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REVIEW

Global spread of the German cockroach, *Blattella germanica*

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Abstract Most people consider cockroaches to be quintessential urban pests, even though very few of the 5000 cockroach species live in urban areas. The German cockroach is the most widespread and common cockroach in urban areas, however how this invasive species has spread globally is poorly understood. We reviewed the published and grey literatures, and museum data, to document the spread of the German cockroach, and how it may have interacted with other urban cockroach species. We found that the German cockroach likely originated from South Asia, was introduced into Europe no later than the 18th century, from where it invaded worldwide. The spread of the German cockroach was facilitated by the improvement of transportation technologies, especially from colonial trading, and indoor heating in cooler climates. Studies of population genetics have found that once introduced into a new location, the German cockroach spread rapidly through local expansion, and this could be within single (large, multiple-story) buildings. This local expansion resulted in displacement of other urban cockroach species, likely due to their small size requiring fewer resources, shorter generation times and so faster evolution, especially for pesticide resistance. These findings may help to identify new pest management methods. Future research could use

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genetic tools at larger scales to map distribution routes across the globe and interaction with pesticides and the evolution of resistance.

Keywords Cosmopolitan urban pest · Pesticide resistance · Spread routes reconstruction · Urban ecology

German cockroaches as the uniquely urban insect

Cockroaches may be the quintessential urban insects, and pests. Although less than 1% of the described cockroach species (~40 species) inhabit human houses, those that do dominate human perception of all cockroach species (Vidlička 2001; Robinson 2005; Bell et al. 2007). They have been considered as "among the most important of the household pests" (Ebeling 1978). Although cockroaches can be allogenic and so cause some medical problems, they are mostly considered nuisance pests (Peterson and Shurdut 1999; Kramer and Brenner 2009). Cockroaches are considered to have moved into human housing from agricultural lands, as urban habitats developed in antiquity in Africa and Asia (Pedigo and Rice 2014), although the evolution of cockroaches (and other organisms) as members of urban communities (and pests) has been little studied (Frankie and Ehler 1978; Schal and Hamilton 1990; McIntyre 2000; Martin et al. 2015).

Among the cockroaches, the German cockroach is of particular interest for several reasons. First, the German cockroach has perhaps a uniquely mysterious origin. It has never been found in natural habitats, and consequently its native range is unknown. Second, it is an invasive species and appears to have displaced other urban cockroach species (Cornwell 1976; Stejskal and Verner 1996), however the German cockroach has rarely been considered from an invasion biology perspective. Third, German cockroaches share their living space with humans and other urban adapted species, but they have not been considered in an urban ecology perspective (Martin et al. 2015; Hulme-Beaman et al. 2016).

Given the ubiquity of the German cockroach in urban habitats, it seems timely to determine the origins and spread of the species. This review aimed to consider all the available information, including the first appearance of the German cockroach in all locations, from museum records, the peer-reviewed literature, official publications of government agencies, and correspondence between entomologists. Specifically, we aimed to determine the possible origin, historical spread and factors that make the German cockroach such a successful invader.

History of urban cockroaches

Etymology reflects urban experience

The history of cockroaches as urban pests is found in their names, although the earliest records do not distinguish between species. The earliest written record was *ή ςίλφη* (Peri Silphes), mentioned by Aristotle in the *Τῶν Περ Τὰ Ζῷα στοριῶν* (History of Animals), written in the late 4th century BC (Vidlička 2001). The name of their order, Blattodea, comes from the Latin "*blattarum*", used by Quintus Horatius Flaccus (Horace) in his epistles (ca. 20 BC), originally meant insects that shun light (Shuckburgh 1888). This word included many household pest insects, including moths and beetles that ate books and clothes (Topsell 1658; Ligon and True 1673), but was narrowed to include cockroaches by themselves ("*fetida blatta*" or stinking moth) by the late 18th century (for a detailed history of nomenclature before 1758, see Vidlička 2001).

The name "cacarootch" was first introduced into English in 1624 from a Spanish word "*cucaracha*", which originated from the Latin "*cuca*", meaning caterpillar. The word "cacarootch" was firstly found in the letter written in Virginia by Captain John Smith, describe the cockroach as "a certaine India bug, called by the Spaniards a cacarootch, the which creeping into chests they eat and defile with their ill-scented dung" (Sherk 2004). The name "cockroach" become widely accepted when Charles Darwin settled it in 1859 (Darwin 1859).

This history is not limited to Europe. On the opposite side of the world, in China, the earliest plausible records were from the Tang dynasty (618–907). The Chinese named cockroaches 蜚蠊 (pronounced "fei-lian") in which 蜚, from dictionary *Erya* 3rd century BC (Chen and Zhang 2007), means the stink bug, and 蠊 from Shuowenjiezi 1st century AD (Duan 1815), means clam-like marine arthropods. Chinese records from the Ming dynasty (1368–

1644) described cockroaches as urban pests, as they were found in kitchens (Wu et al. 1988).

Identity of ancient pests

The identities of the cockroaches infesting these ancient houses are unknown from texts, and physical evidence is lacking. Therefore, in most cases, speculation is the only option. The most parsimonious explanation is that ancient pests remain pests in the modern world as well; e.g. the house mouse *Mus musculus* L. (Boursot et al. 1996; Cucchi et al. 2005). Currently, there are around 40 species of cockroaches found in or around housing in cities around the world, however only half of these species are found commonly, in higher populations, as they are capable of surviving in the dry habitats inside housing (Cornwell 1968, 1976; Ebeling 1978; Robinson 2005; Bell et al. 2007).

