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Predation by an exotic lizard, *Anolis sagrei*, alters the ant community structure in betelnut palm plantations in southern Taiwan

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Abstract. 1. Predators can affect prey directly by reducing prey abundance and indirectly by altering behavioural patterns of prey. From previous studies, there is little evidence that ant community structure is affected by vertebrate predation.

2. Researchers tend to consider the interactions between vertebrate predators and ants to be weak. The present study examined the impact of the exotic invasive lizard, *Anolis sagrei*, on the ant community structure by manipulating the density of lizards within enclosures. The natural density of *A. sagrei* in the field was surveyed and used as the stocking density rate in the lizard-present sub-enclosures.

3. Before the lizard density was manipulated, there was no difference in the ant diversity between sub-enclosures. After the lizard density manipulation, the ant diversity in sub-enclosures with *A. sagrei* present was significantly different from that of enclosures where the lizards were absent, although the overall ant abundance did not differ significantly.

4. The ant diversity difference was generated by a significant reduction of the ant species *Pheidole fervens* in sub-enclosures with *A. sagrei* present. Such an abundance change might be the result of direct predation by the lizards, or it might be generated by a foraging site shift by this ant.

5. The results of this study thus demonstrated that the invasion of an exotic vertebrate can significantly alter the community structure of ants, perhaps through the combined direct and indirect effects of lizards on ants.

Key words. *Norops sagrei*, ants, lizards, *Pheidole fervens*, predation.

Introduction

Predation and competition have been shown to be two major factors affecting prey populations and communities. The effects of predation on prey can be divided into two categories. The first is the direct predation effect, which is also known as the density-mediated effect. In such interactions, predators reduce prey densities mainly by direct predation. Based on past research, the current evidence of direct predation is insufficient, because the dynamic nature of the simultaneous predator–prey interactions renders the impact of predators on prey difficult to observe (Sih, 1984). Empirical evidence of such effects largely came from studies on mammals (Bakker *et al.*, 2005; Delgado García *et al.*, 2005; Lalas *et al.*, 2007); studies examining the impact of predators on arthropods are few (Fincke *et al.*, 1997; Schmitz, 1998; Berger & Wirth, 2004; Recher & Majer, 2006). On the other hand, predators may also impact prey populations or communities through indirect effects, which are also called trait-mediated indirect effects. In such circumstances, prey change their behaviour, morphology or life cycle in response to the presence of predators (Gotelli, 1996; Holway, 1998; Peacor & Werner, 2000; Morrison, 2004). Prey utilise various strategies to avoid predation or to reduce the mortality risk, and thus reduce the effects of predators on them. Sometimes, the indirect effects of predation might generate a greater impact on prey populations and communities than the direct effects (Peacor &

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Werner, 2001; Schmitz *et al.*, 2004). Ultimately, both direct and indirect predation effects can potentially cause the decline of prey abundance and alter the community structure.

In the past, there was little empirical evidence regarding how ant community structures are affected by the aforementioned factors (Andersen, 2000). Recently, numerous studies have been conducted using invasive ants as a model to examine the impact of exotic ant species on native ant communities. The results of several studies showed that the invasion of the exotic ant species, such as the red imported fire ant (*Solenopsis invicta*) (Porter & Savignano, 1990) and the Argentine ant (*Linepithema humile*) (Bond & Slingsby, 1984; Cammell *et al.*, 1996; Holway, 1998; Sanders *et al.*, 2003), generated negative effects on native ant communities by significantly reducing their abundance and diversity. The invasive ants affected the native ant community mostly via competition. Some native ant species are outcompeted by exotic ants and leave the habitat or alter their foraging strategies because the latter are usually better in exploiting resources (Porter & Savignano, 1990; Holway, 1998).

While competition among ant species may generate a variation in ant diversity, predation is rarely considered as a key factor influencing ant communities. Certain predators that specialise on ants, such as antlions (Neuroptera: Myrmeleontidae), have been shown to be able to decrease ant diversities through their predatory effect (Gotelli, 1996). On the other hand, there are fewer studies on the effects of predation of vertebrate predators on ant communities. Although many studies showed that ants are one of the major food items of lizards (Munger, 1984; Pacala & Roughgarden, 1984; Spiller & Schoener, 1990; Dial & Roughgarden, 1995), the impacts caused by these predators on ants are still poorly understood.

