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# Effects of the Brown Anole Invasion and Betelnut Palm Planting on Arthropod Diversity in Southern Taiwan

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**The brown anole (*Anolis sagrei*) occurs naturally in various localities in Central America, and an exotic invasive population was first reported in Sheishan District, Chiayi County, Taiwan, in 2000. Previous studies showed that following the invasion of *A. sagrei*, the diversity and abundance of local terrestrial arthropods, such as orb spiders and arboreal insects, were severely affected. In this study, we assessed the impact of *A. sagrei* on arthropod diversity in Taiwan by comparing spider and insect diversities among betelnut palm plantations, in which this lizard species was either present or absent, and a secondary forest. In addition, enclosures were established in which the density of *A. sagrei* was manipulated to investigate the effect of this predator on spiders. The results of a lizard stomach content analysis showed that spiders comprised 7% and insects 90% of the prey consumed. Among the insects consumed by *A. sagrei*, more than 50% were ants. The abundances of the major arthropod prey of *A. sagrei*, such as jumping spiders and hymenopterans, in the lizard-present sites were much lower than in the lizard-removed sites. The enclosure experiments also showed that predation by the lizards significantly reduced the abundance of jumping spiders. All these results indicated that the introduced lizard greatly affected the diversity and abundance of terrestrial arthropods in agricultural areas in southern Taiwan.**

**Key words:** *Anolis sagrei*, *Areca catechu*, spider, Salticidae, insect, ant

## INTRODUCTION

Invasive species are one of the major factors causing biodiversity loss and economic damage in the world (Williamson, 1996). In Taiwan, the effects of introduced species on the local fauna and flora have received some attention in recent years. However, most research focused on the impact on organisms such as mammals (Wu, 2003), skinks (Zhu, 2002), and woody vegetation (Wu et al., 2004; Chung and Lu, 2006). Here we report the effects of an exotic invasive lizard, the brown anole (*Anolis sagrei*), on the diversity and community structure of terrestrial invertebrates at a locality in southern Taiwan. We also provide information on the impact of betelnut palm (*Areca catechu*) cultivation on the diversity and community structure of terrestrial invertebrates in the same locality.

The brown anole is a diurnal arboreal species that favors a variety of sunny habitat types and areas disturbed by humans. This sit-and-wait (ambush) predator preys on a variety of invertebrates, especially insects (Lee, 2000). Brown anoles are known to have dispersed by vehicular rafting in North America (Campbell, 1996), and their ability to be commensal with humans (Lee, 2000), as well as their adaptability to a variety of food sources, has made this animal a very successful invasive vertebrate. In 2000, this lizard was first recorded as an invasive species in Taiwan (Norval et al., 2002). Densities of the brown anoles in certain areas such as betelnut palm plantations can be very high, reaching about one individual per 4 m$^2$ (S.C. H. and G. N., unpublished data). This density is much higher than that of any of the local reptile species (Lin and Lu, 1982). Previous studies have shown that high densities of *A. sagrei* may greatly affect the diversity and abundance of terrestrial arthropods, and that this lizard causes a decline in the density and abundance of terrestrial arthropods. When *A. sagrei* was experimentally introduced onto small islands, the abundance of web spiders decreased, and consequently the abundance of small aerial insects increased (Spiller and Schoener, 1994; Schoener and Spiller, 1999; Schoener et al., 2002). On the other hand, since insects are also the main food resource of the brown anole (Spiller and Schoener, 1990; Schoener and Spiller, 1999), direct predation by *A. sagrei* will greatly affect insect diversity. For insects directly preyed upon by *A. sagrei*, removal of the lizards resulted in increased abundance (Pacala and Roughgarden, 1984; Dial and Roughgarden, 1995). It is currently unclear how spider and insect communities in southern Taiwan are affected by the brown anole

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invasion.

In Taiwan, another major factor that may seriously affect arthropod diversity is the large-scale transformation of land from broad leaf forests into betelnut palm remove (Aracaceae: *Areca catechu* L.) plantations. The betelnut palm is a tall slender palm (height up to 30 m) originating in Southeast Asia. The distribution of the betelnut palm includes Southeast Asia, East Asia, East Africa, Madagascar, the Arabian Peninsula, Pacific islands, and New Guinea (Staples and Bevacqua, 2006). On some Pacific islands, betelnut palms are grown in home gardens for local consumption. However, in certain regions it is extensively grown as a commercial crop, and the area used for this cultivation keeps expanding.

Vast areas of low elevation broadleaf forests of Taiwan have been cleared to cultivate betelnut palms, from about 1000 ha in the 1960s to up to 40,000 ha in the 1990s, which comprises more than 1% of the overall land area in Taiwan (Lu et al., 2002). Previous studies on the impact of betelnut plantations on ecosystems have focused on abiotic properties such as land soil loss (Lu et al., 1999) or hydrological characteristics (Lu et al., 1996). Compared with the high canopy cover of broadleaf forests, betelnut palm plantations provide sparse cover, because each palm has only 6 to 9 pinnate leaves and therefore allows higher light penetration and intercepts less rainfall (Staples and Bevacqua, 2006). Moreover, the high, structurally simple canopy results in higher topsoil temperature, which severely affects the decomposition rate of organic matter, and consequently the understory vegetation community (Staples and Bevacqua, 2006). In addition, betelnut palm saplings compete poorly with weeds, so during the early stages of cultivation intensive weed management must be performed. Also, during the nut harvesting period, farmers usually apply herbicides on a large scale to clear the ground to have better access to the palms. The vegetation characteristics of betelnut palms, combined with the management regime for maintaining plantations, naturally has an enormous impact on biodiversity in these ecosystems. However, it is currently not clear how the replacement of low-elevation broadleaf forests with betelnut palm plantations affects invertebrate biodiversity.

