or subspecies with one or more non-native records available and aggregated literature records cited on AntMaps.org (Janicki et al. 2016) as well as those returned by searches on the Web of Science database (https://www.webofknowledge.com/ [Accessed 4 January 2019]) and Google Scholar (https://scholar.google.com/ [Accessed 4 January 2019]). We conducted searches using the current valid name for each species as well as synonyms. Distribution records for species were also reviewed from specimens deposited at

the Smithsonian Institution National Museum of Natural History (USNM), Towson University Biodiversity Center (TUBC), and the Florida State Collection of Arthropods (FSCA).

Results

Synopsis of Established, Non-native Species

The list that follows includes all *Nylanderia* species with documented established populations outside of their native ranges:

Nylanderia amia (Forel 1913a)
Nylanderia bourbonica (Forel 1886)
    =*Nylanderia bengalensis* (Forel 1894)
    =*Nylanderia bourbonica hawaiensis* (Forel 1899)
    =*Nylanderia bourbonica skottsbergi* (Wheeler 1922)
    Subspecies:
        Nylanderia bourbonica farquharensis (Forel 1907a)
        Nylanderia bourbonica ngasiyana (Forel 1907b)
Nylanderia clandestina (Mayr 1870)
Nylanderia flavipes (F. Smith 1874)
Nylanderia fulva (Mayr 1862)
    =*Nylanderia fulva fumata* (Forel 1909)
    Subspecies:
        Nylanderia fulva biolleyi (Forel 1908)
        Nylanderia fulva cubana (Santschi 1930)
        Nylanderia fulva fumatipennis (Forel 1915)
        Nylanderia fulva incisa (Forel 1908)
        Nylanderia fulva longiscapa (Forel 1908)
        Nylanderia fulva nesiotis (Wheeler 1919)
Nylanderia glabrior (Forel 1902)
Nylanderia guatemalensis (Forel 1885)
    =*Nylanderia vividula antillana* (Forel 1893)
    Subspecies:
        Nylanderia guatemalensis cocoensis (Forel 1885)
        Nylanderia guatemalensis edenensis (Linsley and Usinger 1966)
        Nylanderia guatemalensis itinerans (Forel 1901a)
Nylanderia jaegerskioeldi (Mayr 1904)
    =*Nylanderia jaegerskioeldi borcardi* (Santschi 1908)
    =*Nylanderia traegaordhi* (Forel 1904)
    =*Nylanderia weissi* (Santschi 1911)
    =*Nylanderia weissi nimba* (Bernard 1953)
    =*Nylanderia zelotypa* (Santschi 1915)
Nylanderia pubens (Forel 1893)
Nylanderia steinheili (Forel 1893)
    Subspecies:
        Nylanderia steinheili minuta (Forel 1893) (unresolved junior primary homonym of *Prenolepis imparis minuta* Emery 1893 [Bolton 2019])
Nylanderia tasmaniensis (Forel 1913b)
Nylanderia vaga (Forel 1901b)
    =*Nylanderia vaga crassipilis* (Santschi 1928a)
    =*Nylanderia vaga irritans* (Santschi 1928b)
Nylanderia vividula (Nylander 1846)
    =*Nylanderia kincaidi* (Wheeler 1906)
    =*Nylanderia picea* (Buckley 1866)
    =*Nylanderia vividula mjobergi* (Forel 1908)
    Subspecies:
        Nylanderia vividula australis (Santschi 1929)

Synopsis of Non-established, Non-native Species

The list that follows includes all species that have records outside of their native ranges, but that do not have established populations in places where they are not native:

Nylanderia braueri (Mayr 1868)
    Subspecies:
        Nylanderia braueri donisthorpei (Forel 1908)
Nylanderia sharpii (Forel 1899)

Synopsis of Species With Dubious or Unverified Records

The list that follows includes all species that have limited non-native records, but these are either doubtful or unconfirmed:

Nylanderia obscura (Mayr 1862)
    Subspecies:
        Nylanderia obscura bismarckensis (Forel 1901b)
        Nylanderia obscura celebensis (Karavaiev 1933)
        Nylanderia obscura minor (Karavaiev 1933)
        Nylanderia obscura papuana (Forel 1901b)
Nylanderia silvestrii (Emery 1906)
    Subspecies:
        Nylanderia silvestrii kuenzleri (Forel 1909)
Nylanderia stigmatica (Mann 1919)
Nylanderia teranishii (Santschi 1937)
Nylanderia vitiensis (Mann 1921)

Species Summaries

Nylanderia amia (Forel 1913a)

Native Range

Nylanderia amia occurs in subtropical and tropical Southeast Asia. Records are known from Taiwan (Terayama 1999), and Guangdong and Fujian Province in China (Wheeler 1930, Ran and Zhou 2013).

Non-native Range

This species is also established in Japan and commonly arrives at Japanese ports, including Tokyo Bay and the Kagoshima Prefecture (Harada 2013, Sakamoto et al. 2016).

Similar Species

Nylanderia amia most strongly resembles and was once considered a subspecies of *N. bourbonica,* until Terayama (1999) elevated it to species status. This species is most likely to be confused with *N. bourbonica*. Specimens of *N. amia* from Taiwan were noted by Trager (1984) to be distinct from *N. bourbonica* in color, size, head width, pubescence, and genitalic structure, though the differences in these traits between the two species were not discussed in detail. In his original description, Forel (1913a) offered the following characters to distinguish *N. amia* from *N. bourbonica*: 1) The head of *N. amia* is slightly longer than broad and does not have a straight posterior margin; and 2) the pubescence is less dense and the standing macrosetae are slightly shorter. A taxonomic revision of Asian *Nylanderia* species is needed to provide a better delimitation of the morphological boundaries between these and other species in the region.

Pest Status and Potential Threat

Although *N. amia* is not native to Japan, there is no evidence that this species is an economically important pest or has adverse ecological impact in its non-native range.

Use in Biological Control

Suenaga (2017) demonstrated that *N. amia* may be used as a biocontrol agent to remove eggs of two moth pests—*Aedia leucomelas* (Linnaeus) and *Spodoptera litura* (Fabricius) (Lepidoptera: Noctuidae)—from sweet potato, *Ipomoea batatas*. Responsible use of this species for biological control would require a better understanding of its biology, interactions with other species (e.g., whether it would also tend to pestiferous plant-sucking insects), and what other unintended effects its application for control could have.

Nylanderia bourbonica (Forel 1886)

Native Range

Nylanderia bourbonica occurs in subtropical and tropical areas of Southern and Southeast Asia. Occurrences are recorded throughout most of China, Vietnam, Myanmar, Bangladesh, Sri Lanka, the southern tip of India, and the Philippines. Two subspecies are known from islands off east Africa. The subspecies *N. bourbonica farquharensis* and *N. bourbonica ngasiyana*—known only from the Seychelles and Comoros respectively—are questionable. If they are indeed native or endemic to these places, they may have been incorrectly described as subspecies of *N. bourbonica*.

Non-native Range

Nylanderia bourbonica is the most widespread of the genus and appears to have been moving across the globe as early as the 1800s. Populations have become established in subtropical and tropical areas worldwide, including those in Australia, Africa, and North America, as well as islands in the South Pacific and the Caribbean. The original description was from an established non-native population on the French island of Réunion, off the east coast of Madagascar (Forel 1886). One record also exists for Saint Helena, Ascension and Tristan da Cunha in the South Atlantic (Wetterer et al. 2007a). In the United States, this species is very common across peninsular Florida. In a list of 'urban pest ants' of peninsular Florida, Klotz et al. (1995) rank *N. bourbonica* as the eighth most abundant pest species. *Nylanderia bourbonica* is a relatively old invader of Florida, with specimens dating back to as early as 1924 in the state (Deyrup 2016). This species has also been reported in Italy (Jucker et al. 2008), the Netherlands (Boer and Vierbergen 2008), and the United Kingdom (Borowiec 2014) in Europe, Quebec in Canada (Francoeur 2010), Missouri and Illinois (Guénard et al. 2017) in the United States, and in New Zealand (Ward et al. 2006). However, no established populations are known from any of these places, probably because of their colder climates. This species is established on multiple continents, but in only a few countries per continent (Bertelsmeier et al. 2017).