Currently, studies examining the impact of predation on ants mainly focus on overall ant abundance (Porter & Savignano, 1990; Gotelli, 1996; Holway, 1998). The major reason for such a trend might be that it is difficult to observe the interactions between predators and particular prey and to determine which kind of prey was really predated upon (Sih, 1984). Very few studies investigated the fluctuations of prey species composition generated by the introduction of predators. However, such information is important in determining how different members of ant communities respond to the presence of predators. The present study examined how the presence of vertebrate predators affected the ant community structures and abundance. It was hypothesised that vertebrate predators would negatively affect the abundance and community structures of ants. To test this hypothesis, enclosures were erected and the density of an exotic lizard, *Anolis sagrei*, was manipulated within these enclosures. The ant community structures in lizard-present and removed enclosures were compared to determine the impact of lizard predators.

Materials and methods

Anolis sagrei

The exotic invasive lizard, the brown anole (*Anolis sagrei*), was first recorded in Taiwan in 2000, and it is hypothesised that this species was accidentally introduced into Taiwan through anthropogenic means (Norval *et al.*, 2002). The brown anole is a diurnal trunk-ground species, which favours a variety of sunny habitat types and areas disturbed by humans. This watch-and-wait (ambush) predator predates upon a variety of invertebrates, especially insects (Lee, 2000), although spiders, isopods, and molluscs are also taken (Rodriguez Schettino, 1999). Results of Huang (2007) showed that ants comprised more than half of the diet of *A. sagrei* in southern Taiwan and among them more than 90% were *Pheidole fervens* (estimated from stomach contents of 230 lizards). *Anolis sagrei* is a well documented invasive lizard species, and introduced populations are known from various parts of the USA (Conant & Collins, 1991; Steven & Lance, 1994; Campbell, 1996, 2003; McAllister *et al.*, 2003; McCoid, 2006; Turnbough, 2006; Wiley *et al.*, 2007), Jamaica (Landwer *et al.*, 1995; Roughgarden, 1995), Grand Cayman (Roughgarden, 1995), Mexico to Belize (Schwartz & Henderson, 1991; Rodriguez Schettino, 1999; Calderon *et al.*, 2003; Zamora-Abrego *et al.*, 2006), Granada (Henderson & Powell, 2005), the West Indies (Greene *et al.*, 2002), and Hawaii (Goldberg & Bursey, 2000; Powell & Pansza, 2005).

Study site and enclosure design

The study site was located in betelnut palm plantations in Santzepu, Sheishan District, Chiayi County, Taiwan (23°25′25″N, 120°29′05″E). This field experiment was conducted from March to October, 2006, in eight pairs of enclosures. Each enclosure was 6 m by 12 m, which consisted of two adjacent sub-enclosures 6 m × 6 m in size (Fig. 1). Poles (180 cm bamboo sticks) were planted 30 cm into the ground at 1.5 m

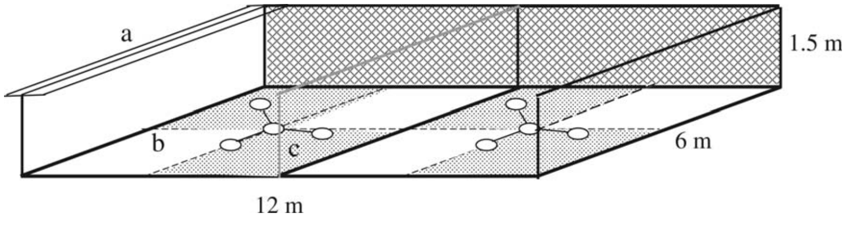

Fig. 1. A schematic diagram showing the enclosure design. A pair of enclosures was 6 by 12 m in size consisting of two sub-enclosures 6 by 6 m. The fence was topped with 40 cm wide slippery plastic to stop lizards from escaping (a). One set of pitfall traps (c) was established in each sub-enclosure. Each sub-enclosure was divided into four quadrants (b) and in each post-manipulation survey ants were collected from two of them (the shaded areas) in an alternate manner.

