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4 Invasions of Terrestrial Arthropods: Mechanisms, Pathways, and Dynamics

4.1 Introduction

Insects and other terrestrial arthropods are particularly notorious as invasive species, both in terms of numbers of species (Hulme *et al.*, 2008) as well as in their ecological (Lodge, 1993; Wilcove *et al.*, 1998) and economic (Pimentel *et al.*, 2000; Pimentel *et al.*, 2005) impacts. Much of the success of terrestrial arthropods as invasive species stems from the same biological features thought to account for their diversity: insects and other terrestrial arthropods are small, often reproduce quickly, have diverse lifestyles, occupy many habitats, and are well protected from the external environment by an exoskeleton (Resh & Cardé, 2009; Gullan & Cranston, 2014). Invasive insects and other arthropods are linked to nearly every human activity. For example, invasive insects and mites include countless domesticated pests in agricultural systems, affecting both plant and animal products. Other arthropods are pests associated with the enterprises of forestry and horticulture. Still more impact urban systems and human health, while others are threats to biodiversity in natural ecosystems. Invasive arthropods play many ecological roles in natural and managed ecosystems, including functioning as all types of consumers (herbivores, predators, parasites, internal and external), but also as vectors of disease for plants and animals. It is this biological and functional diversity of invasive arthropods that makes it difficult to develop simple management strategies for their control, as well as to propose and enact legislation to limit their spread.

Efforts to categorize invasions have provided some structure with which to understand the biology of invasive insects and predict their spread and impact. Particularly useful in this regard has been the distinction between natural dispersal and dispersal associated with human activities (Falk-Petersen *et al.*, 2006), as well as identification of stages of the invasion process itself from dispersal of propagules to successful colonization, and eventual spread and impact, either ecological or economic (Facon *et al.*, 2006; Blackburn *et al.*, 2011). For management, understanding pathways of invasion is critical (Hulme *et al.*, 2008); knowledge of pathways also provides important insights into the interacting biological and socio-economic factors responsible for the spread and impact of invasive species.

In this chapter we use the framework of Hulme *et al.* (2008) to outline the main mechanisms and pathways by which insects and other terrestrial arthropods invade new habitats. We also review novel tools that have contributed to a better understanding of the invasion process and the general trends that these approaches have revealed about insect invasions. Finally, we emphasize the importance of policy and risk assessment in the management of invasive arthropods, and recognize the significant role that they play in both natural and managed ecosystems.

4.2 Mechanisms and Pathways

Hulme *et al.* (2008) identified three mechanisms through which non-indigenous species typically invade new habitats: (1) purposeful importation of a commodity; (2) arrival of a vector involved in transportation; and (3) natural dispersal from another region (Table 4.1). Each of these mechanisms is associated with one or more pathways of invasion: (1) live commodities (organisms for sale) may be released or escape, and other commodities may have associated contaminants; (2) vectors move invasive species as stowaways; and (3) dispersal by invasive organisms may follow corridors or may move unguided. Here, we adopt Hulme *et al.*'s (2008) framework to describe the means by which insects invade new habitats and to illustrate their associated ecological diversity.

Tab. 4.1: Mechanisms, pathways and activities associated with terrestrial arthropod invasions following the invasion classification of Hulme *et al.* (2008).

Mechanism	Pathway	Activity	Insect examples	References
Commodity	Release	Biological control	Ladybird beetles, Coccinellidae Africanized honeybee, *Apis mellifera scutellata*	(Simberloff & Stiling, 1996; Snyder *et al.*, 2004; Majerus *et al.*, 2006; Lombaert *et al.*, 2010; Roderick *et al.*, 2012)
	Escape	Biological control	Asian harlequin ladybird, *Harmonia axyridis*, especially in glass houses	(Majerus *et al.*, 2006)
	Contaminant	Plant trade Wood products Grain Soil	Glassywinged sharpshooter, *Homalodisca vitripennis* Whiteflies, *Bemisia spp.* Hemlock woolly adelgid, *Adelges tsugae* Tephritid fruit flies, *Ceratitus capitata, Bactrocera spp.* Pine beetles, *Dendroctonus spp.* Asian long-horned beetle, *Anoplophora glabripennis* Asian gypsy moth, *Lymantria dispar asiatica* Spider mites, e.g. tomato spider mite, *Tetranychus evansi*	(Clarke *et al.*, 2005; Malacrida *et al.*, 2007; Petit *et al.*, 2008; Petit *et al.*, 2009; Hadjistylli *et al.*, 2010; Nardi *et al.*, 2010; Boubou *et al.*, 2012)

