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1   **International Biodiversity Observation Year in Western-Pacific and Asian Region**

2   **(DIWPA-IBOY): A case report on species rarity and spatio-temporal variability of**

3   **species composition in Lepidoptera and Coleoptera communities from a temperate**

4   **forest of northern Japan**

5

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2

1 **Abstract**

2 An international project, DIWPA-IBOY, took place for simultaneously observing biodiversity throughout

3 the Western-Pacific and Asian Region in 2001 to 2003, as one of core projects for International

4 Biodiversity Observation Year, a crosscutting network activity of DIVERSITAS (An International

5 Programme of Biodiversity Science). DIWPA-IBOY provides extensive data on species diversity

6 obtained by the standardized method. Under this project, 51742 individuals of Lepidoptera and 11633 of

7 Coleoptera were collected by light traps from Tomakomai Experimental Forest of Hokkaido University,

8 one of core DIWPA-IBOY sites, in the cool-temperate region of northern Japan. Based on these data, this

9 study examined the relative abundance distribution (RAD) to evaluate the amount of rare species in

10 Lepidoptera and Coleoptera communities. The beta diversities between sampling seasons, forest strata

11 and trap sites were also assessed to evaluate the spatio-temporal variability of species composition in

12 these communities. In the analysis of RAD, the best-fit model was selected from the log-Normal,

13 Zipf-Mandelbrot and Zipf models differing in the tail length of RAD, i.e., the proportion of rare species.

14 To explore the beta diversity between samples, the abundance-based Jaccard index with unseen species

15 estimator was calculated, and then a hierarchical clustering analysis was conducted. As a result of RAD

16 analysis, the Coleoptera community was regarded as containing a larger proportion of rare species than

17 the Lepidoptera community. The seasonal compartmentalization of community, deduced from the

18 beta-diversity analysis, was finer in Lepidoptera (seven assemblages recognized) than in Coleoptera

19 (three assemblages). The spatial (vertical and horizontal) compartmentalization was negligible in both

20 communities. The coincidence of the larger proportion of rare species and the lower beta diversity

21 between seasons in the Coleoptera community was explained by the longer life spans of beetles compared

22 to moths, based on the assumption that the length of life span acts as a temporal agent for mass effect on

23 the analogy of the migration rate as a spatial agent for mass effect.

24

25 **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

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

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

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

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

1   Gaston 2005). DIWPA-IBOY would provide relatively less biased data, at least comparable across sites,

2   based on the standardized sampling methods (Nakashizuka and Stork 2002).

3   In this paper, the structures of Lepidoptera and Coleoptera communities are examined with special

4   reference to the species rarity and the beta diversity, using samples collected by light traps from a

5   temperate forest of northern Japan in DIWPA-IBOY. In order to assess the community structure in detail,

6   first the seasonal dynamics of species richness and abundance is addressed for each community. Then the

7   species rarity in each community is examined by the analyses of RAD and SAD. The beta diversity as

8   variability of species composition between samples is used to demonstrate the spatio-temporal

9   compartmentalization of each community. Finally, the relationships between the species rarity and the

10   beta diversity are discussed by comparing the features of Lepidoptera and Coleoptera communities. This

11   case report from one of core sites in DIWPA-IBOY will facilitate the comparison of community structure

12   across sites along the nearly global, latitudinal transect of forest ecosystems, which is one of goals aimed

13   in DIWPA-IBOY, based on the unprecedented data obtained by standardized methods from the very wide

14   range.

15

16

17   **Methods**

18

19   Study site

20

21   The samplings were carried out in a temperate deciduous forest of Tomakomai Experimental Forest

22   (TOEF; 42°43' N, 141°36' E, ca. 90 m a.s.l.), Hokkaido, Japan. TOEF is one of the core research sites for

23   DIWPA-IBOY (cf. URL: http://diwpa.ecology.kyoto-u.ac.jp/iboy.htm). This cool-temperate forest

24   receives 1,161 mm of annual precipitation and experiences an average annual temperature of 5.6 °C. Oak

25   (*Quercus crispula*), maple (*Acer mono*) and linden (*Tilia japonica*) dominate the forest. The canopy

26   ranges from 15 to 25 m in height, saplings of the dominant tree species growing on the forest floor.

