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Possible role of weaver ants, *Oecophylla smaragdina*, in shaping plant–pollinator interactions in South-East Asia

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Summary

1. Although theoretical models suggest that ambush predators could have a wide range of ecological and evolutionary effects on plant–pollinator interactions, these models require predators that are both abundant and mobile. Crab spiders, the main model system for studying the effects of ambush predators on plant–pollinator interactions, are neither of these.

2. The weaver ant *Oecophylla smaragdina* is a keystone predator in South-East Asian forests. It uses the flowers of a wide range of native and introduced species as hunting platforms for incoming pollinators. Weaver ants affect the behaviour of flower visitors and the reproductive success of their host plants.

3. Due to their ubiquity and mobility, *O. smaragdina* ants satisfy the assumptions of the theoretical models. They have the potential to affect the structure of pollination networks.

4. *Synthesis*. *Oecophylla smaragdina* in South-East Asia, and possibly other predatory ant species in African and American tropical forests, may play a key role in shaping the ecological and evolutionary trajectories of plant–pollinator interactions.

Key-words: ambush predators, ant–plant interactions, community ecology, crab spiders, determinants of plant community diversity and structure, plant–pollinator interactions, tritrophic interactions

One decade ago, the opening statement of a ground-breaking paper could claim that the effects of predation on pollinators had been largely ignored (Dukas 2001). Since then, it has been suggested that ambush predators – mainly crab spiders, praying mantises and hemipteran bugs that wait on or under flowers for the arrival of unsuspecting pollinators – could affect the distribution patterns of plant species (Suttle 2003), the foraging decisions of pollinators (Jones 2010), the evolution of flower colours (Abbott 2010), the evolution of plant traits that attract ambush predators (Higginson, Ruxton & Skelhorn 2010), and even play a role in regulating the populations of solitary bees (Rodríguez-Gironés 2012).

Ambush predators, particularly crab spiders, have been shown to affect the behaviour of insect pollinators at the inflorescence, plant and patch levels (Dukas 2001, 2005; Schmalhofer 2001; Dukas & Morse 2003), and today it is undisputed that they can alter the behaviour of insect pollinators – although this effect is not universal (Brechbühl, Casas & Bacher 2010; Llandres & Rodríguez-Gironés 2011). Crab spiders may even have top-down indirect effects on the fitness of the plants that harbour them (Suttle 2003; Gonçalves-Souza *et al.* 2008). It is less clear, however, whether they can affect the population dynamics or evolutionary trajectories of their host plants. There is a simple reason why a given abundance of ambush predators should have stronger evolutionary effects on pollinators than plants. Individuals of many species of insect pollinators, particularly bees, can visit thousands of flowers during their lifetime (Müller *et al.* 2006). As a result, the probability that a bee will have a fatal encounter with a predator is much greater than the proportion of flowers harbouring them; it approximates the proportion of flowers with predators multiplied by the number flowers visited in the pollinator's lifetime. Hence, bees are likely to experience high

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selective pressures to avoid predator-harbouring flowers even when the predators occur at low densities (Rodríguez-Gironés 2012; Rodríguez-Gironés & Bosch 2012).

On the other hand, ambush predators only affect the fitness of the plants hosting them or those in their immediate neighbourhood (i.e. in the patch that pollinators are likely to avoid upon detection of the predator's presence). If ambush predators are scarce, few plant individuals will be affected by their presence and, even if they have strong effects on the fitness of these plants, they will represent a weak selection force. As a consequence, we should only expect predators to affect the population dynamics or evolutionary trajectory of their host plant if they are sufficiently abundant. Indeed, the suggestion that the anti-predator response of pollinators could have important effects for plant community composition or for the evolution of floral traits relies on the assumption that ambush predators are both abundant and mobile. As an example of the importance of abundance, population growth of the invasive plant *Leucanthemum vulgare* was only affected significantly by the presence of *Misumenops schlingeri* at occupancy levels above 12% (Suttle 2003), considered to be a high density for crab spiders (Schmalhofer 2001; Dukas & Morse 2003; Llandres, de Mas & Rodríguez-Gironés 2012). As for the importance of mobility, ambush predators could exclude pollinators from rich flowers if they were able to track resources in the environment (Jones 2010). But only mobile predators can track resources and the crab spiders that feed on pollinators are rather sedentary (Morse 2007). For instance, female *Misumenops schlingeri* remained on individual inflorescences for up to two weeks (Suttle 2003).

