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Title

Assessment of higher insect taxa as bioindicators for different logging-disturbance regimes in lowland tropical rain forest in Sabah, Malaysia

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Abstract

One of the serious environmental problems since the 1980s is the conflict between high rate of deforestation and maintenance of healthy ecosystem services and biological values in tropical forests. There is an urgent demand for setting up an appropriate environmental assessment to keep healthy ecosystem functions and biodiversity along with sustainable forest use based on ecology. In this study, we tried to assess logging-disturbance effects on abundances of several flying insect groups (higher-taxon approach) in lowland tropical rain forest, Deramakot Forest Reserve, Sabah, Malaysia, with consideration of seasonal changes and vertical forest stratification. The season was the most important factor affecting the abundances of all the insect groups. Effects of logging disturbance were prominent in the understorey but obscure in the canopy. Changes in physical conditions by logging, possibly increased evaporation by solar radiation, may have decreased the abundance of desiccation-sensitive insects, especially in the understorey. And, there are two probable reasons for the difference between in the understorey and in the canopy: 1) noise effects of various physical, environmental factors may have obscured insect responses to logging disturbance in the canopy; 2) higher spatio-temporal variation in quality and quantity of living food resources such as leaves, flowers and fruits provided in the canopy may have affected the abundance of

their consumer insects independently of logging disturbance. Thus, this study suggests that the abundance of some insect groups at higher-taxon level, especially in the understorey, can be used as bioindicators for assessing effects of logging disturbance on the forest ecosystem.

Key words

Bioindicator, Higher-taxon Approach, Flying Insects, Selective Logging, Tropical Forests

Introduction

A major environmental concern of tropical forest disappearance has been centered on one of the biggest topics in conservation ecology since the 1980s (Bowles et al., 1998).

The importance of ecosystem services and biological values provided from tropical forests has been pointed out by scientists and has been noticed by citizens of the world.

Nevertheless, the disappearance of tropical forests proceeds still at a high rate (Laurance, 1999; Bawa et al., 2004). Main driving forces of deforestation are population pressure,

policies of governments (Laurance, 1998) or financial problems (Wilkie et al., 1992) and those complexes. Under these circumstances, we must renovate policies and

schemes of tropical forest conservation to keep healthy ecosystem functions and biodiversity along with sustainable forest use (Kleine & Heuvelop, 1993; Organisation,

I. T. T., 1990), and must show the tolerance level of forest use based on ecology (Bawa et al., 2004).

The first step to answer this demand is to scientifically but instantly assess current conditions of disturbed and undisturbed environments. Various bioindicators have been applied as useful tools to assess living conditions for organisms, traditionally in aquatic environments (Rosenberg et al., 1986) and recently in terrestrial environments (van Jaarsveld et al., 1998; Baldi, 2003; Ekschmitt et al., 2003; Woodcock et al., 2003). Particularly, invertebrates have an advantage as bioindicators, because of being ubiquitous in a wide range of environments and moderate in the growth rate and population turnover (Hodkinson, 2005).

There are various approaches in bioindicator assessment. Some focus on certain taxa, but others measure the diversity of the whole community at the level of species or higher taxa (McGeoch, 1998; Hodkinson, 2005). Naturally, the higher the taxonomic resolution is, more fine-scaled information on the environment will be gained. However, such a fine-scale assessment at the species level is impractical when using highly diverse taxa such as insects. Identification of species is almost impossible for non-experts, and even for experts; the work necessitates a large amount of labor and time (Oliver & Beattie, 1996; Baldi, 2003; Keith et al., 2004). Recently, instant and

economically reasonable approaches of using higher taxa (family or order) or functional groups for bioindicator assessment have made a presence (Baldi, 2003; Deans et al., 2005).

In this study, we examined the possibility of flying insects at the family level as an environmental indicator of logging disturbance in lowland tropical forests. Flying insects with high mobility have two potential advantages for environmental assessment. Their high dispersion ability enables them to escape rapidly from inconvenient habitats to better ones, implying their sensitivity to disturbance. Secondly, their high mobility enables us to assess relatively wide-range environmental conditions from a fixed point. Our study is the first trial to apply a higher-taxon approach for assessing the impact of logging disturbance on insect communities in lowland tropical forests. The assessment was conducted in Deramakot Forest Reserve, Sabah, Malaysia, where various logging regimes were historically applied to different stands of tropical lowland rain forest. Effects of different degrees of logging disturbance were compared across an array of forest stands differing in applied method of logging operation and time after logging.

Materials and Methods

Location and climate of study site

Deramakot Forest Reserve (DFR), Sabah, Malaysia (5°19' - 20'N, 117°20' -42'E), covers about 55,000 hectares in the east of central Sabah. The climate is marine equatorial, with low variance in monthly mean temperature of about 26°C. Being greatly influenced by the northeast monsoon (November-February) and the southwest monsoon (May-August), the annual precipitation ranges from 1700 to 5100 mm (Kleine & Heuveldop, 1993). The forest of DFR is classified as the *Parashorea tomentella-Eusideroxylon zwageri* type, dominated by Dipterocarps such as *Parashorea tomentella*, *Shorea leptoclados*, *Dryobalanops lanceolata* and *Dipterocarpus caudiferus*, which together make up 40 % of bigger trees (Chey, 2002).