In this study, we quantified the effects of the invasive brown anole and betelnut palm plantations on arthropod diversity in a locality in southern Taiwan. We assessed the impact of *A. sagrei* by comparing the spider and insect diversities in study sites on betel nut palm plantations in which the lizards were either present or removed. We also examined lizard stomach contents to determine whether prey consumption was responsible for the differences in arthropod diversity observed among study sites. Although predation by the brown anole potentially affects arthropod diversity, the complexity and composition of the understory vegetation are also vital determinants. Especially for spiders, guild composition is greatly affected by vegetation structural complexity (Greenstone, 1984; Rypstra et al., 1999; Tsai et al., 2006). Therefore, to clarify the effects of *A. sagrei* and understory vegetation on spider and insect diversities, we also quantified the structural complexities of the vegetation at the three study sites. In addition, we established enclosures in the field and manipulated lizard densities within them to eliminate the confounding effects of habitat heterogeneity and to obtain direct evidence of the impact of *A. sagrei* on arthropods. Finally, we assessed the effects of betelnut palm cultivation on arthropod diversity by comparing the spider diversity of a betelnut palm plantation with that of a nearby broadleaf secondary forest.

## MATERIALS AND METHODS

### Locations and history of study sites

The study sites were located in Santzepu, Sheishan District, Chiayi County, Taiwan. This area is a mosaic of agricultural lands, cultivated areas, residential areas, betelnut palm plantations, and broad leaf secondary forests of various sizes. Sampling plots were established in three study sites: a betelnut palm plantation with *A. sagrei* present (LP site) (23°25'25"N, 120°29'05"E); a betelnut palm plantation with *A. sagrei* removed (LR site) (23°25'23"N, 120°29'15"E); and a secondary broadleaf forest (SF site) (23°25'36"N, 120°29'08"E). In addition to occurring in betelnut palm plantations, *A. sagrei* could also be found in surrounding agricultural fields, orchards, cemeteries, and residential areas. The LP site we chose was in the core area of the known local *A. sagrei* distributional range and had the highest brown anole density (Huang, unpublished data). Densities of *A. sagrei* were still relatively low in betelnut palm plantations in the periphery of the known distributional range. This distribution pattern of *A. sagrei* prevented us from establishing sampling plots on multiple betelnut palm plantations. A betelnut palm plantation in the peripheral area of the *A. sagrei* distribution range was designated as the LR site.

In Santzepu, like other low-elevations areas in western Taiwan, the fragmentation of habitats is remarkable. The great majority of secondary forests in the Santzepu area are quite small and are potentially vulnerable to edge effects, so we chose the largest patch of secondary forest for our sampling plots. The linear distances between the study sites were ca. 300 m. The area of each study site was about 3500 to 4000 $m^2$. At each site, seven plots were established as replicates, 15 to 20 m apart. Each sampling plot was a 5×10 m quadrate with two 5×5 m subplots. Field studies were conducted every month from January 2004 to February 2005. Throughout the study period, several collection trips were carried out each month to remove any brown anoles observed within the LR site.

### *Anolis sagrei* stomach content analysis

We selected a small betelnut palm plot (15×40 m) next to the LP site in which to determine the prey composition of *A. sagrei* by catching lizards for stomach content analysis. Lizards were caught by hand or with fine-meshed fishing scoop nets, or were shot with air pistols. Collections were only carried out between 1400–1600h to ensure that the lizards had enough time to forage. From January 2004 to February 2005, 12 to 20 lizards were collected every month. All lizards collected were injected with 70% ethanol to preserve the stomach contents. In the laboratory, the lizards were dissected by making a mid-ventral incision. Prey items in the stomach of every lizard were identified either to family (spiders) or order (insects), and the numbers of all prey types were recorded. Chi-square tests of homogeneity were used to compare the spider family and insect order composition between lizards' ingested prey and arthropod collections made at the LP site. Similarity in arthropod composition between the stomach contents and study site would indicate that *A. sagrei* simply predated upon what was available in the betelnut palm plantations. A significant difference in the composition would suggest that this lizard selectively hunts for certain prey types.

### Spider and insect diversity survey

Spiders and insects in the study sites were collected each month by using both sweep netting and pitfall trapping. In each plot, spiders and insects in the understory vegetation were collected by sweep netting with a standardized five-minute sampling effort. In addition, in each subplot, a set of pitfall traps was established to collect ground spiders and insects. Each set of pitfall traps consisted of three 500-ml plastic cups arranged in a straight line with two barrier fences between them. Each month the cups were filled with 70% ethanol and left open for a week. Each collection cup was covered with a plastic disc to reduce ethanol evaporation and to prevent rainwater and fallen leaves from entering the cup. Specimens collected were preserved in 70% ethanol and were identified to either species/morphological species (spiders) or order (insects). Previous studies demonstrated that rare spider species were especially vulnerable to *A. sagrei* predation (Spiller and Schoener 1998). To determine whether rare spider species received greater impact from *A. sagrei*, the percentage of each species/morphospecies of spider relative to overall spider abundance was calculated. Following the methods of Spiller and Schoener (1998), we designated species whose abundance comprised less than 3% of the overall spider specimens as rare species.

The spider and insect communities at different sites were quantified by using the abundance of morphological species and orders, respectively. We first used the Bray-Curtis similarity index (Krebs, 1989) to calculate the pair-wise similarities between sampling plots, using the square roots of spider and insect abundance values. The Bray-Curtis similarity values were then used to construct nonparametric multidimensional scaling (MDS) plots, by using the PRIMER program (Clarke and Warwick, 2001) to visually depict clustering patterns among the sampling plots. An analysis of similarity (ANOSIM) (Clarke and Warwick, 2001) test was performed for each pair of study sites to determine the significance level of the sampling-plot clustering patterns. In addition, for both spiders and insects, we calculated the Margalef species richness ($D_{mg}$), Pielou's evenness (J), the Shannon-Wiener function (H'), and Simpson's index (D) for each sampling plot. One-way analysis of variance (ANOVA) tests and LSD mean comparisons were used to compare the values of all indices among the three study sites; these were performed with SYSTAT 9.0 (SPSS, Chicago, IL, USA). The SIMPER function of the PRIMER program (Clarke and Warwick, 2001) was used to determine the contribution of each insect order to the variation in diversity observed among the study sites.