continued **Tab. 4.1:** Mechanisms, pathways and activities associated with terrestrial arthropod invasions following the invasion classification of Hulme *et al*. (2008).

Mechanism	Pathway	Activity	Insect examples	References
Vector	Stowaway	Water transportation (voyaging, rubber tires) Cargo holds Vehicles Animals	Mosquitos, *Culicidae, Aedes spp.* *Gypsy moth, Lymantria dispar dispar* Horse-chestnut leafminer, *Cameraria ohridella*	(Gilbert *et al*., 2005; Johnson *et al*., 2006; Benedict *et al*., 2007)
Dispersal	Corridors	Trails Roadsides	Argentine ant, *Linepithema humile*	(Holway, 1995)
	Unaided	Natural dispersal	Brown planthopper, *Nilaparvata lugens* Colorado potato beetle, *Leptinotarsa decemlineata* Ladybird beetles, Coccinellidae	(Snyder *et al*., 2004; Majerus *et al*., 2006; Lombaert *et al*., 2010; Gillespie *et al*., 2012)

4.2.1 Commodities: Release, Escape, Contaminants

Previous reviews of invasive species (Hulme *et al*., 2008), including insects and other terrestrial arthropods (e.g., Howarth, 1996; Yano *et al*., 1999; Kiritani & Yamamura, 2003; Sax *et al*., 2005) have illustrated the importance of movement of commodities for invasions, a process that is associated with the three following pathways: release, escape, and as contaminants. Live commodities, such as horticultural plants, can become invasive if they escape as weeds to occupy new habitats (see Chapter 3). Similar pathways are possible for insect commodities, such as those intentionally released for biological control. While current programs of biological control using insects are tightly regulated, including pre-release quarantine and host-range testing, some earlier introductions for biological control have had severe negative impacts (Simberloff & Stiling, 1996; Roderick & Howarth, 1999; Snyder *et al*., 2004). For insects, adaptation to novel conditions, particularly novel hosts or new physical environments, is possible in ways not predicted by pre-release testing (Roderick *et al*., 2012). For example, following use in glass houses for biological control, the Asian harlequin ladybird, *Harmonia axyridis,* escaped and became invasive in Britain and elsewhere (Majerus *et al*., 2006; Lombaert *et al*., 2010). Another example of an insect invasion first introduced as a commodity is the release and spread of the more excitable Africanized honeybee, *Apis mellifera scutellata,* in the Americas (Hall & Muralidharan, 1989).

A vast diversity of invasive arthropods are contaminants of commodities, which spread through global trade or other human transport (Hulme *et al*., 2008). Insect contaminants of horticultural, agricultural, and forestry products are particularly important in this regard. Noted examples include *Bemisia* whiteflies, which were moved around the US on ornamental poinsettia and world-wide on other plant species (Perring *et al.*, 1993; Hadjistylli *et al.*, 2010), and the glassy-winged sharpshooter, *Homalodisca vitripennis,* which spread internationally through movement of citrus and vine hosts (Petit *et al.*, 2008). Contaminants of food products also include the recent invasions of Asian citrus psyllid, *Diaphorina citri*; numerous species of fruit flies, *Bactrocera spp.* (Clarke *et al.*, 2005); and the tomato spider mite, *Tetranychus evansi* (Boubou *et al.*, 2012). Movement of wood products, including wooden shipping pallets and lumber, is thought to have spread Asian gypsy moths, *Lymantria dispar asiatica*; pine beetles, *Dendroctonus spp.*; Formosan subterranean termites, *Coptotermes formosanus*; Asian long-horned beetles, *Anoplophora glabripennis*; and Hemlock woolly adelgids, *Adelges tsugae,* to name only a few. Insect contaminants are also common in grain supplies and feed, seeds, stored products, and soil (Hulme *et al.*, 2008). Unfortunately, with an increase in global trade, contaminants of commodities will continue to be a worldwide problem.

