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Tree Species Composition Predicts Epiphytic Lichen Communities in an African Montane Rain Forest

Andreas Frisch¹, Jörgen Rudolphi^{1,2}, Douglas Sheil^{3,4,5}, Alexandro Caruso¹, Göran Thor¹, and Lena Gustafsson^{1,6}

¹ Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7044, SE-750 07, Uppsala, Sweden

² Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Skogsmarksgränd, SE-901 83, Umeå, Sweden

³ Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O. Box 5003, NO-1432, Ås, Norway

⁴ Center for International Forestry Research (CIFOR), GPO Box 113 BOCBD, 1600, Bogor, Indonesia

⁵ Institute of Tropical Forest Conservation, Mbarara University of Science and Technology, PO Box 44, Kabale, Uganda

ABSTRACT

The ecology of many tropical rain forest organisms, not the least in Africa, remains poorly understood. Here, we present a detailed ecological study of epiphytic lichens in the equatorial montane rain forest of Bwindi National Park (331 km²), Uganda. We evaluated all major lichen growth forms, including selected groups of crustose lichens. In 14 transects at elevations of 1290 m to 2500 m, we sampled 276 trees belonging to 60 species. We recorded all lichen species on each tree trunk between ground level and 2 m above the ground, yielding 191 lichen species in 67 genera, with a mean of 4.7 species per tree. We used non-metric multi-dimensional scaling to separate epiphytic lichen assemblages according to tree species composition and elevation. Structural equation modeling indicated that elevation influenced tree species composition and that tree species composition largely determined lichen species composition. Thus, elevation acted indirectly on the lichen assemblages. Further studies examining factors such as bark properties and lichen colonization ecology may clarify what determines the association between tree species and lichen assemblages. The link between lichen assemblages and large-scale elevation patterns, as well as disturbance and regrowth histories, warrants further study. An analysis of lichen species composition on individual tree species that occur over large elevation ranges would distinguish the effect of tree species on lichen assemblages from the effect of elevation and thus climate. Our study highlights the limited extent of our knowledge of tropical epiphytic lichens.

Key words: Bwindi; crustose; equatorial; non-metric multi-dimensional scaling; structural equation modeling; transects; Uganda.

THE ONGOING LOSS OF SPECIES IN THE TROPICS RAISES GLOBAL CONCERNS (Secretariat of the Convention on Biological Diversity 2010); however, the identities of many of the lost and declining species remain unknown. Such knowledge gaps are especially evident for composite organisms such as lichens, the symbiotic associations between a filamentous fungus and one or more photosynthetic organisms including micro-algae, cyanobacteria, or both (Lutzoni & Miadlikowska 2009). Lücking *et al.* (2009) estimated the global number of lichens at 28,000, with 14,000 species in the tropics. In tropical forests, most lichens grow as epiphytes on the bark of trees or on the surface of leaves (Komposch & Hafellner 2000). Little is known about the crustose (crusty, corticolous) epiphytic lichens occurring in tropical forests, whereas many of the foliose (leaf-like) and fruticose (shrubby) species have been described (Aptroot *et al.* 1995, Komposch & Hafellner 2000). Relatively comprehensive studies have characterized the epiphytic lichen communities in some subtropical forests (Li *et al.* 2013). Tropical forest lichen studies have mostly considered the Neotropics and focused on taxonomy,

rather than ecology (see references in Komposch & Hafellner 2000, Cáceres *et al.* 2007). Studies on lichen community ecology in the paleotropics are particularly scarce and include some studies conducted in Southeast Asia (Wolseley *et al.* 1994, Wolseley & Aguirre-Hudson 1997) and tropical Africa (Biedinger & Fischer 1996, Yeshitela 2008). No study has yet examined lichen community ecology in an equatorial African forest.

Elevation is a major determinant of variation in tropical rain forest communities. As elevation increases, temperature decreases, and other abiotic factors (*e.g.*, humidity and sunlight) exhibit local gradients (Richards 1996, Körner 2007, Ghazoul & Sheil 2010). The zonation of forest types shows the most striking biodiversity gradient. In tropical Africa, lowland forests and montane forests are usually distinct and separated by a transition zone. Montane forests are characterized by un-buttressed trees with a height of 20–25 m, with compact crowns and few lianas (Richards 1996, Ghazoul & Sheil 2010).

