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Chapter one

The shifting of ant community structure by predation of lizards

(Anolis sagrei)

Abstract

Predation effects could be achieved by directly reducing prey abundance and by indirectly via altering behavioral patterns of prey. In the past, there was little evidence that ant community structure composition could be affected by vertebrate predations. Researchers tend to consider the interactions between vertebrate predators and ants to be weak. In this study, we examined the impacts of the exotic invasive lizard, *Anolis sagrei*, on ant community structure by manipulating the density of lizards by enclosures. The natural density of *A. sagrei* in the field was surveyed and used as the density in the lizard-present subenclosures. Before lizard density was manipulated, there was no difference in ant diversity between subenclosures. After lizard density manipulation the ant diversity in subenclosures with *A. sagrei* present was significantly different from that of enclosures without, although overall ant abundance did not differ significantly. The ant diversity difference was generated by abundance change of ant species *Pheidole fervens* due to predation pressure of *A. sagrei*. A significantly lower *P. fervens* in subenclosures with *A. sagrei* present might result

from direct predation of lizards, or was generated by foraging site shift of this ant.

Results of this study thus demonstrated that the invasion of an exotic vertebrate could significantly alter the community structure of ants via predation.

Key words: *Anolis sagrei*, *Pheidole fervens*, predation, lizards, ants

沙氏變色蜥之捕食對螞蟻群聚結構之改變

摘要

捕食效應可藉由直接降低獵物數量與經由改變獵物行為模式而間接造成影響。過去研究中，甚少有證據指出螞蟻群聚結構組成是可被脊椎動物之捕食所影響，多數學者亦認為脊椎動物與螞蟻之間的交互關係是很微弱的。於此實驗中，我們以外來種沙氏變色蜥為探討主題，藉由圍籬實驗操控其密度來探討對於螞蟻群聚結構之影響。在調查野外之蜥蜴自然密度後，利用此結果當做具蜥蜴存在之圍籬內蜥蜴密度之依據。在開始對蜥蜴密度進行操控前，兩個處理間的螞蟻多樣性組成並無不同。開始對蜥蜴密度進行操控後，螞蟻多樣性組成在兩種處理下(具蜥蜴存在與不具蜥蜴存在)開始產生顯著差異；而然，螞蟻總數在兩個處理下卻是沒有差異的。螞蟻多樣性之差異主要是因為蜥蜴對熱烈大頭家蟻的捕食而造成其數量之變化。在具蜥蜴存在之圍籬，熱烈大頭蟻數目顯著偏低，而這有可能是因為蜥蜴的直接捕食，亦或是因螞蟻對於覓食地點選擇之改變所造成的。因此，本實驗結果說明外來種脊椎動物可藉由捕食效應而對螞蟻群聚結構造成顯著性改變。

關鍵字：沙氏變色蜥、熱烈大頭家蟻、捕食、蜥蜴、螞蟻

Introduction

Predation and competition have been shown to affect prey population densities. The effects of predation can be divided into two categories. The first is the direct predation effect, predators reduce prey densities mainly by direct predation. Relevant evidence has been shown in mammals (Lalas et al. 2007), birds (Recher and Majer 2006) and insects (Fincke et al. 1997). However, many researches point out that currently the evidence of direct predation is insufficient. Because of the dynamic nature of simultaneous predator-prey interactions, the impacts of predators on prey are difficult to observe (Sih 1984). The other is through indirect effect, in which prey change their behavior, morphology or life cycle in response to the presence of predators (Gotelli 1996, Holway 1998, Morrison 2004). Prey utilize various strategies to avoid the predators or to reduce mortality risk, and thus release the effects of predators on prey. Ultimately, both of these two strategies induce the decline of prey abundance.

In the past, there was little empirical evidence demonstrating ant community structures could be altered by various factors (Andersen 2000). In here, ant community was defined as a group with different populations constructed by different species of ants. However, recently many researches use invasive ants as a model to discuss the impacts of exotic ant species on native ant communities. Results of several

studies showed that the invasion of those exotic ant species, e.g. the imported fire ant (*Solenopsis invicta*) (Porter and Savignano 1990) and Argentine ants (*Linepithema humile*) (Bond and Slingsby 1984, Cammel et al 1996, Holway 1998, Sanders et al. 2003), generated negative effects on native ant communities by significantly reducing their abundance and diversity. Many ant species became rare or even distinct. In addition to impacting native ants, those invader ants also have negative effects on other arthropods, such as isopods (Porter and Savignano 1990), ticks, spiders and predatory beetles (Summerlin et al. 1977, Lofgren and Williams 1984, Long et al. 1987). In addition to exotic ant species, the specific predator of ants, such as antlion (Neuroptera: Myrmeleontidae), has been shown that their predation could decrease the ant diversities (Gotelli 1996). On the other hand, there are fewer studies on the effects of predation of vertebrates on ant communities. Although many studies showed that ants are the major food resource of lizards (Munger 1984, Pacala and Roughgarden 1984, Spiller and Schoener 1990, Dial and Roughgarden 1995, Huang unpublished data), the impacts caused by those predators on ants are still unclear.

However, studies examining the fluctuation of ant abundance mainly focus on ant communities as a whole (Porter and Savignano 1990, Gotelli 1996, Holway 1998). The major reason for such trend might be that it is difficult to observe the interactions between predators and particular prey (Sih 1984) and to determine which kind of prey

was really predated upon. Very few studies investigated the fluctuations of prey species composition generated by the introduction of predators. However, such information is important in realizing how ant community structures respond to the presence of predators. In this study, we examined how the presence of predators affected prey community structures and abundance. Enclosures were established and the density of predators, the *Anolis sagrei* lizard, was manipulated. Ant community structures in lizard-present and removed enclosures were compared to realize the direct and indirect impacts of predators on prey.

Materials and methods

Anolis sagrei

The exotic invasive brown anole, *Anolis sagrei*, was first recorded in Taiwan on 2000 and they might have been accidentally introduced into Taiwan by anthropogenic activities (Norval et al. 2002). Results of a preliminary study showed that ants comprised more than half of the diet of *A. sagrei* and among them more than 90 % were *Pheidole fervens* (number of lizards = 230, number of prey = 2,352). Besides ants, Lepidoptera (especially caterpillars) comprised more than 22 % of the overall diet. In addition to ants and caterpillars, spiders (especially Salticidae and Linyphiidae) were also frequently found in the stomach contents of *A. sagrei*. By comparing the

betelnut palm plantation sites with lizards present and removed, it showed that ant comprised nearly twice amount of ants in lizards removed site than it did in lizards present site. Due to the predation of lizards, the number of Salticidae spiders declined significantly when lizards were present.

Study site and enclosure design

The study sites were located in the 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. There were eight pairs of enclosures and each pair was consisted a lizard-present and a lizard-removed treatment. Each enclosure was 6 m by 12 m, which was consisted of two adjacent subenclosures 6 m × 6 m in size. Poles (180 cm bamboo sticks) were dug into ground for 30 cm and were separated from each other for 1.5 m to serve as supports of the fence. The fence was composed of fine meshed (3 mm × 3mm) plastic sheet which could effectively keep lizards from moving though. The height of fence was 150 cm high from ground surface and was embedded into ground for 15 cm to prevent the lizards from burrowing under it. The fence of the enclosure was topped with a 40 cm wide overhanging barrier made of the slippery plastic so that the lizards could not climb over it. The betelnut palm tree trunks within 1 m of the enclosures (either inside and outside) were surrounded with a round plastic board (40 cm in diameter) at the

same height as the enclosure to prevent the lizards from escaping from tree trunks.

Each subenclosure had a door 1 m in width for easy entrance. During the field experiment, we examined the enclosure once each week to repair the damages.

Manipulating lizard density in enclosure

On April, August and November of 2005, we conducted preliminary surveys to estimate the adult/subadult lizard density in the study site following the method devised by Heckel and Roughgarden (1979). Each survey was conducted on three consecutive days, each day a different color of lead-free paint was used to mark the lizards. The estimated lizard density in the study site was about 4.59 to 10.44 per 36 m² (Fig. 1). Based upon such information, we kept about 4 to 5 lizards in the lizard-present subenclosures and removed all in the lizard-removed subenclosures at the beginning of experiment.

On March 28, 2006, we conducted the first lizard-removal for both subenclosures of all eight pairs of enclosures. On March 30, 2006, four to six adult/subadult lizards were released into the lizard-present subenclosures; and every lizard found in the lizard-removed subenclosures was excluded. For the first five weeks, we surveyed the subenclosure lizard density at night, because they perched on vegetation while they slept and therefore were vulnerable to be caught. Every adult/subadult lizard caught at night during the survey was marked with whit lead-free

paint on the tail. On the subsequent week, whit tail marks enabled us to locate lizards and to recognize whether they existed in the lizard-present subenclosures or not.

Those adult/subadult lizards collected from lizard-removed subenclosures were either released into the lizard-present subenclosures when the lizard density was not high enough, or were released back to the field outside the enclosures. Throughout the field experiment we tried to maintain the male and female ratio inside the enclosure to be around 1 : 2. The adult/subadult lizard density survey was conducted once every week until June 16, 2006. After this date, the lizard density inside subenclosures remained more or less stable and therefore the frequency of lizard density survey was reduced to once every two weeks.

Arthropod sampling

One set of Y-shaped pitfall trap was established in each subenclosure in all eight pairs of enclosures. Each pitfall trap was composed of four 500 ml cups and there were three one-meter-long fences between four cups to intercept the arthropods efficiently. In each survey, the pitfall traps were opened for three consecutive days to collect ground arthropods. To collect above ground arthropods; we divided each subenclosure into four quadrants. We then conducted a five-minute sweep netting to collect arthropods from two of the quadrants. In the next survey the other two quadrants were sampled. Sweep-netting and pitfall trap collection were conducted

once before the lizard density was manipulated to see whether the initial arthropod diversity in subenclosures was similar. In this particular survey all four quadrants in subenclosures were sweep-netted. After lizard density manipulation was started, arthropod survey was conducted once every two or three weeks till the end of experiment. The collected ants were identified to species.

