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Structure and diversity of drosophilid communities in special relation to the three-dimensional structure of forest

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This paper reviews previous works on the vertical distributions of drosophilid flies in various forests ranging from the tropics to the subarctic region, especially along the Asian Green Belt, and addresses relationships between forest structure and drosophilid diversity on various spatial scales from the global to forest-stand ones, based on the data obtained by comparable, standardized collecting methods. The structure-diversity relationships show that on any spatial scales, more complex foliage structure contributes to the higher beta diversity along the vertical dimension and in consequence to higher species diversity in the whole community. Thus, the spatial habitat heterogeneity should be an important factor responsible for global to local variations in drosophilid species diversity. In forests with continuous, closed canopy, the vertical foliage structure defines the physical template of habitats, where inhabitant organisms actually interact with each other under various physical environments, and as a consequence determines the species diversity in inhabitant communities.

1. Introduction

Although there is much controversy for the magnitude of animal species richness on the earth (e.g., Gaston, 1991; Erwin, 1991), many researchers agree that a large part of animal diversity is due to species richness of arthropods, especially associated with the forest canopy in tropical rain forests (Erwin, 1983; Stork, 1988; Wilson, 1988). However, the forest canopy is still a less explored world on the earth. To reveal the great variety of life forms harbored there has been one of major challenges in ecology and biodiversity sciences.

In forest ecosystems, trees as skeleton organisms display leaves three-dimensionally in the aboveground space and construct complex structures in consequence of competition and niche separation for light. In general, the physical environments under the closed canopy are vertically heterogeneous but horizontally relatively homogeneous, resulting in a strato- or gradient-like pattern of physical environments. The stratified distribution of organisms living in such three-dimensional, vertically-structured forest spaces has been so widely documented as a ubiquitous pattern from boreal to tropical rain forests, in various kinds of organisms such as arthropods (Davidson, 1930; Fichter, 1939; Adams, 1941; Bates, 1944; Turnbull, 1960; Nielsen and Ejlersen, 1977; Sutton and Hudson, 1980; Sutton et al., 1983; Moeed and Meads, 1984; Brown et al., 1997; Davis et al., 1997), birds (Colquhoun and Morely, 1943; Stokes and Schultz, 1995), reptiles (Reagan, 1995), and mammals (Harrison, 1962; Francis, 1994; Whitmore, 1998; Bernard, 2001). The habitat heterogeneity hypothesis predicts a positive correlation between habitat complexity and species diversity: the greater the complexity of a habitat, the more the number of species that can co-exist in that habitat (Klopher and MacArthur, 1960; Pianka, 1966). This hypothesis has been tested to explain not only the latitudinal clines of species diversity on the global scale but also between-habitat

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differences on the local scale (see Tews et al., 2004, for review). Apparently, the ability for forests to harbor diverse animal species is not equivalent spatially on global (e.g., tropics vs. other regions), local (e.g., structurally complex vs. simple forests), and even microhabitat (e.g., the canopy vs. other strata) scales. This paper addresses various spatial patterns of diversity in a particular group of insects, drosophilid flies, which are strongly associated with forests in their lives and are commonly distributed across various kinds of forests from the tropics to the subarctic region.

With respect to the vertical distribution of drosophilid flies within forests, since a pioneer work by Basden (1953), only a few, fragmental reports have been published from Europe (Greuter, 1963; Shorrocks, 1975; Lumme et al., 1979), North America (Toda, 1985a), South America (Tidon-Sklorz and Sene, 1992) and Australia (van Klinken and Walter, 2001). In Asia, exceptionally, very intensive and extensive surveys on this subject have been conducted by the nearly identical method of sampling in various forests at many localities ranging from Southeast Asia to East Siberia (Toda, 1977b, 1984, 1985b, 1987, 1992; Beppu, 1980, 1984, 1985, 2006; Kwon and Toda, 1981; Toda and Fukuda, 1985; Toda et al., 1987; Tanabe et al., 2001; Tanabe, 2002; Ishii et al., 2004; Toda, unpublished data).

2. Spatial structure of drosophilid communities in cool-temperate forests

The vertical distributions of drosophilid flies were intensively studied in various cool-temperate forests of northern Japan, by setting specially-designed (for automatically retaining trapped flies into a bottle with fixative solution) traps, Toda's Trap II (Toda, 1977a) baited with fermented banana, vertically from the ground to the canopy. Toda (1977b) first recognized five patterns of vertical distribution among component species of a drosophilid community in a natural, broad-leaved forest, and divided the forest drosophilid community into two subcommunities, the understory and the canopy ones. The two subcommunities were different from each other in the taxonomic and the feeding-guild compositions of component species: the understory subcommunity was characterized by the *Drosophila quinaria* species group and composed mainly of herbage feeders and fungus feeders, while the canopy subcommunity included a number of species of steganine genera *Amiota* Loew, *Phortica* Schiner (cited as *Amiota* in Toda, 1977b) and *Leucophenga* Mik and of typical tree-sap feeders such as the *Drosophila obscura* species group. Toda (1987) further divided each subcommunity into two subassociations: the understory subcommunity into the herbage-layer subassociation and the shrub-layer one, and the canopy subcommunity into the lower subassociation distributed from the subarboreal to the lower canopy layer and the upper one restricted to the canopy layer. This vertically stratified structure of forest drosophilid community is relatively constant throughout the season (Toda, 1977b, 1987), and across natural forests at various localities (Toda, 1977b, 1984, 1987; Beppu, 1980; Toda, unpublished data), though being somewhat obscured in secondary forests with smaller aboveground space (Toda, 1987; Tanabe, 2002).