Logging history in DFR

Logging in DFR began from the southern part, along the Kinabatangan River, in the 1950s. The initially adopted logging method was the Malayan Uniform System, which allowed harvesting of all commercial timber over 45 cm in DBH (Diameter at Breast Height) and subsequent systematic poisoning to unwanted species for promoting

the natural regeneration of saplings and seedlings of commercial trees. This was modified in 1971 to the Sabah Uniform System along with the timber boom having started in the late 1960s (Kleine & Heuvelop, 1993). The method applied heavy machineries without appropriate consideration of forest stand conditions and abandoned all silvicultural treatments except cutting of lianas one year before felling. The minimum DBH for harvesting was 60 cm and felling was assumed to be cycled at 60-year intervals. However, loggers and foresters ignored even those reduced requirements for convenience or profit. As a result, many patches of deforested area have been created in mosaic with residual forests to such a degree that any silvicultural management or rehabilitation procedure has made no sense.

In 1989, the State Forestry Department of Sabah, assisted by the German Government, started a project aimed at introducing sustainable management for timber production, soil conservation, non-timber forest produce and conservation of native flora and fauna in DFR. The introduced logging operation is called Reduced Impact Logging (RIL). RIL is a kind of selective logging, which lays down various guidelines for sustainable forest use, e.g., setting of stream buffer zones, preservation of potential crop trees, and damage assessment after harvesting (Sabah Forestry Department, 1998). By the authentication from the State Government of Sabah, the price of timber from

DFR has royalty in respect of the efforts for sustainable management.

Study plots

To assess logging impact on various components and functions of lowland tropical rain forest ecosystem, in total ten 0.2-hectare study plots were established in different forest compartments in and near DFR: those plots were classified into five groups, each with two replicate plots, under different regimes of disturbance in logging operation and the length of interval after logging. We chose one of the two replicate plots from each group for sampling flying insects. The disturbance regimes were specified by two factors, logging method (RIL or CM: conventional method referring to non-RIL) and interval after logging. The five plots were named according to the disturbance regimes; NIL: primary forest with no impact of logging, CM-70s: harvested in the 1970s by CM, RIL-95: harvested in 1995 by RIL, RIL-00: harvested in 2000 by RIL, and CM-con: continuing to be harvested intermittently by CM.

To estimate the effects of logging on forest environment, six environmental variables were extracted from vegetation data for all trees with DBH over 9 cm in each plot (Seino et al., personal communications): 1) tree species richness (TSR), 2) tree density: number of trees within each plot (TDN), 3) total basal area of trees (BAT), 4)

basal area of *Macaranga* trees (BAM), 5) basal area of commercial (Dipterocarpaceae) trees over 60 cm in DBH (BAC), 6) basal area of small trees below 10 cm in DBH (BAS). In addition, 7) the amount (dry weight) of litter on the ground (ALG) was measured, as the mean of A0-layer samples collected from five 25 cm² quadrats in each plot (Ito & Hasegawa, personal communications). Furthermore, in March 2005, vertical forest structure was measured by a portable lidar system. Details of the system were described in Parker et al. (2004). To measure the vertical forest profiles, each plot was divided into 10 m meshes. Measurements were conducted at 2 m intervals along a mesh line. Summing up the data, i.e., the height from the lidar system to the nearest foliage, for each 10 m section (five measuring points), the foliage densities were calculated at 1 m intervals by MacArthur-Horn method (MacArthur & Horn, 1969). Then, the foliage height diversity was estimated by the Shannon-Wiener index for each 10 m section and 8) the average (FHD) was calculated for each plot as a measure of foliage-layer diversity. As another measure of foliage structure, 9) the horizontal constancy of vertical foliage profile (HCF) was calculated by Kendall's coefficient of concordance for the 1m-interval foliage densities across all 10 m sections within each plot (Tanabe, 2002).

Insect sampling

We employed a bait trap specially designed by Toda (1977) for sampling flying insects in the above-ground forest space. To collect mainly fruit flies (Drosophilidae) the traps were baited with fermented banana (ca. 170 g per trap), but non-drosophilid flies (Diptera), beetles (Coleoptera), bees and wasps (Hymenoptera) were also collected in abundance and other orders more or less.

In order not to disturb the forest floor of study plots by repeated visits to the trapping sites, we selected a tree or two trees just adjacent (within 5 m) to each plot for setting the banana traps (the vegetation was continuous in configuration between respective trapping site and plot). The traps were set vertically from the understorey to the canopy: the lowest trap was set at 0.5 m above the ground surface, the next at 1.5 m, and others at 5 m intervals up to the canopy, the top trap varying in height according to the canopy height of the forest (36.5 m at NIL, 31.5 m at CM-70s, 26.5 m at RIL-95 and RIL-00 and 21.5 m at CM-con). Some (up to four) upper traps were suspended from the same rope with a pulley that was hung from a bough of the selected tree, but the lowest two were tied directly to the trunk of the same tree or a nearby tree.