Of these, just seven species in the families Blattidae and Ectobiidae are found over two or more continents and with high populations in urban housing (Cornwell 1968). Four are widespread, especially in the tropics, but less so in temperate latitudes: the Australian, Brown, Smokybrown and Brown-banded cockroaches. Three are global, found commonly in temperate and even polar latitudes (Cochran 1999): the American, Oriental and German cockroaches (note all common names from the Entomological Society of America). Their successful spread across the world was, in part, favored by their physiological and behavioral characteristics, and their pre-adaptations to their original habitats (Martin et al. 2015).

The four widespread species

The Australian cockroach (*Periplaneta australasiae* Fabricius) is likely native to western Africa, although it was described from specimens collected in south Asia (Shaw 1925). It is a common pest in the tropics around the world, including Central and South America, South and Southeast Asia, and Australia. It is found less commonly in temperate locations in North Asia, North America and Europe, and then usually associated with artificial heating in buildings (Cornwell 1968). The Brown cockroach (*P. brunnea* Burmeister) is likely native to Africa as well, with a current distribution similar to that of the Australian cockroach (Cornwell 1968). The Smokybrown cockroach (*P. fuliginosa* Serville) is native to Asia, probably Japan, then introduced to multiple locations in the subtropics such as Australia, Southeast United States and South America (Appel and Smith 2002). The Brown-banded cockroach (*Supella longipalpa* Fabricius) is native to the west coast of Africa, where natural *Supella* species are found (Cornwell 1968). It was recorded that the Brown-banded cockroach was firstly introduced to the West Indies by slave ships in 1862 (de Saussure 1864). Now the species is widely spread across the tropics as domiciliary pest. There is little information on the spread of these species, in part because they are mostly in the tropics and not in Europe, where many older records were kept, and in part because they are less abundant than the three global species. It is likely that their spread was due to human trade and shipping, as for the global species. Note that the likelihood of successful introduction depends on more than human transportation (Mack et al. 2000; Vršanský et al. 2011), as suggested from other newly emerged pest cockroach species, for example *Ectobius* spp. (Vršanský et al. 2014).

The global species

The American cockroach (*Periplaneta americana* L.) is native to tropical south and west Africa, where wild populations can be found (Princis and Beier 1966). The original common name was “Ship cockroach” (Bell and Adiyodi 1982), and it was likely that the American cockroach spread from Africa to the Americas on ships used for the Slave Trade, perhaps as early as in the 1600 s (Rehn 1945; Peterson 1977). Now it is distributed in human settlements from the tropics to the warm temperate latitudes. The American cockroach is most common in the tropics, such as sub-Saharan Africa, Central and South America, to the southern USA, South and Southeast Asia, and Australia (Bell and Adiyodi 1982). It is found in cooler latitudes in lower numbers and with restricted (usually seasonal) spread, often associated with artificial heating. For example, in the British Isles, American cockroaches were only found in ports and indoors during the cold winter (Ragge 1965).

The Oriental cockroach (*Blatta orientalis* L.), is likely to be from southwest Asia, as wild populations are known from the Crimea and Greece (Beier 1974; Robinson 2005), and its closest relative, *Blatta* *furcata* Karny, is found in North Africa, Israel and Lebanon (Bohn 1984). Princis (1954) also suggested the Near and Middle East origin of the Oriental cockroach based on its closely relatedness to *Shelfordella* species. It is now found most commonly and abundantly in human settlements in temperate zones, in southern Europe, North America, Western and Central Asia, North Africa and Southern Australia (Cornwell 1968), which share similar 'Mediterranean' climates (Csa and Csb in the Köppen climate classification). The Oriental cockroach is probably the earliest pest cockroach species; ootheca have been found wrapped in Ancient Egyptian mummy bandages (Curry 1979). The Oriental cockroach was a pest in Europe in the time of Aristotle (Vidlička 2001). Showing the confusion of identifying native habitats, Linnaeus considered the Oriental cockroach to have originated in the Americas (Linnaeus 1758), while one century later, Brunner von Wattenwyl (1865) considered the Oriental cockroach to be "oriental" because it was associated with the Silk Road. Instead, the Oriental cockroach was most likely transported from the original sources in southwest Asia slowly westwards into Europe through human activities, and finally distributed throughout the entirety of Europe in the 17th century (Rehn 1945). The Oriental cockroach can survive freezing temperatures for hours, so long as it is acclimatized at 15 °C (Mellanby 1939). The ability to acclimate to cold temperature likely enabled the Oriental cockroach to spread into higher and wetter latitudes in the northwest of Europe and establish a year-round presence (Solomon and Adamson 1955).

The German cockroach (*Blattella germanica* L.) is of particular interest because it has the most widespread and truly "cosmopolitan" distribution: it has been found in human dwellings from Alaska to Antarctica, and everywhere between (Chamberlin 1949; Pugh 1994). Like other urban exploiters (McKinney 2002), the German cockroaches have adapted to the full variety of human habitations: from stationary buildings used for housing (houses, apartments, hotels, hospitals and so forth) and other purposes (restaurants, barns, animal housing facilities, warehouses and so forth), to mobile vehicles (ships, trains, trucks and cars, and so forth) (Cornwell 1968). However, the German cockroach has never been observed as an endemic, in natural habitats, and so its origin remains unknown.

