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Invasive arthropods

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Summary
Many arthropod species have been transported around the globe and successfully invaded new regions. Invasive arthropods can have severe impacts on animal and human health, agriculture and forestry, and the biodiversity of natural habitats as well as those modified by humans. The economic and environmental effects of invasion can be both direct, through feeding and competition, and indirect, such as the transmission of pathogens. In this paper, the authors consider ten examples that illustrate the main mechanisms of introduction, the characteristics that enable species to rapidly expand their ranges and some of the consequences of their arrival.

Keywords
Ant – Arthropod – Environmental change – Food security – Global transport – Insect – Invasive species – Mite – Mosquito – Tick.

Introduction

Arthropods account for more than 80% of all described species. Their success is partly due to their capacity to rapidly expand their range and exploit new habitats. Extant subphyla include the Chelicerata (such as spiders, scorpions and ticks), Myriapoda (centipedes and millipedes), Hexapoda (insects) and Crustacea (crabs, lobsters, barnacles and shrimp). Many arthropods are economically important, serving beneficial functions, such as pollination or being farmed for food production, or deleterious functions, such as damaging plant crops or transmitting pathogens. In this paper, the authors consider some important invasive arthropods in detail, examining the circumstances surrounding their introduction, the characteristics that have enabled them to rapidly expand their ranges and some of the consequences of their arrival.

Arthropods possess several characteristics which may help them to be successful invaders. First, most arthropods have at least one life stage which can be passively dispersed. In the case of winged insects, the most readily dispersed stage is often the imago: its relatively small size and capacity for flight renders it particularly suitable for active or passive dispersal on the wind, often over very long distances, as with *Culicoides* and *Bemisia tabaci* (see below). Some spiders and Lepidoptera larvae also achieve airborne dispersal by 'ballooning', producing silk draglines to catch gusts of wind. In the case of crustaceans, the larval stages are typically the most prone to dispersion, often drifting long distances in sea water as meroplankton.

Other arthropods disperse by attaching themselves to other species. For example, adult ticks may be transported long distances while attached to migratory birds, while the bee mite, *Varroa destructor*, spreads through attachment to adult bees when colonies split and through the queen bee trade. Dispersal may also be inadvertently aided by human activities, such as the international transportation of people, foodstuffs and materials (for example, *Aedes albopictus* and *Anoplophora glabripennis*, discussed below), while some species have been intentionally introduced, either for cultivation or to control other invasive species. Readers interested in a more detailed exploration of the possible routes by which arthropod vectors are introduced are directed to the articles by Reiter (93) and Toy and Newfield (118), in Part 1, while invasive crustacea are discussed further by Gherardi (35).

Many introduction events, however, do not result in successful colonisation, either because the local environment is not suitable or simply because of the vulnerability of small founder populations to stochastic forces. Arthropods generally produce very large numbers of offspring with individually low probabilities of survival. This strategy is particularly effective at rapidly exploiting short-term beneficial changes in the environment, such as an absence of local predators, as well as recovering from unfavourable environmental changes (e.g. seasonal changes). Combined with the dispersal abilities noted above, the net effect is that many arthropod species are able to efficiently locate environmentally suitable habitats, even when they are geographically distant from them, and can rapidly exploit alterations to the environment, such as those caused by human activity or seasonality. As a result, many of the most successful and damaging invasive animal species are arthropods (Fig. 1).

Invasive arthropods and health

Arthropods can affect animal and human health in several ways. Some, such as mosquitoes, midges, ticks and mites, feed on body fluids such as blood or haemolymph. This behaviour may directly weaken the host, as in the case of *V. destructor* (see below), but may also transmit pathogens between hosts. Pathogenic effects caused by arthropod pathogens are typically limited by natural selection to maximise their transmission potential, and the arthropods carrying such pathogens are termed 'vectors'. The establishment of invasive arthropod vector populations in a region may aid the later invasion of an exotic vector-borne pathogen or, alternatively, may allow a native pathogen to spread into new species (55) (see also the following section: '*Culicoides imicola* and other biting midges'). Finally, some arthropods thrive on the products and by-products of human activities, such as food waste. Not only do these species cause economic losses from the consumption of such resources, as well as nuisance value, they may also contribute to the transmission of pathogens via other routes, such as the faecal-oral.

