Diversity of Subcortical Arthropod Communities in Tropical and Temperate Forests

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Species diversity of subcortical arthropod communities were assessed in two tropical regions and two temperate regions. In the tropics, communities of subcortical arthropods were more diverse in La Selva, Costa Rica, than on Barro Colorado Island, Panama. Costa Rican communities yielded higher values of both Shannon and Simpson diversity indices than Panamanian communities. Compared to Panamanian communities, Costa Rican ones supported higher measures of both species richness and evenness. Between the two temperate regions, communities of subcortical arthropods in Korea scored consistently higher values of both Shannon and Simpson indices than the ones in eastern Massachusetts, U.S.A. When individual diversity components were compared, however, Korean communities yielded exceptionally high evenness measures but lower species richness than the communities in the U.S.A. Unusually high evenness values of Korean subcortical arthropods were due to extremely low population densities of all component species.

For many plant and animal taxa, diversity is known to be higher in the tropics than in temperate regions (MacArthur, 1972; Terborgh, 1973; Brown and Gibson, 1983; Stevens, 1989; Rosenzweig, 1992). For instance, the number of ant species has been assessed to be 7 in Alaska, 73 in Iowa, 101 in Cuba, 134 in Trinidad, and 222 in Brazil (Stiling, 1992). Plants and their insect herbivores provide another striking example of decreasing species diversity with increasing latitude (Farrell and Mitter, 1993).

Many theories have been advanced to explain why tropical communities harbor greater numbers of species than temperate and arctic ones. Among the better supported are the time theory (e.g., Southwood, 1961; Sanders, 1968; but see Strong 1974), spatial heterogeneity theory (MacArthur and MacArthur, 1961), species-energy or productivity theory (Wright, 1983; see also Turner et al., 1987, 1988), area theory (Darlington, 1959; Terborgh, 1973), competition theory (Dobzhansky, 1950), predation theory (Paine, 1966; Paine and Levin, 1981), and climatic stability theory (Sanders, 1968).

Communities of subcortical arthropods have never been studied with respect to the relationship between diversity and latitude. In the following account I compare diversity measures of subcortical arthropod communites from two tropical regions (Barro Colorado Island (BCI), Panama, and La Selva, Costa Rica) and two temperate regions (Massachusetts, U.S.A., and Korea). The objectives of this study were (1) to investigate similarities and differences in species composition and community structure of subcortical arthropods between tropical and temperate regions, (2) to assess if diversity measures of subcortical communities follow the same general pattern of latitudinal gradient, and (3) to determine which of the theories can explain the patterns of arthropod species diversity under the bark of decaying trees. I also included in this account a discussion of theoretical and/or practical shortcomings associated with species diversity indices currently being used.

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Materials and Methods

Study sites and materials

The study began at the field station of the Smithsonian Tropical Research Institute on Barro Colorado Island (79°50′W, 9°9′N), Panama, in July 1985. Once a decaying tree was located on the forest floor, I gently peeled off its bark and collected the arthropods living underneath the bark. Captured specimens were identified to the species level and counted in numbers. Because most of subcortical arthropods could not readily be given species names, however, the majority of the specimens were classified into morpho-species groups. I avoided excessive and often destructive collecting activities by simply counting individuals of the arthropods, once they were given proper species names or at least tentative morpho-species ranks.

Field sampling and counting were continued on and off on BCI until August 1988. About half of the island is covered by mature semideciduous forest that has been relatively undisturbed over the past 200-400 years, while the other half is covered by young semi-decidous forest less than 100 years old (Foster and Brokaw, 1982). More details on the climate, vegetation, and habitats of BCI are available in Croat (1978) and Leigh et al. (1982).

Much the same studies were conducted at the field station of the Organization for Tropical Studies in La Selva (84°3′W, 10°25′N), Costa Rica, during July-August 1986 and May-June 1987. La Selva station is situated in lowland evergreen forest that is contiguous to a large area of relatively little disturbed tropical forests (Janzen, 1983). Janzen (1983) also provides a general description of the vegetation as well as habitat and climate in La Selva and neighboring regions.