Similar Species

Distinguishing *N. bourbonica* from *N. vaga* is particularly challenging in that the two are widely distributed and are morphologically very similar, with strong intraspecific variation observed among colonies of each species. However, *N. bourbonica* workers are not known to have strong variation in color and are all dark brown, while *N. vaga* is known to range from pale yellow-brown to black (Sarnat and Economo 2012). Although both species have dense pubescence on the dorsal surface of the mesosoma, *N. bourbonica* also has pubescence on the mesopleuron and *N. vaga* does not (Sarnat

and Economo 2012). Workers of *N. bourbonica* are also relatively large compared to most other *Nylanderia* species, including *N. vaga* (Wilson and Taylor 1967). Additional distinguishing characters are still needed to clarify the taxonomy of these morphologically variable species and facilitate their diagnosis. *Nylanderia bourbonica* is also very similar to *N. amia*, but the head of *N. bourbonica* is approximately equal in width and length with a straight posterior margin, and the body overall has denser pubescence and slightly longer macrosetae.

Pest Status and Potential Threat

Although this tramp ant is very widespread, it is not known to be a serious pest. *Nylanderia bourbonica* is best described as a nuisance or 'picnic pest' in outdoor eating areas and seldom enters buildings in large numbers (Deyrup et al. 2000), probably only doing so to seek shelter from cold weather (Trager 1984). Bananas from Hawai'i have been known to suffer superficial, cosmetic damage from formic acid secretions released by *N. bourbonica* (Nelson and Taniguchi 2012). While damaged bananas may not be harmful to consumers, the blemishes could make them less marketable.

Nylanderia braueri (Mayr 1868)

Native Range

Nylanderia braueri Occurs in the forests of New South Wales, Australia (Taylor et al. 1985).

Non-native Range

The two specimens in the type series for the subspecies *N. braueri donisthorpei* (Forel 1908) are not from the native range, but were instead collected from Kew Gardens, London, England. Currently, no populations are known to be established outside of the native range of this species.

Taxonomic Status

Based upon review of the original description (Forel 1908) and examination of images of the type series (AntWeb CASENT0903129, CASENT0911015), the subspecies *N. braueri donisthorpei* appears to be a synonym of *N. braueri* and may be treated as such when the *Nylanderia* of Australasia are revised. In his description, Forel himself admitted that these two named entities are morphologically identical.

Pest Status and Potential Threat

Although the type material was described from a non-native population in London, England, there is no evidence that this species is a pest or poses any threat as an invasive species.

Nylanderia clandestina (Mayr 1870)

Native Range

Nylanderia clandestina occurs in subtropical and tropical Southeast Asia, with records in Vietnam (Forel 1911), Malaysia (Overbeck 1924), and Java (Chapman and Capco 1951).

Non-native Range

Nylanderia clandestina is also found on the Caroline and Marshall Islands in the Pacific Ocean (Clouse 2007). This species is spread regionally among islands adjacent to its native range (Bertelsmeier et al. 2017).

Pest Status and Potential Threat

No records from the literature indicate whether *N. clandestina* is a pest or has adverse ecological effects in areas where it is not

native. However, *N. clandestina* is one of several known ant associates of a facultatively myrmecophilous lycaenid butterfly, *Lampides boeticus* (Fiedler 2006, Obregon-Romero and Gil-T 2011), which is a known pest to legume crops including fava beans (*Vicia faba*) and garden peas (*Pisum sativum*) (Lohman et al. 2008). *Lampides boeticus* ranges across Europe, Africa, South and Southeast Asia, and Australia. Ant associates of myrmecophiles have been known to indirectly abet plant damage (Hosseini et al. 2017), and ant–caterpillar interactions could promote diet breadth and host-range evolution in lycaenids (Forister et al. 2011), amplifying the economic impact of associated pest species.

Nylanderia flavipes (F. Smith 1874)
Native Range
Nylanderia flavipes occurs in temperate deciduous forests of China, South Korea, North Korea, and Japan.

Non-native Range
In the United States this species was first collected outside its native range in a Philadelphia, Pennsylvania park in 1939, though it went undiagnosed for over four decades. Trager (1984) at first thought that the Philadelphia specimens—along with others from Pittsburgh and Long Island—were of a northern variant of *N. faisonensis* but determined that they were *N. flavipes*. Since its arrival to the United States, *N. flavipes* has become established as a dominant urban ant in the northeastern part of the country and is one of the most common ants on Broadway in New York City (Pećarević et al. 2010). Records also exist for Boston, Massachusetts (Clark et al. 2011), Washington, DC, and Cleveland, Ohio (Ivanov and Milligan 2008). Its range extends as far west as Indiana (Carroll 2011) and as far south as South Carolina (Janicki et al. 2016). While this species is not established in Northern Europe, reports exist for plant product inspection interceptions in the Netherlands (Boer and Vierbergen 2008) and a colony within tulip bulbs in Kew Gardens, London, England (Donisthorpe 1908).

There are two hypotheses as to how this species arrived and became established in the United States. Fisher and Cover (2007) posited that *N. flavipes*, along with another ant species, *Vollenhovia emeryi*, may have come from Japan in a shipment of 3,020 cherry trees gifted to the United States by the Japanese government in 1912. The trees arrived in Washington, DC and were planted around the Tidal Basin. Another scenario was proposed by Trager (1984), who speculated that *N. flavipes* could have entered the country in potted plant materials or mushroom-growing logs carried by Chinese or Japanese immigrants in the early 20th century. The latter seems more likely, as Trager also noted that the American population probably originated from China based on similarity in color, as Japanese specimens are distinctly darker. Although this species is found on at least two continents, it has a limited regional distribution and is spread mainly among adjacent countries (Bertelsmeier et al. 2017).

Dubious Records
Possible misidentifications exist for records from rice fields and some other unreported areas in the Philippines (Way et al. 1998), as the low latitude and open habitat are uncharacteristic for the species (Wetterer 2011). Similarly, records from Taiwan and Sumatra are also doubtful, as *N. flavipes* is unlikely to persist in hot, tropical climates. A misidentified specimen on the island of Niue in the South Pacific was determined to be *N. vaga* (Wetterer 2006). All confirmed established, non-native records of *N. flavipes* are in mainland, temperate areas and there is no evidence that this species is common on islands or in coastal habitats.

Espadaler and Collingwood (2001) reported a population in Barcelona, Spain that was later determined to instead be *N. vividula* (Gomez and Espadaler 2006). In the Middle East, there are records from Iran, United Arab Emirates, Oman, and Yemen (Collingwood and Agosti 1996, Collingwood et al. 1997, Collingwood and van Harten 2001, Dezhakam and Soleyman-Nejadian 2002, Paknia et al. 2008). However, based on this species not being known to tolerate the arid climate of these regions, misidentification of these specimens is likely (Ivanov and Milligan 2008, Wetterer 2011). There are also reports of an established population of *N. flavipes* in the urban area of Ciudad Victoria, Mexico (Rosas-Mejía and Vásquez-Bolaños 2013), but this could be another case of misidentification—presumably of *N. vividula*—and warrants further investigation.

Similar Species
This species is most often confused with *N. faisonensis* and *N. vividula* from the Nearctic, though only the latter of the two is also found outside the United States. *Nylanderia flavipes* is best distinguished from both of these by its small, but visible ocelli, arched mesosoma, and the overall more yellowish hue of the body, legs, and sometimes the anterior-most part of the gaster (Trager 1984). In contrast, both *N. faisonensis* and *N. vividula* tend to be dark brown, with the mesosoma sometimes lighter brown than the head and gaster. *Nylanderia faisonensis* has tan to whitish meso- and metacoxae, relatively longer legs and antennal scapes, and a relatively narrower head. *Nylanderia vividula* has much sparser cephalic pubescence than both *N. flavipes* and *N. faisonensis*. *Nylanderia flavipes* is considered the Asian cognate of *N. faisonensis*, as the two share a number of morphological similarities and both specifically inhabit moist deciduous forests in their native ranges (Trager 1984). In this regard, it is notable that *N. flavipes* has spread across the northern part the range of *N. faisonensis* but may be excluded by *N. faisonensis* in more southern areas, where *N. flavipes* could probably otherwise thrive.

Biology and Natural History
Colonies are usually small and have, on average, approximately 100 workers. This species is both monogynous and polydomous (Ichinose 1986). Colonies are known to frequently move and establish multiple nest sites, and sometimes colony fission occurs when seasonal change in nestmate recognition causes satellite sites to become independent (Ichinose 1991).

