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

Corresponding author: Sven P. Batke [1,2,3] Email: batkesp@tcd.ie, Phone: +353 (0)86 665 24 59 Address: Botany Department, Trinity College Dublin, College Green, Dublin.

Co-authors:

Brian R. Murphy[1,2], Email: murphb16@tcd.ie

Nicholas Hill [3], Email: nejmhill@gmail.com

Daniel L. Kelly [1,2], Email: DKELLY@tcd.ie

1. Department of Botany, Trinity College Dublin, College Green, Dublin 2, Ireland.

2. Trinity Centre for Biodiversity Research, Trinity College Dublin, Ireland

3. Operation Wallacea, Hope House, Old Bolingbroke, Lincolnshire, UK

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.

Keyword: mosses, epiphyte, Honduras, microclimate, elevation

1.1 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, 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 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.

2.1 Materials and methods

2.1.1 Data collection

Climate data were collected over a 12-mo period within 20 large mature trees (ten needle-leaved conifers and ten broadleaved angiosperms) in Cusuco National Park (CNP), Honduras (15º32'31"N, 88º15'49"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 × 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.

2.1.2 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).

3.1 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 (minimum temperature = 2%) were poorly predicted from bryophyte cover alone (Table 1). However, when elevation was included in the model, the overall model fits for RH and temperature were improved by 21% (maximum RH) and 80% (mean temperature) respectively. Although canopy position did contribute to the model performance, the contributions were small when modeled together with bryophyte cover (mean RH = 11%; minimum temperature = 3%; Table 1). The only statistically significant correlations of RH to bryophyte cover at the different canopy positions were to mean and minimum RH and maximum and minimum temperature in the upper canopy (Table 2 and Figure 1). Bryophyte cover increased with mean RH and minimum temperature (Figure 1). In summary, mean temperature explained most of the cover of bryophytes when elevation was included (overall model fit = 82%). Similarly, maximum RH explained most of the cover of bryophytes when elevation was included (overall mode fit = 23%; Table 1). Canopy position did not contribute much to the model performance but the correlations varied between different canopy positions (Figure 1).

RH (maximum RH = 12%) and temperature (mean temperature = 17%) were poorly predicted from lichen cover alone (Table 1). However, as with bryophyte cover, when elevation was included in the model, the overall model fits for RH and temperature with lichen cover were improved by 15% (maximum RH) and 68% (mean temperature) respectively. Including canopy position in the models did not increase model performance (Table 1). However, compared to bryophyte cover, RH and temperature were more strongly correlated to lichen cover at the different canopy positions (Table 2 and Figure 1). Mean and maximum RH were statistically correlated to lichen cover at the middle and upper canopy. Also, minimum RH was statistically correlated to lichen cover at the lower canopy (Table 2 and Figure 1). Temperature showed a similar pattern with the only difference being the correlation between minimum temperature and lichen cover in the upper canopy (Table 2 and Figure 1). Lichen cover decreased with maximum RH, and, with the exception of the lower canopy, increased with maximum temperature (Figure 1). In summary, maximum temperature explained most of the cover of lichens, when elevation was included (overall model fit = 85%). Similarly, maximum RH explained most of the cover of lichens when elevation was included (overall mode fit = 27%; Table 1). Finally, compared to bryophyte cover, canopy position was more important when lichen cover was correlated to climate variables (Table 2 and Figure 1).

Table 1. Mixed effects linear models correlating air RH and temperature to visually estimated bryophyte and lichen cover at different heights within the canopy (i.e. Position) and between high and low elevation sites (i.e. Elevation asl.). The models that present most of the variation in the data and had the lowest AIC scores are highlighted in bold and their significance level are marked by asterisks (***p < 0.01 and *p < 0.05).

