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Current Opinion in Insect Science

Human-mediated dispersal in insects

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Central to the problem of biological invasions, human activities introduce species beyond their native ranges and participate in their subsequent spread. Understanding human-mediated dispersal is therefore crucial for both predicting and preventing invasions. Here, we show that decomposing human-mediated dispersal into three temporal phases: departure, transport and arrival, allows to understand how the characteristics of human activities and the biological traits of species influence each phase of the dispersal process, and ultimately govern invasion pathways in insects. Integrating these precise mechanisms into future invasion models should increase their realism and generalization for any potential insect invader. Moreover, understanding these mechanisms can provide insight into why some invasive insects are more widely distributed than others, and to estimate risks posed by species that have not yet been introduced.

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Current Opinion in Insect Science 2019, **35**:96–102

This review comes from a themed issue on **Global change biology**

Edited by **Arnaud Sentis** and **Nicolas Desneux**

https://doi.org/10.1016/j.cois.2019.07.005

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Introduction

All species are restricted in their geographical ranges. These limits are determined by the species' adaptations to the environment within their range, interspecific interactions and dispersal barriers [1]. Over the last few centuries however, humans have increasingly facilitated species' movements beyond their historical ranges [2,3] and the rate of new species introductions continues to rise due to the ongoing globalization of trade and travel [4,5]. Some introduced species are able to establish and become invasive, that is, they cause ecological or economic impacts in their introduced range [6]. These alien invasive species are the second most common cause of recent species extinctions, after biological resource usage [7]. In terrestrial ecosystems, insects are generally the most common and damaging group of animal invaders [8]. They cause a range of impacts on biodiversity, ecosystem services (such as nutrient cycling and carbon storage), or human and animal health, generating economic costs of at least 70 billion US$ annually [8,9]. Because of their small size, insects are easily transported by accident through human activities [10•]. In addition, they are sometimes introduced intentionally to serve as biological control agents, food or even as pets [11•].

Human-mediated dispersal is increasingly recognized as a key issue in invasion science [12,13••]. In numerous recent studies, genetic analyses have been used to reconstruct the global spread of many invasive insects [e.g. 14,15]. Most of these studies have found that individual histories of insect invasions tend to be complex and include frequent jump dispersal, multiple introduction events and back-introductions into native ranges [16]. Interestingly, introduced populations often become sources of new introductions via secondary introductions, a phenomenon termed the 'bridgehead effect' [15,17•,18]. This is a positive feed-back process whereby invasions generate new invasions and significantly contribute to rising invasion rates worldwide [19]. Yet, new invasions do not occur with equal probability across space and are linked to the intensity of human activities. It has been shown that countries with higher economic activity [20], population density [21] or human footprint [22] tend to receive a greater number of invasive species. However, proxies of human activities are typically general and have often been found to be poor predictors of new invasions [23]. Thorough knowledge of human-mediated transport is necessary to understand the precise mechanisms involved in the dispersal process and predict future invasion risk.

