DISCUSSION

Passalid beetles were more abundant under logs with higher microbial activity, probably because higher microbial biomass provides beetles with a larger food source. Logs at an intermediate level of decay may provide an ideal habitat in which passalids can burrow, feed, reproduce. Abiotic factors such as temperature, moisture, and diameter of the log did not appear to be important determinants of abundance. Number of adult beetles was not correlated with number of larvae indicating that passalid beetles do not neccessarily reproduce in the same places they feed. Some logs that appeared to be suitable habitat harbored no beetles (8 of 36 logs), suggesting that beetle distribution patterns could be a function of dispersal as well as habitat quality. If so, there should be a relationship between passalid abundance and the proximity of other logs, but we were unable to test for these spatial patterns in our study.

Because we could not survey mite abundance in the substrate under fallen logs, we are unable to make definitive conclusions about what determines mite abundance and distribution. Beetle size appears to be more important than beetle colony size. We offer two hypotheses to explain patterns in mite abundance: (1) mites feed on some part of the beetle, either a fungus growing on them, or a fluid secreted, and therefore will only be found on beetles, regardless of physical factors, or (2) mites feed on microbes associated with the decaying logs as do passalids, and simply use the beetles for transportation (phoresy) to other logs. Either hypothesis could explain why we found more mites on larger beetles. The mite community probably contained at least two guilds, which we were unable to distinguish: orobatid mites that are grazers of fungi and predatory mites that feed on the orobatids. Further studies examining the relationship between mite abundance in the substrate, mite guild composition, and soil respiration rate could provide insight into the nature of the symbiosis between phoretic mites and passalid beetles.

LITERATURE CITED

White, R.E. 1983. Peterson Field Guides; Beetles. Houghton, Mifflin Company, New York, USA.

SPECIES RICHNESS OF LICHENS IN SUN AND SHADE HABITATS

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Abstract. Comparisons of species richness may depend upon the spatial scale that is considered. Species richness in a localized area may or may not be representative of species richness in habitat patches or across habitat patches. We compared species richness at different spatial scales in the lichens that occupy logs in sun and shade habitats at Cerro de La Muerte, Costa Rica. Lichen densities and total species richness were greater on logs in the sun than on logs in the shade. Competition with mosses likely limits lichen density in shade habitats. Within each habitat, species richness increased as sample area and the number of logs sampled increased. Average species richness within 15 x 15 cm plots was greater in the sun than in the shade (4.7 vs. 2.7 species per plot). Thus, more species of lichens coexisted in close proximity in habitats with higher lichen abundanceWithin an average log in the sun habitat, compare to an average log in the shade habitat, the cumulative number of species increased more quickly with increased sample area. Furthermore, the increase in species richness with the addition of new habitat patches (logs) was greater in the sun habitat than in the shade habitat. The increase in species richness across logs suggests that logs within habitats differ in their suitability for different lichen species, or that there are limitations on lichen dispersal among logs, or both. Because of competative exclusion by mosses, lichens may attain their greatest densities and diversity in habitats (dry sunny logs) where they have lower growth rates than in other habitats (moist shaded logs). If so, lichen species most common in shade habitats may be those with the highest intrinsic growth rates and strongest competitive abilities.

Key Words: lichens,, diversity, species richness, alpha diversity, beta diversity, gamma diversity

INTRODUCTION

Lichens exist where few other organisms can survive by enduring extreme environmental conditions such as high levels of dessication. Lichen density increased with canopy openness in Cerro de la Muerte, Costa Rica, presumably due in part to the ability of lichens to withstand high levels of irradiance (Hansel et al. 1996). High lichen density could result from a few lichen species dominating an environment or from a diverse community of coexisting lichen species. We tested whether species richness of lichens was higher in sun habitats than in shade habitats. Because patterns of species richness can differ at different spatial scales, we compared species richness in small subplots (15 x 15 cm), and tested for differeneces between habitats in the rate at which new species were added with the inclusion of subplots in the same habitat patch (a fallen log) and with the inclusion of other habitat patches (other fallen logs).