			Humidity			**Temperature**		
Group	**Dependent**	**Independent**	**AIC**	**R^2**	**p**	**AIC**	**R^2**	**p**
	Max.	Elevation	**1249.6**	**0.22**	**<0.01*****	2021.1	0.19	<0.01***
	Max.	Position	1350.4	0.001	0.33	2079.0	0.07	<0.01***
	Mean	Elevation	1890.5	0.20	<0.01***	**1000.7**	**0.80**	**<0.01*****
	Mean	Position	1961.7	0.05	<0.01***	1691.3	0.001	0.48
	Min.	Elevation	3008.4	0.04	<0.01***	1530.4	0.57	<0.01***
	Min.	Position	2980.7	0.10	<0.01***	1861.3	0.01	0.02*
Bryophyte								
	Max.	Bryophyte	1348.8	0.002	0.18	2099.9	0.02	<0.01***
	Max.	Bryophyte:Position	1353.8	0.001	0.44	2076.1	0.08	<0.01***
	Max.	Bryophyte:Elevation	**1247.0**	**0.23**	**<0.01*****	2016.3	0.21	<0.01***
	Max.	Bryophyte:Position:Elevation	1258.4	0.22	<0.01***	1970.3	0.30	<0.01***
	Mean	Bryophyte	1957.0	0.06	<0.01***	1690.0	0.0004	0.36
	Mean	Bryophyte:Position	1940.6	0.11	<0.01***	1696.1	0.01	0.74

	Mean	Bryophyte:Elevation	1863.4	0.26	<0.01***	**995.7**	**0.82**	**<0.01*** **
	Mean	Bryophyte:Position:Elevation	1828.9	0.33	<0.01***	1002.7	0.82	<0.01***
	Min.	Bryophyte	2987.4	0.09	<0.01***	1857.2	0.02	<0.01***
	Min.	Bryophyte:Position	2947.7	0.18	<0.01***	1858.2	0.03	<0.01***
	Min.	Bryophyte:Elevation	2969.1	0.13	<0.01***	1505.9	0.59	<0.01***
	Min.	Bryophyte:Position:Elevation	2923.2	0.24	<0.01***	1502.4	0.60	<0.01***
Lichen								
	Max.	Lichen	1299.2	0.12	<0.01***	2092.3	0.04	<0.01***
	Max.	Lichen:Position	1301.4	0.12	<0.01***	2071.2	0.09	<0.01***
	Max.	Lichen:Elevation	**1226.2**	**0.27**	**<0.01*** **	2011.1	0.22	<0.01***
	Max.	Lichen:Position:Elevation	1227.4	0.28	<0.01***	1966.4	0.31	<0.01***
	Mean	Lichen	1945.3	0.09	<0.01***	1613.5	0.17	<0.01***
	Mean	Lichen:Position	1933.6	0.12	<0.01***	1617.3	0.17	<0.01***
	Mean	Lichen:Elevation	1880.5	0.23	<0.01***	**937.4**	**0.85**	**<0.01*** **
	Mean	Lichen:Position:Elevation	1846.2	0.30	<0.01***	938.7	0.85	<0.01***
	Min.	Lichen	3021.0	0.01	<0.05*	1813.3	0.12	<0.01***
	Min.	Lichen:Position	2977.6	0.12	<0.01***	1807.6	0.14	<0.01***
	Min.	Lichen:Elevation	2999.6	0.06	<0.01***	1498.8	0.60	<0.01***
	Min.	Lichen:Position:Elevation	2954.0	0.18	<0.01***	1500.2	0.61	<0.01***

Table 2. Bryophyte and lichen cover coefficients of determination (R^2) for mean, maximum and minimum RH and temperature for each canopy position. The R^2 values that were highly significant ($p < 0.01$) are marked by ***.

		RH			Temperature		
Type		Mean	Max.	Min.	Mean	Max.	Min.
Bryophyte							
	Lower	0.06	0.04	0.13	0.05	0.001	0.02
	Middle	0.01	0.01	0.03	0.01	0.004	0.01
	Upper	0.07***	0.002	0.11***	0.002	0.03***	0.08***
Lichen							
	Lower	0.02	0.07	0.03***	0.02	0.01	0.04
	Middle	0.08***	0.07***	0.002	0.19***	0.02***	0.004
	Upper	0.12***	0.15***	0.004	0.19***	0.11***	0.03***

