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Editorial overview: Social insects as invasive species

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Invasive species pose severe threats to biodiversity and the environment. For example, many introduced plants and animals cause the displacement and even extinction of species native to the environments they invade [1,2]. Introduced species also alter biological interactions and degrade ecosystems in the process. Human food supplies and economies are likewise subject to threats from invasive species [3]. Unfortunately, these problems are only growing in importance; continued globalization and climate change will increase the likelihood of species invasions and exacerbate their effects.

Social insects are among the most widespread and damaging of invasive species [4]. Social insects, which generally include termites, ants, social bees, and social wasps, are defined as displaying a division of labor among reproductive and nonreproductive castes. This division of labor represents a fundamentally important evolutionary development and major transition in biological history akin to the transition from unicellular to multicellular organisms [5]. As a result of their unique biology, social insects are ecologically dominant [6]. And a great variety of social insects have been introduced to non-native habitats. This has resulted in changes in biodiversity, put extinction pressure on local taxa, and caused substantial economic damage. For example, invasive termites destroy human structures and inflict substantial economic harm [7]. Introduced ants are major nuisances and extirpate native species [8]. And invasive social bees and social wasps harm native taxa and become extreme pests [9]. Scientists continue to be interested in how and why social insects are such ecologically dominant and destructive invasive taxa [10,11].

This issue of *Current Opinion In Insect Science* explores social insects as invasive species. The collected papers take a variety of approaches, and each provides insight into the causes and consequences of social insect invasions, viewed through the lens of contemporary research questions. Two of the studies take a global view. Bertelsmeier investigates how human trade has facilitated the spread of invasive social insects. Social insects have been moved around the world for hundreds of years. However, Bertelsmeier identifies two waves of relatively recent spread of invasive species, the first from 1850 to 1914 and the second from 1960-today, which coincide with advances in transportation networks and increased globalization. She points out that it is generally difficult to know how and when relatively ancient invasions occurred. Invasion patterns are often complex and may involve multiple introductions before establishment. Hotspots for invasions generally include islands and habitats that have been modified by humans. However, different social insect taxa are likely to be transported through different means, owing to their distinct life history traits.

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Menzel and Feldmeyer consider another globally important factor that might affect social insect invasions—climate change. Climate change poses a major threat to the biodiversity of flora and fauna around the world. But how does this influence the spread of invasive social insects? The authors point out that social insects are, from some perspectives, not so different from other insects. However, social insects do possess traits that might cause their responses to climate change to differ from those of solitary insects. Social insects tend to be relatively sessile; that is, the colonies of many social insect species typically do not move once established. However, many social insects can engineer their nests, which can provide a buffer against changing environmental conditions. In contrast, a factor that could dampen the long-term adaptive potential of social insects is their apparent reduction in effective population size relative to other insects. The authors conclude that the effects of climate changes on social insect taxa will largely depend on the particular species characteristics and life history traits.

Two studies from this issue take an ecological approach to understanding the impacts of invasive social insects. Holway and Cameron focus on ant invasions. They consider one of the major mechanisms by which invasive ants acquire nutrients, which is by scavenging for food. Ants are excellent scavengers. And many invasive ants seem to be adept at locating food sources and scavenging for resources. The authors point out how little is known about the ecology of invasive social insects, in general, and how invasive social insects acquire resources, in particular. Indeed, a great deal more research is needed to understand 'energy transfers within and between the green and brown food webs.'

Eyer and Vargo consider the importance of breeding ecology to invasive insect societies. Plasticity in colony structure is thought to be associated with invasiveness in many taxa. For example, it has long been recognized that some invasive social insects undergo dramatic changes to their colony and social structure during the invasion process. Many invasive ants have multiple queens per colony and some even form large supercolonies. Such supercolonies can come to dominate a local ecosystem. However, changes in colony characteristics do not seem to be generally associated with the invasive status of social insects. The authors point out that unorthodox mating systems or inbreeding may enhance invasion success and conclude that species invasions provide excellent opportunities for studying evolution and adaptation.

Fournier and Aron explore the genetics of social insect invasions by focusing on the importance of hybridization. They first discuss the theoretical benefits of hybridization during biological invasions. Hybridization can act to increase population density, genetic variation, and trait variation. Although hybridization has been documented with some introductions, the authors find that hybridization upon invasion is highly taxon-dependent. Moreover, it is not clear if hybridization is associated with a general increase in invasion success. The authors explore the reasons why hybridization may, or may not, be important to the life history of invasive social insects.

Hagan and Gloag also take a genetic approach to investigating invasive social insects. They discuss how the unusual mechanism of sex determination in hymenopteran social insects may affect invasion success. Hymenopteran insects are haplodiploid and many hymenopteran taxa show an associated complimentary sex determination system. This sex determination mechanism makes hymenopteran social insects particularly vulnerable to inbreeding because of costly diploid male production. Indeed, the authors describe complimentary sex determination as an 'Achilles heel for social insect invaders.' Nevertheless, many hymenopteran social insects are excellent invaders, owing in part to mechanisms that enhance levels of genetic diversity within colonies. The authors describe how behavioral, social, and reproductive mechanisms preserve and restore genetic diversity through genetic bottlenecks associated with species introductions.

Finally, several reviews in this issue provide a taxon-centric view of research in invasive social insects. Russo *et al.* specifically investigate the biology of introduced bees. Bees hold an unusual place in the discussion of invasive social insects because bees have great economic importance as pollinators. In fact, the managed honey bee is deliberately introduced throughout the world. Thus the authors distinguish between 'managed' status and 'invasive' status. They suggest that species introduction, management, and sociality all interact as factors contributing to the threat level to native bee species. Russo *et al.* propose a 'managed-to-invasive species continuum' to describe this threat level. They note that introduced bees can affect the availability of resources, such as non-native plants, and may also compete for nesting sites. Moreover, highly social bee species may be particularly problematic because of their generalist diets, propensity to spread disease, and high densities.

Wilson Rankin introduces the problems associated with invasive wasps. She considers emerging themes in the invasive wasp literature. Recently, the spread of invasive hornets, such as the so-called murder hornet, *Vespa mandarinia*, made a splash in the popular media. However, invasive *Vespula* species have remained the major focus of those studying invasive wasps because *Vespula* colonies consume huge amounts of prey and have substantial ecological and economic impacts. Recent studies of *Vespula* have focused on the ecological mechanisms for success. In addition, Wilson Rankin explains how the integration of molecular genetic approaches has assisted in addressing biological questions about social wasp invasions.

Finally, Evans provides new insights into the biology of invasive termites. Invasive termites are a major economic problem in many parts of the world. However, the movement of invasive termites into natural habitats is not well studied. Evans suggests that termite invasions seem slower than invasions of other social insects because termite breeding systems take longer to generate large population sizes. He then discusses the ecological impact of invasive termite species. Overall, there is a great deal more that needs to be learned about invasive termites, which often operate inconspicuously in the environment.

The articles presented in this issue provide an outstanding overview of contemporary research on invasive social insects. They demonstrate diverse approaches to studying invasive species and provide new insights into the causes and consequences of social insect invasions from genetic and ecological perspectives. Future studies should continue in this vein. For example, there is a need to better understand the proximate mechanisms involved in the arrival, spread, and establishment of invasive social insects. There is also much to learn about the ecological interactions of social insects in new habitats and how climate change and habitat modification will influence range limitations. Although invasive social insects are remarkable and ubiquitous, there is still a great deal left to understand about how and why they survive and ultimately flourish in their new environments.

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