METHODS

We compared lichen diversity and abundance on the trunks of fallen trees in sunny and shaded habitats of an old growth *Quercus*-dominated forest on 28-29 January, 1998 at Estacion Biologica Cuerici, Cerro de la Muerte, Costa Rica. The study site was at 2900 ± 100 m elevation. Within each habitat, we sampled lichens in ten 15 x 15 cm plots on each of eight haphazardly selected fallen logs. Beginning at one end of each log, we sampled plots every 25 cm along a longitudinal transect centered on the top of the log, alternating plots on either side of the transect. Within each plot, we recorded the presence and absence of 67 recognized morpho-species of lichen. We also recorded total percent cover of lichen, total percent cover of moss, and percent uncolonized space. For consistent lichen identification, we used a voucher catalog of morpho-species that we carried with us throughout the sampling. Lichen morpho-species were classified as one of four morphotypes (crustose, foliose, fruticose and thread-like). We measured canopy coverage over each log with a spherical densiometer.

We compared lichen diversity between habitats at three levels of increasing spatial scale. We defined alpha diversity as the average number of species per 15 x 15 cm plot. Beta diversity was defined as the rate at which new species accumulated as the sample area increased from one plot to ten plots within a log.

Gamma diversity was defined as the increase in number of species per eight 15 x 15 cm sample plots if those plots were taken from eight different logs (Quantity A) compared to if they were taken from a single log (Quantity B). Quantity A was estimated as the average total number of unique species found in five random samples of eight 15 x 15 cm plots, with each plot drawn from a different log. Quantity B was estimated as the average total number of unique species per eight 15 x 15 cm plots drawn from the same log. For Quantity B, we derived one estimate for each log based on eight random samples of eight 15 x 15 cm plots, then averaged the individual estimates for each log.

We used an ANOVA to compare canopy coverage and percent of log substrate covered in sun and shade habitats. Alpha diversity was compared between habitats using a nested ANOVA with habitat as a fixed effect and logs nested within habitat as a random effect. Beta and gamma diversity were compared between habitats with a student's t-test. We used chi-square analyses to test the null hypothesis that proportions of the four lichen morphotypes would be the same in sun and shade habitats.

RESULTS

We found 67 species of lichens in 160 15 x 15 cm plots. Canopy coverage (± SE) averaged 33.4 ± 5.0 % over logs in the sun habitat vs. 91.3 ± 1.2 % over logs in the shade habitat (F_{14} = 126.12, P < 0.001). As reported by Hansel et al. (1996), lichens were more abundant in the sun habitat than the shade habitat and mosses showed the opposite pattern.

Species richness per 15 x 15 cm plot (alpha diversity) was higher in the sun habitat than in the shade ($F_{1, 14}$ = 5.65, P = 0.032; Table 2). In the sun habitat compared to the shade habitat, there was a greater increase in species richness as sample area increased from one 15 x 15 cm plot to ten 15 x 15 cm plots (higher beta diversity, compare slopes in Figure 1; T_8 = 2.73, p < 0.05; Table 2). For both habitats, species richness in eight plots was greater when plots were drawn from different logs (Quantity A from methods, solid squares in Figure 2) compared to when plots were drawn from the same log (Quantity B in methods, open squares in Figure 2). This difference was significant in the sun habitat (T_7 = 3.39, P < 0.01; Fig. 1) and nearly significant in the shade habitat (T_7 = 1.95, P < 0.10). The increase in species richness as samples are drawn from across logs vs. within logs (gamma diversity, difference between solid and open squares in Figure 1) was 7.4 species vs. 4.2 species.

Sun and shade habitats contained similar proportions of lichen species of each morphotype (Table 3). However, there were differences between habitats in the representation of morphotypes as species occurrences (where one species occurrence = one species of a particular morphotype within one plot; Table 3). Overall, 30 of 50 species in the sun habitat were restricted to the sun habitat in our sampling (unique species, compared to 17 of 36 species in the shade habitat). Furthermore, the two habitats differed in the proportion of unique species representing the four morphotypes (Table 3), with the species richness of crustose morphotypes being much higher in the sun habitat than in the shade habitat. The relative frequency of rare and common species was similar between the sun and shade habitats (Fig. 2). Of the 67 species, fifteen appeared in only one plot, while two ubiquitous species of thread-like lichen occurred in 35 - 45% of all plots.