To summarize, although theory suggests that ambush predators could play an important role in shaping the patterns of plant–pollinator interactions, studies with crab spiders provide little support for this claim. Mantises and hemipteran bugs have been much less studied in this context, but they tend to occur at even lower densities on flowers, which makes them even less likely to affect plant community composition through the behavioural changes they induce in foraging pollinators. Our hypothesis, therefore, is that where crab spiders are the main predators ambushing at flowers, as is the case in temperate meadows, ambush predators can have large effects on pollinator behaviour, but they will have only modest effects on plant populations and plant–pollinator interactions at the community level. Things, however, can be otherwise in the tropics, due to the presence of highly mobile, ubiquitous ambush predators: aggressive predatory ants. Although ants can affect plant fitness in a diversity of ways, such as by damaging flowers (Galen & Geib 2007), predating on seeds or dispersing them (Brown & Human 1997) and removing herbivores (Llandres, Rodríguez-Gironés & Dirzo 2010), in what follows we concentrate on their effects on plant–pollinator interactions.

Ants are abundant and diverse in most habitats. Many ant species are opportunistic foragers, consuming flower nectar when available (Herrera, Herrera & Espadaler 1984). In particular, certain species are able to displace, through interference or exploitation competition, other flower visitors (Lach 2007, 2008). Ants can have direct effects on plant pollination success, damaging flowers during nectar consumption (Galen & Geib 2007), and indirect effects, mediated by changes in pollinator behaviour. These indirect effects can be negative (Ness 2006) or positive (Altshuler 1999) for plant reproduction. As a result, ants have imposed strong evolutionary pressures on plant traits. Indeed, it is well known that many flowers produce ant repellents at the time of anthesis (Willmer & Stone 1997; Raine, Willmer & Stone 2002). These ant repellents have generally been assumed to minimize exploitation (Ghazoul 2001; Junker & Bluthgen 2008) and interference (Willmer & Stone 1997; Raine, Willmer & Stone 2002; Junker, Chung & Bluthgen 2007) competition between ants and pollinators.

Exploitation and interference competition need not be the only mechanisms through which ants affect plant–pollinator interactions. Although ants are not normally considered flower-dwelling ambush predators, we argue here that this vision may need to be revised – at least in the tropics. *Oecophylla smaragdina* (Fabricius) (weaver ants; possibly several cryptic species) are ubiquitous in any habitat with trees from Sri Lanka and India, through southern China, South-East Asia, and Melanesia to northern Australia (Crozier *et al.* 2010). They are numerically co-dominant in natural ecosystems ranging from Australian tropical savanna (Arnan, Gaucherel & Andersen 2011) to lowland rain forest in New Guinea (Klimes *et al.* 2011) and Borneo (Davidson *et al.* 2007), and they are abundant enough to be effective in controlling pests in a wide range of tree crops (Crozier *et al.* 2010). Colonies defend huge, three-dimensional territories, and the major workers (the only caste outside the nests) are aggressive generalist predators that can affect plant–pollinator interactions. For example, *O. smaragdina* workers repel pollinators from *Nephelium lappaceum* (Tsuji *et al.* 2004) and pollen thieves from *Melastoma malabathricum* (Gonzálvez *et al.* 2013), while they are active hunters of fig wasps (Ranganathan & Borges 2009). Although the negative effect of ants on pollinator visit rate has previously been attributed to the territorial behaviour of the ants (Tsuji *et al.* 2004; Gonzálvez *et al.* 2013), *O. smaragdina* ants are also known to raid bee nests (Seeley 1983), making it likely that weaver ants would use flowers as hunting platforms.