27   Deciduous trees break buds in early to mid May, and shed their leaves in late October.

28

29   Light trap sampling

6

1

2 The whole sampling procedure followed the IBOY manual (Nakashizuka and Stork 2002). Three sets of

3 two traps, one at the ground level (1 m from the ground level) and the other in the canopy at the height of

4 15.8, 16.3 and 17.1 m from the ground level, were operated simultaneously at three randomly determined

5 points within a square one-hectare plot (100 m × 100 m), where the tree species composition was

6 relatively uniform. Trapping was repeated at monthly intervals from March to November 2001. Traps

7 were run for three nights on each monthly sampling event, avoiding the week around the full moon. They

8 were emptied daily for the trapping period. Thus, in total, 126 samples (seven months × two strata × three

9 locations × three days) were collected in this study. Traps run from about 5.00 p.m. throughout the night.

10 The catches were first sorted at the order level, and then the specimens of Lepidoptera and Coleoptera

11 were identified to species and counted by taxonomic experts, H. Kogi and A. Kashizaki, respectively.

12

13 Statistical analysis

14

15 To estimate the total species richness, the mean species accumulation curve (SAC) with its standard

16 deviation was calculated by random permutations (1000 times) of 126 samples, one trap-night sample

17 being the unit for permutation (Gotelli and Colwell 2001). The extrapolated species richness in the

18 species pool was reckoned by estimating the number of the undetected species and adding it to the

19 observed species richness (Colwell and Coddington 1994). The bootstrap estimate and its standard error

20 (Smith and van Belle 1984) were calculated to reckon the potential species pool.

21   The relative abundance distributions in Lepidoptera and Coleoptera were fitted to three statistical

22 models with maximum likelihood method. Log-Normal model, Zipf model and Zipf-Mandelbrot model

23 were examined. The log-Normal model assumes that the logarithmic abundances follow the Normal

24 distribution (Preston 1948, 1962). The Zipf model can be regarded as power law, and is denoted as

25 follows:

26

27 $f(x) = c \cdot x^a,$

28

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

1   modified from Zipf model by adding a parameter b, giving the following formula (Mandelbrot 1982;

2   Frontier 1985):

3

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

5

6   The Zipf model has the longest tail corresponding to rare species among the three models. The tail of

7   log-Normal model is the shortest. The best-fitted model was selected according to Akaike's information

8   criterion (AIC).

9   The numbers of species were plotted to abundance classes representing Preston's octaves at the

10   base of 2, and then the left-truncated Normal distribution of the Preston model (Preston 1948, 1962) was

11   fitted to observed frequencies of species with maximum likelihood method. The expected frequency $f(x)$

12   at abundance octave x is defined as follows:

13

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

15

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

17   at the mode.

18   In evaluation of beta diversity between samples, the daily variability was ignored by summing up

19   three-night samples at a given trap in each month. This resulted in a total of 42 samples (seven seasons ×

20   two strata × three sites) of which species compositions were compared. The spatio-temporal variability of

21   species composition was measured by means of abundance-based Jaccard index with estimator for the

22   effect of unseen shared species proposed by Chao et al. (2005), and then was graphically presented by a

23   similarity matrix. To demonstrate the compartmentalization in each community, agglomerative

24   hierarchical clustering (Kaufman and Rousseeuw 2005) was conducted by UPGMA (unweighted

25   pair-group method with arithmetic mean) based on dissimilarities (beta diversities) between 42 samples.

26   The dissimilarity was defined as one minus the abundance-based Jaccard index. The all analyses were

27   performed under the R environment for statistical computing (R Development Core Team 2005), and

28   with its contributed package Vegan (Oksanen et al. 2005).

29

1

2 **Results**

3

4 Seasonal dynamics and species richness

5

6 In total, 51742 individuals of 892 Lepidopteran species, and 11633 individuals of 355 Coleopteran

7 species were collected by the 126 trap-night samplings (the original dataset not shown but downloadable

8 from DIWPA-IBOY [Forest Ecosystem] Database:

9 http://diwpa.ecology.kyoto-u.ac.jp/IBOY/LoginForm.aspx). In both Lepidoptera and Coleoptera, July was

10 the richest in the numbers of species and individuals collected (Fig. 1).

