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SPECIES DIVERSITIES OF HERPETOFAUNAL SAMPLES FROM SIMILAR MICROHABITATS AT TWO TROPICAL SITES[1]

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Abstract. Amphibians and reptiles were collected from tree buttresses in two different regions to determine whether within-habitat species diversity differences were evident. Using the method suggested by Pielou (1966), the average species diversity per individual was $H' = 1.92 \pm .47$ for the collection of amphibians and reptiles taken from tree buttresses in a tropical dry forest formation in Thailand, $H' = 4.95 \pm .84$ for the tree buttress collection taken in Ecuador. Part of the within-habitat diversity differences are due to a difference in kind of organism: a large number of terrestrial frogs are present in Ecuador; there are no terrestrial frogs from the Thai site. Other differences are also operating, however. The number of lizard species are comparable in the two collections (8 from Thailand, 10 from Ecuador), yet the Brillouin diversity measure of the Ecuadorian lizard collection was $NH = 2.24$, higher than the diversity of the Thai lizard collection, $NH = 1.25$. The diversity differences are postulated to be due to different sizes of the total forest herpetofaunas of the two regions.

INTRODUCTION

The rolc of within- and/or among-habitat differences in explaining species diversity gradients has been a topic of much discussion based primarily on hypotheses with few direct data. The purpose of this paper is to examine the species diversities of amphibians and reptiles from apparently similar microhabitats from two different tropical forests. If the two forests are thought of as collections of microhabitats, certain of the microhabitats are equivalent, but the total number of microhabitats differ in each forest. If diversity differences are due solely to among-habitat differences, the diversities of similar microhabitats should be similar, but the total diversities would differ because of the unequal number of microhabitats in each forest. If within-habitat diversity differences are present in addition to among-habitat differences, the diversities of similar microhabitats will differ. Analysis of diversity differences between similar microhabitats should allow distinction of whether or not within-habitat differences are operating.

The microhabitat we examined was the tree buttress. The two study sites were in Thailand and Ecuador. The Thai site, the Sakaerat Experimental Station, lies approximately 250 km NE of Bangkok. The forest sampled was a dry evergreen forest, which has a Tropical Dry bioclimate according to Holdridge's (1964) classification. The site in Amazonian Ecuador, Limoncocha, lies on the Rio Napo, near the equator. The forest sampled has a Tropical Moist bioclimate (Holdridge 1964).

METHODS AND MATERIALS

The tree buttress increases the interface of tree and ground. We examined this interface for reptiles and amphibians. The ground surface lying among buttress extensions was examined, the surface litter was removed by hand, and the surface soil was turned by either hoe (Thailand) or machete (Ecuador). The buttress system was examined to the point where the buttress originated from the trunk or to eye level in the few cases where the buttresses were taller than the collectors. When individual animals were captured, we recorded their exact location as well as the diameter of the tree at breast height. The sampling in Thailand was done in conjunction with random quadrat sampling, and covered the 10-month period of March–December 1969. The sampling in Ecuador was done specifically to determine the composition of the buttress herpetofauna and was done in June and July of 1971. In Ecuador, additional information on the extent of the buttresses and extent of litter lying between the buttresses was also recorded and an effort was made to sample the trees randomly. The data on tree diameters, buttress diameters, degree of leaf litter development, and occurrence of animals are available on request from the first author to anyone who wishes to utilize them. The Thai specimens are in the collections of the Field Museum of Natural History; the Ecuador specimens are in the collections of the Los Angeles County Museum of Natural History.

Pielou's (1966) method and the Brillouin (1956) measure are used to determine the species diversities of the two collections. The Pielou method allows determination of a standard error and has already been used in analyzing quadrat data for amphibians and reptiles (Lloyd, Inger, and King 1968). In this case, each "quadrat" is a tree buttress that had amphibians or reptiles associated with it. Empty tree buttresses were not used.

THE TREE BUTTRESS AS A MICROHABITAT

The tree buttress system has evolved as a support system for the tall, monolayered trees of tropical forests. The buttress consists of flat, triangular plates

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which are confluent with the base of the tree trunk and extend into the ground.

The buttresses are discrete units, easy to recognize and sample. The similarity in appearance of the buttresses at the two sites prompted Heyer, who was present at both sites, to initiate the comparative sampling in Ecuador. As far as we know, there is no information indicating whether or not amphibians and reptiles utilize tree buttresses distinctively with respect to either tree trunks or forest floor. However, the tree buttress has distinctive features which would be recognized by amphibians and reptiles: (1) crevices often form where the buttress joins the trunk, providing hiding places for lizards, (2) leaf litter is deeper between the buttresses than on surrounding ground, (3) caverns are often formed where the buttress, ground, and trunk meet, providing hiding places for surface animals.

In Thailand, the dry evergreen forest was sampled over the entire year. An example illustrates that the species are not restricted to tree buttresses, but are commonly associated with them. Sixty-nine of 360 specimens (19%) of *Riopa bowringi*, the commonest forest floor lizard, were found in tree buttresses.

Species Diversity Results

The following 12 species of amphibians and reptiles were collected from tree buttresses in Thailand.