The only thorough study of epiphytic lichens along an elevation gradient in tropical moist forests reported to date covered elevations from 1000 to 4000 m in the Columbian Andes (Wolf 1993). The only elevation study from Africa to consider lichens examined epiphytic vegetation in the dry and montane forests of

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⁶Corresponding author; e-mail: lena.gustafsson@slu.se

Rwanda and Zaïre (now the Democratic Republic of Congo) (Biedinger & Fischer 1996).

Here, we report the first detailed ecological study of epiphytic lichen composition in an African rain forest, *i.e.*, the Bwindi Impenetrable National Park (henceforth ‘Bwindi’) in Uganda. We examined all major growth forms of lichens, including the important, but rarely studied, families of crustose lichens. We aimed to clarify how epiphytic lichen species assemblages vary with location. Specifically, we wanted to test the hypothesis that elevation is the main factor determining the composition of epiphytic lichen assemblages, and more important than properties of the host, *i.e.*, tree species composition.

METHODS

BWINDI NATIONAL PARK.—Bwindi Impenetrable National Park in southwest Uganda (Fig. S1) occupies an area of 331 km² with an elevation range of between 1200 m and 2600 m above sea level (asl.). This UNESCO World Heritage Site represents one of the few East African forests where lowland and montane vegetation types meet. The park lies in the rugged Kigezi Highlands and the terrain slopes from the comparatively high, deeply dissected south and southeast region to the lower north and northwest region. The bedrock comprises Precambrian shale phyllite, with some quartzite, schist, and localized granite (Howard 1991). Soils mostly include well-differentiated humic ferralsols with abundant organic matter and moderate to high acidity (Twongyirwe *et al.* 2011, 2013). The local climate has two rainfall peaks, March to May and September to November. Mean annual rainfall ranges from 1392 mm (elevation 1890 m) to 1826 mm (elevation 1494 m), and mean annual temperature ranges from 16.4°C (elevation 2300 m) to 21.7°C (elevation 1433 m) (Institute of Tropical Forest Conservation (ITFC) <http://www.itfc.org>, 22/7/2013).

The Albertine Rift region, which includes Bwindi, is the most vertebrate species-rich region of comparable size in Africa (Plumptre *et al.* 2007). Bwindi also has among the most diverse

composition of flora in East Africa, with over 1000 identified flowering plant species, including *ca.* 320 tree and shrub species and more than 100 species of ferns (ITFC herbarium data, unpubl. data). Of additional biogeographical interest, Bwindi lies between the East African and West African floras, regions which have separated and reconnected many times through geological time (Couvreux *et al.* 2008). Bwindi also has half of the world’s endangered mountain gorillas (*Gorilla beringei beringei*) (McNeilage *et al.* 2006).

Densely populated, cultivated areas surround this forest (Olupot *et al.* 2009, Twongyirwe *et al.* 2013). Natural disturbances in the area include localized landslides, elephants, and occasional fires following droughts. Bwindi is among the best-protected forests in Africa, but small-scale human activities remain locally significant (including tourist trails and resource collection, both legal and illegal). In the past, timber cutting, artisanal gold mining, illegal forest clearing, and anthropogenic fires threatened the region (Babaasa *et al.* 2004, Olupot *et al.* 2009).

SAMPLING.—Bwindi includes Eastern, Western, and Northern sectors (Fig. S1). We sampled five areas within the park: Byumba (Northern sector), Buhoma (Western sector), Center, Ruhija, and Rushaga (all Eastern sector) (Fig. S1). These areas broadly represent the park’s terrain and forests, including differences in elevation, human impact, and tree communities. Ruhija and Rushaga have the highest elevation (Eastern sector; 1910–2500 m asl.) and Byumba has the lowest (Northern sector 1290–1660 m asl.) (Table 1). Human impact mostly occurs in Ruhija and Rushaga and along the margins bordering the agricultural landscape, but only limited human impact occurs in the Center.