11 The results of SAC analyses are shown in Fig. 2, separately for Lepidoptera and Coleoptera. The

12 species richness of Lepidoptera was steeply accumulated in the range of smaller sample sizes, but in

13 Coleoptera gradually approached the asymptote. The extrapolated species richness predicted by means of

14 bootstrap estimator was 962.0 ± 15.7 (SE) and 419.2 ± 19.1 (SE) in Lepidoptera and Coleoptera,

15 respectively, implying that 92.7 % of species was sampled for Lepidoptera, but 84.7 % for Coleoptera

16 (Fig. 2).

17

18 Relative abundance distribution

19

20 In Lepidoptera, the log-Normal RAD model was best fitted (Fig. 3a). In contrast, Zipf-Mandelbrot model

21 was selected as the best model in Coleoptera (Fig. 3b). SAD was less left-truncated in Lepidoptera than in

22 Coleoptera (Fig. 3c, d). Both results from RAD and SAD analyses indicated that the Coleoptera

23 community had more singletons and undetected species compared with the Lepidoptera community.

24

25 Spatio-temporal beta diversity

26

27 Seasonal compartment structures are clearly represented within both Lepidoptera and Coleoptera

28 communities (Fig. 4). Lepidoptera community markedly demonstrated high similarity of species

29 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.

11

12

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

11

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

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

Acknowledgements

1 **References**

2

3 Blackburn TM, Gaston KJ (2003) Macroecology: concepts and consequences. Cambridge University

4   Press, Cambridge

5 Chao A, Chazdon RL, Colwell RK, Shen TJ (2005) A new statistical approach for assessing similarity of

6   species composition with incidence and abundance data. Ecol Lett 8:148-159

7 Colwell RK, Coddington JA (1994) Estimating terrestrial biodiversity through extrapolation. Philos Trans

8   R Soc Lond Biol 345:101-118

9 Condit R, Pitman N, Leigh EG, Chave J, Terborgh J, Foster RB, Nunez P, Aguilar S, Valencia R, Villa G,

10   Muller-Landau HC, Losos E, Hubbell SP (2002) Beta-diversity in tropical forest trees. Science

11   295:666-669

12 Connolly SR, Hughes TP, Bellwood DR, Karlson RH (2005) Community structure of corals and reef

13   fishes at multiple scales. Science 309:1363-1365

14 Crist TO, Veech JA, Gering JC, Summerville KS (2003) Partitioning species diversity across landscapes

15   and regions: A hierarchical analysis of alpha, beta, and gamma diversity. Am Nat 162:734-743

16 Fisher AG, Corbet SA, Williams SA (1943) The relation between the number of species and the number

17   of individuals in a random sample of an animal population. J Anim Ecol 12:42-58

18 Frontier S (1985) Diversity and structure in aquatic ecosystems. Oceanogr Mar Biol 23:253-312

19 Gaston KJ (1994) Rarity. Chapman & Hall, London

20 Gaston KJ, Blackburn TM (2000) Pattern and process in macroecology. Blackwell Science, Oxford

21 Gering JC, Crist TO (2002) The alpha-beta-regional relationship: providing new insights into

22   local-regional patterns of species richness and scale dependence of diversity components. Ecol