Unknown origin of the German cockroach

Out of Africa to Europe?

The earliest records of the German cockroach are from Europe, where it is believed to have arrived during the 7 years War (1756–1763) (Rehn 1945). The common names given to the cockroach varied according to the combatants: Russians called it the "Prussian cockroach" and their opponents called it the "Russian cockroach" (Rehn 1945). Linnaeus named the species after the location from which his specimens were collected (originally *Blatta germanica*), and this eventually became its modern common name (Linnaeus 1767).

Although named in Europe, it was clear that the German cockroach did not originate there. Although fossil records indicate genus *Blattella* was cosmopolitan (Vršanský et al. 2011) and appeared in Europe 45 million years ago (Vršanský 2008), it is not likely that the modern distribution of German cockroaches is relevant to the ancient distribution of extinct *Blattella* species. Apart from the recognition of a new species during the 7 years War, there are no other *Blattella* species in Europe. Rehn (1945) speculated the German cockroach was brought into Europe following the route of Oriental cockroach; and that it remained confined to Southern Russia for a few centuries, until the 30 years War (1618–1648) brought it into Western Europe. The African origin was based on Rehn's (1945) claim of 15 intimately related species found in northeastern Africa.

More likely out of Asia

The "out-of-Africa" hypothesis was questioned when Princis and Roth, discovered the majority of species of *Blattella* (28 of 54) were endemic to Asia (Princis 1950; Roth 1997; Wang et al. 2010). They also noted that the German cockroach was morphologically more similar to Asian than African species, which suggested it was more closely related to the former. Princis and Roth considered the Asian cockroach (*Blattella asahinai* Mizukubo) from South Asia (Sri Lanka, Myanmar, and Northeastern India) to be particularly similar to the German cockroach (Princis 1958; Roth 1985). Their observations were corroborated by interbreeding experiments in the lab (although only sterile offspring were produced) (Roth

1970), and molecular phylogenetic data, with the German cockroach clustered with Asia species (Mukha 2002; Mukha et al. 2010).

The "out-of-Asia" hypothesis is the most widely accepted scenario currently. However, there are difficulties with this hypothesis. First, not one wild population of the German cockroach has been found in Asia. Consequently, second, there is no clear transport route from Asia to Eastern Europe, especially to Russia and Prussia. Note that the Ottoman Empire was not involved in the 7 year's War, when the German cockroach was first recorded in Europe. This is in contrast to the Oriental cockroach, which likely moved through Ottoman Empire trade routes.

Spread of the German cockroach

The timing of the worldwide spread of the German cockroach may be inferred from written records, including insect specimens in museum collections (detailed list Table. S1). We used these records to map the first recorded occurrence of German cockroach in specific countries or geographic regions (Fig. 1). The very first specimen of the German cockroach was recorded from Denmark in 1763 and known as *Blatta transfuga* (Brünnich 1763; Princis 1969), (later examined by Linnaeus and re-named *Blatta germanica*) (Linnaeus 1767). The first occurrence of the German cockroach outside Europe was from New York, United States, when the Croton Aqueduct was constructed in 1842. New Yorkers believed that the aqueduct brought the pest to the city, and so called German cockroaches "the Croton bugs" (Copeland 2003). By the late 19th century German cockroaches presented throughout almost the entirety of Europe (Bolivar 1884; Miall 1886; Huldén and Huldén 2003), and in most other continents. Their abundance increased during the first half of the 20th century, especially in ports extensively trading with Europe. The current distribution of the German cockroach was probably shaped in the early 20th century.

