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ABSTRACT

Climate change is causing decreased moisture levels during the dry season on the Pacific slope of the Monteverde cloud forest in Costa Rica. This alteration could be harmful to the abundant epiphytic, poikilohydric bryophyte and lichen community by causing range shifts, which could lead to local extinctions. I investigated the potential impact of changing moisture levels by establishing a baseline of the current distribution of bryophytes, bare bark, and crustose, foliose, and fruticose lichens between 1550-1750m in the cloud forest at the Monteverde Biological Station. I determined the percentage cover of each organism and the canopy cover for each cardinal direction at intervals of 20m of increasing elevation. I found a higher abundance of bryophytes and a lower abundance of crustose lichens at the higher elevations while the foliose and fruticose lichens did not illustrate a trend. There was a strong negative correlation between the bryophytes and crustose lichens that seemed both causal and correlated with elevation.

Distribución de líquenes y briófitos en un gradiente altitudinal del bosque nuboso de Monteverde, Costa Rica

RESUMEN

El cambio climático está menguando el nivel de humedad durante la estación seca en la Vertiente del Pacífico de Monteverde, Costa Rica. Esta alteración podría perjudicar la abundancia de la comunidad de plantas epífitas como briófitos poiquilotermos y líquenes al causar cambios en los rangos de humedad, lo que podría promover extinciones locales. Investigué el impacto potencial del cabio de los niveles humedad estableciendo una línea de base de la distribución actual de briófitas, corteza desnuda, y líquenes incrustantes, foliosos y fruticosos entre los 1550 y 1750 metros de elevación en la Estación Biológica Monteverde. Determiné el porcentaje de cobertura de cada organismo y del dosel en cada punto cardinal a intervalos de 20 m de incremento en elevación. Encontré mayor abundancia de briófitas y menor abundancia de líquenes incrustantes en las elevaciones altas, mientras que los líquenes foliosos y fruticosos no mostraron ninguna tendencia. Hubo una correlación negativa entre briófitos y líquenes incrustantes que pareció tanto causal y correlacionado con la elevación.

Climate change is altering the precipitation regimes of cloud forests (Karmalkar et al. 2008; Goldsmith et al. 2013; Nair et al. 2003), which could cause an organismal range shift. Highly abundant and diverse communities of lichens and bryophytes are found in the lower montane wet forest (1450-1600m) and lower montane rain forest (1550-1850m) of the Monteverde cloud forest, because frequent mist and clouds are characteristic of these zones along with a mean annual rainfall of 1850-4000mm and 3600-8000mm, respectively (Nadkarni and Wheelwright 2000). Increasing sea surface temperatures may be leading to an increase in the base height of the cloudbank thus producing longer mist-free periods along the Pacific side of the Monteverde cloud forest during the dry season (Karmalkar et al. 2008; Goldsmith et al. 2013; Nair et al. 2003). Longer dry periods and a decrease in vertical and horizontal rainfall could cause moisture stress that would be detrimental to the epiphyte community (Karmalkar, Bradley, and Diaz 2008), which includes both bryophytes and lichens. Moisture levels increase with elevation in the cloud forest, thus the rising cloudbank and decreased precipitation during the dry season could lead to a range shift of lichens and bryophytes. Vegetative range shifts can lead to the loss of a species or population as the habitable range of an organism decreases or as invading organisms capable of thriving under the new climatic conditions outcompete the pre-existing organism (Saikkonen et al. 2012).