Culicoides imicola and other biting midges

Culicoides biting midges (Diptera: Ceratopogonidae) transmit several important veterinary diseases, including bluetongue virus (BTV) and African horse sickness (AHS). Until recently, the main vector species in Africa, the Middle East and Europe was thought to be *C. imicola* (Kieffer).

While the exact historical limits of this species in southern Europe are unknown, distribution studies suggest that it has spread into new regions in Greece (84), Spain (101) and France (25) during the last 20 or 30 years, although recent studies have found little evidence for further expansion since 2000 (20). Molecular studies also support a recent European expansion (17, 79). *Culicoides imicola* is typically found in consistently warm regions with dry summers (89), and climate change is believed to have increased the suitability of many parts of southern Europe for the species (88). The dispersal of *Culicoides* on the wind is thought to be the principal method by which these species colonise new patches of habitat, and has also been implicated as the source of several outbreaks of *Culicoides*-transmitted pathogens, such as BTV and AHS virus (AHSV) (35, 105, 106, 107). The geographical expansion and increasing density of *C. imicola* populations in southern

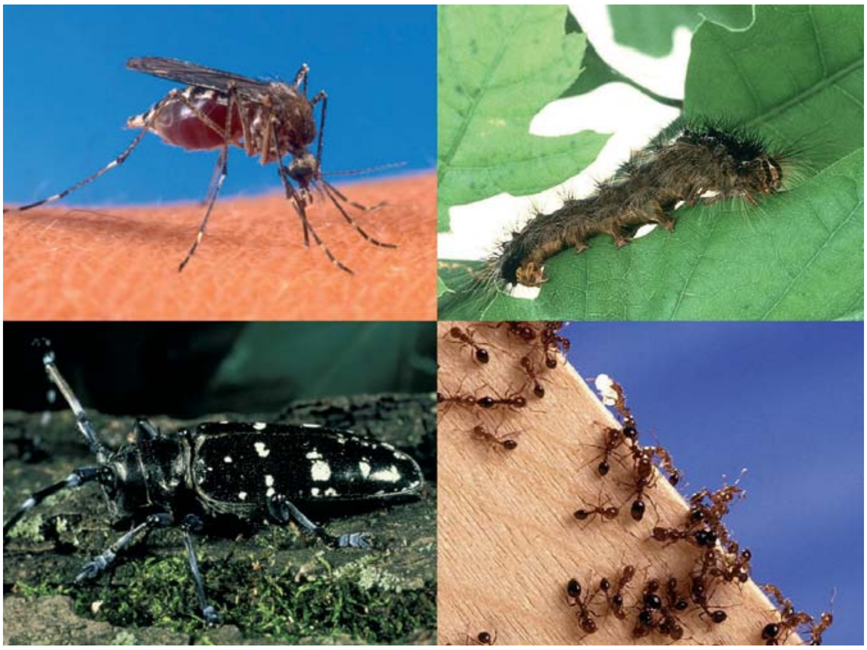

Fig. 1
Some important invasive species
Clockwise from top left: *Aedes albopictus*, *Lymantria dispar*, *Solenopsis invicta*, *Anoplophora glabripennis*
Source: United States Department of Agriculture

Europe are thought to have been key factors in the emergence of BTV in southern Europe since 1998 (90). Moreover, the increased exposure of Palearctic livestock-biting *Culicoides* species to BTV may have encouraged the adaptation of the virus to these species, indirectly facilitating the more recent expansion of BTV into northern Europe since 2006.

The economic damage caused by BTV is difficult to estimate as many of the costs are indirect, for example, as a result of trade restrictions. However, one recent study (120) suggests that the cost of the recent emergence in northern Europe in 2006 and 2007 was around €200 million to the Netherlands alone. African horse sickness results in the rapid death of 80% or more of infected horses, and a similar emergence of AHSV in Europe would have far more devastating economic consequences.