Statistical analyses

Paired *t*-tests were used to compare the abundance of various arthropods in lizard-present and lizard-removed subenclosures. Quantities compared included abundance of overall ants and abundance of *Pheidole fervens*. In addition, we also compared the community structures of ants in subenclosures subjected to different treatments. Bray-Curtis similarity index was used to calculate the similarity between subenclosures and such data was used to construct multi-dimensional scaling (MDS) plots. ANOSIM (analysis of similarity) was then used to determine the significance level. Bray-Curtis similarity calculation, MDS plotting and ANOSIM tests were all conducted using PRIMER v5.1 (Clarke and Warwick 2001). The contribution of each ant species to the observed community structural difference between lizard-present and lizard-removed subenclosures was analyzed by the SIMPER function of PRIMER (Clarke and Warwick 2001)

Results

Lizard density censuses

Five weeks after lizard density manipulation, the number of adult/subadult *A. sagrei* in lizard-present subenclosures reached about six and was significantly higher than that in lizard-removed subenclosures ($t = 9.807, p < 0.01$) (Fig. 2). In May, the density of adult/subadult lizard inside the lizard-present subenclosures dropped but increased steadily subsequently. Eventually the adult/subadult lizard density reached around seven per subenclosure on October (Fig. 2), although in September the density somewhat declined. Throughout the experiment in each month the average density of adult/subadult *A. sagrei* in lizard-present subenclosures was significantly higher than that in lizard-removed subenclosure (Fig. 2, Table 1). On July, due to the disturbance of typhoon and subsequent bad weathers the adult/subadult lizard density census could not be completed so the data was not available.

Beside *A. sagrei*, one *Japalura swinhonis*, two tropical house geckos and one *Dinodon rufozonatum* were found in lizards-present enclosures. One *J. swinhonis*, two *Mobuya longicaudata* and four tropical house geckos comprised in lizards-removed subenclosures. Therefore, the impacts from lizards on arthropods in subenclosure were mostly resulted from *A. sagrei*, while other lizard species consisted little impacts on them; which means that these two types of enclosures were under homogeneous

condition.

The effect of lizards on ant abundance and community structures

Eight species of ants were found in the study site (*Pheidole fervens*, *Paratrechina kraepelini*, *Pachycondyla luteipes*, *Iridomyrmex anceps*, *Ochetellus glaber*, *Pheidole formosensis* stat. n., *Polyrhachis dives* and *Strumigenys minutula*). *Pheidole fervens*, *Paratrechina kraepelini* and *Pachycondyla luteipes* were the dominant ant species. The abundance fluctuation of difference species of ants were given in table 2. Before the manipulation of adult/subadult *A. sagrei* density, ant communities in two types of subenclosures did not differ significantly (ANOSIM test, $R = -0.093$, $p = 0.877$) (Fig. 3a). However, after adult/subadult lizard density manipulation ant communities in two types of subenclosures differed significantly (ANOSIM test, $R = 0.214$, $p = 0.035$) (Fig. 3b). The reason for the observed ant community structural difference was the abundance reduction of *P. fervens* due to predation by *A. sagrei*. Results of SIMPER tests showed that this ant species alone was accounted for more than 60 % of the observed community composition difference between two types of enclosures (Table 3). Before adult/subadult lizard density manipulation the abundance of *P. fervens* did not differ significantly between two types of subenclosures ($t = -0.945$, $p = 0.376$) (Fig. 4a). After manipulating the density of lizards, the number of *P. fervens* in lizard-present subenclosures was significantly

lower than that in lizard-removed enclosures. Before the manipulation of adult/subadult lizard density, the overall ant abundance did not differ significantly between two types of subenclosures ($t = -1.661$, $p = 0.141$) (Fig. 4b). Despite a dramatic abundance difference of *P. fervens* between two types of subenclosures, after adult/subadult *A. sagrei* density manipulation, the overall ant abundance did not differ significantly ($t = -0.898$, $p = 0.398$), although that of lizard-present subenclosures was somewhat lower (Fig. 4b).

Discussions

Results of past studies showed that competition was the major mechanism affecting ant communities (Porter and Savignano 1990, Holway 1998, Vanderwoude et al. 2000, Sanders et al. 2003, Ness and Bronstein 2004). Even though Gotelli (1996) and Morrison (2004) explicitly showed that antlions could shift ant communities by predation, they did not examine the impacts on ant community structural composition. There is still no evidence that presence of a particular vertebrate predator could alter the whole ant community structural composition. Results of our study showed that the invasive lizard, *A. sagrei*, preyed on large number of one particular ant species and consequently altered the overall ant community structure. Such pattern is rarely verified on vertebrates. Although Munger (1984) demonstrated that horned lizard

predation affected particular species of ants; how this vertebrate impacted the whole ant community structure was not clear. In this study, *A. sagrei* is the top predator in betelnut palm ecosystem and there are few organisms to compete with or predate on this lizard. Even though other reptiles (e.g. *J. swinhonis*, tropical house geckos, *D. rufozonatum* and *M. longicaudata*) also presented few numbers in this study site, the relative population size compared with *A. sagrei* were divergent and the impacts led by them on arthropods were minor compared with that by *A. sagrei*. Results of previous studies showed that *A. sagrei* could affect orb-web spiders and aerial arthropods through either predation or competition (Spiller and Schoener 1988, 1990, 1994, Schoener and Spiller 1996, Spiller and Schoener 1998, Schoener and Spiller 1999, Schoener et al. 2002). However, currently the relationship between *A. sagrei* and ants is still poorly understood and some researches considered that the interactions between these two organisms might be weak (T. Schoener, personal communication). Although many studies showed that competition and predation are two major mechanisms that predators influenced the ant communities; few examined the interaction between predator and each member of the ant community. In this study we found that the invasive *A. sagrei* had a significant impact on ant community structure. Furthermore, we provided evidence that the abundance fluctuation of one major ant prey that lizards preferred, *P. fervens*, played a crucial role in influencing

the ant community structure.

Pheidole fervens are omnivores (Brwon Jr. 2000) and they collect various types of items such as honey dew, seeds and insects (Japanese Ant Image Database 2003). The moving trains of *P. fervens* form a superhighway to transport food resource or move to satellite nests on the ground surface (C. C. Lin, personal communication). The train of moving ants generates distinct mobile images and makes these ants easy targets for *A. sagrei* to pick up. However, while the number of workers returning from particular foraging area declines, fewer and fewer ants might be sent to that area to avoid the decline of the colony size (C. C. Lin, personal communication). Therefore, a lower *P. fervens* abundance in subenclosures with lizards present not only resulted from lizards' direct predation; but potentially could also be generated by changes in ants' foraging decisions. Studies by Gotelli (1996) and Morrison (2004) also showed that foraging behavioral changes of ant workers could cause the change of ant diversity or ant community structure. When we manipulated the lizard density by establishing enclosures, the number of *P. fervens* that were sent to lizard-present subenclosures should be similar to that before enclosure establishment, because lizard density within and outside the subenclosures was the same. However, in the subenclosures with lizards removed, possibly due to lower predation pressure from lizards and thus the higher return rate of ants, more and more ants were sent to these

areas rather than those with lizards present.

Other ant species such as *Paratrechina kraepelini* search for food resources individually but carry food items back to the nest together (C. C. Lin, personal communication). Because *P. kraepelini* usually move on the ground or tree trunks individually, compared with the group-moving *P. fervens*, their chance of being detected by lizards might be much lower. On the other hand, *Pachycondyla luteipes* search for food resources individually then recruit other ants to bring food back. They are generalist predators or scavengers and some species of this genus are specialists on termites (Australian Ant Online 2001). Because the foraging behaviors of these two dominant ant species differed from that of *P. fervens*, they received much less predation pressure from *A. sagrei*. The other five ant species comprised less than 15 individuals in the whole survey and therefore it is difficult to assess the impacts of lizards on them.

Ants play very important roles in ecosystems and their biomass could reach around 15 % of total animal biomass in tropical areas such as Central Amazon rain forests (Fittkau and Klinge 1973). Many studies use ants as an indicator of the quality of soil, because ants can easily and reliably be used to monitor the sustainability of soil (Lobry de Bruyn 1999). Folgarait (1998) pointed out that ants can influence the utilization of soil of 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*) on soil movement can reach 80 % of overall contribution of total soil fauna. Hence, when ants were severely preyed upon, the significant change in ant community might potentially impact ecosystem functioning. *Anolis sagrei* had been introduced into Taiwan for at least seven years and available evidence showed that the number of ants consumed by lizards was incredibly high. In average, every *A. sagrei* consumed about 3.5 ants per day and the total number of lizards in the study site was about 1015 [10.15 individuals/ 36m² x 3600 m² (total study area)]. In other words, over 3500 ants were consumed by *A. sagrei* everyday. Therefore, the parts of ecosystem functioning participated by ants would potentially be impacted. In this study, we only examined short term ant community changes due to large predation pressure from lizards. If we consider the long time existence of this invasive lizard in the study site, the actual influence on ant community and ecosystem functioning should be much higher than what is observed in this short term study. Further effects are needed to realize whether the changes in ant community due to lizard predation would affect functioning of the ecosystem, especially the litter layer.

At the beginning of lizard density manipulation, we purposely elevated the lizard density within the lizards-present subenclosures. Therefore, on average, over six

lizards were released into each lizards-present subenclosure to enhance lizard density variation between two types of subenclosures. In April, due to the changes of lizard density survey procedures and thus less disturbance, the density of lizards declined and was similar to the density in the field. Because the breeding season of *A. sagrei* was from March to October, the density of *A. sagrei* increased gradually during this period. In August, the density of *A. sagrei* was the highest because more resource were available in the field. In September, due to two typhoons, the population size of *A. sagrei* was reduced. In October, the study site received less disturbance and therefore the population size of *A. sagrei* remained stable and fluctuated less.