Varying tolerances to saturation is a distinctive difference between lichens and bryophytes. They are poikilohydric, meaning that they cannot regulate water loss and thus their water content is determined by their surroundings. Lichens are composed of both a mycobiont (fungus) and a photobiont (algae or bacteria), which photosynthesizes and transfers carbon to the fungus (Brodo and Sharnoff 2001). Lichens can have three life forms—crustose, foliose, and fruticose—that vary in morphology and physiology (Brodo and Sharnoff 2001). Crustose lichens have a lower surface area to volume ratio that supports greater tolerance to desiccation and they are less likely to be found at higher elevations where foliose and fruticose lichens are generally more prevalent (Bässler et al. 2015). Foliose and fruticose lichens may be more common at higher elevations because their branched morphology better allows them to take advantage of the higher moisture conditions thereby outcompeting the crustose lichen (Bässler et al. 2015). However, for lichens maximal rates of photosynthesis seem to be reached at around 35-70% saturation, and prolonged saturation may even cause death (Mulkey, Chazdon, and Smith 1996). Mosses, liverworts, and hornworts are bryophytes and, unlike lichens, they prefer the perpetually saturated conditions of the cloud forest (Lowman and Bruce 151-158). However, they are also capable of withstanding desiccation under drier conditions (Proctor 2007), which may permit an overall larger range than lichens.

Lichens and bryophytes illustrate similarities in their reproductive strategies, as most of these two types of organisms are able to reproduce sexually and asexually. Foliose and fruticose lichens can reproduce sexually and asexually, though many genera of crustose lichens depend on sexual reproduction because they do not have specialized vegetative structures (Bowler and Rundel 1975). Foliose and fruticose lichens reproduce asexually through vegetative fragmentation during which a portion of the lichen breaks off and, if transported to a suitable habitat, is able to grow (Bowler and Rundel 1975). These life forms also have sexual pathways for reproduction through spores or reproductive structures (Bowler and Rundel 1975). Sexual reproduction can be less successful than vegetative propagules because with the former the structures must land near a free-living photobiont, which is rare (Bowler and Rundel 1975;

Lutzoni and Miadlikowska). This is a limitation that bryophytes do not face, though they also reproduce sexually and asexually. For sexual reproduction, the spores are wind-disseminated and germinate if they land in an appropriate habitat (Vashishta 2). Asexual reproduction occurs when part of the bryophyte gametophyte is separated and dispersed or gemmae, undifferentiated cells, are released and able to reach suitable substrate (Ramawat, Mérillon, and Shivanna 69). As these two organisms both require an available space on similar substrate, there is likely a competition for space.

Elevational gradients may be seen as a way to study the effects of global warming and the underlying purpose of my study is to establish a baseline of the distribution of epiphytic lichen life forms and bryophytes in the Monteverde cloud forest at the Monteverde Biological Station. I hypothesized that the different tolerances of bryophytes and lichens to moisture would cause a distinctive prevalence along an elevational gradient. I predicted an increase of bryophytes, fruticose lichens, and foliose lichens with elevation and a subsequent decline in the abundance of crustose lichens. The crustose lichens are tolerant of dry conditions, but the high moisture levels present at the higher elevations of the Monteverde cloud forest may not provide an environment conducive for the growth of these lichens; however, bryophytes do not face this limitation. Additionally, I predicted that the wider range of moisture conditions that bryophytes are able to tolerate would lead to an overall greater abundance of this organism. This investigation aimed to compare the abundance and distribution of lichens and bryophytes along an elevational gradient in the Monteverde Biological Station cloud forest from 1550m to 1750m.

MATERIALS AND METHODS

I conducted my observations along the Principal and Division Trail at the Monteverde Biological Station in Costa Rica during the second week of May 2016. This area is primary forest that experiences occasional disturbances by landslides. I sampled two trees from the sides of the trail (based on their accessibility) at 20m increments from 1550m to 1750m, resulting in a sample size of 22 trees. I used an altimeter, calibrated daily, to determine elevation. I estimated percentage cover of bryophytes (Figure 1), bare bark, and crustose (Figure 2), foliose (Figure 3), and fruticose lichens (Figure 4) using a 12cm^2 gridded transparency with 9 squares and a total of 54 holes 6mm in diameter (a standard hole punch size) (Figure 5). For each tree, I measured diameter at breast height (dbh) and tied a string 6cm above this point. I then pinned the transparent grid to the string on the northern side of the tree, determined using a compass, and identified the organism beneath each circle within each square of the grid. In order to correctly ascertain the identity of each organism, I used a photographic guide compiled by José Luis Chaves and conferred with Fern Perkins, who is affiliated with the Monteverde Institute. Additionally, I measured canopy cover with a spherical densiometer. I repeated this procedure for the east, south, and west side of the tree. I marked the tree with flagging tape so that I could return if necessary.

