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ABSTRACT

The purpose of this study was to determine the community composition, S, H, E, N, and $_{Smarg}$ of arthropods living in epiphytic moss mats on vertical gradients, in the elfin forest of Monteverde, Costa Rica. Past studies have shown that moss mats alter biotic factors of the surrounding environment by increasing moisture and decreasing temperature variation. Moss samples were collected from 1 m, 7 m, and 15 m from nine trees between 1725 m and 1800 m and dried using Berlese funnels. Arthropods were separated by order and morphospecies. N was highest at 15 m, Smarg and S were highest at 1m, and H^1 and E were highest at 7 m. High abundance of arthropods at 1m and 15m, stems from the presence of one morphospecies of arthropod found in high numbers at each height but in patchy distributions. These results point to variable resource distribution at 1m and 15m rather than height as the main factor behind moss-dwelling arthropod community makeup.

RESUMEN

El propósito de este estudio debía determinar la composición de la comunidad, S, H', E, N, y S_{marg} de artrópodos que viven en esteras de musgo de epiphytic en declives verticales, en el bosque mágico de Monteverde, Costa Rica. Los estudios del pasado han mostrado esas esteras de musgo alteran los factores no bióticos del ambiente circundante aumentando la humedad y la variación disminuyente de la temperatura. Las muestras del musgo se reunieron de 1M, de 7 M, y de 15 M de nueve arboles entre 1725 M y 1800 M y secaron utilizando los embudos de Berlese. Los artrópodos fueron separados por la orden y morphospecies. N era más alta en 15 M, Smarg y S eran más altos en 1 M, y H^1 y E eran más altos en 7 M. La abundancia alta de artrópodos en 1 M y 1 5 M, proviene de la presencia de un morphospecies de artrópodo encontró en números altos en cada altura pero en distribuciones desiguales. Estos resultados señalan a la distribución variable del recurso en 1 M y 15 M antes que la altura como el factor principal detrás de constitución de comunidad de artrópodo de morada de musgo.

INTRODUCTION

The elfin forest of Monteverde, Costa Rica is characterized by soggy soils, high ambient moisture and strong winds. These abiotic factors create a habitat of dwarfed trees with thick moss mats growing epiphytically on their trunks. (Nadkarni and Wheelwright, 2000). These epiphytic moss mats have been found to maintain higher levels of moisture (Allen, 1994) as well as decreased variation in temperature (Conrachen, 1999). This microhabitat provides an ideal environment for arthropods, which are greatly influenced by relative humidity and temperature fluctuations (Bergst, 1995).

The canopy of the elfin forest is characterized by high temperature variation, and increased exposure to wind and sunlight, leading to lower moisture retention despite higher rainfall (Nadkarni and Lowman, 1995). These factors often lead to altered community structure in the canopy. Nadkarni and Longino (1990), working with arthropods in leaf litter on a vertical gradient in Monteverde, found that the abundance decreased from the ground to the canopy for all groups other than ants, and that some taxa were completely absent from the canopy. While the abiotic variation from the ground to the canopy leads to low arthropod abundance it provides an ideal environment for moss, which enjoys an overall higher primary productivity and thus is found in thicker mats in the canopy.

Moss mats are thicker in the canopy due to higher exposure to moisture from mist and rain, as well as greater exposure to light, therefore increasing the amount of photosynthesis. This increased thickness in the canopy should lead to higher retention of moisture as well as more nutrients. The greater habitat area, moisture and nutrient availability may further improve the microhabitat in which arthropods flourish. Booth and Usher (1984) found that increased dry biomass of moss and overall levels of nutrients were directly correlated with arthropod abundance. Furthermore, Tanaka and Tanaka (1982) found that general arthropod abundance in the West Indies was 2.3 times higher during the wet season. Working in Monteverde, Afashi (2001) also found that moss-dwelling arthropod diversity, richness, and abundance all increased with elevation, due to increased levels of moisture found at higher elevations. The findings of these two studies suggest both a heavy dependence of arthropods on moisture, and that moss, in the presence of higher levels of moisture can support more arthropods. This idea is the basis for the possibility that moss found higher in the canopy, having higher nutrients, dry biomass and water content should provide a more suitable environment for arthropods.