Toda (1987, 1992) investigated horizontal aspects in the three-dimensional structure of forest drosophilid community by covering the forest edge and/or gaps in study sites, and revealed that the living space of canopy subcommunity was remarkably lowered to the level of herbage layer at the forest edge but, on the other hand, that the understory subcommunity retreated interiorly from the forest edge. Moreover, Toda (1992) estimated, based on behavioral responses (i.e., the degree of vertical habitat segregation) of drosophilid flies to the vegetation structure, the subjective habitat patchiness or 'ecological neighbourhood' influential to the three-dimensional distribution of a forest drosophilid community to be on the scale of 110–450 m^2, corresponding well with the most prevalent size of canopy gaps occurring in various forests. Tanabe (2002) quantified the degree of stratification, i.e., the horizontal constancy of vertical distribution pattern, in each component species by observing their distributions at replicate plots within each study site of four forests with markedly different vertical foliage structures. Comparing the values among species and among forests, he found a tendency that feeding-specialist species depending on a particular food substrate, for example tree sap, showed highly predictable patterns of vertical stratification, while genelarist species showed non-stratified and/or highly variable patterns of vertical distribution.

As schematically shown in Fig. 1, the living space

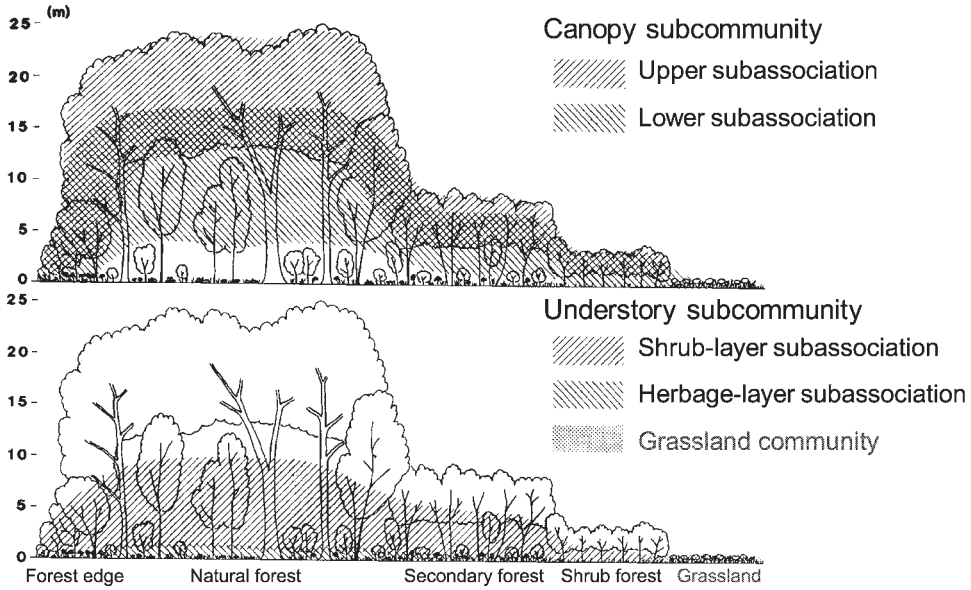

Figure 1 : Spatial structure of a drosophilid community in cool-temperate forests of northern Japan. [Reproduced with partial modification from Toda (1987) under the permission from Tokai University Press.]

of a forest drosophilid community is largely divided into two layers, the outer foliage layer (the canopy plus the edge) and the inner understory layer. This habitat stratification corresponds to the separation between production space and decomposition space in a forest ecosystem, probably reflecting the difference in food substances provided to drosophilid flies there. In addition to the primary separation between the underground and the aboveground forest ecosystems, this compartmentalization of the aboveground space should be fundamental for all organisms living there, as Richards (1983) argued, "More important than the stratification of the trees is the boundary between the euphotic zone in which the crowns are more or less fully exposed to sunlight (the 'canopy'), and the shaded oligophotic zone (the 'undergrowth') beneath."

3. Latitudinal cline

The gradient of species richness increasing from the poles to the equator is the most widely recognized pattern on the global scale. Such latitudinal gradients in species richness occur in diverse ecosystems such as open oceans, coasts, forests, deserts, rivers, lakes, etc. However, most of evidence for such clines is based on records of species in local fauna and/or flora across latitudes. If we want to evaluate the biodiversity, taking relative abundances of component species into account, across any transects, we need data taken quantitatively by standardized methods. There may be, however, very few such data for latitudinal clines of animal diversity. Nearly infinite numbers of surveys and samplings must have been conducted for animal diversity all over the world, but only few data may be comparable across localities because of differences in methods. Even slight differences in the design of sampling devices or in survey intensity bring about method-specific biases in samples and/or data. Here, latitudinal patterns of some biodiversity properties in drosophilid communities are presented, based on comparable data obtained by the completely standardized method across a wide range of latitudes from the equator to the subarctic region.