I used R programming (R Core Development Team, 3.1.2) for the statistical testing. I performed ANOVA tests to measure the differences between mean organismal cover and their potential interactions with elevation, canopy cover, dbh, and cardinal direction. Additionally, I performed a correlation to measure the interaction between the bryophyte and crustose lichen cover and a regression to test the interaction between the proportion of bryophyte and crustose lichen cover with increasing elevation.

Figure 1. Mat of bryophytes at 1700m

Figure 2. Crustose lichens at 1600m (left) and 1500 m

Figure 3. Foliose lichen with fruiting bodies (red) at 1700m

Figure 4. Fruticose lichens at 1650m (left) and 1500m

Figure 5. The transparent grid was pinned 6cm above dbh for each cardinal direction and used to determine percentage cover by identifying the organism beneath each hole-punched circle.

RESULTS

I identified 4,637 organisms or sections of bare bark beneath the holes of my transparent grid: 2,955 (63.7%) bryophytes, 798 (17.2%) crustose lichens, 700 (15.1%) bare bark, 169 (3.6%) other organisms, 13 (0.3%) foliose lichens, and 2 (0.04%) fruticose lichens (Figure 6). The northern and western aspects, facing away from the valley, had identical average canopy cover at 95.0% while the southern aspect had 93.2% and the eastern aspect had 92.4% average canopy cover. The overall average canopy cover was 93.9%. The average dbh was 18.7 ± 7.6cm.

The data reveal that bryophyte cover increased (Figure 7; R^2=0.23, P=0.02, N=22) while crustose lichen cover decreased (Figure 8; R^2=0.37, P=0.003, N=22) with increasing elevation. I expected an increase in fruticose and foliose lichen with elevation, but they were both rare within my sampling area. Thus, along the elevational gradient, only crustose lichens and bryophytes exhibited significant changes in abundance. These two types of organisms displayed a strong negative correlation, with crustose lichen abundance decreasing as bryophyte abundance increased (Figure 9; r=-0.85, P<0.001, N=22). Additionally, the proportion of crustose lichens to byrophytes decreased with increasing elevation (R^2=0.19, P=0.04, N=22). Furthermore, there was overall a greater abundance of bryophytes in comparison to crustose lichen (t_{41}=7.80, P<0.001). The three-way ANOVA between organismal cover and cardinal direction, dbh, and canopy cover did not yield significant interactions.