To evaluate the possibility that *O. smaragdina* plays an important role in structuring plant–pollinator interactions in South-East Asia and tropical Australia, we checked for the presence of weaver ants on a wide range of flowers within their habitat and observed their interactions with flower-visiting insects. Rather than focusing on specific taxa or a particular location, we made wide-ranging observations in different localities over the complete geographic range of the ant species, from southern China (April–August 2011; northern limit) and Sri Lanka (July 2006; west limit) through South-East Asia (February–July, 2010) and into north-east Australia (April 2008 and May 2009; south-east limit). We looked for plant individuals satisfying the following conditions: they were in bloom, they were patrolled by *O. smaragdina,* and they received pollinators. Plant individuals without *O.*

smaragdina were not included in the sample because it is impossible to decide whether weaver ants would use those flowers as hunting platforms if given the chance, while plants that received no pollinators in a 15-min observation period were excluded because the absence of ants at flowers could simply be explained in terms of economic profitability. Because our aim was to assess the use of flowers as hunting platforms by *O. smaragdina* ants, we did not census the local abundance of plants and ants, or the proportion of plants and flowers harbouring ants. Individual plants were observed for 15 min, and we typically observed three to five individuals per species, depending on availability – although for some species, when plants of small size grew in clumps, the number of individuals observed was much higher. Due to the relatively low sampling effort per plant species, it is important to note that we are only reporting true positives, not true negatives – that is, further work might show that *O. smaragdina* ants hunt pollinators at flowers where we failed to observe them. The results of our observations are summarized in Table 1.

Except in Singapore, where most of our observations were performed in suburban areas, *O. smaragdina* ants were very abundant: far more abundant than all other ambush predators combined. Although we did not quantify the proportion of flowers patrolled by weaver ants systematically throughout our survey, several observations suggest that these are generally high. In rural Singapore (late March 2010), 27 ± 5% (mean ± SEM) of *M. malabathricum* flowers were patrolled by *O. smaragdina* ants (Gonzálvez *et al.* 2013) and a *Xanthostemon chrysanthus* tree harbouring an *O. smaragdina* colony had over 60% of inflorescences patrolled by ants, with an average of 3.7 ants per occupied inflorescence. Moreover, while weaver ants patrolling *Turnera ulmifolia* at a suburban garden in Sri Lanka were present at only 1% of the flowers, they captured *Trigona* bees at 28% of the flowers they occupied.

Overall, we observed *O. smaragdina* ants at plants of 48 species in 32 families that were in bloom and attracting pollinators at the time of the observations. In 31 of the 48 plant species, we observed ants patrolling flowers. We observed ants attacking flower visitors at all these 31 species (successfully capturing bees and other visitors at 15 of them; Fig. 1) and drinking nectar at only three species: *Heliconia psittacorum* L.f., *Costus woodsonii* and *C. speciosus* (Koen. ex Retz) Sm. In six of the plant species where ants did not patrol flowers, ant repellents may have precluded them from doing so: in these species, ants were attacking approaching bees from branches, and in three of them, we observed successful captures (*Cinnamomum iners*, *Syzygium cumini* and *Mallotus barbatus*). It is also worth noting that in seven of the species where we observed successful captures from flowers (*Ficus semicordata*, *Turnera ulmifolia*, *Calliandra emarginata*, *Mallotus barbatus*, *Asystasia gangetica*, *Bidens alba* and *Musa acuminata*) and three of the species where we observed unsuccessful attacks (*Catharanthus roseus*, *Clerodendrum* sp. and *Costus woodsonii*), the observations were made in the secondary, hunting, territory of the ants – making it highly unlikely that the ants were simply defending their territory. Cooperative hunting tactics, with nearby individuals rapidly coming to the aid of the ant that first attacks the bee, allow *O. smaragdina* to capture pollinators considerably larger than themselves (Wojtusiak, Godzinska & Dejean 1995). We observed *O. smaragdina* capturing *Apis cerana* from eight plant species, *A. mellifera* from *Bidens alba* and *Nomia strigata* from *Melastoma malabathricum* (Table 1).