Pest Status and Potential Threat
Despite its prevalence in North America, this species is not considered a pest. Its impact on native species is unknown but thought to be minimal. In urban areas it appears to thrive most in parks, gardens, and medians with planted trees (Pećarević et al. 2010, Wetterer 2011). The southward expansion of its range is unlikely because of its preference for temperate woodland habitat and possible exclusion by *N. faisonensis* (Trager 1984). Tending of a coccid pest of citrus (*Nipaecoccus viridis*) by this species has been reported from Khuzestan, Iran (Dezhakam and Soleyman-Nejadian 2002).

Nylanderia fulva (Mayr 1862)
Native Range
Nylanderia fulva ranges across most of South America, as far south as Buenos Aires, Argentina and northward into Bolivia and Brazil (up to Mato Grosso and Bahia) in the central part of the continent. There are six additional subspecies: 1) *N. fulva biolleyi* in Sao Paulo, Brazil; 2) *N. fulva cubana* in Cuba and Costa Rica;

3) *N. fulva fumatipennis* in Salta, Argentina and Santa Catarina, Brazil; 4) *N. fulva incisa* in Costa Rica; 5) *N. fulva longiscapa* in Rio de Janeiro, Brazil; and 6) *N. fulva nesiotis* in the Galapagos.

Non-native Range

Records of this species also exist for Colombia, Costa Rica, Cuba, Dominican Republic, Galapagos Islands, Haiti, Jamaica, Lesser Antilles, Mexico, Puerto Rico, and the United States. The first known record of *N. fulva* in the United States was in Brownsville, Texas in 1938 (Trager 1984). The earliest known record of this species as a pest may have been in a hospital in Miami, Florida in 1990; an infestation that was originally attributed to *N. pubens* (Klotz et al. 1995). Without any specimens available it is difficult to confirm which species was responsible, but the described behavior implicates *N. fulva*. *Nylanderia fulva* first became established in Houston, Texas, United States in 2002 but was named as *N.* sp. nr. *pubens* (Meyers and Gold 2008). The correct name of this invasive ant was later determined by Gotzek et al. (2012), a decade after its first confirmed record in the United States. By then it had already spread across the Gulf Coast to Florida. It is likely that this species has arrived at ports of entry multiple times independently, and possible routes of entry include the ports of Houston, Mobile, Jacksonville, and Savannah. Niche models have indicated that other areas of high climatic suitability for this species include Hawai'i, central Africa, eastern Madagascar, Southeast Asia, eastern Australia, and northern parts of New Zealand (Kumar et al. 2015). This species has a regional distribution is spread mainly among adjacent countries (Bertelsmeier et al. 2017).

Dubious Records

Bernard (1950) reported a non-native population of *N. fulva*—or at least a close relative—in the park of Santa Lucia along the French Riviera, west of Saint-Raphael, France. This population was first noticed in 1939, when it cohabited the park with around eight other ant species and consisted of at most ten percent of the total ant population. By 1950 the population reached swarm status and had eliminated all other ants in the park, including the Argentine ant, *Linepithema humile*. Unfortunately, Casevitz-Weulersse and Galkowski (2009) were unable to verify these reports, as specimen records do not exist in the literature and no such specimens could be found in the Bernard collection. No other citations exist for this population, which appears to have since died out. The subspecies *N. fulva nesiotis* has dubious records in Ecuador (Fernández and Sendoya 2004).

Similar Species

The workers and queens of this species are virtually indistinguishable from those of *N. pubens*. Currently, diagnosis is only possible by comparing male genitalia of these two species (Trager 1984, Gotzek et al. 2012). *Nylanderia fulva* males have parameres that are less sclerotized and more elongate, tapered, and triangular in profile view, and with fewer macrosetae arranged irregularly on the paramere margins. In contrast, the parameres of *N. pubens* are more sclerotized and more rounded in profile, with dense, long macrosetae that are arranged in a fan-like configuration. In cases where a male specimen is not available, observation of nesting and behavioral characteristics may distinguish these species. *Nylanderia fulva*, at least in its invaded range, makes its presence known by the way it blankets the environment with massive numbers of workers, which are sometimes accompanied by many queens. Invading populations of *N. fulva* often reach

extreme densities that suddenly die off after about 10 yr, in a pattern that has been called 'boom and bust' (Wetterer et al. 2014). *Nylanderia fulva* and *N. pubens* appear to be sympatric in the Caribbean and possibly southern Florida in the United States, though the last known record of *N. pubens* in southern Florida is from 1994. It is not known whether it persists there today (Gotzek et al. 2012).

Biology and Natural History

Colonies are polygynous and polydomous, and invading populations in the southeastern United States are unicolonial due to a genetic bottleneck after invasion (Eyer et al. 2018). *Nylanderia fulva* is unlike any other *Nylanderia* species in that colonies (at least in areas where it is not native) reproduce by fission, which is one of several life history traits likely to have contributed to its invasion. Established populations often produce very high densities of individuals that cover the ground surface. Colonies usually establish nests in preexisting cavities rather than by excavating soil. These cavities may either be the abandoned or conquered nests of other ant species and arthropods, or in debris on the surface of the soil (LeBrun et al. 2013). Inadvertent transport by humans is facilitated by this behavior, as colonies are also known to nest in objects such as potted plants (e.g., ornamentals) or garbage that may be relocated.

High similarity in heterozygosity between queens and workers indicates that both castes are probably produced through classic sexual reproduction (Eyer et al. 2018). Nuptial flight activity was recently described by Wang et al. (2016). Although males fly throughout the year, they do not reach peak activity until summer. Alate queens are produced en masse once a year in late summer but are not known to fly. The queens may instead use pheromonal cues to attract the flying males.

Interactions with the red imported fire ant (*Solenopsis invicta*) may have also promoted the spread of *N. fulva* across the southeastern United States. These two species have similar native ranges and have been natural enemies since before their invasions of North America (Kronauer 2014). Although the workers of *N. fulva* are smaller and will lose in one-on-one interactions, they frequently outnumber those of *S. invicta* and are adept at displacing fire ant populations (LeBrun et al. 2013) in part due to their ability to simultaneously detoxify fire ant venom and kill fire ants by secreting large quantities formic acid (Chen et al. 2013).

In addition to displacing invasive species such as *S. invicta*, non-native *N. fulva* populations also have negative impacts on the biodiversity of native wildlife, including vertebrates such as small mammals, reptiles, and ground-nesting birds (LeBrun et al. 2013). Endangered species like the Attwater's prairie chicken may be threatened by the spread of *N. fulva* (Meyers and Gold 2008). Although the effects of *N. fulva* on native wildlife are apparent, colonies may have difficulty remaining established for extended periods of time.

Pest Status and Potential Threat

In addition to the adverse ecological impacts outlined above, *N. fulva* invasions also have severe agroeconomic impacts. Adverse effects were first seen in Colombia as early as the 1940s, where *N. fulva* was intentionally introduced as a biological control agent against leaf-cutting ants (*Atta* spp.) and venomous snakes (Zenner-Polania 1990), but then became a serious pest in orchards due to its mutualistic association with coccids (Campos-Farinha and Zorzenon 2005). On the island of St. Croix, locals blamed *N. fulva* for serious damage to crops (e.g., coconuts) through tending hemipteran pests (Wetterer and Keularts 2008).

Livestock and zoo animals confined by fences and cages or restrained by tethers are incapable of escaping swarms of ants. While *N. fulva* cannot sting, colonies reach such high densities that animals—including rabbits, chickens, and even cattle—may suffer irritation from biting and formic acid secretions, incur injuries such as blindness, or asphyxiate from the sheer number of ants occluding their airways (Zenner-Polania 1990, Wetterer and Keularts 2008). Attacks on domestic and zoo animals may result in either mortality or expensive veterinary bills. Honey bee colonies in Texas, United States have also been raided by *N. fulva*, which eat the bee larvae and use the hives as their own nests (Harmon 2009).

An infestation at the Jacksonville Zoo and Gardens in Jacksonville, Florida, United States has been ongoing since as early as the late 1990s, where the ants have been known to be a nuisance to visitors and animals, and at one point reached high enough densities to render the zoo train inoperable due to the volume of ants on the tracks (Meyers and Gold 2008). Infestations have also been responsible for power outages and expensive damage to electronics, as colonies have been known to nest in electrical equipment and cause electrical shorts. Meyers and Gold (2008) described several rolling power outages in Deer Park, Texas, United States due to high populations of *N. fulva*, and an infestation of the Johnson Space Center in Houston, which caused concerns for both human safety and potential loss of scientific data.