Aedes albopictus and other invasive mosquitoes

Native to China, Korea and Japan, the Asian tiger mosquito, *Aedes albopictus* (Skuse) (Diptera: Culicidae), has spread to most continents and major land masses during the last 50 years, largely as a result of human activity, with only Australia and New Zealand free from invasion (29, 40, 67). First discovered in the United States in 1983, it spread rapidly through eastern North America and is now commonly found in 36 states, as well as in Central and South America (2, 29, 40, 41, 67). In Europe, *A. albopictus* was first detected in Albania in 1979 and then discovered in Italy in the 1990s (73, 94). Once having entered Europe, *A. albopictus* spread to other areas of the continent and has been found, although not always established, in Belgium, Spain, the Netherlands, France and Germany (29, 31, 102). An aggressive human biter and nuisance pest, concern over the spread of *A. albopictus* focuses on its potential role as a vector of a number of viruses, including:

– dengue fever
– chikungunya
– Eastern, Western and Venezuelan equine encephalitis
– Sindbis virus
– Ross River virus
– Mayaro virus
– Japanese encephalitis virus
– West Nile virus
– yellow fever virus (2, 73).

The 2007 outbreak of chikungunya virus in Italy was supported by the establishment of *A. albopictus* in the area before the arrival of the virus (95).

Several characteristics contribute to the ability of *A. albopictus* to spread over large distances and rapidly colonise new areas. As the flight range of the mosquito is quite short, long-range colonisation is the result of accidental, passive transportation. *Aedes albopictus* lays its eggs in water within small pools in rocks, trees, holes and, importantly, in manufactured containers, such as tyres (29, 40, 55, 73, 92). The eggs are resistant to desiccation, enabling them to survive transportation. Once in a temperate location, some strains of *A. albopictus* lay 'diapausing' or hibernating eggs, in response to low temperatures and short photoperiods, allowing the mosquito to overwinter and establish permanent populations in temperate areas where other mosquitoes, such as *A. aegypti*, cannot (31, 73). The –5°C cold-month isotherm marks the maximum northward expansion of *A. albopictus* in Asia and North America, providing a potential range throughout southern and central Europe, as far north as the Arctic Circle on the west coast of Norway (73).

Aedes aegypti (L.) (Diptera: Culicidae) is another invasive container-breeding mosquito. It occurs as two subspecies: *A. aegypti formosus*, a sylvatic, zoophilic strain found only in sub-Saharan Africa and of little global significance, and *A. aegypti aegypti*, which often breeds in water containers and feeds almost exclusively on humans (104).

The use of water containers for breeding by the latter subspecies has facilitated its expansion into all tropical and subtropical regions of the world, while its predominantly human-biting behaviour makes it an effective vector of several viruses, including yellow fever and dengue. It is likely that *A. aegypti* reached the Americas in the drinking water aboard slave ships from the 15th to 19th Centuries, where it caused large outbreaks of dengue and yellow fever in the 18th Century (114). Shipping also brought the domestic form of *A. aegypti* to Asia in the following centuries, where it became the dominant *Aedes* species, and troop movements during World War II brought the mosquito to the Pacific islands (34, 114). The species was apparently eradicated from large areas of Central and South America, using DDT, in the 1940s and 1950s, but these areas were rapidly recolonised when control efforts were reduced in the 1960s (39).

A related species, *Aedes* (Finlaya) *japonicus japonicus* (Theobald) (Diptera: Culicidae), has recently expanded its range for similar reasons. Also of Asian origin, it arrived in the United States in 1998 (85). It has since established populations throughout much of the eastern United States and southern Canada and continues to spread (26, 74). In 2007 and 2008, *A. japonicus* was recorded as having established itself in Belgium and subsequently in Switzerland and Germany (103, 122). The human biting habits of *A. japonicus* implicate the species as a 'bridge' vector for West Nile virus, allowing transmission of the virus from the avian population to humans (74, 103). Laboratory studies have demonstrated that *A. japonicus* is a highly efficient vector of West Nile virus and St. Louis encephalitis, and West Nile virus has been isolated from wild-caught specimens in the United States (74).

