Invasive ant establishment, spread, and management with changing climate

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Abstract

Ant invasions and climate change both pose globally widespread threats to the environment and economy. I highlight our current knowledge of how climate change will affect invasive ant distributions, population growth, spread, impact, and invasive ant management. Invasive ants often have traits that enable rapid colony growth in a range of habitats. Consequently, many invasive ant species will continue to have large global distributions as environmental conditions change. Distributions and impacts at community scales will depend on how resident ant communities respond to local abiotic conditions as well as availability of plant-based carbohydrate resources. Though target species may change under an altered climate, invasive ant impacts are unlikely to diminish, and novel control methods will be necessary.

Introduction

Ant invasions involve the establishment of non-native ant species in new environments with amenable abiotic conditions followed by population growth as food and nesting resources are acquired. Impacts of ant invasions are often realized when incipient populations achieve exceedingly high abundance and outcompete or harass native fauna, facilitate outbreaks of honeydew-producing pest insects, disrupt ecological processes, or threaten human health or livelihoods [1,2]. Of the over 16,000 described ant species [3], about 200 are known to have established outside of their native range (alien ants), and 19 of these are currently considered invasive due to their ecological and environmental impacts [4].

Climate change also threatens ecological processes and human well-being. Temperature, rainfall, and atmospheric carbon dioxide concentration are measurably deviating from historical norms and already changing population growth rates, species distributions, and species interactions across taxa [5-7]. Future abiotic change and the specific responses of biotic communities will be multi-faceted and vary with scale and geography. My aim here is to provide a broad overview of how some of the common components of climate change (increased temperatures, drought, more variable rainfall, increased carbon dioxide) will affect the introduction, establishment, spread, and management of invasive ants (Figure 1).

Transportation, introduction, and establishment of invasive ants

With increasing global population and trade, opportunities for species transport are set to continue to increase over the coming decades [8]. Small size and ability to persist in close association with humans enable many ant species to hitchhike in a variety of commodities [9,10]. The ability to found a population from a single mated queen, or in some cases with just workers and brood, increases the probability of establishment.

Once transported to a new location, an introduced species must establish under local abiotic conditions before it can spread. Species distribution models for 15 invasive ant species based on 19 bioclimatic variables and combining six future climate change scenarios predict a 6.3-35.8% increase in suitable land area for five species, a 2.6-64.3% decrease in suitable land for eight species, and little net change for two species [11*]. Overall, by 2080, 37% of land area in biodiversity hotspots in predicted to be suitable for one or more invasive ant species compared to 14.6% in the rest of the world [11*]. Increases in abiotically suitable locations and subsequent establishment will likely increase potential for further spread as more locations act as bridgeheads [12]. Decreasing time in transit or changing abiotic filters may also increase opportunity for additional species or populations to survive such that species that are alien, but not invasive, or that have not yet moved beyond their native range, may emerge as new priority invaders. Though predictions of future distributions under climate change come with many caveats, they collectively indicate that invasive ants will continue to threaten biodiversity and livelihoods.

Invasive ant spread and impact

Following establishment, the spread and impact of introduced ants is dependent on their population growth, which in turn is linked to their reproductive capabilities and capacity to adapt to their new environment. Spread and impact are also defined by the ability to compete with resident ant species, often related to the monopolization of plant-based carbohydrate resources (Figure 1). Population growth, spread, and impact of invasive ants are all multifaceted processes that will be influenced by the response of invasive ants and the species with which they interact to climate change.

Population growth and competition with resident ant species

Population growth in a new environment requires adapting to a new habitat, and this adaptability to will benefit invasive ants as the climate changes. The eusocial lifestyle generally affords ants flexibility to adapt to changes in their environment [13**,14**]. Particular traits such as fast brood development, dependent colony founding, dynamic nestmate recognition thresholds, nest site flexibility, high aggression, wide geographic ranges, and uniform worker sizes are predicted to confer some resilience to environmental change [15**], and are common among invasive ant species. Invasive ants also tend to have broad diet breadth and rapid colony growth in response to high resource availability [13**]. They tend to thrive in disturbed environments [1], which may advantage them following extreme events such as floods, fires, and cyclones. Invasive species have almost always gone through a genetic bottleneck in their introduction phase, which should limit their ability to adapt to changes in conditions in their novel range. However, low genetic diversity in an introduced ant population often reduces intraspecific aggression and allows allocation of workers away from defense and toward resource acquisition, ultimately enabling extremely high population density [1,16].

