Research paper

Application of Necrophilous Beetles to Long-term Monitoring of a Forest Ecosystem Associated with Climatic Change

Wenbe Hwang,[1)] Chao-Nien Koh[2,3)]

【Summary】

We used necrophilous beetles for the long-term monitoring of biodiversity in the Hapen Nature Preserve in northern Taiwan, evaluating changes in the species compositions of beetle communities in 2 different habitats over a 6-yr period. The species richness, individual numbers, and diversity indices of the beetles were significantly higher in a forest habitat than in a meadow habitat. The species similarity between the beetle communities in the 2 habitats was 3.95%. Differences in species richness and heterogeneity of the vegetation may have affected the compositions of the beetle communities in the 2 habitats. Compared to non-baited pitfall traps, the species richness and individual numbers were greater in baited pitfall traps. Different dominant structures of beetles between non-baited and baited traps were demonstrated. We suggest using baited traps to investigate the effects of global warming on compositions of necrophilous beetle communities. We selected 42 species of necrophilous beetles representing 7 families as indicator species for long-term monitoring of biodiversity during the survey periods. Diversity indices of beetles monitored in the meadow habitat significantly increased in 2006 compared to those in 2001. The community similarity between the 2001 and 2006 survey periods was only 14.7% for the meadow habitat. In the forest habitat, the diversity indices varied and significantly differed among 2001, 2006, and 2007, despite the annual individual numbers not significantly differing. Based on comparisons of data from 2001 with those from the 2006 and 2007 survey periods, beetle-community similarities in the forest habitat were 49.0 and 44.9%, respectively. Variations in species compositions of beetle communities in the 2 habitats in different years may have been due to changes in the ambient temperature. Moreover, communities of necrophilous beetles in the meadow habitat were probably more strongly influenced by changes in temperature than those in the forest habitat.

Key words: necrophilous beetles, bait effect, biodiversity, community structure, long-term monitoring.

Hwang W, Koh CN. 2013. Application of necrophilous beetles to long-term monitoring of a forest ecosystem associated with climatic change. Taiwan J For Sci 28(2):83-96.

[1)] Department of Ecoscience and Ecotechnology, National Univ. of Tainan, 33 Shulin St., Sec. 2, West Central Dist, Tainan 70005, Taiwan. 國立臺南大學生態科學與技術學系，70005台南市中西區樹林街二段33號。

[2)] Department of Forest Protection, Taiwan Forestry Research Institute, 53 Nanhai Rd., Taipei 10066, Taiwan. 林業試驗所森林保護組，10066台北市南海路53號。

[3)] Corresponding author, e-mail:nien@tfri.gov.tw 通訊作者。

Received March 2013, Accepted May 2013. 2013年3月送審 2013年5月通過。

研究報告

氣候變遷下親屍性甲蟲在森林生態系統長期監測的應用

黃文伯[1)] 葛兆年[2,3)]

摘 要

以親屍性甲蟲長期監測北台灣哈盆自然保留區之生物多樣性，並評估6年間林地與草地之親屍性甲蟲在物種組成上的變化。林地親屍性甲蟲之種豐富度、個體數及多樣性皆顯著高於草地，且兩地群聚組成之相似度僅3.95%，其差異可能與兩地植被種豐富度及歧異度不同有關。誘餌掉落式陷阱相較於無誘餌掉落式陷阱捕獲較多的甲蟲物種數及個體數，且兩種陷阱中，捕獲量大的物種並不相同，我們建議採用誘餌掉落式陷阱調查研究全球暖化對親屍性甲蟲群聚組成之影響。本研究在受屍體誘餌吸引的甲蟲中選定7科42種甲蟲做為長期監測物種。2006年草地監測之甲蟲多樣性較2001年顯著提高，且兩年群聚相似度僅14.7%。林地的多樣性在2001、2006與2007年間有顯著的差異，惟監測甲蟲個體數在3年間無顯著差異，而後兩年與2001年的群聚相似度分別為49.0及44.9%。氣溫的改變可能是不同年間親屍性甲蟲群聚產生變動的原因之一，草地群聚變動較大似乎受氣溫變化影響較大。

關鍵詞：親屍性甲蟲、誘餌效果、生物多樣性、群聚結構、長期監測。

黃文伯、葛兆年。2013。氣候變遷下親屍性甲蟲在森林生態系統長期監測的應用。台灣林業科學 28(2):83-96。

INTRODUCTION

Variations in insect life histories as a result of changes in abiotic factors in the environment are generally thought to be associated with the soil matrix and climatic conditions, and the effects of changes in ambient temperature are particularly significant (Sparks et al. 1995, Sota 1996, Blanckenhorn 1997, Tatar et al. 1997). Among biotic factors, competitors and available resources are considered to affect the population dynamics of insects (Sota 1996, Smith and Merrick 2001). Carcasses are highly nutritious, but such resources are often scarce (Hanski and Cambefort 1991). The decomposition of a carcass is affected by the temperature, humidity, and type of habitat (Payne 1965, Nabaglo 1973, Swift et al. 1979). Temperature and humidity are the main factors affecting microbial activity, which affects the decomposition rate of a carcass (Swift et al. 1979). Within the carcass microhabitat, the most important community members are arthropods, with Coleoptera, Diptera, Hymenoptera, and Araneida comprising 78~90% of animals on the carcass (Payne 1965, Johnson 1975). The presence of insects accelerates the decomposition of carcasses (Payne 1965, Putman 1978). The rate of development of Diptera larvae increases at higher temperatures (Nishida 1984), indirectly affecting the length of time during which carcass resources are available. Changes in climatic conditions cause variability in the environment, and this affects resource availability and the species using the resources. In particular, the species composition and population density of decomposers, such as coprophagous and necrophagous beetles, are significantly impacted by such climatic changes (Hanski and Cambefort 1991, Martin-Piera and Lobo 1993).