4.2.2 Vectors: Stowaways

A fourth pathway for terrestrial arthropods to arrive in new habitats is as stowaways associated with some vehicle or animal vector; this pathway is common for many invasive plants and animals (see Chapters 1, 2, 3, 5, 6). For example, the Polynesian tiger mosquito, *Aedes polynesiensis,* is thought to have stowed away in water containers transported by ancient Polynesians when voyaging across the Pacific. More recently, the Asian tiger mosquito, *Aedes albopictus*, travelled in water found inside discarded automobile tires (Benedict *et al.*, 2007). The glassy-winged sharpshooter, *Homalodisca vitripennis,* and many other species have been observed in the cargo holds of airplanes (Liebhold *et al.*, 2006), and bedbugs, *Cimex lectularius,* move with human belongings (Saenz *et al.*, 2012), presumably in luggage. Flightless gypsy moths, *Lymantria dispar dispar,* have been spread through transport on vehicles in North America (Johnson *et al.*, 2006), a vector which has also been proposed for spread of the horse-chestnut leafminer, *Cameraria ohridella*, in Europe (Gilbert *et al.*, 2005).

Many arthropods are transported to new habitats in association with other animals (Chapter 6). For example, the distribution of ticks carrying Lyme disease is associated with vertebrate hosts (Ostfeld *et al.*, 2006; Swei *et al.*, 2011). Insects can also be vectored by birds, sometimes over great distances, either as external stowaways or in bird guts inside seeds (Gillespie *et al.*, 2012). Finally, humans transport their own domesticated arthropod parasites, especially lice and mites.

4.2.3 Dispersal: Corridors or Unguided

Hulme *et al.* (2008) recognized two pathways of dispersal, either along dispersal corridors or unguided (unaided). While dispersal corridors are likely more important for freshwater aquatic species than for terrestrial species (see Chapters 3, 5), terrestrial arthropods can also disperse to new areas facilitated by ecological corridors, including disturbed roadsides, railways, or walking trails. For example, the invasive Argentine ant, *Linepithema humile*, moves along roads and trails into native forest in Hawaii where it is a serious ecological pest (Krushelnycky & Gillespie, 2008). Terrestrial arthropods can also spread unguided by corridors from one area to another. As one might expect, this pathway is common for insects with great aerial dispersal ability, such as the rice brown planthopper, *Nilaparvata lugens*, which is known to move seasonally between tropical and temperate regions in South East Asia (Denno & Roderick, 1990; Mun *et al.*, 1999; Zhu *et al.*, 2000). However, even less dispersive insects can move efficiently, locally and regionally: examples include the Colorado potato beetle, (Grapputo *et al.*, 2005); various ladybird coccinellid beetles (Snyder *et al.*, 2004; Majerus *et al.*, 2006; Lombaert *et al.*, 2010); and many species of ants (Holway *et al.*, 2002).

4.3 New Tools and Approaches

Invasive insects and other terrestrial arthropods are model systems for the study of invasive species, in that their effects are important economically and ecologically, their distribution is global, and many species are easily collected and monitored. Much of our current understanding of insect invasions comes from new research approaches. Active areas of research include the use of molecular population genetics facilitated by high-throughput DNA sequencing to infer the origins of colonization events and other features of demographic history (Davies *et al.*, 1999b; Estoup & Guillemaud, 2010; Boubou *et al.*, 2012). In this regard, insect collections are proving invaluable as sources of DNA for studies of origins in addition to providing documentation of historical ranges (Carey, 1991; Suarez & Tsutsui, 2004; Malacrida *et al.*, 2007; Marsico *et al.*, 2010). Insects in collections can also provide information on food webs and other ecological interactions, such as through examination of pollen or stable isotopes (Hobson *et al.*, 2012). Recent advances in making predictions of range expansion associated with global change, especially with changes in climate and land use, are possible through using collection data, online databases, niche modeling, and integral projection models (Suarez *et al.*, 2001; Migeon & Dorkeld, 2006-2015; Rapacciuolo *et al.*, 2012; Meynard *et al.*, 2013; Berkeley, 2014; Merow *et al.*, 2014; DAISIE, 2015). Finally, citizen science is allowing the public to participate in large scientific endeavors and at the same time benefit from new knowledge. Insect-related examples of citizen science include identification tools, including *Discover Life* (Pickering,