Studies have demonstrated that *A. albopictus* out-competes other *Aedes* mosquito species for resources in the larval habitat, leading to the dominance of *A. albopictus* and the replacement of native *Aedes*, and even of the invasive *A. aegypti* in some areas where their ranges overlap (54, 55, 68). The replacement of *A. aegypti*, an efficient vector of dengue and yellow fever, by the less efficient vector, *A. albopictus*, may actually result in a net gain for human health, if disease outbreaks caused by the latter are less severe (29).

Rhipicephalus (Boophilus) microplus, the cattle tick

The cattle tick, *Rhipicephalus (Boophilus) microplus* (Canestrini) (Acari: Ixodidae), is an important pest that feeds on cattle and deer but can be carried by other large mammals. Native to India, Indonesia and Japan, it can now also be found in the tropical and subtropical regions of Africa, Australia and the Americas (23, 32, 69, 112). *Rhipicephalus microplus* causes heavy losses to the cattle industry through its feeding activities, inducing anaemia, weight loss and reduced milk production (53). It also acts as the major vector for the protozoan parasites *Babesia bigemina* and *B. bovis*, which cause babesiosis or cattle fever; pathogens whose distributions have expanded alongside their tick vector (23, 32). Unable to move far on its own, *R. microplus* is spread by the movement of its hosts while it is feeding. The practice of moving cattle by driving them allows the tick to be transported for large distances and, despite animal movement restrictions, *R. microplus* is now endemic in many areas of the world (23). Although it has recently been eradicated from the United States, through acaricide dips and stringent disease controls, it is often found in quarantine stations on the Mexican border (19), and so continues to threaten the United States cattle industry. Accumulated losses, direct and indirect, due to babesiosis in the United States before the eradication of *R. microplus*, have been estimated at approximately US$3 billion (19).

Further discussion of the invasion of exotic ticks and tick-borne pathogens, and their importance for livestock, can be found in the article by Barré and Uilenberg (6).

Varroa destructor

The European honey bee, *Apis mellifera* (L.) (Hymenoptera: Apidae), has been used by humans as a crop pollinator and producer of honey for centuries. However, humans also transported *A. mellifera* to Russia in the early 20th Century, where its sibling species, the Asian honey bee, *A. cerana*, exposed *A. mellifera* to the parasitic bee mite, *Varroa destructor* (Anderson, Trueman) (Acari: Varroidae) (previously described as *V. jacobsoni* Oud.). The exchange of bees across the globe has accelerated the spread of *Varroa* mites (82). Present in Eastern Europe in the 1960s, *V. destructor* moved west, entering the rest of Europe and appearing in the United States in 1987 (82). New Zealand was reached by 2000, resulting in Australia being the only country not to be invaded by the mite (36). *Apis mellifera* is very sensitive to *Varroa* infestations and serious colony losses have been incurred (49). In addition to direct losses caused by feeding, *V. destructor* is a vector of bee viruses and bacteria. Untreated bee colonies generally die within two to three years, a consequence which has resulted in the complete disappearance of wild bee colonies in many regions. The potential cost of *Varroa* infection to the Australian economy has been estimated at US$16.4 million to US$38.8 million per year (21). Control of *V. destructor* has been made more difficult as resistance to acaricides has evolved in the mite population (72), and no eradication strategies are currently considered feasible (62).

Invasive arthropods and agriculture

The production of vegetables, cereals, fruit, timber and other plant-derived products relies on a relatively small number of plant species. Transporting these plants and their products to new regions has also helped to spread the arthropods that feed on them. A large proportion (40%) of the most damaging arthropod pests of agriculture and forestry are invasive species, causing approximately US$13.5 billion in crop losses and management costs each year in the United States, as well as US$2.1 billion in costs to the forestry industry *per annum* (86). As in the case of human and animal health, discussed above, invasive arthropods may damage plants directly, through consumption, or indirectly, by transmitting pathogens, particularly in the case of sap-feeding arthropods, such as the cotton whitefly, *Bemisia tabaci*.