References

- Andersen, A. N. 2000. Global ecology of rainforest ants: Functional groups in relation to environmental stress and disturbance. Pp. 25-34. In Agosti, D., Majer, J. D., Alonso, L. E. and Schultz, T. R. 1st eds. *Ants: standard method for measuring and monitoring biodiversity*. Smithsonian institution press. Washington, USA.
- Australian Ants Online. 2001. Available at <http://www.ento.csiro.au/science/ants/> (accessed February of 2007)
- Bond, W. and Slingsby, P. 1984. Collapse of an ant-plant mutualism: the Argentine ant (*Iridomyrmex humilis*) and myrmecochorous Proteaceae. *Ecology* 65: 1031-1037.
- Brown Jr., W. L. 2000. Diversity of ants. Pp. 45-79. In Agosti, D., Majer, J. D., Alonso, L. E. and Schultz, T. R. 1st eds. *Ants: standard method for measuring and monitoring biodiversity*. Smithsonian Institution Press. Washington, USA.
- Cammell, M. E., Way, M. J. and Paiva, M. R. 1996. Diversity and structure of ant communities associated with oak, pine, eucalyptus, and arable habitats in Portugal. *Insectes Sociaux* 43: 37-46.
- Clarke, K. R. and Warwick, R. M. 2001. *Change in marine communities: an approach to statistical analysis and interpretation*. 2nd edn. PRIMER-E Ltd. Plymouth.
- Dial, R. and Roughgarden, J. 1995. Experimental removal of insectivores from rain

- forest canopy: direct and indirect effects. *Ecology* 76: 1821-1834.
- Fincke, O. M., Yanoviak, S. P. and Hanschu, R. D. 1997. Predation by odonates depresses mosquito abundance in water filled tree holes in Panama. *Oecologia* 112: 244-253.
- Fittkau, E. J. and Klinge, H. 1973. On biomass and trophic structure of the Central Amazonian rain forest ecosystem. *Biotropica* 5: 2-14.
- Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. 1998. *Biodiversity and Conservation* 7: 1221-1244.
- Gotelli, N. J. 1996. Ant community structure: effects of predatory ant lions. *Ecology* 77: 630-638.
- Heckel, D. G. and Roughgarden, J. 1979. A technique for estimating the size of lizard populations. *Ecology* 60: 966-975.
- Holway, D. A. 1998. Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. *Oecologia* 116: 252-258.
- Humphreys, G. S. 1994. Bioturbation, biofabrics and the biomantle: an example from the Sydney Basin. *Developments in Soil Science* 22: 421-436.
- Japanese Ant Image Database. 2003. Available at <http://ant.edb.miyakyo-u.ac.jp/E/index.html> (accessed February of 2007)
- Lalas, C., Ratz, H., McEwan, K. and Mcconkey, S. D. 2007. Predation by New

- Zealand sea lions (*Phocarctos hookeri*) as a threat to the viability of yellow-eyed penguins (*Megadyptes antipodes*) at Otago Peninsula, New Zealand. *Biological Conservation* 135: 235-246.
- Lobry de Bruyn, L. A. 1999. Ants as bioindicators of soil function in rural environments. *Agriculture, Ecosystems and Environment* 74: 425-441.
- Lofgren, C. S., and Williams, D. F. 1984. Polygynous colonies of the red imported fire ant, *Solenopsis invicta* (Hymenoptera Formicidae) in Florida. *Florida Entomologist* 67: 484-486.
- Long, W. H., Nelson, L. D., Templet, P. J. and Viator, C. P. 1987. Abundance of foraging ant predators of the sugarcane borer in relation to soil and other factors. *Journal of the American Society of Sugar Cane Technology* 7: 5-14.
- Morrison, L. W. 2004. Spatiotemporal variation in antlion (Neuroptera: Myrmeleontidae) density and impacts on ant (Hymenoptera: Formicidae) and generalized arthropod foraging. *Ecology and Population Biology* 97: 913-922.
- Munger, J. C. 1984. Long-term yield from harvester ant colonies: implications for horned lizard foraging. *Ecology* 65: 1077-1086.
- Ness, J. H. and Bronstein, J. L. 2004. The effects of invasive ants on prospective ant mutualists. *Biological Invasions* 6: 445-461.

- Norval, G., Mao, J. J., Chu, H. P. and Chen, L. C. 2002. A new record of an introduced species, the brown anole (*Anolis sagrei*) (Dumeril & Bibron, 1837), in Taiwan. *Zoological studies* 41: 332-336.
- Pacala, S. and Roughgarden, J. 1984. Control of arthropod abundance by *Anolis* lizards on St. Eustatius (Neth. Antilles). *Oecologia* 64: 160-162.
- Porter, S. D. and Savignano, D. A. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* 71: 2095-2106.
- Recher, H. F. and Majer, J. D. 2007. Effects of bird predation on canopy arthropods in wandoo *Eucalyptus wandoo* woodland. *Austral Ecology* 31: 349-360.
- Sanders, N. J., Gotelli, N. J., Heller, N. E. and Gordon, D. M. 2003. Community disassembly by an invasive species. *PNAS* 100: 2474-2477.
- Schoener, T. W. and Spiller, D. A. 1996. Devastation of prey diversity by experimentally introduced predators in the field. *Nature* 381: 691-694.
- Schoener, T. W. and Spiller, D. A. 1999. Indirect effects in an experimentally staged invasion by a major predator. *American Naturalist* 153: 347-358.
- Schoener, T. W., Spiller, D. A. and Losos, J. B. 2002. Predation on a common *Anolis* lizard: can the food-web effects of a devastating predator be reversed? *Ecological Monographs* 72: 383-407.
- Sih, A. 1984. The behavioral response race between predator and prey. *American*

Naturalist 123: 143-150.

Spiller, D. A. and Schoener, T. W. 1988. An experimental study of the effect of lizards on web spider communities. *Ecological Monographs* 58: 57-77.

Spiller, D. A. and Schoener, T. W. 1990. Lizards reduce food consumption by spiders: mechanisms and consequences. *Oecologia* 83: 150-161.

Spiller, D. A. and Schoener, T. W. 1994. Effect of top and intermediate predators in a terrestrial food web. *Ecology* 75: 182-196.

Spiller, D. A. and Schoener, T. W. 1998. Lizards reduced spider species richness by excluding rare species. *Ecology* 79: 503-516.

Summerlin, J. W., Hung, A. C. F. and Vinson, S. B. 1977. Residues in nontarget ants, species simplification and recovery of populations following aerial applications of mirex. *Environmental Entomology* 6: 193-197.

Vanderwoude, C., Lobry de Bruyn, L. A. and House, A. P. N. 2000. Response of an open-forest ant community to invasion by the introduced ant, *Pheidole megacephala*. *Austral Ecology* 25: 253-259.

Figures

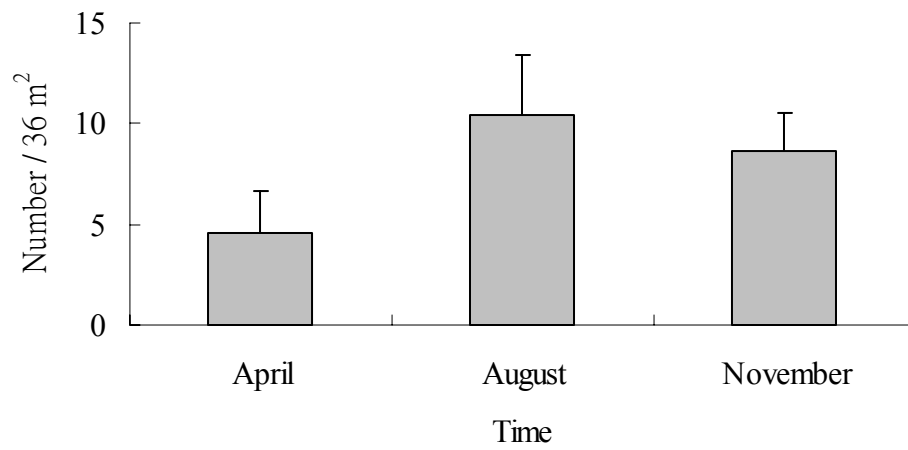


Fig. 1. Mean (\pm SE) estimated adult/subadult lizard density of the betelnut palm plantation in three months of 2005.

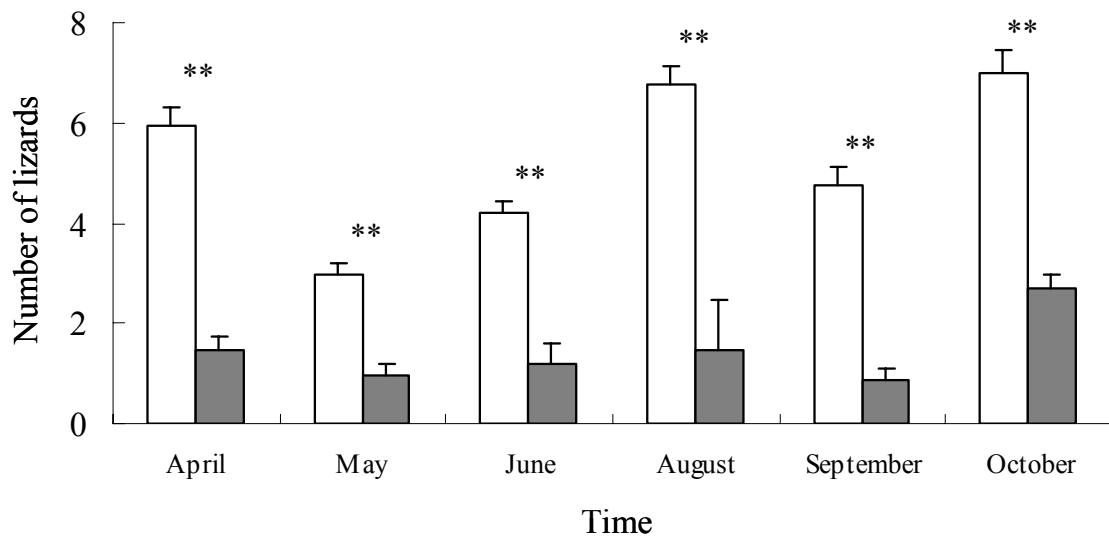


Fig. 2. Mean (\pm SE) number of adult/subadult *Anolis sagrei* in lizard-present (open bars) and lizard-removed (gray bars) subenclosures in different months of 2006. (** : $p < 0.01$)