Baited trapping of insects can reflect the biodiversity in different ecosystems under different seasonal climatic conditions. Competition for limited, variable food resources results in the differentiation of ecological niches and subtle changes in the life history of species (Sauer 1986, Sauer et al. 1986). When the carcass decomposition rate is rapid during hot summer months, the opportunity and available time for feeding greatly decrease, and the reduction in feeding frequency causes beetles to go into estivation until the temperature drops in autumn (Hwang and Shiao 2011). Thus, such species may be present in different ecosystems at different times based on the stenothermic characteristics of the species (Hwang 2006). Under the effects of climate warming, the rapid decomposition of carcass resources will lead to more-intense competition, thereby affecting the status of some stenothermal species. According to the regional climate model, a species should migrate to regions at a higher latitude with a similar native climate when global warming occurs (Parry and Carter 1989). The migration or disappearance of stenothermal species will, however, likely alter the species diversity within affected communities.

To select an indicator species for long-term monitoring, we compared species compositions of necrophilous beetles in carcass microhabitats of meadow and forest ecosystems. The aim of our study was to evaluate the impact of long-term climate changes on the species composition and community structure of necrophilous beetles.

MATERIALS AND METHODS

We performed our study in the Hapen Nature Preserve of northern Taiwan (24°45'N, 121°34'E). The study area is subtropical, with an elevation of 600~800 m. To collect necrophilous beetles, 2-km transect lines were set up in forest and meadow areas near the Hapen River. Along each transect line, 8 sampling plots were selected at 200-m intervals. One baited pitfall trap and 1 non-baited pitfall trap were buried in each sampling plot. The 2 traps were separated by at least 5 m.

Pitfall traps were constructed by burying a 20-cm length of PVC pipe (15 cm in diameter) vertically in the ground with 1 end of the pipe flush with the surface. A 500-ml plastic cup was placed at the bottom of the pipe to collect trapped animals. Small holes in the bottom of the plastic cup allowed moisture to drain away. A tight-fitting funnel was placed inside the upper region of the plastic cup to prevent the escape of the trapped animals. A 3600-cm^2 section of fine-gauge metal mesh was placed on the ground over the trap entrance to prevent the capture of subterrestrial animals, and a 16×16-cm opening was cut in the mesh to expose the trap entrance. The mesh was fixed to the ground with pegs. A 20×20×10-cm metal cage with a mesh size of 4 cm^2 was placed directly over the trap entrance to prevent vertebrates from accessing the trap. The cage was fixed to the ground mesh with nylon cable ties. The top of the cage was covered with a 20×20-cm transparent acrylic plate to protect the trap and the cage from rain. An 8.5-cm plastic Petri dish was suspended inside the cage to support the bait. A fresh carcass (approximately 20 g) of a 4- to 5-wk-old mouse was placed in the Petri dish as bait. No Petri dish was placed in non-baited traps.

The first survey was performed in 2001, from February 2001 to January 2002. Traps were baited twice each month. During the 4-d period following baiting, beetles were collected from both non-baited and baited traps. The methods used for the 2006 (February 2006 to January 2007) and 2007 (February 2007 to January 2008) survey periods were equivalent to those used in 2001, except that baiting and collection were performed once monthly. However, meadow areas were not surveyed during the 2007 period. To analyze changes in species compositions, data from 2006 and 2007 were compared to data from the first 4-day collection period for each month in 2001.

All captured, non-target species were immediately released on the sampling plot. Captured beetles were immersed in 75% ethanol, and species were identified. Specimens that could not be keyed to a single species were marked as a morphological species. To detect differences in attraction to the bait, we compared numbers of each species that were collected in baited traps each month with those collected in non-baited traps.

Species richness and individual numbers were compared using the Shannon-Wiener Diversity Index (H'):

$H' = -\Sigma\, p_i \log_e p_i$;

where p_i is the proportion of individuals of species i in a community.

To compare the beetle species similarity among different habitats during the same period and during different periods within a single habitat, we used the Wainstein Similarity Index (K_w). When the species compositions of the 2 communities in the spatial or the temporal habitats are completely consistent, the value of K_w is 100, and when the 2 communities completely differ, the value of K_w is 0, according to the following equations:

$K_w = R_e \times J$;

where R_e is Renkonen's coefficient and J is Jaccard's coefficient.

$R_e (\%) = \Sigma \min (p_{i1}, p_{i2})$ and

$J = c \times 100 / (S_1 + S_2 - c)$;

where p_{i1} is the proportion of individuals of species i in the first community; p_{i2} is the proportion of individuals of species i in the second community; S_1 is the species richness in the first community; S_2 is the species richness in the second community; and c is the number of species present in both communities.

The dependency data from 12 mo were analyzed using the Wilcoxon signed-ranks test (WSRT) or Friedman-test to compare species richness, individual numbers, and H' of the beetle communities, the attractive effect of the baiting technique for species richness, and annual individual numbers of each species for each habitat ($p < 0.05$). All analyses were conducted using SPSS vers. 20 (SPSS, Chicago, IL, USA).