As reviewed in Section 2, drosophilid species segregate their microhabitats from each other in the aboveground space from the ground to the forest canopy. It is, then, expected that their biodiversity is much affected by the forest structure, especially the foliage stratification, which becomes simpler toward high latitudes. Fig. 2 shows results of a transect study on vertical distributions of drosophilid flies along the Asian Green Belt from a tropical rain forest in Sumatra to a boreal forest in East Siberia and even to a subarctic forest near the northern limit of timber line in the Mackenzie delta of Canada. Sampling procedures were standardized, setting the same banana traps (Toda's Trap II) vertically from the ground to the canopy (Toda and Kitching, 2002), although the number of traps varied among localities according to the heights of studied forests. The diversity of each local drosophilid community was evaluated by three measures, the species richness *S*,

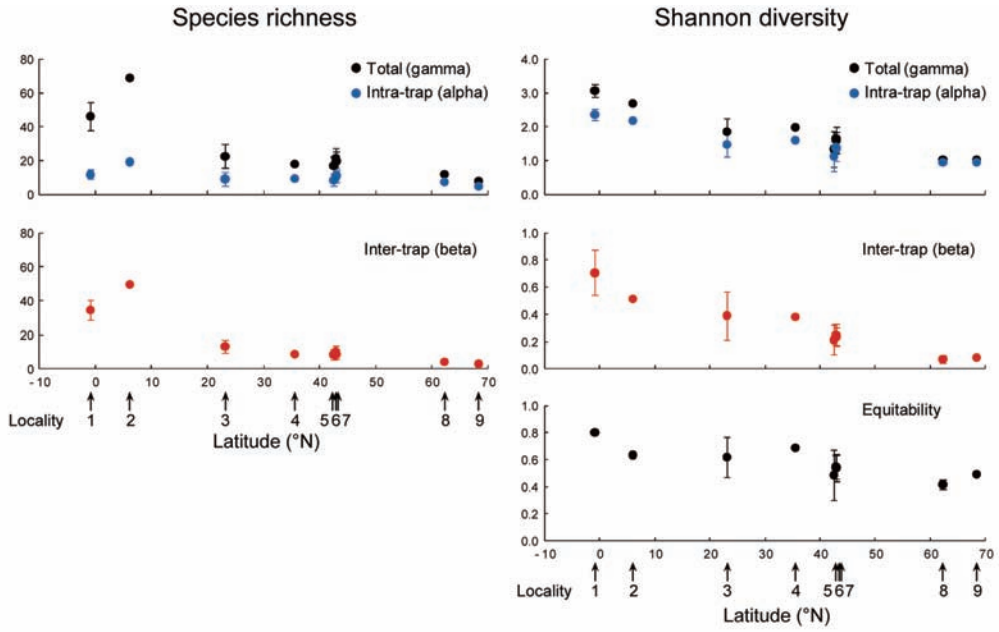

Figure 2 : Latitudinal clines of species richness, Shannon diversity (H') and equitability (Pielou's J') in forest drosophilid communities; for the first two measures, the total (gamma) diversity was partitioned into the intra-trap (alpha) and the inter-trap (beta) diversities. The mean and standard deviation (error bar) were calculated for weekly samples. Localities (latitude, the number of traps, the height of top trap, the number of weekly samples): 1) Padan, Sumatra, Indonesia (53' S, 10, 45 m, 3); 2) Poring, Sabah, Malaysia (6°5' N, 10, 40 m, 1); 3) Dinghushan, Guangdong, China (23°8' N, 7, 26 m, 35); 4) Ashiu, Kyoto Pref., Japan (35°30' N, 5, 15.7 m, 1); 5) Tomakomai, Hokkaido, Japan (42°30' N, 6, 13 m, 15); 6) Koryukozan, Hokkaido, Japan (42°51' N, 5, 16.5 m, 8); 7) Misumai, Hokkaido, Japan (42°57' N, 5, 14 m, 9); 8) Spaskayapad, Yakutia, Russia (62°14' N, 4, 10 m, 4), 9) Inuvik, Northwest Territories, Canada (68°22' N, 4, 10.5 m, 1).

the Shannon H' index and the equitability of Pielou's J':

$$H' = -\sum(n_i/N)\ln(n_i/N) \quad (1)$$

$$J' = H'/\ln S \quad (2)$$

where N is the total number of individuals, and n_i is the number of individuals of species i. In addition, for the first two measures, the total (gamma) diversity was partitioned into the intra-trap (alpha) and the inter-trap (beta) diversities along the vertical dimension of forest structure, according to the concept of "additive partitioning of species diversity" (Levins, 1968; Tanabe et al., 2001; Veech et al., 2002). Gamma diversity was based on summed data for all traps in each plot. Alpha diversity was estimated as the average of species richness or as the weighted (by the sample size) average of Shannon diversity calculated for each trap. Beta diversity caused by sample compositional differences among traps was calculated as the difference between the gamma and the alpha diversities (= gamma − alpha). The sampling frequency (sampling was repeated usually at weekly intervals) varied among localities, due to opportunity and conditions of field research: sampling was carried out nealy throughout the seasons at a few localities, but only once or twice at some localities. Therefore, the above diversity measures were presented as the means for weekly samples, with the standard deviations to show the seasonal variations in the cases of long-term sampling.