intervals to serve as supports of the fence. The fence consisted of fine meshed (3 mm × 3 mm) plastic sheet, which could effectively keep the lizards from moving through it. The height of the fence was 150 cm from the ground surface and it was embedded 15 cm deep into the ground to prevent the lizards from burrowing under it. The fence of the enclosure was topped with a 40 cm wide overhanging barrier made of a slippery plastic so that the lizards could not climb over it. The betelnut palm tree trunks that were within 1 m of the fences of the enclosures (on both sides of the fence) were collared with a round plastic board (40 cm in diameter) at the same height as the enclosure to prevent the lizards from escaping or entering via jumping from the tree trunks. During the field experiment, the enclosures were examined once each week to maintain and repair any potential damage to fences.

Manipulating lizard density in enclosures

In April, August, and November of 2005, preliminary surveys were conducted to estimate the lizard densities in the study site following the method devised by Heckel and Roughgarden (1979). In this study only adult [snout–vent length (SVL) range: male $>$ 45 mm; female $>$ 42 mm] and subadult (SVL range: male, 39–45 mm; female, 34–42 mm) *A. sagrei* were used. Each survey was conducted on three consecutive days, and on each day a different colour of lead-free paint was used to mark the lizards. The estimated lizard densities in the study site were 4.59 ± 2.11 in April, 10.44 ± 3.01 in August, and 8.62 ± 1.86 in November (individuals per 36 m^2). Results of a preliminary study showed that in this study site, the home ranges of male and female *A. sagrei* were estimated to be 1 to 4 and 3 to 8 m^2 respectively (S. Huang, unpublished data). Based upon such information, it was estimated that the maximum density in sub-enclosures of an area of 36 m^2 was about nine lizards (three males and six females). On 28 March 2006, we conducted the first lizard removal from both types of sub-enclosures of all eight enclosure pairs. On 30 March 2006, four to six lizards were released into the lizard-present sub-enclosures (according to the estimated lizard density in April); and every lizard found in the lizard-removed sub-enclosures was removed again. For the first 5 weeks, the sub-enclosure lizard density was surveyed at night, because they were easier to count or remove as they slept perching on the vegetation. Every lizard caught at night during the survey was marked on the tail with white lead-free paint. In the subsequent weeks, white tail marks enabled us to locate lizards and to recognise whether they existed in the lizard-present sub-enclosures. Lizards collected from inside the lizard-removed sub-enclosures were either released into the lizard-present sub-enclosures when the lizard density was not high enough, or were released back into the field outside the enclosures. Throughout the field experiment we tried to maintain a 1:2 male to female ratio inside the sub-enclosures. The lizard density survey was conducted once every week until 16 June 2006. After this date, the lizard density inside the sub-enclosures remained more or less stable and the frequency of the lizard density surveys was therefore reduced to once every 2 weeks to minimise disturbances inside the enclosures.

Ant sampling

One Y-shaped pitfall trap set was established in each sub-enclosure in all eight pairs of enclosures (Fig. 1). Each pitfall trap set was composed of four 500 ml cups, with three 1 m long fences between the four cups to enhance ground ant interception efficiency. During each survey, the pitfall traps were filled with 200 ml of 70% alcohol and were opened for three consecutive days to collect ground arthropods. To collect above-ground ants; we divided each sub-enclosure into four quadrants (Fig. 1) and conducted a 5 min sweep netting to collect ants from two of the quadrants during each survey. During the following survey the other two quadrants were sampled with the same methods. Sweep-netting and pitfall trapping were conducted once before the lizard density was manipulated to see whether the initial arthropod diversity in the sub-enclosures was similar to that at the end. In this particular survey all four quadrants in the sub-enclosures were sweep-netted. After the initiation of lizard density manipulation, arthropod surveys were conducted once every 2 or 3 weeks until the end of the experiment. Ant specimens collected were identified to species and samples from all post-manipulation surveys were pooled for statistical analyses to control for the potential effects of seasonality.