Three HOBO Pro RH Temp data loggers (MicroDAQ.com, Contoocook, NH, USA) were equidistantly placed along each transect approximately 5 cm from each trap in the different habitats. The ambient temperature and relative humidity were recorded at 30-min intervals. The temperature accuracy and range were ±0.2 and -30~50℃, respectively.

RESULTS

During the 2001 survey period, 8022 beetles of 254 species in 30 families were collected in the traps. The K_w value between the forest and meadow habitats was 3.95%, with 63 species found in both habitats. The species richness, individual number, and diversity of all collected beetles were significantly higher in the forest habitat than in the meadow habitat (WSRT: species richness, $p < 0.01$; individual number and diversity, $p < 0.05$, $n = 12$) (Fig. 1).

Bait effect

The species richness of beetles was significant higher in baited traps than in non-baited traps in the meadow area (WSRT: $p <$

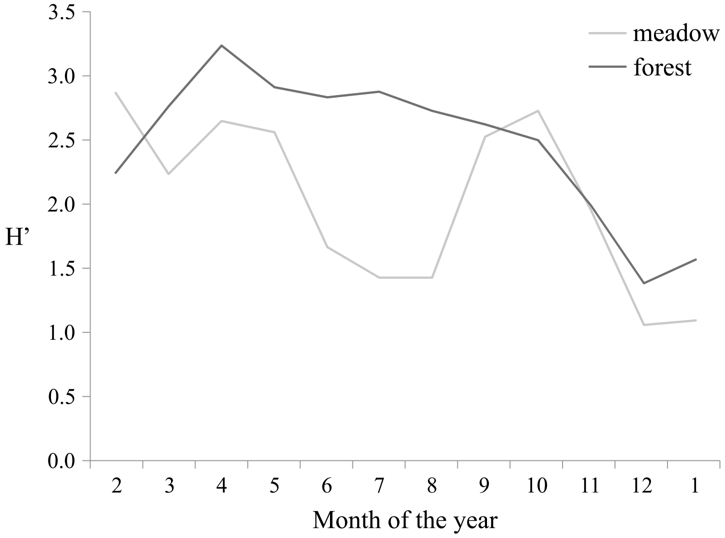

Fig. 1. Shannon-Wiener Diversity Index (H') of all collected beetles in a meadow habitat and forest habitat during 2001 in the Hapen Nature Preserve.

0.01, $n = 12$) and in the forest area (WSRT: $p < 0.01$, n = 12) (Fig. 2a). The individual number of beetles was significant higher in baited traps than in non-baited traps in the meadow area (WSRT: $p < 0.01$, $n = 12$) and in the forest area (WSRT: $p < 0.01$, $n = 12$) (Fig. 2b). The K_w between non-baited and baited traps was 4.11% during 2001.

Selection of monitored species

The majority of the trapped beetles were from the Carabidae (11.3%), Histeridae (1.7%), Hydrophilidae (11.3%), Leiodidae (12.5%), Scarabaeidae (9.6%), Silphidae (2.1%), Staphylinidae (45.8%), and Trogidae (2.1%) families. These 8 families represented 96.4% of the trapped beetles. Results of the WSRT analysis showed that almost all species of these 8 families were significantly attracted to carcass-baited traps. Two species of the Carabidae family were significantly attracted to baited traps (WSRT: $p < 0.05$, n = 12), *Pheropsophus javanus*, a meadow species, and *Pheropsophus beckeri*, a forest species. The remaining species of the Carabidae that were collected were not significantly attracted to baited traps (WSRT: $p > 0.05$, n = 12). Because only 1 species of the Carabidae was collected in both types of habitat, carabids were not considered for monitored species. From the remaining 7 beetle families, we selected 42 species that were significantly attracted to baited traps (WSRT: $p < 0.05$, $n = 12$) as indicator species of environmental changes. We chose the 2 most prevalent species of the Hydrophilidae, *Cercyon* sp. (87.9%) and *Magasternum* sp. (10.2%), as indicator species because individual numbers of the other 5 species were statistically low. Similarly, *Margarinotus multidens* (92.9%) and *Mar. formosanus* (5.0%) of the Histeridae were selected. All 6 species of the Leiodidae were selected. Of the trapped Scarabaeidae members, 766 individuals of 20 species were dung beetles that were significantly attracted to carcass bait (WSRT: $p < 0.05$, $n = 12$). All dung beetle species of the Scarabaeidae were identified. Excluding herbivorous scarab species, 20 dung beetle species were selected. All 3 species of the Silphidae were selected