All the diversity measures, except for the intra-trap (alpha) species richness that was nearly constant across the latitudinal transect, decreased almost monotonically from the tropical forests to the boreal and subarctic ones. Thus, forest drosophilid communities showed a clear latitudinal cline, increasing southward, of the overall local (gamma) diversity. For the species richness, this cline (of gamma diversity) can be attributed mainly to the southward increasing vertical beta diversity, i.e., the rate of species turnover due to their micorhabitat segregation between strata from the understory to the canopy, which should be promoted by the larger (higher) and more finely stratified aboveground space in forests at lower latitudes. For the Shannon diversity, both alpha and beta diversities contributed to the southward increasing gamma diversity. And, the similarly southward increasing equitability indicates that relative abundances of component species are more balanced with each other in forest drosophilid communities at lower latitudes, probably reflecting the finer-grained niche space there.

4. Tree shape, forest structure and diversity of drosophilid community in boreal and temperate birch forests

Many hypotheses have been proposed to explain latitudinal clines of species diversity on the earth. Rohde (1992) reviewed a number of hypotheses and pointed out the logical circularity in many of them related to biotic factors, including 'biotic spatial heterogeneity' which this paper focuses on. He argued that those hypotheses are based on the assumption of higher diversity of some particular organisms, e.g., trees for the present case, in the tropics. Brown and Gibson (1983) claimed that ultimately, all general patterns of biodiversity must be attributed to physical causes. To explain the latitudinal cline of biodiversity, but only its northern part, in forest drosophilid communities from a bottom-up approach, Tanabe et al. (2001) compared tree shape, foliage structure and diversity of drosophilid community between two birch forests latitudinally about 20° apart from each other: one at Spaskayapad (62°14' N, 129°39' E) in East Siberian boreal region and the other at Nakagawa (44° 50' N, 142°15' E), Hokkaido in cool-temperate region.

Paltridge (1973) and Kuuluvainen (1992) showed theoretically the extreme importance of sun angle, which is determined by latitude, in shaping tree crowns. According to Kuuluvainen's (1992) simulations, latitudinally different light regimes are influential on the efficiency of photosynthesis in trees with different crown shapes; trees with planar crowns are more efficient at lower latitudes, while those with narrowly conical crowns are more efficient at higher latitudes. In reality, white birch (*Betula platyphylla* Sukatchev) trees had different crown shapes between the two surveyed forests; trees in the temperate forest had shallower and more planar crowns than those in the boreal forest (Fig. 3A). This indicates that the theory based on light regimes is applicable to the variation in crown shape of the same species, even within a small latitudinal range.

Based on the latitudinal cline of tree crown shape, Terborgh (1985) proposed a model to explain a latitudinal gradient in the vertical complexity of forest structure. According to his model, in tropical forests shallowly dome-shaped crowns permit sunlight to penetrate the canopy at shallow angles and enable the second foliage layer to develop close to the canopy. This process is potentially repeated, producing the third, fourth or more layers. However, in boreal forests, where trees with narrowly conical crowns are dominant, direct sunlight can pass through the canopy only at deep angles, so that establishment of a subcanopy layer is not possible. The observed difference in vertical complexity of foliage structure between the boreal and temperate birch forests supported Terborgh's (1985) theory. The temperate forest was more complex in the vertical foliage structure than the boreal forest; the former was characterized by the clearly two-layered foliage profile with the larger foliage height diversity (*FHD*) measured by the Shannon index, whereas the latter profile was less stratified, being distributed somewhat continuously from the ground to the canopy at lower densities and resulting in the smaller *FHD* (Fig. 3B). In addition, the horizontal connectivity of canopy foliage was significantly stronger, represented by a smaller proportion of gap, in the temperate forest than in the boreal one.