It is clear from Table 1 that *O. smaragdina* ants make widespread use of flowers as hunting platforms. Because they are ubiquitous and mobile (Crozier *et al.* 2010), they have the potential to affect the relationships between plants and their pollinators at both ecological and evolutionary time-scales, as predicted by recent models (Suttle 2003; Abbott 2010; Higginson, Ruxton & Skelhorn 2010; Jones 2010; Rodríguez-Gironés 2012). Although the system has received little attention, published data and the observations conducted for this study suggest that pollinators avoid *O. smaragdina* ants, showing behavioural responses similar to those used to avoid other ambush predators (Tsuji *et al.* 2004; Gonzálvez *et al.* 2013).

We now turn to the effect of weaver ants on their host plants. Depending on the costs and benefits that flower-patrolling ants impose on the plants, flowers patrolled by weaver ants could have higher or lower reproductive success than ant-free flowers. Pollinator effectiveness depends on the number of pollen grains removed and/or deposited per flower visit, which together with pollen quality determine per-visit pollinator effectiveness, and the rate at which pollinators visit flowers. Ants can affect both terms of the equation. Consider first per-visit effectiveness. Interference competition between bee species can increase the rate of between-plant movements and therefore enhance fruit and seed set (Greenleaf & Kremen 2006; Carvalheiro *et al.* 2011). Likewise, it has been suggested that aggressive ants at flowers may reduce the number of flowers that bees visit per plant, favouring outcrossing and increasing seed set per bee visit (Altshuler 1999). In this way, *O. smaragdina* could affect the per-visit effectiveness of pollinators. Ants can also increase or decrease pollinator visit rates. Thus, *O. smaragdina* ants reduce the pollination success of *Nephelium lappaceum* because pollinators avoid plants with ant nests (Tsuji *et al.* 2004). In the case of *M. malabathricum*, however, the pollinators actually prefer plants with ant nests, which have higher fruit set and seed set than plants without ant nests (Gonzálvez *et al.* 2013). This preference is mediated by the effect of weaver ants on pollen thieves: although the flowers of *M. malabathricum* attract a wide array of visiting bees, they are pollinated almost exclusively by large carpenter bees, *Xylocopa* spp. (Gross 1993). *Oecophylla smaragdina* ants deter small bees, which remove pollen but are poor at transferring and depositing it from and into other flowers. Carpenter bees, which are too big to be affected by ant attacks, experience reduced interspecific exploitation competition at plants with ant nests and, as a result, concentrate their foraging effort on these plants. Interestingly, *M. malabathricum* flowers attract *O. smaragdina* ants during anthesis with a so-far-unidentified cue (Gonzálvez *et al.* 2013).

Table 1. Plants in bloom where we observed *Oecophylla smaragdina* ants. The table indicates whether ants patrolled flowers and their reaction towards flower visitors. In the ant response column, cells are left empty when we observed no ants at flowers, while NBV indicates that bees did not visit ant-harbouring flowers (although they visited nearby flowers of the same plant) and NR indicates that ants did not respond to the arrival of flower visitors. Species are sorted in alphabetical order within families