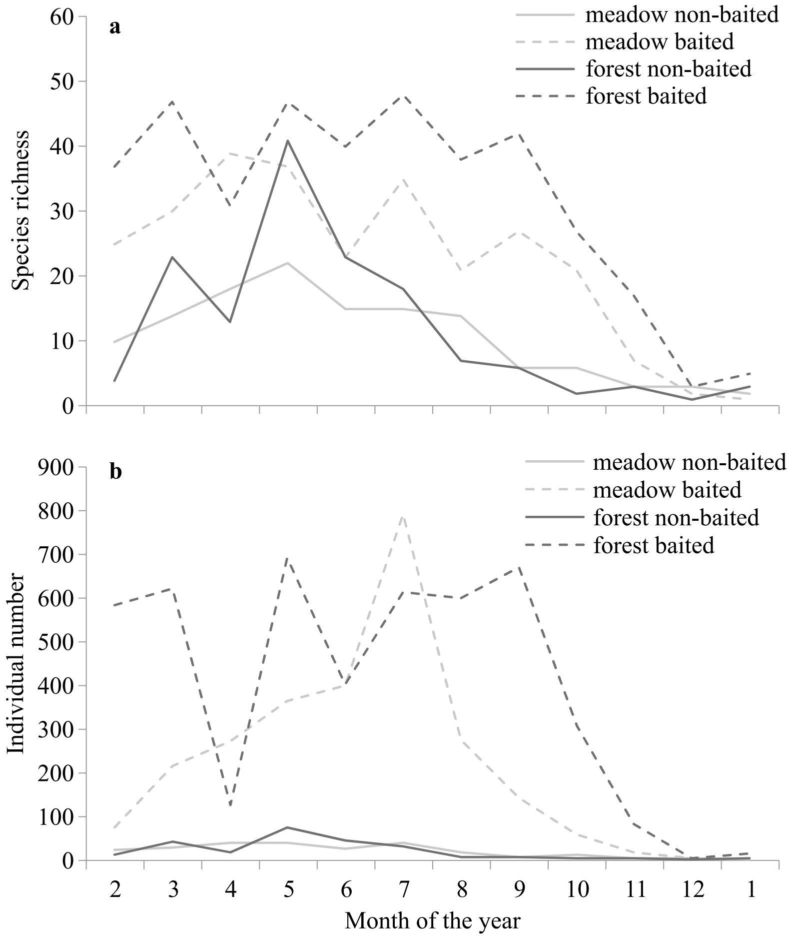

Fig. 2. Species richness (a) and individual number (b) of beetles collected using non-baited and baited pitfall traps from February 2001 to January 2002 in a meadow habitat and forest habitat in the Hapen Nature Preserve.

because they were significantly attracted to baited traps (WSRT: $p < 0.05$, $n = 12$). In total, 107 species of the Staphylinidae were collected. However, because of identification difficulties and statistically low individual numbers for many of the species, statistically significant results of the analysis to assess bait attraction were obtained for only 6 staphylinid species (WSRT: $p < 0.05$, n = 12). Thus, *Anotylus* sp. 6 (25.8%), *Aleochara nigra* (21.3%), *Philonthus longicornis* (11.7%), *Oxytelus* sp. 3 (11.5%), *Philonthus* sp. 1 (5.8%), and *Anotylus* sp. 3 (3.1%) were selected as indicator species. All species of the Trogidae were selected.

Changes in diversity in the meadow habitat

We used 42 necrophilous beetle species in 7 families as indicator species to compare species compositions between the 2001 and 2006~2007 survey periods. In the meadow habitat, 11 species were collected in 2006 that had previously been collected in 2001 only in the forest habitat. Although the numbers of 8 species increased in the meadow in 2006, the total number of beetles of all species collected was 63.7% lower in 2006 than in 2001 (Fig. 3). A comparison of individual numbers in the meadow habitat in 2001 with those in 2006 showed that individual numbers in the 2 yr did not significantly differ (WSRT: $p = 0.29$, n = 12).

Diversity indices of necrophilous beetle communities were significantly higher in 2006 than in 2001 (WSRT: $p < 0.01$, $n = 12$) (Fig. 4). The results indicate that the attractive effects of baiting were lower in 2006 than in 2001. The K_w value of comparisons of beetles

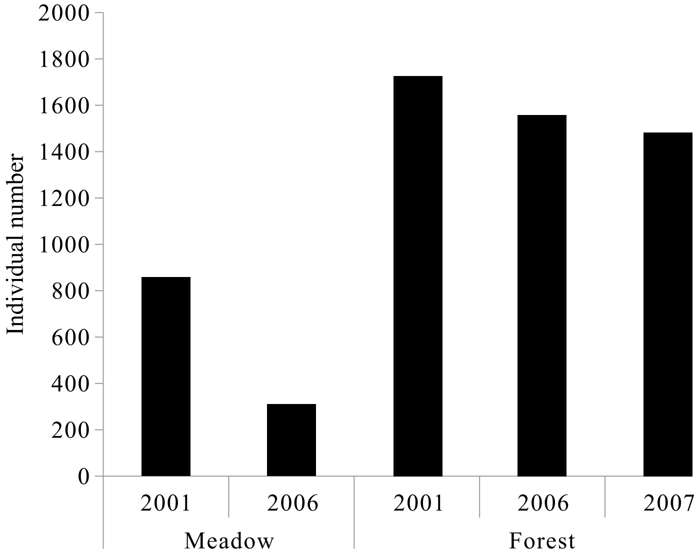

Fig. 3. Individual numbers of 42 monitored necrophilous beetle species in a meadow habitat in 2001 and 2006 and in a forest habitat in 2001, 2006, and 2007 in the Hapen Nature Preserve.

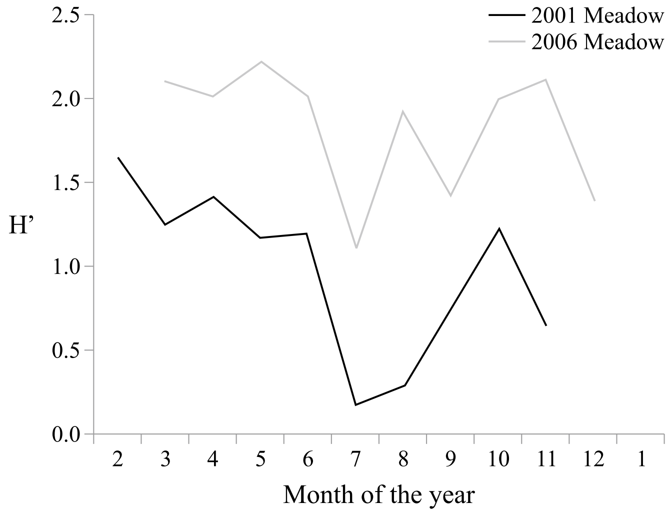

Fig. 4. Shannon-Wiener diversity index (H') of 42 monitored necrophilous beetle species collected in baited pitfall traps in a meadow habitat in 2001 and 2006 in the Hapen Nature Preserve.

collected in the meadow in 2001 and 2006 was 14.7%.