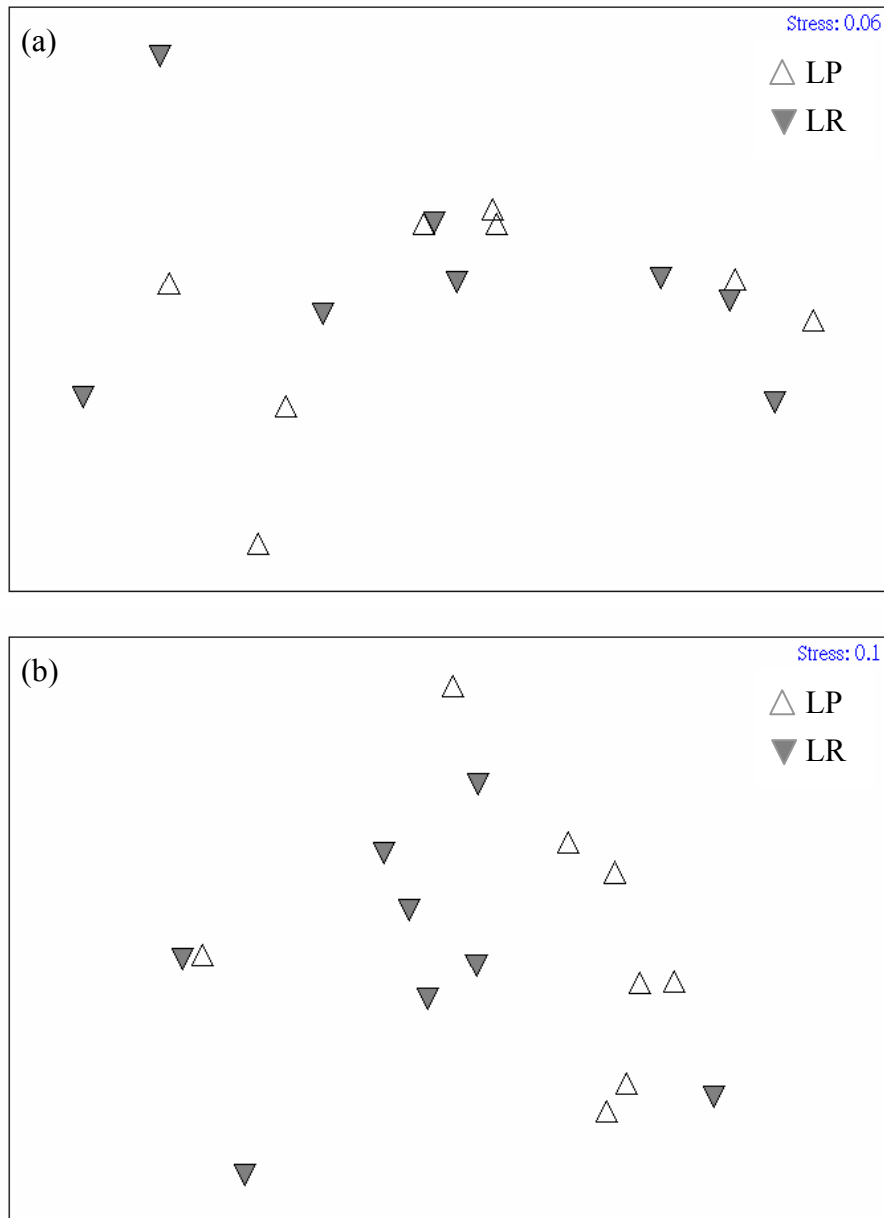


Fig. 3. The MDS plots of lizard-present (LP) and lizard-removed (LR) subenclosures generated by ant species composition before (a) and after (b) lizard density manipulation.

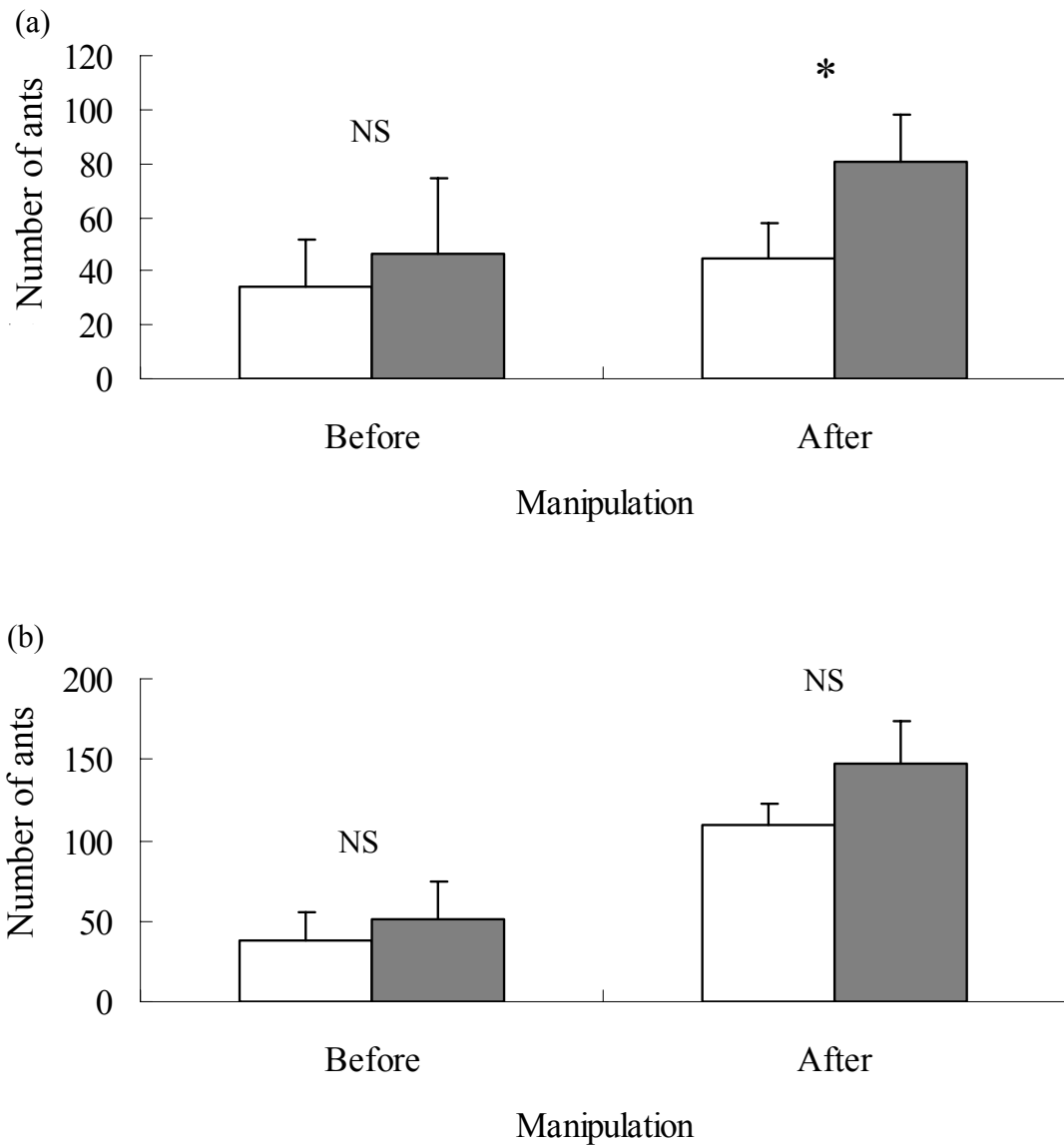


Fig. 4. Mean (\pm SE) abundance of *Pheidole fervens* (a) and overall ant species (b) in lizard-present (open bars) and lizard-removed (gray bars) subenclosures before and after lizard density manipulation. (NS: non-significant at $\alpha = 0.05$ level; *: $p < 0.05$)

Tables

Table 1. Results of paired t -tests comparing number of adult/subadult *A. sagrei* between lizard-present and lizard-removed subenclosures in various months of 2006.

Month	t	p
March to April	9.801	<0.001
May	6.394	<0.001
June	5.636	<0.001
August	10.624	<0.001
September	4.651	0.002
October	9.911	<0.001

Table 2. The abundance of different species of ants from two types of enclosures

before and after lizard density manipulation.

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

Table 3. The results of SIMPER tests analyzing contribution of dominant ant species to the observed ant community structure difference.

Species	Mean Dissimilarity	Dissimilarity/SD	Contribution (%)	Cumulative (%)
<i>Pheidole fervens</i>	27.39	1.79	60.33	60.33
<i>Paratrechina kraepelini</i>	9.43	1.25	20.76	81.09
<i>Pachycondyla luteipes</i>	6.75	1.14	14.87	95.96

Chapter two

The effect of invasive lizard, *Anolis sagrei*, on litter decomposition in a betelnut palm ecosystem

Abstract

Litter decomposition rate is an important factor affecting nutrient recycling in the detritus ecosystem. Collembola are among the most abundant micro-detritivores in leaf litter and play the key roles in the functioning. Collembola influence the litter decomposition rate directly by feeding on litters and indirectly by consuming the fungi involved in the detritus recycling process. Ground spiders such as the family Lycosidae is the major predator of collembola and some genera of ants also take collembola as major prey resource. In this study, we established enclosures to manipulate the density of an invasive lizard, *Anolis sagrei*, to determine whether the introduction of this lizard would indirectly affect collembola abundance and diversity by predated their predators such as ants and spiders, and consequently affecting litter decomposition rate. We surveyed the natural density of *A. sagrei* and used that as the density in lizard-present subenclosures. After the manipulation, the overall ant abundance did not differ between two lizard-present and lizard-removed subenclosures. The abundance of *Strumigenys* ant, the collembola specialist, was very

low, so its impact on collembola could not be assessed. After lizard density manipulation although the abundance of jumping spiders (Salticidae) differed significantly, that of the major spider predator of collembola, the wolf spider (Lycosidae), showed no significant change. Neither abundance nor diversity of collembola differed significantly between two types of subenclosures. Congruent with such results were the litter decomposition rates, which also showed no significant differences. Results of this study showed that although presence of the invasive *A. sagrei* altered ant community structure, this lizard did not significantly affect major predators of collembola and thus collembola abundance and consequently litter decomposition was not impacted.