Biological Control

Two potential biocontrol agents have been proposed for management of *N. fulva*. The first to be described is a microsporidian parasite (*Myrmecomorba nylanderiae*) that affects all life stages, causes reduced melanization and abdominal distention in adults, and is transovarially transmitted (Plowes et al. 2015). The second to be described is a single-stranded RNA virus called *Nylanderia fulva virus I* (NfV-1) and is only known to be spread by horizontal transmission (Valles et al. 2016a).

Nylanderia glabrior (Forel 1902)

Native Range

Nylanderia glabrior occurs across Australia and some nearby Pacific Islands, including New Guinea, Fiji, Caroline Islands, Solomon Islands, Lord Howe Island, and Norfolk Island.

Non-native Range

This species has becomeestablished in New Zealand and Pacific Islands farther east, including the Samoan Islands and Society Islands.

Similar Species

Forel (1902) noted that workers of *N. glabrior* are nearly identical to those of *N. rosae* in Australia and that the two species can only be distinguished by the male genitalia. In the Pacific islands, *Nylanderia glabrior* is most similar to *N. vaga* and *N. vitiensis*. This species can be distinguished from *N. vaga* by its relatively smaller eye size (<35 facets per eye) and the absence of pubescence on the first gastral tergite. *Nylanderia vitiensis* is considered endemic to Fiji, has smaller eyes (<10 facets), and is pale yellow-brown, while *N. glabrior* is darker brown in overall color (Sarnat and Economo 2012).

Pest Status and Potential Threat

There is no evidence that this species is a pest or poses any threat as an invasive species.

Nylanderia guatemalensis (Forel 1885)

Native Range

This species ranges as far south as Parana, Brazil in central South America, and into southern portions of Central America. *Nylanderia guatemalensis* has also been reported from Cuba, Jamaica, the Dominican Republic, and the Lesser Antilles, but it is not clear if it is native to these areas. The subspecies *N. guatemalensis cocoensis* is reported from Cocos Island (Kempf 1972). However, Smith et al. (2013) made note that *N. guatemalensis cocoensis* would likely be elevated to full species (*N. cocoensis*) in a modern taxonomic revision. *Nylanderia guatemalensis edenensis* was described by (Wheeler 1924) from a series of eight workers and one dealate queen collected on Eden Rock in the Galapagos, and this is the only known locality for this taxon. The subspecies *N. guatemalensis itinerans* is reported from mainland Costa Rica, Hispaniola, the Lesser Antilles, Trinidad and Tobago, Ecuador, and Ceara, Brazil (Kempf 1972, Brandao 1991).

Non-native Range

The established range of this species includes the Galapagos Islands, Cocos Island, and Florida, United States. In Florida, *N. guatemalensis* is most often found nesting in the leaf litter of mesic, disturbed areas and sometimes undisturbed hammocks of Dade, Broward, and Monroe counties. It is less common farther north to Hillsborough and Indian River counties (Deyrup et al. 2000). The subspecies *N. guatemalensis itinerans* has a non-native record in the Galapagos (Kempf 1972). *Nylanderia guatemalensis* has a regional distribution and is spread mainly among adjacent countries (Bertelsmeier et al. 2017).

Similar Species

This species is very similar in geographic range, size, and appearance to *N. steinheili*, and records of *N. guatemalensis* may be misidentifications of *N. steinheili* (Wetterer et al. 2016). Additionally, records from Texas (O'Keefe et al. 2000) and Arizona (Cole 1937) in the United States are likely misidentifications of *N. vividula*, of which *N. guatemalensis* was once considered a subspecies. One character useful for distinguishing *N. guatemalensis* (and several other species not native to the United States) from Nearctic natives such as *N. vividula* is the relatively dense pubescence found all over the body, as Nearctic species have little to no pubescence (Kallal and LaPolla 2012). Revisionary work of the Neotropical *Nylanderia* is needed to clarify the difficult taxonomy involving both native and non-native species in this region.

Pest Status and Potential Threat

Much like *N. bourbonica*, this species is an occasional nuisance pest of outdoor eating areas but rarely enters buildings in large numbers (Deyrup et al. 2000). It is unknown how much of an impact this species has on native species.

Nylanderia jaegerskioeldi (Mayr 1904)

Native Range

This species is native throughout the Middle East and Africa, as far south as Mozambique and as far west as Guinea.

Non-native Range

Nylanderia jaegerskioeldi seems to have spread westward from the Middle East and across the Mediterranean Sea (Collingwood and Agosti 1996). The non-native range includes several countries ringing the Mediterranean Basin: Morocco and Algeria in northwestern Africa; Turkey and Iraq in the Middle East; and Portugal, Spain, and Greece in Europe. The first record for the Iberian Peninsula

is from 2000, when about ten workers were found foraging on a mulberry tree (*Broussonetia papyrifera*) in Nijar, Spain (Espadaler and Collingwood 2001). In Portugal, the first reports of this species were from 2012, in landscaped and disturbed areas near the coast (Obregón Romero and Reyes López 2012). *Nylanderia jaegerskioeldi* has also become established on the Canary and Madeira Islands off the western coast of Africa, the Balearic Islands east of Spain, and the island nation of Cyprus. In the Canary Islands, this species has been found in disturbed areas on Tenerife (Espadaler and Bernal 2003) and El Hierro (Espadaler 2007). The first report of *N. jaegerskioeldi* in Madeira was from urban gardens in Funchal, and Wetterer et al. (2007b) suspected that this was a recent establishment.

Similar Species

The workers of *N. jaegerskioeldi* are morphologically indistinguishable from those of *N. natalensis*, which occurs in southern Africa (Botswana, South Africa, Mozambique, and Zimbabwe). The only way to tell these two species apart using morphology is through examination of males (LaPolla et al. 2011b). The males of *N. jaegerskioeldi* are more pubescent than those of *N. natalensis* and several genitalic characters are particularly useful for species-level diagnosis.

Pest Status and Potential Threat

In the Arabian Peninsula this species is a common nuisance pest of households and often occurs in irrigated and shaded areas outdoors (Collingwood et al. 1997). The arrival of this species to the Iberian Peninsula and Mediterranean areas seems to have occurred through the transport of ornamentals from Africa to Andalusia, Levante, and Algarve (Obregón Romero and Reyes López 2012). In Puerto de la Cruz in the Canary Islands this species was found in abundance in flower pots (Espadaler and Bernal 2003), the transport of which has been and continues to be a major contributor to the spread of tramp ant species.

Nylanderia obscura (Mayr 1862)

Native Range

Nylanderia obscura occurs across Australia, New Guinea, Borneo, Sulawesi, the Solomon Islands, New Caledonia, Lord Howe Island, and Norfolk Island. There are four additional subspecies: 1) *N. obscura bismarckensis* from New Guinea, the Bismarck Archipelago, and the Solomon Islands; 2) *N. obscura celebensis* from Sulawesi; 3) *N. obscura minor* from Java and the Maluku Islands; and 4) *N. obscura papuana* from New Guinea.

Dubious Records

Nylanderia obscura was reported in Hawai'i (Forel 1899), but this report was later determined to be a misidentification of *Nylanderia bourbonica* (Wheeler 1934).

Similar Species

This species is most similar to *N. vaga*, which was once classified as a subspecies of *N. obscura*, but raised to full species by Emery (1914) based on differences in mesosomal macrosetae counts. Emery assigned *N. vaga* to the 'N. *vividula* group', species of which have four total pairs of erect macrosetae on the mesosoma: two on the pronotum and two on the mesonotum. In contrast, he assigned *N. obscura* to the '*fulva* group', species of which have other hairs, almost as long, in addition to the four pairs seen in 'N. *vividula* group' species. Characterization and delimitation of *N. vaga*, *N. obscura*, and other Australasian *Nylanderia* species is sorely needed.

Pest Status and Potential Threat

This species has been observed tending to a major pest of sugar cane: the sugarcane mealybug, *Saccharicoccus sacchari* (Hemiptera: Pseudococcidae) (De Barro 1990). Given that ant species rarely form obligate, one-to-one mutualisms with their trophobiotic associates (Hölldobler and Wilson 1990), it is likely that *N. obscura* also opportunistically tends to other honeydew-producing insects.