TABLE 1. Abundance of lichens and mosses, and amount of uncolonized area in sun and shade habitats. F-statistic tests the null hypothesis that habitats do not differ.

	% coverage		$F_{1, 14}$	P
	Sun	Shade		
Lichen	39.5	9.00	15.7	0.001
Moss	26.9	51.9	3.83	0.07
Uncolonized	33.6	34.1	0.22	0.64

TABLE 2. Alpha, beta and gamma diversity between sun and shade habitats (mean ± SE).

	α-diversity[a]	β-diversity[b]	γ-diversity[c]
Sun	4.71 ± 0.54	1.37 ± 0.16	7.40
Shade	2.71 ± 0.64	0.84 ± 0.12	4.20

[a]Each SE based on SD and n of 8 logs.

[b]Each SE based on SD and n of 8 plots.

[c]It was not possible to estimate SEs for γ-diversity,

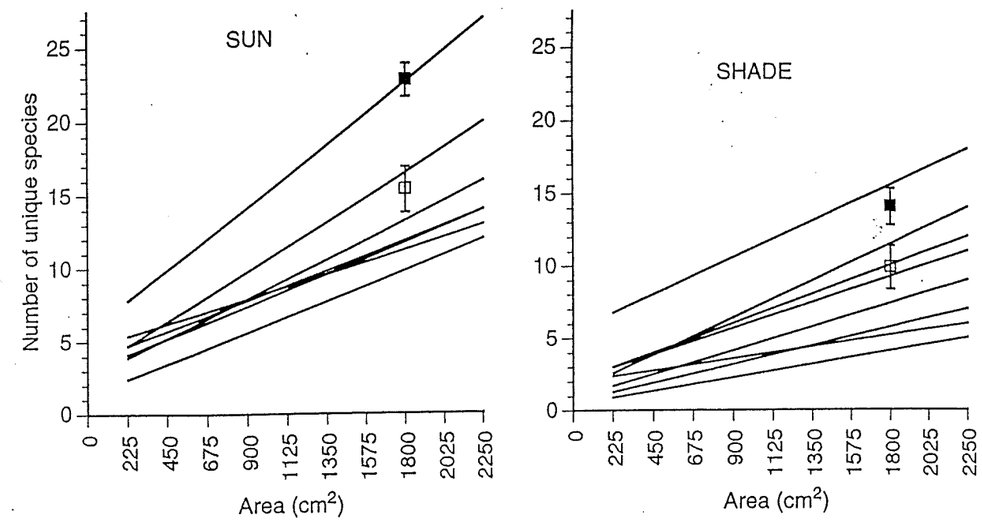

FIG. 1. Species richness in sun and shade habitats. Each line represents one log, with the endpoints indicating the average number of species per subplot (at 225 cm^2) and the total number of species in all 10 subplots (at 2250 cm^2). The slope of the lines represents beta diversity. the difference between the open and closed symbols at 1800 cm^2 represents gamma diversity (the increase in species richness if the 8 subplots are taken from 8 different logs vs. a single log).

TABLE 3. Distribution of lichen species between sun and shade, within four morphotype categories. Chi-square statistics test the null hypthesis that the proportion of species (or occurrences) representing the morphotypes did not differ between habitats (df = 3).

	Number of species		Number of occurrences		Number of species unique to habitat	
	Sun	Shade	Sun	Shade	Sun	Shade
Crustose	23	10	92	54	17	5
Foliose	12	15	88	80	5	8
Fruticose	7	4	78	6	5	2
Thread-like	8	7	123	78	3	2
	χ^2 = 4.17		χ^2 = 40.72***		χ^2 = 5.55*	

