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**International Biodiversity Observation Year in Western-Pacific and Asian Region
(DIWPA-IBOY): A case report on species rarity and spatio-temporal variability of
species composition in Lepidoptera and Coleoptera communities from a temperate
forest of northern Japan**

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Abstract

An international project, DIWPA-IBOY, took place for simultaneously observing biodiversity throughout the Western-Pacific and Asian Region in 2001 to 2003, as one of core projects for International Biodiversity Observation Year, a crosscutting network activity of DIVERSITAS (An International Programme of Biodiversity Science). DIWPA-IBOY provides extensive data on species diversity obtained by the standardized method. Under this project, 51742 individuals of Lepidoptera and 11633 of Coleoptera were collected by light traps from Tomakomai Experimental Forest of Hokkaido University, one of core DIWPA-IBOY sites, in the cool-temperate region of northern Japan. Based on these data, this study examined the relative abundance distribution (RAD) to evaluate the amount of rare species in Lepidoptera and Coleoptera communities. The beta diversities between sampling seasons, forest strata and trap sites were also assessed to evaluate the spatio-temporal variability of species composition in these communities. In the analysis of RAD, the best-fit model was selected from the log-Normal, Zipf-Mandelbrot and Zipf models differing in the tail length of RAD, i.e., the proportion of rare species. To explore the beta diversity between samples, the abundance-based Jaccard index with unseen species estimator was calculated, and then a hierarchical clustering analysis was conducted. As a result of RAD analysis, the Coleoptera community was regarded as containing a larger proportion of rare species than the Lepidoptera community. The seasonal compartmentalization of community, deduced from the beta-diversity analysis, was finer in Lepidoptera (seven assemblages recognized) than in Coleoptera (three assemblages). The spatial (vertical and horizontal) compartmentalization was negligible in both communities. The coincidence of the larger proportion of rare species and the lower beta diversity between seasons in the Coleoptera community was explained by the longer life spans of beetles compared to moths, based on the assumption that the length of life span acts as a temporal agent for mass effect on the analogy of the migration rate as a spatial agent for mass effect.

Keywords Beta diversity, Insect community, Mass effect, Relative abundance distribution, Species rarity

1 **Introduction**

2
3 Concern about rapid species loss and anthropogenic alteration of natural habitats has emphasized the need
4 to monitor the changes in species diversity as one of the features of biological communities.
5 DIWPA-IBOY aimed at inventorying and monitoring biodiversity in a network of many observation sites
6 distributed along the “Asian Green Belt”, an almost continuous forest cover stretching from the taiga of
7 eastern Siberia to the forests of eastern Australia. In DIWPA-IBOY, the sampling methodology was
8 standardized to allow and facilitate comparisons among sites and along some environmental gradients
9 (Nakashizuka and Stork 2002). The surveys having been conducted under this methodology in each
10 observation site are now providing informative data on biodiversity.

11 Species diversity can be partitioned among different components; alpha, beta, and gamma
12 diversities. A large number of studies have focused on local alpha diversity and regional gamma diversity
13 (for reviews see Gaston and Blackburn 2000; Blackburn and Gaston 2003), whereas species turnover or
14 beta diversity among communities has received little attention, although it captures a fundamental aspect
15 of variability of species diversity within space and time (Lande 1996; Koleff et al. 2003). Another feature
16 of community is the predominance of rare species (Colwell and Coddington 1994). Explaining genesis
17 and maintenance mechanisms of rare species in a community is one of the most challenging themes in
18 recent ecological research (Hubbell 2001).

19 The first aspect examined in this study is species rarity. The quantification of the species rarity in a
20 community has been tried by means of relative abundance distributions (RAD, reviewed by Tokeshi
21 1993; Tokeshi 1999). The geometric shape of empirical RAD that can be shown by the plot of
22 logarithmic species abundance to species rank order provides intuitive information on the species rarity in
23 a focal community. The rare species in the RAD are represented as the species of the lower ranks, for
24 example, singletons and doubletons. The statistical models for estimation of RAD are based on specific
25 statistical distribution, although these do not explain any ecological processes. Log-Normal (Preston 1948,
26 1962), Zipf (Zipf 1966) and Zipf-Mandelbrot (Mandelbrot 1982; Frontier 1985) models differ in the
27 length of tail which shows the proportion of rare species involved in the RAD. The procedure to fit these
28 models to the empirical data, and then to select a best-fitted model, allows a comparison among
29 communities in terms of species rarity. Furthermore, in the log-Normal model, species rarity can be

1 shown by species abundance distribution (SAD), the species frequency plot against the population
2 abundance expressed as a logarithm to the base 2, which is Preston's octave (Preston 1948, 1962). The
3 position of the octave mode would suggest the proportion of rare species in the community, although the
4 log-Normal model is usually truncated on the left.