The more suitable conditions of moss mats, for arthropods, as compared with other habitats, such as leaf litter, are likely enough to overcome the harsher conditions normally found in the canopy. I hypothesize that species richness, diversity, evenness and number of moss-dwelling arthropods will increase with the height of moss mats, due to the higher levels of moisture, higher moss thickness and greater amounts of nutrients found in the canopy.

MATERIALS AND METHODS

Research was conducted in Monteverde, Puntarenas, Costa Rica in the elfin forest above the Estación Biológica de Monteverde. All work was conducted between 1725m and 1800m. Samples of a single moss morphospecies were collected at 1m, 7m and 15m from trees with dbh greater than 85cm between 0900hrs and 1400hrs. Trees were chosen that had a high abundance of moss and were easily accessible. To normalize the volume of samples a 251cm^3 tuna can was filled by pulling moss off of the trunk by hand and immediately emptying the can into labeled plastic bags. Whenever possible, samples were taken from the north side of trees to control for variation in mist levels arising from Northeast trade winds. As moss was pulled off of the tree any arthropods that were seen on the bark were also collected.

Each moss sample was split in half and placed in a Berlese funnel until completely dry (1-2 days). Mesh was placed over the top of the funnels to prevent outside arthropods from entering. Samples were examined under a dissecting microscope and arthropods were identified to order and morphospecies and placed into labeled vials. The specimens were used as a morphospecies library to help with later identification. Dry moss was examined for any arthropods that had not left the moss.

Control funnels, without moss, were also placed under lights to determine if arthropods that were not in the samples were capable of entering the funnels. The controls were used to calibrate for the number of individuals of each morphospecies present in the funnels that had not come from the samples. This number was then subtracted from the number of the corresponding morphospecies found in the sample funnels.

Statistical Analysis: All Data

Overall species diversity, Shannon-Weiner diversity index, species richness, species number, and S_{marg} were calculated for the three heights, using all of the data. A modified, pairwise t-test was performed on the Shannon-Weiner diversity index to test whether there was a significant difference in diversity between heights. Sorenson's quantitative indices were calculated for each pair of heights and comparisons were made for differences in abundance. Any cases in which orders were absent from a height were noted.

Statistical Analysis: Calibrated Data

The number of individuals of each morphospecies in the control cups was noted and that quantity was subtracted from the morphospecies in the test samples. The same statistical analyses were conducted.

RESULTS

All Data

The lowest species richness, S_{marg}, and number of individuals were found at but the highest diversity and evenness were found at 7m (Fig. 1, 2, 3, 4, and 5). Diversity was significantly higher at 7m than at 15m ($t = 2.17$). The community at heights 1 and 15 were most similar ($Cs = 0.93$), and were least similar at heights 7 and 15 ($Cs = 0.60$). The abundance of individuals at heights 1 and 7 were also fairly dissimilar ($Cs = 0.66$).

Orders Diptera, Coleoptera, Hymenoptera, Acari, Hemiptera, Isopoda, Isoptera, Araneae and the subclass Diplopoda were found at all heights. Lepidoptera and Collembola, and the subclass Chilopoda were only found at one height (15m, 1m, 1m respectively) and at low abundances (Table 1). Gastropoda, the only non-arthropod order, and Orthoptera were found in low abundance at 1m and 15m (Table 1). The most abundant orders were Diptera, Acari, Coleoptera, Hymenoptera and Araneae. Diptera and Hymenoptera (mainly the family Formicidae) had very high abundances at 15m and 1m respectively but in patchy distributions (Table 2). Acari and Coleoptera were most abundant at 15m, while Araneae was relatively consistent at all heights (Table 1).

Calibrated Data

Diversity was significantly higher at 7m than at 15m ($t = 3.09$), and significantly higher at 1m than 15m ($t = 2.27$). The composition at heights 1 and 15 were most similar ($Cs = 0.84$), with heights 7 and 15 being nearly as similar ($Cs = 0.82$). The composition at heights 1 and 7 were most dissimilar ($Cs = 0.66$).

