Advances in understanding and predicting the spread of invading insect populations

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Highlights

Spread is a critical stage of the biological invasion process

Novel uses of data sources facilitate our ability to estimate spread rates

Advances in modeling aids in understanding the factors affecting spread dynamics

Understanding and predicting spread enhances decision-making in management

Abstract

Understanding and predicting the spread of invading insects is a critical challenge in management programs that aim to minimize ecological and economic harm to native ecosystems. Although efforts to quantify spread rates have been well studied over the past several decades, opportunities to improve our ability to estimate rates of spread, and identify the factors, such as habitat suitability and climate, that influence spread, remain. We review emerging sources of data that can be used to delineate distributional boundaries through time and thus serve as a basis for quantifying spread rates. We then address advances in modeling methods that facilitate our understanding of factors that drive invasive insect spread. We conclude by highlighting some remaining challenges in understanding and predicting invasive insect spread, such as the role of climate change and biotic similarity between the native and introduced ranges, particularly as it applies to decision-making in management programs.

Introduction

Spread: the process by which a species moves from one area to another. Animals have been on the move for millennia, sometimes as part of migratory behavior, more often in search of food. Insects, the first group of organisms to evolve flight capability more than 300 million years ago, have been constantly on the move in search of resources to exploit. Owing to their small size and persistence, they are also adept at hitchhiking on products moved by humans, a pathway at least as old as the ancient Silk Route that linked Asia with Africa and Europe. Nowadays, with globally connected economies and transportation networks, products are continuously moved around the world, occasionally leading to the unwanted arrival of new species into new areas. This arrival stage, as the first stage of the biological invasion process, is often the product of long distance, anthropogenically-mediated spread. Upon establishment, species spread to new areas through both short- and long-range movement, with the latter often human-assisted. Attempts to predict and understand the spread of invading insects, from the mechanisms that facilitate arrival to the processes that affect spread post-establishment, have a long history dating at least to the late 1800s given the economic importance of invasive insects as agricultural pests. In this review, we examine recent methods in understanding and predicting invasive insect spread. We first focus on data sources that can be used to quantify spread rates. We then discuss advances in modeling methods that enhance understanding of the factors mediating and affecting invasive insect spread. We conclude by highlighting the importance of understanding invasive insect spread in the development of management programs, and the effect that climate change could have on spread dynamics.

Data sources to estimate invasive insect spread

The spread of any invading organism is defined by the spatial displacement in its distribution through time. Thus, any attempt to quantify spread requires knowledge of where an organism is over at least two time periods. Earlier methods to quantify spread relied on crude approximations of spatial boundaries, and whatever methods were available to detect the organism [1]. The identification and synthesis of species-specific semiochemicals facilitated the development of more sensitive insect trapping devices that more precisely defined spatial boundaries. Methods to use space-time data to estimate spread rates have been refined over the years, from linear regression techniques to spatially-explicit approaches that can account for anisotropic spread [2]. Regardless of the method to estimate spread, distributional data collected through time is still required. In this section, we highlight the use of Digital Earth data, citizen-science collected data, and genetic data derived useful in estimating distributional ranges for quantifying spread rates (Fig. 1).

Digital Earth Data

Digital Earth data have increased dramatically over the past several years, facilitating many avenues of research [3]. An early use of such data to estimate insect presence was reported by Rousselet et al. [4], who used Google Street View to map the distribution of pine processionary, *Thaumetopoea pityocampa* (Denis & Schiffermüller). Using drone technology to assess insect presence or damage levels to guide pest management decisions [5] could also be useful in estimating the space-time distributions needed to quantify spread. Remote-sensed data in ecological applications is now several decades old, but there are still opportunities to apply this technology for smaller organisms such as insects [6*]. For example, Park et al. [7] used a drone equipped with a multispectral camera to detect trees suspected to be infected with pine wilt disease, which is caused by a nematode vectored by *Monochamus* species. Due to the labor and resources required to monitor an invading species across a landscape using trapping devices, Digital Earth Data could facilitate efforts to delineate spatial boundaries through time needed to estimate spread. However, limitations in microclimatic data, which are particularly important in affecting poikilothermic organisms, could affect the ability to estimate changes in spatial distributions through time [8]. For example, phenological predictions of the occurrence of life stages, some of which could be the stage sampled in invasive insect management programs (i.e., pheromone-baited traps aimed at detecting adults), might be over- or underestimated if broad-scale weather data do not sufficiently account for microclimatic variation.

