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Short Communication

Can air humidity and temperature regimes within cloud forest canopies be predicted from bryophyte and lichen cover?

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ABSTRACT

The use of bryophyte and lichen cover as a proxy for air relative humidity (RH) and temperature in tropical forests has been widely proposed. Many studies that have assessed the usefulness of such indicators have mostly focused on estimates from ground observations. Here we identify the usefulness of bryophyte and lichen cover to estimate RH and temperature along montane cloud forest canopies in Cusuco National Park, Honduras. We used correlation analysis to identify the contribution of height above ground level (i.e. canopy position) and elevation (asl.) on the cover of bryophytes and lichens and in relation to temperature and RH measured over a 12-mo period. We found that maximum RH and mean temperature was best explained by bryophyte cover when elevation was included in the model ($R^2 = 0.23$ and $R^2 = 0.82$ respectively). Elevation explained the largest proportion of variance in that model (22–82%). On the other hand, maximum RH and minimum temperature were best explained by lichen cover and elevation ($R^2 = 0.27–0.85$). RH and bryophyte cover were positively correlated (best fit model: $R^2 = 0.11$) and RH and lichen cover negatively correlated (best fit model: $R^2 = 0.12$). The correlation between temperature and bryophyte cover was positive (best fit model: $R^2 = 0.03$) and the correlation between temperature and lichen cover, with the exception of the lower canopy, was positive (best fit model: $R^2 = 0.09$). We conclude that estimates that use bryophyte and lichen cover as a proxy for RH and temperature need to consider the effects of differences in elevation between sites. Our results have also shown that including canopy position in models, that predict microclimate data from bryophyte and lichen cover, did not increase the explanatory power of such models.

1. Introduction

The use of non-vascular epiphytes such as bryophytes and lichens as indicators for environmental conditions such changes and climates has frequently been proposed (Zotz and Bader, 2009; Boltersdorf et al., 2014; dos Santos et al., 2014) and several studies have proposed the use of indicator taxa for that purpose (Holz and Gradstein, 2005; Normann et al., 2010). In tropical cloud forests, lichens and bryophytes are often very plentiful and they cover large surface areas of the vascular plant flora as epiphytes and hyper-epiphytes (Gradstein and Pocs, 1989). Humid montane forests in particular show increased species richness, abundance and biomass of non-vascular epiphytes, in comparison to lowland forests (Frahm, 1990; Frahm and Gradstein, 1991; Wolf, 1994; Wagner et al., 2014). Bryophytes and lichens show clear zonations within forest canopies, but both groups show different patterns in their distribution (Cornelissen and Steege, 1989; León-Vargas et al., 2006; Cornelissen et al., 2007). Their vertical and horizontal distribution is mostly attributed to microclimate gradients within the canopy (Wolf, 1993; Acebey et al., 2003; Wagner et al., 2014). The diffusion of sunlight through the canopy makes the air in the upper canopy warmer and lighter, whereas the air in the lower canopy is often cooler and denser, resulting in a stable temperature stratification within the canopy (Szarzynki and Anhuf, 2001). Relative air humidity (RH) is generally higher in the lower canopy and temperature displays a reversed pattern (Batke and Kelly, 2014).

Collecting data on the microclimate of a forest is often time-consuming and costly. Because the cover of bryophytes and lichens is closely coupled to the microclimatic conditions within a forest

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canopy, it has been proposed that bryophyte cover [and to some extent lichen cover and growth (Shukla et al., 2013)] can be used as a proxy for RH and temperature (Gradstein and Pocs, 1989; Frahm and Gradstein, 1991; Karger et al., 2012). For example, the relationship between bryophyte cover and RH in tropical forests was recently investigated by Karger et al. (2012). Their study investigated 26 study sites in tropical forests in Costa Rica, Ecuador and the Philippines and found that, across their study sites, bryophyte cover was only weakly correlated with RH. However, after separating highland (1800–3500 m asl.) from lowland sites (<1800 m asl.), RH showed a significant positive relationship with bryophyte cover ($R^2 = 0.36–0.62$). In contrast, temperature was only correlated to bryophyte cover in the lowlands ($R^2 = 0.36$). Karger et al. (2012) suggested that these results can be used to make relatively good estimates of the RH in a given study site when bryophyte cover is used as a proxy. The usefulness of lichen cover as an indicator for RH and temperature in tropical forests on the other hand, has been less well studied. Pearson (1969) found in Minnesota that trees that were located further from the edge of the forest showed significantly lower RH and an approximately 50% increase in lichen cover. His data suggested that increased light and temperature levels and the lower RH outside the denser forest, provided more optimal growing conditions for a number of lichen species. Although the lichen cover on average was lower on trees in the interior of the forest, lichens were still abundant in the crowns of the trees.