5 The second aspect considered in this study is beta diversity among assemblages. Beta diversity is
6 defined as the diversity among two or more assemblages changing in composition, for example, along
7 spatial or temporal gradients (Lande 1996). Under a given regional diversity, as the beta diversity
8 increases, local species compositions differ more remarkably from one another with a smaller overlap of
9 species among them (Koleff et al. 2003). The beta diversity is measured by means of the statistics of
10 'similarity' or 'dissimilarity' indexed among assemblages (Koleff et al. 2003). Although measurements of
11 beta diversity had been based on presence-absence data among assemblages in most of previous
12 publications (e.g., Koleff et al. 2003; Tuomisto et al. 2003), Chao et al. (2005) indicated that such
13 classical indices using presence-absence data could be highly sensitive to sample size, especially for
14 assemblages with numerous rare species. Theoretical approaches to these problem (Condit et al. 2002;
15 Plotkin and Muller-Landau 2002; Chao et al. 2005) are ongoing, but there are still few applications of
16 such new beta diversity measurements to empirical data (e.g., Latimer et al. 2005; Novotny and Weiblen
17 2005).

18 Beta diversity will provide other perspectives on species rarity (Gaston 1994; Kunin and Gaston
19 1996). The point for consideration is whether spatio-temporal variation in community composition
20 affords opportunities for rare species to persist. The proportion of rare species in a community may be
21 influenced by dispersal ability and habitat requirement of individual species which generate beta diversity
22 (Tuomisto et al. 2003; Legendre et al. 2005). Developing hypotheses on the relationship between species
23 rarity and beta diversity will shed more light on species diversity and community assembly in the future.

24 However, some deficiencies in data quality have prevented the analyses of RAD and beta diversity.
25 In most field surveys, because it is virtually impossible to detect all species and their relative abundance
26 in a focal community (Chao et al. 2005), the samples collected should be strongly biased. For example,
27 Connolly et al. (2005) have demonstrated that the spatial scale of sampling could affect the shape of RAD
28 in the coral and reef fish communities. Less biased and refined extensive data of species and their relative
29 abundances are necessary for the robust estimation of RAD and beta diversity (e.g., Williamson and

Gaston 2005). DIWPA-IBOY would provide relatively less biased data, at least comparable across sites, based on the standardized sampling methods (Nakashizuka and Stork 2002).

In this paper, the structures of Lepidoptera and Coleoptera communities are examined with special reference to the species rarity and the beta diversity, using samples collected by light traps from a temperate forest of northern Japan in DIWPA-IBOY. In order to assess the community structure in detail, first the seasonal dynamics of species richness and abundance is addressed for each community. Then the species rarity in each community is examined by the analyses of RAD and SAD. The beta diversity as variability of species composition between samples is used to demonstrate the spatio-temporal compartmentalization of each community. Finally, the relationships between the species rarity and the beta diversity are discussed by comparing the features of Lepidoptera and Coleoptera communities. This case report from one of core sites in DIWPA-IBOY will facilitate the comparison of community structure across sites along the nearly global, latitudinal transect of forest ecosystems, which is one of goals aimed in DIWPA-IBOY, based on the unprecedented data obtained by standardized methods from the very wide range.

Methods

Study site

The samplings were carried out in a temperate deciduous forest of Tomakomai Experimental Forest (TOEF; 42°43' N, 141°36' E, ca. 90 m a.s.l.), Hokkaido, Japan. TOEF is one of the core research sites for DIWPA-IBOY (cf. URL: <http://diwpa.ecology.kyoto-u.ac.jp/iboy.htm>). This cool-temperate forest receives 1,161 mm of annual precipitation and experiences an average annual temperature of 5.6 °C. Oak (*Quercus crispula*), maple (*Acer mono*) and linden (*Tilia japonica*) dominate the forest. The canopy ranges from 15 to 25 m in height, saplings of the dominant tree species growing on the forest floor. Deciduous trees break buds in early to mid May, and shed their leaves in late October.