We established 14 transects between 1290 m and 2500 m asl (Table 1) and positioned the transects from valley bottoms to ridgetops, to include the characteristic, small-scale topographical variation within Bwindi. We used the following criteria to locate and orient transects: (1) slopes spanning at least 200 m in elevation; (2) relatively undisturbed forest with old trees; and

TABLE 1. *Sampling design.*

Study areas	Transects (number)	Plots valley bottom (number)	Plots mid-slope position (number)	Plots ridgetops (number)	Surveyed trees (number)	Elevation (range for transects, m)	Main tree species
Buhoma	3	6	10	6	66	1470–1900	<i>Leptonichia mildbraedii</i> , <i>Strombosia scheffleri</i> , <i>Newtonia buchananii</i> , <i>Markbamia lutea</i> , <i>Carapa grandiflora</i> ,
Byumba	3	5	10	7	66	1290–1660	<i>Leptonichia mildbraedii</i> , <i>Strombosia scheffleri</i> , <i>Allanblackia kimbiliensis</i> , <i>Sapiam ellipticum</i> , <i>Lansonia lucida</i> , <i>Polyscias fulva</i>
Center	2	4	8	4	48	1800–2150	<i>Strombosia scheffleri</i> , <i>Carapa grandiflora</i> , <i>Beilschmidia</i> sp., <i>Pittosporum manii</i>
Ruhija	4	5	10	5	60	2020–2500	<i>Strombosia scheffleri</i> , <i>Olinia usambarensis</i> , <i>Olea capensis</i> , <i>Podocarpus milanjanus</i>
Rushaga	2	3	6	3	36	1910–2220	<i>Strombosia scheffleri</i> , <i>Carapa grandiflora</i> , <i>Psychotria mabonii</i>

For location of study areas, see Fig. S1.

(3) accessible from the base camp within one field day. Transects varied in length and were oriented in a straight line in the direction of the slope. On hilltops, valley bottoms, and at one or two intermediate levels along the slope, we established one or two circular plots 10 m in diameter. We established 92 plots with between 4 and 8 plots per transect, and between 12 and 22 per study area (Table 1). The following criteria guided plot establishment: (1) ≥ 60 percent tree canopy cover; (2) no major disturbance (trails, cutting or other human signs, large herbivores, or fire); (3) no atypical or highly localized features such as springs or rock exposures. The length of the slope and the structure and quality of the forest in transects determined the number of plots at each elevation (one or two). Within elevations (hilltops, slopes, valley bottoms), we placed plots ≥ 100 m apart. When reaching the elevation, we continued 30 steps parallel to the slope and then chose the closest suitable patch of forest. A central tree in the patch and the two nearest trees within 5 m of this tree were selected, meeting the criteria below, resulting in three trees per plot. Criteria for included trees were: (1) ≥ 10 cm dbh (diameter at breast height, at 1.3 m) and (2) no visible damage to the trunk ≤ 2 m in height. We excluded multi-stemmed trees, tree ferns, palms, lianas, and bamboo. Each transect had 12 to 24 trees (depending on the number of plots), and we examined 276 trees.

We determined the species of each sampled tree, following nomenclature used in the ITFC herbarium (updated in 2012 to follow the African Plant Database, see <http://www.ville-ge.ch/musinfo/bd/cjb/africa/index.php>). We noted all lichen species on the trunk from ground level to 2 m above the ground. We recorded the dominant tree species and canopy cover (subjectively estimated in 10% intervals) and measured the dbh for each sampled tree.

LICHEN IDENTIFICATION.—We collected small fragments of all lichen species from all sampled trees for later identification and deposited duplicate specimens in Herbarium UPS, Uppsala University, Sweden and in the ITFC herbarium in Bwindi. Species identification included morphological examination of specimens as well as the identification of diagnostic lichen secondary metabolites using high-performance thin layer chromatography (HPTLC) (Arup *et al.* 1993). Macrolichens identification used Swinscow and Krog (1988), with some name changes according to Index Fungorum (<http://www.indexfungorum.org>). Crustose lichens encountered in the study included the species-rich and ecologically significant orders Arthoniales and Ostropales, as well as selected smaller groups such as the calicioid lichens and *Lepraria* (e.g., Vezda 1966, Tibell 1987, Torrente & Egea 1989, Thor 1990, Grube 2001, Staiger 2002, Frisch 2006, Rivas Plata *et al.* 2006, 2010, Sérusiaux *et al.* 2006, Aptroot *et al.* 2009, Ertz 2009, Lücking *et al.* 2009, Saag *et al.* 2009, Frisch & Thor 2010, Tibell & Frisch 2010). Appendix S1 lists all species included in this analysis.