Nylanderia pubens (Forel 1893)

Native Range

The native range of this species is thought to include much of the Caribbean and parts of northern South America, with records from the Lesser Antilles, Puerto Rico, Hispaniola, Cuba, Colombia, and Panama.

Non-native Range

In the United States, *N. pubens* has been found in southern Florida, mostly around Miami. However, this species may have been extirpated from the area as a result of invasion by *N. fulva*. The last verified specimen records of *N. pubens* from Florida dates to 1994 (Wetterer et al. 2014). The first published record of *N. pubens* in Florida was by Trager (1984), with earlier specimens dating back to 1953 (Deyrup et al. 2000). Specimens were also collected from USDA greenhouses in Washington, DC (Trager 1984), and outside of the United States a non-native record exists for the Galapagos Islands. This species has a local distribution with low spread beyond its native range (Bertelsmeier et al. 2017).

Similar Species

Workers and queens of *N. pubens* are morphologically indistinguishable from those of *N. fulva*. The only way to discriminate between these two species using morphology is through observation of male genitalic characters (see full discussion above in the *N. fulva* section), but genetic sequence data have also been used to delimit these two species (Gotzek et al. 2012). Nesting and foraging behaviors, including the distinct 'boom and bust' pattern observed in non-native *N. fulva* populations, may be useful for distinguishing these two species in the field (Wetterer et al. 2014, 2016). *Nylanderia pubens* colonies maintain lower worker densities than invasive *N. fulva*. Nesting and foraging behaviors of *N. pubens* and *N. fulva* are not well characterized, and more complete natural history description from the native range would be helpful for distinguishing and managing these non-native species.

Pest Status and Potential Threat

This species is considered a minor and localized nuisance pest; it may sometimes enter households (Klotz et al. 1995, Deyrup et al. 2000).

Nylanderia sharpii (Forel 1899)

Native Range

Nylanderia sharpii occurs across eastern China, as far south as Guangdong Province and as far north as Liaoning Province.

Non-native Range

The type series (worker, queen, and male) for this species was described from a colony found in Honolulu, Hawai'i on plants shipped from China (Forel 1899). However, no additional colonies have since been reported and this species is not known to have any populations established outside of its native range.

Similar Species

Upon viewing Forel's (1899) original drawings, Wilson and Taylor (1967) noted that this species is indistinguishable from *N. vaga*, with

the exception of male genitalic characters: parameres of *N. sharpii* males are narrower and more tapered than those of *N. vaga*, and are distinctly serrate along the ventral margins.

Pest Status and Potential Threat

There is no evidence that this species is a pest or poses any threat as an invasive species.

Nylanderia silvestrii (Emery 1906)

Native Range

Nylanderia silvestrii occurs in moist tropical and subtropical forests of southern South America. Records exist for Uruguay and parts of Argentina. The subspecies *N. silvestrii kuenzleri* is native to Argentina.

Dubious Records

A dubious record from the Global Ant Biodiversity Informatics Project (GABI_00149658) (Guénard et al. 2017) exists for the Mentawai Islands in Indonesia.

Pest Status and Potential Threat

It is unlikely that this species has established populations anywhere outside of its native range. No information in the literature indicates whether this species is or could become a pest or invasive species.

Nylanderia steinheili (Forel 1893)

Native Range

Records exist for most of southern Central America, Colombia, Venezuela, and parts of northern and eastern Brazil. This species is also reported throughout the West Indies, but its native status in this region is uncertain. The subspecies *N. steinheili minuta* was described by Forel (1893) from Saint Vincent in the Antilles.

Non-native Range

This species has become established in the Galapagos Islands (Wauters et al. 2016), urban areas of Buenos Aires, Argentina (Josens et al. 2016), and the Seychelles (Fisher 1997). In Florida, United States, *N. steinheili* occurs from the south-central part of the peninsula south into the Florida Keys (Moreau et al. 2014, Deyrup 2016). It is thought to be excluded from the northern part of the state by cold weather. *Nylanderia steinheili* has been intercepted in Europe, though no populations have become established, likely limited by the colder climate. In Norway, *N. steinheili* was found in the tropical house of 'The Little Zoo' in Brokelandsheia and probably arrived through the transport of plants from Costa Rica (Gjershaug and Staverlokk 2016). This species was also intercepted by the Plant Protection Service in the Netherlands in 1980 (Boer and Vierbergen 2008).

Similar Species

This species is very similar in geographic range, size, and appearance to *N. guatemalensis*, and at least some records of *N. guatemalensis* may actually be *N. steinheili* (Wetterer et al. 2016). See discussion above in the *N. guatemalensis* section for more information, including diagnostic characters that separate these two species. Additionally, some records of *N. fulva* in central South America may in fact be misidentified *N. steinheili*.

Pest Status and Potential Threat

Nylanderia steinheili only nests outdoors and is not known to be a pest species (Deyrup 2016). Like *N. faisonensis,* this species often prefers to nest in and around buried twigs in leaf litter. It therefore

seems as though *N. steinheili* could supplant *N. faisonensis* in southern Florida, where *N. faisonensis* is relatively uncommon (Deyrup 2016).

Nylanderia stigmatica (Mann 1919)

Native Range

Records of this species are only known from the Solomon Islands and Vanuatu.

Dubious Records

A single worker record was reported for the Samoan Islands (Santschi 1928b, Wheeler 1935), but later considered doubtful since no other extensive ant collections (1938–1940 and 1956–1962) included *N. stigmatica* (Wilson and Taylor 1967).

Similar Species

Nylanderia stigmatica is a distinctive species with workers that have a dorsally flattened mesosoma and very long, slender scapes (Wilson and Taylor 1967).

Pest Status and Potential Threat

An extensive review of the literature on *N. stigmatica* found no confirmed records anywhere beyond its native range. This species is currently of no concern as a pest or invasive species.

Nylanderia tasmaniensis (Forel 1913b)

Native Range

This species is native to southeastern Australia, in the states of New South Wales and Tasmania.

Non-native Range

Nylanderia tasmaniensis has become established in New Zealand (Ward and Edney-Browne 2015).

Similar Species

The worker of this species is very similar to that of *N. braueri*, except that the head is wider and the scapes are shorter (Forel 1913b).

Pest Status and Potential Threat

No information in the literature indicates whether this species is or could become a pest or invasive species.

Nylanderia teranishii (Santschi 1937)

Native Range

A single record exists for this species in Kinki, Japan (Santschi 1937).

Unverified Records

There is one unverified record of this species in Xizang, China (Ran and Zhou 2013).

Pest Status and Potential Threat

No information in the literature indicates whether this species is a pest or invasive species.

Nylanderia vaga (Forel 1901b)

Native Range

This species is native to Australia, New Guinea, the Lesser Sunda Islands, Norfolk Island, and the Bismarck Archipelago.

Non-native Range

Established, non-native records of this species exist for Sulawesi, in addition to islands all throughout the South Pacific, from Australasia to as far east as the Galapagos Islands, and as far north as Hawai'i. *Nylanderia vaga* has been intercepted in New Zealand, but no records of established populations are known to exist there. This species has a transcontinental distribution and is established in multiple major world regions, but in only a few countries per region (Bertelsmeier et al. 2017).

Unverified Records

Two records for this species in Southeast Asia await verification. One is a specimen in the Australian National Insect Collection (ANIC) that was collected from Vietnam (GABI_00352716) (Guénard et al. 2017), and the other is from the Philippines, where it was reportedly very common in rice fields (Way et al. 1998).

Dubious Records

The Skottsberg expedition (1907–1909) collected a single *Nylanderia* species (*N. bourbonica*) on the island of Juan Fernandez off the Chilean coast, which (Wheeler 1922) misidentified as *N. vaga*.