Whereas the ability to achieve high population densities is a common component of ant invasiveness, achieving numerical dominance requires outcompeting resident ants for resources. Resident ant communities themselves will be adapting to abiotic changes. Individual thermal tolerance in combination with behavior [17,18], diet [19], interaction with other ant species [20,21], and land use [22-24] will affect ant population growth and composition of ant assemblages, potentially decreasing their assemblage stability [25]. Although species and community level responses will vary, some general trends are predicted. Species that are more specialized in their nest requirements and task partitioning, or are generally less phenotypically plastic, are expected to be more vulnerable to climate change [13**,15**]. Communities that lose specialists will tend towards ant assemblage simplification and may be more prone to invasion by introduced ants. The risk may be tempered if resident dominant ant species more suited to the abiotic conditions provide biotic resistance [26,27]. Ant communities in the tropics are likely to be most affected by climate change because they experience narrower temperature ranges, and tropical species are more likely to exist near their thermal tolerance [14**]. Temperate regions may have some increases in ant abundance and richness with rising temperatures leading to higher productivity, at least in the near-term [28], which may reduce their vulnerability to invasion.

Invasive and other ants will also likely be challenged by greater fluctuation in moisture availability with climate change. Ants protect themselves from desiccation with a layer of cuticular hydrocarbons (CHCs), which also are central to nestmate recognition and communication and facilitate division of labor and colony organization [29]. More viscous CHC layers are more protective against water loss, but communication requires some fluidity of the CHC layer [29]. Thus, selection for survival with increasing aridity may come at a cost to chemical signaling. Further investigation of CHC profiles is necessary to understand potential trade-offs between functions [29]. Another possibility is that CHC profiles will converge as habitats become more homogenized, which may decrease territoriality and thus lessen one barrier to high population densities for ants generally [15**]. Such possible changes may reduce the competitive advantage of invasive ant species, which commonly trade-off intraspecific territoriality for high population density [1].

Responses of invasive and other ants to future climate changes will depend on characteristics of ant species and the broader ecological community. Behavioral and phenotypic plasticity will be advantageous [13**,15**], but is unlikely to completely explain future ant invasions. Current global geographic distributions of invasive ants compared to alien ants indicate that invasive ants have not shifted their niche, suggesting that biotic interactions and human-associated dispersal are key to invasive ant spread and impact [30]. For example, the Asian needle ant (*Brachyponera chinensis*) has an inflexible, narrow climatic niche but still displaces native ant species because it is aggressive and its lack of genetic diversity enables it to form large colonies of multiple interacting nests (supercolonies) [31*]. Long-term prediction of invasive ant spread and impact is further complicated by invasive ants themselves being agents of environmental change and the many unanswered questions about their population booms and busts [32].

Acquiring plant-based carbohydrate resources

The availability of plant-associated carbohydrate-rich resources is often a key factor in population growth for invasive ants that are able to pass through abiotic filters and establish. Honeydew from sap-sucking insects increases invasive ant colony growth [33-35] and abundance [36,37] across multiple species and geographic locations [38*]. Floral and extrafloral nectar are also widespread carbohydrate-rich resources linked to invasive ant success [39-42]. Invasive ants visiting plant-associated carbohydrate-rich resources often affect other insect-plant interactions with consequences for pollinators [43,44], plant reproduction [45,46], and herbivory [47].

The availability of honeydew to invasive ants depends on the honeydew producers, their host plants and natural enemies, and resident ants, all of which may respond to climate change independently. At the community level, climate change is unlikely to cause honeydew producers to become too rare to influence ant invasions. The existing mutualisms between invasive ants and sap-sucking hemipterans are non-specialized and occur despite the interactors usually sharing no evolutionary history. Many hemipterans recorded as important to ant invasions are themselves introduced, or at least widespread [38*], and thus likely to thrive on numerous host plants in a variety of habitats. Interactions with bugs native to the ants' introduced range may also be important for facilitating invasion [37]. Honeydew producers may benefit from intermittent drought due to increased nitrogen availability in phloem [48], which may reduce honeydew excreted per individual [49]. Elevated carbon dioxide and/or temperature affect population growth, behaviour, honeydew production, and chemical communication of sap-sucking insects sometimes to the benefit of the ants or their trophobionts, but often dependent on host plants, seasonal timing, ant attendance, or natural enemies [7,50-54]. Phenological and spatial mismatches characteristic of lagged responses to warming are more likely between species that share an evolutionary history [5], but more work is required to understand its importance for mymrecophilous bugs and their host plants. Future studies encompassing a broad range of taxa and climates will be most helpful in developing more precise predictions about the role of honeydew in ant invasions and how changes in the mutualism may affect broader impacts of ant invasions.

Climate change is also anticipated to affect floral and extrafloral nectar availability, which would have consequences for invasive ants and their impacts. In several plant species, water stress reduces flower abundance, nectar volume, or flower size [55-58] as well as investment in extrafloral nectar [59,60], but see [61]. Elevated carbon dioxide, temperature, or their combined effects can change the distribution of floral [62,63] or extrafloral nectar [64,65] across space or time, within individual plants or at the community level. As with honeydew, invasive ants readily consume floral and extrafloral nectars despite usually sharing no evolutionary history with their producers and therefore may be quicker to adapt to spatial or temporal changes in availability of these resources than the co-evolved organisms they are intended to attract.