Bemisia tabaci, the cotton whitefly

One of the most successful invasive arthropods is *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae), known by several common names, including the 'cotton whitefly' and the 'sweet potato whitefly'. This aphid-like insect has been recorded on every continent except Antarctica (10). *Bemisia tabaci* is highly polyphagous, with more than 600 plant species recorded as hosts (83). Direct feeding by the insect can cause crop damage; however it is the plant viruses that *B. tabaci* transmits that cause the greatest losses (51). Over 100 plant viruses are transmitted by *B. tabaci*, including cassava mosaic virus and tomato yellow leaf curl virus. These viruses can result in up to 100% yield loss (24, 51). Tropical and subtropical regions are most affected, with cotton, cabbage, bean, cassava, cucurbit, sweet pepper and tomato crops being particularly damaged (10). In temperate climes, the insect is a pest of glasshouses. The winged adults are capable of passive aerial dispersal over large distances and this high mobility is compounded by the ease with which it is transported by trade in plants and plant products. Together, these have resulted in the global expansion of its range. Its small size belies a huge reproductive potential that can result in explosive population growth. Resistance to insecticides with different modes of action has been recorded in *B. tabaci*, increasing the difficulty of its control (22, 27).

Ceratitis capitata, the Mediterranean fruit fly

A major pest of economic importance, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), the Mediterranean fruit fly, attacks the fruit of more than 200 host plants, especially thin-skinned, succulent fruits (65). Eggs are laid under the skin of fruit which may allow infested fruit to be transported without detection. Native to the Mediterranean Basin and Africa, *C. capitata* has established populations across many of the fruit-growing regions of Central and South America and the Pacific, and has only been prevented from establishing itself on the mainland of the United States by extensive and expensive eradication programmes, using insecticides, sterile insect release and other techniques (7, 8, 18, 43, 71, 121). Its successful colonisation of new and diverse habitats has been enhanced by its ability to adapt to cooler climates than other fruit flies can tolerate, as well as its wide host range (71). These traits have allowed *C. capitata* to become a serious international pest of fruit agriculture (8, 71). The economic cost of the potential establishment of this pest in California has been estimated to be US$1 billion per year (7).

Lymantria dispar, the gypsy moth, and other defoliators

The gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae), is native to Europe and Asia, where the larvae feed on a large number of plant species but are particularly associated with *Quercus* (63). Populations are defined by irregular, explosive outbreaks, typically lasting one to five years (28). Mass defoliation by high densities of larvae can result in tree death and loss of production in forests and profound ecological disruption (63, 64). Large areas of forest can be completely defoliated, opening the canopy and having a severe impact on the biodiversity of native species. Repeated defoliation over a number of outbreak years may kill the affected trees. *Lymantria dispar* was introduced to North America from France in 1868 and has subsequently spread over a vast area of the eastern United States and Canada (63, 91, 116). The United States spends US$11 million per year on *L. dispar* control and local eradication (86), but efforts to stop the spread have been only partially successful (108, 116, 127). Females of the *L. dispar* strain present in North America are flightless, and dispersal is by the silk ballooning of first instar larvae and the translocation of egg masses, which are laid on any object near a host plant (63, 91). Therefore, human movement can easily spread the moth to new areas. Climate change may allow areas in the west of North America, where establishment has not yet occurred, to become more suitable for the gypsy moth (66).

Other invasive species that cause defoliation in trees are *Adelges piceae* (Ratz.) (Hemiptera: Adelgidae), the balsam woolly adelgid, and *A. tsugae* (Annand) (Hemiptera: Adelgidae), the hemlock woolly adelgid.

In its native range of Europe and Asia, the feeding habits of *A. piceae*, a tiny aphid-like insect, cause few adverse effects on the trees upon which it feeds. However, in its introduced range in North America, fir trees are highly sensitive to feeding, as no new needles replace those attacked, resulting in defoliation and death of the tree (87, 109). *Adelges tsugae*, native to Japan and China, feeds on hemlock and, in North America, where it has become invasive, causes a similar pattern of defoliation and tree death of host species (50, 128). Eggs and hatchlings of both species are spread by the wind and human movement of timber. The impact on timber production by both species is substantial and consequent or 'knock-on' effects on other species reliant on the host trees, such as tree-nesting birds, have also been reported (56, 86). *Adelges piceae* is now widespread throughout North America, while *A. tsugae* is currently invasive in the eastern United States (81, 87).