Changes in diversity in the forest habitat

A comparison of the species composition of beetles from baited traps in the forest habitat in 2001 with those in 2006 and 2007 showed that species richness and the number of individuals progressively decreased, with the number of individuals decreasing by 10% in 2006 and 14% in 2007 (Fig. 3), despite fluctuations in the diversity indices (Friedman-test: $p < 0.05$, $n = 12$) (Fig. 5). Comparisons of individual numbers in the forest habitat in 2001, 2006, and 2007 showed that individual numbers in the 3 yr did not significantly differ (Friedman-test: $p = 0.86$, n = 12). The species composition in the forest habitat also shifted over time. The K_w value of comparisons of beetle species collected in 2001 and 2006 was 49%. Further analysis yielded K_w values of 44.9 and 61.7% for comparisons of data for 2001 and 2007 and for 2006 and 2007, respectively, indicating that similarity in species composition had declined over time.

Changes in the annual average temperature

We recorded temperatures during the 2001, 2006, and 2007 survey periods to compare differences in monthly average temperatures between 2001 and 2006~2007. Data from the 2006 and 2007 survey periods were combined, and data for the months of November 2006 and 2007 were eliminated from the analysis because data from November 2006 were lost as the result of a typhoon. Comparison of the monthly average temperatures in 2001 indicated a warm winter and early spring phenomena in 2006~2007 (WSRT: $p < 0.05$, $n = 5$ from December to April). Annual average temperatures in 2001 and 2006~2007 were 18.2 and 18.6℃, respectively (Fig. 6).

DISCUSSION

Distributions of many terrestrial organisms are currently shifting in latitude or elevation in response to climate changes (Konvicka et al. 2003, Chen et al. 2011), and the range of shift of each species is dependent on multiple intrinsic species traits and extrinsic drivers of change (Chen et al. 2011). We suggest that

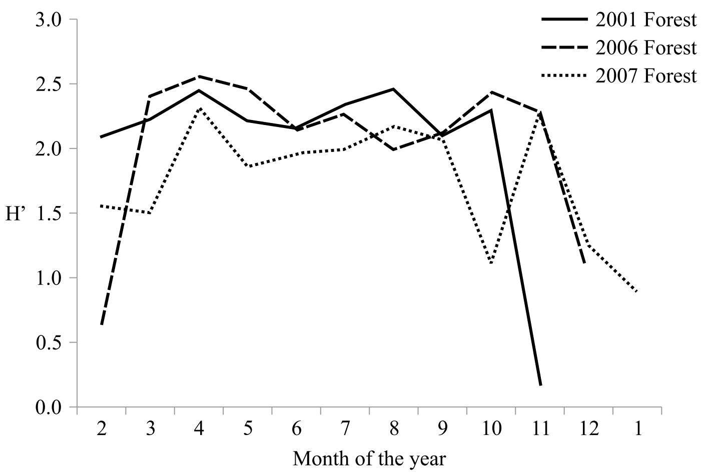

Fig. 5. Shannon-Wiener diversity index (H') of 42 monitored necrophilous beetle species collected in baited pitfall traps in a forest habitat in 2001, 2006, and 2007 in the Hapen Nature Preserve.

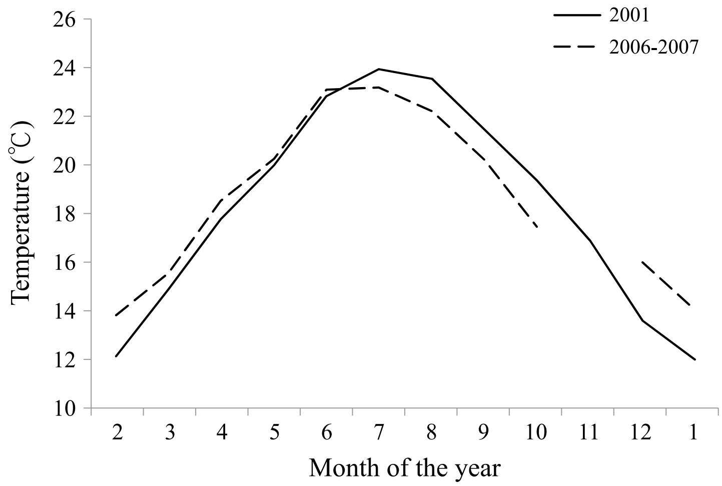

Fig. 6. Monthly average temperatures from February 2001 to January 2002 (2001) and February 2006 to January 2008 (2006-2007). Data for November 2006 and 2007 were not included because the data for November 2006 were lost as the result of a typhoon that corrupted the thermometers during that period.

external drivers affect the diversity of a community. The carcass decomposition rate is influenced by the ambient temperature (Swift et al. 1979). Thus, detritivores that use carcasses as their microhabitat are suitable indicators for assessing impacts of global warming on biodiversity. We selected the Hapen Nature Preserve in subtropical Taiwan as a research site because it was previously shown to have a high diversity and species richness of necrophilous beetles (Hwang 2006).