### Quantification and composition survey of vegetation structure

Three height levels of the vegetation structure in the betelnut palm plantations were quantified: canopy, understory, and litter. Measurements were made in each 5×5 m subplot. A Nikon 4500 digital camera fitted with a fish-eye lens was used to take hemispherical photos of the canopy. The photographs were transformed into black and white images to better distinguish between the canopy and the sky. A Gap Light Analyzer Ver. 2.0 (Frazer et al., 1999) was used to estimate the percentage of canopy coverage. We quantified the vertical density of the understory vegetation with a method similar to that used for canopy cover, but a pink cardboard panel (53×76 cm) was used as the background. A person held the cardboard panel vertically at each of the four cardinal edges of each subplot, at three height levels (ground to 60 cm; 70 to 130 cm; 140 to 200 cm). Standing in the middle of the plot, the photographer took images of the panel and the vegetation in front of it with a Nikon 4500 digital camera. The percent coverage of the cardboard by vegetation was used as an indication of the vertical vegetation density. On each subplot, the quantity of leaf litter was estimated by collecting litter from six 25×25 cm quadrates. The litter was dried in an oven at 60°C for 48 h, and the dry weight was used as an estimate of litter quantity. The percent coverages of the canopy and understory, and dry litter mass, were measured once each month for each sampling plot, and mean values were analyzed. One-way ANOVA tests and LSD mean comparisons were used to compare these vegetation structural characteristics among the three study sites.

### Enclosure design, lizard density survey, and spider sampling

Eight enclosures (6×12 m) were established in the LP site in 2006, and each was divided into two sub-enclosures (6×6 m). Poles (180 cm bamboo sticks) were planted 30 cm deep into the ground at 1.5 m intervals to serve as supports for a fence. The fence consisted of fine-mesh (3 mm×3 mm) plastic sheets that effectively prevented lizards from moving though. The height of the fence was 150 cm from the ground surface, and part of the fence was embedded into the ground 15 cm deep to prevent lizards from burrowing underneath. The fence of the enclosure was topped with a 40-cm-wide overhanging barrier made of a slippery plastic to prevent the lizards from climbing over. All betelnut palm trunks that were within 1 m of either side of the fences of the enclosures were collared with a circular plastic board (diameter 40 cm, height 150 cm) to prevent the lizards from escaping or entering via the tree trunks. During the field experiment, we examined the enclosures once each week to repair any potential damage to fences.

In April, August, and November 2005, we conducted preliminary surveys to estimate lizard densities in the study sites, following the method of Heckel and Roughgarden (1979). For this part of the study, only adult (SVL range: male>45 mm; female>42 mm) and sub-adult (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 color of lead-free paint was used to mark the lizards. On 28 March 2006, we conducted the first lizard removal from both types of sub-enclosures in all eight enclosure pairs. On 30 March 2006, four to six lizards were released into the lizard-present sub-enclosures according to the lizard density estimated in April (Fig. 6), and every lizard found in the lizard-removed sub-enclosures was removed. Throughout the field experiment, a 1:2 male to female sex ratio was maintained in the lizard-present sub-enclosures.

One Y-shaped pitfall trap set was established in each sub-enclosure. Each pitfall trap set consisted of four 500-ml cups, with three one-meter-long fences between the four cups to enhance the spider interception efficiency. During each survey, the pitfall traps were opened for three consecutive days to collect ground spiders. To collect above-ground spiders, we divided each sub-enclosure into four quadrates and conducted a 5-min sweep netting to collect arthropods from two of the quadrates during each survey. During the following survey, the other two quadrates were sampled in the same manner. Sweep netting and pitfall trapping were conducted once before the lizard density was manipulated to see whether the initial spider abundance in the sub-enclosures was similar. In this particular survey, all four quadrates in the sub-enclosures were sweep netted. After initiation of the lizard density manipulation, spider surveys were conducted once every two or three weeks until the end of the experiment. Most spider specimens collected were identified to family, but salticids were identified to morphospecies. Samples from all post-manipulation surveys were pooled for statistical analyses to control for the potential effects of seasonality. The abundance of the dominant spider families (Salticidae, Linyphiidae, and Oxyopidae), estimated from stomach content samples obtained from the two types of sub-enclosures, was compared by using a paired *t*-test. The abundance of each morphological species of jumping spiders was divided by the overall spider specimen abundance to determine whether the species was rare.

## RESULTS

### *Anolis sagrei* stomach content analysis

A total of 230 lizards were collected, and 155 spider specimens (comprising 6.6% of all prey items) were obtained from their stomachs. Of these specimens, 47 belonged to the family Linyphiidae and 44 to Salticidae, representing 30.3% and 28.4% of the overall spider prey, respectively. Of the rest of the spider specimens, 28 were unidentifiable and the remaining 15 were members of the families Araneidae, Ganphosidae, Lycosidae, Oxyopidae, Pholcidae, Thomisidae, and Theridiidae (Fig. 1A). In total, 2181 insect specimens, comprising 93.36% of all prey items, were retrieved from the lizards' stomachs. The main insect order preyed upon by the lizards was Hymenoptera, which represented more than half the insects consumed (Fig. 1B). More than 95% of the hymenopterans consumed by the lizards were ants. The second most abundant insect prey was Lepidoptera (22.4%), followed by Hemiptera (8%) and Coleoptera (6.5%). The remaining insect orders comprised less than 5% of the stomach contents.

## Spider diversity survey

During the study period, 4013 spiders were collected, and among them 1989 were adults (Fig. 2). From the three study sites, 205 morphological species from 24 families were recorded. In total, 1538 spiders were collected from the LP site (Fig. 2A), consisting of 83 morphological species from 19 families. At the LP site, the dominant families were Oxyopidae and Linyphiidae. In total, 980 spiders were collected from the LR site (Fig. 2B), consisting of 90 morphological species from 19 families. At the LR site, Oxyopidae and Linyphiidae were also the dominant spider families. In the SF site 1495 spiders were collected, consisting of 139 morphological species from 21 families. At the SF site, the dominant families were Linyphiidae, Lycosidae, and Salticidae (Fig. 2C). Overall spider abundance was significantly higher