Key words: Collembola, Lycosidae, *Strumigenys*, litter decomposition, *Anolis sagrei*

外來種沙氏變色蜥對檳榔園中落葉分解率之影響

摘要

落葉分解率是底棲生態系中影響養份循環的重要因子；跳蟲則是落葉層中數量最多的小型分解者，並且還在生態功能性上扮演關鍵角色。跳蟲會藉由直接分解掉落葉或是間接地經由消化底層養份循環過程中的真菌來影響落葉分解率。地表蜘蛛如狼蜘蛛科蜘蛛是跳蟲的主要捕食者；且有些屬的螞蟻亦以跳蟲為主要的食物來源。在此實驗中，我們以建立圍籬來操控外來種沙氏變色蜥密度觀察此外來種蜥蜴的引入是否會藉由捕食跳蟲的捕食者，如螞蟻及蜘蛛進而間接影響到跳蟲的數目、多樣性及落葉分解率。我們先調查了沙氏變色蜥的自然密度，並利用此密度當做圍籬內蜥蜴密度操控的依據。在開始對蜥蜴密度進行操控後，螞蟻的總數於有蜥蜴存在及蜥蜴移除組間是沒有差異。偏好捕食跳蟲之姬瘤顎蟻屬螞蟻數目極低，因此它們對跳蟲所造成之衝擊並無法評估。雖然跳蜘蛛科蜘蛛數目在開始對蜥蜴密度開始進行操控後有顯著差異；但因跳蟲的主要捕食者狼蜘蛛科蜘蛛數目在操控前、後並無不同，以致跳蟲數目及多樣性在兩種處理皆未達顯著之差異。落葉分解率之結果在兩個處理間亦未達顯著之差異，此與跳蟲之結果相符。此研究之結果顯示，雖然外來種沙氏變色蜥之存在會改變螞蟻群聚結構組成，但此蜥蜴卻不會顯著地藉由影響跳蟲的捕食者，亦或是跳蟲本身進而間接影響落葉分解率。

關鍵字：跳蟲，狼蛛科，姬瘤顎蟻屬，落葉分解，沙氏變色蜥

Introduction

Litter decomposition rate is an important factor affecting the nutrient recycle rate of detritus ecosystem (Seastedt 1984, Hasegawa and Takeda 1995, Bradford et al. 2002). In the detritus ecosystem, arthropods play the key roles in the functioning (Folgarait 1998, Lawrence and Wise 2000, Lensing et al. 2005). Collembola are among the most abundant microbi-detritivores in leaf litter and their density could reach the level of one hundred thousand or more per square meter (Hopkin 1997). Collembola influence the litter decomposition rate directly by feeding on litter and indirectly by consuming the fungi involved in the detritus decomposition process (Parkinson et al. 1979, Seastedt 1984, Hasegawa and Takeda 1995). In spite of great population of collembola in detritus ecosystem, spiders are the most abundant macrofaunal invertebrate predators in terrestrial ecosystems (Wise 1993, Nyffeler 2000). Previous studies showed that in detritus ecosystems, particularly wolf spiders of the family Lycosidae, particularly, predate upon collembola as main food resource (Lawrence and Wise 2000, Lensing et al. 2005). Results of several manipulative studies showed that when spiders in the system were removed, the number of collembola increased significantly (Lawrence and Wise 2000, Wise 2004). The predation of spiders on collembola consequently generates indirect impacts on litter decomposition rate. In other words, the nutrient recycling of detritus ecosystem is also

affected by spiders.

Exotic invasive lizard, *Anolis sagrei*, was first recorded in Chiayi, Taiwan in 2000 (Norval et al. 2002). From previous study, the diet of *A. sagrei* estimated from stomach content was mostly ants and spiders (Huang, unpublished data). Many predators, e.g. predaceous mites, carabid beetles, ants and spiders use collembola as major prey resource (Hopkin 1997). Among ants, the genus *Strumigenys* preferentially predate upon collembola as major prey item (C. C. Lin, personal communication). In spiders, wolf spiders of the family Lycosidae are reported to be another major predator of collembola (Lawrence and Wise 2000, Wise 2004). However, jumping spiders of the family Salticidae, which comprises a large proportion in lizards' diet composition, resemble wolf spiders in many aspects of foraging behaviors. Jumping spiders pursue prey actively, and search for prey in understory and ground levels. In this study, we evaluated whether the presence of an invasive lizard might indirectly affect collembola abundance and diversity by predated upon their predators such as ants and spiders. The density of adult/subadult *A. sagrei* was manipulated by enclosures and the effects of such treatments on ant, spider, collembola abundance and litter decomposition rate were assessed.

Material and Methods

Study site and enclosure design

The study sites were located in the 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. There were eight pairs of enclosures and each pair consisted of a lizard-present and a lizard-removed treatment. Each enclosure was 6 m by 12 m, which consisted of two adjacent subenclosures 6 m × 6 m in size. Poles (180 cm bamboo sticks) were dug into ground for 30 cm and were separated from each other for 1.5 m to serve as supports of the fence. The fence was composed of fine meshed (3 mm × 3mm) plastic sheet which could effectively keep lizards from moving through. The height of fence was 150 cm high from ground surface and was embedded into ground for 15 cm to prevent the lizards from burrowing under it. The fence of the enclosure was topped with a 40 cm wide overhanging barrier made of the slippery plastic so that the lizards could not climb over it. The betelnut palm tree trunks within 1 m of the enclosures (either inside and outside) were surrounded with a round plastic board (40 cm in diameter) at the same height as the enclosure to prevent the lizards from escaping from tree trunks. Each subenclosure had a door 1 m in width for easy entrance. During the field experiment, we examined the enclosure once each week to repair the damages. The

study site was not conducted fertilization by farmers; in other words, there was no any procedure was conducted to enhance the fertile of land.

Manipulating lizard density in enclosure

On April, August and November of 2005, we conducted preliminary surveys to estimate the lizard density in the study site following the method devised by Heckel and Roughgarden (1979). The adult and subadult lizards were used only to calculate the lizard density and to release into the lizards-present subenclosures. Each survey was conducted on three consecutive days, each day a different color of lead-free paint was used to mark the lizards. The estimated lizard density in the study site was about 4.59 to 10.44 per 36 m² (Fig. 1). Based upon such information, we kept about 4 to 5 lizards in the lizard-present subenclosures and removed all in the lizard-removed subenclosures at the beginning of experiment.

On March 28, 2006, we conducted the first lizard-removal for both subenclosures of all eight pairs of enclosures. On March 30, 2006, four to six lizards were released into the lizard-present subenclosures; and every lizard found in the lizard-removed subenclosures was excluded. For the first five weeks, we surveyed the subenclosure lizard density at night, because they perched on vegetation while they slept and therefore were vulnerable to be caught. Every lizard caught at night during the survey was marked with whit lead-free paint on the tail. On the subsequent week,

whit tail marks enabled us to locate lizards and to recognize whether they existed in the lizard-present subenclosures or not. Those lizards collected from lizard-removed subenclosures were either released into the lizard-present subenclosures when the lizard density was not high enough, or were released back to the field outside the enclosures. Throughout the field experiment we tried to maintain the male and female ratio inside the enclosure to be around 1 : 2. The lizard density survey was conducted once every week until June 16, 2006. After this date, the lizard density inside subenclosures remained more or less stable and therefore the frequency of lizard density survey was reduced to once every two weeks.

Arthropod sampling

One set of Y-shaped pitfall trap was established in each subenclosure in all pairs of enclosures. Each pitfall trap was composed of four 500 ml cups and there were three one-meter-long fences between four cups to intercept the arthropods efficiently. In each survey, the pitfall traps were opened for three consecutive days to collect ground arthropods. To collect above ground arthropods; we divided each subenclosure into four quadrants. We then conducted a five-minute sweep netting to collect arthropods from two of the quadrants. In the next survey the other two quadrants were sampled. Sweep-netting and pitfall trap collection were conducted once before the lizard density was manipulated to see whether the initial arthropod diversity in

subenclosures was similar. In the survey all four quadrants in subenclosures were sweep-netted. After lizard density manipulation was started, arthropod survey was conducted once every two or three weeks till the end of experiment. The collected ants were identified to species, spiders were identified to family and collembola were identified into morphological species. The number of Collembola was transformed with exponential function to calculate their diversities.

Litter decomposition estimation

The decomposition rate of dehydrated betelnut leaves was used as an indicator to estimate the impacts of detritus fauna such as collembola and other organisms on litter decomposition. Each litterbag contained 6 g of dehydrated leaves of betelnut palm *Areca catechu* L. and six litterbags were placed inside each subenclosure. The leaves were dehydrated under 60 °C for 72 hours and the litterbag was 15 by 15 cm in size with a 3 mm mesh size. Litter decomposition rate estimation were conducted twice, one in the summer and the other in the autumn. The summer survey began on July, 7, 2006 and the litterbags were taken back to laboratory after two, three and five weeks. The autumn survey began on September, 18, 2006 and the litterbags were taken back to laboratory after two, five and nine weeks. The litters were taken out from the litterbag and rinsed up with water to remove the mud on the surface and put into oven under 60 °C for 72 hours. The dry weight of the remaining litter was substrated from

the original weight to calculate litter decomposition rate.

Statistical analyses

Paired *t*-tests were used to compare the abundance of various arthropods in lizard-present and lizard-removed subenclosures. Quantities compared included abundance of overall ants, abundance of Lycosidae, Salticidae and collembola. In addition, we also compared the community structures of collembola in subenclosures subjected to different treatments. Bray-Curtis similarity index was used to calculate the similarity between subenclosures and such data was used to construct multi-dimensional scaling (MDS) plots. ANOSIM (analysis of similarity) was then used to determine the significance level. Bray-Curtis similarity calculation, MDS plotting and ANOSIM tests were all conducted using PRIMER v5.1 (Clarke and Warwick 2001). Paired *t*-tests were used to compare litter decomposition rates between subenclosures with *A. sagrei* present or removed.

Results

Lizard density censuses

Five weeks after lizard density manipulation, the number of *A. sagrei* in lizard-present subenclosures reached about six and was significantly higher than that in lizard-removed subenclosures ($t = 9.807, p < 0.01$) (Fig. 2). In May, the density of

lizard inside the lizard-present subenclosures dropped but increased steadily subsequently. Eventually the lizard density reached around seven per subenclosure on October (Fig. 2), although in September the density somewhat declined. Throughout the experiment in each month the average density of *A. sagrei* in lizard-present subenclosures was significantly higher than that in lizard-removed subenclosure (Fig. 2, Table 1). On July, due to the disturbance of typhoon and subsequent bad weathers the lizard density census could not be completed so the data was not available.