We conducted sampling four times, in July to August and in October to November, 2003 and in January to February and in April to May, 2004. During each sampling

period trapped insects were collected and trap baits were renewed three times at 10-day intervals. All samples were preserved in 70 % ethanol and carried to Hokkaido University (Japan). Collected insect specimens were identified to family for Diptera, Coleoptera and Hymenoptera, but to order for the others.

Analyses

Consolidation of environmental variables

The disturbance of logging itself is initially represented by direct loss of commercial timber and soil agitation. As time goes by, however, those direct effects of logging seem to be concerned with various aspects of forest succession. With the thought of this complexity, we summarized the nine measured environmental variables as a few major axes of a standardized Principal Component Analysis (PCA). Since PCA axes are, by definition, orthogonal and independent of one another, this procedure creates composite, independent, environmental variables and avoids the danger of spurious correlations, i.e., multicollinearity (Voigt et al., 2003).

Effects of logging disturbance on insect abundance

Effects of logging disturbance were examined for the abundance of the following

seven insect families with the total number of collected individuals more than 500: Drosophilidae, Phoridae, Sciaridae, Muscidae, Nitidulidae, Staphylinidae and Apidae, the first four belonging to Diptera, the next two to Coleoptera, and the last to Hymenoptera.

Considering the vertical stratification of insect communities within forest, we focused on two extreme strata, the understorey (the lowest two traps) and the canopy (the highest two). Although the actual height of canopy varied among the study plots, the canopy was the uppermost stratum with similar characteristics such as dense foliage and being exposed to the outer, open environment, and therefore comparable across the plots. On the other hand, intermediate strata varied in number and environmental conditions, with difficulty for objective comparison, among the study plots. The data from traps other than the lowest and the highest two were excluded from the analyses.

Generalized Linear Models were adopted to estimate effects of logging disturbance (R Development Core Team, 2004), separately for the abundance of each insect group in the understorey and in the canopy. In this study probability distributions were assumed to be of Poisson, and link functions were set to logarithmic function. In addition to the composite, environmental variables, season was incorporated into the analyses as a categorical variable: the four sampling periods were each coded by three

binary, dummy variables (SV1, 2 and 3).

From all the possible models (including the null model with no variables) differing in composition of incorporated covariates (the composite, environmental variables) and cofactor (season), the best model was selected with Akaike's Information Criteria (AIC) (Akaike, 1973). The deviance improvement was evaluated for each variable incorporated into the selected model. Its percentage to the deviance of null model can be regarded as a relative explanatory power of each variable.

Results

Consolidation of environmental variables

PCA axes were calculated for the original data of the nine environmental variables at the five study plots (Table 1). Nearly all (92 %) of the total variance in the original data was explained by the first two PCA axes, 57.8 % by Axis 1 and 34.1 % by Axis 2. Biplot of the environmental variables and the study plots on these axes is shown in Fig. 1. The principal component coefficients (loadings) of the environmental variables for the two axes are shown in Table 2. Fig. 1 and Table 2 show that four environmental variables, BAC, BAT, BAM and FHD are represented mostly by Axis 1, and that ALG, and HCF are represented by Axis 2. However, the variance for the remaining three variables, TSR, TDN and BAS, are explained by both axes in combination.

Among the four environmental variables well represented by Axis 1, BAM was negatively correlated with BAC, BAT and FHD. *Macaranga* are major pioneer plants in Southeast Asian tropics, rapidly entering deforested areas. Gap formation by selective logging would promote the growth of *Macaranga* rapidly and such simultaneous forest regeneration may reduce vertical complexity of foliage, FHD. On the other hand, harvesting of big commercial trees directly reduces BAC and eventually BAT. Thus, Axis 1 can be interpreted as representing direct effects of selective logging. As for Axis 2, ALG was negatively correlated with HCF (strongly), TDN and BAS (partially). Interpretation of these correlations is difficult, except for partial correlation between TDN, BAS and HCF: the promotion of young tree growth (BAS) would partly contribute to the increase of the tree density (TDN) and more number of small trees, which are highly variable in height according to the growth rates of different tree species under the light conditions of stands, may result in high degrees of HCF. To interpret the negative correlations between ALG and these three variables, we need more information, for example on the rates of supply and decomposition of litter and relations between nutrient cycling and plant growth.

The positions of study plots on Axis 1 are consistent with the interpretation of this axis. NIL with no logging disturbance and CM-con with the strongest disturbance were

plotted at the opposite extremes, and the other three study plots, CM-70s, RIL-95 and RIL-00, with moderate disturbance but varying in logging method and interval after logging were at intermediate positions. However, the positions along Axis 2 are difficult to be interpreted as mentioned above, varying especially among the moderately disturbed plots.