Taller forests have a much stronger vertical gradient in microclimate regimes compared with shorter forests (Sillett and Antoine, 2004). It is therefore likely that the cover estimates of bryophytes (and lichens) show much stronger vertical dissimilarities in taller forests (McCune et al., 2000). Studies that estimate bryophyte and lichen cover from the ground rely heavily on an open understory and the use of binoculars (Gradstein et al., 2003). Estimates that are based on ground observations are likely to be less accurate compared to estimates that use direct branch observations, e.g. through rope-climbing methods (McCune and Lesica, 1992).

In this study, we investigated the correlations between temperature and RH and bryophyte and lichen cover along the whole vertical length of a tall forest canopy in Honduras. We aimed to investigate whether bryophyte and lichen cover can be used as a proxy for RH and temperature along the full vertical forest profile. It was predicted that bryophyte and lichen cover on individual branches will change with height in the canopy. Bryophytes grow frequently in conditions were moisture levels are high and are in effect shade plants (León-Vargas et al., 2006). Their cover is largely determined by the loss of water from exposure (e.g. sun light). As they become light-saturated at relatively low levels, deeply shaded places such as the lower canopy are thus better for water conservation (Proctor, 1990). Lichens on the other hand grow more plentifully on more exposed sites in the canopy (Pearson, 1969) where temperatures and light levels are higher. The upper branches in a tree are also much younger, provide less favorable conditions to bryophytes and hence reduce competition from bryophytes (Wolseley and Aguirre-Hudson, 1997).

Our hypotheses were (i) that RH and bryophyte cover are positively correlated, both being highest in the lower canopy and lowest in the upper canopy and (ii) that RH and lichen cover are negatively correlated. (iii) The reverse patterns were expected for the correlations with temperature.

2. Materials and methods

2.1. Data collection

Climate data were collected over a 12-month period within 20 large mature trees (ten needle-leaved conifers and ten broadleaved angiosperms) in Cusuco National Park (CNP), Honduras (15°32′31″ N, 88°15′49″ W). Ten trees including both life-forms (one conifer and one broadleaved tree per plot) were located within five low elevation cloud forest plots (<1450 m asl.) and ten trees in five high elevation cloud forest plots (1800–2000 m asl.). We selected different host life-forms, as previous studies have shown that the cover of non-vascular epiphytes can vary between different host life-forms and species, which is often a result of differences in bark properties and tree height (Wolf, 1994). Due to significant logging and farming activities at low elevation sites (>1450 m asl.), the elevation gradient was relatively low. Minimum distance between plots (150 m × 150 m) was 50 m. Luscar EL-USB-2 data loggers ($n = 70$) were used to measure RH and temperature at 10-min ($n = 8$) or hourly ($n = 62$) intervals between June 2012 and June 2013. The 10-min interval measurements for eight of the data loggers were averaged to hourly measurements for the analysis. The loggers were suspended at three different heights within the canopy namely the lower, middle and upper third of the canopy. As described in Batke and Kelly (2014), the height of each logger depended on the total tree height and each loggers was at the same horizontal distance from the bole of the tree (i.e. the inner canopy). Some of the data loggers were paired, in order to assess recording precision. Branches that were located between two logger-levels were assigned a canopy position based on their distance to the nearest data logger. Mean ± SD tree height was 40.4 m ± 9.9 m [see Batke and Kelly, 2014 for more details on the forest plots]. We used rope climbing techniques to sample every branch along the whole tree for bryophyte and lichen cover. The height of each branch was measured using a tape measure from the center of each branch. Branches that grew vertically and branches that grew across different canopy zones were subdivided and treated separately. Bryophyte and lichen cover were visually estimated for each branch (and bole), using a 0–100% scale with 5% intervals.

2.2. Data analysis

From the data logger measurements (number of repeated measures = 386,469) we calculated the mean, maximum and minimum temperature and RH for each canopy position, viz. lower, middle and upper canopy. We used linear regression and Linear Mixed Effect Models to identify the effects of canopy position and elevation on the cover of bryophytes and lichens and their relationships to temperature and RH. RH and temperature were treated as dependent variables, whereas canopy position, elevation, bryophyte and lichen cover were treated as independent variables. We analyzed mean, minimum and maximum microclimate variables separately. Tree identity was treated as a random variable but was not included in any further analysis as the contribution of tree identity to the models was low (0.2% of variance explained).

To identify the model that best explained humidity and temperature, the models were tested using ANOVA comparisons and the model with the lowest Akaike Information Criterion (AIC) was retained. Elevation was included as a continuous variable and canopy position as a categorical variable. The correlations between RH/temperature and height in the canopy were demonstrated in previous work (Batke and Kelly, 2014). All calculations were done in ‘R’ (R Developing Core Team, 2011).

3. Results

Elevation explained 22% of the data when modeled for maximum RH and 80% when modeled for mean temperature (Table 1). Canopy position showed much weaker correlations, with the best-fit models explaining 10% of minimum RH and 7% of maximum temperature (Table 1). RH (mean RH = 6%) and temperature