Anoplophora glabripennis, the Asian long-horned beetle, and other wood-boring beetles

Anoplophora glabripennis (Motschulsky) (Coleoptera: Cerambycidae), the Asian long-horned beetle, is one of a number of invasive wood-boring beetles. Eggs are laid under the bark of trees and the larvae feed on the cambium layer and pupate in the xylem. Repeated attack weakens branches, disrupts water and nutrient flow and ultimately kills the tree (5, 76, 80). The beetle is a destructive pest in its native range of eastern China and Korea and has been accidentally introduced into North America and southern Europe. Important routes of introduction include wood packaging material and bonsai plants from Asia (117).

Local eradication can be achieved by removing and replacing infested trees but, in the United States, this has incurred estimated costs of US$41 billion (3, 5). The success of *A. glabripennis* as an invasive species may be due to its unusually large host range. Most wood-boring insects specialise in dealing with the natural defences of a few host species and many rely on the compromised defences of stressed hosts to allow the larvae to feed (76), but *A. glabripennis* attacks many tree species without needing the host to be stressed (80). Where it is invasive, *A. glabripennis* has also expanded its host range to exploit the new host species which it has encountered (76).

The ability to adapt to local hosts demonstrated by *A. glabripennis* is also demonstrated in two other invasive bark beetles: *Ips typographus* (L.) (Coleoptera: Scolytinae) and *Dendroctonus valens* (LeConte) (Coleoptera: Scolytinae). Widely distributed in its native range of North America, *D. valens* has shown an ability to use new hosts within its introduced range in China, adapting to these new hosts more readily than other scolytid bark beetles (30). *Ips typographus* can overcome the defences of healthy spruce trees during eruptions, as well as those of stressed trees or trees that have previously been damaged. Widely distributed across Europe and Asia, *I. typographus* is considered to be a very serious forestry pest (4). Both *D. valens* and *I. typographus* are introduced by accidental transport through the international timber trade, and have the potential to expand their range further (52).

Invasive arthropods and biodiversity

The ecological impacts of invasive species include direct and indirect effects on native plants, animals and whole ecosystems (56). Direct predation on and competition with native organisms may lead to the displacement or extinction of the native populations. This impact on biodiversity is seen particularly within island habitats where, in the past, such competition has been minimal, due to the isolation of the indigenous populations. Indirect and ecosystem-level effects are also important and complex ecosystem processes may be disrupted by the presence of alien invasive insect species.

Further discussion of the impact of invasive species on biodiversity can be found in Morand (75) and Hoffmann (44).

Invasive ant species

Ants are easily transported by human movements and by trade (45, 61, 70). While most introduced ant species remain confined to human-modified habitats, several are successful invaders of more natural environments and six are recognised as among the most destructive of all invasive arthropod species (47, 61). Invasive ant species share characteristics that allow successful establishment of a colony in new areas: the species are typically unicolonial, forming 'super colonies' of genetically similar, non-aggressive, interconnected nests. Males mate with more than one female and the females leave the home nest on foot, rather than undergoing a mating flight. They have the ability to nest in a number of habitats; in particular, disturbed areas. They are omnivorous and quick to use food sources and are very aggressive towards other ant species, whose nests they raid (42, 46, 47, 70). Invasive ants often expand their range at the expense of native ant species, and the number of invasive ants can exceed that of all the native ant species within a comparable area (47). The loss of native ant species has important implications for the ecological processes that these insects provide, such as seed dispersal and predation, but the invasive ants may not (61, 98). Serious negative effects have been recorded not only on other ant species but also through the disruption of invertebrate and vertebrate ecosystems (44, 57, 78, 98, 125). Invasive ants have proven difficult to control and impossible to eradicate, once established (47).