All GLM analyses were carried out using these two PCA axes as composite, environmental variables, Com1 and Com2. The first variable represents the intensity of logging disturbance, but the second represents an unknown factor independent of logging disturbance but related to the amount of ground litter, the tree density or horizontal constancy of foliage.

Effects of logging disturbance on insect abundance

Understorey

The selected models were divided into two categories, one including all environmental variables for Drosophilidae, Phoridae, Nitidulidae, Staphylinidae and Apidae and the other not including Com2 for Sciaridae and Muscidae. The pattern of spatio-temporal variation in abundance predicted from the selected model is shown in comparison with the observed pattern, separately for each insect group, in Fig. 2. Table 3 shows the

parameter estimate for each environmental variable incorporated into the selected model for each insect group, and Table 5 the improved deviance and its percentage. The selected models fairly improved deviance (53.97 % to 85.45 %). The most important factor explaining the deviance was Season in all the selected models, except for that of Muscidae. Com1 representing the logging disturbance impact was the most important in Muscidae and the second important in the other families, suggesting that all the insect groups concerned, especially Sciaridae and Muscidae for which Com2 has been excluded from the models, can be used as indicators for assessing impact of logging disturbance.

Canopy

The selected models for canopy communities were different in the incorporated variables and/or their relative importance from those for understorey communities in all insect groups except for Drosophilidae and Nitidulidae. The selected models improved 25.34 % to 66.74 % of the deviance and season was also the most important variable in all the insect groups except for Apidae (Table 5), and Muscidae was independent of Com1 and Com2. For Sciaridae in contrast to the results for the understorey communities, Com1 was excluded from the selected model instead of Com2 (Table 5).

In Phoridae, Staphylinidae and Apidae, the relative importance of Com1 and Com2 was reversed between the understorey and the canopy: Com2 was the most important in Apidae (Table 5). Even in Drosophilidae and Nitidulidae, for which Com1 was also the second important variable, the percentage improvement of deviance by this variable was less in the canopy than in the understorey (Table 5). The parameter estimates for Com1 were positive in Phoridae and Apidae, implying positive effects of logging disturbance on these insects in the canopy (Table 4). Thus, the patterns of abundance variation across the study plots were different between in the understorey and in the canopy: effects of logging disturbance were less clear on canopy communities than on understorey ones (Figs. 2 and 3).

Discussion

Seasonality in abundance of every insect group studied was apparent as in previous works (Wolda, 1980; 1988; Kato et al., 1995). Additionally, our study showed that the seasonal fluctuations in tropical insect populations were strong enough to exceed the effects of logging disturbance. This result is consistent with the study by Hill et al. (2003). Even in the tropics near the equator, monitoring of insect communities should be done in the same season, or ideally throughout a year. Another point to be taken into consideration is the interaction between logging disturbance and seasonal effects.

Silviculture treatments such as logging alter physical structure of forest stands and change microclimate conditions there (Aussenac, 2000). Unfortunately, our study was too small in the spatial scale to detect such interactive effects. More spatially scaled-up research is needed to evaluate the interaction effects.

The logging disturbance (Com1) was detected as the most or second important, environmental factor, which generally caused the decrease in abundance of all the insect groups concerned, in the understorey communities. In the canopy, however, the insect groups except Drosophilidae and Nitidulidae responded differently to the logging disturbance: Com2 was the most or second important. What is the reason for this difference in insect responses to the logging disturbance between the understorey and the canopy? First, consider the difference in physical environment between the two strata. The understorey is the innermost part of forest and well buffered by foliage cover from the external, physical environment, e.g., solar radiation, wind, rainfall and so on (Lee, 1978; Parker, 1995). On the other hand, the canopy is the outermost part exposed to radical changes in weather conditions. It seems likely that in the understorey, all the insect groups would have responded similarly to changes in some environmental factors caused by logging disturbance under well-buffered, stable conditions of other factors. For example, probably decreased humidity due to increased evaporation by solar

radiation would have decreased the abundances of desiccation-sensitive insects such as most of the studied Dipteran families with small body size. In the canopy, however, the impact of logging disturbance, if present, may have been obscured for most of the insect groups studied, probably due to noise effects of spatio-temporal variation in a number of physical, environmental factors. Another possible reason for not detecting of logging impact on the canopy insect communities is high heterogeneity of food resources there. Main food resources for insects in the understorey are dead and/or decayed, organic matters such as leaf litter, fallen logs, (decayed) barks and fruits, or fungi and microbes growing on such dead matters. On the other hand, the canopy provides insects mainly with living food resources such as leaves, flowers and fruits. In general, living vegetable matters are spatio-temporally more variable in both quality and quantity than dead matters, according to leaf ages and species-specific characters of living plants (Coley, 1983; Coley & Barone, 1996). The quality of dead matters on the understorey is considered to be less species-specific and much influenced by physical, environmental factors such as temperature and humidity. Thus, logging disturbance may have affected the abundance of understorey insects through changes in their food resources. On the other hand, the abundance of canopy insects utilizing highly diverse food resources may have been determined by various factors independent of logging disturbance. Most of

the Dipteran families studied depend on dead, organic matters or fungi/microbes on them, spend their larval stages in soil, and have an important role for organic decomposition in forest ecosystem (Schaeffer & Schauer mann, 1990; Frouz, 1999). Responses of Dipteran families in the understorey, especially Muscidae and Sciaridae, might be related to some changes in decomposition system by logging disturbance.