23   Lett 5:433-444

24 Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and

25   comparison of species richness. Ecol Lett 4:379-391

26 Hubbell SP (2001) The unified neutral theory of biogeography and biodiversity. Princeton University

27   Press, Princeton

28 Kaufman L, Rousseeuw PJ (2005) Finding groups in data: an introduction to cluster analysis. Wiley, New

29   York

1   Koleff P, Gaston KJ, Lennon JJ (2003) Measuring beta diversity for presence-absence data. J Anim Ecol

2   72:367-382

3   Kunin WK, Gaston KJ (1996) The biology of rarity: causes and consequences of rare-common

4   differences. Chapman & Hall, London

5   Lande R (1996) Statistics and partitioning of species diversity, and similarity among multiple

6   communities. Oikos 76:5-13

7   Latimer AM, Silander JA, Cowling RM (2005) Neutral ecological theory reveals isolation and rapid

8   speciation in a biodiversity hot spot. Science 309:1722-1725

9   Legendre P, Borcard D, Peres-Neto PR (2005) Analyzing beta diversity: Partitioning the spatial variation

10   of community composition data. Ecol Monogr 75:435-450

11   Mandelbrot BB (1982) Fractal geometry of nature. W. H. Freeman, San Francisco

12   McGill BJ (2003) Does Mother Nature really prefer rare species or are log-left-skewed SADs a sampling

13   artefact? Ecol Lett 6:766-773

14   Mouquet N, Loreau M (2003) Community patterns in source-sink metacommunities. Am Nat

15   162:544-557

16   Murakami M, Yoshida K, Hara H, Toda MJ (2005) Spatio-temporal variation in Lepidopteran larval

17   assemblages associated with oak, *Quercus crispula*: the importance of leaf quality. Ecol Entomol

18   30:521-531

19   Nakashizuka T, Stork N (2002) Biodiversity research methods: IBOY in Western Pacific and Asia. Kyoto

20   University Press, Kyoto & Trans Pacific Press, Melbourne

21   Novotny V, Basset Y (2000) Rare species in communities of tropical insect herbivores: pondering the

22   mystery of singletons. Oikos 89:564-572

23   Novotny V, Weiblen GD (2005) From communities to continents: beta diversity of herbivorous insects.

24   Ann Zool Fenn 42:463-475

25   Oksanen J, Kindt R, O'Hara RB (2005) Vegan: Community Ecology Package version 1.6-10.

26   Plotkin JB, Muller-Landau HC (2002) Sampling the species composition of a landscape. Ecology

27   83:3344-3356

28   Preston FW (1948) The commonness and rarity of species. Ecology 29:254-283

29   Preston FW (1962) The canonical distribution of commonness and rarity, Part 1 and 2. Ecology

1   43:182-215, 410-432

2   R Development Core Team (2005) A language and environment for statistical computing. R Foundation

3   for Statistical Computing, Vienna, Austria

4   Shmida A, Wilson MR (1985) Biological determinants of species diverity. J Biogeogr 12:1-20

5   Smith EP, van Belle G (1984) Nonparametric-estimation of species richness. Biometrics 40:119-129

6   Solé RV, Alonso D, McKane A (2002) Self-organized instability in complex ecosystems. Philos Trans R

7   Soc Lond Biol 357:667-681

8   Stork NE, Hammond PM, Russell BL, Hadwen WL (2001) The spatial distribution of beetles within the

9   canopies of oak trees in Richmond Park, UK. Ecol Entomol 26:302-311

10   Tokeshi M (1993) Species abundance patterns and community structure. Adv Ecol Res 24:111-186

11   Tokeshi M (1999) Species coexistence. Blackwell, Oxford

12   Tuomisto H, Ruokolainen K, Yli-Halla M (2003) Dispersal, environment, and floristic variation of

13   western Amazonian forests. Science 299:241-244

14   Veech JA, Summerville KS, Crist TO, Gering JC (2002) The additive partitioning of species diversity:

15   recent revival of an old idea. Oikos 99:3-9

16   Whittaker RH (1965) Dominance and diversity in land plant communities. Science 147:250-260

17   Williamson M, Gaston KJ (2005) The lognormal distribution is not an appropriate null hypothesis for the

18   species-abundance distribution. J Anim Ecol 74:409-422

19   Zipf GK (1966) Human behaviour and the principle of least effort. Hafner, New York

Figure legends

2

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

4 communities.

5

6 Fig. 2 Species accumulation curves (SAC) in Lepidoptera and Coleoptera communities, estimated by

7 permutation on the basis of one trap-night sample as the unit. Standard deviations of SAC are denoted as