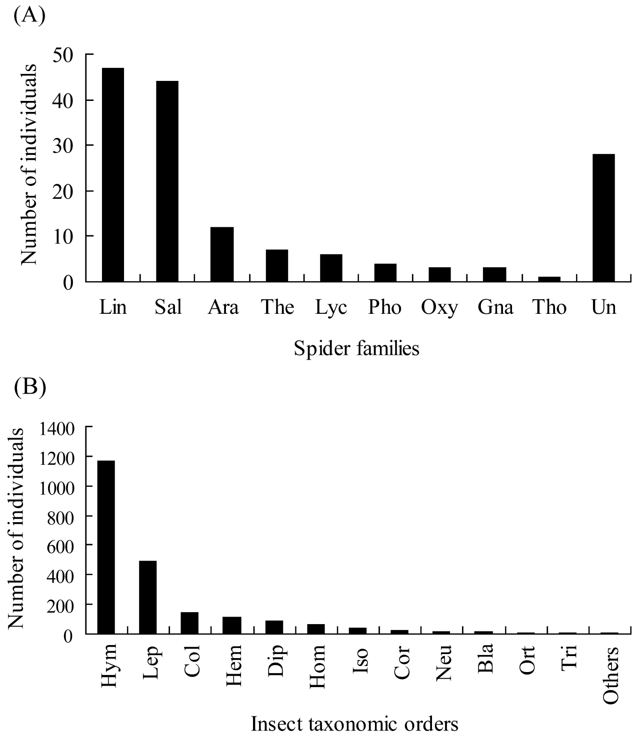

**Fig. 1.** **(A)** Spider specimens retrieved from the stomach contents of *A. sagrei*, categorized according to family. Lin, Linyphiidae; Sal, Salticidae; Ara, Araneidae; The, Theridiidae; Lyc, Lycosidae; Pho, Pholcidae; Oxy, Oxyopidae; Gna, Gnaphosidae; Tho, Thomisidae; un, unknown. **(B)** Insect specimens retrieved from the stomach contents of *A. sagrei*, categorized according to order. Hym, Hymenoptera; Lep, Lepidoptera; Col, Coleoptera; Hem, Heminoptera; Hom, Homoptera; Iso, Isoptera; Cor, Corrodentia; Neu, Neuroptera; Bla, Blattaria; Ort, Orthoptera; Tri, Trichoptera.

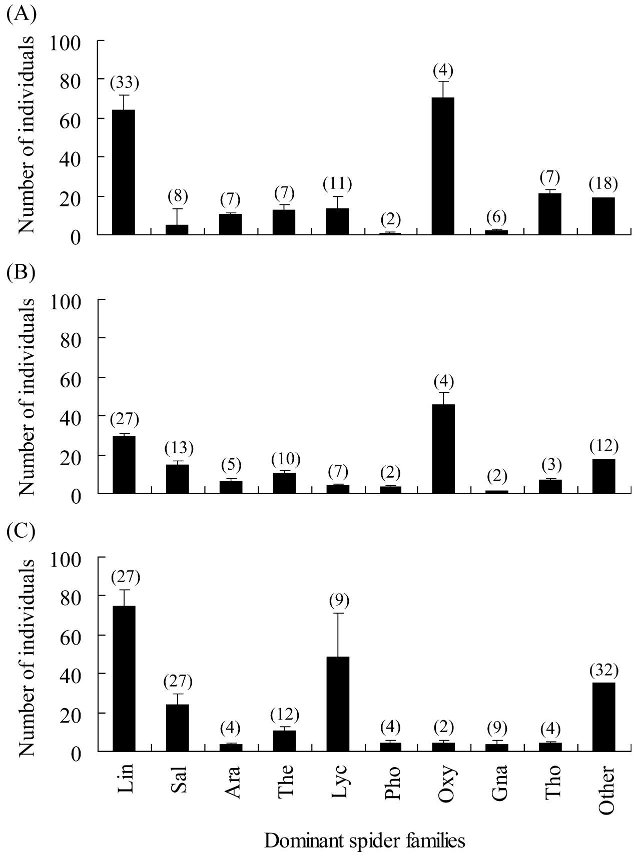

**Fig. 2.** Mean (±SE) abundance of individuals of the dominant spider families in the sampling plots in the **(A)** lizard-present, **(B)** lizard-removed, and **(C)** secondary forest sites. Numbers in parenthesis indicate the number of morphological species. See Fig. 1 for abbreviations.

**Table 1.** Results of one-way ANOVA tests and LSD mean comparisons comparing the abundance of individuals of **(A)** dominant spider families and **(B)** dominant insect orders collected from sampling plots in the lizard present (LP), lizard removed (LR) and secondary forest (SF) sites.

| (A) Spiders | | | |
|---|---|---|---|
| Families | *F* | *p* | LSD |
| Linyphiidae | 16.827 | 0.000 | SF=LP>LR |
| Oxyopidae | 56.451 | 0.000 | LP>LR>SF |
| Lycosidae | 1.484 | 0.253 | SF=LP=LR |
| Salticidae | 11.259 | 0.001 | SF=LR>LP |
| Araneidae | 10.141 | 0.001 | LP>LR=SF |

| (B) Insects | | | |
|---|---|---|---|
| | *F* | *p* | LSD |
| Hymenoptera | 8.244 | 0.003 | SF>LR>LP |
| Diptera | 11.877 | 0.001 | SF>LP>LR |
| Coleoptera | 3.191 | 0.065 | SF≧LP=LR |
| Hemiptera | 1.424 | 0.267 | LR=LP=SF |
| Lepidoptera | 6.733 | 0.007 | LP≧SF=LR |

at the LP site than at the LR site (*F*=11.073, *p*=0.006). The abundance of the most dominant spider families differed significantly among the three sites (Table 1A). The abundance of Salticidae, a major spider prey of *A. sagrei*, was significantly higher at the SF and LR sites. However, the abundance of Linyphiidae, another major spider prey of *A. sagrei*, was significantly higher at the SF and LP sites (Fig. 2, Table 1A). There were 8, 13, and 27 morpho-species of salticids at the LP, LR, and SF sites, respectively. Each salticid species collected in this study comprised less than 3% of the overall spider abundance, and therefore all salticids were rare species.