Family	Plant species	Locality	Ants at flowers	Flower visitors	Ant response
Acanthaceae	*Asystasia gangetica* (L.) T. Anderson	Bin[a]	Yes	*Apis cerana*	Captures
Acanthaceae	*Thunbergia grandiflora* Roxb.	XTBG[b]	Yes	*Xylocopa* sp.	
Anacardiaceae	Unidentified species	XTBG[b]	No	*Trigona* sp	Attacks (from branches)
Apocynaceae	*Catharanthus roseus* (L.) G. Don	Bin[a]	Yes	*Trigona* sp.	Attacks
Arecaceae	*Adonidia merrillii* (Becc.) Becc.	WCP[c]	Yes	*Apis cerana*	Captures
Arecaceae	*Archontophoenix alexandrae* (F. Muell.) H. Wendl & Drude	Kuch[d]	Yes	*Trigona* sp.; *Apis dorsata*	Captures (*Trigona*)
Asteraceae	*Bidens alba* (L.) DC.	AB[e]	Yes	*Apis mellifera*	Captures
Asteraceae	*Sphagneticola trilobata* (L.) Pruski	Kuranda[f]	No	*Apis mellifera*; butterflies	
Bignoniaceae	*Tecoma stans* (L.) Juss.ex Kunth	YK[g]	No	*Trigona* sp.	
Costaceae	*Costus woodsonii* Maas	KRP[h]	Yes	Flies	Attacks
Cucurbitaceae	*Momordica charantia* L.	Cairns[i]	No	*Xylocopa* sp.; *Trigona* sp.; *Apis mellifera*	
Dilleniaceae	*Dillenia suffruticosa* (Griff. ex Hook. f. & Thomson) Martelli	SBW[j]	Yes	*Xylocopa* sp., *Apis cerana,* small flies	Attacks
Euphorbiaceae	*Mallotus barbatus* Müll. Arg.	XTBG[b]	No	*Trigona* sp; *Apis cerana*	Captures (from branches)
Fabaceae	*Andira inermis* (W. Wright) Kunth ex DC.	Kuch[d]	No	*Trigona* sp.; *Apis dorsata*	
Fabaceae	*Bauhinia blakeana* Dunn.	Kuch[d]	Yes	*Trigona* sp.	Captures
Fabaceae	*Bauhinia variegata* L.	XTBG[b]	Yes	*Xylocopa* sp.	Attacks
Fabaceae	*Caesalpinia pulcherrima* (L.) Sw.	KRP[h]	Yes	*Trigona* sp.	NR
Fabaceae	*Callerya atropurpurea* (Wall.) Schot	McRR[k]	Yes	*Xylocopa latipes*; hornets, lycaenids	Attacks
Fabaceae	*Callerya* sp.	XTBG[b]	No	Halictid bees	
Fabaceae	*Calliandra emarginata* (Humb.& Bonpl. ex Willd.) Benth.	NUS[m]	Yes	*Apis cerana*	Captures
Fabaceae	*Cassia auriculata* L.	XTBG[b]	Yes	*Xylocopa* sp.	Attacks
Fabaceae	*Cassia fistula* L.	WCP[c], XTBG[b]	Yes	*Apis cerana*; *Xylocopa* sp.	Attacks
Fabaceae	*Erythrina crista-galli* L.	WCP[c]	Yes	*Apis cerana*	Captures
Fagaceae	*Castanopsis indica* (Roxb.) Miq.	XTBG[b]	No	Flies, small bees	Attacks (from branches)
Gentianaceae	*Fagraea fragrans* Roxb.	WCP[c]	No	*Apis cerana*	NBV
Goodeniaceae	*Scaevola taccada* (Gaertn.) Roxb.	Bin[a]	Yes	*Trigona* sp.; *Xylocopa* sp.; Halictidae; flies	Captures (*Trigona* and halictidae)
Lamiaceae	*Callicarpa glabrifolia* S. Atkins	Kuch[d]	Yes	*Trigona* sp.	Attacks
Lamiaceae	*Clerodendrum* sp.	Kuch[d]	Yes	*Trigona* sp.	Attacks
Lamiaceae	*Gmelina asiatica* L.	XTBG[b]	Yes	*Xylocopa* sp.	NBV
Lamiaceae	*Orthosiphon aristatus* (Bl.) Miq.	JCU[l]	No	*Trigona* sp.	
Lauraceae	*Cinnamomum iners* Reinw.	Kuch[d]	No	*Trigona* sp.	Captures (from branches)
Lecythidaceae	*Couroupita guianensis* Aubl.	WCP[c]	No	*Apis cerana*	Attacks from branches
Lythraceae	*Lagerstroemia speciosa* (L.) Pers.	WCP[c]	Yes	*Apis cerana*; *Xylocopa* sp.	NR
Melastomataceae	*Melastoma malabathricum* L.	McRR[k]	Yes	*Nomia strigata*; *Xylocopa* sp.; *Amegilla* sp.	Attacks and captures (*Nomia strigata*)
Moraceae	*Ficus semicordata* Buch. Ham. ex Sm.	XTBG[b]	Yes	Fig wasps	Captures
Musaceae	*Musa acuminata* Colla	XTBG[b]	Yes	*Apis cerana*	Captures
Myrtaceae	*Syzygium campanulatum* Korth.	KRP[h]	No	Small bees, beetles, flies and butterflies	
Myrtaceae	*Syzygium cumini* (L.) Skeels	Kuch[d]	No	*Trigona* sp.	Captures (from branches)
Myrtaceae	*Xanthostemon chrysanthus* (F. Muell.) Benth.	NUS[n]	Yes	*Apis cerana*	Captures
Nyctaginaceae	*Bougainvillea* sp.	Kuch[d]	No	*Trigona* sp.	
Passifloraceae	*Turnera ulmifolia* L.	Bin[a], Kegalle[n]	Yes	*Trigona* sp.; *Apis cerana*	Captures (*Trigona*, *Apis cerana*)
Piperaceae	*Piper umbellatum* L.	XTBG[b]	No	Flies, *Apis cerana*, *Apis florea*	
Pittosporaceae	*Pittosporum tobira* (Thunb.) W.T. Aiton	XTBG[b]	No	*Apis* sp.	