Anthropogenic disturbance especially by logging on natural forest ecosystems has been greatly intensified since the 1960s in Southeast Asia (Brookfield & Byron, 1990), causing deterioration of ecosystem functions and mass extinction of biological species (e.g., Laurance, 1999). In the last decade, effects of clear felling or selective logging on invertebrates have been studied (Holloway et al., 1992; Chey et al., 1997; 2002; Willott, 1999; Willott et al., 2000; Chung et al., 2000; Lewis, 2001; Eltz et al., 2002; 2003; Samejima et al., 2004). Their findings have suggested a possibility to apply those invertebrate responses for assessing the impact of logging disturbance on ecosystem functioning. However, such scientific assessment is not yet enough as to keep the balance between forest harvesting and natural revegetation (Laurance, 1999). It is an urgent demand to assess current and future threats of ecosystem degradation for planning effective managements of ecosystem maintenance, sustainable use and remediation. Higher-taxon approach seems to be the most realistic in its convenience

and cost efficiency to this current demand. In this context, the present study showed possible effectiveness of such an approach. However, the patterns observed in the present study may be highly dependent on the particular sampling method by banana-baited trap. The obtained samples do not cover all members of the selected taxa, even for Drosophilidae, and the sampling efficiency, if comparable across different environments for each taxon, should vary among the different taxa. For generalization, more evidence should be obtained by different sampling methods.

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Table 1. Original data for nine environmental variables at each study plot.

| Plot | TSR ^a | TDN ^b | FHD ^c | HCF ^d | BAT ^e (m ²) | BAM ^f (m ²) | BAC ^g (m ²) | BAS ^h (m ²) | ALG ⁱ (g) |
|--------|------------------|------------------|------------------|------------------|------------------------------------|------------------------------------|------------------------------------|------------------------------------|----------------------|
| NIL | 50 | 151 | 2.606 | 0.677 | 7.853 | 0.107 | 2.402 | 0.053 | 50.572 |
| CM-70s | 35 | 102 | 2.300 | 0.398 | 7.694 | 0.317 | 2.026 | 0.046 | 78.734 |
| RIL-95 | 40 | 154 | 2.239 | 0.630 | 7.590 | 0.297 | 1.534 | 0.074 | 28.964 |
| RIL-00 | 33 | 128 | 2.123 | 0.476 | 7.155 | 1.048 | 1.253 | 0.074 | 63.580 |
| CM-con | 25 | 126 | 2.088 | 0.635 | 4.089 | 1.976 | 0.000 | 0.090 | 53.678 |

^aTree species richness.

^bNumber of trees.

^cFoliage height diversity.

^dHorizontal constancy of vertical foliage.

^eTotal basal area of trees.

^fBasal area of Macaranga trees.

^gBasal area of commercial (Dipterocarpaceae) trees over 60cm in DBH.

^hBasal area of small trees below 10cm in DBH.

ⁱThe amount (dry weight) of litter on the ground.

Table 2. The eigenvector coefficients of a standardized PCA for nine environmental variables.

| Environmental variables | Axis 1 | Axis 2 |
|-------------------------|---------|---------|
| TSR | -0.9125 | -0.3215 |
| TDN | -0.2767 | -0.9484 |
| FHD | -0.8832 | -0.1582 |
| HCF | -0.0272 | -0.9453 |
| BAT | -0.9465 | 0.0614 |
| BAM | 0.9822 | 0.0288 |
| BAC | -0.9901 | 0.1320 |
| BAS | 0.8503 | -0.4959 |
| ALG | 0.0269 | 0.9765 |

Note: The eigenvalues of the axes represented are: Axis 1 = 0.5788, Axis 2 = 0.3413 (sum = 92% of total variance explained).

Table 3. Parameter estimates of the selected model to explain spatio-temporal variation in abundance of each insect group in the understorey.

| Insect group | Intercept | Com1 | Com2 | SV1 | SV2 | SV3 |
|---------------|-----------|---------|---------|---------|---------|---------|
| Drosophilidae | 6.0156 | -0.3737 | -0.1331 | 0.0237 | 0.8823 | 0.8644 |
| Phoridae | 2.8015 | -0.2336 | -0.1728 | 0.5496 | 1.4537 | 1.6963 |
| Sciaridae | -0.0458 | -0.9641 | -* | 1.6094 | 1.1896 | 3.2415 |
| Muscidae | 2.4301 | -0.6352 | - | -0.8522 | -0.5819 | -1.2238 |
| Nitidulidae | 4.6603 | -0.2441 | -0.1125 | -0.3223 | 0.3257 | 0.3231 |
| Staphylinidae | 5.2393 | -0.4524 | -0.2490 | -2.1484 | -0.4730 | -1.3183 |
| Apidae | 1.2659 | -0.2904 | -0.2224 | 0.5521 | 1.1664 | 0.4229 |

* Not selected.