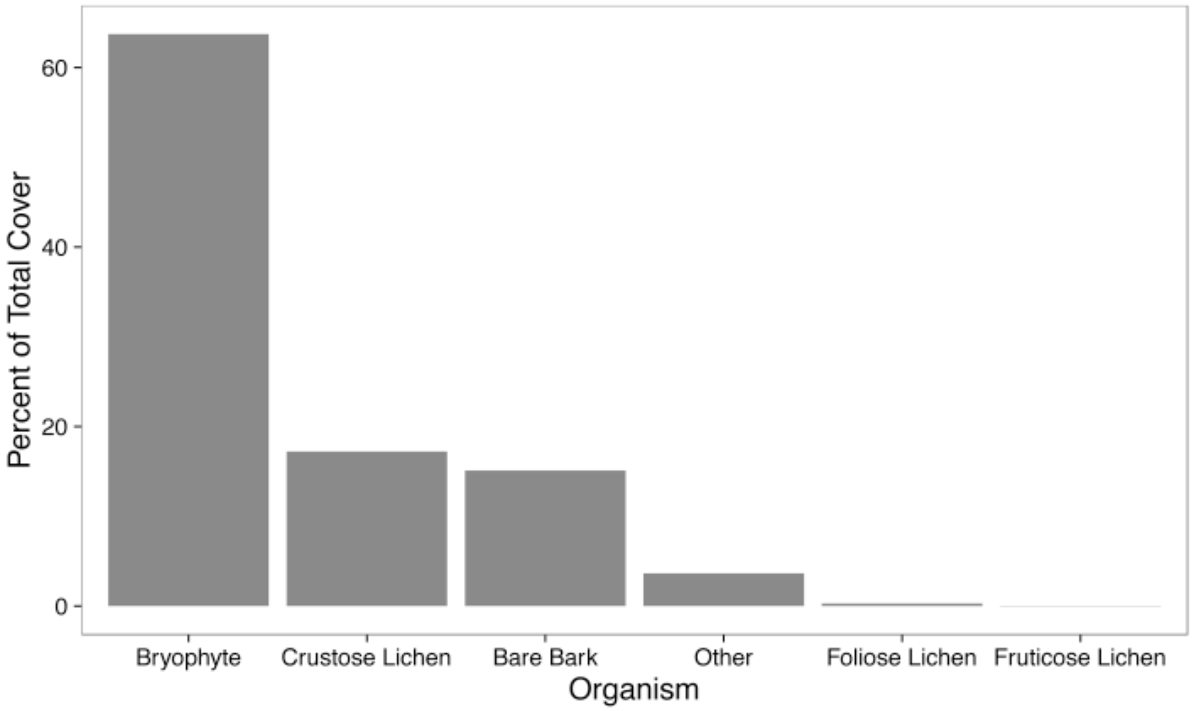

Figure 6. The percentage of each organism found using the transparent grid across the 22 trees and cardinal directions. The percentage is out of the total 4,637 identifications.

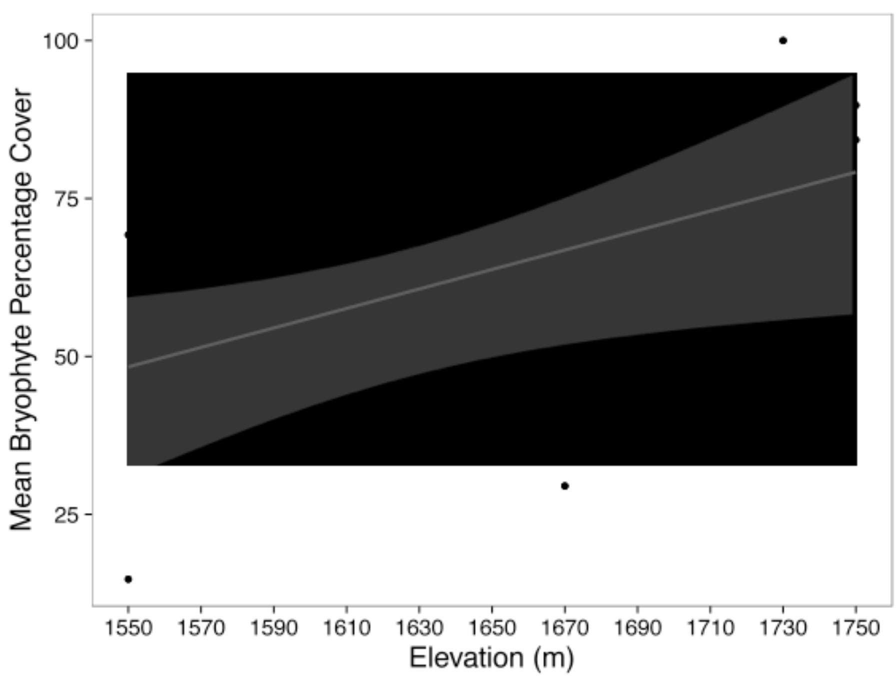

Figure 7. Mean bryophyte percentage cover across cardinal direction for the 22 trees increased with elevation. The shaded portion represents a 95% confidence interval.