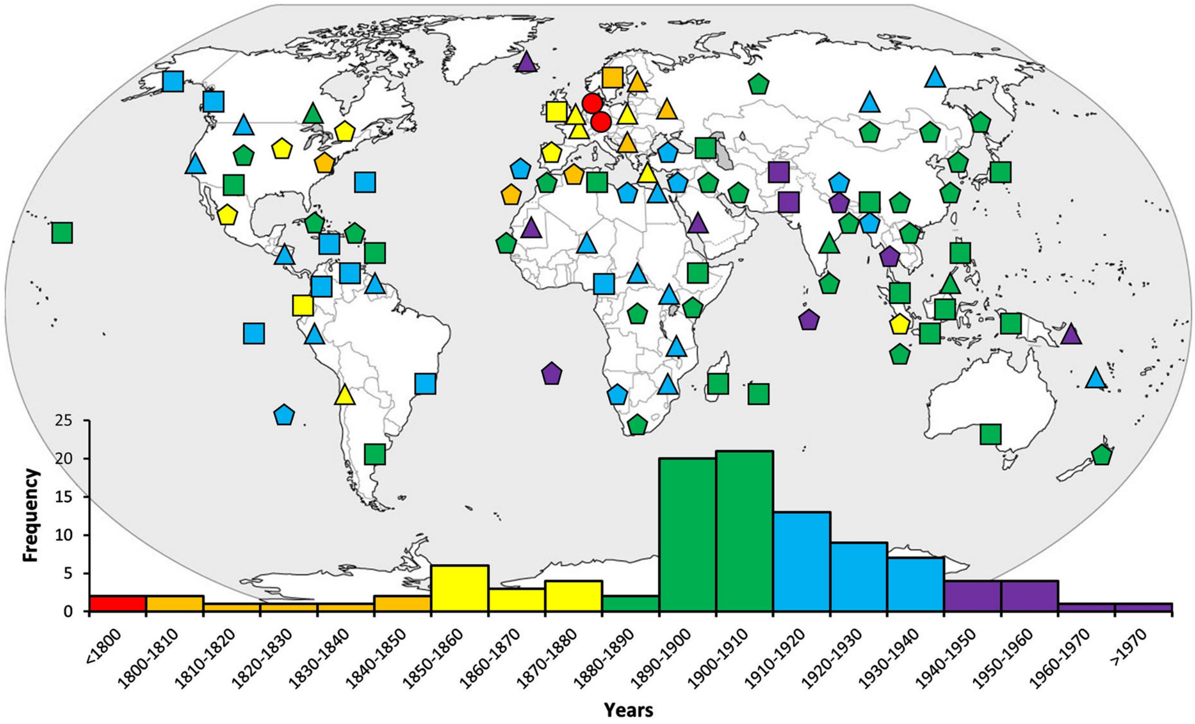

Fig. 1 Map summarizing the first reports of German cockroach around the world. Each point indicates the first occurrence of German cockroach in a specific region. Colors represent 30 years-time periods, the first decade of which is represented by triangles, the second decade by rectangles and the third decade by pentagons. The histogram indicates the number of reports for each 10-year-interval. For detailed information, refer to Table S1

Historical records of spread

It is likely that the invasion and establishment of German cockroach in Europe occurred over a long period of continuous trading, probably from Asia. Historical records of trade between Europe and Asia before the 17th century with information about pests would be most helpful. Unfortunately, such records are rare, and the few that exist do not provide sufficient information to distinguish cockroach species.

There are useful records from the early 20th century, suggesting that German cockroach spread rapidly outside of Europe at that time (Fig. 1). Sea and land transport increased in number and speed, due to the introduction of steam engines. Furthermore, aspects of urban environments became increasingly similar, including the forms of construction of human buildings and city layouts (Martin et al. 2015). The homogenization of the urban environment would allow for easy colonization by "pre-adapted" urban exploiter species, including German cockroaches (Martin et al. 2015). Hotels and hospitals provide two examples: German cockroaches were first reported from these buildings, in many cases (Burgess and Chetwyn 1979; Kutrup 2002; Shahraki et al. 2013).

Historical records have disadvantages. First, not all countries/regions have records. Second, for those that do, the records may indicate when an entomologist able to identify the species was present, rather than the time the German cockroach arrived in the particular region. Third, the records usually lack information on transport, such as mode (ship, train, etc.) and from where. Fourth, there is conflicting information from different sources. For example, some reports claimed that German cockroach first arrived in Japan via cargo ship in the 1950 s (Hitomi 1957), but the earliest museum specimen collected from Japan was dated from 1891. This may suggest a fifth issue, that German cockroaches may have been introduced many times, as population genetic studies have shown.

Genetic data to map spread

In lieu of historical records, genetic methods have been used to explore the relationships among populations of various invasive species worldwide (Ascunce et al. 2011; Boissin et al. 2012; Lombaert et al. 2014). A similar approach could be used to determine the global spread of German cockroach. To date, there are only a few population genetics studies available, and most of these studies are focused on local spread; in France (Cloarec et al. 1999; Jobet et al. 2000), the United States (Mukha et al. 2007; Booth et al. 2010; Crissman et al. 2010) and China (Tang et al. 2016), rather than long distance spread (trans-Atlantic, Vargo et al. 2014). Though these studies cannot be used to draw a global picture, they shed light on the spread of German cockroaches that complements historical records, as they uncover some important patterns during the spread and establishment of the German cockroaches.

First, spread of the German cockroach resembles the process of biological invasions. All studies found evidence of loss of genetic variation, bottleneck effects, and founder effects (Cloarec et al. 1999; Jobet et al. 2000; Booth et al. 2010; Mukha et al. 2007; Crissman et al. 2010; Vargo et al. 2014; Tang et al. 2016). Some of these effects are due to inbreeding, which is common in all invasive species (Fitzpatrick et al. 2011). This includes German cockroach populations (Booth et al. 2010; Crissman et al. 2010), even though they tend to avoid sibling mating (Lihoreau et al. 2008; Lihoreau and Rivault 2010). Three different phenomena commonly observed in biological invasion scenarios (Guillemaud et al. 2011): bridgehead effect, admixture and multiple introductions, were also observed among German cockroach populations (Tang et al. 2016).

Second, previous observations (Owens and Bennett 1982; Rivault 1989) of the limited mobility of German cockroach in urban environments were supported by recent population genetic studies. According to their genetic analyses, Crissman et al. (2010) inferred that the German cockroach population unit in Rayleigh, North Carolina in the USA, is comprised of the individuals within the same building (in other words, different buildings have separate populations). This suggests that urban environments provide German cockroaches with a highly-fragmented habitat, in which all the populations are isolated. This finding was then supported by more genetic studies that reported highly significant level of differentiation among German cockroach populations between buildings in France (Jobet et al. 2000), in rural North Carolina (Booth et al. 2010), multiple cities in the USA and eastern Europe (Vargo et al. 2014) and in China (Tang et al. 2016), even though overall genetic variance (allelic richness) was low.

This probably indicates that introductory events are rare but chance of a successful establishment is high.

