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Colony–colony interactions between highly invasive ants

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Abstract

Among invasive species, ants are a particularly prominent group with enormous impacts on native biodiversity and ecosystem functioning. Globalization and on-going climate change are likely to increase the rate of ant invasions in the future, leading to simultaneous introductions of several highly invasive species within the same area. Here, we investigate pairwise interactions among four highly invasive species, *Linepithema humile*, *Lasius neglectus*, *Pheidole megacephala* and *Wasmannia auropunctata*, at the whole colony level, using a laboratory set-up. Each colony consisted of 300 workers and one queen. The number of surviving workers in the competing colonies was recorded daily over 7 weeks. We modelled the survival of each colony during pairwise colony interactions, using a nonlinear model characterizing the survival dynamics of each colony individually. The least dominant species was *P. megacephala*, which always went extinct. Interactions among the three other species showed more complex dynamics, rendering the outcome of the interactions less predictable. Overall, *W. auropunctata* and *L. neglectus* were the most dominant species. This study shows the importance of scaling up to the colony level in order to gain realism in predicting the outcome of multiple invasions.

Zusammenfassung

Unter den invasiven Arten sind Ameisen eine ganz besonders auffällige Gruppe mit enormen Auswirkungen auf heimische Arten und Ökosystemfunktionen. Die Globalisierung und anhaltender Klimawandel werden wahrscheinlich in der Zukunft die Rate an Ameiseninvasionen erhöhen, was zu simultanen Einführungen von mehreren invasiven Arten in der gleichen Region führen kann. Hier untersuchen wir paarweise Interaktionen zwischen vier hoch invasiven Arten, *Linepithema humile*, *Lasius neglectus*, *Pheidole megacephala* und *Wasmannia auropunctata*, indem wir Konfrontationen zwischen ganzen Kolonien in einem Laborversuch durchführen. Jede Kolonie bestand aus 300 Arbeiterinnen und einer Königin. Die überlebenden Arbeiterinnen in konkurrierenden Kolonien wurden täglich über einen Zeitraum von sieben Wochen gezählt. Wir haben die Überlebensrate je Kolonie während der paarweisen Interaktionen modelliert, indem wir die Koloniedynamik mit einem nichtlinearen Model charakterisierten. Die am wenigsten dominante Art war *P. megacephala*, welche immer ausgestorben ist. Die Interaktionen zwischen den restlichen drei Arten zeigten eine komplexere Dynamik, die das Ergebnis der Interaktionen weniger vorhersehbar machte. Insgesamt waren *W. auropunctata* und *L. neglectus* die dominantesten Arten. Diese Studie zeigt die Bedeutung von

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Experimenten auf dem Kolonie-Niveau, um realistischere Ergebnisse zu bekommen und das Resultat multipler Invasionen vorhersagen zu können.

Keywords: Biological invasions; Invasive ants; Colony behaviour; Interference competition; Colony survival; *Linepithema humile*; *Lasius neglectus*; *Pheidole megacephala*; *Wasmannia auropunctata*

Introduction

On-going globalization and tourism facilitate species movements across the world and the rates of new species introductions are exploding (Essl et al., 2011). As a result, biological invasions are increasingly threatening biodiversity. Among invasive species, ants (*Formicidae*) are a particularly prominent group. Owing to their small size, they can be easily transported by accident on plants, fresh products, timber, shipment containers or personal items (Suarez, Holway, & Ward, 2005). More than 200 ant species have been transported by humans and introduced outside their native range (Suarez, McGlynn, & Tsuitsui, 2010), but there are potentially even more exotic ant species which have established outside of their native range (Miravete et al., 2014). A subset of these exotic species has become invasive and has enormous impacts on native biodiversity, ecosystem functioning and animal or human health (Holway, Lach, Suarez, Tsutsui, & Case, 2002; Lach & Hooper-Bui, 2010; Rabitsch, 2011). In addition, many species can invade houses, destroy electrical equipment and impact agriculture, causing high economic losses (Pimentel, Zuniga, & Morrison, 2005). A total of 19 species has been listed as highly invasive by the IUCN invasive species specialist group (IUCN SSC Invasive Species Specialist Group, 2012) and 5 species are even on the IUCN "100 of the world's worst invasive alien species" list (Lowe, Browne, Boudjelas, & De Poorter, 2000). Very few native species have been shown to be able to resist the most harmful invasive ant species (e.g. Masciocchi, Farji-Brener, & Sackmann 2009; Blight, Provost, Renucci, Tirard, & Orgeas 2010; Cerdá, Angulo, Caut, & Courchamp 2012). Invasive ants are frequently very aggressive and behaviourally dominant species (Holway et al., 2002). Interference competition between invasive and native ant species is relatively well studied, but interactions between invasive ant species remain poorly known. It is unclear how two invasive ant species would interact, should they be simultaneously introduced within the same area. Generally, in regions where multiple invasions have occurred, invasive ants do not co-exist in the same area (Lebrun & Feener, 2007; Krushelnycky & Gillespie, 2010; Spicer Rice & Silverman, 2013). A recent modelling study has identified large uninvaded areas that may be suitable for 15 of the 'worst' invasive ants (Bertelsmeier, Luque, Hoffmann, & Courchamp, 2015b). The suitable range of several highly invasive ants overlaps substantially, creating large potential invasion "hotspots". However, predictive species distribution modelling does not take into account biotic interactions (Guisan & Thuiller, 2005). Therefore it is important to investigate whether a single top dominant ant species may ultimately prevail, displacing other aggressive, yet less competitive invasive species.

Classically, species interactions have been investigated in community studies, using pitfall traps to record the numerical dominance of different species and with baits to observe behavioural interactions (Cerdá, Arnan, & Retana, 2013). In the case of interactions between multiple invasive ant species, this is not possible because they usually do not co-occur in the same areas yet, although they may interact in the future. To circumvent this difficulty, studies have used behavioural assays under laboratory conditions, placing one or several workers of different species in a petri dish and recording their interactions. Several previous studies on behavioural interactions have carried out this type of laboratory experiments, yet it remains rare in the literature on interference competition (Buczkowski & Bennett, 2008; Blight et al., 2010), especially among invasive ants (but see Kirschenbaum & Grace, 2008). However, these interference experiments in petri dishes are based on single worker interactions and it is unclear whether results from these experiments can be extrapolated to the colony level (but see Holway and Suarez, 2004 for an experimental colony confrontation between the Argentine ant and a native competing species). For example, the low number of workers used (either single workers or groups of 10–25) does not allow species to display interference strategies depending on a minimum number of workers (Buczkowski & Bennett, 2008). Further, the presence of resources or a territory is known to influence behaviours, and thus dominance hierarchies (Tanner & Adler, 2009). Clearly, experiments under more realistic conditions are needed – at the whole colony level in the presence of a queen and over an intermediate to long time span.

Here, we investigate the dominance relationships of four of the worst invasive ant species (*Linepithema humile*, *Lasius neglectus*, *Pheidole megacephala* and *Wasmannia auropunctata*, see Appendix A, Table S1 for details on these species), using dyadic interactions at the colony-level. These species might colonize the same areas in the future, according to a recent modelling study (Bertelsmeier et al., 2015b). To increase realism, we provided the species with sufficient space to avoid confrontations (unlike the small petri dishes) and we monitored the survival daily over 6 weeks.