Diptera was the only order that was affected by excluding all control morphospecies. Diptera decreased significantly and was no longer the most abundant order (Table 1).

Table 1. Number of individuals per order by height of moss-dwelling arthropods, and Gastropods, in the elfin forest of Monteverde, Costa Rica. Changes from the calibrated data in parentheses.

	Height (m)			
Order	1	7	15	Total
Orthoptera	1	0	1	2
Isoptera	4	4	8	16
Hemiptera	5	5	4	14
Lepidoptera	0	0	1	1
Diptera	13	5	67 (9)	85 (27)
Coleoptera	11	9	21	41
Hymenoptera	50	3	5	58
Collembola	1	0	0	1
Acari	18	21	27	66
Araneae	7	11	4	22
Isopoda	3	3	2	8
Chilopoda	4	0	0	4
Diplopoda	6	1	2	9
Gastropoda	2	0	3	5
Total	125	62	145	332

Table 2. Abundance by tree of moss-dwelling Formicidae and Diptera in the elfin forest of Monteverde, Costa Rica. Formicidae in parentheses

	Height (m)		
Tree	1	7	15
1	4 (0)	0 (0)	0 (0)
2	4 (0)	0 (0)	0 (0)
3	0 (0)	0 (0)	1 (0)
4	0 (0)	1 (0)	37 (0)
5	1 (0)	2 (0)	0 (0)
6	3 (0)	1 (0)	24 (0)
7	0 (0)	0 (0)	2 (0)
8	0 (0)	0 (0)	1 (0)
9	1 (45)	1 (0)	2 (0)

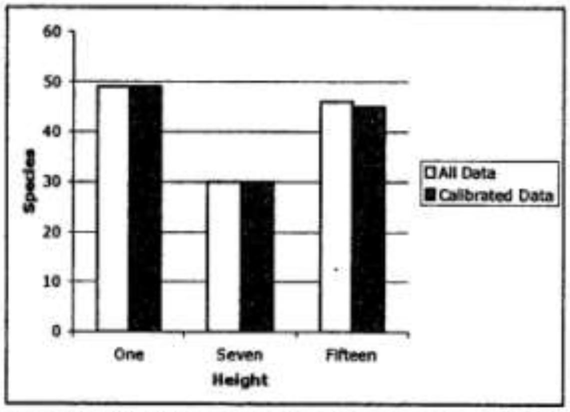

Figure 1. Species vs. height for moss-dwelling arthropods in the elfin forest of Monteverde, Costa Rica. Calibrated data excludes control species

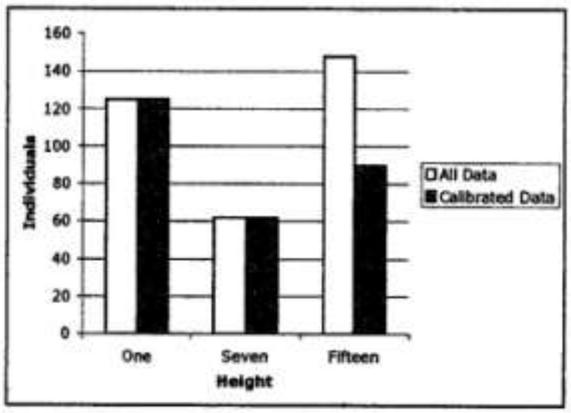

Figure 1. Individuals vs. height for moss-dwelling arthropods in the elfin forest of Monteverde, Costa Rica. Calibrated data excludes control species

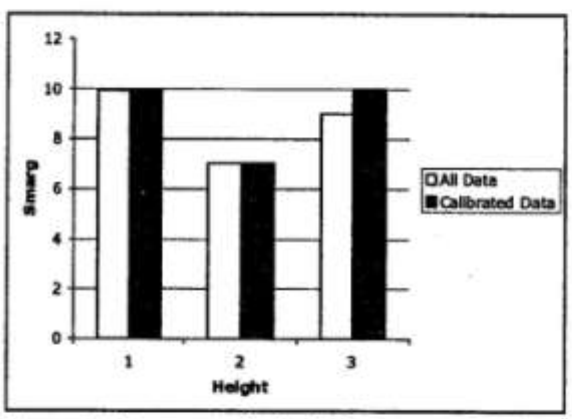

Figure 1. Smarg vs. height for moss-dwelling arthropods in the elfin forest of Monteverde, Costa Rica. Calibrated data excludes control species