The MDS plot generated from spider morphological species compositions (stress=0.1) showed that the sampling plots at each site clustered together and were separated from those of the other sites (Fig. 3A). Among sampling plots at the three sites, those at the SF site showed greater scatter. The results of the ANOSIM tests based upon similarities estimated by spider morphological species showed that the spider composition of the three sites differed significantly (Table 2). Total species number, density, and Margalef species richness were significantly higher for the plots at the SF site than for those at the betelnut palm plantation sites (Table 3). Sampling plots at the LP site exhibited higher species number and density, but lower Margalef species richness, than those at the LR site. However, the evenness, Shannon-Weiner function, and Simpson index values at the LR site were the highest among the three sites.

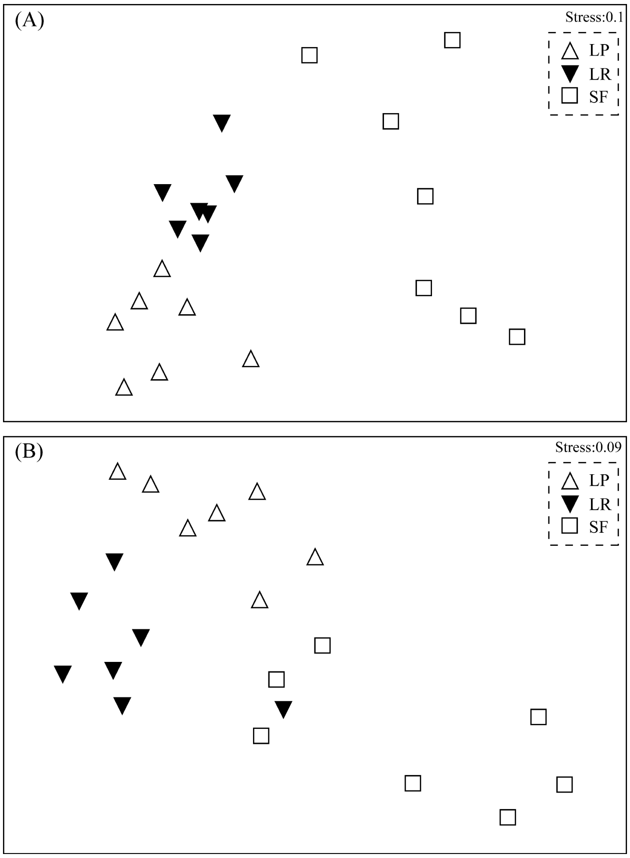

**Fig. 3.** MDS plots of the sampling plots in the lizard-present (LP), lizard-removed (LR), and secondary forest (SF) sites, generated from data on the compositon of **(A)** spider morphological species and **(B)** insect orders.

### Insect diversity survey

In total, 108,151 insects from 16 orders were obtained during the study period. The abundances of the dominant insect orders at the LP site were either significantly higher than (e.g., Diptera and Lepidoptera) or similar to (Coleoptera and Hemiptera) those at the LR site (Fig. 4, Table 1B). However, the abundance of hymenopterans at the LP site was significantly lower than that at the LR site (Fig. 4, Table 1B). The abundances of the dominant insect orders at the SF site were significantly higher than, or similar to, those in the betelnut palm plantation plots (Table 1B). The abundances of hymenopterans, dipterans, and coleopterans at the SF site were 1.5 to 2 times higher than those at the LP and LR sites (Fig. 4). On average, the densities of dominant insect orders from sampling plots at the SF site were 1.8 to 2 times higher than those at the betelnut palm plantation sites (Table 4).

Of the three study sites, the LR site had the lowest evenness, Shannon-Wiener function, and Simpson index

**Table 2.** Results of the pair-wise ANOSIM tests comparing the spider species and insect order compositions in sampling plots in the lizard present (LP), lizard removed (LR), and secondary forest (SF) sites.

| Comparison | Spider species composition | | Insect order composition | |
|---|---|---|---|---|
| | *R* | *p* | *R* | *p* |
| Global R | 0.719 | 0.001 | 0.629 | 0.001 |
| LP vs. LR | 0.762 | 0.002 | 0.647 | 0.002 |
| SF vs. LR | 0.751 | 0.001 | 0.616 | 0.002 |
| LP vs. SF | 0.902 | 0.004 | 0.707 | 0.002 |

**Table 3.** Number of spider species, mean (±SE) spider density, richness ($D_{mg}$), evenness (J), Shannon-Wiener function (H'), and Simpson index (D) for sampling plots in the lizard present (LP), lizard removed (LR), and secondary forest (SF) sites in southern Taiwan, and the results of ANOVA tests and LSD mean comparisons.

| Habitat | Species | Density | $D_{mg}$ | J | H' | D |
|---|---|---|---|---|---|---|
| LP | 110 | 83.43± 7.87 | 7.00±0.44 | 0.87±0.01 | 2.99±0.09 | 0.93±0.01 |
| LR | 90 | 53.71± 3.55 | 7.02±0.48 | 0.93±0.01 | 3.12±0.08 | 0.96±0.003 |
| SF | 139 | 148.43±27.1 | 7.06±0.41 | 0.78±0.02 | 2.78±0.07 | 0.9±0.01 |
| *F* | | 8.700 | 2.009 | 8.929 | 7.245 | 7.645 |
| *p* | | 0.002 | 0.163 | 0.002 | 0.005 | 0.004 |
| LSD | | SF>LP=LR | SF>LR>LP | LR>LP=SF | LR>LP=SF | LR≧LP=SF |