To clarify the preference of beetle species for carcasses, we compared the capture rate in baited traps with that of non-baited traps. The combination of a pitfall trap and certain attractants, such as lighting (Heap 1988) and various types of bait, was shown to be effective for collecting both a greater number of different species and greater numbers of individuals. Thus, we used carcass bait to attract a large number of necrophilous beetles. Comparisons of the beetle species composition between non-baited and baited traps showed different dominance structures (K_w, 4.11%). The number of individuals and number of species in our baited traps were higher than those in non-baited traps. The capture of beetles in non-baited traps may be considered to be a result of random movement. With regard to the feasibility of studying global warming, the use of baited pitfall traps enables investigators to focus more on changes in ambient temperatures, compared to the fewer numbers of individuals and species randomly captured in non-baited pitfall traps.

We selected the most prevalent species of the 7 remaining families of the necrophilous beetles that were collected in our study as indicator species for our analysis, all of which are known to occur in carcass microhabitats. Beetles of the genus *Margarinotus* in the family Histeridae feed on dipteran eggs and larvae that also inhabit the carcass (Kovarik and Caterino 2000). Terrestrial beetles of hydrophilid species were observed in mud, feces, carcasses, and decomposing leaf litter (Sowig and Wassmer 1994). Adults of the

Leiodidae feed on mushrooms, rotting fruit, or corpse microorganisms (Chandler and Peck 1992). Dung beetles of the Scarabaeidae feed on both feces and carcasses (Hanski 1983, Boonrotpong et al. 2004). The 3 most common carrion beetles in Taiwan are necrophagous (Chen 2008, Hwang and Shiao 2008, Su 2010). Demonstrating relatively greater temperature sensitivity, *Nicrophorus nepalensis* is known to exhibit estivation and hibernation behaviors (Hwang and Shiao 2011). Of the Staphylinidae, only the *Aleochara*, *Anotylus*, *Oxytelus*, and *Philonthus* genera are known to be necrophilous. However, species of the Staphylinidae were the most prevalent in our study. Adults of the genus *Aleochara* feed on carrion, and the larvae feed on pupae of dipterans (Kemner 1926, Peschke and Fuldner 1977, Klimaszewski 1984). Beetles of the genus *Oxytelus* were observed to feed on feces and carrion (Hanski 1987). *Anotylus* acts as predator on carcasses, feeding on fly pupae (Omar et al. 1991), and *Philonthus* feeds on fly eggs and maggots (Hu and Frank 1997). Of the Trogidae, adults and larvae often emerge during the late stage of decomposition, feeding on feathers, fur, and skin (Gennard 2007). Each group of necrophilous beetles has special ecological functions in the carcass microhabitat. Thus, we selected 42 species of 7 families as indicator species for environmental monitoring.

Carcass feeding is also influenced by the decomposition rate. When the temperature is lower, the development of fly maggots feeding on a carcass is slower (Nishida 1984). Among abiotic factors, temperature likely has the greatest impact on the decomposition rate (Swift et al. 1979) with higher rates of decomposition associated with shorter feeding periods. This also results in a shorter period during which necrophilous animals can locate a carcass. Consequently, the numbers of species and individuals that are able to use carcass resources are also reduced. This may lead to competitive exclusion between species using the same resources (MacArthur and Levins 1964, Levins 1968). Therefore, changes in ambient temperature indirectly affect the species composition of the community of necrophilous animals in carcass microhabitats. To observe ambient temperature changes during the 2001 and 2006~2007 survey periods, the average monthly and annual temperature were determined. We found that the monthly average temperatures during the spring and winter months and the average annual temperature were higher during the 2006~2007 period. These data imply that the availability of carrion resources was reduced during these periods, and that competition among necrophilous beetle species increased. Consequently, populations of weak competitors may have decreased. Each species has unique adaptations to temperature. Thus, if the average ambient temperature of an ecosystem increases, a cool stenothermic species may migrate to higher latitudes that are similar to the species' native climate (Parry and Carter 1989). For example, the behavior activity of *Nicrophorus nepalensis* decreases when the ambient temperature exceeds 26℃ (Hwang and Shiao 2011). The peak activity periods of *N. nepalensis* in our study were during March and October in 2001 in Hapen Nature Preserve. However, the peak activity period in autumn shifted to November in 2006. The 1-mo delay in the activity period during the fall may have significant impacts on subsequent hibernation and breeding periods. In 2007, the major activity period of *N. nepalensis* shifted to April, and numbers of beetles collected in February, March, and May were much lower than those observed in 2001. This may indicate that the activity period was shortened as a result of increasing temperatures at the beginning of the year and during the summer, while the life history of *N. nepalensis* did not significantly chang.