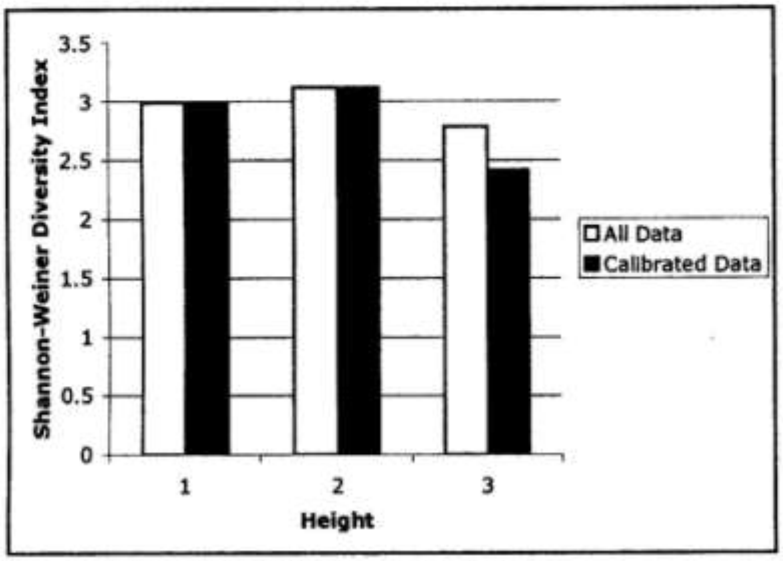

Figure 1. H' vs. height for moss-dwelling arthropods in the elfin forest of Monteverde, Costa Rica. Calibrated data excludes control species

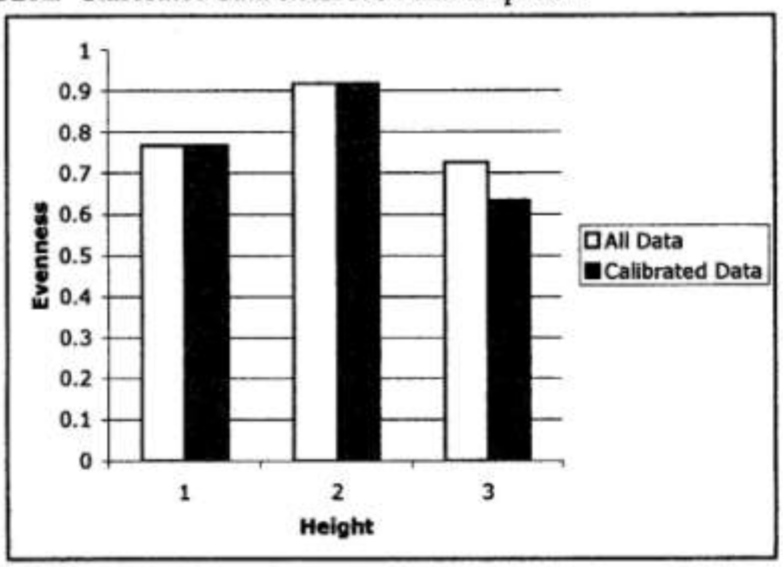

Figure 1. Evenness vs. height for moss-dwelling arthropods in the elfin forest of Monteverde, Costa Rica. Calibrated data excludes control species

DISCUSSION

I hypothesized that species richness, abundance, S_{marg}, diversity, and evenness would increase with height due to the microclimate caused by moss mats. Due to high arthropod abundance at 15m and 1m and the patchy distribution and abundance of morphospecies at these heights it can be concluded that height is not the driving force behind variation in moss-dwelling arthropod communities. The abiotic factors of the canopy appear to be ameliorated by moss mats but the deciding factor for community composition is most likely patchy resource availability at the high and low ends of the trees, which leads to variation in moss mat microclimates across samples. This patchy resource availability comes from varying environmental factors. Sunlight and wind variation are still greatest in the canopy, while at ground level, the most variable factors are sunlight and moisture as well variation in proximity to high abundances of ground dwelling arthropods such as ants. These variations in abiotic factors would lead to patchy distribution of resources and variable abundance of arthropods high in trees and low to the ground. This variation is likely the reason for patchy distribution and abundance of one morphospecies of Formicidae at 1m and one of Diptera at 15m. The high abundance of these two morphospecies leads to the higher evenness and therefore higher diversity at 7m.