Table 1. *(continued)*

Family	Plant species	Locality	Ants at flowers	Flower visitors	Ant response
Rubiaceae	*Ixora chinensis* Lam.	XTBG[b]	Yes	Butterflies; Syrphid flies	
Rubiaceae	*Ixora* sp.	Kuch[d]	Yes	*Trigona* sp.	NR
Rubiaceae	*Morinda angustifolia* (Roxb.) Hook.	XTBG[b]	Yes	Flies	Attacks
Solanaceae	*Solanum trilobatum* L.	XTBG[b]	Yes	*Xylocopa* sp.	Attacks
Vitaceae	*Cissus hastata* Miq.	Kuch[d]	Yes	*Trigona* sp.	Attacks

[a] Bintan, Indonesia.
[b] Xishuangbanna Tropical Botanical Garden, Yunnan Province, China.
[c] West Coast Park, Singapore.
[d] Kuching, Borneo, Malaysia.
[e] Airlie Beach, Queensland, Australia.
[f] Kuranda, Queensland, Australia.
[g] Yorkeys knob, Queensland, Australia.
[h] Kent Ridge Park, Singapore.
[i] Cairns, Queensland, Australia.
[j] Sungei Buloh Wetland Reserve, Singapore.
[k] MacRitchie Reservoir, Singapore.
[l] James Cook University Campus, Queensland, Australia.
[m] National University of Singapore campus, Singapore.
[n] Kegalle, Sri Lanka.

Fig 1. (a) Weaver ant waiting for floral visitors on a *Scaevola taccada* flower. (b) Weaver ants ambushing *Apis cerana* on *Xanthostemon chrysanthus* flowers. (c–e) Successful captures of *A. cerana* on (c) *Xanthostemon chrysanthus*, (d) *Erythrina crista-galli* and (e) *Archontophoenix alexandrae* flowers. (f) *Trigona* bee captured by weaver ants on *Bauhinia blakeana* flowers.

The effect of *O. smaragdina* ants on the pollination of *M. malabathricum* flowers has wider implications. It is often assumed that flowers produce ant-repellent substances to prevent ants from consuming their nectar (Junker & Bluthgen 2008) or from scaring their pollinators (Willmer & Stone 1997). In the latter scenario, production of ant repellents would only make sense when pollinators are at risk from ant attacks. We can therefore predict that the evolution of ant repellents is more likely when flowers are pollinated mainly by susceptible, small insects (such as flies, butterflies or small to medium-sized bees) than when they are pollinated by large animals (including birds and bats, but also large bees), safe from ant attacks.