Third, though dispersal between buildings is difficult, local expansion is still the major force for the regional spread of the German cockroach. The population genetic studies found that the local population growth rate is much higher than the migration rate (Cloarec et al. 1999; Crissman et al. 2010); this means that most new colonization events of the German cockroach are radiations from regional trading centers, i.e. the bridgehead populations. Fast local population growth will facilitate spread by improving local adaptation, reducing the impact of bottleneck effects (Nei et al. 1975; Fitzpatrick et al. 2011) and creating a higher level of genetic differentiation among populations (Cloarec et al. 1999; Booth et al. 2010; Crissman et al. 2010; Vargo et al. 2014; Tang et al. 2016). One piece of evidence showing the local growth rate is higher than the migration rate comes from Isolation by Distance analysis (IBD) (Wright 1943). IBD can be interpreted as populations within smaller geographical ranges are more genetically related compared to populations in a greater geographical range. Though IBD was interpreted differently in previous, smaller scale, German cockroach population genetic studies, later studies with relatively larger geographical scale show significant IBD (Vargo et al. 2014; Tang et al. 2016). There is one exception (Cloarec et al. 1999), however this anomaly may be explained by the marker: allozymes. The allozymes used did not provide enough resolution to differentiate the genetic distance in two geographical scales, or alternatively, the marker was subjected to selective forces (Parker et al. 1998).

Forth, IBD in previous studies has indicated different spread patterns at different geographical scales. Some observed IBD may be the artifacts of comparisons between different geographical scales. For example, Tang et al. (2016) reported IBD using pairwise distance from both within city and between city comparisons; the scattering of IBD data points can be considered to be stepped, instead of linear. This is because there is low level genetic differentiation between populations within buildings, medium level differentiation between buildings within cities, then high level differentiation between cities. Note that IBD is relatively weak when considered at each geographical scale separately.

Urban ecology of the German cockroach

The worldwide spread the German cockroach in the urban landscape is due in part to the combined effects of abiotic, and biotic factors pertinent the German cockroach, and in part to human factors. The major biological and ecological factors include a short life span, a preference for warm temperatures, a social lifestyle, a preference for the food and shelter in urban environments, and the presence of other competing cockroach species. The human factors include assisted transport, food supplies, and pest control measures, including insecticides.

Size and lifespan

The German cockroach could be more ‘r-selected’ than other urban pest cockroach species, due to its size and lifespan. The German cockroach is smaller, 10–15 mm long, than other major pest cockroaches (e.g. American cockroach size 28–44 mm long) (Cornwell 1968). Thus, for a given amount of resources, the smaller bodied German cockroach is able to sustain a larger population relative to larger bodied species. Commensurate with its smaller size, the lifespan of the German cockroach is about half that of other pest species, and therefore will have more generations in any given time period than other pest species (Cornwell 1968).

The life history traits have two effects on invasion and urban ecology of the German cockroach: one may limit their spread, whereas the other may increase their competitiveness. First, a shorter lifespan requires shorter transportation times, when no or few food resources are available—thus limiting spread (Willis and Lewis 1957). Consequently, German cockroaches may have relied on a series of stepping stone journeys. The earliest European records of “hitchhiking” German cockroaches seem to support this suggestion, and it was described as “brought around European soldiers’ meal baskets”; in other words, by land, with provisions (Brünnich 1763). However, as human technology progressed, transportation became faster, and thus shortened the duration of travel. Perhaps it is not surprising that the greatest expansion of German cockroach distribution occurred in the 20th century.

Second, the smaller size and the shorter life span usually results in a faster potential rate of increase of population size. These may result in a faster potential rate of evolution, thus potentially increasing adaptability. It is possible German cockroaches have evolved greater tolerances, e.g. to insecticides, than other pest cockroach species (See Fig. 2). If so, then this would allow German cockroaches to adapt to new environmental circumstances more rapidly, such as new building materials, new food types, and other human factors. Moreover, the faster reproductive rate decreases the vulnerability to bottleneck effects, which facilitates the overall plasticity to deal with stress and fluctuated environment, especially for re-colonization after local elimination (Flegr 2013).

Temperature and humidity

The German cockroach is likely (sub)tropical, like congeneric species, with an optimal temperature range of 25–32 °C (Roth 1985), which is about 5 °C higher than that for the Oriental cockroaches (Gunn 1935). Consequently, its activity and distribution in temperate latitudes, such as in Europe, North America and northern Asia, are limited to warm seasons and indoor habitats (Ragge 1965). Human technology has improved indoor conditions for the German cockroaches, in particular, heating and insulation in buildings. In addition, heat from mechanical and electrical engines (in compressors, such as refrigerators, air conditioning etc., for elevators, escalators, generators, etc.) likely improved survival for this tropical species in temperate locations; indeed German cockroaches are well known to live around electrical circuitry in buildings (Huang and Zhang 2010).