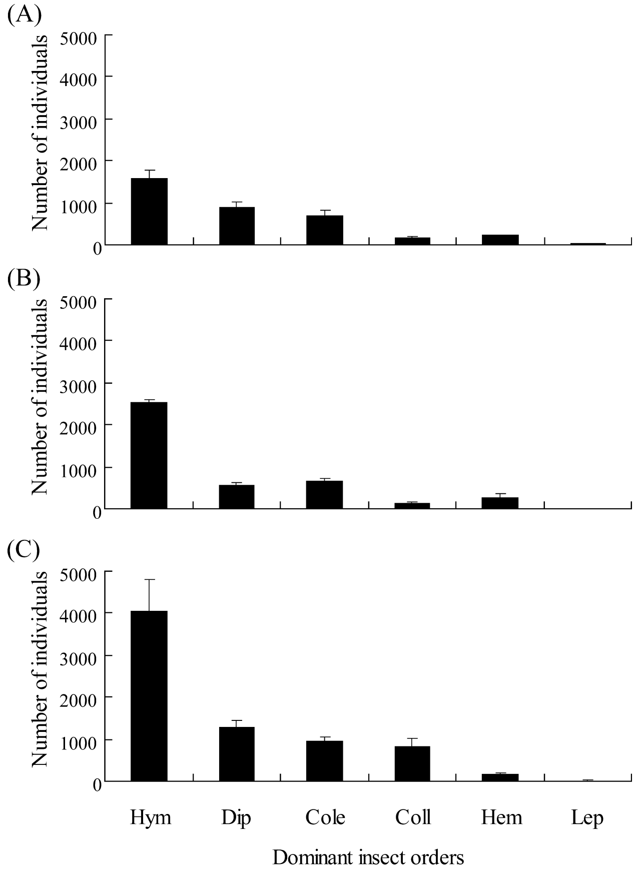

**Fig. 4.** Mean (±SE) abundance of individuals of the dominant insect orders in the sampling plots in the **(A)** lizard-present, **(B)** lizard-removed, and **(C)** secondary forest sites. See Fig. 1 for abbreviations.

values (Table 4). The MDS plot (Fig. 3B, stress=0.09) constructed from the insect order composition showed that the sampling plots at each site clustered together. The plots in the secondary forest showed greater scatter than those at the betelnut palm plantation sites. The ANOSIM tests showed that the insect composition differed significantly among the three study sites (Table 2). The SIMPER tests showed that hymenopterans alone contributed 27% of the variation in insect diversity observed between the LP and LR betelnut palm plantation sites (Table 5). Dipterans were another major contributor (Table 5), accounting for about 17% of the variation in insect diversity between the LP and LR sites.

### Comparison of arthropod diversity and lizard prey composition

Spider family and insect order compositions at the LP site were significantly different from those determined from the stomach contents of the lizards ($\chi^2$=24127.93, $p<0.001$ for spiders and $\chi^2$=1282.76, $p<0.001$ for insects). This incongruence indicated that *A. sagrei* did not simply consume what was available in the habitats, but selectively hunted certain prey types. A comparison of the spider and insect compositions of the lizard stomach contents and those recorded at the LP site indicated that selective hunting for linyphiid and salticid spiders and hymenopteran and lepidopteran insects was the main reason for the observed incongruence.

### Composition and structure of the understory vegetation

The main understory herbaceous plants at the LP site were *Ageratum houstonianum*, *Bidens pilosa, Drymaria diandra, Cleome rutidosperma, Melastoma candidum, Passiflora suberosa*, and *Phyllanthus* sp. The dominant plants at the LR site were *Ageratum conyzoides*, *Ampelopsis brevipedunculata* var. *hancei*, *D. diandra*, and *Panicum*

**Table 4.** Number of insect orders, mean (±SE) insect density, richness ($D_{mg}$), evenness (J), Shannon-Weiner function (H'), and Simpson index (D) for sampling plots in the lizard present (LP), lizard removed (LR) and secondary forest (SF) sites in southern Taiwan, and the results of ANOVA tests and LSD mean comparisons.

| Sites | Orders | Density | $D_{mg}$ | J | H' | D |
|---|---|---|---|---|---|---|
| LP | 13 | 3710.14± 348.94 | 1.41±0.07 | 0.6 ±0.02 | 1.51±0.03 | 0.71±0.01 |
| LR | 15 | 4213.71± 335.61 | 1.37±0.04 | 0.5 ±0.02 | 1.25±0.06 | 0.58±0.03 |
| SF | 14 | 7520.14±1012.22 | 1.34±0.06 | 0.54±0.02 | 1.37±0.06 | 0.65±0.03 |
| *F* | | 10.208 | 0.407 | 5.857 | 6.816 | 6.144 |
| *P* | | 0.001 | 0.672 | 0.061 | 0.006 | 0.009 |
| LSD | | SF>LR=LP | LP=LR=SF | LP=SF>LR | LP=SF>LR | LP=SF≧LR |

**Table 5.** Results of SIMPER tests analyzing the contribution of various insect orders to the observed insect composition differences between sampling plots at the lizard present and lizard removed sites.

| Insect Order | Mean dissimilarity | Dissimilarity/ SD | Contribution % | Cumulative % |
|---|---|---|---|---|
| Hymenoptera | 4.09 | 1.7 | 27.72 | 27.72 |
| Diptera | 2.57 | 1.53 | 17.4 | 45.13 |
| Coleoptera | 1.41 | 0.99 | 9.54 | 54.66 |
| Collembola | 1.33 | 1.69 | 9.04 | 63.7 |
| Others | 1.31 | 2.19 | 8.86 | 72.56 |
| Hemiptera | 1.31 | 0.98 | 8.86 | 81.42 |
| Orthoptera | 0.75 | 2.1 | 5.06 | 86.47 |
| Lepidoptera | 0.58 | 1.64 | 3.95 | 90.42 |

*maximum*. There were also woody plants at the LP site. Overall, plant diversity at the LP site was higher than at the LR site. Significant differences in canopy openness were found among the three sites (Table 6). Canopy openness was the lowest in the secondary forest, followed by the LR site (Fig. 5A). The vertical density of the understory vegetation was significantly lower at the LR site than at the LP and SF sites (Fig. 5B), but was not significantly different between the latter two (Table 6). These results indicate that the understory vegetation was structurally more complex at the LP site than at the LR site. The average mass of the litter did not differ significantly among the three sites (Table 6, Fig. 5C).