Diversity of subcortical arthropods in temperate regions were assessed in various parts of the eastern Massachusetts (72°50′-70°30′W, 41°50′-42°40′N), U.S.A., and South Korea (126°55′-129°30′E, 33°20′-38°15′N). Samplings in Massachusetts were done sporadically during 1986-1990 and those in Korea between October 1994 and April 1997. Collection sites in Korea included Mt. Sorak, Mt. Chumbong, Mt. Ungil, Mt. Kwanak, Mt. Worak, Mt. Minjuji, and Mt. Halla. Forests in both regions were mostly mixed ones of deciduous and coniferous trees.

Data analysis

To avoid unusually low measures from entering the data pool and thus shifting means unrealistically low, only the data collected from logs whose diameters were equal to or greater than 30 cm. For each data set the following four diversity measures were calculated: (1) species richness (S), the total number of species in a community; (2) Shannon diversity measure (Shannon and Weaver, 1949) defined as

$$H = -\sum_{i=1}^{s} P_i \log P_i \quad ;$$

(3) Simpson diversity measure (Simpson, 1949) defined as

$$D = \sum_{i=1}^{s} P_i^2 \quad ;$$

(4) Williams' model-free evenness measure (Williams, unpub. ms.) defined as

$$H = 1 - \sqrt{\frac{S \sum_{i=1}^{s} P_i^2 - 1}{S - 1}}$$

Table 1. Values (mean±SD) of Shannon (H) and Simpson (D) indices for subcortical arthropod communities in Costa Rica, Panama, Korea, and the U.S.A. Numbers in parentheses denote sample sizes

	Costa Rica (39)	Panama (87)	Korea (34)	U.S.A. (13)
H	1.365±0.234	1.155±0.257	0.788±0.378	0.745±0.242
D	0.662±0.091	0.549±0.146	0.373±0.192	0.351±0.137

where P_i is the relative frequency of the ith species.

Results

The decreasing pattern in latitudinal gradient of diversity is in general well supported by the present study. Diversity measures turned out to be generally higher in tropical regions than in temperate ones (Tables 1 and 2). Subcortical arthropod communities in two tropical regions were more diverse than those in temperate regions, although the exact pattern of decreasing diversity with increasing latitude at a finer scale did not meet the expectation. Communities at La Selva, Costa Rica, supported greater values of both Shannon and Simpson indices than the Panamanian communities (Table 1), although La Selva is located higher in latitude than Barro Colorado Island, Panama. Subcortical arthropod communities at La Selva harbored on average more species whose distributions were also more even (Table 2).

Somewhat conflicting pictures emerged between the samples from South Korea and eastern Massachusetts, U.S.A. Subcortical arthropod communities in Korean forests had higher measures of both Shannon and Simpson indices (Table 1), although they actually harbored smaller numbers of species (Table 2). Although eastern Massachusetts is located at higher latitudes than South Korea, rotting logs in Korean forests had consistently lower species richness measures than those in the United States. Korean samples yielded higher values of both Shannon and Simpson indices probably due to their unusually high evenness measures (Table 2 and Fig. 1). A majority of arthropods in subcortical communities of Korea existed so consistantly in low numbers that relative abundances of species did not vary much at all.

Tropical communities of subcortical arthropods were dominated by termites, ants, and beetles. Ant colonies occurred frequently in rotting logs in eastern Massachusetts. In Korean forests, however, ants, termites, and beetles seldom inhabited, and instead, predatory centipedes were among the most numerous arthropods. How such communities with predators more abundant than potential prey can be maintained remains unresolved.

In general, subcortical arthropod communities in Costa Rica were most diverse with a slight exception of an unusually high evenness values of subcortical arthropod communities in Korea (Fig. 1). Costa Rican

Table 2. Values (mean±SD) of the ordered couple (S, E) for subcortical arthropod communities in Costa Rica, Panama, Korea, and the U.S.A.