To adapt to the urban and indoor environment, pest cockroach species have to deal with food depletion

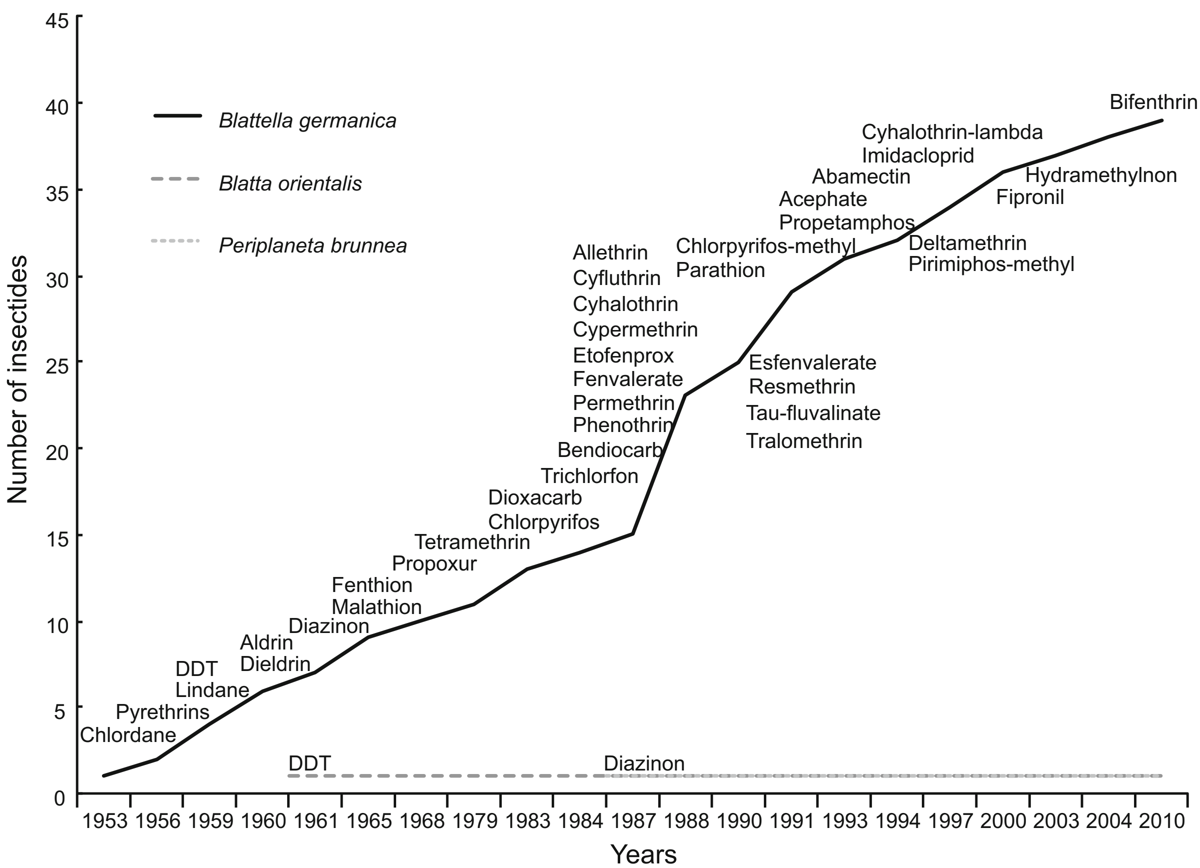

Fig. 2 Cumulative curves of records on insecticide resistance of pest cockroaches. Note that there is no recorded insecticide resistance for four of the major pest species: *Periplaneta americana*, *P. australasiae*, *P. fuliginosa*, *Supella longipalpa*. For detailed information, refer to Table S2

(Hulme-Beaman et al. 2016) and water deprivation (Grandcolas 1998). However, previous studies that compared desiccation tolerance and starvation found that the German cockroach was more vulnerable compared to other pest cockroach species (Gunn 1935; Willis and Lewis 1957; Appel et al. 1983). Rapid body water loss (Gunn 1935), developmental deficit and reproductive reduction (Durbin and Cochran 1985) were detected when the German cockroach was under dry experimental conditions, especially when the dry condition was long and continuous.

From the aspects of invasion and urban ecology, the German cockroach does not appear to have significant advantage to urban environmental conditions, compared to other pest cockroach species. This may help to explain, the German cockroach's relatively later global spread than other global pest cockroach species. The short lifespan and physiological requirements of the German cockroach might have prevented its spread until the development of faster transportation technology and the improvement of the indoor environment, especially heating.

Behavior

Though sensitive to unfavorable environmental conditions, the fact that German cockroach is a ubiquitous urban pest suggests it has physical and physiological advantages derived from its more organized and social aggregations. Many pest cockroaches are gregarious (Roth and Willis 1960; Roth and Cohen 1973), which allows more individuals to survive in small harborages in human dwellings (Grandcolas 1998). German cockroach aggregations are considered to display the most advanced organization among pest cockroach species (Rust et al. 1995; Lihoreau et al. 2012), leading to greater population density and greater individual fitness (Izutsu et al. 1970). There is evidence that the German cockroach displays better foraging organization (Durier and Rivault 2001; Jeanson and Deneubourg 2006) and greater ability to manipulate its micro-environments; mainly by increasing temperature (Lihoreau and Rivault 2008) and humidity (Dambach and Goehlen 1999).

German cockroaches can display unusual behaviors when they are in low population densities. Isolated outside of their group, individual German cockroaches suffer from "isolation syndrome". The symptoms of this syndrome include delay of the imaginal molt (Izutsu et al. 1970), delay of sexual maturation (Gadot et al. 1989; Holbrook et al. 2000) and disorder of behavior, such as stronger exploration-avoidance, reduced foraging and reduced assessment of mating partner quality (Lihoreau et al. 2009). Most of the symptoms are virtually unknown in other pest cockroach species (Lihoreau et al. 2012). Low population densities lead to low cuticular hydrocarbons, which regulate social organization (Danchin et al. 2004), which are the cues that mediate aggregation (Rivault et al. 1998), kin recognition (Lihoreau et al. 2007; Lihoreau and Rivault 2009) and collective decisions (Rivault et al. 1998; Miller and Koehler 2000; Jeanson and Deneubourg 2006; Lihoreau et al. 2010).