8 vertical lines. Horizontal lines indicate the richness of potential species pools extrapolated by means of
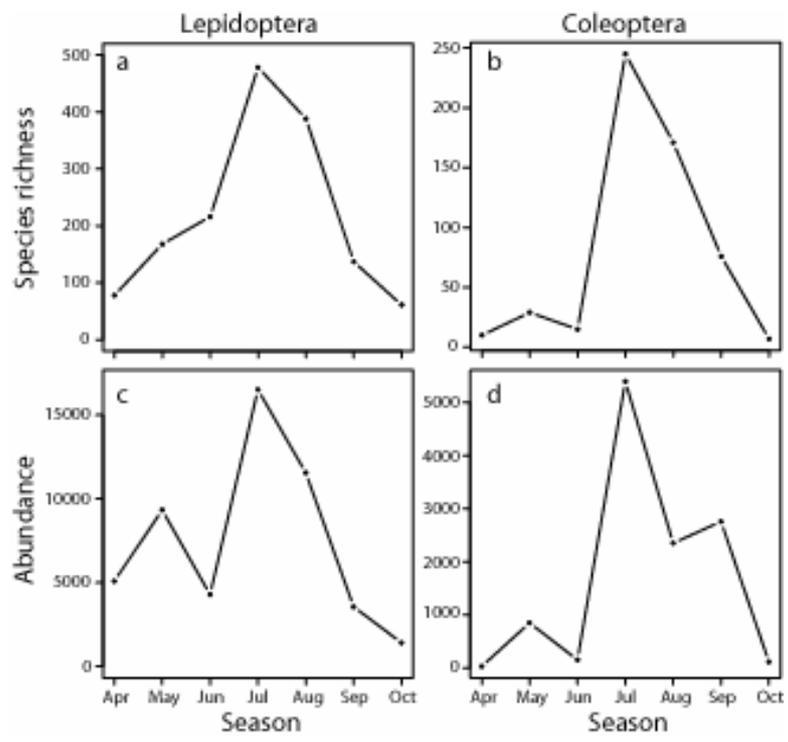
9 bootstrap estimator.

10

11 Fig. 3 Relative abundance distribution (RAD) and species abundance distribution (SAD) on doubling

12 octaves of abundance in Lepidoptera (a, c) and Coleoptera (b, d) communities. In RAD, solid line

13 represents the fitted log-Normal model, broken line the Zipf-Mandelbrot model, and dotted line the Zipf

14 model, and of them the selected best model is shown with bold line. In SAD, fitted truncate log-Normal

15 model is shown with solid line, with indication of the mode by vertical line and the standard deviation by
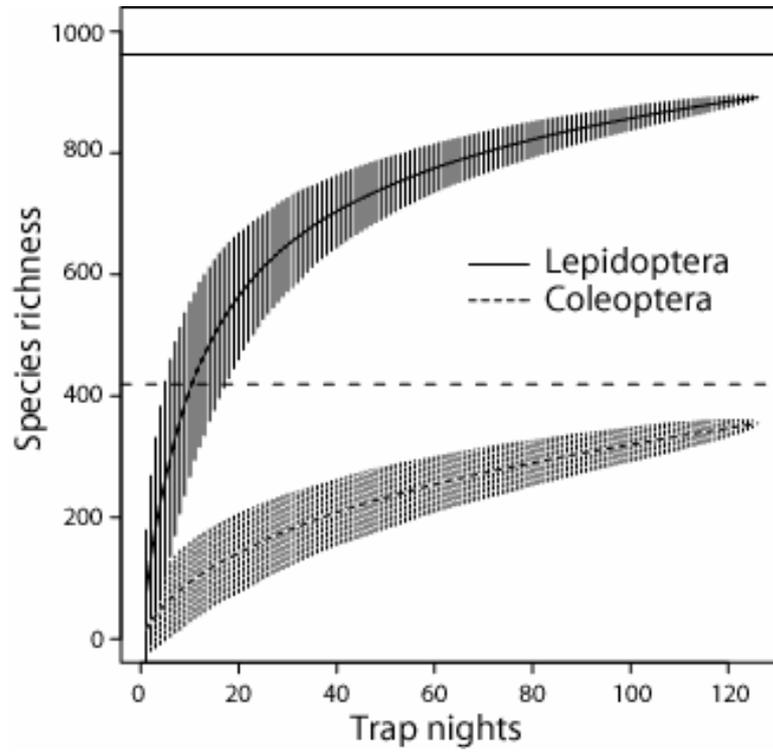
16 horizontal line.

17

18 Fig. 4 Spatio-temporal similarity matrices and compartment structures in Lepidoptera (a, c) and

19 Coleoptera (b, d) communities. The similarity matrix comprises gray-scaled cells representing

20 species-composition similarities between 42 samples (seven months [from April to November] × two

21 strata [C: canopy, G: ground] × three trap sites [1, 2, and 3], pooling the three trap-nights data for each

22 trap): the gray-scale ranges from black (the maximum similarity = 1) to white (the least similarity = 0).