Citizen-scientist collected data

Many invasive insects have been first reported by the public. In fact, in a study of insect eradication outcomes, programs that were initiated following passive detection methods (e.g., public vigilance), were more successful than those that relied on host or habitat searches by management agencies [9]. The widespread adoption of cellular phones over the past two decades has undoubtedly facilitated the collection of space-time data from citizens, such as the use of Smartphone apps to identify invasive species and provide the data needed to estimate spread [10*]. Not surprisingly, citizen-scientist collected data has been used to monitor the spread of invasive insects [11] and can be combined with climatic models to project invasive insect spread [12]. However, the potential for misidentification, especially true for a group as speciose as insects, remains a challenge [13].

Genetic techniques

The use of genetic techniques, such as DNA barcoding [14], in invasive species monitoring programs has greatly increased over the past several years. Biosurveillance based on genetic techniques can be used to monitor all stages of the biological invasion process, including species origins and spread [15]. DNA metabarcoding techniques can be used in multi-species identification from specimens collected, for example, from trapping devices [16], which can provide insight into the arrival stage and hence, the product of initial spread from a native area. The invasion history of an organism may also be ascertained using genetic approaches. For example, Bras et al. [17] used the genetic architecture of box tree moth, *Cydalima perspectalis* (Walker), in its native and invaded range to ascertain primary and secondary introduction events. Ortego et al. [18] used genetic tools to ascertain introduction frequency and spread of the North American boatman, *Trichocorixa verticalis* (Fieber). Lastly, an emerging tool in invasive species detection is the use of environmental DNA (eDNA) in which genetic material deposited by an organism is analyzed to ascertain presence, such as from soil or plant samples [19**]. Although eDNA is useful for detection in space, it currently lacks a precise temporal signature needed to estimate spread.

Modeling invasive insect spread

Insect spread is the result of interactions among various mechanisms, most importantly population growth and dispersal [20]. Species with high dispersal capabilities but reduced growth rates might be diluted in space and may not readily establish, while species with rapid growth but low dispersal capabilities might spread slowly. Furthermore, waiting times between arrival and establishment can be affected by environmental and anthropogenic variables [21]. Modeling each mechanism individually (dispersal and growth), and describing spread at an integrated level, furthers our understanding of the factors that affect the spread of invading species (Fig. 1). Here we review recent innovative approaches to understanding population growth, dispersal, and integrated spread.

Population growth

Population growth factors, such as survivorship and reproductive rates, can provide a potential indication of the spread of an invading species, regardless of dispersal capability. Among insects, temperature and host availability are often the main drivers affecting population growth. Insect phenological models describing the development rate of life-stages as a function of temperatures can assess where a species could potentially establish [22]. Ecophysiological models using spatially explicit growth rates and estimates of habitat suitability can also predict potential distributions [23], as can models that use other environmental factors such as humidity [24]. Species distribution models, which consider the correlation between bioclimatic variables and species occurrence, can be populated with data, including with data collected through citizen science efforts [12], to build niche models, and refined to consider habitat data from the native and invaded areas [25], or microclimates in urban versus non-urban areas [26]. Combining evolutionary dynamics with environmental data can substantially refine predictions from niche models [27*]; indeed, Gougherty and Davies [28*] highlighted the importance of host tree phylogenetic diversity on the geographic extent of non-native insects.