From an urban ecological perspective, aggregation and social behaviors are necessary for the species introduced to the urban environment to become "urban exploiters"—the most derived class of urban adapted species (Kark et al. 2007). This is even more important for the German cockroach than for other pest cockroach species, due to the greater limitations on individuals in the urban environment. From the perspective of biological invasion, the social behavior explains the higher local expansion, after the bridgehead effect. Compared to those already established German cockroach populations, newly introduced individuals may have reduced competitiveness after suffering the isolation during hitchhiking (Lihoreau et al. 2012).

Insecticide resistance

The German cockroach is resistant to 42 active ingredients (Zhu et al. 2016), from most major groups of synthetic insecticides (Naqqash et al. 2016) (organocholrides, organophosphates, carbamates, synthetic pyrethroids, neonicotinoids, oxadiazines, and phenyl pyrazoles; see Fig. 2 and Table S2). Resistance has increased over time; it was first observed with chlordane in Texas in March 1952 (Heal et al. 1953); to date, there are more than 279 cases reported worldwide (Arthropods Resistant to Pesticides Database, accessed 14th May 2018). Resistance to insecticides is rarer in other pest species of cockroaches: only two examples are known, for the Brown cockroach in the United States resistant to diazinon (Mallis et al. 1986) and the

Oriental cockroach in France and Germany resistant to DDT (Webb 1961).

There are three major mechanisms of insecticide resistance in the German cockroach: behavioral resistance, physiological resistance and metabolic detoxification (Liu et al. 2005; Zhu et al. 2016). All three mechanisms involve inheritable genetic changes, mostly point mutations (Naqqash et al. 2016). The spread of insecticide resistance can due to multiple independent mutation and duplication events, or a single mutation spread with multiple introductory events, or a complex process involving multiple independent mutation events, followed by multiple introductions, gene flow and local selection (ffrench-Constant et al. 2000; Labbe et al. 2005). For the German cockroach, it is likely that the various genes responsible for insecticide resistance would follow different patterns of spread around the world. However, there are as yet no studies that examine the global genetic patterns for insecticide resistant-associated genes in the German cockroach.

Competition with other species

If the German cockroach is better adapted to urban environments than other pest cockroach species (Roth and Willis 1960; Bell et al. 2007; Lihoreau et al. 2012; Limoee 2012), then we would expect the German cockroach to out-compete the other species over time. To test this expectation, we gathered field reports of cockroach infestations from eight countries, and compared the proportions of each pest cockroach species over time (Table. S3). The proportion of German cockroach infestations increased through time in all instances, supporting the contention that German cockroaches are more competitive in urban environments (Fig. 3).

There is additional, though anecdotal, evidence that the German cockroach will or has replaced the other established pests species in human households. Darwin noted this in the first edition of Origin of Species: "In Russia the small Asiatic cockroach has everywhere driven before it its great congener" (i.e. the American cockroach and other species of *Peripleneta*, which were in the same genus as the German cockroach at the time) (pp. 76, Darwin 1859). Weidner's observations over half of the 20th century in Germany witnessed the German cockroach replacing the Oriental cockroach (Weidner 1983). Cornwell (1968) mentioned that post-war buildings with central heating had significantly higher ratio of the German cockroach to those without heating in the UK. Stejskal and Verner (1996) observed the changing dominance from the Oriental cockroach to the German cockroach in Czechoslovakia within two decades (1960s–1980s) and suggested this was a widespread trend in Europe.

The increase in German cockroach infestations may be due to causes other than greater competitiveness. It is possible that other pest cockroach species have been controlled more successfully through the use of insecticides or other pest management methods. There are a few studies that indicate an overall decline in cockroach infestation regardless of species in Denmark (Rasmussen and Nielsen 1997), Switzerland (Landau et al. 1999) and New Zealand (Robinson 1999), due to comprehensive pest management approaches. Under such circumstances, only those strains with resistance will increase, which may favor the German cockroach, as it has great insecticide resistance.

Origin of the German cockroach: a hypothesis

Although the recent spread and rise to urban dominance of the German cockroach during the 20th century appears to be understood, at least in part, the origin of the species remains obscure. The closest relatives are Asian, yet there are no wild populations of the German cockroach in Asia. Here we propose an explanation of the evolution of the German cockroach, based on and consistent with, the current knowledge. This includes comparisons with other invasive *Blattella* species, known dates of introductions around the world, and the specific biology and ecology of the German cockroach.

Comparisons with known invasive *Blattella* species

There are three *Blattella* species from Asia, related to the German cockroach, which have recent—and documented—invasion histories. These are the previously mentioned and closely related Asian cockroach, plus the Field cockroach and the False German cockroach (Roth 1985). These three species may provide insights into the origins and spread of the German cockroach.