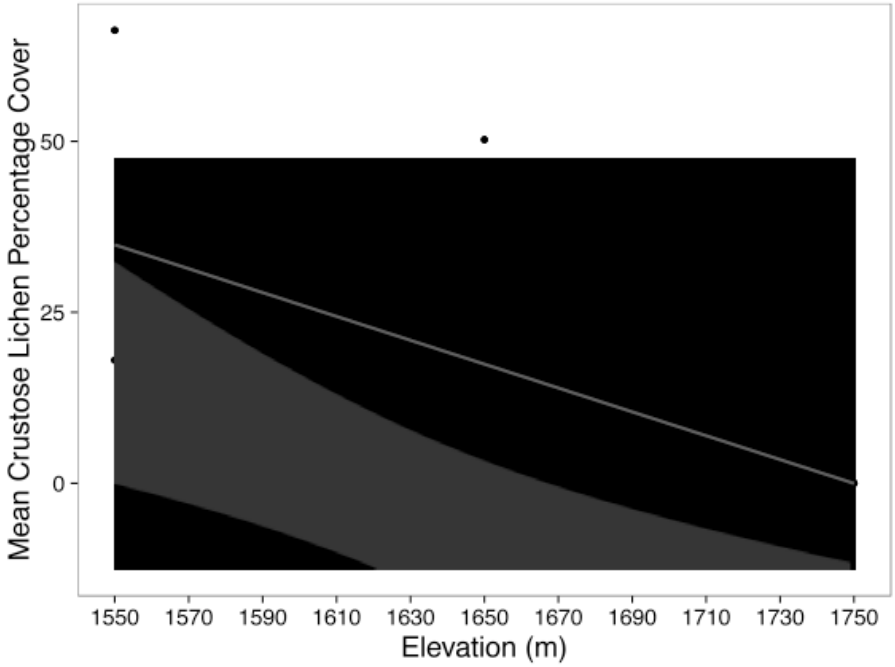

Figure 8. Mean crustose lichen percentage cover across cardinal direction for the 22 trees decreased with elevation. The shaded portion represents a 95% confidence interval.

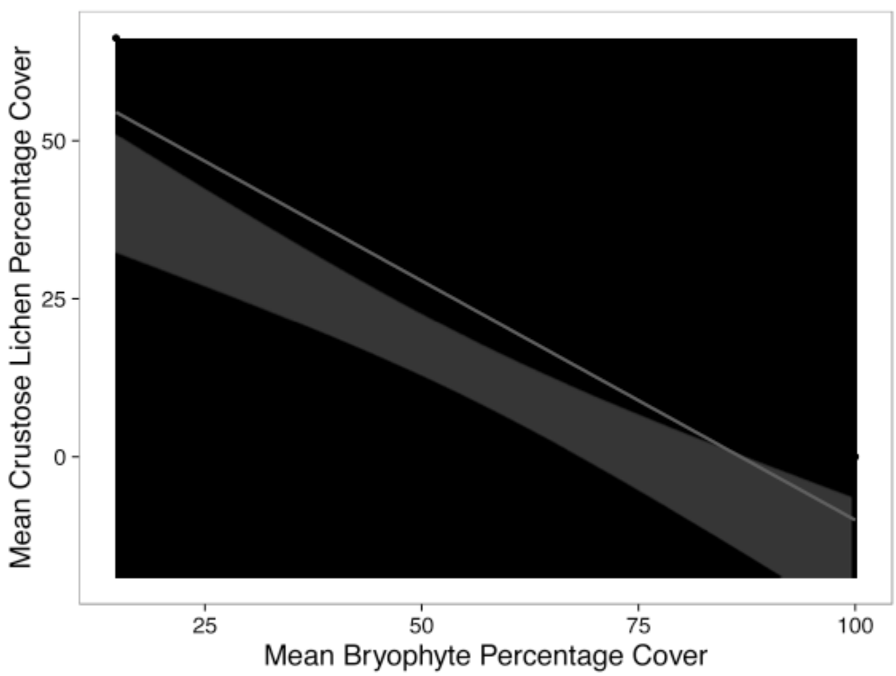

Figure 9. The strong negative correlation illustrates that as the cover of bryophytes increases the cover of crustose lichen decreases. The shaded portion represents a 95% confidence interval.