Similar Species

Nylanderia vaga is especially difficult to distinguish from *N. bourbonica* because *N. vaga* is widely distributed and extremely morphologically variable. *Nylanderia bourbonica* is consistently dark brown and has pubescence on the mesopleuron while *N. vaga* ranges in color from pale yellow-brown to black and lacks mesopleural pubescence (Sarnat and Economo 2012). Individuals of *N. vaga* have been misidentified in the past as *N. vividula* in Fiji (Mann 1921) and may have also been confused with *N. vitiensis* (Cheesman and Crawley 1928). *Nylanderia vaga* is also very similar to *N. obscura*, of which it was once considered a subspecies, until (Emery 1914) elevated it to species based on differences in mesosomal macrosetae counts. According to Emery, *N. vaga* has exactly four pairs of erect macrosetae on the mesosoma—two on the pronotum and two on the mesonotum—while *N. obscura*, in addition to having these four pairs of macrosetae, has other erect macrosetae on the mesosoma that are almost as long. *Nylanderia vaga* may represent a complex composed of multiple distinct species. As a result of its wide distribution and high morphological variation, delimitation of *N. vaga* and discrimination from closely related species presents an ongoing challenge.

Pest Status and Potential Threat

This species has been associated with cosmetic damage to bananas in Hawai'i due to formic acid secretions, making the fruit less marketable (Nelson and Taniguchi 2012). This species is not considered an ecological threat despite its widespread across a variety of habitats on Pacific islands (Berman et al. 2013).

Nylanderia vitiensis (Mann 1921)

Native Range

This species is considered endemic to the islands of Fiji.

Dubious Records

Records of this species from the Society Islands and Tuamotu Islands are currently considered dubious and may instead be *N. glabrior* or *N. vaga*.

Similar Species

This species is most similar to *N. glabrior* and *N. vaga*. *Nylanderia vitiensis* can be distinguished from both species by its relatively smaller eyes and paler, more yellow color. *Nylanderia glabrior* is dark yellow-brown and *N. vaga* displays great variation in color, from pale yellow-brown to black (Sarnat and Economo 2012).

Pest Status and Potential Threat

No information in the literature indicates whether this species is a pest or invasive species.

Nylanderia vividula (Nylander 1846)

Native Range

Nylanderia vividula is one of few species in the genus found in both the eastern and western United States, and occurs in open, disturbed habitats across the southern half of the country. This species is considered native to Texas and Mexico, as well as countries throughout Central America, the West Indies, and northern and eastern South America (Deyrup 2016). The subspecies *N. vividula australis* is reported only from Paraná, Brazil (Santschi 1929).

Non-native Range

This species is established, but probably not native to the southeastern United States, Bermuda, Chile, southern Europe, and the Middle East (Deyrup 2016). Most records from before 1984 in Florida, United States are misidentifications; the earliest verified records from Florida date to 1982 (Deyrup et al. 2000). This species has been found in northern European greenhouses since at least its original description (Nylander 1846); the type series was collected in Finland (Trager 1984, Deyrup 2016). *Nylanderia vividula* is also listed as an established, non-native species to Libya, Egypt, Zaire, Zanzibar, Madagascar, Mascarene Islands, the Seychelles, Southeast Asia, and several Pacific Islands. However, many of these records may be misidentifications of other species. For example, a worker, queen, and male from Mauritius (AntWeb CASENT0059600, CASENT0058913, and CASENT0058918) and a worker from the Solomon Islands (AntWeb CASENT0219750) all have scapes with higher erect macrosetae counts than what is typical for specimens from North America, suggesting that they belong to a different, albeit morphologically similar, species group. This species is established on multiple continents, but in only a few countries per continent (Bertelsmeier et al. 2017).

Dubious Records

Records from Fiji (Mann 1921) were later reported to be misidentifications of *N. vaga* (Wilson and Taylor 1967, Sarnat and Economo 2012).

Similar Species

Nylanderia vividula has been confused with three other widespread species with established, non-native records: *N. flavipes*, *N. guatemalensis*, and *N. vaga* (see discussions on each of these species above). In the United States, *N. vividula* could be confused with four other native species: *N. parvula*, *N. concinna*, *N. faisonensis*, and *N. terricola*. *Nylanderia vividula* workers are best distinguished from those of *N. parvula* by the presence of large, erect macrosetae on the antennal scapes, and from those of *N. concinna* and *N. faisonensis* by the relative sparsity of hairs on the posterior part of the head that makes head of *N. vividula* look especially shiny (Deyrup 2016). Workers of *N. vividula* and *N. terricola* are virtually impossible to distinguish, as morphological characters are often unreliable. *Nylanderia vividula* typically has a more quadrate head with subparallel lateral margins and larger eyes relative to head length in comparison to *N. terricola*, which has an ovate head with convex lateral margins and smaller eyes relative to head length

(Kallal and LaPolla 2012). Western variants of *N. terricola* are also relatively lighter in color (Kallal and LaPolla 2012). This species is very similar to *N. sharpii* from China, and records of *N. vividula* in Asia may be misidentifications.

Natural History

This species typically nests in soils with large amounts of clay or organic matter, or in cavities or debris on the soil surface (Graham et al. 2008). In the southeastern United States, *N. vividula* and the red imported fire ant (*Solenopsis invicta*) often co-exist in open areas such as fields and lawns (Deyrup 2016), and declines of *N. vividula* populations are correlated with increases in those of *S. invicta* (Shawler et al. 1989, Wojcik 1994).

Pest Status and Potential Threat

Although this species may be widespread, it is not known to be a pest (Deyrup et al. 2000). In fact, the established, non-native range of *N. vividula* is likely to have been overestimated due to misidentifcation of other, similar-looking species.

Discussion

Prevention and management of invasive species depend, fundamentally, on reliable identification of species of concern. However, diagnostic tools that can link species to names, geographic distributions, and behaviors are lacking for many groups of insects that can be considered emerging threats. This is in part due to the classic 'taxonomic impediment': in the face of vast numbers of species which remain undescribed, taxonomic progress is slow. Even among named taxa, assessing the risk of invasion can be challenging when species' life histories are poorly characterized.

A proactive approach to overcoming the taxonomic impediment for emerging invasive threats would ideally focus on species that are likely candidates as future invasive species; that is, known tramp species that frequently live with and are inadvertently transported by humans. Tramp species of ants and other social insects that are especially successful outside of their native ranges often possess a suite of life history traits associated with invasion: adaptation to frequent environmental disturbance, polygyny (multiple queens), polydomy (multiple nests per colony), and unicoloniality (lack of nestmate vs. non-nestmate recognition) (Suarez and Tsutsui 2008). Prioritizing taxonomic resolution of those groups that are poorly understood and contain adventive species that possess these traits will set the stage for correctly diagnosing these insects when and if they are identified as species of concern. Using the ant genus *Nylanderia* as an example, we outline how new tools and technologies—ranging from genomic techniques and comprehensive bibliographies, to aggregated distributional information—can make it possible to taxonomically target species of greatest concern.

Nylanderia Taxonomy

Like many taxa that are speciose, widespread, and poorly characterized, the ant genus *Nylanderia* is rife with taxonomic confusion. It includes over a dozen tramp species that are often mistakenly assumed to be native where they are not, and at least one species (*N. fulva*) is considered a serious invasive pest. Clear delimitation and identification of species has been hindered by a lack of distinguishing morphological characters in this group and, as a result, hundreds of species await description. Needless to say, a comprehensive global revision of the genus has never been undertaken.

In groups such as *Nylanderia* where morphology alone cannot be used for delimiting and distinguishing species, other tools are needed. Integrative taxonomic study is especially important in challenging groups such as *Nylanderia* for establishing predictive frameworks to identify species that are likely to cause adverse economic and ecological impacts because effective invasive species prevention and mitigation programs are always dependent on unambiguous identification.

Pest Status of *Nylanderia* Species

Review of published literature and museum records of the 20 *Nylanderia* species with non-native records revealed that only 13 have verified established records (Fig. 1). Of these 13, only nine are currently considered to be pests or mutualists of pests. *Nylanderia fulva* is currently the sole pest of economic importance, although at least four other species are either occasional indoor or outdoor nuisance pests or are of potential agronomic, economic, or ecological concern: *N. bourbonica, N. vaga, N. guatemalensis, N. jaegerskioeldi, N. pubens, N. clandestina, N. flavipes,* and *N. obscura* (Table 1). At least four species—*N. clandestina, N. flavipes, N. fulva,* and *N. obscura*—have been observed in association with various hemipteran and lepidopteran pests of economic importance. Ants can indirectly increase abundances of honeydew-producing insects that vector causative agents of plant diseases (Krushelnycky et al. 2005). Two additional species—*N. braueri* and *N. sharpii*—have been reported outside of their native ranges, but have not yet become established in places where they are not native. Eleven species that have been documented outside of their native ranges are not currently considered pests at all; only limited evidence exists of their non-native status (Table 1).