Country	(S, E)	n
Costa Rica	(10.571±3.409, 0.386±0.126)	39
Panama	(9.429±2.370, 0.359±0.164)	87
Korea	(6.571±1.618, 0.553±0.117)	34
U.S.A.	(7.429±1.902, 0.241±0.103)	13

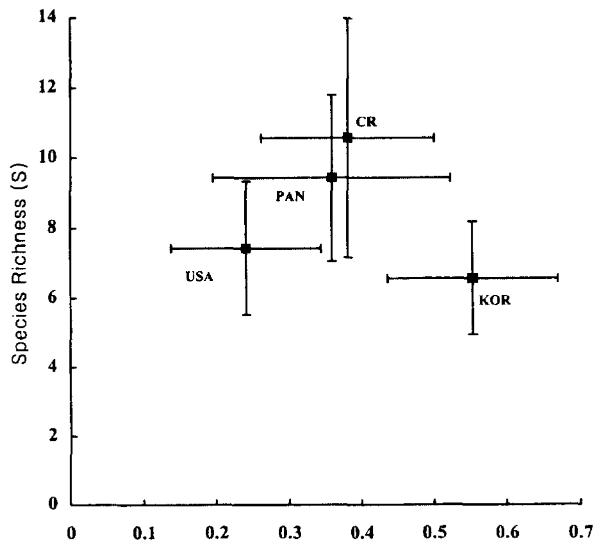

Fig. 1. Graphic representation of the ordered couple (S, E) for subcortical arthropod communities in Costa Rica (CR), Panama (PAN), Korea (KOR), and the U.S.A. (USA). Vertical and horizontal bars denote standard deviations.

subcortical arthropod cummunities supported greater measures of both Shannon and Simpson indices (Table 1) and higher species richness and evenness (Fig. 1). Subcortical arthropod communities in Korea supported the lowest species richness but the highest evenness (Fig. 1).

Discussion

Latitudinal gradients: patterns and theories

Among the proposed theories to explain latitudinal diversity gradients, the spatial heterogeneity theory and competition theory could not be tested in this study, although both theories are generally well accepted in other studies (Rozenzweig and Abramsky, 1993). The species-energy theory may explain gross-level differences in diversity measures between the tropical and temperate regions in this study. Abundances of arthropods in subcortical communities were considerably higher in the tropics than in temperate regions (Choe, unpublished data).

The area theory and climatic stability theory provide some clues to why communities at La Selva, Costa Rica, are more diverse than the ones on BCI, Panama. As discussed above, BCI is an island of relatively small area, whereas the forest at La Selva is connected to a much larger forest. Furthermore, the climate at La Selva tends to be less variable than that of BCI. While there is a distinct seasonality in terms of relative humidity on BCI, a dry season is almost non-existent or not as distinct at La Selva. The dry season usually starts in December and lasts until April on BCI, although the timing and duration of dry and rainy season vary considerably (Rand and Rand, 1982).

The time theory can be both supported and rejected by the results of this study. Being a man-made island, half of the forest on BCI is relatively young (Foster and Brokaw, 1982). This may explain why subcortical arthropod communities on BCI are less diverse than those at La Selva. When diversity measures of subcortical arthropod communities were compared between tropical and temperate regions in this study, however, a very different prediction could be put forth. Since fallen trees rot much faster in the tropics (Choe, unpub. data) and thus allow less time for communities to develop, the time theory should predict lower diversity measures in subcortical arthropod communities in the tropics than in temperate regions.

The time theory has received varying degrees of both acceptance and rejection in other studies as well. While Southwood (1961) found good correlations between insect diversity and tenure length of British trees, Strong (1974) and Stong et al. (1977) revealed that abundances of insects associated with trees were explained better by the area theory than by the time theory.

Finally, the predation theory may provide some marginal clues to how subcortical arthropod communities in Korea could produce higher values of both Shannon and Simpson indices than those in eastern Massachusetts, U.S.A., while they actually supported fewer species. It is possible that the commonly occurring predatory centipedes in fact hold populations of most other subcortical species down at low levels and thus allow more species to coexist. However, further studies are needed to demonstrate if indeed the centipedes play a role of keystone predators (*sensu* Paine, 1966) in subcortical communities of Korean forests.