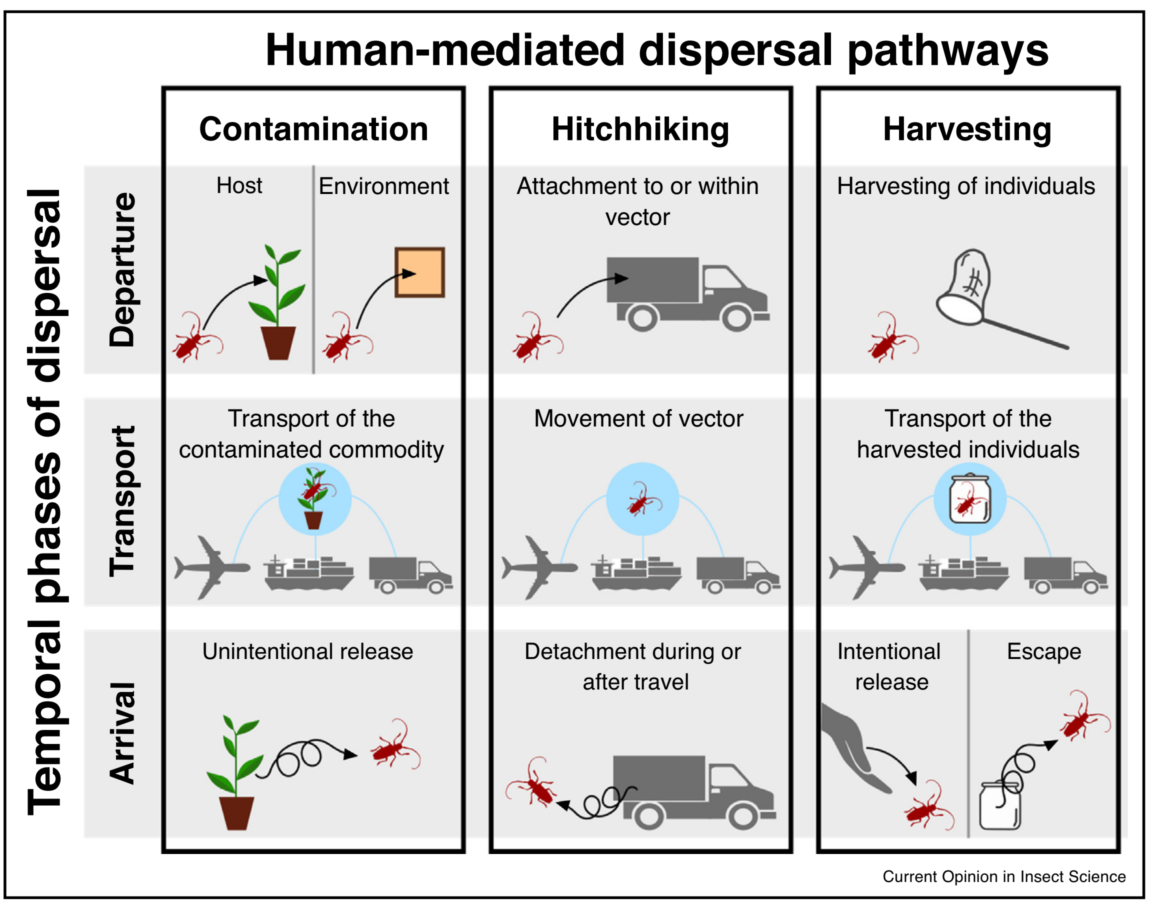
To achieve this, we propose distinguishing between three temporal phases in the human-mediated dispersal process (departure, transport and arrival), as these phases uniquely affect spread dynamics and the geography of invasions [13••,24]. Recognizing each of these phases is important for three reasons. First, it facilitates identifying the characteristics of different human activities that are key drivers of each dispersal phase. Second, it aids understanding of how human-mediated dispersal filters species based on their biological traits. Finally, it provides a basis for the prediction of invasion risk and the allocation of resources for managing the dispersal process.

Three phases in the human-mediated dispersal of insects

Like natural dispersal [25,26], human-mediated dispersal can be decomposed into three phases: departure, transport and arrival ([13••]; Figure 1). Departure covers the initiation of the dispersal process, for example, when a host substrate containing insects is loaded onto a transport vector, when insects attach to a potential transport vector or when insects are captured for shipping. Transport is the movement phase of the dispersal process; it can be performed by any type of vector, for example cars, trains, boats or airplanes. Arrival is the final phase of the dispersal process, when insects become disassociated with the transport vector, when they are released (intentionally or not), or when they escape captivity. Each phase is influenced by human activities that vary enormously in their frequency, spatial scale and direction.