2009) and *iNaturalist* (Ueda & Loarie, 2013), as well as targeted research focusing on changing geographic distributions, such as the *Lost Ladybug Project* (Cornell University, 2014).

4.4 The Invasion Process

Because of their worldwide economic importance, particularly as pests of agriculture, as urban associates, and as vectors of human disease, the invasion process of many terrestrial arthropods has been studied in great detail. Several common themes emerge that often characterize arthropod invasions:

- Invading populations can be small in size, and often with invasive genotypes unrepresentative of the species as a whole; examples include tephritid fruit flies; mites; mosquitoes (*Culicidae* spp.); and ants (Davies *et al.*, 1999a; Fonseca *et al.*, 2000; Holway *et al.*, 2002; Navajas & Boursot, 2003; Roderick & Navajas, 2003; Navajas *et al.*, 2009). That invasions of terrestrial arthropods can be successful despite small initial population sizes, and thus low genetic diversity that should limit potential adaptation, is a paradox (but see below).
- Many insect invasions involve cryptic invasions of more than one colonization event. For example, molecular genetic studies of medflies, *Ceratitis capitata*, olive flies, *Bactrocera oleae*, oriental fruit flies, *Bactrocera dorsalis*, and other tephritid fruit flies show that multiple, often cryptic invasions are common (Davies *et al.*, 1999a; Clarke *et al.*, 2005; Nardi *et al.*, 2005; Malacrida *et al.*, 2007; Nardi *et al.*, 2010). Similar results have been found in Bemesia whiteflies (Hadjistylli *et al.*, 2010), glassy-winged sharpshooters, *Homalodisca vitripennis* (Petit *et al.*, 2008), Colorado potato beetles, *Leptinotarsa decemlineata* (Grapputo *et al.*, 2005), and other terrestrial arthropods, particularly mites (Boubou *et al.*, 2012). Mixing or hybridization associated with multiple colonization events may increase the genetic variation in colonizing populations, which in theory should contribute to the ability of invasive populations to adapt to novel conditions.
- In many invasive arthropod species, invading populations originate from populations that were invasive elsewhere. An example is the serial invasion history of the medfly, *Ceratitis capitata*, which originated in sub-Saharan Africa and spread to the Mediterranean, and then world-wide (Davies *et al.*, 1999a). Another example is the spread of the glassy-winged sharpshooter from one island to the next within and between island archipelagoes in French Polynesia (Petit *et al.*, 2008). Such species may have overcome limitations of small populations and low genetic diversity through selection in previous colonization episodes.
- A lag period of many generations may occur before the populations reach a size large enough to be noticed or to cause economic damage. Examples include the gypsy moth, *Lymantria dispar dispar* (Johnson *et al.*, 2006), and light brown apple moth *Epiphyas postvittana* (Suckling & Brockerhoff, 2010), among others.

– Species interactions, or lack thereof, are critical in many insect invasions, especially escape from competitors and enemies (Torchin *et al.*, 2003). Other interactions among species may facilitate arthropod invasions, such the presence of host plants or other resources (Leong *et al.*, 2014). For example, the Colorado potato beetle is thought to have moved from native solanaceous species to potatoes with the arrival of European settlers in the American West (Grapputo *et al.*, 2005). For sap-feeding insects, microbe symbionts may provide essential amino acids necessary to switch to new plant host species (McFall-Ngai *et al.*, 2013).