23 The compartment structure was deduced from UPGMA. Path-length distance indicates
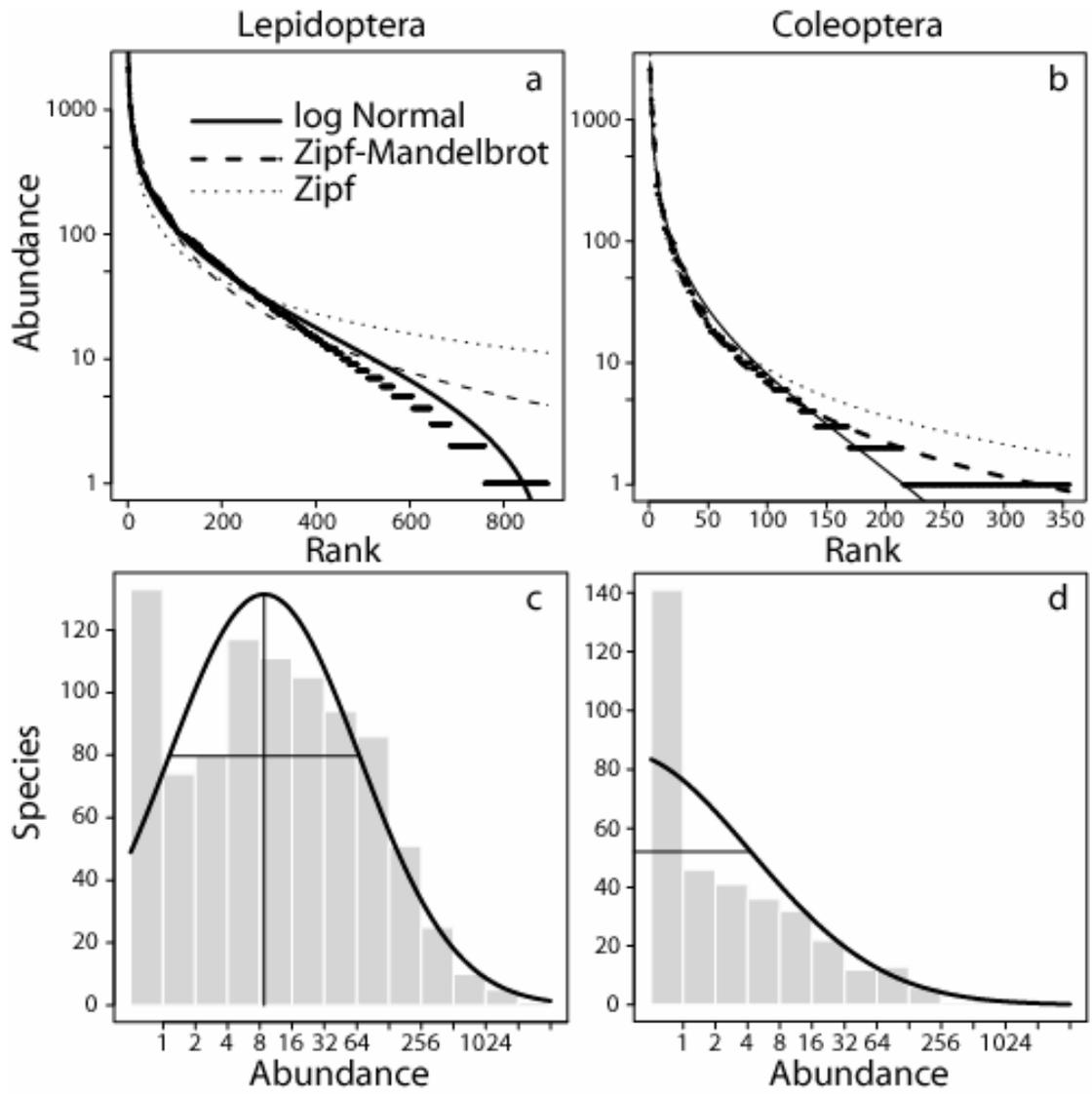
24 species-composition dissimilarity.

1   Fig. 1

1   Fig. 2

1   Fig. 3

1   Fig. 4

2