## Results of the enclosure experiments

The estimated lizard densities in April, August, and November 2005 at the LP site ranged from 4 to 10 individuals per 36 $m^2$ and were 9 to 18 times those at the LR site (Fig. 6). Five weeks after the lizard density manipulation, the number of *A. sagrei* in the lizard-present sub-enclosures reached about six, similar to the natural lizard density in April 2005. Eventually the lizard density reached about seven to nine animals per sub-enclosure, and it remained more or less stable until the end of the experiment. The average number of jumping spiders of the family Salticidae did not differ significantly between the two types of sub-enclosures before the manipulation (effect size [ratio of lizard-removed treatment to control]=0.83, $t$=0.180, df=7, $p$=0.862) (Fig. 7a). After the lizard density manipulation, the average number of salticids declined significantly in the lizard-present sub-enclosures (effect size=2.22, $t$=-2.434, df=7, $p$=0.045)

**Table 6.** Results of the ANOVA tests and LSD mean comparisons comparing canopy openness, vertical density of understory vegetation, and litter mass among the three study sites.

| Vegetation structure | *F* | *p* | LSD |
|---|---|---|---|
| Canopy openness | 44.625 | <0.001 | LP>LR>SF |
| Vegetation vertical density | 7.469 | 0.001 | LP=SF>LR |
| Litter mass | 0.187 | 0.83 | LP=LR=SF |

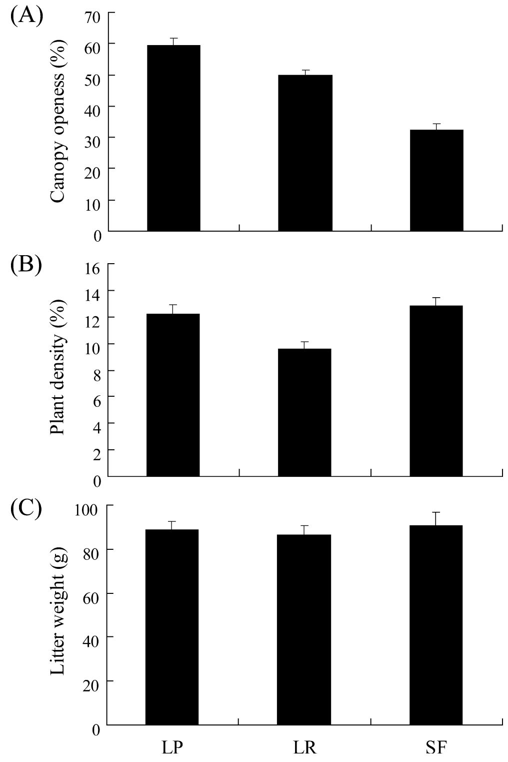

**Fig. 5.** Mean (±SE) canopy openness **(A)**, plant density **(B)**, and dry litter weight **(C)** in the sampling plots in the lizard-present (LP), lizard-removed (LR), and secondary forest (SF) sites.

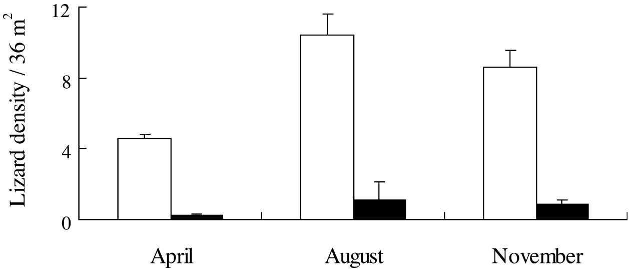

**Fig. 6.** Mean (±SE) estimated *Anolis sagrei* density (per 36 $m^2$) at the lizard-present (open bars) and lizard-removed (closed bars) betelnut palm plantation sites in April, August, and November 2005.

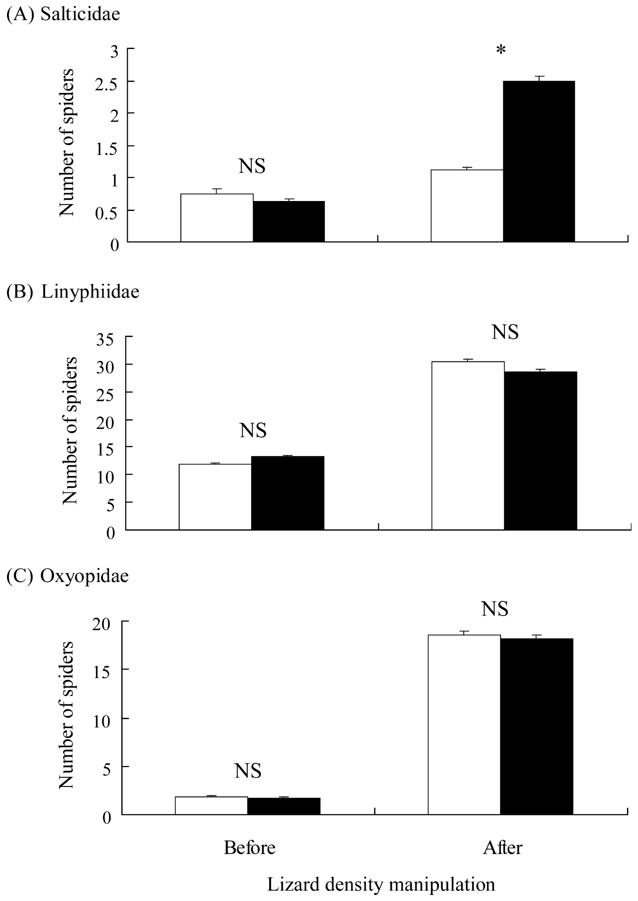

**Fig. 7.** Mean (±SE) abundance of **(a)** Salticidae, **(b)** Linphiidae, and **(c)** Oxyopidae in the lizard-present (open bars) and lizard-removed (closed bars) sub-enclosures before and after *Anolis sagrei* density manipulations. NS, non-significant at $\alpha$=0.05; *, $p$<0.05.

(Fig. 7a). Four and 10 salticid morphospecies were found in the lizard present and removed treatments, respectively. All salticids comprised less than 3% of the overall spider abundance and were thus rare species. The average number of spiders of the family Linyphiidae was not significantly different between the two types of sub-enclosure, neither before (effect size=1.12, *t*=–0.553, df=7, *p*=0.597) nor after (effect size=0.94, *t*=0.359, df=7, *p*=0.730) the lizard density manipulations (Fig. 7b). Besides Linyphiidae, the abundance of the lynx spiders (Oxyopidae) was also high at the study sites. The abundance of oxyopids was similar between the two types of sub-enclosure, both before (effect size=0.93, *t*=0.174, df=7, *p*=0.867) and after (effect size=0.98, *t*=0.119, df=7, *p*=0.909) the lizard density manipulations (Fig. 7c).