As well as affecting the ecological and evolutionary trajectory of specific plant species, *O. smaragdina* ants might affect the structure of entire communities. Plant–pollinator networks are the result of ecological processes operating at different temporal and spatial scales. Trait complementarity and exploitation barriers play a key role during network build-up (Santamaría & Rodríguez-Gironés 2007). Under trait complementarity, the similarity between the reward that the plant has to offer and the resource that the pollinator seeks determines whether species pairs interact. Barriers, on the other hand, are plant phenotypic traits that prevent certain pollinator species from accessing the reward. In a sense, *O. smaragdina* ants behave as indirect exploitation barriers: only pollinators with a low susceptibility to predation (e.g. those with large body sizes) will exploit flowers commonly associated with predatory ants. The balance between exploitation and complementarity among the processes that operate during network build-up affects the topology of the ensuing network. In particular, stronger barriers lead to more nested communities (Santamaría & Rodríguez-Gironés 2007). We can therefore expect that the nestedness of plant–pollinator networks will increase when *O. smaragdina* ants are present. The presence of ants could also increase the modularity and decrease the connectivity of the community, because susceptible pollinators will specialize on ant-free flowers to reduce predation risk and non-susceptible pollinators will concentrate on ant-harbouring flowers to reduce intraspecific competition for resources (Gonzálvez *et al.* 2013). In turn, these topological properties (nestedness, connectivity and modularity) are known to affect the ecological properties of the network, such as its robustness to external perturbations (Bascompte 2009).

We predict that other ant species will ambush pollinators at flowers in tropical Africa and the Neotropics, where other arboreal ants occupy the ecological niche filled by *O. smaragdina* in South-East Asia. In particular, a very similar species in the same genus, *O. longinoda*, occupies the same habitats and ecological niche in a broad band across equatorial Africa (Wojtusiak, Godzinska & Dejean 1995). In many plant species, flowers are frequently visited by pollinators, and it may be faster and easier to capture insects by ambushing at flowers than searching through the vegetation. We should therefore expect predatory ants to use many flowers as hunting platforms. Indeed, the production of ant repellents by flowers of African (Willmer & Stone 1997) and American (Raine, Willmer & Stone 2002) plant species suggests that ants interfere with the pollination process in these continents. Just as in South-East Asia, we should expect flowers to produce ant repellents if they rely mainly on small bees for their pollination, but not if their most effective pollinators are not susceptible to predation by weaver ants. As a result, at the landscape level there will be a mosaic of flowers with and without ant repellents, with and without predatory ants, and this heterogeneity should affect the foraging behaviour of pollinators, the structure of pollination networks and the reproductive success of plants.

The structure and stability of ecological communities cannot be understood from knowledge of a single type of interactions, such as predator–prey or plant–pollinator interactions, but from the complex interplay of them all (Melián *et al.* 2009). In particular, it has been suggested that the stability of communities is strongly dependent on the proportion of mutualistic interactions (Mougi & Kondoh 2012). *Oecophylla smaragdina* is a keystone predator species, very abundant and broadly distributed throughout tropical South-East Asia and north-east Australia (Crozier *et al.* 2010). As we have documented, these ants often use flowers to ambush foraging bees. The presence of ants at flowers, by altering the foraging behaviour of bees, can affect the relationship of a plant with its flower visitors, modulating the evolution of flower traits (Gonzálvez *et al.* 2013). Due to the abundance of ants, however, we hypothesize that the topology of plant–pollinator networks will differ between communities where ants are present and absent, and that flowers will follow different evolutionary pathways depending on whether their main pollinators are susceptible or not to the attack of *O. smaragdina* ants. To check these predictions, it will be important not only to carry out more studies of ant impacts on plant–pollinator pairs, but also to conduct community-level studies, using the comparative method to trace the evolution of ant repellents across plant lineages and comparing the topology of pollinator networks in localities with and without *O. smaragdina* ants. Furthermore, to assess the generality of our observations, future work must evaluate whether African and American ant species use flowers as hunting platforms in the way that *O. smaragdina* ants do.

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