INFLUENCE OF ABIOTIC FACTORS ON LICHEN AND MOSS COMMUNITY STRUCTURE IN A HIGH ELEVATION TROPICAL HABITAT

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Abstract. Moss and lichen distribution was examined over a range of abiotic factors at the Cuerici Biological Reserve in Costa Rica. The importance of abiotic factors in general, and the relative influence of individual factors, varied across hierarchical levels of community organization. Diversity and species richness increased with elevation, while total coverage did not correlate with any of the abiotic factors measured. Lichen increased with light and decreased with moisture. Moss increased with moisture and decreased with light. Structurally similar functional groups showed a broad array of complex responses to most environmental variables measured, while only half of the individual morphotypes sampled responded to abiotic influences. These results suggest that processes which generate patterns in community properties such as diversity differ from those responsible for distributions of individual species or higher taxa.

Key words: Abiotic factors, bryophytes, community structure, diversity, elevational gradients, lichens, mosses.

"I am but slight lichen, you are my rock, and there ain't nothing gonna scrape me off."

INTRODUCTION

The community structure of bryophytes and lichens is presumbably shaped by the complex interplay of many factors including competition, dispersal, and the abiotic environment. For example, abiotic environmental gradients may directly limit distribution of a species, or may indirectly alter the outcome of interspecific competition. Lichens and mosses can provide dramatic insight into how environmental conditions can determine community structure because they have less well defined vascular systems and less differentiation into specialized organs. This simplicity limits the range of possible physiological responses and life history strategies that they can utilize to respond to shifting abiotic variables. Lichens and mosses, two physiologically distinct taxa with very different life histories, coexist across broad environmental gradients in the cloud forest. If they vary in their responses to the abiotic environment, this suggests that the effects of environmental factors on community structure is, in part, a function of the physiology of organisms within the community.

While physiology may influence distribution and abundance of individual taxa across environmental gradients, other processes like dispersal and disturbance may drive community-level patterns of diversity and richness. Because different processes may be important at different levels of organization, the lichen and moss community as a whole may show patterns that cannot be easily predicted from patterns and processes at the level of populations or individuals. We searched for evidence of community organization at four hierarchical levels: the lichen and moss community, lichens and mosses as taxa, functional groups of species that share similar morphological characteristics and individual morphotypes. If there are emergent properties at the community level, composite variables such as species richness, diversity and total cover should respond to different suites of abiotic factors than do individual taxa or functional groups.

METHODS

Moss and lichen coverage was examined in relation to four abiotic gradients: moisture, bark characteristic, canopy coverage, and elevation. Sampling was done on 25-26 January 1996 at the Cuerici Biological Reserve, a *Quercus*-dominated forest at 2700-3000 m asl, in Costa Rica. At 30 study sites, each separated by 100 meters, an area of 200 cm^2 was examined on a randomly selected portion of the nearest fallen log, standing tree, and overhanging branch. Percent cover was estimated for all lichens, mosses, and other species. Substrate moisture was ranked on an ordinal

scale of increasing wetness from 1 to 5. Bark texture was classified as rough, moderate or smooth. Canopy coverage was estimated as percentage of sky visible through an imaginary core (30 m in diameter) extending up from the sample site. Elevation was ranked on an ordinal scale of increasing altitude from 1 to 4. Mosses and lichens were separated into 83 morphotypes, which were then divided into 11 functional groups according to morphological similarities (Figure 1).

Covariance between environmental variables was small ($r^2 < 0.25$ for all correlations), so stepwise multiple regressions were used to isolate factors that explained the most variance in percent cover of each taxa. We developed similar multiple regressions models for other dependent variables including the 11 functional groups, total moss and lichen cover, moss and lichen richness, total species richness, and Shannon-Weiner Diversity Index. We only report relationships that were significant in the multiple regression (a = 0.05). Interactions that seemed to result from only one or two outlier sample plots were considered spurious and were excluded.

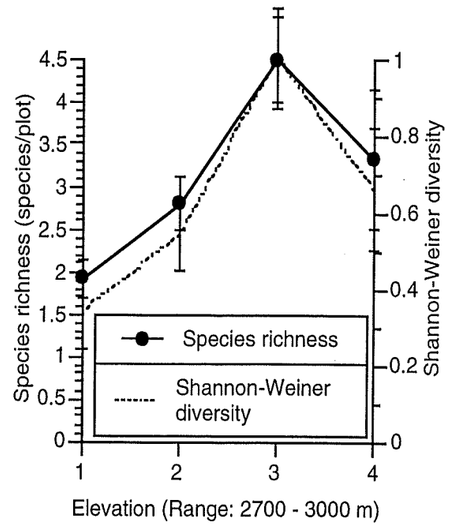

Fig. 2. Species richness and Shannon-Weiner diversity for mosses and lichens at as a function of elevation at Cuerici Biological Reserve, Costa Rica.