Table 4. Parameter estimates of the selected model to explain spatio-temporal variation in abundance of each insect group in the canopy.

| Insect group | Intercept | Com1 | Com2 | SV1 | SV2 | SV3 |
|---------------|-----------|---------|---------|---------|---------|---------|
| Drosophilidae | 6.1739 | -0.1693 | 0.0154 | 0.8352 | 0.1926 | 0.7593 |
| Phoridae | 1.7641 | 0.1552 | 0.1831 | 1.6161 | 0.5306 | 1.3524 |
| Sciaridae | -0.5758 | -* | 0.3489 | 2.3979 | 0.9808 | 2.8526 |
| Muscidae | 0.3365 | - | - | 0.1335 | -0.5596 | 1.0498 |
| Nitidulidae | 5.3558 | -0.1663 | -0.0736 | 0.3615 | 0.3531 | 1.1726 |
| Staphylinidae | 5.5102 | -0.0497 | 0.1152 | -0.6204 | -0.8816 | -0.5360 |
| Apidae | 1.7421 | 0.1907 | 0.4455 | 1.2347 | 0.6451 | 0.7239 |

* Not selected.

Table 5. Percentage deviance improved by selected model and each incorporated variable (calculated when fitted singularly) for each insect group in the understorey and in the canopy.

| Insect group | Deviance improved (%) | | | | | | | |
|---------------|-----------------------|-------|-------|----------------|--------|-------|-------|----------------|
| | Understorey | | | | Canopy | | | |
| | Season | Com1 | Com2 | Selected model | Season | Com1 | Com2 | Selected model |
| Drosophilidae | 44.81 | 36.02 | 7.57 | 85.45 | 45.07 | 10.16 | 0.05 | 57.97 |
| Phoridae | 53.67 | 8.83 | 5.26 | 66.77 | 49.36 | 2.88 | 4.47 | 57.22 |
| Sciaridae | 54.64 | 30.01 | -* | 84.65 | 49.85 | - | 9.08 | 58.99 |
| Muscidae | 30.07 | 45.67 | - | 75.82 | 25.27 | - | - | 25.34 |
| Nitidulidae | 28.68 | 27.16 | 7.54 | 61.51 | 57.63 | 7.61 | 1.81 | 66.74 |
| Staphylinidae | 42.76 | 18.71 | 7.79 | 66.48 | 48.09 | 1.04 | 6.11 | 55.18 |
| Apidae | 30.46 | 15.74 | 10.04 | 53.97 | 23.12 | 1.74 | 25.20 | 52.05 |

* Not selected.

Figure legends

Fig. 1. PCA biplot for relations between environmental variables and study plots.

Environmental variables are shown with vectors and study plots with circles.

Fig. 2. Seasonal and among-plot variations in abundance of each insect group in the understorey: observed value (bar) and prediction from the selected model (dot with line).

Fig. 3. Seasonal and among-plot variations in abundance of each insect group in the canopy: (see legend of Fig. 2 for further explanation.