In the calibrated data the high abundance of dipterans disappears. This finding is concurrent with the results of Nadkarni and Longino (1990) who did not find a high level of dipterans in canopy or ground leaf litter in Monteverde. In the original data the higher abundance at 15m comes from one morphospecies of Dipterans that was found in variable abundance between samples. The presence of Dipterans in moss can be explained by the fact that they lay eggs in areas with high moisture (Borror, 1989), which would lead to increased numbers of young Dipterans found in moss samples. The higher abundance of Dipterans in the canopy most likely comes from their ability to reach canopy heights, allowing them to use an area that has less competition (Majer, 1990), making them more prone to variation. This would also make them more dependent on resource availability and they would likely be more abundant in moss that is better at retaining moisture and decreasing temperature variation.

The relatively high abundance of arthropods at 1m is due to the presence of 45 individuals of one species of army ant found at one site. Army ants have patchy distributions as they are always moving and have no permanent nest; furthermore they travel in large groups that branch off in many directions to forage for insects (Holldobler and Wilson, 1990). This behavior, could explain why they were only found at one site and in high abundance. The complete lack of ants in any other samples is contradictory to Nadkarni and Longino's (1990) findings, which showed that ants were among the most well represented taxa in leaf litter in the canopy and understory in Monteverde. This contradiction can be explained by Longino (2000) who states that most ants in the Monteverde canopy make their nests on obscure areas of trees such as the ends of branches. The lack of ants in other samples is consistent with the findings of both Majer et al (2001) and Janzen et al (1976) who found reduced ant abundance above 1500 meters as well as very patchy distributions of ants at all elevations. When the findings of these past studies are considered along with the basic foraging behavior of ants it becomes apparent why they would only be found at low heights. Considering these factors, non-ant arthropod abundance is still highest at 15m even with all controls excluded.

Other than Hymenoptera and Diptera, the next most abundant orders of arthropods were Acari and Coleoptera. The abundance of both taxa increased with height. These findings are consistent with Nadkarni and Longino (1990) who also found high Acari and Coleoptera abundance in the canopy. That mites and beetles are abundant at all heights is congruent with the fact that they are both among the most abundant and diverse groups of arthropods on earth (Houck, 1994 and Borror et al 1989). Both Acari and Coleoptera, being such diverse orders would be able to withstand large fluctuations between moss mats; individual morphospecies may change but abundance would remain relatively constant. This is reflected in the high species richness of both orders. Araneae, also a very well represented order at all heights was most likely present as predators in arthropod communities. For all of these orders, abundance was relatively consistent at all heights (table 1). These findings are in contrast to the Nadkarni and Longino study (1990), which showed a decrease in abundance of all arthropod groups, other than ants, with height. Since their study was performed on leaf litter, this difference supports the idea that moss mats create microhabitats for arthropod communities in the canopy.

Another major difference from the Nadkarni and Longino (1990) study comes in the almost complete lack of Collembolans, and the low abundance of Crustaceans. Low abundance of both taxa is most likely due to the fact that both feed on decaying matter and detritus (Borror et al 1989), which is most likely found in low quantity in moss mats.

When compared with the Nadkarni and Longino study (1990), which was also done in Monteverde, my results most likely point to the creation of microhabitats within moss communities that ameliorate the abiotic factors in the canopy. The higher abundance of arthropods at 15m and 1m, caused by the patchy distribution and abundance of one morphospecies each of Diptera and Formicidae reflects a microclimate caused by the moss that does not vary on a vertical gradient but rather from tree to tree dependent on varying resources that stem from patchy abiotic factors.

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