## DISCUSSION

This study showed that the transformation of lowland broadleaf forests into betelnut palm plantations severely affects the diversity and abundance of terrestrial arthropods. While there were about 140 species of spiders in the sampling plots in the broadleaf forests (SF site), only 90 species of spiders were collected from the lizard-removed betelnut palm plantation plots (LR site). Overall spider abundance in the sampling plots in the broadleaf forest was two to three times that at the betelnut palm plantation sites. The composition of spider communities also differed significantly between two types of habitats. In the betelnut palm plantation plots, a more open canopy induced the growth of dense herbaceous plants, of which the majority were monocotyledons. Such dense, grassy, ground-level vegetation is not suitable for the ground-weaving linyphiid and wandering lycosid spiders. However, this habitat is favorable for the arboreal oxyopid spiders. On the other hand, there was a higher diversity of dicotyledonous herbaceous plants in the understory of the broadleaf forest, and this habitat type could potentially provide more resources for insects of various foraging modes. Consequently, the abundance of most orders of insects was higher in the broadleaf forest.

Salticids and linyphiids were the main spider prey consumed by *A. sagrei*. Salticids are brightly colored arboreal hunters and actively search for prey in understory vegetation (Foelix, 1996). *Anolis sagrei* is a diurnal sit-and-wait predator (Schwartz and Henderson, 1991) that usually catches actively moving, visually conspicuous prey (Schoener, 1968). Our field surveys and enclosure experiments both showed that direct predation pressure from *A. sagrei* was the main mechanism behind the decline in salticid diversity and abundance. Although the species diversity of salticids is high, about 4000 documented species (Proszynski, 2007), most species are usually rather low in abundance. In both our field surveys and enclosure experiments, salticid species comprised less than 3% of the overall spider abundance. Since most salticids were rare, the loss of low numbers of them tended to dramatically reduce their overall diversity in a habitat. In the enclosure experiment, after the lizard density manipulations, the number of salticid species of the lizard present treatments was less than half that of the lizard-removed treatments. This indicates that rare species, such as many salticids, are more vulnerable to the introduced brown anole and face a larger threat of extinction.

Lynx spiders (Oxyopidae) and jumping spiders (Salticidae) are both diurnal, arboreal hunters (Uetz et al., 1999) with well-developed vision (Song et al., 1999), and are similar in size. However, very few oxyopids were found in the stomach contents of *A. sagrei*. At the betelnut plantation sites, lynx spiders were far more abundant than jumping spiders. However, *A. sagrei* consumed considerably more jumping spiders than lynx spiders, and a possible explanation for this result is that the body coloration of lynx spiders provides a certain degree of camouflage. Lynx spiders on our study sites (mostly *Oxyopes lineatipes*) are green in body coloration, and they usually rest on vegetation to ambush prey. Jumping spiders, on the other hand, are often brightly colored (Foelix, 1996). The bright body coloration and high mobility of jumping spiders may make them visually conspicuous to *A. sagrei* and thus more vulnerable to predation. On the other hand, although linyphiids were the major spider prey of *A. sagrei*, predation pressure from this lizard did not significantly impact linyphiid abundance in the betelnut palm plantations. The field surveys showed that linyphiids were more abundant in sampling plots at the LP site than at the LR site. This abundance pattern might have been generated by the higher structural complexity of the understory vegetation at the LP site. When we conducted enclosure experiments to control for the confounding effects of vegetation heterogeneity, linyphiid abundance did not significantly differ between the two sub-enclosure types. Of the various spider families sampled in the Santzepu area, linyphiids were highest in abundance, whereas they comprised only 3% of the prey consumed by *A. sagrei*; the number of linyphiids consumed by lizards might thus have little impact on this family's abundance. We conclude from the results of the field surveys and enclosure experiments that the complexity of the understory vegetation was the major determinant of linyphiid abundance, and that predation by *A. sagrei* did not play a significant role.

While the higher insect diversity at the SF site was generated mainly by vegetation characteristics, differences in insect diversity between the two betelnut palm study sites might have been generated by both vegetation composition and *A. sagrei* predation. A more diverse community of herbaceous dicotyledonous plants at the LP site might have maintained a more diverse and abundant insect assemblage, since the abundances of most insect orders (except for hymenopterans) at the LP site were higher than or similar to those at the LR site. However, the abundance of insects that received heavy predation pressure from the lizards was lower at the LP site. In this study, even though we quantified insect diversity by identifying insect specimens only to taxonomic order, we still found significant differences in insect composition between the LP and LR sites. The SIMPER analyses showed that these composition differences were generated by much lower hymenopteran abundance at the LP site. The stomach content analyses showed that among hymenopterans, ants were the main prey items of *A. sagrei*. The dominant ant species found in the stomach contents was *Pheidole fervens*. In the study sites, this ant usually formed supply lines along the ground or on the trunks of betelnut palms, and we frequently observed *A. sagrei* perching on betelnut palm trunks picking off *P. fervens* one by one from a line of moving ants. This persistent predation pressure from *A. sagrei* might have severely lowered the ant abundance at the LP site.

Previous studies have demonstrated that *A. sagrei* prefers open, disturbed habitats (Losos et al., 1993; Rodriguez Schettino, 1999). Betelnut palm plantations, which are widely distributed at low elevations all over Taiwan, are a suitable habitat for this lizard. *Anolis sagrei* was recently found in a locality in eastern Taiwan (M. C. Du, personal communication), and this dispersal was without a doubt due to anthropogenic activities. If appropriate measures are not taken, this highly dispersive and competitive lizard may eventually spread into betelnut palm plantations all over Taiwan. In this study, although *A. sagrei* were quite abundant at the LP site, and even though individuals were observed on the edge of the secondary forest, very few of them were observed in the secondary forest site (about 0.0025 / 100 $m^2$; Huang, unpublished data). The high canopy coverage of the SF site might have prevented this invasive lizard from establishing a stable population. We thus suggest that ultimately the best method to prevent the brown anole from spreading and to conserve arthropod diversity in Taiwan would be to reestablish large areas of broadleaf forests. If this goal cannot be feasibly achieved, at least the areas of betelnut palm cultivation should be limited and should be surrounded by large areas of secondary forest.

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