* P < 0.05; ** P < 0.01; *** P < 0.005

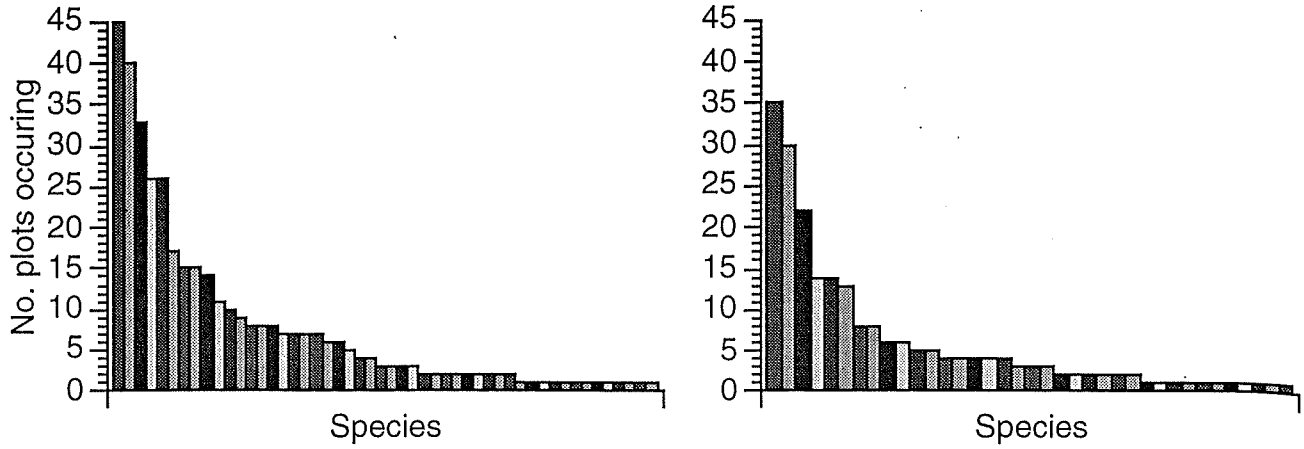

FIGURE 2. Pattern of ranked species abundance in sun and shade habitats.

DISCUSSION

There was higher abundance of lichens, in the sun habitat, as previously reported for this study site (Hansel et al. 1996). Furthermore, the sun habitat, compared to the shade habitat had higher species richness of lichens across all three spatial scales that were investigated (alpha, beta, and gamma diversity). The greater alpha diversity within plots in the sun habitat indicates that more species of lichens coexisted in close proximity in habitats with higher lichen abundance. Higher beta and gamma diversity in the sun habitat indicate that the number of species increases at a greater rate with increasing area in the sun habitat, both as area is added within a habitat patch (log) and as additional habitat patches are added. There was a greater increase in species richness when area is added from another log vs. area added on the same log in both habitats (gamma diversity). This suggests that logs within a habitat differ in their suitability for different lichen species, or that there are limitations on lichen dispersal among logs, or both.

Interspecific competition with mosses may be a key limitation on lichen diversity in the shade habitat. In the sun habitat, low water availability probably limits moss growth and survival, leaving more vacant substrate for colonization by lichens. However, lichens have very low intrinsic growth rates (compared to mosses or perhaps any other photosynthetic organisms). Consequently, wherever moisture availability allows the growth of mosses or other competitors (e.g., on shady logs), lichens are likely to occur in reduced abundance even if the shaded, moister logs could provide more rapid lichen growth in the absence of competitors. This hypothesis could be tested in long term studies of lichen growth rates in sun and shade habitats with and without the removal of competitors. If this hypothesis is true, lichen communities attain their greatest diversity in habitats that do not allow the highest potential growth rate (dry, sunny logs). An additional prediction of this model is that the lichen species that occur most commonly in shaded habitats are those with the highest intrinsic growth rates and perhaps the most efficient dispersal systems. Comparisons of competitive abilities and dispersal efficacy in sun and shade lichen species could be a fertile area for future research.

LITERATURE CITED

Hansel, C. H, J. Z. Ruben, and P.P. C. Shelby. 1996. "Influence of abiotic factors on lichen and moss community structure in a high elevational tropical habitat." Pp. 57-61 *in* A. L. Mannan and D. S. Canny, editors. Dartmouth Studies in Tropical Ecology. Dartmouth College, Hanover, NH. USA.