Different beetle species display different habitat preferences (Hwang 2006). In addition to the effects of temperature on insect activity (Kaspari et al. 2000, Haysom et al. 2004), environmental illumination also affects the activity of ground-dwelling beetle species (Antvogel and Bonn 2001). The species richness and number of individuals of consumers in habitats are indirectly influenced by the affects of illumination on the species richness of the vegetation (Scherber et al. 2010) and the heterogeneity of the habitat (Butterfield et al. 1995). Higher heterogeneity and a greater abundance of resources in a habitat result in the survival of a greater number of species (Ricklefs and Lovette 1999). In our study, all vegetation species were dwarf herbaceous in the meadow habitat which received intense, direct sunlight. However, the species richness and heterogeneity of vegetation were higher in the forest habitat than in the meadow habitat. The diversity of trapped beetles was lower in the meadow habitat than in the forest habitat. Thus, differences in species richness and heterogeneity of vegetation between the habitats may have affected the diversity of heterotrophic animals in general. The climatic warming observed in 2006~2007 resulted in different degrees of impact on the necrophilous beetle communities in the 2 habitats. The structure of the community shifted more dramatically in the meadow habitat than in the forest habitat. In 5 yr, there was a decrease of 63.7% in the number of beetles in the meadow habitat, whereas only a 10% reduction was observed in the forest habitat. The community similarity of beetles in the meadow habitat between in 2001 and 2006 was only 14%, while 50% similarity was maintained in the forest habitat. The biomass of vegetation and the vertical space are smaller in the meadow habitat than in the forest. With a low heat capacity coefficient, the thermal buffer effect will be weaker in the meadow environment than in the forest. Greater exposure to high-intensity sunlight and a larger temperature difference between day and night occur in the meadow habitat, compared to the forest habitat. Thus, impacts of the climate warming should be greater in the meadow habitat than in the forest. The thermal buffer effect could explain different degrees of impact on necrophilous beetle communities between the 2 habitats.

While it is reasonable to assume that a warmer climate will accelerate carcass decomposition, the actual rate will also be affected by the carcass size, exposure to water and sunlight, microbial activity, and the feeding of scavengers (Chaloner et al. 2002, Fenoglio et al. 2010). During our 6-yr monitoring period in the subtropical Hapen Nature Preserve, changes in the species composition of thermally sensitive necrophilous beetles produced significant changes in both the meadow and forest habitats. Necrophilous beetles are important decomposers, and changes in their species composition likely affect nutrient cycling in an ecosystem. Thus, our study may provide indirect evidence of the impact of climate warming on nutrient cycling. Moreover, monitoring longer-term trends of variations in the species composition of necrophilous beetles is needed.

ACKNOWLEDGEMENTS

We wish to thank M. Baehr (Carabidae), C.-F. Lee (Hydrophilidae), I. Lobl (Pselaphinae), K. Masumoto (Scarabaeidae), S. Mazur (Histeridae), S. Nomura (Pselaphinae), M. Perreau (Leiodidae), and H. Schillhammer (Staphylinidae) for their help with taxonomic identifications. We also thank J.T. Chao for invaluable field site access and assistance. This research was supported by grants from the National Univ. of Tainan (99AB2-14 and AB100-319) and Taiwan National Science Council (NSC97WFA0F00038).

LITERATURE CITED

Antvogel H, Bonn A. 2001. Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. Ecography 24:470-82.

Blanckenhorn WU. 1997. Altitudinal life history variation in the dung flies *Scathophaga stercoraria* and *Sepsis cynipsea*. Oecologia 109:342-52.

Boonrotpong S, Sotthibandhu S, Pholpunthin, C. 2004. Species composition of dung beetles in the primary and secondary forests at Ton Nga Chang Wildlife Sanctuary. Sci Asia 30:59-65.

Butterfield J, Luff ML, Baines M, Eyre MD. 1995. Carabid beetle communities as indicator of conservation potential in upland forest. For Ecol Manage 79:63-77.

Chandler DS, Peck SB. 1992. Diversity and seasonality of leiodid beetles (Coleoptera: Leiodidae) in an old-growth forest and a 40-year-old forest in New Hampshire. Environ Entomol 21:1283-93.

Chaloner DT, Wipfli MS, Caouette JP. 2002. Mass loss and macroinvertebrate colonisation of Pacific salmon carcasses in south-eastern Alaskan streams. Freshw Biol 47:263-73.

Chen KH. 2008. Studies on biology of *Calosilpha cyaneocephala*. Master's thesis. Chiayi, Taiwan: National Chiayi Univ. 96 p.

Chen IC, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333 (6045):1024-6.

Fenoglio S, Bo T, Cammarata M, Malacarne G, Del Frate G. 2010. Contribution of macro- and micro-consumers to the decomposition of fish carcasses in low-order streams: an experimental study. Hydrobiologia 637:219-28.

Gennard DE. 2007. Forensic entomology: an introduction. New York: Wiley. 224 p.

Hanski I. 1983. Distributional ecology and abundance of dung and carrion-feeding beetles (Scarabaeidae) in tropical rain forests in Sarawak, Borneo. Acta Zool Fenn 167:1-45.

Hanski I. 1987. Nutritional ecology of dung and carrion-feeding insects. In: Slaniki F Jr and Rodrigues JG, editors. Nutritional ecology of insects, mites, spiders and relateds invertebrates. New York: Wiley. p 837-83.

Hanski I, Cambefort Y. 1991. Ecology of dung beetles. Princeton, NJ: Princeton Univ. Press. 481 p.

Haysom KA, McCracken DI, Foster GN, Sotherton NW. 2004. Developing grassland conservation headlands: response of carabid assemblage to different cutting regimes in a silage field edge. Agric Ecosyst Environ 102:263-77.

Heap MA. 1988. The Pit-Light, a new trap for soil-dwelling insects. J Aust Entomol Soc 27:239-40.

Hu GY, Frank JH. 1997. Predation on the horn fly (Diptera: Muscidae) by five species of *Philonthus* (Coleoptera: Staphylinidae). Environ Entomol 26:1240-6.