DISCUSSION

This study aimed to compare the distribution of bryophytes and lichens along an elevational gradient and found a significantly different trend between the two organisms. Crustose lichens and bryophytes were the dominant competitors within the system as folicose and fruticose lichens were rare. Perkins, who is currently sampling lichen diversity in the Monteverde area, also has not encountered many fruticose lichens in her sampling (pers. comm.), though the reason behind their rarity is unclear.

In agreement with my prediction, bryophyte percentage cover was highest at the higher elevations while crustose lichen was highest at the lower elevations. The shifting abundance of crustose lichens and bryophytes is likely explained by the differences in moisture along the elevational gradient. Flock (1978) and Robinson and coworkers (1989) looked at terrestrial lichens and bryophytes along a soil moisture gradient and saw highest bryophyte diversity in the wetter sites. Additionally, Wolf (1993), who studied bryophyte and lichen diversity and biomass in the northern Andes, found a decrease in crustose lichen with altitude. In contrast, Grytnes and coworkers (2006), working in western Norway, found no bryophyte elevational trend. The concurring and contrasting results regarding lichen and bryophyte abundance seem to suggest, as predicted, that moisture as a result of elevation rather than elevation itself is more important in determining distribution. Crustose lichens are tolerant to desiccation and thus seem able to compete successfully with bryophytes for space at the lower, drier elevations. In contrast, the sustained moisture of the higher elevations is likely detrimental to the crustose lichens because it could limit CO_2 diffusion from the photobiont to the mycobiont (Lowman and Bruce 153), which is not a restrictive factor for the byrophytes.

Bryophytes were found in greater abundance than crustose lichens at all elevations above and below the demonstrated trough around 1650m. This suggests that crustose lichens are more sensitive to the environmental pressures of fluctuating moisture. The different moisture conditions along the elevational gradient likely presents habitats with varying degrees of suitability for crustose lichen spores and free-living algae or bacteria, which is critical because many genera reproduce sexually. It is possible that the lower, drier elevations did not provide a suitable habitat for the free-living algae or bacteria thereby allowing bryophytes to dominate there. Additionally, the higher elevations may be too saturated for efficient transfer of photosynthesis products to the fungi. The peak of crustose lichen percent cover around 1650m may represent the optimal conditions for this organism. This elevation is a transitional area between lower montane wet forest and lower montane rain forest that may offer the ideal level of moisture for the crustose lichen, thereby allowing it to outcompete the bryophytes for space. The corresponding bryophyte trough seems to suggest that the strong negative correlation between the two types of organisms is causal in nature. However, this correlation is also likely influenced by elevation. At the higher, wetter elevations where the crustose lichens may be unable to persist there is available space, which the data suggest is taken advantage of by bryophytes.

In future studies, I would measure bark pH, thickness of the lichen and bryophyte layer, and moisture levels. Bark pH would be a useful indicator of bark chemistry and how this affects the community composition. I predict that more acidic bark would display a different organismal cover than more basic bark. Additionally, bryophyte biomass appeared to change considerably with elevation, but was not accounted for in my sampling process. I predict that there would be an increase in biomass as elevation and moisture increases. Finally, rain gauges, along with a device to measure horizontal precipitation, placed at several elevations along the gradient would allow for a direct measurement of the interaction between moisture and organismal bark cover as opposed to the indirect measurement using elevation. I predict that the moisture levels would have a strong positive correlation with the elevational gradient. If this study were repeated in several years, I might expect the crustose lichen cover to increase at the higher elevations as a result of decreasing moisture due to climate change

To summarize, my results supported the prediction that bryophytes would increase and crustose lichens would decrease along an increasing elevational gradient and that there was greater overall bryophyte cover. However, the data did not support the prediction regarding the increase in foliose and fruticose lichens because they were essentially absent from the sampling areas.

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