This comprehensive review offers both reassurance and cause for concern. The discovery that the majority of the 20 putative tramp *Nylanderia* species are not currently problematic pests is comforting. On the other hand, it is alarming that nine species of *Nylanderia*, many of which are challenging to identify, have repeatedly and successfully established populations outside of their native ranges. Even the dubious records of *Nylanderia* species outside their native ranges highlight the challenge of identifying *Nylanderia* species in a global context; these records indicate how difficult it can be to tell harmful, non-native species apart from poorly known (or unknown) native species. *Nylanderia* species' pest-like tendencies and track record of repeated arrivals through human transport suggests that the species highlighted here could be at early stages of becoming invasive. In time and if left unchecked, further spread of these species could occur. Awareness of these potential new pests and emerging threats is a first step toward preventing new invasions. The next step is to ensure that species identities are reliably linked to the names, distributions, biology, and natural history of these ants.

Morphological Identification

Workers, and even queens, of many *Nylanderia* species offer few reliable diagnostic morphological characters. However, males across ant genera offer additional useful characters among species for which males have been described (Deyrup and Cover 2004, Lapolla et al. 2012, Boudinot 2013, Boudinot et al. 2013). *Nylanderia* males are often very distinct at the species level, even when worker and queen characters alone are insufficient for identification (Gotzek et al. 2012, Kallal and LaPolla 2012). Although they are much less commonly encountered than foraging workers, males may be collected in abundance during mating season; especially at lights. Associating males with workers and queens of the same species may not be possible when based solely on morphology. Whenever possible, collecting full
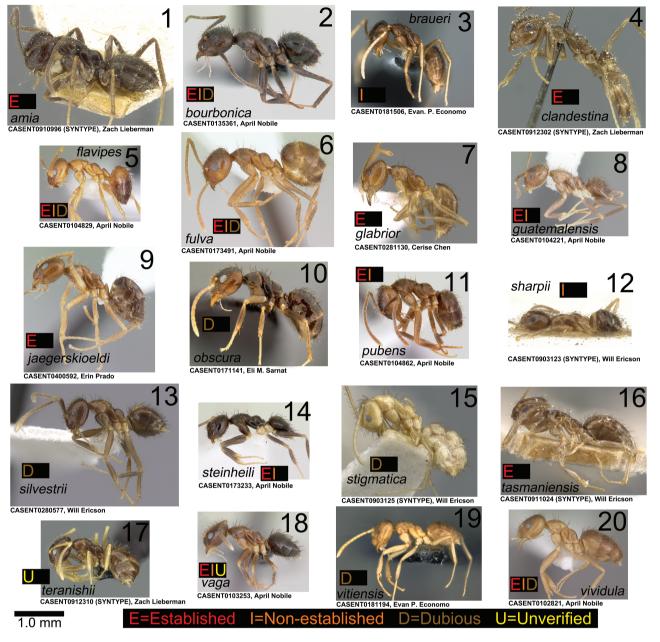
Fig. 1. Profile images (to scale) for all 20 *Nylanderia* species with non-native records. Images from AntWeb 2019. Specimen ID and image credit are provided below each image.

nest series including workers, queens, and males directly from colonies is recommended to improve the likelihood of accurate species identification.

Behavior

Diagnostic characters exist beyond morphological structures, and associated behavioral or ecological traits can prove useful for pest species discrimination (e.g., in leaf-cutter ants: Fowler and Robinson 1979, Forti et al. 2006). In practice, pest management professionals and field biologists may rely on behavioral or colony-level characters (e.g., worker movement, foraging behavior, trailing patterns, polygyny, polydomy, nest location, etc.) to help identify species or at least determine an action plan for management (National Research Council 1969, Holway and Suarez 1999). For example, *Nylanderia fulva* exhibits distinct quick and erratic movement patterns, high

population densities, and a preference for nesting in preformed soil cavities and surface debris (LeBrun et al. 2013). These traits can be effective in discriminating this species from others, especially when a microscope is not available.

Taxonomic Quandaries

Three *Nylanderia* species groups include widespread, poorly delimited, and difficult-to-identify species of known or potential economic concern. Currently, each group includes one pair of morphologically similar species: 1) the *N. fulva* complex (*N. fulva* and *N. pubens*); 2) the *N. guatemalensis* complex (*N. guatemalensis* and *N. steinheili*); and 3) the *N. bourbonica* complex (*N. bourbonica* and *N. vaga*). Species delimitation in each complex is founded on tenuous evidence at best, and current species-level hypotheses seem unlikely to persist after

Table 1. Summary of pest status and non-native record types for each *Nylanderia* species with non-native records

| Species name | Record types | | | | Pest status | | | | | | Plant |
	Established	Non-established	Dubious	Unverified	Outdoor	Indoor	Agronomic	Livestock	Horticultural	Urban	Pest Mutualist
N. amia	✔										
N. bourbonica	✔	✔	✔		✔	✔	✔				
N. braueri		✔									
N. clandestina	✔										✔
N. flavipes	✔	✔	✔							✔	✔
N. fulva	✔	✔	✔		✔	✔	✔	✔	✔	✔	✔
N. glabrior	✔										
N. guatemalensis	✔	✔			✔	✔					
N. jaegerskioeldi	✔				✔	✔			✔	✔	
N. obscura			✔								✔
N. pubens	✔	✔			✔	✔				✔	
N. sharpii		✔									
N. silvestrii			✔								
N. steinheili	✔	✔									
N. stigmatica			✔								
N. tasmaniensis	✔										
N. teranishii				✔							
N. vaga	✔	✔		✔			✔				
N. vitiensis			✔								
N. vividula	✔	✔	✔								
Total	13	10	8	2	5	5	3	1	2	4	4

Data compiled from AntMaps.org and literature records.

taxonomic revision. For example, color is often cited to distinguish *N. bourbonica* from *N. vaga*. However, *N. vaga* can vary from pale yellow-brown to black, and individuals on the darker end of the spectrum are difficult to distinguish from *N. bourbonica* (Sarnat and Economo 2012). These complexes are currently unresolvable with morphology alone. Because of this, the integration of genetic or genomic data will be helpful for species delimitation and reconstructing phylogeny.

Summary

Nylanderia is an example of a lineage with multiple tramp species for which species-level identification is difficult, and where taxonomic preparedness will facilitate management and preempt misdiagnosis of invasive species before they become a problem. Associating species with their morphology, life history, behavior, ecology, and geographic distribution is necessary in order to develop resources for the identification of problematic species. Below is a discussion of the tools and practices that can facilitate taxonomic resolution of historically challenging groups, such as *Nylanderia*.

Tools and Technology

Taxonomic Tools and Online Resources

Tools (e.g., dichotomous keys, field guides, collections of images and descriptions, distribution maps, etc.) for identification of species in taxonomically difficult groups should ideally be easy to understand and use a variety of methods to help users—often non-experts, but professionals on the front lines battling non-native populations—distinguish species in field and lab settings. Dichotomous or multi-entry identification keys should keep broad audiences in mind and include, ideally, illustrations or photographs representing all castes, life stages, and morphs of each species. Images or descriptions of

the extended phenotype, such as shape or size of nest entrances, organization of foraging trails, and appearance of preferred habitat are also valuable for field identification. Minimizing technical jargon is helpful, as is including a glossary of terms specific to the taxonomic group.

Among the most valuable and least celebrated tools for advancing revisionary taxonomy in any group are compilations of taxonomic, geographic, and ecological information. The field of myrmecology, for example, has benefitted from easy access to a number of accessible online resources. Especially useful are an updated catalogue of the group's taxonomy (Bolton et al. 2006, Bolton 2019), bibliographies of all published taxonomic literature (Ward et al. 1996), type specimen data and images (AntWeb 2019), distribution maps (Janicki et al. 2016, Guénard et al. 2017), and natural history information and identification keys to specific taxa (AntWiki 2019). The availability of these resources in the past 20 years has introduced remarkable stability and consensus to the taxonomy of ants, and has facilitated advances that would have previously been difficult, if not impossible.