The difference in diversity between the two drosophilid communities in the temperate and boreal birch forests accorded with the trend of global latitudinal cline. As expected from the habitat heterogeneity hypothesis, the drosophilid community in the temperate forest was more diverse in all examined measures than that in the boreal forest (Fig. 4). The difference in species richness between the two communities was substantially attributed to the impoverishment of canopy-dwelling species in the boreal forest; the understory subcommunity had almost the same species richness in both forests. This must be related to the differences in foliage structure between the two forests. Fig. 5 shows schematically tree shapes, foliage structures and drosophilid communities in the two surveyed forests. As indicated by the lower horizontal connectivity of foliage, the canopy layer that consists of trees with deep, narrow crowns is highly rugged in the boreal forest. On the other hand, the canopy of the temperate forest, being formed by trees with shallow, somewhat spherical crowns due to more horizontal display of leaves, is more continuously waved. In addition, the boreal forest is vertically less stratified than the temperate forest. Thus, the depauperation of the canopy subcommunity in the boreal forest may have been caused by intensified competitive exclusion due to the reduction of living space or carrying capacity and the reduced degree of habitat

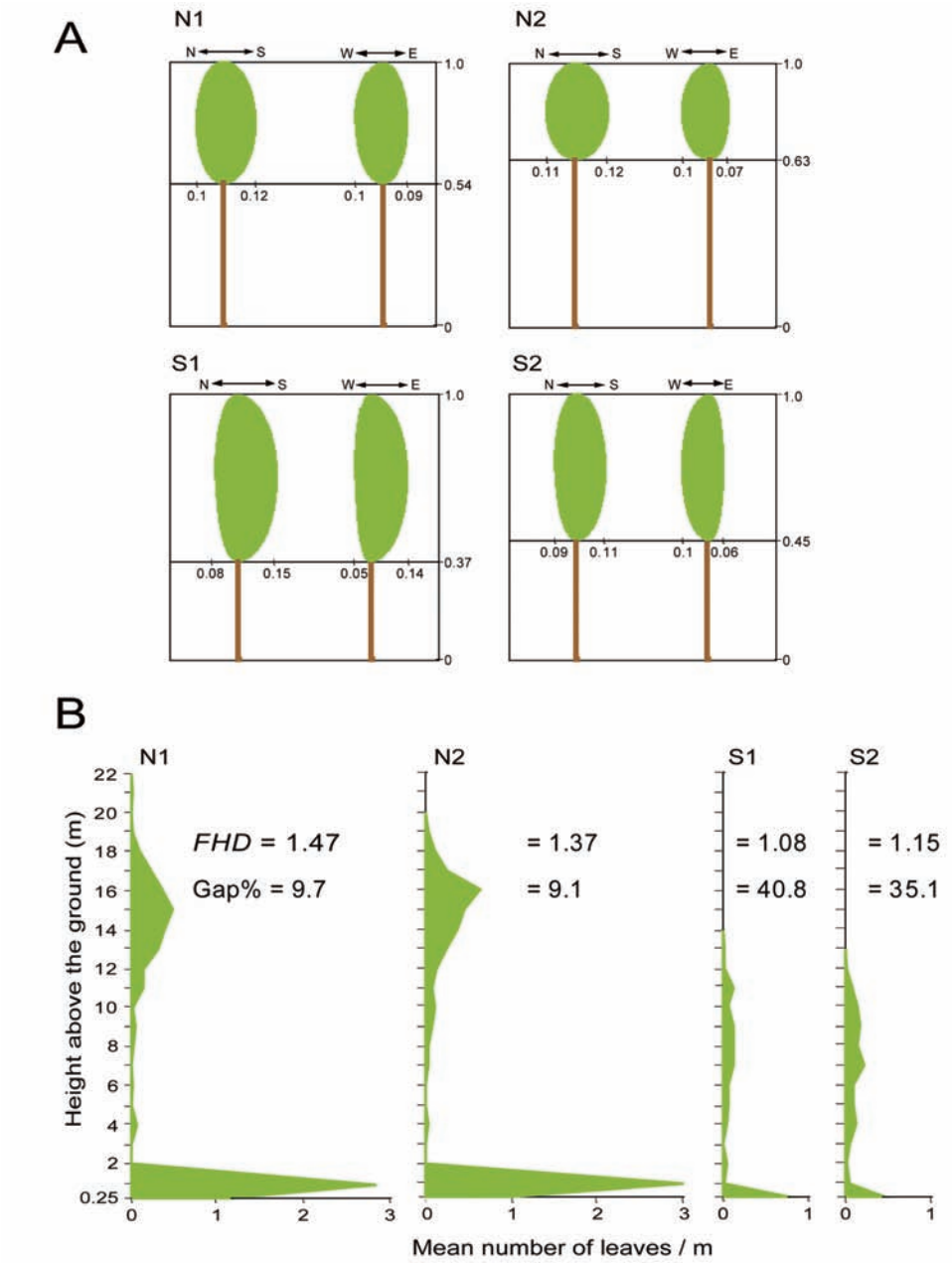

Figure 3：Average shape of white birch (*Betula platyphylla*) canopy trees (A) and average foliage height profile (B) in a cool-temperate forest (Nakagawa: N1, N2) and a boreal forest (Spaskayapad: S1, S2). In both forests, two study plots (10 m × 10 m quadrat) were established, near the center of which the traps were set vertically with a rope-pulley system. For all trees (≥ 1.5 m high) within each study plot, the following items were measured and/or recorded: species, the location on X-Y coordinates, tree height, trunk diameter at breast height (ca. 1.3 m high), height at the base of the lowest living branch, and crown radii in the four directions of cardinal points from the tree base. For comparisons of tree shape between localities and between plots, white birch that was common to both localities was selected in order to exclude the species-specificity in tree shape. In addition, the data for vertically erect canopy trees were used for calculation of the average shape to minimize the variation due to shading and leaning effects. To measure the vertical foliage distribution, MacArthur and Horn's (1969) camera method was employed (cf. Toda, 1992). The camera was equipped with a focusing screen with a grid of 16 intersections (focusing points) in the view field. The plot profile was obtained by averaging profiles at 36 intersections of 2 m mesh grid within each plot. Foliage height diversity (*FHD*) was measured by Shannon index, and the proportion of gap was calculated as the ratio of focusing points encountering the sky to the total points sampled within each plot. [Reproduced with partial modification from Tanabe et al. (2001) under the permission from Ecological Society of Japan.]

segregation.