Native to South America, the Argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae), has successfully invaded Mediterranean-type (dry and impoverished) habitats throughout the world, including the western United States, Australia and the Mediterranean Basin (14, 48, 96, 97, 98, 111, 113). Exhibiting all the characteristics of an invasive ant species described above, *L. humile* displaces native ant species through aggression and competitive exclusion wherever it has been found, in agricultural, urban and natural environments (13, 14, 46, 48, 98, 100, 119).

Solenopsis invicta (Buren) (Hymenoptera: Formicidae), the red imported fire ant, is another notorious invasive ant. Native to South America, *S. invicta* was introduced into the United States during the 1930s and has since spread to 13 states, the Caribbean islands, Australia and New Zealand (16, 77). An aggressive ant with a painful sting, it is a voracious predator and may interfere with biological control in many crops, displacing native ant and other arthropod species (33, 47, 57, 123). In the state of Texas, the impact of *S. invicta* on livestock, wildlife and public health is estimated to be US$300 million per year (86). Similar species of invasive fire ants, with the same capacity for disruption, are *S. geminata* (F.) and *Wasmannia auropunctata* (Roger) (47, 61, 110).

The big-headed ant, *Pheidole megacephala* (F.), and the yellow crazy ant, *Anoplolepis gracilipes* (Smith), both out-compete other ant species, even to the point of eradicating native species (9, 45). Both species now exhibit widespread distributions. *Pheidole megacephala* is native to Africa but is now present throughout temperate and tropical zones of the world and has invaded large areas of Australia, while *A. gracilipes* is native to Mexico and has spread through much of the Indo-Pacific region, South America and the Caribbean (9, 47, 70, 126).

Harmonia axyridis, the harlequin ladybird

The Harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), also known as the multicoloured Asian lady beetle, is highly variable in coloration. In its native range in Asia, it is a voracious predator of aphids, psyllids and scale insects (1, 58). The appetite of its larvae and the ease with which it could be cultured identified *H. axyridis* as a potential biological control agent for aphids in many crop systems. First used in North America in 1916 (37), the first established feral population was recorded in that continent in 1988. It subsequently spread rapidly across North America, where it has become the dominant ladybird species in many regions (58, 59, 115). A similar rapidity of spread occurred in Western Europe, after the first introduction of the insect in 1982 (1, 11). The spread accelerated from 2002, and the beetle arrived in the United Kingdom (UK), through non-deliberate introduction and flight from the continent. It has become widespread in the UK within a short time (12, 99).

Harmonia axyridis has been blamed for the decline of native ladybird species, both in agricultural and natural ecosystems. As a generalist polyphagous predator, *H. axyridis* competes for resources with native predators and also preys on those species with which it competes, a phenomenon known as intra-guild predation. This can result in not only a loss of biodiversity where *H. axyridis* has become the dominant ladybird species, but also a loss in effective natural pest control, as populations of native predators are reduced (1, 15, 59, 124). The competitiveness of *H. axyridis* over native ladybird species is aided by more rapid development and more generations per year, as it does not require a winter dormancy period for reproduction (60, 124).

Table I
Some key characteristics of the invasive arthropod species discussed in the text

Species	Historical range	Destructive in historical range?	Introduced range	Mechanism of introduction: Natural	Human-made, accidental	Human-made, deliberate	Primarily associated with human-made habitats?	Broad host range?	Disease vector?
Culicoides imicola	Africa	Y	Southern Europe	x			N	Y	Y
Aedes albopictus	Asia	Y	Global tropical to temperate except Australia & New Zealand		x		Y (artificial sites for oviposition)	Y	Y
Rhipicephalus microplus	Asia	Y	Tropical to subtropical Africa, Australia & Americas, except United States		x		N	Y	Y
Varroa destructor	Asia	N	Global except Australia	x	x		Y (beehives)	N	Y
Bemisia tabaci	Not known	–	Global	x	x		Y (glasshouses)	Y	Y
Ceratitis capitata	Mediterranean & Africa	N	Historical plus the Americas and Pacific islands		x		Y	Y	N
Lymantria dispar	Europe & Asia	N	Historical plus North America			x	N	Y	N
Anoplophora glabripennis	Asia	Y	Historical plus North America & southern Europe		x		N	Y	N
Invasive ants	Variously in South & Central America, Africa	N	Global		x		N	Y	N
Harmonia axyridis	Asia	N	Asia, North America, Europe			x	N	Y	N