STATISTICAL ANALYSES.—We used non-metric multi-dimensional scaling (NMDS) and structural equation modeling (SEM) to investigate the relationship between explanatory variables and the

species composition of epiphytic lichens. The analyses involved two steps. First, we conducted separate NMDS analyses for trees and for epiphytic lichens, and fitted the environmental variables study area, elevation, canopy cover, and dbh onto the ordinations using 999 permutations. For elevation, canopy cover, and dbh, we used transect averages. As we sampled only three trees in each plot, we used the proportion of the total number of trees in transects for each tree species in the analyses of tree species composition and the proportion of occupied trees in each transect for each lichen species in the analyses of lichen species composition. In the analyses of lichen species composition, we also used the coordinates in the tree species ordination along the NMDS axis 1 as an explanatory variable. Second, using SEM, we analyzed the effects of elevation and tree species composition (*i.e.*, NMDS coordinates along axis 1 in the tree species ordination) on lichen species composition. The coordinates along NMDS axis 1 in the lichen ordination were used as the response variable. The powerful, multivariate technique of SEM can simultaneously detect and evaluate direct and indirect effects. We compared different models using both ANOVA and AIC. As a complement to the SEM, we performed a Mantel test of the correlation between the tree and lichen species dissimilarity matrices. We performed Pearson correlation analyses and set the number of permutations to 999, using R (v. 3.1.1) with the add-on packages *vegan* (Oksanen *et al.* 2013) and *lavaan* (Rosseel 2012).

We performed indicator species analysis (ISA) in PC-ORD (McCune & Mefford 2011) to assess which lichen species and tree species, respectively, were characteristic of different elevations. We classified the 14 transects into three groups of elevation ranges: 1390–1670 m, >1670–2090 m, and >2090–2380 m, based on their average elevation. ISA calculates the average abundance of each species in each group and divides that by the sum of average abundances across all groups (relative abundance). The number of sample units in each group in which the species is present is then divided by the total number of sample units in these groups (constancy). The product of the relative abundance and constancy is multiplied by 100 and forms the ‘indicator value’ (IV), ranging from 0 to 100. We evaluated the statistical significance of IV-values using the Monte Carlo technique with 1000 permutations (McCune & Mefford 2011).

RESULTS

SPECIES NUMBERS.—We recorded 191 lichen species belonging to 67 genera (Appendix S1). The most species-rich orders were Arthoniales (34% of all recorded species), Lecanorales (23%), Ostropales (20%), and Teloschistales (12%). We identified 94 taxa to the species level (49% of all taxa), including 11 that are only tentatively named. Most unnamed species belonged to the large heterogeneous, crustose genera *Arthonia* (12), *Herpothallon* (6), *Lepraria* (6), *Oppegapha* (6), and *Arthotbelium* (5), as well as *Graphis* (6), and the lichen parasitic genus *Cbaenothecopsis* (6). With the exception of *Oppegapha*, all these genera are under-studied in Africa. Four taxa could not be determined to the genus level and we included these as Arthoniaceae 1, Roccellaceae 1, Sporodochia

1, and Squamules 1. Of the recorded lichen species 68 percent were crustose, 26 percent foliose, and 6 percent foliose.

We recorded a total of 1089 lichen occurrences (*i.e.*, separate records on different trees), with the most common species being *Chrysothrix candelaris* (63 occurrences), *Lepraria aureoflocculosa ined* (62), and *Cryptothoria paleotropica* (59) (Appendix S1), all with a leprose or byssoid thallus organization. Nearly half of the lichen species (45%) were recorded only once. Each plot (three trees) had an average of 10.2 lichen species, varying between 1 and 25, and each tree had an average of 4.7 lichen species, varying between 0 and 17. The average number of lichen species per tree was 4.0 in Buhoma, 4.5 in Byumba, 4.0 in Center, 4.5 in Ruhija, and 5.7 in Rushaga.