The manner by which human activities drive the three phases of the dispersal process also depends on the pathway through which insects are dispersed [27]. The human activities dispersing insects can be classified into three types of pathways: contamination, hitchhiking and harvesting (Figure 1). The contamination pathway corresponds to the transportation of a commodity contaminated by insects (eggs, larvae or adults) either because the commodity is the insect's natural host (e.g. plants, mammals) or its immediate environment (e.g. soil, water) [10•]. For example, invasive fire ants (*Solenopsis invicta*) were shown to be dispersed during road maintenance by the transport of soil from invaded depots to maintenance sites (i.e. road shoulders) [28]. In the hitchhiking pathway, insects actively attach to an object not directly related to their natural environment (e.g. shipping container, car) [10•]. For instance, gypsy moths sometimes lay eggs on cars and trucks that are then transported while the vehicles travel, and the larvae eventually detach from these vectors after hatching [29]. The harvesting pathway consists of the intentional capture of insects by humans for some, often commercial, purpose (e.g. pet trade, biological control) [11•]. This last pathway

Figure 1



Decomposing human-mediated dispersal into three phases: departure, transport and arrival, for each invasion pathway. Contamination and hitchhiking pathways are accidental while in the harvesting pathway, species are intentionally captured and transported but arrival can be either intentional (release) or unintentional (escape).

leads to introductions either by intentional release or subsequent escape from captivity [2] (Figure 1). European bumblebees (*Bombus terrestris*) have been harvested and reared commercially for pollination purposes. They were directly released into the wild in New Zealand and escaped from glasshouses in Japan, two areas where they are now invasive [30].

Importantly, the characteristics of how humans travel or transport commodities (such as the distance travelled, the type and amount of transported commodities; Table 1) and the biological traits of species selectively transported by human-mediated dispersal (such as morphology, life histories or behavior; Table 2) depend both on the dispersal phase (i.e. departure, transport and arrival) and the dispersal pathway (i.e. contamination, hitchhiking or harvesting) [13••].

Characteristics of human activities

Departure phase. The key aspect of this dispersal phase is the number of individuals of a species that leave their native (or invasive) range. This population level of departure determines propagule pressure, a central feature of invasion success [31]. The quantity of transported commodities and traffic volume are important for the contamination and hitchhiking pathways, respectively, because they affect the frequency of dispersal events (propagule numbers), and the number of individuals transported per dispersal event (propagule size) [31,32•]. In the harvesting pathway, the frequency of departure typically depends on commercial factors such as costumers' demand or harvesting cost [11•].

Transport phase. The distance of human-mediated dispersal can vary strongly with different human activities. This is especially important for the contamination and harvesting pathways where species are less likely to interrupt the transport phase by detaching during travel, in contrast with the hitchhiking pathway [13••]. The structure of the different transport networks also influences the direction of dispersal [33,34], leading to a higher propagule pressure in the most connected areas [35•]. The properties of transportation networks, such as their connectedness and the existence of highly connected transportation hubs are potential drivers of bridgehead effects [19]. Finally, the probability of survival of insects during transport depends on factors such as the duration of the transport, exposure to extreme temperatures or limited access to food and water [36••]. These external conditions are more relevant during accidental transport rather than in the harvesting pathway where transport is intentional and designed to keep the species alive. However, in the contamination pathway, insects are often transported with hosts which may provide ideal conditions for surviving transport over long distances.

Arrival phase. Arrival is generally the most studied phase of human-mediated dispersal in insects because the introduction of species into a new location is typically the only phase of human-mediated dispersal easily

Table 1

Characteristics of human activities affecting each phase of human-mediated dispersal in each pathway. Associated references indicate papers that mention the relationship. References with an asterisk correspond to studies on taxa other than insects