Statistical analyses

Paired *t*-tests were used to compare the abundance of the various ant species in the lizard-present and lizard-removed sub-enclosures. In addition, the community structures of the ants in the sub-enclosures subjected to different treatments was also compared. The Bray–Curtis similarity index was used to calculate the similarity between the sub-enclosures. Pairwise Bray–Curtis similarities were first square-root transformed to downweight the influence of dominant ant species and the transformed data were used to construct the multi-dimensional scaling (MDS) plots.

An analysis of similarity (ANOSIM) test was then used to determine whether the ant diversities (considering both species composition and abundance) differed significantly between the sub-enclosures with and without lizards. The Bray–Curtis similarity calculation, MDS plotting, and ANOSIM tests were all conducted using PRIMER v5.1 (Clarke & Warwick, 2001). The contribution of each ant species to the observed community structural difference between the lizard-present and lizard-removed sub-enclosures was analysed by the SIMPER function of PRIMER (Clarke & Warwick, 2001).

Results

Anolis sagrei *density censuses*

Five weeks after the lizard density manipulations, the number of *A. sagrei* in the lizard-present sub-enclosures reached about six (similar to the natural lizard density in April). In May, the density of the lizards inside the lizard-present sub-enclosures dropped but increased again steadily. Eventually the lizard density reached about seven per sub-enclosure in October (Fig. 2). Throughout the experiment the average density of the *A. sagrei* in the lizard-present sub-enclosures was significantly higher than that in the lizard-removed sub-enclosures ($t = 9.801$, $P < 0.001$ in April; $t = 6.394$, $P < 0.001$ in May; $t = 9.801$, $P < 0.001$ in June; $t = 10.624$, $P < 0.001$ in August; $t = 4.651$, $P = 0.002$ in September; $t = 9.911$, $P < 0.001$ in October, d.f. = 7 for all tests). In July, due to the disturbance of typhoons and subsequent bad weather the lizard density censuses could not be conducted, and the data for that period were not available. Except for *A. sagrei*, throughout the experiment a total of one *Japalura swinhonis* (Swinho's tree lizard), two *Hemidactylus frenatus* (Pacific house gecko), and one *Dinodon rufozonatum* (Asian king snake) were found in the lizard-present sub-enclosures. During the same period of time a *J. swinhonis*, two *Mabuya longicaudata* (long-tail skink) and four *H. frenatus* were found in the lizard-removed sub-enclosures. All these reptiles were removed from the enclosures. Since the abundances of the other lizards were very low, the observed arthropod diversity variation between sub-enclosures should be generated by *A. sagrei* predation.

The effect of Anolis sagrei *on ant abundance and community structures*

A total of eight species of ants were found in the study site (Table 1) and among them *Pheidole fervens*, *Paratrechina kraepelini*, and *Pachycondyla luteipes* were the dominant species. Before lizard density manipulation, the ant communities in the two types of sub-enclosures did not differ significantly (ANOSIM test, $R = -0.085$, $P = 0.924$) (Fig. 3a). However, after the manipulation the ant communities in the two types of sub-enclosures differed significantly (ANOSIM test, $R = 0.150$, $P = 0.039$) (Fig. 3b). The major contributor of the observed ant community structural difference was the abundance reduction of *P. fervens*. Results of the SIMPER tests showed that this ant species alone accounted for more than 35.51% of the observed community composition difference between the two types of enclosures (Table 2). Before lizard density manipulation the abundance of *P. fervens* did not differ significantly between the two types of sub-enclosures ($t = -0.945$, d.f. = 7, $P = 0.376$) (Fig. 4a). After the manipulation, the abundance of *P. fervens* (pooled from all post-manipulation samplings) in the lizard-present sub-enclosures was significantly lower than that in the lizard-removed sub-enclosures (Fig. 4a). Before the manipulation of lizard density, the overall abundance of ants other than *P. fervens* did not differ significantly between the two types of sub-enclosures ($t = -0.244$, d.f. = 7, $P = 0.814$) (Fig. 4b). After the *A. sagrei* density manipulation the overall non-*P. fervens* ant abundance (pooled from all post-manipulation samplings) did not differ significantly ($t = -0.125$, d.f. = 7, $P = 0.904$),

Table 1. The abundance of ant species from two types of sub-enclosures before and after *Anolis sagrei* density manipulation (LP, lizard-present sub-enclosures; LR, lizard-removed sub-enclosures).