The above results in combination support the habitat heterogeneity hypothesis, i.e., the positive correlation between habitat complexity and animal diversity, and suggest that a physical environmental factor, i.e., the sun angle, could be potentially important in producing latitudinal clines of diversity in animal communities inhabiting the aboveground space of forest through changes in plant structure at the individual and community levels.

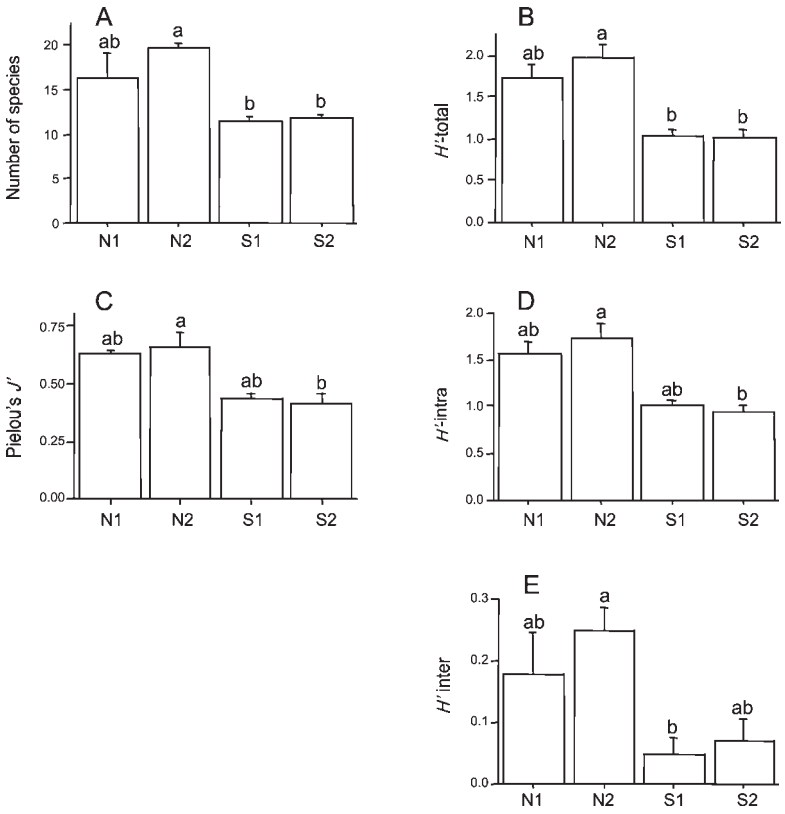

Figure 4：Means and standard deviations (error bars) of the number of species (A), the total (gamma) diversity measured by Shannon H' (B), the equitability of Pielou's J' (C), the intra-trap (alpha) diversity as the mean of H' for trap samples (D), and the inter-trap (beta) diversity as H'-total - H'-intra (E) at each plot in Nakagawa and Spaskayapad. The means and standard deviations were calculated for four weekly samples obtained at each study plot. The letters above the error bars indicate the results of Tukey-type multiple comparisons between the four plots; the same letters indicate non-significant differences ($P > 0.05$).