Light trap sampling

The whole sampling procedure followed the IBOY manual (Nakashizuka and Stork 2002). Three sets of two traps, one at the ground level (1 m from the ground level) and the other in the canopy at the height of 15.8, 16.3 and 17.1 m from the ground level, were operated simultaneously at three randomly determined points within a square one-hectare plot (100 m × 100 m), where the tree species composition was relatively uniform. Trapping was repeated at monthly intervals from March to November 2001. Traps were run for three nights on each monthly sampling event, avoiding the week around the full moon. They were emptied daily for the trapping period. Thus, in total, 126 samples (seven months × two strata × three locations × three days) were collected in this study. Traps run from about 5.00 p.m. throughout the night. The catches were first sorted at the order level, and then the specimens of Lepidoptera and Coleoptera were identified to species and counted by taxonomic experts, H. Kogi and A. Kashizaki, respectively.

Statistical analysis

To estimate the total species richness, the mean species accumulation curve (SAC) with its standard deviation was calculated by random permutations (1000 times) of 126 samples, one trap-night sample being the unit for permutation (Gotelli and Colwell 2001). The extrapolated species richness in the species pool was reckoned by estimating the number of the undetected species and adding it to the observed species richness (Colwell and Coddington 1994). The bootstrap estimate and its standard error (Smith and van Belle 1984) were calculated to reckon the potential species pool.

The relative abundance distributions in Lepidoptera and Coleoptera were fitted to three statistical models with maximum likelihood method. Log-Normal model, Zipf model and Zipf-Mandelbrot model were examined. The log-Normal model assumes that the logarithmic abundances follow the Normal distribution (Preston 1948, 1962). The Zipf model can be regarded as power law, and is denoted as follows:

$$f(x) = c \cdot x^a,$$

where c is the scaling parameter, and a is a decay coefficient (Zipf 1966). The Zipf-Mandelbrot model is

modified from Zipf model by adding a parameter b , giving the following formula (Mandelbrot 1982; Frontier 1985):

$$f(x) = c \cdot (x + b)^a,$$

The Zipf model has the longest tail corresponding to rare species among the three models. The tail of log-Normal model is the shortest. The best-fitted model was selected according to Akaike's information criterion (AIC).

The numbers of species were plotted to abundance classes representing Preston's octaves at the base of 2, and then the left-truncated Normal distribution of the Preston model (Preston 1948, 1962) was fitted to observed frequencies of species with maximum likelihood method. The expected frequency $f(x)$ at abundance octave x is defined as follows:

$$f(x) = S_x \cdot \exp(-(\log_2(x) - \mu)^2 / 2\sigma^2),$$

where μ is the location of the mode, σ is the standard deviation, and S_x is the expected number of species at the mode.

In evaluation of beta diversity between samples, the daily variability was ignored by summing up three-night samples at a given trap in each month. This resulted in a total of 42 samples (seven seasons $\times$ two strata $\times$ three sites) of which species compositions were compared. The spatio-temporal variability of species composition was measured by means of abundance-based Jaccard index with estimator for the effect of unseen shared species proposed by Chao et al. (2005), and then was graphically presented by a similarity matrix. To demonstrate the compartmentalization in each community, agglomerative hierarchical clustering (Kaufman and Rousseeuw 2005) was conducted by UPGMA (unweighted pair-group method with arithmetic mean) based on dissimilarities (beta diversities) between 42 samples. The dissimilarity was defined as one minus the abundance-based Jaccard index. The all analyses were performed under the R environment for statistical computing (R Development Core Team 2005), and with its contributed package Vegan (Oksanen et al. 2005).

Results

Seasonal dynamics and species richness

In total, 51742 individuals of 892 Lepidopteran species, and 11633 individuals of 355 Coleopteran species were collected by the 126 trap-night samplings (the original dataset not shown but downloadable from [DIWPA-IBOY \[Forest Ecosystem\] Database: http://diwpa.ecology.kyoto-u.ac.jp/IBOY/LoginForm.aspx](http://diwpa.ecology.kyoto-u.ac.jp/IBOY/LoginForm.aspx)). In both Lepidoptera and Coleoptera, July was the richest in the numbers of species and individuals collected (Fig. 1).

The results of SAC analyses are shown in Fig. 2, separately for Lepidoptera and Coleoptera. The species richness of Lepidoptera was steeply accumulated in the range of smaller sample sizes, but in Coleoptera gradually approached the asymptote. The extrapolated species richness predicted by means of bootstrap estimator was 962.0 ± 15.7 (SE) and 419.2 ± 19.1 (SE) in Lepidoptera and Coleoptera, respectively, implying that 92.7 % of species was sampled for Lepidoptera, but 84.7 % for Coleoptera (Fig. 2).