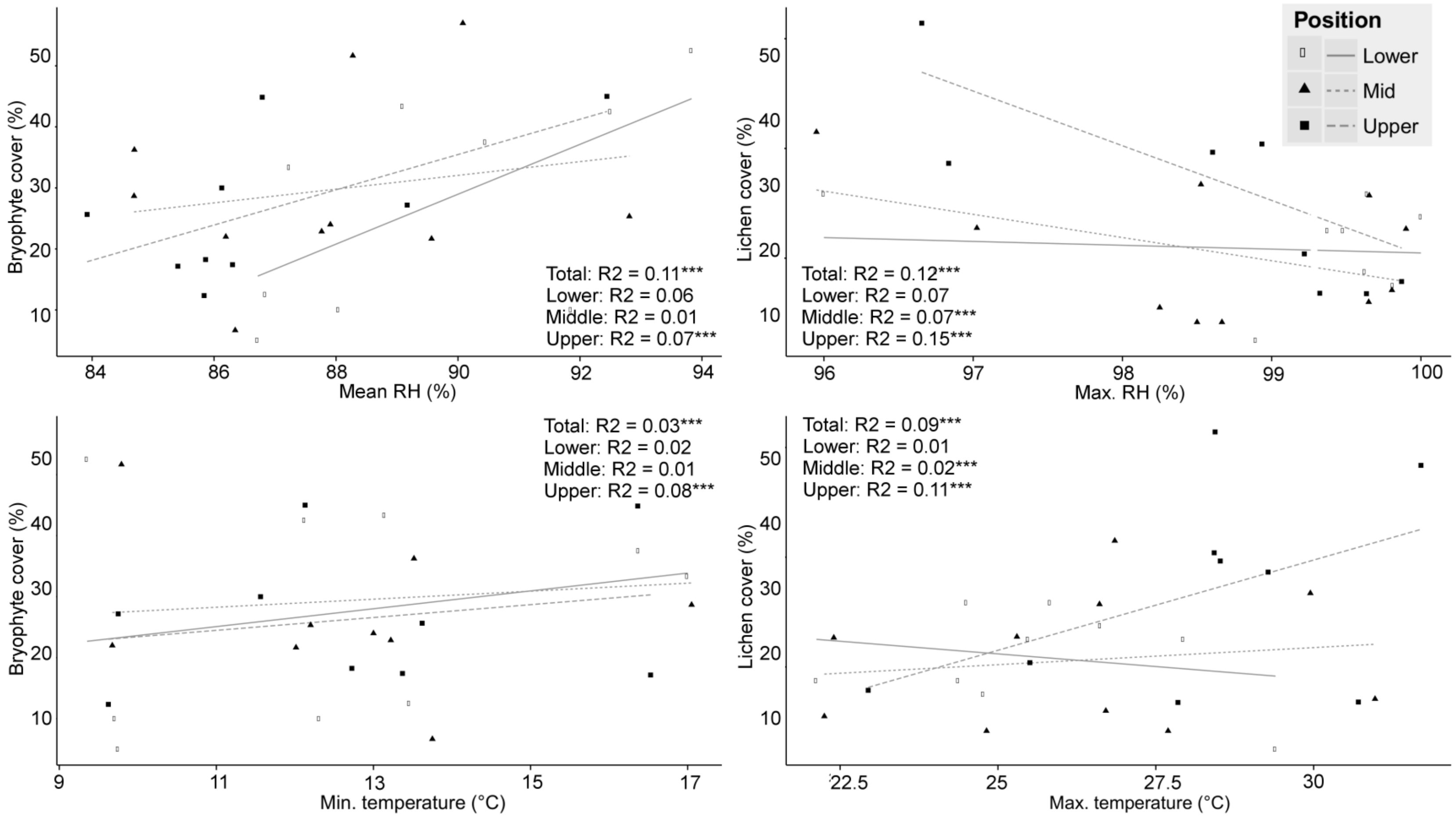

Figure 1. Relationships of bryophyte and lichen cover on canopy branches at different canopy positions per plot with RH and temperature. Following the best fit models, the mean RH and minimum temperature correlations for bryophyte cover are presented and the maximum RH and maximum temperature correlations for lichen cover. The solid lines represent the linear fit for the lower canopy, the dotted lines represent the linear fit for the middle canopy and the dashed lines represent the linear fit for the upper canopy (***p < 0.01).