TREE SPECIES AND ENVIRONMENTAL FACTORS.—We recorded 60 tree species among the 276 trees included in the sample plots (Appendix S2). The total number of tree species per study area varied between 18 and 24. The most common tree species were *Strombosia scheffleri* (31 trees), *Leptonichia mildbraedii* (25), and *Carapa grandiflora* (15). Dominant tree species differed between study areas, Table 1. For 28 percent of the tree species, we found only one tree individual; by contrast, for 25 percent of the tree species, we found more than five individuals. For tree species with more than five individuals, the following had the most lichen occurrences per tree: *Polyscias fulva* (a mean of 6.0 lichen occurrences per tree),

Newtonia buchananii (5.6), and *Leptonichia mildbraedii* (5.0). The trees had an average dbh of 101 cm (range 10–306 cm) and the transects had an average canopy cover of 73 percent (range 60–79%).

VARIATION IN LICHEN SPECIES COMPOSITION WITH ENVIRONMENTAL FACTORS.—The composition of epiphytic lichens correlated significantly with tree species composition and elevation (Figs. 1 and 2).

We compared two structural equation models, with and without a ‘direct effect’ of elevation on lichen species composition, and found that the most parsimonious model did not include any significant direct effect of elevation on lichen species composition (χ^2 : 2.87, Δ AIC: 1.13; Fig. 3). The model showed that elevation had a significant relationship with tree species composition ($P < 0.001$) and that tree species composition had a significant relationship with lichen species composition ($P < 0.001$). The indirect relationship between elevation and lichen species composition was also significant ($P < 0.001$). The Mantel test confirmed this result as it showed a significant correlation between the dissimilarity matrices of the tree and lichen species (Mantel r : 0.70, $P = 0.001$).

SPECIES INDICATIVE OF DIFFERENT ELEVATIONS.—Tree species characteristic of specific elevations (ISA P -values ≤ 0.10) were

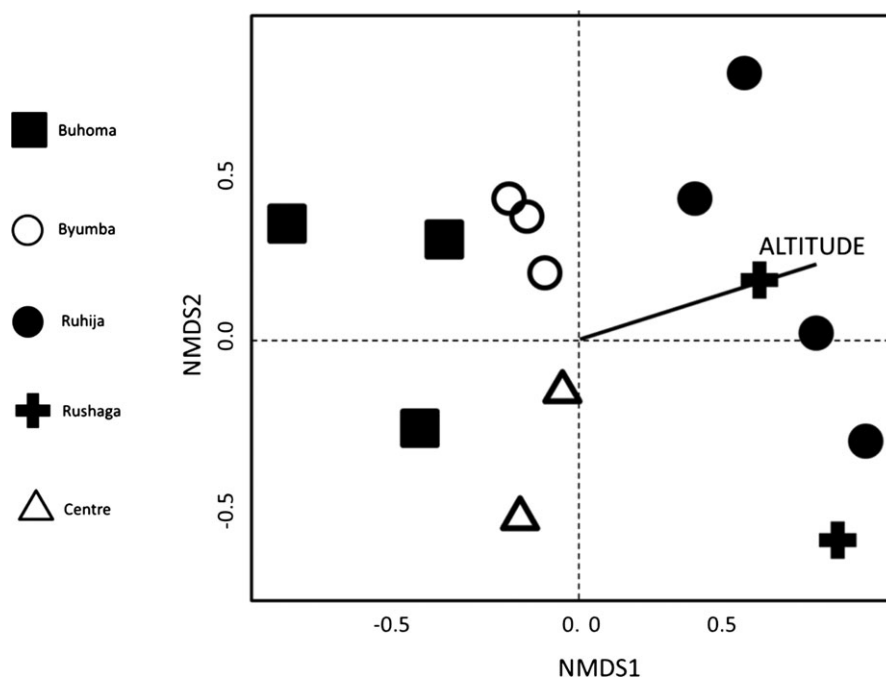


FIGURE 1. Non-metric multi-dimensional scaling graph showing differences in tree species composition among study areas (Fig. S1). The analysis was made at the transect level and the line indicates a significant correlation between tree species composition and elevation ($P = 0.001$). The final three-dimensional solution was reached after three iterations with a final stress of 0.07. The three-dimensional solution was selected over a two-dimensional solution, as it reduced stress by more than 0.05 (from 0.14). The plot shows only the first two dimensions. The procrustean root mean square error (rmse) for the final solution was 0.0013, with a maximum residual of 0.0034.