Hwang W. 2006. Konkurrenz und Aasnutzung necrophager und necrophiler Käfer in Nord- und Südtaiwan mit einem Beitrag zur Biologie von *Nicrophorus nepalensis* Hope (Coleoptera: Silphidae). PhD dissertation, Albert-Ludwigs-Univ. Freiburg. 108 p.

Hwang W, Shiao SF. 2008. Use of carcass by burying beetles *Nicrophorus nepalensis* Hope (Coleoptera: Silphidae). Formosan Entomol 28:87-100.

Hwang W, Shiao SF. 2011. Dormancy and the influence of photoperiod and temperature on sexual maturity in *Nicrophorus nepalensis* (Coleoptera: Silphidae). Insect Sci 18:225-33.

Johnson MD. 1975. Seasonal and microseral variations in the insect population on carrion. Am Midl Nat 93(1):79-90.

Kaspari M, O'Donnell S, Alonso L. 2000. Three energy variables predict ant abundance at a geographical scale. Proc R Soc B-Biol Sci 267:485-9.

Kemner NA. 1926. Zur Kenntnis der Staphyliniden-Larven. II. Die Lebensweise und die parasitische Entwicklung der echten Aleochariden. Entomol Tidskr 47:133-70.

Klimaszewski J. 1984. A revision of the genus *Aleochara* Garvenhorst of America north of Mexico (Coleoptera: Staphylinidae: Aleocharinae). Mem Entomol Soc Can 129:211.

Kovarik PW, Caterino MS. 2000. Histeridae. In: Arnett RH, Thomas MC, editors. American beetles. Vol. 1. Boca Raton, FL: CRC Press. p 212-27.

Konvicka M, Maradova M, Benes J, Fric Z, Kepka P. 2003. Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale. Global Ecol Biogeogr 12:403-10.

Levins R. 1968. Evolution in changing environments. Monogr Populat Biol 2:120.

MacArthur R, Levins R. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proc Natl Acad Sci USA 51:1207-10.

Martin-Piera F, Lobo JM. 1993. Altitudinal distribution patterns of cropo-necrophage Scarabaeidea in Veracruz, Mexico. Coleopts Bull 47:321-34.

Nabaglo L. 1973. Participation of intertebrates in decomposition of rodent carcass in forest ecosystem. Ekol Polska 21:251-69.

Nishida K. 1984. Experimental studies on the estimation of postmortem intervals by means of fly larvae infesting human cadavers. Jpn J Legal Med 38:24-41.

Omar B, Sulaiman S, Jeffery J. 1991. *Anotylus latiusculus* (Kraatz) (Coleoptera: Staphylinidae) parasitizing the puparium of *Musca domestica* L. in Malaysia. Jpn J Sanit Zool 42(2):147-9.

Parry ML, Carter TR. 1989. An assessment of the effects of climatic change on agriculture. Climatic Change 15:95-116.

Payne JA. 1965. A summer carrion study of the baby pig *Sus scrofa* Linnaeus. Ecology 46:592-602.

Peschke K, Fuldner D. 1977. Übersicht und neue Untersuchungen zur Lebensweise der parasitoiden Aleocharinae (Coleoptera: Staphylinidae). Zool Jahrbucher Syst 104:242-62.

Putman RJ. 1978. Patterns of carbon dioxide evolution from decaying carrion. Decomposition of small mammal carrion in temperate systems, 1. Oikos 31:47-57.

Ricklefs RE, Lovette IJ. 1999. The roles of island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. J Anim Ecol 68:1142-60.

Sauer KP. 1986. Strategien zeitlicher und räumlicher Einnischung. Verh Dtsch Zool Ges 79:11-30.

Sauer KP, Spieth HR, Grüner C. 1986. Adaptive significance of photoperiodism in Mecoptera and Lepidoptera. In: Taylor F, Karban R, editors. The evolution of insect life cycles. New York, Berlin, Heidelberg: Springer. p 153-72.

Scherber C, Heimann J, Köhler G, Mitschunas N, Weisser WW. 2010. Functional identity versus species richness: herbivory resistance in plant communities. Oecologia 163:707-17.

Smith RJ, Merrick MJ. 2001. Resource availability and population dynamics of *Nicrophorus investigator*, an obligate carrion breeder. Ecol Entomol 26:173-80.

Sota T. 1996. Altitudinal variation in life cycles of carabid beetles: life cycle strategy and colonization in alpine zones. Arctic Alpine Res

28:441-7.

Sowig P, Wassmer T. 1994. Resource partitioning in coprophagous beetles from sheep dung: phenology and microhabitat preferences. Zool Jahrbucher Syst 121:171-92.

Sparks TH, Buse A, Gadsen RJ. 1995. Life strategies of *Carabus problematicus* (Coleoptera: Carabidae) at different altitudes on Snowdon, North Wales. J Zool 236:1-10.

Su HH. 2010. The morphology, development, behaviors, and interspecific competition of *Nicrophorus concolor* Kraatz (Coleoptera: Silphidae). Master's thesis. Tainan, Taiwan: National Univ. of Tainan. 62 p.

Swift MJ, Heal OW, Anderson JM. 1979. Decomposition in terrestrial ecosystems. London: Blackwell Scientific Publication. 372 p.

Tatar M, Gray DW, Carey JR. 1997. Altitudinal variation for senescence in *Melanoplus* grasshoppers. Oecologia 111:357-64.