4.1 Discussion

Our results showed that most of the variability in the climate data was best explained by the difference in elevation between sites. The position of the data loggers along the vertical canopy profile accounted for only a small proportion of the data variability and RH and temperature were only poorly predicted from bryophyte and lichen cover when they were modeled as the only independent variable in the correlation. The best-fit models were: maximum RH correlated to bryophyte cover and elevation (R^2 = 0.23), mean temperature correlated to bryophyte cover and elevation (R^2 = 0.82), maximum RH correlated to lichen cover and elevation (R^2 = 0.27) and mean temperature correlated to lichen cover and elevation (R^2 = 0.85). The importance of elevation in explaining the cover of bryophytes was previously demonstrated by Karger et al. (2012). They demonstrated that elevation explained much of the variability in bryophyte cover between sites. In their study high elevation sites had a better fit for RH (R^2 = 0.62) compared to low elevation sites (R^2 = 0.36). However, the fit was only better for low elevation sites when bryophyte cover was correlated to temperature (low: R^2 = 0.36; high: R^2 = 0.01). In the present study elevation alone improved the model fit by 17%-80% when modeled with bryophyte cover and 15%-68% when modeled with lichen cover. In particular, the models of mean temperature and elevation showed strong correlations when modeled for bryophyte and lichen cover (Table 1). Our hypotheses that (i) RH and bryophyte cover are positively and (ii) RH and lichen cover are negatively correlated were confirmed. However, the strength of the correlations was weak and differed between canopy positions; the strongest correlations were observed in the upper canopy (Table 2 and Figure 1). The hypothesis that (iii) temperature and bryophyte cover are negatively correlated was not confirmed. Likewise, the predicted positive correlations between temperature and lichen cover was not confirmed for the lower canopy (Figure 1).

Wolf (1993) pointed out that the correlation between bryophyte cover and elevation is most likely the result of increased RH and a decrease in temperature with elevation. His as well as our results demonstrated the importance of including elevation as a variable in any non-vascular epiphyte cover estimate that assess the correlation between climate variables and their cover. Biomass assimilate of bryophytes is optimal at low light intensities and at temperatures below 25 °C; conditions that are frequently observed at high elevation sites and in the lower canopy. At low elevation sites and at greater height in the canopy biomass assimilations are often lower, most likely due to higher temperatures and the resulting higher nocturnal respiration rates (Frahm 1990, Frahm and Gradstein 1991, Bader et al. 2013, Wagner et al. 2014). Additionally, long periods of high RH allow for longer periods of photosynthetic activity by reducing the risk of damage from desiccation (Vanderpoorten and Goffinet 2009). Poikilohydric canopy species in particular are significantly more affected by the decrease in RH and increased exposure to desiccation by wind in the upper canopy (Sillett and Antoine 2004). Lichens are less tolerant to water over-saturation and hence grow in more exposed conditions such as the upper canopy (Gehrig-Downie et al. 2011). Moreover, lichen cover in the middle and upper canopy is often much higher compared to the lower canopy (Lang et al. 1980, Kelly et al. 2004, Batke 2012). This is most likely a result of more suitable growing conditions (e.g. increased solar radiation in the upper canopy) and possibly due to reduced competition from bryophytes on such sites. It has also been suggested that lichen cover (and their distribution) is less affected by microclimate variables at a stand level compared to a regional level (Giordani and

Incerti 2008). If this is the case, this would explain the low correlation of climate variables to lichen cover in our study.

The low contribution of canopy position to our models suggests that the height in the canopy is not a strong contributing factor when correlating climate variables to bryophyte and lichen cover at a stand level. Thus, ground cover estimates in our study site would have been sufficient to predict RH and temperature, once elevation was included in the models. We confirmed the view (Sillett and Antoine 2004) that bryophyte cover increased and lichen cover decreased with increases in RH. However, we were unable to detect a negative correlation between temperature and bryophyte cover, and we only found a positive correlation between temperature and lichen cover in the middle and upper canopy (i.e. the best fit model). The weak correlations between mircoenvironmental variables and bryophyte and lichen cover could be because our data were collected at different resolutions. Bryophyte and lichen cover data were collected on an individual branch level, whereas microclimate measurements were not available for each individual branch; instead measurements were taken from three canopy zones (i.e. lower, middle and upper canopy). Branches that were located between individual data loggers could have experienced different microclimate conditions to those branches that were located directly next to a logger. Having one data logger per branch would have been desirable and would have resulted in a more comprehensive sample design. However, this was not feasible here.