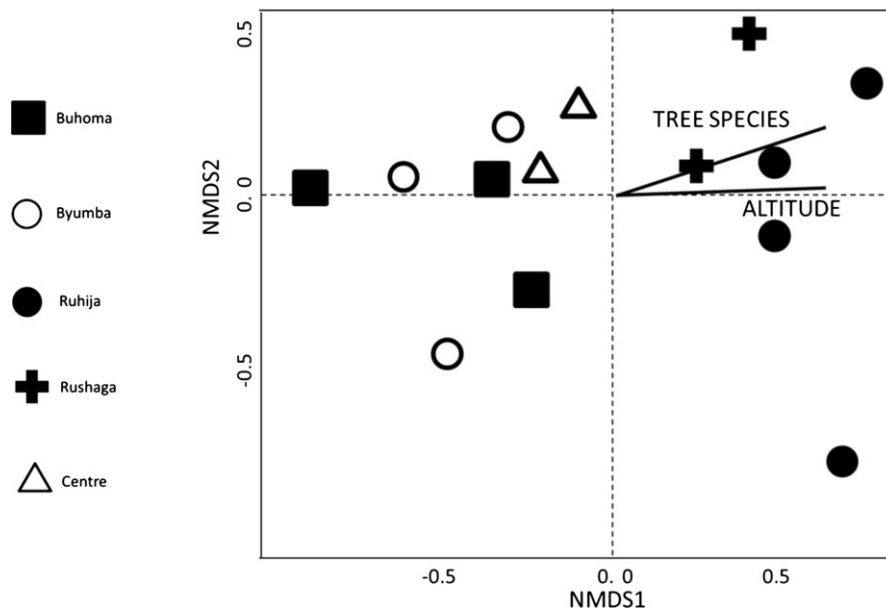


FIGURE 2. Non-metric multi-dimensional scaling (NMDS) graph showing differences in lichen species composition among study areas (Fig. S1). The analysis was made at the transect level and the lines indicate significant correlations between species composition and elevation ($P = 0.001$) and tree species composition (*i.e.*, coordinates for NMDS axis 1 in the NMDS for trees, Fig. 2; $P = 0.001$). The final, three-dimensional solution was reached after 17 iterations with a final stress of 0.09. The three-dimensional solution was selected over a two-dimensional solution as it reduced stress by more than 0.05 (from 0.15). The procrustean rmse for the final solution was 0.00059, with a maximum residual of 0.0012.

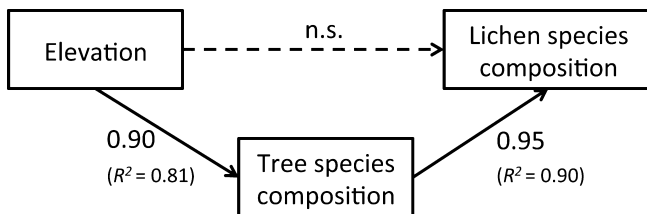


FIGURE 3. Structural equation modeling. Values on the arrows indicate standardized parameters and R^2 values are given in parentheses. The non-significant (n.s.) path is indicated by a dashed arrow.