Results

Species richness in the moss and lichen community was greatest at elevation three (≈ 2850-2925 m asl, Figure 2). Lichen richness increased with elevation, but moss richness did not correlate with any environmental factors. Shannon-Weiner diversity responded similarly to elevation, and also increased with canopy openness (Figure 3). As canopy openness increased, lichen cover increased but moss cover decreased (Figure 4). The opposite was true of substrate moisture: moss cover increased with moisture, and lichen cover decreased (Figure 5).

Of the 11 functional groups, 4 responded to water, 1 responded to elevation, and 1 responded to canopy openness (Table 1). For 4 functional groups, no factor was significant. Three functional groups showed significant interactions: creeping low mosses were particularly abundant on logs in high light conditions; high moisture had a strong positive effect on mosses that stuck up from the substrate when they grew on trees but not on logs; and branching lichens grew at lower light levels in wet habitats than they did in dry habitats.

Of the 83 morphotypes, 43 appeared in only one plot (Figure 6). We analyzed the 8 morphotypes that appeared in at least 10 percent of the tree and log

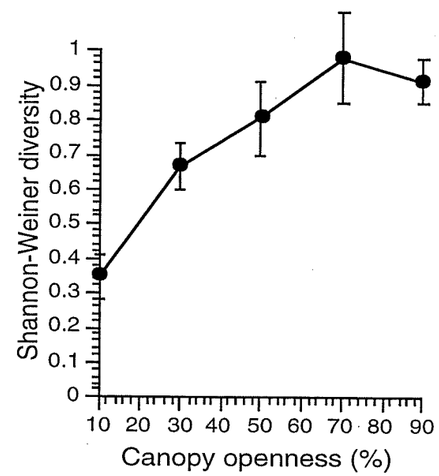

Fig. 3. Shannon-Weiner diversity for mosses abd lichensas a function of canopy openness at Cuerici Biological Reserve, Costa Rica.

plots. Of these, 1 morphotype decreased in abundance with elevation, one with water, and 1 with canopy openness. For another morphotype, cover increased with light on logs but not on trees. Percent cover of one morphotype peaked at higher moisture levels on logs than on trees.

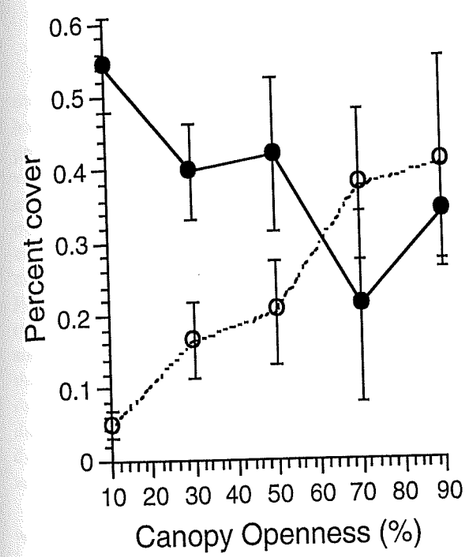

Fig. 4. Lichen and moss cover as a function of canopy openness at Cuerici Biological Reserve, Costa Rica.

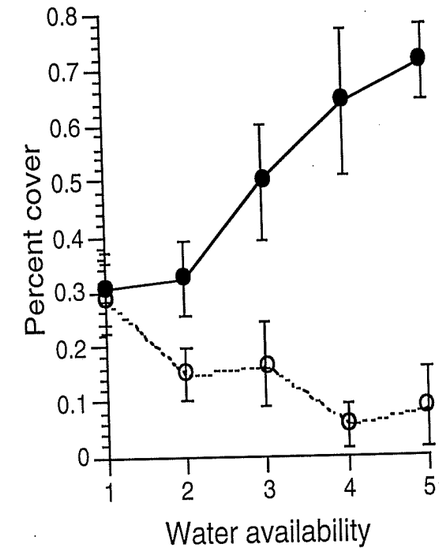

Fig. 5. Lichen and moss cover as a function of water level at Cuerici Biological Reserve, Costa Rica (higher numbers = greater moisture).