Biochemical Assays

Biochemical tools offer considerable promise for rapid field identification. For example, lateral flow immunoassays have recently been used to confirm identification of imported fire ants (*S. invicta* and *S. richteri*) through the detection of unique venom proteins (Valles et al. 2016a, Valles et al. 2017). There could be immense value in developing similar tools for other invasive species (such as *N. fulva*) if unique and targetable proteins can be identified.

Phylogenetics and Phylogenomics

The use of single-gene sequencing has been a standard approach to molecular phylogenetic study for several decades, but much larger datasets are increasingly becoming available as genome-scale data

become more affordable to generate. Phylogenomic data are now regularly used as the basis for revisionary taxonomy and guiding nomenclatural change in historically intransigent taxa. A variety of high-throughput methods have been developed for capturing reduced representation genomic data, including restriction site-associated DNA sequencing (RADseq) (Davey and Blaxter 2011, Andrews et al. 2016), transcriptomics (Mittapalli et al. 2010, Zhang and Yuan 2013), anchored-hybrid enrichment (AHE) (Lemmon et al. 2012, Lemmon and Lemmon 2013, Breinholt et al. 2018) and targeted enrichment of ultraconserved elements (UCEs) (Faircloth et al. 2012, Branstetter et al. 2017). All of these techniques offer the benefit of large amounts of genomic data and can be employed for resolving questions at different evolutionary time scales; e.g., reconstructing deep-level phylogenies, delimiting sister species, or even describing population-level processes.

UCEs have been shown to be especially valuable in insects and are increasingly being leveraged in studies of Hymenoptera. Although protocols for UCE capture were originally developed to study vertebrates (Faircloth et al. 2012, Lemmon and Lemmon 2013), they have been adapted for use in various insect orders, including Coleoptera (Van Dam et al. 2017), Hemiptera (Kieran et al. 2019), and Hymenoptera (Faircloth et al. 2015, Bossert et al. 2019, Branstetter et al. 2018). Many of the loci which are sequenced after UCE enrichment have yet to be identified, but they are conserved all across animal taxa from sponges to humans (Ryu et al. 2012). The utility of these regions lies in the fact that the UCE regions themselves are invariant across evolutionarily distant organisms, but the flanking regions increase in variability with distance from the core. As a result, UCEs are easy to acquire and compare across taxa at multiple evolutionary time scales. In ants, UCEs have been used to resolve phylogeny at the subfamily and tribal level (Blaimer et al. 2015, Branstetter et al. 2017) and within select ant genera (Blaimer et al. 2016, Ješovnik et al. 2017). A recent UCE bait set developed for capturing genomic data from ants targets 2,590 loci from across the entire genome (Branstetter et al. 2017). The availability of this bait set, optimized for this family, will facilitate comparative genomic study across lineages within ants.

Applied Genomics for Species Identification

Genetic and genomic data can also facilitate rapid species-level identification. This approach can be valuable when timely diagnosis at the species level is critical and when taxonomic expertise is limited. DNA 'barcoding' uses a 600 base pair sequence of mitochondrial DNA (mtDNA) to identify individual species for which a reference sequence exists (Hebert et al. 2003). This technology has technical and practical limitations such as those associated with mtDNA inheritance and difficulty with determining how to apply and standardize a barcoding species concept (Rubinoff et al. 2006). Another shortcoming of mtDNA barcoding is that a single marker on its own cannot reliably capture speciation and delimit species (Edwards and Bensch 2009). Despite these drawbacks, mtDNA barcodes and other single-gene markers are convenient and inexpensive for diagnosis in taxa that are thoroughly catalogued and for which a strong taxonomic framework exists. Currently, the taxonomic browser for the Barcode of Life Data System (BOLD; Ratnasingham and Hebert 2007) shows over 3,000 *Nylanderia* specimen records and more than 2,000 of those have barcodes. The database also currently has a large collection of specimens that have been assigned interim species names, which reflects the need for a global taxonomic revision of the genus. Because of the unresolved state of *Nylanderia* taxonomy it is not yet known whether barcoding can effectively diagnose *Nylanderia* species, especially for the purpose of screening for non-native species at ports of entry. Beyond the scale (and affordability) of mtDNA and single-gene markers, genomic barcoding harnesses as many as thousands of different loci for the purpose of cataloging and identifying species and is therefore more robust, but lacks the standardization necessary to link newly collected genomic data to traditional genetic datasets. Recently, UCE and mtDNA barcodes have been used in tandem to overcome the drawbacks of both types of data (Zarza et al. 2018). Given that UCE and other genomic loci are already being extracted from insects for phylogenetic study, it may not be long before these markers can be adopted for barcode-based, cryptic insect species identification.

Monitoring and Management

The most cost-effective way to manage invasive species is to proactively monitor for them, detect their arrival early, and have infrastructure in place to take immediate preventative action in the early stages of invasion (Myers et al. 2000, Krushelnycky et al. 2005). Realistically, prioritization of invasive species that require urgent action should follow a standardized scale that predicts the species' degree of impact (Blackburn et al. 2014): a form of invasive species triage. Management practices rely upon strong foundational taxonomy and predictive accuracy because timely and accurate diagnosis of invasive species must happen before it is too late for containment and eradication. Prevention is especially cost efficient (although hard to quantify) because it reduces the need for full-scale invasive species quarantine or eradication programs, which are rarely employed for invasive ant species. Even well-funded programs, however, are not guaranteed to prevent the spread of or eradicate invasive species after establishment. Red imported fire ants stand as a cautionary example; despite considerable investment of funding, labor, and time, efforts to eradicate *S. invicta* from both the United States and Australia have failed (Drees and Gold 2003, Buhs 2004, Tschinkel 2006, Magee et al. 2016).

Surveillance

Taxonomic tools are especially important for professional identifiers involved in surveillance and monitoring at ports of entry. Challenges abound based on the sheer volume of cargo: in the United States, shipping container inspection rates of less-than five percent (Kempinski and Murphy 2016) are typically based on perceived risk, and inspectors are burdened with the broad responsibility of intercepting threats unrelated to biological invasion, such as explosives, narcotics, chemical weapons, hazardous chemicals, radioactive materials, and humans (Valković et al. 2004, Longo 2010). Because surveys primarily focus on lists of target species deemed most likely to arrive and cause damage (Bishop and Hutchings 2011), many groups that are less well understood taxonomically may not be recognized as important. The probability of non-native species establishment increases with species that exert high propagule pressure from unchecked, repeated arrivals (Suarez et al. 2005). Taxa that are frequently moved via human-mediated dispersal should be cataloged and databased to increase the probability of interception and reduce the amount of genetic variation and load of individuals that arrive through ports of entry. In Australia, some common problems with documentation of non-native species at ports include: 1) failure to consult taxonomic experts for identification; 2) lack of native species documentation; and 3) no consideration that new non-native records may instead be undescribed native species (Bishop and Hutchings 2011). Overcoming these issues requires a

strong emphasis on taxonomic preparedness and awareness of native species around ports.

Concluding Remarks

In some regards, our taxonomic goals and challenges have remained unchanged for hundreds of years—we endeavor to describe the breadth of life on Earth by delimiting and naming individual species. Because of the increased pace of species' range expansions around the world, it is more important than ever to make progress in our ability to distinguish and identify widespread, morphologically similar species. The incorporation of new tools and technology into traditional taxonomy are already part of the approach to addressing global species invasions.

This review of non-native and invasive *Nylanderia* species highlights a practical need for taxonomic attention to problematic species, regardless of taxonomic group. One of the great challenges of our time is to prevent and manage invasive species spread; our inability to reliably associate specimens with stable, clearly delimited names complicates this task. Genomic data represent an underused but significant resource in invasive species management because on a basic level, they help establish taxonomic preparedness, and on an applied level they can be leveraged for rapid species-level identification of species that are otherwise unidentifiable.

The ant genus *Nylanderia* may represent a substantial emerging threat, and clarifying the taxonomy and developing diagnostic tools in this group will facilitate *Nylanderia* species delimitation, diagnosis, risk assessment, and proactive management. More broadly, many other insect groups with derelict taxonomy persist as emerging threats. Taxonomic preparedness is key for early detection and rapid management of invasive species and can be achieved through the development of identification tools and resources, but this remains unattainable in groups with large numbers of undescribed or poorly delimited species. Moving forward, the integration of genomic tools and technology with traditional taxonomic endeavors and natural history description will prime professionals on the front lines to meet the challenge of managing and preventing the spread of problematic invasive species.

Acknowledgments

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