Dispersal

The spread of invasive insects often proceeds through stratified dispersal, which combines short and long distance dispersal. Short distance dispersal is usually related to species dispersal capabilities, while long-distance dispersal is more often associated with human-mediated dispersal. Dispersal kernels are commonly used to quantify species movement, with various techniques, such as mark-release-recapture, used to calibrate them. More recently, flight mill data [29] was used to parameterize a model to estimate dispersal of the pine wood nematode vector, *Monochamus galloprovincialis* (Olivier), in forest ecosystems. Genome-wide SNP markers have been used to infer dispersal by analyzing colonization dynamics across an invaded range [30]. Other recent advances include using least-cost path analysis to model dispersal trajectories in heterogeneous landscapes [31], dynamic representations of landscape connectivity to better account for variation in dispersal when the structure of habitats change over time [32], and using abiotic factors, such as temperature and light conditions, to quantify flight probability [33], all of which can affect the diffusion coefficient.

Long-distance movement of invading insects remains a challenge due to its stochasticity. Efforts to consider long-distance movement include quantifying the role atmospheric-mediated dispersal [34], and human-mediated dispersal such as the effects of spatial heterogeneity in human population density at the source and destination [35]. Given the role of humans in moving invasive species, attempts to understand long-distance movement continue to focus on trade [36] and visitation networks [37] including the transportation of infested material [38]. Modeling spread dynamics can also serve to test different dispersal scenarios and determine if spread is attributable to human vectors [39].

Integrated models

Models that combine population growth given local bioclimatic conditions, innate dispersal capabilities, and human-mediated movement hold promise for understanding invasive insect spread [40]. However, given the complexity, relatively few models describe growth and dispersal simultaneously [41**]. Combining components in an integrated model could be used to better understand spread. For example, dispersal could be reduced to potential entry points (i.e., through human-mediated dispersal) and combined with habitat suitability to assess invasion risk [42]. Considering phenology during the transportation stage along trade routes also informs the probability of human-mediated long-distance movement [43]. Among herbivorous insects, it is crucial to consider interactions between the insect and its host plant in terms of phylogeny [44] and habitat connectivity [45]. Some models account for multiple interactions, such as the interactions among the invading insect, its host plant, fire, and drought [46] or the interplay between insects and fungal pathogens [47]. The effectiveness of control measures on spread can also improve understanding of invasion dynamics; for example, Cacho and Hester [48] describe the dynamics between an invading species and biological control agents to determine conditions needed for biocontrol success.

Remaining challenges

Despite recent attempts to understand the effect of control measures on spread, more work is needed in this area especially with regard to tactics that could be implemented in the near future. Although insect phenology has been considered in efforts to predict the area of potential establishment, its role in spread remains unclear. Furthermore, when considering climate change, insect species could adapt either by shifting their seasonality to match changing thermal conditions, dispersing to more favorable areas, or both [49*]. Phenology can also interact with spatial spread in climate-driven range expansions [50]. Lastly, environmental resistance is an important factor in spread that deserves greater attention, even though modeling species interactions to assess habitat invasibility can be complex. Considering biotic similarity between species communities in the native and invaded range could be useful in assessing environmental suitability [51*].

Acknowledgements

PCT acknowledges support from the David R.M. Scott Endowed Professorship in Forest Resources at the University of Washington.