Shortcomings of diversity and evenness indices

The Shannon (Shannon and Weaver, 1949) and the Simpson (Simpson, 1949) indices are among the most commonly used diversity indices in ecology. By their nature and design, however, diversity measures confound species richness (number of species) with species evenness (proximity to a uniform distribution). A community is said to be diverse when it supports many species and their abundances are fairly even. On the contrary, a community has low diversity when the species are few and their abundances are uneven.

Nonetheless, communities with more species whose relative abundances are highly uneven may in fact yield lower diversity measures than communities with relatively fewer but more evenly distributed species (Patil and Taillie, 1977). The fact that Korean samples showed higher scores of commonly used diversity indices than eastern Massachusetts samples regardless of their low species richness illustrates the problems associated with many diversity indices.

Information is lost by collapsing richness and evenness into a singles number. To compensate this problem, ecologists created evenness or equitability ratios to gain information on relative abundances. One of the most frequently used evenness indices is J' (Pielou, 1969), which is H/ln S where H is the Shannon diversity index and S is the number of species. However, this and all other diversity-associated evenness indices are not independent of species richness, which is in turn dependent on sample size (Hurlbert, 1971; Magurran, 1988).

A new evenness index, E, independent of any particular diversity index, has been proposed by Williams (unpub. ms.). On purely geometric grounds, this so-called model-free index measures evenness as the relative distance from the totally even midpoint in a multidimensional vector space. Williams also argued that a community would be better described by a set of two numbers, i.e., species richness (S) and evenness (E), than by a single measure of diversity. Thus Williams suggested that we present diversity profiles of biological communities as the ordered couple (S, E). This way we get information on how many species are in a community as well as how evenly they are distributed there.

This study nicely demonstrates that it is much more informative to describe a biological community with its species number (S) and distribution evenness using an index free of influences of diversity measures. Williams' evenness index appeared to accurately assess the degree of equitability in relative distribution of species. Thus, I echo Williams' suggestion of describing biological communities using the ordered couple rather than single diversity measures.

The ordered couple method will be particularly useful in environmental impact analysis. If a biological community loses some of its component species due to human interference but somehow its evenness increases for whatever reasons, the clearly damaged community may be evaluated unfairly as a community whose overall diversity has improved. A graphic representation of the ordered couple such as the one in Fig. 1 may help us quickly assess characteristics of communities in terms of species richness and evenness, and allow quick comparisons among communities.

Paucity of subcortical arthropod communities in Korea

Korean subcortical arthropod communities turned out to be seriously depauperate in this study. They supported the smallest numbers of species among all four study sites. Although their evenness measures were the highest, such exceptional values were the results of unsually low population densities of all component species. It is particularly noteworthy that Korean subcortical arthropods occurred in lower species number and population size than those in eastern Massachusetts, which is located higher in latitude.

Although detailed food-web analyses were not conducted, subcortical arthropod communities in the two tropical regions and eastern Massachusetts appeared to have a normal pyramid structure. On the other hand, Korean communities of subcortical arthropods were dominated by centipedes, potential predators for various arthropods living underneath the bark. Such an inverted pyramid of numbers cannot be maintained unless the biomass of prey has an extremely high turnover rate (Stiling, 1992). In any case, I could not find any sign of large amounts of energy being processed by any potential prey at any time during the entire field season.

Reasons for this reverse pattern of latitudinal gradient and inverted food chain structure were not systematically investigated, but one clear difference between the two regions was relative humidity in rotting logs. Rotting logs in Korean forests were so dry that their woody cambia often appeared unpenetrable. Low humidity in the forest interior would inbihit decomposition processes, which in turn slows down nutrient recycling in the forest ecosystem. Low measures of species richness and population density in subcortical arthropod communities may be indicative of overall decrease in species diversity in Korean forests. Thus, the results of this study warrants further investigations of species diversity and structure of forest communities in Korea.

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