The effect of lizards on ants, spiders and collembola

There was no significant difference in overall ant abundance between lizard-present and removed subenclosures (Fig. 3). The abundance of the genus *Strumigenys* obtained from traps was very low (five individuals) and therefore statistic analysis was not feasible. The abundance of Lycosidae did not differ significantly between lizard-present and removed subenclosures either before lizard density manipulation ($t = -1.000, p = 0.351$) or after ($t = 1.101, p = 0.307$) (Fig 4a). Salticidae showed no significant difference on abundance between two treatments before lizard densities were manipulated ($t = 0.18, p = 0.862$). However, after the manipulation, the abundance in the lizard-present subenclosures was significantly lower ($t = -2.434, p = 0.045$) (Fig. 4b). There was no significant difference on number of collembola between two treatments either before ($t = -0.764, p = 0.47$) or after manipulation ($t =$

-1.069, $p = 0.321$) (Fig. 5). The ANOSIM results from Bray-Curtis similarity that generated by morphological species composition showed no significant difference between two treatments before ($R = -0.069$, $p = 0.763$) and after ($R = -0.009$, $p = 0.448$) lizard density manipulation. The MDS-plots estimated from collembola morphospecies composition showed no clustering between subenclosures of two treatments before (Fig. 6a) or after (Fig. 6b) lizard densities manipulation.

The effects of lizards on litter decomposition rates

In the summer survey, when the litter was kept in the field for two weeks, the decomposition rate between two types of subenclosures differed significantly ($t = -1.931$, $p = 0.043$). However, when the litter was kept for three or five weeks, no significant difference in decomposition rate was found (three weeks: $t = -1.388$, $p = 0.182$; five weeks: $t = 0.136$, $p = 0.894$) (Fig. 7a). In the autumn survey, no difference in litter decomposition rate was found no matter the litter was kept in the field for two ($t = -1.617$, $p = 0.127$), five ($t = -1.507$, $p = 0.153$) or nine ($t = -0.827$, $p = 0.422$) weeks (Fig. 7b).

Discussions

Results of this study showed that the impacts of lizards on collembola were slight, because lizards only predated small number of predators of collembola. In a

previous study, results of stomach content analysis showed that collembola comprised only around 0.18 % of prey consumed by *A. sagrei* (Huang, unpublished data).

Therefore, it was unlikely that *A. sagrei* would impact collembola population via direct predation. However, collembola consist small size and soft body material; this make them easier to be digested. Unlike insects or spiders, collembola do not consist exoskeleton; without those morphological exoskeleton makes them more difficult to be identified. In this case, we considered that collembola were predated small population and the direct interactions between lizards and collembola were minor.

Some researches (Lawrence and Wise 2000, Lawrence and Wise 2004, Wise 2004) showed that certain ground spiders, particular Lycosidae, preyed on collembola and could reduced the number of collembola substantially. Kajak (1995) pointed out that through predation, spiders not only affected decomposers' abundance but also influenced litter decomposition rate indirectly. Since collembola did not seem to be affected by direct predation by *A. sagrei* and spiders did not receive heavy predation pressure from lizard; the impacts of *A. sagrei* on collembola in the betelnut palm ecosystem were weak. Salticidae actively hunt for prey in understory plantation as well as grounds. In this study, about half of the Salticidae specimens were collected from pitfall trap sampling. Although the habitats of Salticidae overlapped with that of collembola, it is possible that Salticidae did not prey heavily on collembola as did

Lycosidae. On the other hand, only few Lycosidae were present in the study site. Low density of wolf spiders suggested that the predatory interactions between Lycosidae and collembola were not as strong as that reported in other studies (Lawrence and Wise 2000, Lawrence and Wise 2004, Wise 2004). Kajak (1995) reported that collembola are one of the major prey consumed by ground webbing spiders, Linyphiidae. In this study, Linyphiidae were abundant in the study site and *A. sagrei* consumed a considerable amount of them (Huang, unpublished data). However, this spiders' high abundance in betelnut palm plantations might have buffered the predation pressure from *A. sagrei*. Therefore, *A. sagrei* were not able to affect the survival of collembola indirectly by preying on spiders.

In addition to spider predators, some ants such as member of the genus *Strumigenys* are specialists on collembola (Japanese Ant Image Database 2003). In this study, we did find *Strumigenys* ants in the study site. However, they only comprised a very small proportion of overall ant community in the study site. Furthermore, while ants such as *Pheidole* aggregate and form a conspicuous moving train, *Strumigenys* usually move solitarily. Such behavioral trait makes them unlikely to be predated by *A. sagrei*. Therefore, in the betelnut palm plantation ecosystem, the links between ants and collembola were also weak and direct or indirect significant impacts on collembola from ants could not be detected. Although predation of *A.*

sagrei significantly impacted ant community, since the collembola specialist *Strumigenys* were scarce and were not affected, collembola diversity as well as litter decomposition rate did not differ between subenclosures with or without *A. sagrei*.

Besides spiders and ants, there are many other animals which can potentially be predators of collembola. Hopkin (1997) observed that young toads, blackbirds and robins occasionally consume collembola. Collembola were also retrieved from stomach contents of birds in English woodlands (Betts 1955). Many predators such as harvestmen, pseudoscorpions and mites are also the potential predators of collembola (Hopkin 1997). Gasc et al. (1983) reported that in French Guyana, around 30% to 48% of food items small lizards consumed were collembola. Except predators, other soil animals such as earthworms also play important roles in regulating soil organism communities. Szlavecz (1985) demonstrated that the burrows created by earthworms helped generate more suitable microhabitats, which increased the abundance of soil animals such as collembola (Dózsa-Farkas 1978). In this study, in addition to ants and spiders, we did not consider the effects of other organisms. Some of such organisms might not be well controlled and such compounding effects might have prevented us from detecting the impacts of *A. sagrei* on collembola and litter decomposition. At the beginning of experiment we expected to see a difference in litter decomposition between subenclosures with lizards present or removed. However, the results showed

that except in the very beginning of the survey, basically density of *A. sagrei* had no effect on litter decomposition rates. Such results were congruent with the facts that the abundance and diversity of collembola did not differ between two types of subenclosures.

In past, few studies examined the relationships between ants and collembola. In this study, we observed that some ants were carrying collembola, although we were not sure whether ants took collembola as food resource or for other purposes. Due to the high sensitivity of ants during predation, they tend to drop food items they are carrying when disturbed (Halaj et al. 1997). Therefore, more sophisticated experiments are needed to test the exact relationships between ants and collembola. Several studies showed that removing macroinvertebrates affected the carbon content of soil during decomposition procedure in the meadow ecosystem (Kajak 1997) or in Amazonian tropics (Vasconcelos and Laurance 2005). Macroarthropods influence litter decomposition mostly though affecting microinvertebrates or microbial decomposers (Scheu 1993, Hunter et al. 2003). Besides collembola, there are many different kinds of macroinvertebrates [e.g. termites (Silva et al. 1985), earthworm (Reagan and Waide 1996), Formicidae, Araneae, and Lepidoptera (Hunter et al. 2003)] and microinvertebrates [e.g. mites and nematode (Hopkin 1997)] that can function as decomposers. They can affect litter decomposition rate through influencing fungal and

bacterial population (Scheu 1993). Therefore, besides collembola, many macro- and micro-invertebrates are substantially involved in litter decomposition process and they play various roles and affect ecosystem of functioning differently (Spain and Feuvre 1987). In this study, it is possible that certain decomposers that were not manipulated or controlled actually play important roles in betelnut palm plantation detritus ecosystem. A following up experiment with more biotic and abiotic factors controlled may help reveal the relationships among lizards, ants, collembola and ecosystem functioning.



References

- Betts, M. M. 1955. Food of titmice in oak woodland. *Journal of Animal Ecology* 24: 282-323.
- Bradford, M. A., Tordoff, G. M., Eggers, T., Jones, T. H. and Newington, J. E. 2002. Microbiota, fauna, and mesh size interactions in litter decomposition. *Oikos* 99: 317-323.
- Clarke, K. R. and Warwick, R. M. 2001. Change in marine communities: an approach to statistical analysis and interpretation. 2nd edn. PRIMER-E Ltd. Plymouth.
- Dózsa-Farkas, K. 1978. Die bedeutung zweier Enchytraeiden-Arten bei der Zersetzung von Hainbuchenstreu in mesophilen Laubwäldern Ungarns. *Acta Zoologica Academiae Scientiarum Hungaricae* 24: 321-330
- Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. 1998. *Biodiversity and Conservation* 7: 1221-1244.
- Gasc, J. P., Betsch, J. M. and Massoud, Z. 1983. Selective predation by sauria on collembolan in the dense, humid forest litter in French Guiana. *Bulletin de Lasociete Zoologique de France-Evolution et Zoologie* 108: 467-476.
- Halaj, J. Ross, D. W. and Moldenke, A. R. 1997. Negative effects of ant foraging on spiders in Douglas-fir canopies. *Oecologia* 109: 313-322.
- Hasegawa, M. and Takeda, H. 1995. Changes in feeding attributes of four

- collembolan populations during the decomposition process of pine needles.
Pedobiologia 39: 155-169.
- Heckel, D. G. and Roughgarden, J. 1979. A technique for estimating the size of lizard populations. *Ecology* 60: 966-975.
- Hopkin, S. P. 1997. *Biology of the Springtails (Insecta: Collembola)*. Oxford University Press. New York.
- Hunter, M. D., Adl, S., Pringle, M. and Coleman, D. C. 2003. Relative effects of macroinvertebrates and habitat on the chemistry of litter during decomposition. *Pedobiologia* 47: 101-115.
- Japanese Ant Image Database. 2003. Available at <http://ant.edb.miyakyo-u.ac.jp/E/index.html> (accessed February of 2007)
- Kajak, A. 1995. The role of soil predators in decomposition processes. *European Journal of Entomology* 92: 573-580.
- Kajak, A. 1997. Effects of epigeic macroarthropods on grass litter decomposition in mown meadow. *Agriculture, Ecosystems and Environment* 64: 53-63.
- Lawrence, K. L. and Wise, D. H. 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. *Pedobiologia* 44: 33-39.
- Lawrence, K. L. and Wise, D. H. 2004. Unexpected indirect effect of spiders on the rate of litter disappearance in a deciduous forest. *Pedobiologia* 48: 149-157.