Manipulation	Before		After	
Sub-enclosure	LP	LR	LP	LR
Pheidole fervens	274	371	355	648
Paratrechina kraepelini	23	30	345	419
Pachycondyla luteipes	12	7	145	101
Iridomyrmex anceps	–	–	15	6
Pheidole formosensis stat. n.	–	1	5	7
Ochetellus glaber	–	–	8	1
Polyrhachis dives	–	–	3	1
Strumigenys minutula	–	–	1	–

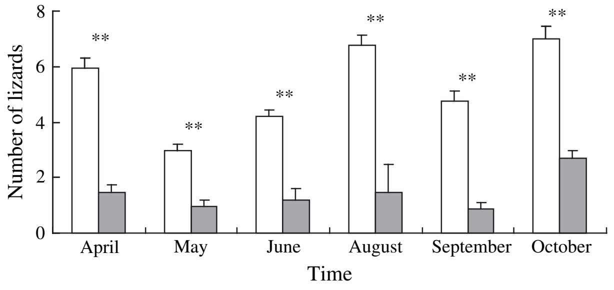

Fig. 2. Mean (+SE) numbers of *Anolis sagrei* in lizard-present (open bars) and lizard-removed (filled bars) sub-enclosures. The numbers represent results of manipulation (**$P < 0.01$).

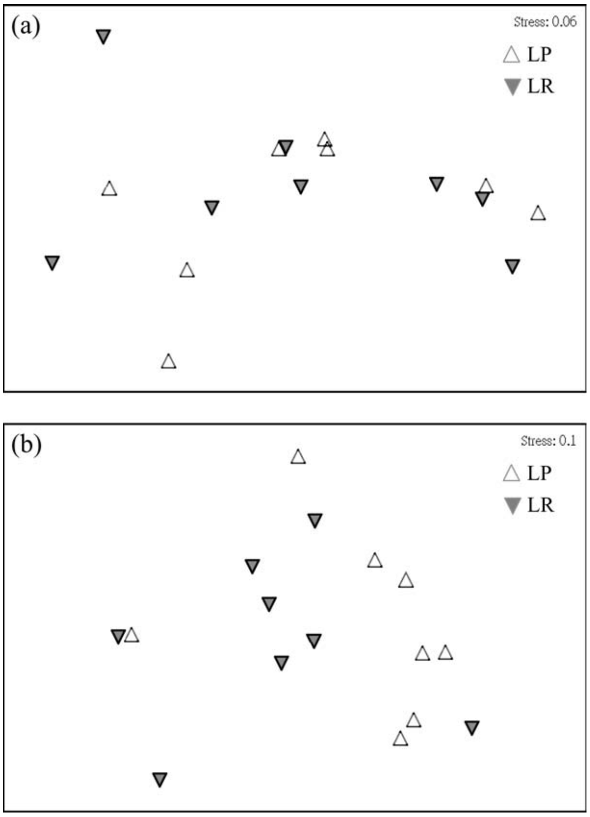

Fig. 3. The multi-dimensional scaling plots of lizard-present (LP) and lizard-removed (LR) sub-enclosures generated by ant species composition before (a) and after (b) *Anolis sagrei* density manipulation.

Table 2. The results of SIMPER tests analysing the contributions of three dominant ant species to the observed ant community composition difference.

Species	Mean dissimilarity	Dissimilarity/ SD	Contribution (%)	Cumulative (%)
Pheidole fervens	8.90	1.79	35.51	35.51
Pachycondyla luteipes	5.20	1.61	20.73	56.24
Paratrechina kraepelini	4.28	1.23	17.09	73.32

although that of the lizard-present sub-enclosures was somewhat lower (Fig. 4b).