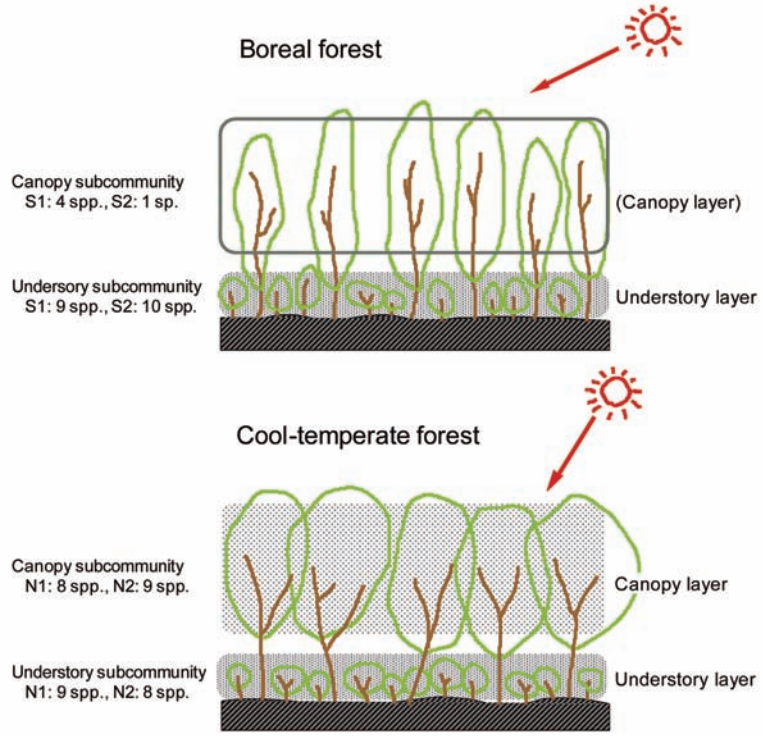

Figure 5：Schematic representation of sun angle, tree shape, forest structure and drosophilid community in boreal and cool-temperate birch forests, with indication of the numbers of species in canopy and understory subcommunities at each study plot.

5. Structure-diversity relationships on the local and forest-stand scales

Along the Asian Green Belt, the regional drosophilid species-pool, which should largely be a historical product of the past geological and biological processes, decreases in parallel with reducing complexity of forest structure from the tropics to the subarctic region; the Drosophilidae is considered to have originated and more diverged in the tropics (Throckmorton, 1975). Under such a latitudinal cline of regional species richness, nevertheless, Tanabe et al. (2001) showed that the forest structure was at least partly responsible for the depauperation of drosophilid canopy subcommunity in the boreal birch forest. In order to evaluate more accurately effects of the forest structure itself on the diversity of animals living there, it is necessary to compare animal communities among structurally different forests under the same regional species-pool. On a local scale, the forest structure changes both temporally according to vegetational succession (Aber, 1979) and spatially according to climatic and/or edaphic conditions (Aber et al., 1981; Terborgh, 1985). We present here some results of such a comparison among cool-temperate deciduous broad-leaved forests with different structural complexity.

Four structurally different forests (S1, S2, S3 and S4) were selected as study sites in the Tomakomai Experimental Forest (TOEF) of Hokkaido University, southern Hokkaido, Japan. The vertical foliage profiles were different among the four forests (Fig. 6), especially between the first two and the last two sites, and the average tree heights were 5–6 m, 11–12 m, 17–18 m, and 20–21 m, respectively, indicating a stepwise increment of each 4–5 m in forest height from S1 to S4. Four replicate survey plots were established in each site. The banana traps (Toda's Trap II) were set in the vertical arrangement at each plot and the trap heights (0.5, 1.5, 6.5, 11.5 and 16.5 m) were held almost constant over all sites (see Tanabe, 2002, for details of the study design).

Three habitat variables were measured at each plot: foliage height diversity (*FHD*), horizontal heterogeneity in vertical foliage distribution and the number of tree species. The second measure was calculated as the beta component of the foliage height diversity (*FHD*) among four subplots in a plot, according to the concept of additive partitioning of diversity. There were no correlations between these three variables across plots. Two diversity measures were calculated for the drosophilid community sampled at each plot: the total species richness excluding singletons as occasional migrants and the between-trap diversity in species composition. The latter was evaluated by Whittaker's (1960) *Bw*:

$$Bw = S/\alpha - 1 \quad (3)$$

where S is the total number of species, and α is the mean number of species per trap. These two diversity measures showed significantly positive correla-

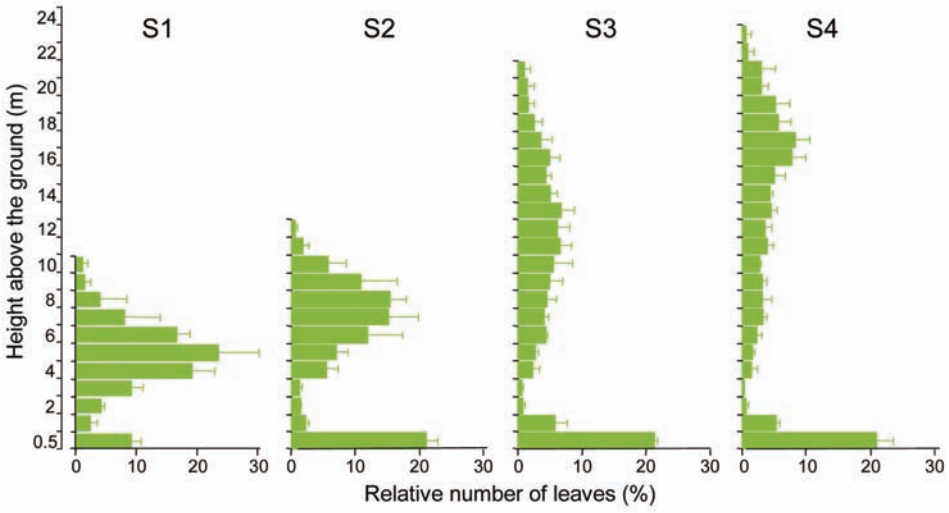

Figure 6 : Average vertical foliage profiles, with standard deviation of relative foliage density at each height (error bar), among four plots in four study sites, which were established in cool-temperate deciduous broad-leaved forests at different successional phases in the Tomakomai Experimental Forest of Hokkaido University, southern Hokkaido, Japan (42°40' N, 141°141' E).