- Lensing, J. R., Todd, S. and Wise, D. H. 2005. The impact of altered precipitation on spatial stratification and activity-densities of springtails (Collembola) and spiders (Araneae). *Ecological Entomology* 30: 194-200.
- Norval, G., Mao, J. J., Chu, H. P. and Chen, L. C. 2002. A new record of an introduced species, the brown anole (*Anolis sagrei*) (Dumeril & Bibron, 1837), in Taiwan. *Zoological Studies* 41: 332-336.
- Nyffeler, M. 2000. Ecological impact of spider predation: a critical assessment of Bristowe's and Turnbull's estimates. *Bulletins of British Arachnological Society* 11: 367-373.
- Parkinson, D., Visser, S. and Whittaker, J. B. 1979. Effects of collembolan grazing on fungal colonization of leaf litter. *Soil Biology and Biochemistry* 11: 529-535.
- Reagan, D. P. and Waide, R. B. 1996. *The Food Web of a Tropical Rain Forest*. The University of Chicago Press. Chicago.
- Scheu, S. 1993. Cellulose and lignin decomposition in soils from different ecosystems on limestone as affected by earthworm processing. *Pedobiologia* 37: 167-177.
- Seastedt, T. R. 1984. The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology* 29: 25-46.
- Silva, S. I., MacKay, W. P. and Whitford, W. G. 1985. The relative contributions of termites and microarthropods to fluff grass litter disappearance in the

Chihuahuan Desert. *Oecologia* 67: 31-34.

Spain, A. V. and Feuvre, R. P. L. 1987. Breakdown of four litters of contrasting quality in a tropical Australian rainforest. *Journal of Applied Ecology* 24: 279-288.

Szlavec, K. 1985. The effect of microhabitats on the leaf litter decomposition and on the distribution of soil animals. *Holarctic Ecology* 8: 33-38.

Vasconcelos, H. and Laurance, W. F. 2005. Influence of habitat, litter type, and soil invertebrates on leaf-litter decomposition in a fragmented Amazonian landscape. *Oecologia* 144: 456-462.

Wise, D. H. 1993. *Spiders in Ecological Webs*. Cambridge University Press, Cambridge.

Wise, D. H. 2004. Wandering spiders limit densities of a major microbe-detritivore in the forest-floor food web. *Pedobiologia* 48: 181-188.

Figures

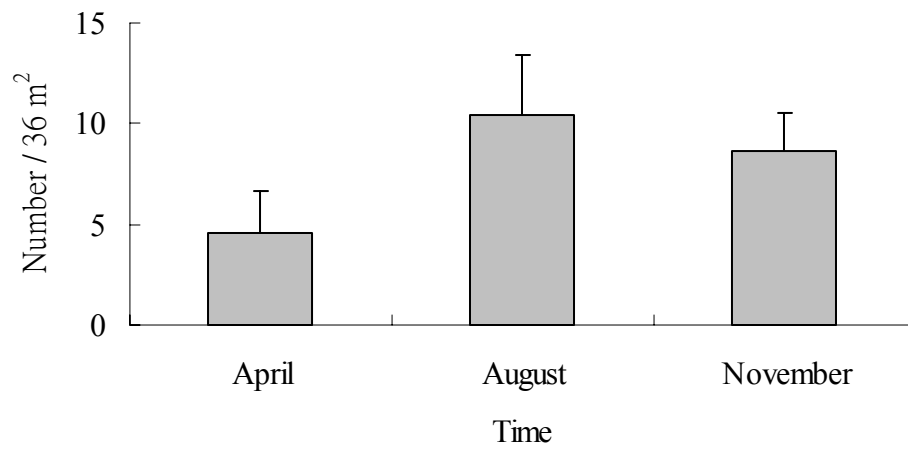


Fig. 1. Mean (\pm SE) estimated adult/subadult lizard density of the betelnut palm plantation in three months of 2005.

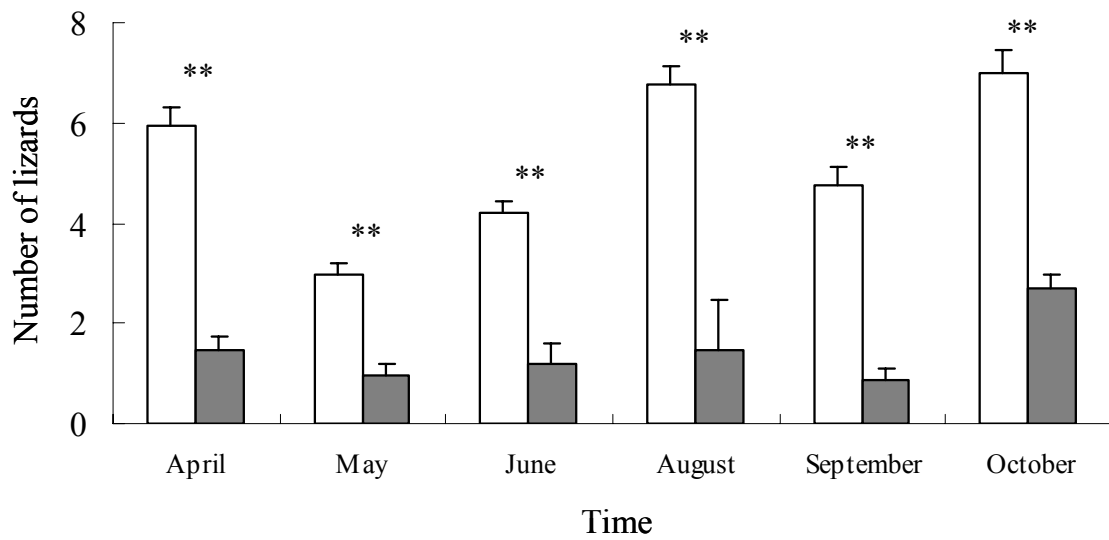


Fig. 2. Mean (\pm SE) number of adult/subadult *Anolis sagrei* in lizard-present (open bars) and lizard-removed (gray bars) subenclosures in different months of 2006. (** : $p < 0.01$)

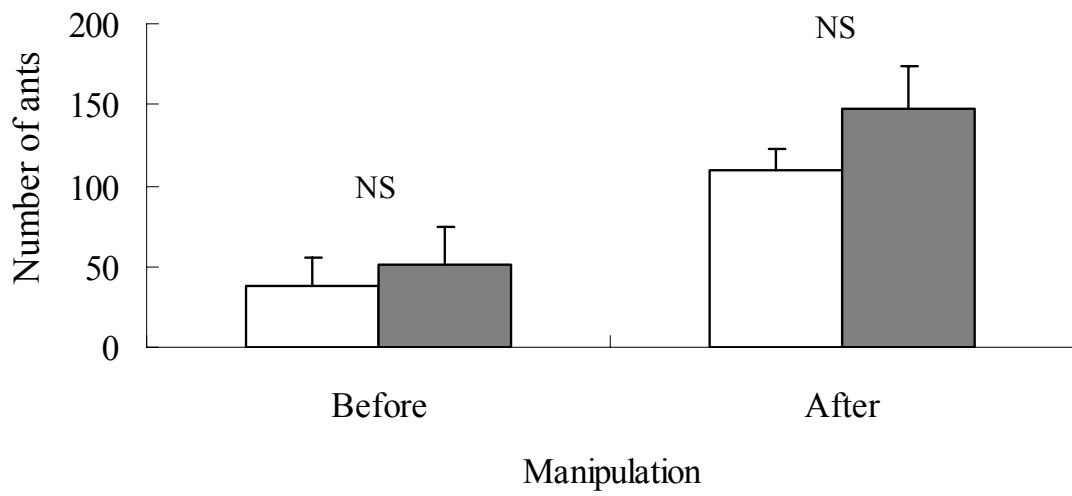


Fig. 3. Mean (\pm SE) of the abundance of overall ant species in lizard-present (open bars) and lizard-removed (gray bars) subenclosures. (NS: non-significant at $\alpha = 0.05$ level)

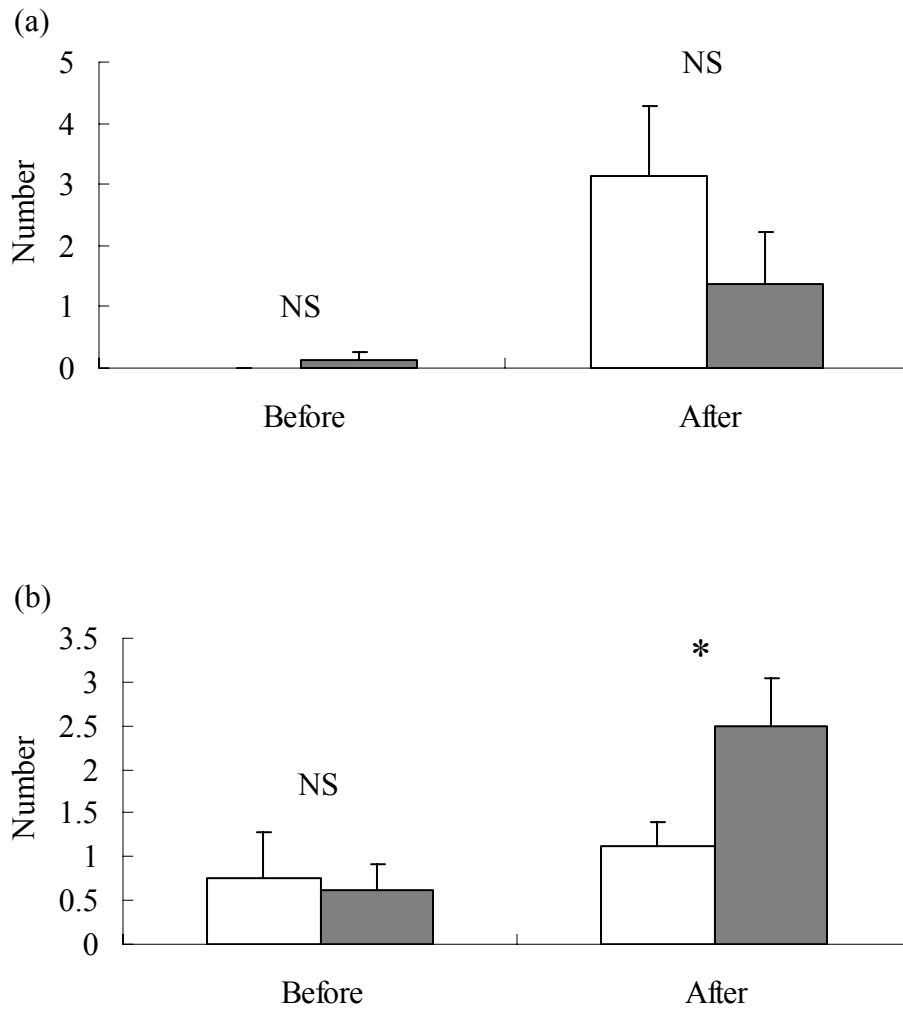


Fig. 4. Mean (\pm SE) abundance of Lycosidae (a) and Salticidae (b) in lizard-present (open bars) and lizard-removed (gray bars) subenclosures before and after lizard density manipulation. (NS: non-significant at $\alpha = 0.05$ level; *: $p < 0.05$)