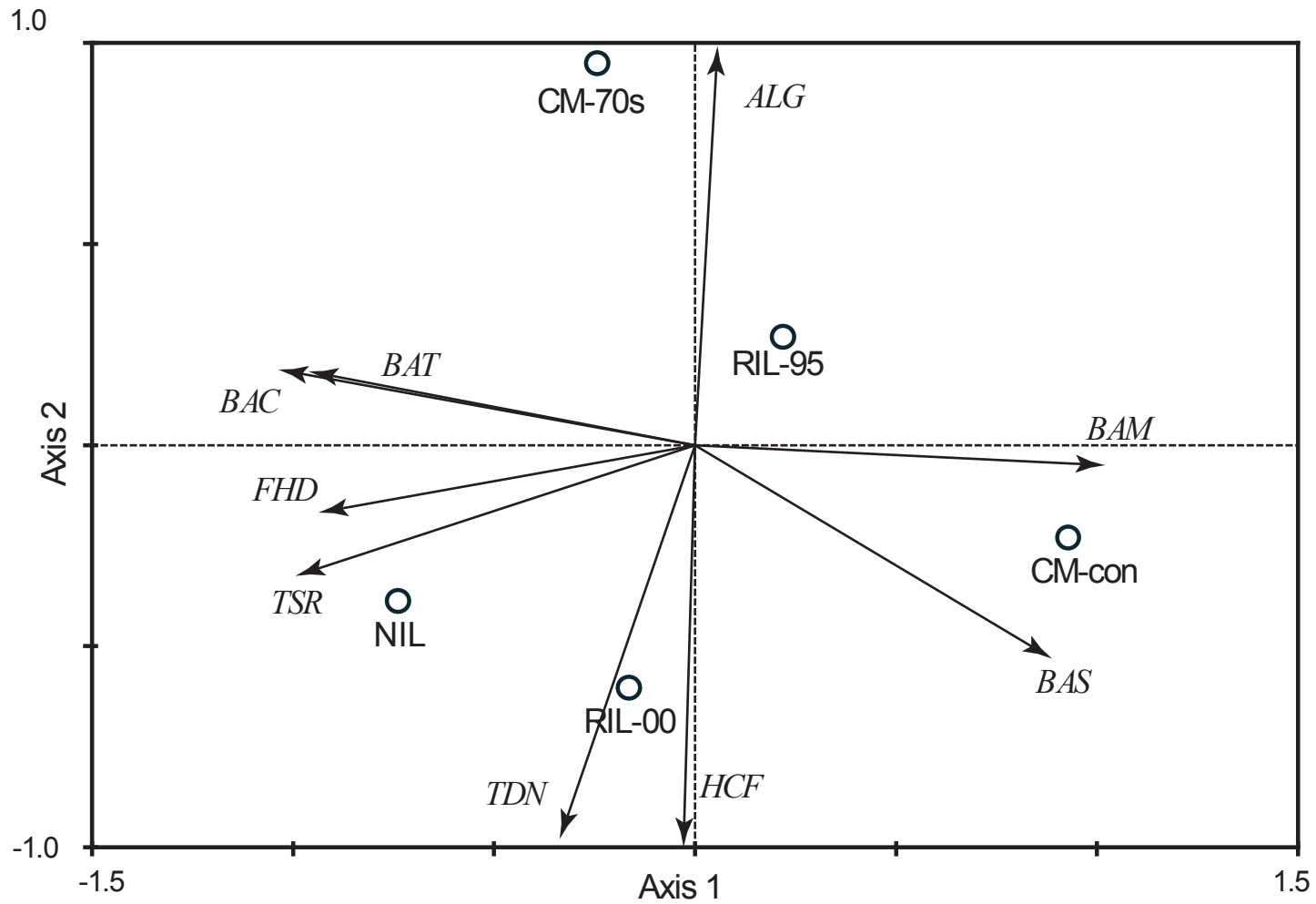


Fig. 1. PCA biplot for relations between environmental variables and study plots. Environmental variables are shown with vectors and study plots with circles.