Characteristics of human activities

Temporal phases of dispersal	Parameters of human-mediated dispersal	Human-mediated dispersal pathways: Contamination	Hitchhiking	Harvesting
Departure	Frequency of departure	**Probability of contamination:** - Type of commodity (e.g. soil, plants, wood) [10, 75*] - Amount transported (propagule size) [68] - Frequency of transport (propagule number) [68]	**Probability of attachment:** - Type of vector (e.g. car, boat, train) [13*, 24*, 32] - Number of vectors (i.e. traffic volume) [73*] - Artificial light [47]	**Probability of capture:** - Consumer' demand [71*, 76*] - Harvesting cost - Regulations (e.g. import bans) [72*]
	Survival	- Treatment by exporter [39]	- Treatment by exporter [39]	- Quality of capture (harvesters' experience)
Transport	Distance of dispersal	- Type of human activity (e.g. domestic, industrial) [10, 13*] - Distance traveled by humans [13*, 80]	- Type of human activity (e.g. domestic, industrial) [10, 13*] - Distance traveled by humans [13*]	- Distance between species and costumers [72*]
	Direction of dispersal	- Topology of transportation networks [33, 35, 19] - Human history (e.g. human colonization) [70]	- Topology of transportation networks [33*, 35, 19] - Human history (e.g. human colonization) [70] - Regulations (e.g. import bans) [72*]	- Location of species and customers [72*]
	Survival	- Duration [82] - Temperature range - Oxygen, water and food availability	- Duration - Temperature range - Oxygen, water and food availability	- Quality of transport (e.g. mail, package, service delivery) - Period of the year (i.e. winter in north hemisphere)
Arrival	Frequency of arrival	**Probability of leaving commodity:** - Number of transportation events [66, 73*]	**Probability of detachment:** - Number of vectors (i.e. traffic volume) [73*] - Type of vector - Vibrations	**Probability of escape:** - Quality of containment [11, 38] - Owner experience **Probability of intentional release:** - Type of human activity (e.g. biocontrol, pet trade) [11] - Owner's knowledge about invasion risks - Owner's age - Species' price/ any value
	Survival	- Treatment by importer [39, 74, 75*] - Import control/quarantine [74, 55, 75*] - Proximity to suitable habitats or hosts	-Treatment by importer [39, 74, 75*] - Import control/quarantine [55, 74, 75*] - Proximity to suitable habitats or hosts	- Regulations (e.g. import bans) [74*] - Proximity to suitable habitats or hosts

Table 2

Species traits and demographic parameters can be under selection in each phase of human-mediated dispersal in each pathway. Associated references indicate papers that mention the relationship. References with an asterisk correspond to studies on taxa other than insects

Traits and demography of insect species

Temporal phases of dispersal	Parameters of human-mediated dispersal	Human-mediated dispersal pathways: Contamination	Hitchhiking	Harvesting
Departure	Frequency of departure	**Probability of contamination:** - Size/density of populations [48, 69] - Hiding/Nesting behavior [10, 57, 63*] - Interactions with plants, animals (e.g. parasites) [10] - Phenology [81]	**Probability of attachment:** - Size/density of populations [48, 69] - Oviposition behavior [57] - Foraging behavior [66] - Attachment ability [52*, 68*] - Phenology [81] - Attraction to artificial light [47]	**Probability of capture:** - Size/density of populations [48, 69] - Size of individuals [11, 76*] - Aesthetics (e.g. color, spines) [11] - Growth rate, generation time [11] - Rarity [78*, 79*]
	Survival	- Resistance to treatments - Cuticule thickness (i.e. resistance to crushing) [68]	- Resistance to treatments	
Transport	Distance of dispersal		- Timing of detachment (e.g. eggs hatching) - Attachment ability [68*]	
	Direction of dispersal			
	Survival	- Resistance to stressful conditions (e.g. starvation, dehydration) [36] - Diapause [77*]	- Resistance to stressful conditions (e.g. starvation, dehydration) [36, 52*]	
Arrival	Frequency of arrival	**Probability of leaving commodity:** - Size (detectability)	**Probability of detachment:** - Phenology - Efficiency of attachment [52*]	**Probability of escape:** - Size [38] - Behavior [38] - Flight ability [38] **Probability of intentional release:** - Known invasive status
	Survival	- Resistance to treatments [83]	- Resistance to treatments [83]	

observed [37]. In the harvesting pathway, the quality of containment (e.g. the facilities and boxes in which insects are kept or reared) will influence the probability of escaping captivity [38]. In the two other pathways, quarantine requirements and phytosanitary treatments implemented at ports of entry (e.g. fumigation, cold/heat treatments, irradiation) are often implemented to reduce the insects' probability of surviving the arrival phase [39].