Frogs
  Family Microhylidae
    Microhyla inornata – 1 individual
Lizards
  Family Gekkonidae
    Cyrtodactylus angularis – 1
    Peropus mutilatus – 2
  Family Scincidae
    Davewakeum miriamae – 4
    Leiolopisma reevesi – 8
    Leiolopisma siamensis – 6
    Mabuya multifasciata – 1
    Riopa bowringi – 69
    Sphenomorphus maculatus – 1
Snakes
  Family Colubridae
    Liopeltis scriptus – 2
    Oligodon cyclurus – 1
    Psammodynastes pulverulentus – 1
Total Number of Individuals – 97

From tree buttresses in Ecuador we collected the following 33 species:

Caecilians
  Family Caeciliidae
    Caecilia sp. – 1 individual
Frogs
  Family Bufonidae
    Bufo typhonius – 9
  Family Dendrobatidae
    Colostethus brunneus – 8
    Phyllobates femoralis – 14
    Phyllobates parvulus – 12
    Phyllobates pictus – 1
  Family Hylidae
    Hyla bokermanni – 2
    Hyla funerea – 2
    Hyla garbei – 1
  Family Leptodactylidae
    Eleutherodactylus acuminatus – 1
    Eleutherodactylus brevicrus – 1
    Eleutherodactylus conspicillatus – 7
    Eleutherodactylus ockendeni – 1
    Eleutherodactylus sulcatus – 2
    Eleutherodactylus variabilis – 1
    Eleutherodactylus sp. A – 11
    Eleutherodactylus sp. B – 2
    Ischnocnema quixensis – 1
    Leptodactylus discodactylus – 1
    Leptodactylus mystaceus – 3
    Leptodactylus wagneri – 5
  Family Microhylidae
    Chiasmocleis ventrimaculatus – 15
    Hamptophryne bolivianus – 10
Lizards
  Family Gekkonidae
    Gonatodes concinnatus – 10
    Pseudogonatodes sp. – 3
  Family Iguanidae
    Anolis sp. – 3
    Enyalioides laticeps – 2
  Family Teiidae
    Iphisia elegans – 2
    Leposoma parietale – 3
    Ophiognomon abendrothii – 3
    Prionodactylus argulus – 3
    Ptychoglossus brevifrontalis – 2
    Tupinambus nigropunctata – 1
Snakes
  Family Colubridae
    Rhadinaea brevirostris – 1
Total Number of Individuals – 143

The Pielou (1966) method yields diversity values for collections in which the organisms are patchily distributed and are sampled by examining random portions of the habitat (not necessarily the animal populations themselves). The average diversity of amphibians and reptiles was calculated by the Brillouin (1956) measure in successively larger samples as suggested by Pielou (1966) for the Thai and Ecuadorian collections (Fig. 1). The Brillouin measure is:

$$NH = \log_2 N! - \sum_{i=1}^{s} \log_2 n_i! \,, \qquad (1)$$

where N is total individuals, n_i are the individuals in each species, and H is the mean diversity per individual in the collection itself. Once there is no change in diversity as sample size increases, the mean of successive values of h_k can be used as an estimator of H'. Values for h_k are determined as

$$h_k = \frac{(N_k H_k - N_{k-1} H_{k-1})}{(N_k - N_{k-1})} \qquad (2)$$

where the subscripts refer to the number of quadrats accumulated thus far in the process. For the Thai data, H' estimates were begun with the 50th buttress, for the Ecuadorian data, the 85th buttress (Fig. 1). We repeated the entire process 10 times, shuffling the data cards prior to each new estimation. The definitive estimates of H' and its standard error are the medians of the 10 runs. For the Thai data, $H' = 1.92 \pm .47$, for the Ecuador data, $H' = 4.95 \pm .84$.

The Brillouin measures of diversity for the total collections are for the Thai data, $NH = 1.58$, for the Ecuador data, $NH = 3.92$. The diversities of the two collections are clearly different. One obvious difference between the collections is the importance of frogs in each. However, the number of lizard species is comparable in the two collections. The lizard subsets of the two collections were analyzed in the same manner as the total collections. Fig. 2 indicates the accumulative values of H. Estimates of H' were begun with the 20th buttress for the Thai data (Fig. 2), at the point where H stabilizes. The average of 10 estimates of H' and the associated standard error for the Thai lizard data is $H' = 1.53 \pm .30$. Obviously the estimates of H have not leveled off for the Ecuadorian data (Fig. 2). The Brillouin measure provides a better measure in this case for the lizard components.