Funding

This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

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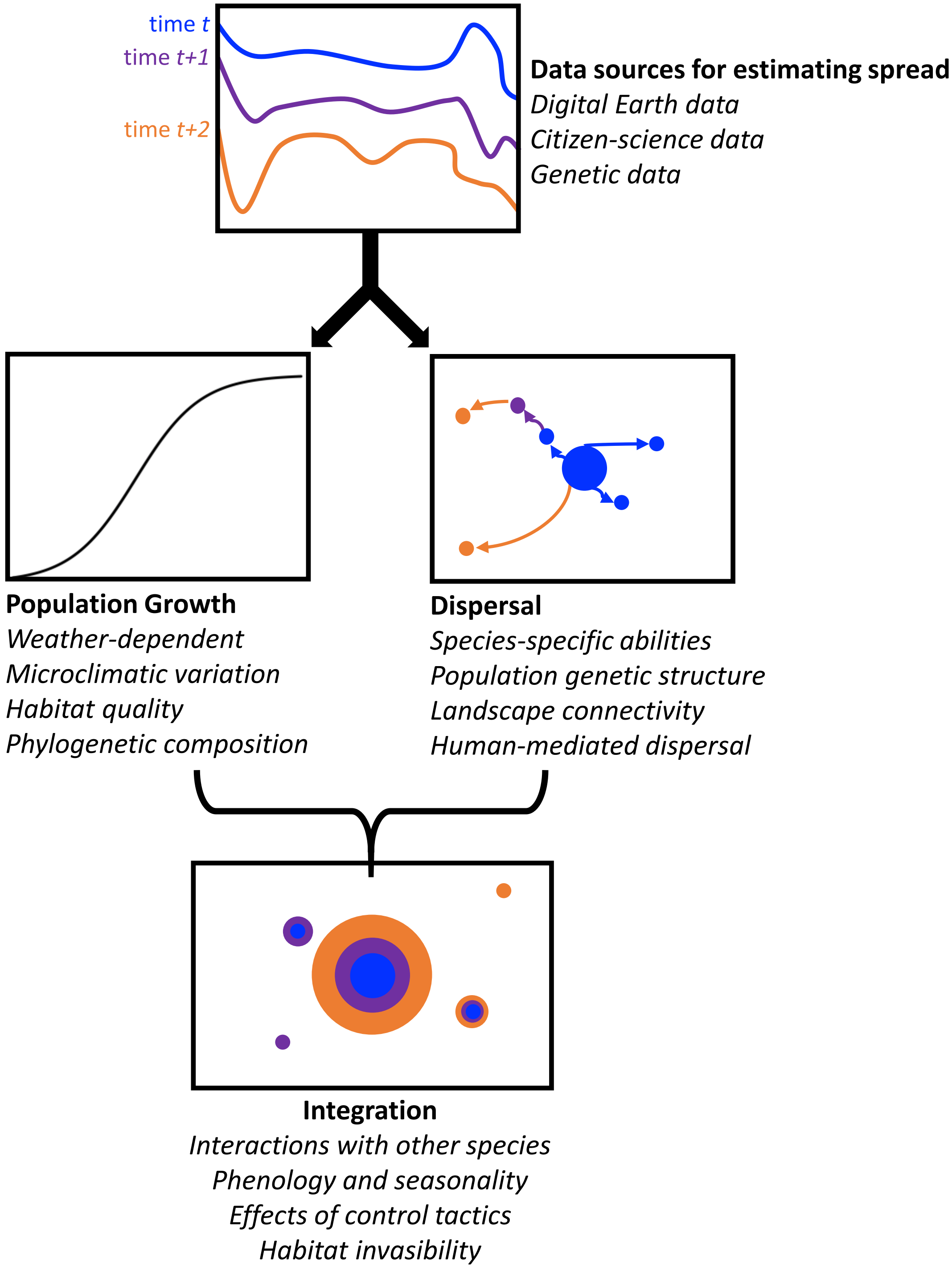
This study proposed an alternative approach to predict the spread of non-native species by considering the environmental resistance of the recipient region; although applied to global avifauna, this study provides an important perspective for the spread of invading insects species.

Figure legend

Figure 1. The spread of invasive insects involves quantifying the change in distributional ranges through time, and innovative data sources can be used to delineate spatial boundaries. Spread itself is largely a component of two processes: population growth and dispersal, each of which can be considered separately and be affected by different factors, such as habitat quality for population growth and landscape connectivity for dispersal. Models that integrate population growth and dispersal provide an opportunity to better understand and predict spread.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time t+2
Data sources for estimating spread
Digital Earth data
Citizen-science data
Genetic data
Population Growth
Weather-dependent
Microclimatic variation
Habitat quality
Phylogenetic composition
Dispersal
Species-specific abilities
Population genetic structure
Landscape connectivity
Human-mediated dispersal
Integration
Interactions with other species
Phenology and seasonality
Effects of control tactics
Habitat invasibility

Figure 1