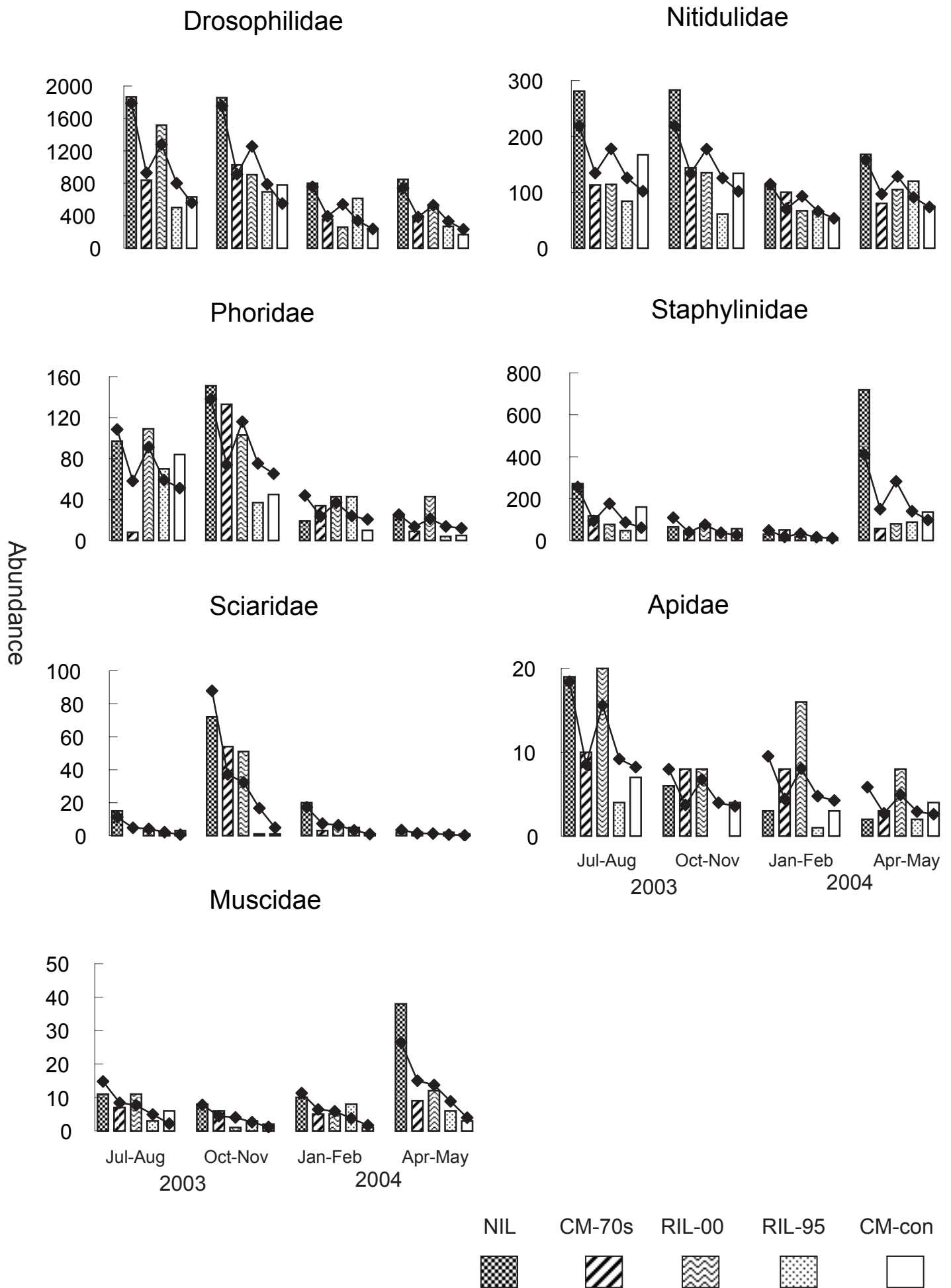


Fig. 2.

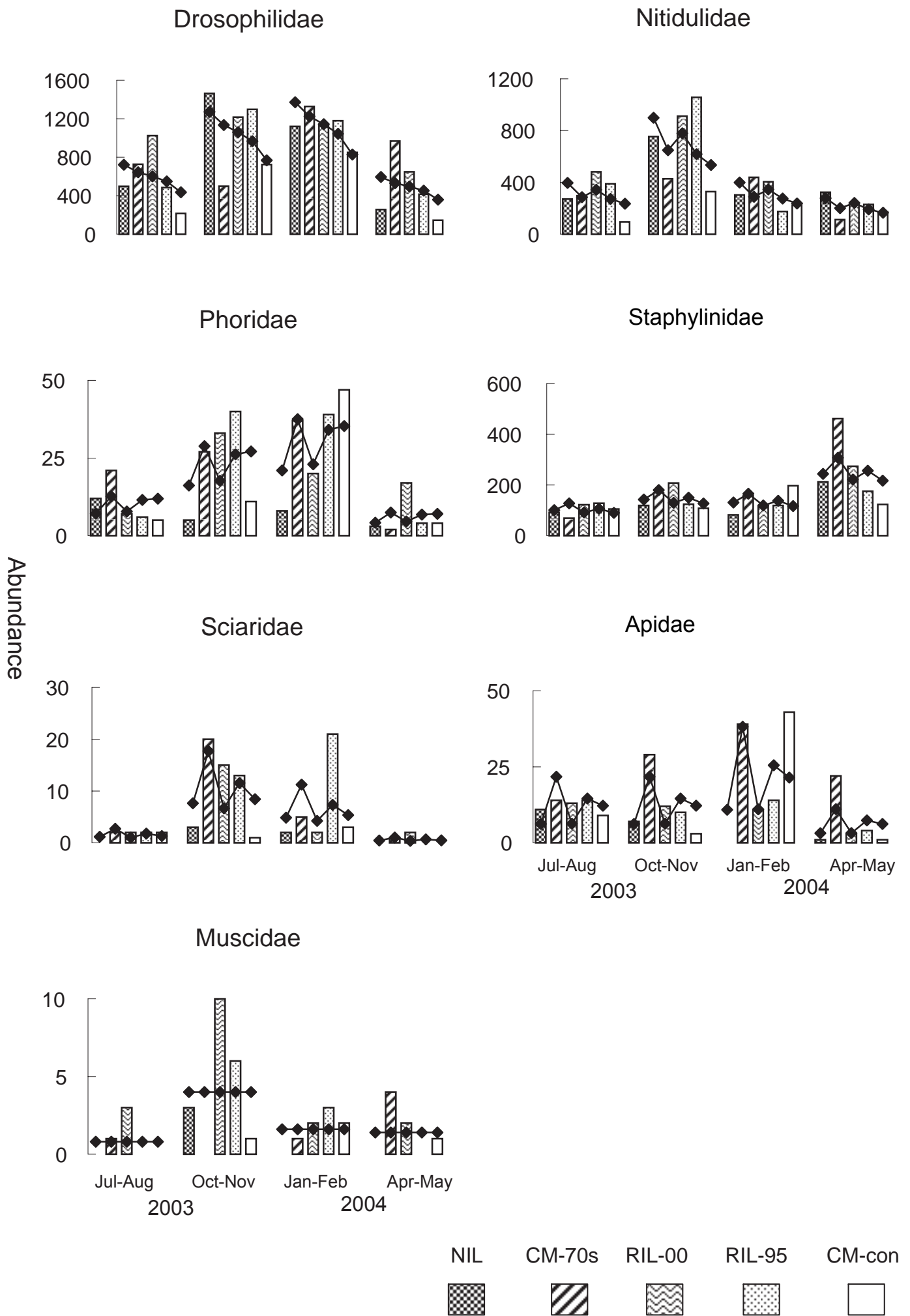


Fig. 3.