4.5 Policy and Management

Understanding the mechanisms of invasion and associated pathways is critical for management, including monitoring, interception, and policies to restrict trade (Hulme, 2006; Petit *et al.*, 2009). Knowledge of pathways is also necessary to predict future spread and impact. Where invasions involve mechanisms associated with commodities or human activity, such information can aid in understanding the process of invasion. For example, when invasive arthropods are contaminants of commodities, the occurrence and traits of contaminants can be at least partially understood by the commodity itself (Hulme *et al.*, 2008). Likewise, understanding vectors of transportation provides testable hypotheses for the spread of species associated with those vectors (Carey, 1991). For example, airplane and shipping routes, coupled with climate matching, predict aspects of insect invasions (Liebhold *et al.*, 2006; Tatum & Hay, 2007).

4.6 Risk Assessment

Risk assessment associated with predicting the spread and impact of invasive species is difficult in general and particularly so for insects and other arthropods (Shogren, 2000). In part, this is because a changing environment and novel sets of species interactions create uncertainties, but also because invasive propagules can be rare (Drake & Lodge, 2006; Simberloff, 2009; Gillespie *et al.*, 2012). Also, there are few incentives for studying the risk of invasions for non-economic species. For example, national and international initiatives such as the European Food Safety Authority (2015) and USDA APHIS (2015) focus on species of commercial interest but are less concerned about risks to natural environments (but see Gilioli *et al.*, 2014). Risk assessment is a major research gap in the study of invasive species and a topic that will become even more critical in the context of global change in climate and land use (Barnosky *et al.*, 2012).

4.7 Living with Invasive Arthropods

Established insect populations are difficult to eradicate, prompting a reanalysis of both their new roles in ecological communities and our public perception of non-native species (Davis *et al.*, 2011; Richardson & Ricciardi, 2013). In most cases, management must necessarily turn from eradication to mitigation and adaptation and, where control is still an option, policy makers must prioritize efforts on the early stages of invasion, and particularly exclusion (Simberloff, 2009; Simberloff *et al.*, 2012). Exclusion is a difficult task and one that is a prime focus for national and international plant health agencies (e.g., EFSA, 2015; USDA APHIS, 2015). A key question is how invasive species will respond to global climate change and what the resulting impacts will be (Barnosky *et al.*, 2012; Biermann *et al.*, 2012). Will invasive insect species move to more suitable climates, adapt to new climates, or die out? Clearly, invasive arthropods are a global problem, and any solutions will necessarily be multidisciplinary and require international collaboration.

4.8 Conclusions

Terrestrial arthropod invaders are diverse and are associated with many pathways of introduction. New tools, including collection science, molecular population genetics, computational modeling, climate/niche modeling, and integral population modeling are providing novel insights into the dynamics of invasions of terrestrial insects and other arthropods. Many invasive populations of terrestrial arthropods are the result of multiple, often cryptic, colonization events, which adds genetic diversity to founding populations but also complicates management. Terrestrial arthropod populations are difficult to eradicate once established, so the best strategy for management is limiting propagules and establishment.

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In a nutshell

- Terrestrial arthropods are important as invasive species in terms of species numbers as well as ecological and economic impacts.
- Characteristics of terrestrial arthropods, their life histories, and their diversity of lifestyles, contribute both to their success and to difficulty in their management.
- Insects and other terrestrial arthropods illustrate the full range of invasion mechanisms and associated pathways; many are contaminants of commodities.
- New tools, including molecular population genetics, high throughput sequencing, computational methods, climate modeling, and collection science are providing novel insights into the dynamics of invasions.
- Invasive terrestrial arthropods often show a pattern of serial invasions, in which an invasive population gives rise to new invasive populations.
- Many invasive arthropod populations are the result of multiple, often cryptic, colonization events, which adds genetic diversity to founding populations but also complicates management. Invasive populations often stem from other invasive populations.
- Population lags are common, in which invasive populations grow undetected for many generations before reaching a threshold where they become abundant enough to be noticed or cause economic damage.
- While knowledge of mechanisms and pathways is critical to management of invasive arthropods, management is most effective at the early stages of the invasion process, particularly by preventing the initial colonization.
- As a result of their success, invasive terrestrial arthropods are now important elements of biological communities in both managed and natural ecosystems.

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