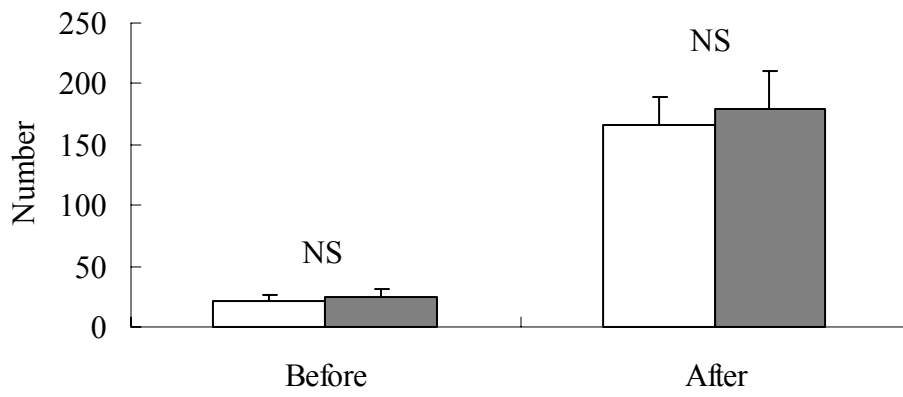


Fig. 5. Mean (\pm SE) abundance of Collembola in lizard-present (open bars) and lizard-removed (gray bars) subenclosures before and after lizard density manipulation.

(NS: non-significant at $\alpha = 0.05$ level)

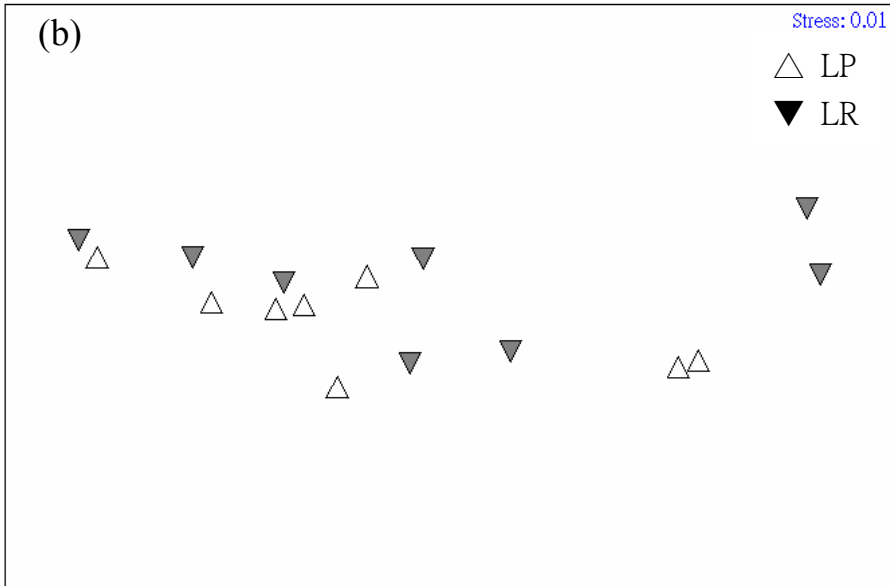
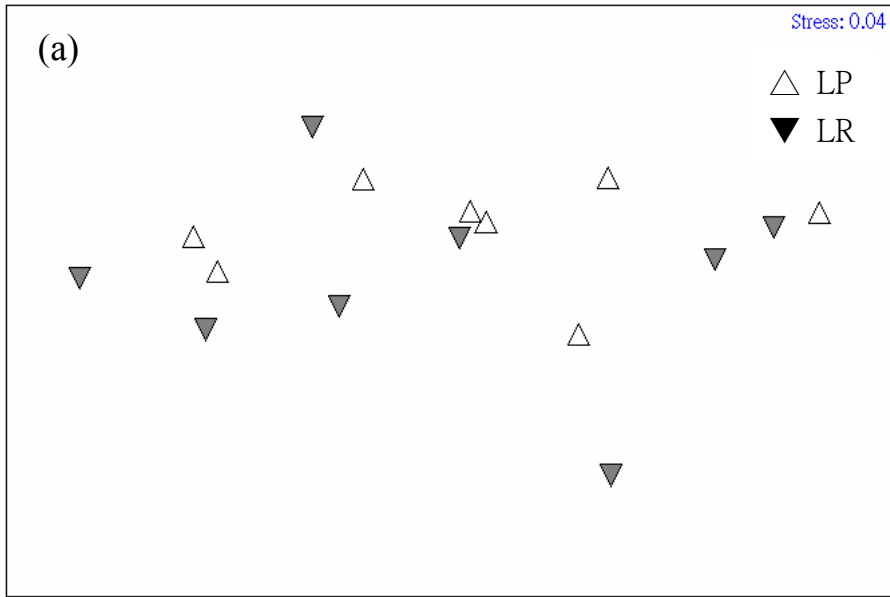


Fig. 6. The MDS plots of lizard-present (LP) and lizard-removed (LR) subenclosures generated by morphological species composition of Collembola before (a) and after (b) lizard density manipulation.

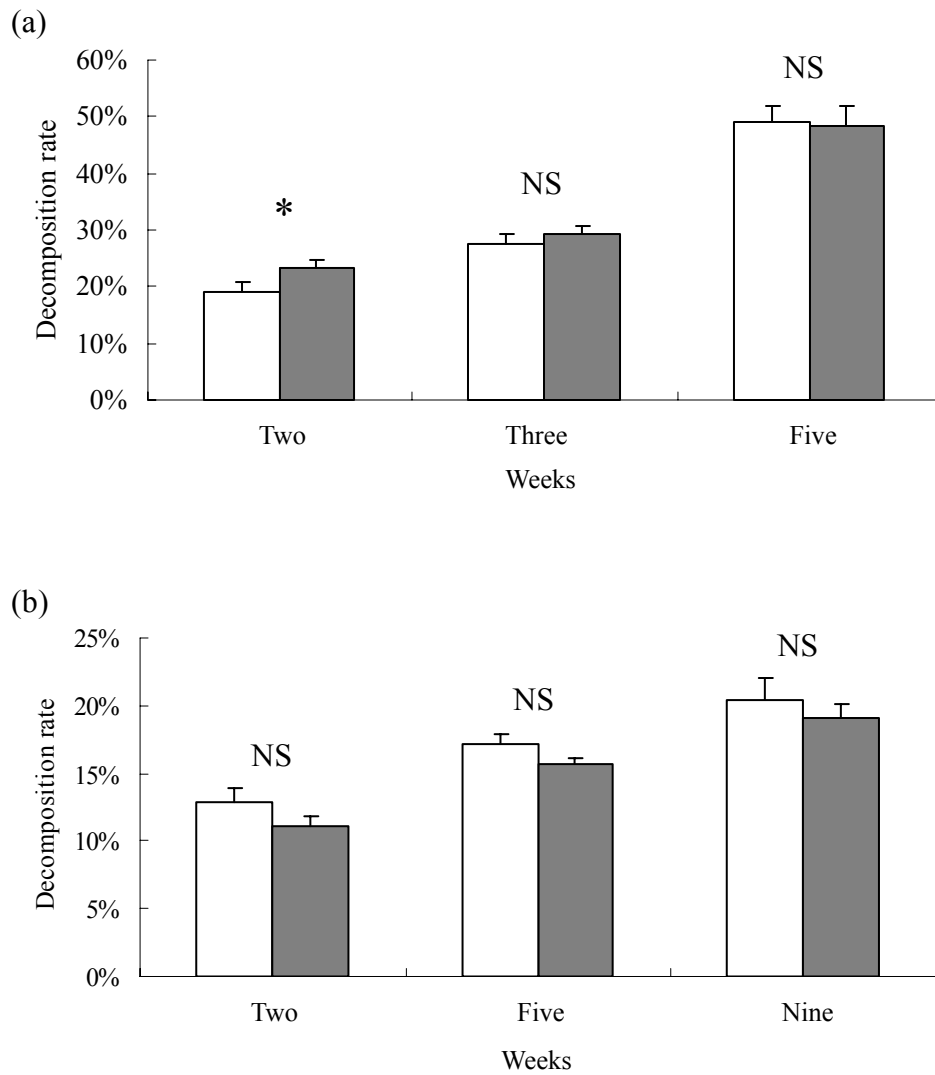


Fig. 7. Mean (\pm SE) decomposition rates of litters placed in subenclosures with lizard present (open bars) or removed (gray bars) for different number of weeks conducted in summer (a) and autumn (b).

Table

Table 1. Results of paired *t*-tests comparing number of *A. sagrei* between

lizard-present and lizard-removed subenclosures in various months of 2006.

Month	<i>t</i>	<i>p</i>
March to April	9.8007	<0.001
May	6.394	<0.001
June	5.636	<0.001
August	10.624	<0.001
September	4.651	0.002
October	9.911	<0.001