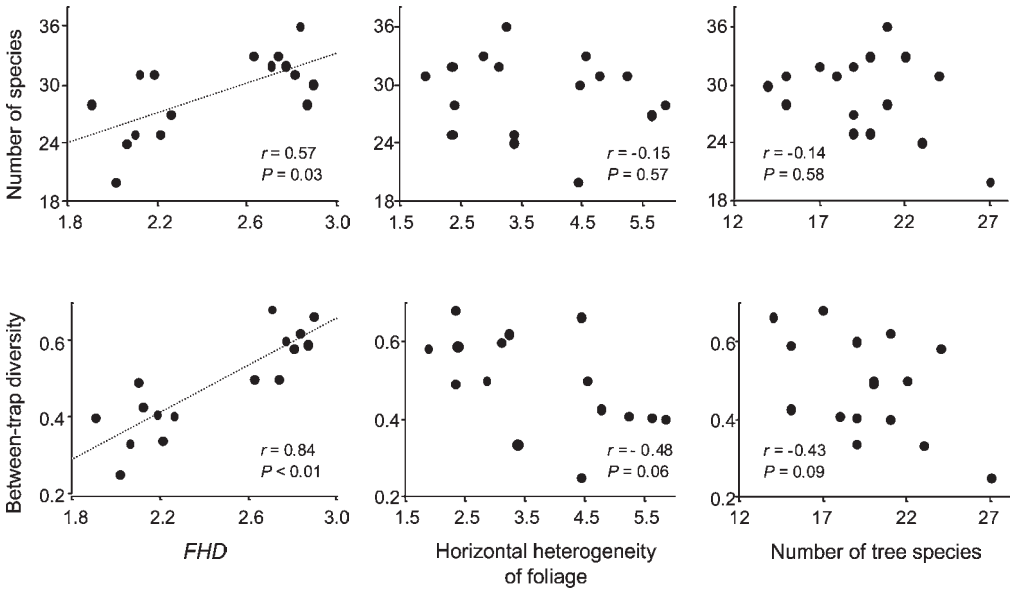

Figure 7 : Relations between drosophilid species diversity evaluated by two measures, species richness excluding singletons and between-trap diversity (Whittaker's *Bw*, see text) in species composition, and three habitat variables, foliage height diversity (*FHD*), horizontal heterogeneity of vertical foliage structure (the beta component of *FHD*, see text for details) and the number of tree species at 16 study plots (4 plots × 4 sites) in the Tomakomai Experiment Forest of Hokkaido University. Correlation coefficients (r) and P-values were based on Spearman's rank correlation tests.

tions only with *FHD* (Fig. 7). This is consistent with the patterns of drosophilid diversity on larger scales; i.e., the vertical foliage structure, *FHD*, influences the species diversity in forest drosophilid communities through limiting the degree of vertical microhabitat segregation among component species.

Furthermore, a number of studies have found vertical gradients of biodiversity in forests, with species-rich faunas at the canopy stratum (Erwin, 1983; Wilson and Peter, 1988; Stork, 1993). This within-forest pattern of variation in biodiversity is often independent of differences in stand-level structural properties. For example, in TOEF, Tanabe (2002) and Ishii et al. (2004) showed that the total number of drosophilid species collected at a stratum (trap height) increased from the ground to the canopy, and that this pattern was consistent among the forests differing markedly in vertical foliage structure. They suggested an important role of the unvarying nature of within-stand environmental gradients under the continuous, closed canopy in organizing forest drosophilid communities.

6. Implications for conservation of biodiversity and ecosystem functions in forests

The recent mass extinction of biological species (Chapin et al., 2000; Dirzo and Raven, 2003), caused by human activities, has resulted in serious deterioration of natural ecosystems. Ecosystems that lack their intrinsic complexity and functions cannot support diverse forms of life and will thus lead to further loss of biodiversity. This "degradation spiral", i.e., a positive feedback between loss of biodiversity and deterioration of ecosystem performances, will lead to the "crisis" of global ecosystems. The critical issue at present is to avoid triggering the "ecosystem degradation spiral". Biodiversity science, as a new multidisciplinary science, should contribute to developing a strategy for proper management of ecosystems, providing scientific data, predictions, and proposals for human societies to conserve biodiversity, its interactions and evolution in ecological complexity, and sustainable production by ecosystems of goods and services that meet human needs.

Summarizing this review, we emphasize that taking into account the three-dimensional structure of forest vegetation is essential for understanding the total amount and the uneven distribution of diversity in insect communities living there. As for drosophilid flies, it is a general pattern from boreal to tropical forests that the diversity of a local community is supported primarily by the vertical complexity of foliage stratification and secondarily by the horizontal variation in forest structure. If higher diversity of insects reflects and/or supports healthy functioning of forest ecosystem (it should be documented by fur-

ther studies), to maintain the complexity of three-dimensional forest structure is important for humankind to receive goods and services from forest ecosystems in a sustainable manner.

Acknowledgements

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