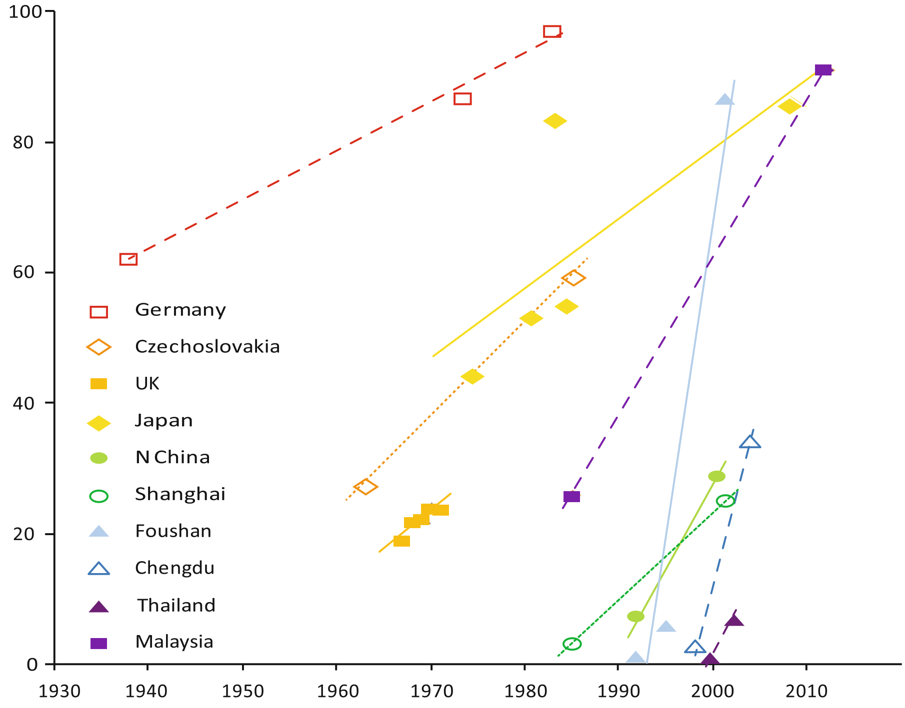

Fig. 3 Scatter plots showing the proportion of German cockroach among cockroaches captured in human household of different locations. For detailed information, refer to Table S3

The Asian cockroach, *Blattella asahinai*, was first discovered and named in Okinawa, Japan, in 1981 (Mizukubo 1981). Roth later examined samples of *Blattella* collected in South Asia and described *Blattella beybienkoi* in 1985 (Roth 1985) that he later synonymized with *B. asahinai* (Roth 1986). The natural range of Asian cockroach is in South Asia around the Bay of Bengal (Roth 1985); the individual discovered by Mizukubo was invasive to Okinawa (Roth 1986). The Asian cockroach is invasive in the southeastern United States (Roth 1986; Austin et al. 2007; Snoddy and Appel 2008; Appel et al. 2009), where it is relatively abundant in agricultural landscapes. It is considered to be a nuisance pest, a potential contaminant of agricultural products, not considered as an important pest because it does not eat living plant tissue, but feeds on leaf litter and rotten fruit. Some have even considered the Asian cockroach beneficial as it consumes eggs of other agricultural pest species (Pfannenstiel et al. 2008).

The Field cockroach (*Blattella vaga* Hebard) and the False German cockroach (*Blattella lituricollis* Walker) have less complicated histories. Field cockroaches are native to Pakistan and Afghanistan, and are reported as invasive in the central United States (Roth 1985). False German cockroaches are native to East and Southeast Asia, and likely invasive to some Pacific Islands, South Africa, Kenya and some Atlantic Islands (Roth 1985; Roth and Rivault 2002; Boyer and Rivault 2003, 2006). Similarly to the Asian cockroach, these two species are nuisance pests in agricultural landscapes as they feed on leaf litter and cause little damage.

These three invasive species, and other *Blattella* species considered as pests to some degree, differ from the German cockroach in where they are found. The other *Blattella* species are found mostly outside human dwellings (Roth 1986; Austin et al. 2007); only the German cockroach is found exclusively inside human dwellings (Robinson 2005). It is possible these three *Blattella* species may resemble an earlier stage of the German cockroach in their process of domestication, with the adaptation to human household environment a recent development (Appel et al. 1983; Grandcolas 1998; Tsai and Lee 2001).

Urban Europe is the original habitat

It is clear from the above three examples that several *Blattella* species from southern Asia can be transported and establish invasive populations in new countries. It is likely that some individuals (or oothecae) of these species, were collected along with the agricultural produce, and then transported to new locations. At the new location, those that were deposited in agricultural areas found food and an environment similar to the one they had left behind.

We suggest a similar scenario for the initial spread of the German cockroach. Populations of the Asian cockroach from southern Asia were transported inside agricultural produce, possibly along trade routes of the Ottoman Empire. These ancestors of the German cockroach hitchhiked through Arabia, Turkey or Italy (Genoa or Venice) and into Europe perhaps via the Amber Route or the Danube River. However the cold European winters killed these tropical insects, except for those that found warm refuge habitats, such as heated buildings. Over time the isolated indoor population became progressively better adapted to indoor habitats. Once the German cockroach had evolved as a distinct indoor species, dependent on humans and their buildings, they could spread to other urban areas. The rise of European countries as global powers may have enabled the spread of German cockroaches from Europe to their colonies.

The above suggestion of evolution of the German cockroach in Europe and then spread from Europe worldwide, is the most intuitive scenario according to extant records and genetic evidence. However, it is not the only possible scenario, for example, it is possible that the Asian cockroach, ancestors of the German cockroach, were brought to more than one urban area, in Arabia and Africa before Europe. It is possible they evolved and spread worldwide through multiple dispersal events from these multiple urban locations. Only a global scale population genetic analysis, using genetic markers with high variability, will be able to test our hypothesis.

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