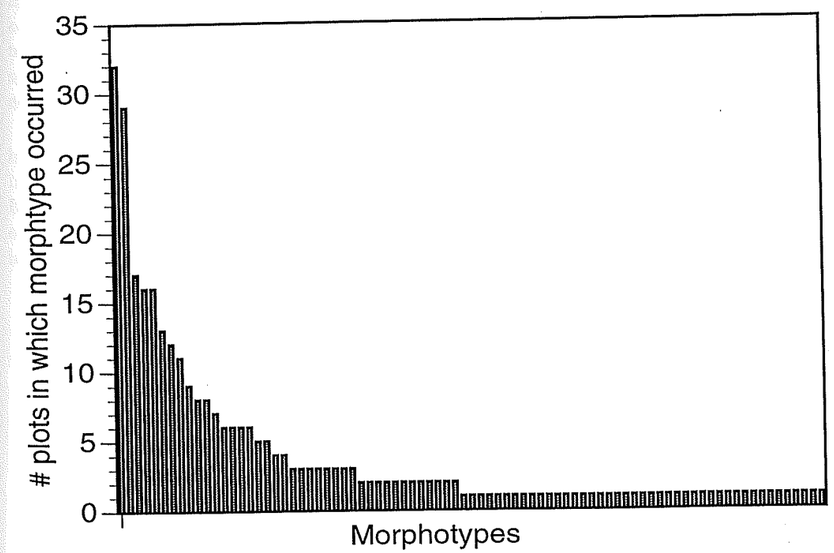

Figure 6: Occurrence frequency of 83 lichen and moss morphotypes in 90 plots placed on logs, trunks and branches at Cuerici Biological Reserve, Costa Rica.

Table 1. Main effects and interactions of abiotic factors on an assortment of dependent variables describing lichen and moss communities at Cuerici Biological Reserve, Costa Rica. Models developed using stepwise multiple regressions (n = 60 sample plot except as noted)

	Main effects					Interactions				
Dependent variable	Habitat b	Elevation	Water level	Canopy openness	Habitat elevation	Habitat x water	Habitat x canopy	Elevation x water	Elevation x canopy	Water x canopy	r 2 for model.
Species richnessa		++									0.09
Shannon-Weiner diversity		+									0.20
Total cover				+							—
Moss richnessa											—
Moss cover			+++							+	0.29
Lichen richnessa		+++									0.16
Lichen cover			-								0.25
Functional groups c				+++							0.25
Branching moss, no microphylls					-						0.08
Thick not grassy moss		—	+								0.25
Moss which sticks up from substrate			-					++			0.14
Creeping low moss							—				—
Grassy moss				+							0.20
Broad microphylls											—
Hanging moss											—
Hanging moss with no microphylls			-								0.13
Crustose lichens											0.30
Foliose lichens			-								—
Branching lichens										+++	0.32

a Analysis includes data from branch, log, and trunk plots (n = 90).
b Habitat is defined as log, trunk or branch.
c Dependent variables are percent cover attibuted to each functional group.
- negative relationship, p < 0.05; -- negative relationship p < 0.01; --- negative relationship, p < 0.001;
+ positive relationship, p <0.05; ++ positive relationship, p < 0.01; +++ positive relationship, p < 0.001.

Discussion

The importance of abiotic factors in general, and the relative influence of individual factors, varied across levels of community organization. Different processes may generate the patterns we observed at various levels of the community. Species richness and diversity of the entire bryophyte and lichen community were affected by elevation, and, to a lesser extent, light levels; whereas the abundance of both mosses and lichens was affected by water and light. Functional groups showed a broad array of complex responses to most environmental variables measured. At the lowest level, only about half of the eight morphotypes frequent enough to be analyzed responded to abiotic influences. This suggests that distributions of species may be linked to factors we did not measure such as disturbance, competition, and/or dispersal.

The increase in richness with elevation contrasts with the pattern of decreasing richness with increasing elevation observed in many other communities (Begon et al. 1990). This pattern seemed driven by lichen richness since moss richness increased only slightly with elevation. If lichen is dispersal limited, increased richness may be the result of higher winds at higher elevation. Total percent cover did not appear to be affected by any abiotic factors. The extent of moss and lichen communities on logs and trees may instead be limited by periodic disturbances such as bark sloughing or the dynamic growth and decay of the organic substrate.

Mosses and lichens were both strongly influenced by light and moisture gradients, but they showed inverse responses to both factors (Figures 4 and 5). Both groups require the same basic resources— nutrients, light, and water— but their responses may be influenced by their different physiologies and life histories. Water, for example, may be particularly important to moss because of its free-swimming gametes. In addition to physiological constraints, the inverse responses we observed in moss and lichen may result from competition whose outcome is dependent on environmental factors. Alternatively, past competition may have resulted in niche differentiation that is no longer reinforced by contemporary selection.

The distributions of 7 of the 11 functional groups correlated with abiotic factors. Moss and lichen morphology may be related to environmental adaptation, or morphologies may simply correspond to taxonomic divisions whose members exhibit similar responses to the abiotic environment.

The structure of moss and lichen communities is strongly affected by abiotic factors, but the factors affecting community variables like diversity and richness do not necessarily appear to be those influencing functional groups or individual taxa. Future studies of community structure should focus on elucidating mechanisms responsible for patterns observed at different levels of community organization. Dynamic processes affecting substrates might limit the influence of environmental gradients, and might explain community-level patterns such as the large area of apparently favorable substrate that remains free of mosses and lichens. Given the relatively slow growth rate of mosses and lichens, disturbance may have long-lasting effects on patterns of abundance and diversity.

Literature Cited

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