Discussion

Ants play very important roles in ecosystems and their biomass could reach about 15% of the total animal biomass in tropical areas such as the Central Amazonian rain forests (Fittkau & Klinge, 1973). Many studies use ants as an indicator of the soil quality, because ants can easily and reliably be used to monitor the sustainability of the soil (Lobry de Bruyn, 1999). Folgarait (1998) pointed out that ants can influence the utilisation of the soil by other organisms by creating and modifying microhabitats; therefore ants can be regarded as the physical ecosystem engineers. Humphreys (1994) also showed that the contribution of funnel ants (*Aphaenogaster longiceps*) to soil movement can reach as much as 80% of the overall contribution of the total soil fauna. Nevertheless, ants also interact with other organisms by serving as symbionts, predators, or prey (see review by Schultz & McGlynn, 2000). Hence, when ants are severely predated upon, the significant changes in the ant community might potentially impact the functioning of ecosystems and numerous organisms that interact with ants.

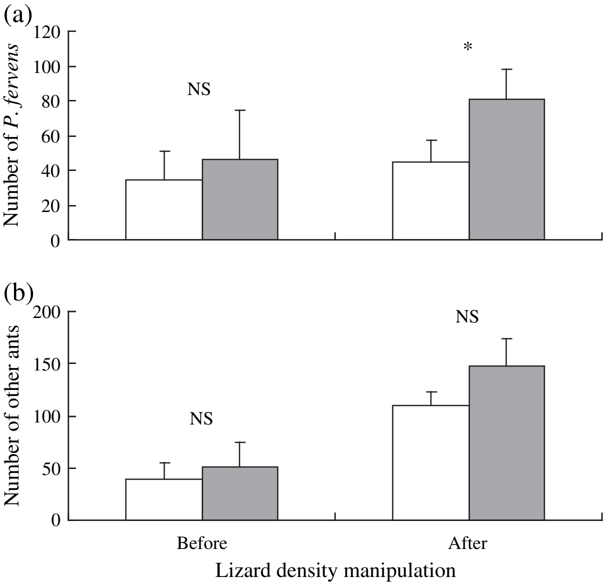

Fig. 4. Mean (+SE) abundance of *Pheidole fervens* (a) and overall non-*P. fervens* ants, (b) in lizard-present (open bars) and lizard-removed (grey bars) sub-enclosures before and after lizard density manipulation (NS, non-significant at $\alpha = 0.05$ level; $^*P < 0.05$).

Results of past studies showed that competition among ant species was the major mechanism affecting ant communities (Porter & Savignano, 1990; Holway, 1998; Vanderwoude *et al.*, 2000; Sanders *et al.*, 2003; Ness & Bronstein, 2004). Even though Gotelli (1996) and Morrison (2004) explicitly showed that antlions could affect overall ant communities by predation, they did not examine the impact on ant community structural composition. There is still no empirical evidence that the presence of a particular vertebrate predator could alter ant community structural composition. Results of the present study show that the invasive lizard, *A. sagrei*, preyed on a large number of one particular ant species and consequently altered the overall ant community structure, and such a phenomenon appears to be rarely reported. Although Munger (1984) demonstrated that horned lizard predation affected a particular species of ants, how this vertebrate impacted the whole ant community structure was not reported. In the present study, *A. sagrei* is the top predator in the betelnut palm plantation ecosystem where few organisms compete with or prey on this lizard. Even though there were other reptiles in the study site, the abundance as a whole was low and therefore should play a minor role in affecting the ant community. Results of previous studies showed that *A. sagrei* could affect orb-web spiders and aerial arthropods through either predation or competition (Schoener & Spiller, 1996, 1999; Spiller & Schoener, 1988, 1990, 1994, 1998; Schoener *et al.*, 2002). However, the relationship between *A. sagrei* and ants is still poorly understood, and some researchers considered that the interactions between these two organisms might be weak (T. W. Schoener, pers. comm.). Although many studies showed that competition and predation are two major mechanisms influencing ant communities (e.g. Sanders & Gordon, 2003), few examined the interaction between the vertebrate predator and each member of the ant community. The present study provides evidence that the abundance fluctuation of one major ant prey that lizards prefer plays a crucial role in influencing the ant community structure.