Finally, the logistical difficulties of ascending into the canopy make it desirable to use estimates of lichen and bryophyte cover from the ground, to predict RH and temperature regimes for the whole forest stand (Pardow et al. 2012). Our results showed that in our study area only a small proportion of mircoenvironmental variables were explained by bryophyte and lichen cover estimates. Most of the variation in climate data was better explained by our models that included elevation as an independent variable. We therefore do not think that RH and temperature can be predicted entirely from bryophyte and lichen cover at CNP. Moreover, we did not find much support that would have suggested that the inclusion of canopy position, in bryophyte and lichen cover estimates, would have increased the predictive power of our models.

Acknowledgments

This project was funded by Trinity College, The University of Dublin, the Rufford Foundation and Operation Wallacea. We thank José Omar Arteaga Mesía (local guide) for his help with the data collection.

References

Acebey, A., S. R. Gradstein, and T. Krömer. 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. Journal of Tropical Ecology **19**:9-18.

Bader, M. Y., T. Reich, S. Wagner, A. S. González González, and G. Zotz. 2013. Differences in desiccation tolerance do not explain altitudinal distribution patterns of tropical bryophytes. Journal of Bryology **35**:47-56.

Batke, S. 2012. A preliminary survey of epiphytes in some tree canopies in Zambia and the Democratic Republic of Congo. African Journal of Ecology **50**:343-354.

Batke, S. P., and D. L. Kelly. 2014. Tree damage and microclimate of forest canopies along a hurricane-impact gradient in Cusuco National Park, Honduras. Journal of Tropical Ecology **30**:457-467.

Boltersdorf, S. H., R. Pesch, and W. Werner. 2014. Comparative use of lichens, mosses and tree bark to evaluate nitrogen deposition in Germany. Environmental Pollution **189**:43-53.

Cornelissen, J. H. C., S. I. Lang, N. A. Soudzilovskaia, and H. J. During. 2007. Comparative cryptogam ecology: a review of bryophyte and lichen traits that drive biogeochemistry. Annals of Botany **99**:987-1001.

Cornelissen, J. H. C., and H. T. Steege. 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. Journal of Tropical Ecology **5**:131-150.

Frahm, J.-P. 1990. Bryophyte phytomass in tropical ecosystems. Botanical Journal of the Linnean Society **104**:23-33.

Frahm, J.-P., and S. R. Gradstein. 1991. An altitudinal zonation of tropical rain forests using byrophytes. Journal of Biogeography **18**:669-678.

Gehrig-Downie, C., A. Obregón, J. Bendix, and S. R. Gradstein. 2011. Epiphyte biomass and canopy microclimate in the tropical lowland cloud forest of French Guiana. Biotropica **43**:591-596.

Giordani, P., and G. Incerti. 2008. The influence of climate on the distribution of lichens: a case study in a borderline area (Liguria, NW Italy). Plant Ecology **195**:257-272.

Gradstein, S. R., N. M. Nadkarni, T. Krömer, I. Holz, and N. Nöske. 2003. A protocol for rapid and representative sampling of vascular and non-vascular epiphyte diversity of tropical rain forests. Selbyana **24**:105-111.

Gradstein, S. R., and T. Pocs. 1989. Bryophytes.*in* H. Lieth and M. J. A. Werger, editors. Ecosystems of the World - Tropical rain forest ecosystems; biogeographical and ecological studies. Elsevier Scientific, Amsterdam.

Holz, I., and S. R. Gradstein. 2005. Cryptogamic epiphytes in primary and recovering upper montane oak forests of Costa Rica: species richness, community composition and ecology. Plant Ecology **178**:89-109.

Karger, D. N., J. Kluge, S. Abrahamczyk, L. Salazar, J. Homeier, M. Lehnert, V. B. Amoroso, and M. Kessler. 2012. Bryophyte cover on trees as proxy for air humidity in the tropics. Ecological Indicators **20**:277-281.