Managing ant invasions under a changing climate

Invasive ant management is currently largely reliant on insecticides [66], which may become less effective as the climate continues to change [67]. To maximize efficacy and reduce risks to non-target species, tailoring applications of insecticidal bait to match the diurnal and seasonal activity patterns of the target ant species is essential, especially for large-scale programs. Aseasonal rainfall and temperatures and increased frequency of extreme weather events reduce both the predictability of ant foraging patterns and the frequency of ideal weather conditions for applying insecticidal bait [68]. Higher temperatures may increase insecticide detoxification due to higher enzymatic activity [67]. Even increased sensitivity to an insecticide would be problematic, however, given that to eliminate the colony workers need to remain alive long enough to share the bait with nestmates. Investment in improved biosecurity and development of more targeted methods (e.g., RNAi [69] may be a useful way forward to avoid the potentially diminishing efficacy of insecticides.

Conclusion

Invasive ants collectively will continue to have wide global distribution and impact. Even if the geographic distribution of some of the most currently damaging species declines, the global species pool of alien and other ants is rich, and new invaders may emerge. The greatest insights may come from determining which aspects of climate change disproportionately affect or favor invasive ants relative to native ants based on traits associated with invasiveness. Climate change effects on the resident ant community and on the availability of plant-based carbohydrate-rich resources are complex and occur across multiple ecological scales and will continue to be important to understanding future ant invasions. A key challenge for the future is understanding the interplay between species' physiological tolerances to abiotic conditions and the community context under which challenging conditions occur.

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Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

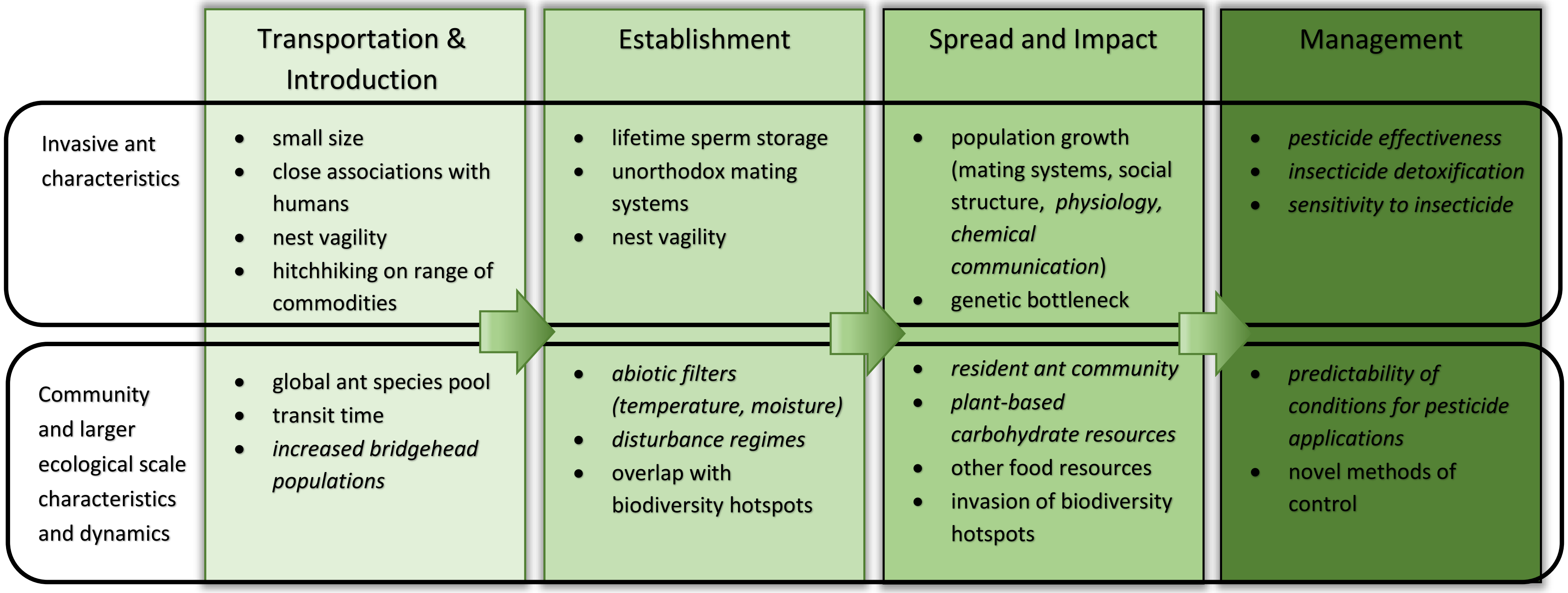

Figure 1. Stages of ant invasion with some of the important characteristics of invasive ants and community and larger scale dynamics relevant to each phase. Characteristics in italics are those currently predicted will be affected by climate change. See text for discussion and references.