Pheidole fervens are omnivores (Brown, 2000) and they collect various types of items such as nectar, seeds, and insects (Ant Database Group, 2003). The moving trains of *P. fervens* form a superhighway to transport food resources or to move to satellite nests on the ground surface (C.-C. Lin, pers. comm.). Lizard species can be categorised as very active, cruising predators (*widely foraging*), or as sedentary, ambush predators (*sit-and-wait*) based upon their foraging modes (Huey & Pianka, 1981; Pianka & Vitt, 2003). *Anolis sagrei* is a sit-and-wait predator that feeds during the entire day (Schwartz & Henderson, 1991), and would thus be expected to prey on more active prey (Huey & Pianka, 1981) that is mobile on the surface and visually conspicuous (Pianka & Vitt, 2003). The train of moving ants generates such distinct mobile images and makes these ants easy targets for *A. sagrei.* However, when the number of foragers returning from a particular area declines, fewer and fewer ants might be sent to that area (C.-C. Lin, pers. comm.). Therefore, a lower *P. fervens* abundance in sub-enclosures with lizards present not only resulted from lizards' direct predation; but potentially could also be generated by changes in the ants' foraging decisions. Studies by Gotelli (1996), Morrison (2004), and Sanders & Gordon (2003) also showed that foraging behavioural changes of ant workers could cause the change of ant diversity or ant community structure. When the lizard density was manipulated by establishing enclosures, the numbers of *P. fervens* that were sent to lizard-present sub-enclosures should be similar to that before the enclosure establishment, because the lizard density within and outside the sub-enclosures was the same. However, in the sub-enclosures with lizards removed, possibly due to lower predation pressure from lizards and thus the higher return rate of the worker ants, more and more ants might be sent to these areas rather than those with the lizards present. Currently, there is no way to identify the mechanisms generating the observed *P. fervens* abundance changes because the experimental design does not allow such evaluation. It is also possible that the combined direct and indirect effects of lizard predation are responsible for the observed results.

Other ant species such as *Paratrechina kraepelini* search for food resources individually but carry food items back to the nest together (C.-C. Lin, pers. comm.). Because *P. kraepelini* usually move on the ground or tree trunks individually, compared with the group moving pattern of *P. fervens*, their chance of being detected by the lizards might be much lower. On the other hand, *Pachycondyla luteipes* searches for food resources individually, then recruits other members to bring the food back to the nest. They are generalist predators or scavengers and some species of this genus specialise in predating on termites (Shattuck and Barnett, 2001). The foraging behaviours of these two dominant ant species differ from that of *P. fervens* and they might have received much less predation pressure from *A. sagrei.* Therefore, the abundance of these two dominant ant species did not differ between the two types of sub-enclosures even after lizard density manipulation. In addition to these three dominant ant species, there were five more ant species. However, their abundance was very low (less than 15 specimens) and consequently it was difficult to assess the impact of the lizards on them.

Conclusion

In this study, evidence from enclosure experiments showed that local ant communities were significantly altered by an exotic lizard. *Anolis sagrei* has been in Taiwan for more than 7 years and available evidence showed that the number of ants consumed by these lizards was high (Huang, 2007). Therefore, the parts of the ecosystem functioning and biotic interactions in which ants play a significant role would potentially be impacted. The present study only examined the short-term ant community changes due to the large predation pressure from *A. sagrei.* If the long-term existence of this invasive lizard in the study site is considered, the actual influence on the ant community and ecosystem functioning should be much greater than what was observed in this study. Since it is quite possible that this lizard will spread in Taiwan similarly to how it has in other parts of the world, further efforts are needed to determine whether, and to what extent, changes in ant communities due to lizard predation affect the functioning of the ecosystem, especially in the litter layer.

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