Relative abundance distribution

In Lepidoptera, the log-Normal RAD model was best fitted (Fig. 3a). In contrast, Zipf-Mandelbrot model was selected as the best model in Coleoptera (Fig. 3b). SAD was less left-truncated in Lepidoptera than in Coleoptera (Fig. 3c, d). Both results from RAD and SAD analyses indicated that the Coleoptera community had more singletons and undetected species compared with the Lepidoptera community.

Spatio-temporal beta diversity

Seasonal compartment structures are clearly represented within both Lepidoptera and Coleoptera communities (Fig. 4). Lepidoptera community markedly demonstrated high similarity of species composition in each month, whereas the similarity among seasons was consistently kept lower (Fig. 4a, c).

1 This notable similarity in each month shows that the species composition of moths having emerged in
2 each month is distinct, and regularly turns over from month to month. The effect of spatial stratification
3 and horizontal heterogeneity on the compositional similarity in Lepidoptera was not observed (Fig. 4a, c).

4 On the other hand, Coleoptera community showed the complicated similarity pattern. In each
5 season of May to June (spring), July to August (summer), and September to October (autumn), the high
6 similarity of species composition was found (Fig. 4b, d). Thus, the Coleoptera community was divided
7 into three seasonal compartments. The Coleopteran species composition in April was similar to that in
8 September and October (Fig. 4b, d). This is due to the emergence of bark beetles (Cryptophagidae) and
9 leaf beetles (Chrysomelidae) in both spring and autumn, implying that they over-winter by adult. Also in
10 Coleoptera, the effect of spatial stratification and horizontal heterogeneity was not discerned.

13 Discussion

14
15 The Coleoptera community contained more number of rare species than the Lepidoptera community (Fig.
16 3). Of 355 Coleopteran species collected, 141 (39.7 %) were singletons and 46 (13.0 %) doubletons,
17 whereas of 892 Lepidopteran species, 133 (14.9 %) were singletons and 74 (8.3 %) doubletons (Fig. 3a,
18 b). This difference was shown in SADs (Fig. 3c, d): the SAD was more left-truncated in Coleoptera than
19 in Lepidoptera, with the mode at the singleton class. SAD displays a strongly right-skewed pattern, if the
20 sampling is insufficient in comparison to the focal community size (Fisher et al. 1943; Preston 1948,
21 1962; Whittaker 1965; Gaston and Blackburn 2000). The bias to higher proportion of rare species can be
22 generated as an artifact due to sampling error (McGill 2003). For example, attractancy of the light traps
23 might be lower for Coleopteran species than for Lepidopteran species. However, in this study, the sample
24 sizes, 51742 individuals of Lepidoptera and 11633 of Coleoptera, were much larger than those in
25 previous studies dealing with the shape of RAD or SAD for invertebrates (cf. Williamson and Gaston
26 2005). Moreover, because a large proportion of species in the potential species pool has been sampled in
27 this study (92.7 % in Lepidoptera and 84.7 % in Coleoptera; Fig. 2), sampling error would be less likely,
28 if not ruled out, to cause the differences in the proportion of rare species between Lepidoptera and
29 Coleoptera communities.

1 The compositional dissimilarity stemmed from stratification between canopy and forest floor or the
2 horizontal heterogeneity among trap sites was found in neither Lepidoptera nor Coleoptera (Fig. 4),
3 although such spatial heterogeneity of species composition was observed in many insect communities
4 living on foliage (Stork et al. 2001; Murakami et al. 2005). Because light trap attracts flying insects from
5 a relatively wide range, species turnover would be difficult to be detected in space at such scales as within
6 the 1 ha survey plot or about 15 to 17 m between the forest floor and the canopy. On the other hand,
7 temporal pattern of species turnover was obvious in the two communities. Based on the seasonal
8 variability of species composition, the Lepidoptera community was partitioned into distinct seven
9 assemblages (Fig. 4), whereas the Coleoptera community was compartmentalized into three assemblages.
10 The seasonally finer compartmentalization in the Lepidoptera community suggests that Lepidoptera
11 adults have shorter life spans, and that species composition turns over every month. On the other hand,
12 the three compartments in Coleoptera community are relatively loose and complicated, probably due to
13 longer adult life spans in Coleoptera than in Lepidoptera.