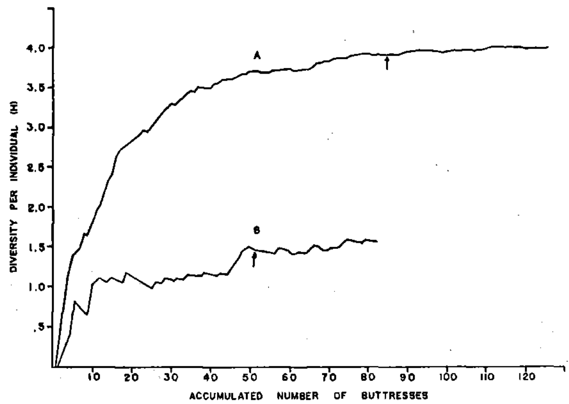

FIG. 1. Successive values of average diversity of amphibians and reptiles collected in tree buttresses from a moist tropical forest in Ecuador (curve A) and a dry evergreen forest in Thailand (curve B). The H was recalculated (Equation 1) following the addition of each buttress to the total collection, taking the buttresses in random order. Buttresses beyond the points indicated by the arrows were used to obtain h_k of equation 2.

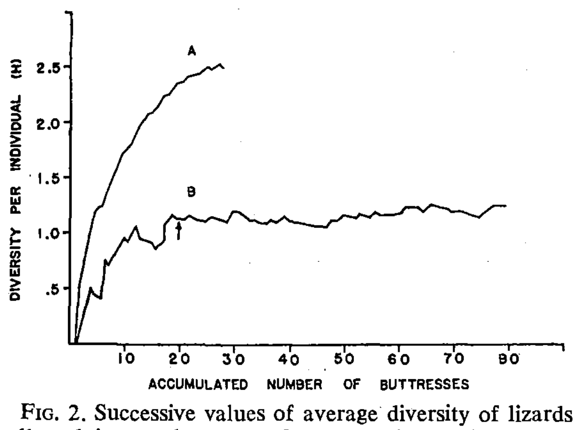

FIG. 2. Successive values of average diversity of lizards collected in tree buttresses from a moist tropical forest in Ecuador (Curve A) and a dry evergreen forest in Thailand (Curve B). See legend for Fig. 1 for further explanation.

For the Thai lizards, $NH = 1.25$, for the Ecuador lizards, $NH = 2.24$. The Ecuadorian lizard collection is clearly more diverse than the Thai lizard collection from tree buttresses.

DISCUSSION

The most obvious aspect of the difference in diversities between the Thai and Ecuadorian collections is the relative role that frogs play in each collection. In Thailand, only a single frog was taken from the buttress microhabitat. In Ecuador, 21 species of frogs were collected from the buttress microhabitat. This difference correlates with differences in anuran reproductive biology in the two regions. Two dominant frog groups of the buttress fauna from Ecuador have terrestrial breeding habits, or nearly so. Frogs of the genus *Eleutherodactylus* have direct development; eggs are laid in moist terrestrial situations, and small adults hatch from the eggs. Male frogs of the family Dendrobatidae transport larvae from small puddle to small puddle in the forest; the frogs are terrestrial and do not require large rain pools or ponds for any portion of their life histories. Frogs with life cycles approaching direct development are exceptional in the anuran fauna of Southeast Asia. The herpetofaunas of Southeast Asia and South America have undergone essentially independent evolutionary histories and indicate that differences in species diversity may be due in part to phylogenetic differences when faunas are compared from differing biogeographic areas.

Even though the lizards of the two collections are distinct at the generic level, there are no obvious differences in biology such as is the case for the anurans. In fact, the gekkonids seemed to be ecological equivalents in both regions, inhabiting the buttress crevices on the trunks; and skinks, iguanids, and teiids were found in the buttress-litter-soil interface. A burrowing lizard was present in each area, *Dave-wakeum miriamae* in Thailand, *Ophiognomon abendrothii* in Ecuador. The differences in diversities of the two collections cannot be correlated with phylogenetic differences as such, but rather reflect differences due to the within-habitat component of species diversities. Karr (1971) has demonstrated that the among-habitat component of diversity does not account for the total diversity differences of temperate and tropical bird communities in the New World, but that within-habitat diversity differences are also operating. These conclusions corroborate those of Orians (1969) based on bird community comparisons from different vegetation formations in Central America. Both authors attribute the within-habitat avian diversity differences to the addition of new food categories in the more complex vegetation formations. Such an explanation is not likely for the within-habitat diversity differences noted here, especially for the lizards. Although gut analyses have not been performed on the species involved, it is highly likely that all of the lizards are insectivorous, selecting food items on the basis of size rather than kind. Two hypotheses seem plausible to account for the within-habitat diversity differences between the two collections: (1) The tree buttress microhabitat is actually more complex in Ecuador than in Thailand. It may be that the amphibians and reptiles recognize differences that are not obvious to us; (2) More species occur in buttresses in Ecuador because there are more species in the surrounding forest. In 10 months of intensive collection at Sakaerat, 74 species of amphibians and reptiles were taken from the dry evergreen forest. Field parties from the University of Kansas have collected approximately 180 species of amphibians and reptiles from Santa Cecilia, Ecuador, just north of our Ecuadorian study site (Dr. William E. Duellman, personal communication). The tree buttresses of Ecuador will always have a greater waif fauna than those of Thailand, analogous to island situations as studied by Mac Arthur and Wilson (1967), resulting in a higher diversity. The second hypothesis is consistent with the conclusions drawn from bird studies (Karr 1971, Orians 1969) and the reality that a forest is more than the sum of its parts.

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