Characteristics of human-mediated dispersal can be modeled to predict the associated risks, and these predictions gain realism when they explicitly consider different parameters involved in each dispersal phase [40,41]. Focusing on the characteristics of human activities could be utilized in generalizable models that can be adapted for a wide range of human activities and various types of insects dispersed by humans through the same pathway [42]. This is important because building a specific human-mediated dispersal model for individual species is both challenging and time-consuming [42].

Species' traits and demography

The different phases of human-mediated dispersal also favor different sets of biological traits. In plants, traits such as large and heavy seeds are favored in the harvesting pathway while the contamination and hitchhiking pathways favor small seed size [43]. Less is known about the traits facilitating transport by insects, though it is clear that species that have historically invaded various world regions are a non-random sample of the global species pools [36••,44,45]. Small sized insects are less likely to be observed and therefore more likely to contaminate material in shipments. For example, small sap-feeding insects are commonly transported with imported live plants [46]. Attraction to light may facilitate association with ships and other transport vectors and thus facilitate transport of insects in the hitchhiking pathway [47].

Departure phase. A high population size and density should increase the probability of being collected accidentally or voluntarily by humans, and thereby increase the frequency of departure [48•,49]. These demographic traits are likely selected for in all three pathways. In the harvesting pathway, insect characteristics such as large body size and fast growth rate increase the probability of being harvested by humans for both the pet trade, and human and pet food [11•]. In the contamination pathway, a strong association with plant species is likely favored, given that plants and parts of plants (e.g. seeds, roots, fruits) are economically important and a frequently transported commodity [46]. This association is the main hypothesis for why Hemiptera and other sap-feeding species are overrepresented among introduced insects [50].

Transport phase. Traits such as higher resistance to stressful conditions such as starvation, dehydration or exposure to toxins during transport are important for surviving the transport phase [36••,51,52]. These traits are likely to be especially favored in the contamination and hitchhiking pathways. Insects that have an extended sessile dormant stage (e.g. diapause or estivation) may be more successfully transported in the hitchhiking pathway. Such traits may not be necessary in the contamination or harvesting pathway as they provide life-sustaining conditions.

Arrival phase. In contamination and hitchhiking pathways, imported commodities and arriving vectors may be subjected to phytosanitary treatments or inspection at ports [53]. Behavior and physiology of some species may make them more resistant to phytosanitary treatments [54]. Small body size (and thus poor detectability) can increase the probability of insects evading detection [46,55]. In the harvesting pathway, small body size, flight abilities or high levels of exploratory behavior might increase the probability of escaping captivity.

The concept that invasions filter species based on their traits is not new [56]. However, studies of differences in traits between native and invasive species (or populations) generally focus on ecological filtering after human-mediated dispersal, that is, during the establishment stage. For example, successful invaders may have a higher competitive ability than native species (or populations) [57–60] or be pre-adapted to new environmental conditions in their introduced range [58,61,62]. Only recently has human-mediated dispersal started to be discussed as an ecological filtering force or selective pressure that might select species or phenotypes based on their propensity to disperse by human activities [13••,36••,63]. Therefore, improving our knowledge on traits favoring species during each dispersal phase is crucial for understanding why some insects are more widely distributed than others [5,64] or for predicting invasion risks of species that may be introduced in the future [40,48•].

Conclusion

In this short review, we do not aim to provide an exhaustive list of factors influencing human-mediated dispersal in insects. Rather, we hope to stimulate further theoretical and experimental research considering phases and pathways as distinct selective filters acting before the establishment and spread of invasive populations. Prevention has been recommended as generally the most efficient approach for managing invasions [65]. Thus, improved knowledge of the drivers of human-mediated dispersal is essential for identifying some of the best options for preventing human activities from dispersing insects at all spatial scales.

Conflict of interest statement

Nothing declared.

Acknowledgements

CB, JMWG and GFM were supported by the University of Lausanne and funding by Canton of Vaud. AML was supported by grant EVA4.0, No. CZ.02.1.01/0.0/0.0/16_019/0000803 from OP RDE.

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