14 The higher proportion of rare species in Coleoptera community than in Lepidoptera community can
15 also be attributed to the difference in life history between Coleoptera and Lepidoptera. Novotny and
16 Basset (2000) revealed that the number of rare species was inflated by a constant influx of immigrants
17 from the other habitats, namely "mass effect" (cf. Shmida and Wilson 1985). They also suggest that the
18 excess of rare species due to the mass effect would counterintuitively decrease beta diversity. Recent
19 demographic models also predict that the inflation of rare species is facilitated by the increasing rate of
20 dispersal among habitat patches (Solé et al. 2002; Mouquet and Loreau 2003). These models explain that
21 differences in species composition result from spatially limited dispersal of species.

22 Arguments on the mass effect have been directed to the spatial migration. In this study, however,
23 the temporal (seasonal) pattern of changes in species composition was clear in both Coleoptera and
24 Lepidoptera communities, and the difference in seasonal compartmentalization between the two
25 communities would suggest the source of rare species. The relationship between the proportion of rare
26 species and the seasonal turnover of species composition can be explained by analogy with arguments on
27 spatial mass effect. Our observation that Coleoptera community contained more rare species and showed
28 lower seasonal beta diversity, but that Lepidoptera contained less rare species and exhibited higher
29 seasonal beta diversity suggests some temporally working mass effect. Here, suppose that life span acts as

1 a temporal agent for mass effect on the analogy of immigration rate as a spatial agent for mass effect. The
2 lower seasonal discontinuity, namely the lower seasonal beta diversity, in Coleoptera community should
3 represent longer adult life spans of Coleoptera compared with those of Lepidoptera. In turn, the longer
4 life spans would enhance the proportion of rare species in the community. Such a linkage between the
5 species rarity and the temporal compartmentalization of community as suggested by the present study
6 should be examined in other taxonomic communities, at other geographic locations, and on other scales
7 for its validity.

8 Our exploration on species rarity and beta diversity in the two insect communities provides some
9 suggestive information for future research. From the definition, beta diversity certainly relies on
10 spatio-temporal scales for resolution of community structure. We need to specify the cause for beta
11 diversity on the concerned scale and evaluate contribution of rare species to beta diversity. Additive
12 partitioning approach (e.g., Gering and Crist 2002; Veech et al. 2002; Crist et al. 2003) for analyzing
13 species diversity may afford new insights into the source of rare species. Relative contributions of rare
14 species to alpha, beta and gamma diversities and their roles in a focal ecosystem are challenging subjects
15 to be examined. Furthermore, since DIWPA-IBOY biodiversity inventories range from the taiga of
16 eastern Siberia, across tropical rain forests, to the temperate forests of eastern Australia, comparison of
17 the communities along this latitudinal transect will offer an opportunity to study geographic variation in
18 species rarity and macroecological patterns of species turnover.

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22
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Figure legends

Fig. 1 Seasonal dynamics of species richness and abundance in Lepidoptera (a, c) and Coleoptera (b, d) communities.

Fig. 2 Species accumulation curves (SAC) in Lepidoptera and Coleoptera communities, estimated by permutation on the basis of one trap-night sample as the unit. Standard deviations of SAC are denoted as vertical lines. Horizontal lines indicate the richness of potential species pools extrapolated by means of bootstrap estimator.

Fig. 3 Relative abundance distribution (RAD) and species abundance distribution (SAD) on doubling octaves of abundance in Lepidoptera (a, c) and Coleoptera (b, d) communities. In RAD, solid line represents the fitted log-Normal model, broken line the Zipf-Mandelbrot model, and dotted line the Zipf model, and of them the selected best model is shown with bold line. In SAD, fitted truncate log-Normal model is shown with solid line, with indication of the mode by vertical line and the standard deviation by horizontal line.

Fig. 4 Spatio-temporal similarity matrices and compartment structures in Lepidoptera (a, c) and Coleoptera (b, d) communities. The similarity matrix comprises gray-scaled cells representing species-composition similarities between 42 samples (seven months [from April to November] $\times$ two strata [C: canopy, G: ground] $\times$ three trap sites [1, 2, and 3], pooling the three trap-nights data for each trap): the gray-scale ranges from black (the maximum similarity = 1) to white (the least similarity = 0). The compartment structure was deduced from UPGMA. Path-length distance indicates species-composition dissimilarity.

1 Fig. 1

1 Fig. 2

1 Fig. 3

1 Fig. 4

2