Y: yes
N: no

Conclusions

Arthropods have been successfully invading new geographical areas throughout recorded history but, in more recent times, human factors have accelerated this process. While certain species, such as *Culicoides* and *B. tabaci*, rely primarily on natural routes of dispersal, such as flight on the wind, the introduction of other species into new regions, such as *A. albopictus*, is partly or wholly the result of human movement and increasing global trade. Some insects, such as *L. dispar* and *H. axyridis*, were initially introduced into new countries and regions deliberately. Although strict quarantine and inspection requirements are now enforced in many areas, invasive arthropods are often inconspicuous or live in cryptic habitats and can be transported undetected.

Many different types of arthropod can be invasive, and the examples already discussed include Diptera, Arachnida, Coleoptera, Hymenoptera, Hemiptera and Lepidoptera. Certain ecological characteristics may make a species more likely to successfully establish itself following introduction. The likelihood of successful establishment in a new region depends upon the availability of a suitable habitat, which is more likely for those species that are either generalists or adapted to habitats resulting from human activity. As can be seen in Table I, every one of the species discussed above is either a generalist or primarily associated with human-made habitats, or both. Since most plant species are now cultivated as a monoculture, and since the introduction of a species into a new region often releases that species from predation pressures, arthropods may reach much higher population densities in their introduced range than in their historical range. As a result, species which may not be destructive in their historical range may cause considerable damage after their introduction into a new one. This may result in economic costs, costs to animal and human health, and damage to local ecosystems. Many arthropods also transmit pathogens and the establishment of such vector species may facilitate or initiate outbreaks of disease. Moreover, the same characteristics that aid the introduction and establishment of invasive arthropod species into new regions make their control and eradication more difficult, and their reintroduction more likely.

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Invasion par les arthropodes

C.J. Sanders, P.S. Mellor & A.J. Wilson

Résumé

De nombreuses espèces d'arthropodes ont été transportées aux quatre coins du globe et ont réussi à s'établir dans de nouvelles régions. L'impact des arthropodes envahissants peut être néfaste pour la santé animale et humaine, ainsi que pour l'agriculture, la sylviculture et la biodiversité des habitats naturels ou modifiés. Les invasions par des arthropodes ont des effets économiques et environnementaux directs, qui concernent leur mode d'alimentation et les effets de la compétition, et indirects, à travers la transmission d'agents pathogènes. En se basant sur dix exemples concrets, les auteurs retracent les principaux mécanismes associés à l'introduction de ces espèces, ainsi que les caractéristiques qui leur permettent de se propager rapidement et les conséquences notables de leur introduction.

Mots-clés

Acarien – Arthropode – Changement environnemental – Espèce envahissante – Fourmi – Insecte – Moustique – Sécurité alimentaire – Tique – Transport mondial.

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Invasión por artrópodos

C.J. Sanders, P.S. Mellor & A.J. Wilson

Resumen
Muchas especies de artrópodos han sido desplazadas por todo el planeta y han invadido con éxito nuevas regiones. La presencia de artrópodos invasores puede acarrear graves perjuicios para la salud pública, la sanidad animal, la agricultura y silvicultura y la diversidad biológica de los hábitats, sean éstos naturales o modificados por el hombre. Los efectos económicos y ambientales de la invasión pueden ser a la vez directos, en cuyo caso pasan por el consumo de alimentos y la competencia, e indirectos, por ejemplo con la transmisión de patógenos. Los autores exponen diez ejemplos que ilustran los principales mecanismos de introducción, las características que permiten a las especies diseminarse con rapidez y algunas de las consecuencias que se siguen de su llegada.

Palabras clave
Artrópodo – Cambio ambiental – Especie invasora – Garrapata – Hormiga – Insecto – Mosquito – Polilla – Seguridad alimentaria – Transporte mundial.

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