Kelly, D. L., G. O'Donovan, J. Feehan, S. Murphy, S. O. Drangeid, and L. Marcano-Berti. 2004. The epiphyte communities of a montane rain forest in the Andes of Venezuela: patterns in the distribution of the flora. Journal of Tropical Ecology **20**:643-666.

Lang, G. E., W. A. Reiners, and L. H. Pike. 1980. Structure and biomass dynamics of epiphytic lichen communities of Balsam fir forests in New Hampshire. Ecology **61**:541-550.

León-Vargas, Y., S. Engwald, and M. C. F. Proctor. 2006. Microclimate, light adaptation and desiccation tolerance of epiphytic bryophytes in two Venezuelan cloud forests. Journal of Biogeography **33**:901-913.

McCune, B., and P. Lesica. 1992. The trade-off between species capture and quantitative accuracy in ecological inventory of lichens and bryophytes in forests in Montana. The Bryologist **95**:296-304.

McCune, B., R. Rosentreter, J. M. Ponzetti, and D. C. Shaw. 2000. Epiphyte habitats in an old conifer forest in western Washington, U.S.A. The Bryologist **103**:417-427.

Normann, F., P. Weigelt, C. Gehrig-Downie, S. R. Gradstein, H. J. M. Sipman, A. Obregon, and J. Bendix. 2010. Diversity and vertical distribution of epiphytic macrolichens in lowland rain forest and lowland cloud forest of French Guiana. Ecological Indicators **10**:1111-1118.

Pardow, A., C. Gehrig-Downie, R. Gradstein, and M. Lakatos. 2012. Functional diversity of epiphytes in two tropical lowland rainforests, French Guiana: using bryophyte life-forms to detect areas of high biodiversity. Biodiversity and Conservation **21**:3637-3655.

Pearson, L. C. 1969. Influence of temperature and humidity on distribution of lichens in a Minnesota bog. Ecology **50**:740-746.

Proctor, M. C. F. 1990. The physiological basis of bryophyte production. Botanical Journal of the Linnean Society **104**:61-77.

R Developing Core Team. 2011. R: a language and environment for statistical computing R Foundation for Statistical Computing, R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Santos, N. D. d., D. P. d. Costa, L. S. Kinoshita, and G. J. Shepherd. 2014. Windborne: Can liverworts be used as indicators of altitudinal gradient in the Brazilian Atlantic Forest? Ecological Indicators **36**:431-440.

Shukla, V., D. Upreti, and R. Bajpai. 2013. Lichens to biomonitor the environment. Springer, Lucknow.

Sillett, S. C., and M. E. Antoine. 2004. Lichens and bryophytes in forest canopies. Page 544 *in* M. D. Lowman and H. B. Rinker, editors. Forest canopies. Elsevier Academic Press, USA.

Szarzynki, J., and D. Anhuf. 2001. Micrometerological conditions and canopy energy exchanges of a neortopical rain forest (Surumoni-Crane project, Venezuela). Plant Ecology **153**:231-239.

Vanderpoorten, A., and B. Goffinet. 2009. Introduction to bryophytes. Cambridge University Press Cambridge, Cambridge.

Wagner, S., M. Bader, and G. Zotz. 2014. Physiological ecology of tropical bryophytes. Pages 269-289 *in* D. T. Hanson and S. K. Rice, editors. Photosynthesis in bryophytes and early land plants. Springer Netherlands.

Wolf, J. D. 1994. Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. Vegetatio **112**:15-28.

Wolf, J. H. D. 1993. Diversity patterns and biomass of epiphytic bryophytes and lichens along an altitudinal gradient in the Northern Andes. Annals of the Missouri Botanical Garden **80**:928-960.

Wolseley, P. A., and B. Aguirre-Hudson. 1997. The ecology and distribution of lichens in tropical deciduous and evergreen forests of northern Thailand. Journal of Biogeography **24**:327-343.

Zotz, G., and M. Bader. 2009. Epiphytic plants in a changing world-global: change effects on vascular and non-vascular epiphytes. Pages 147-170 Progress in Botany. Springer.