Beilschmiedia sp., *Leplea mayombensis*, and *Leptonichia mildbraedii* (elevation 1390–1670 m), *Carapa grandiflora* (>1670–2090 m), and *Olea capensis*, *Olinia usambarensis*, and *Podocarpus milanjanus* (>2090–2380 m). The following lichens were typical for elevation 1390–1670 m: *Cryphonina palaeotropica*, *Heterodermia obscurata*, *Leptogium azureum*, *Ocellularia* 2, and *Squamules* 1, for >1670 m–2090 m: *Diorrygia* 1, *Herpothallon* 5, *Lepraria* 1, *Lepraria aureoflocculosa ined.*, *Lepracaulon arbuscula*, *Opegrapha* 5, and *Parmelinopsis minarum*, and for >2090 m–2380 m: *Chiodecton sorediatum*, *Gyalecta* 11, *Lepraria* 2, *Mazosia* 1, *Nyungvea pallida*, and *Opegrapha trilocularis*.

DISCUSSION

Our main finding was that tree species composition is strongly related to, and likely determines, epiphytic lichen assemblages in our study sites at Bwindi. Elevation also has an important effect

but, for the Bwindi sites, acts indirectly by influencing the tree species composition. This result may be surprising as climatic variation along elevation gradients is widely invoked to explain biodiversity patterns in the tropics (*e.g.*, Richards 1996, McCain 2005) and elsewhere (*e.g.*, Becker *et al.* 2007), and climate has a key influence on the growth and vitality of epiphytic lichens (Ellis 2012). However, several studies show that tree species composition acts as a strong driver of epiphytic lichen composition (Cleavitt *et al.* 2009, Mezaka *et al.* 2012, Odor *et al.* 2013). Also, the limited elevation range (1290 m to 2500 m asl) examined here may not have revealed the distribution limits of many lichen species, although this range in elevation implies a wide temperature range, possibly 6–7°C. Further, although a national park, human disturbance still affects parts of Bwindi, possibly masking the effects of elevation on lichen species composition. Larger sample sizes will likely reveal more complex mechanisms; however, inaccessibility and rugged terrain restrict fieldwork in Bwindi.

How does the species of a tree determine the lichen community it supports? The bark likely acts as one main factor (Wolf 1993, 1994, Ellis 2012). For instance, Cáceres *et al.* (2007) found that the properties of bark determine the local distribution of several crustose epiphytic lichens within an Atlantic rain forest in northeastern Brazil. As lichens lack structures similar to roots, they rely on their surroundings for nutrients and water (Rundel 1982). The nutrient content and pH likely vary between tree species, and tree species are often classified as either ‘rich bark’ or ‘poor bark’ species (Barkman 1958). Bark structure influences water-holding capacity, as bark can have very smooth, thin layers

or deeply fissured, porous structures. We encourage further studies on bark chemistry of tree species important to the epiphytic lichens in Bwindi, such as *Polyscias fulva*, *Newtonia buchananii*, and *Leptonichia mildbraedii* and also comparisons with less-important tree species.

Disturbances, including human influence, may act as a strong indirect determinant for lichen flora. For instance, numerous studies in forests worldwide have found that many epiphytic lichens respond negatively to timber harvesting (e.g., Lesica *et al.* 1991, Rolstad *et al.* 2001, Kantvilas & Jarman 2006). In Bwindi National Park, much of the forests contain large gaps and the forest has a mosaic of open and denser canopies. Past logging caused many of the gaps, although some openings also occurred under more or less natural conditions (Babaasa *et al.* 2004). At the establishment of the park in the 1990s, only about 10 percent of the forest had escaped any timber extraction (Howard 1991). Of our study areas, Rushaga and Ruhija have experienced the most disturbances, as they are close to densely populated areas and regularly frequented by elephants. In Rushaga, we struggled to identify slopes that fulfilled our criteria for forest cover. The Center study area, situated furthest from the forest edge, experienced the least disturbance. However, even this area has open valley bottoms with sparse vegetation, most likely due to large mammals. Although our analyses indicate a major, direct role of the tree species composition on epiphytic lichen composition, further understanding will require more investigation of the effect of humans and large herbivores (aside from any influence on the tree community).

The identification of fruticose and foliose lichens followed the concept of species as outlined in the macrolichen flora of East Africa (Swinscow & Krog 1988), with nomenclature adjusted to recent changes in classification. Crustose lichens were mostly identified to the genus level only, using a combination of morphological and chemical criteria. This approach was necessary due to the lack of adequate identification literature and the poor knowledge of crustose rain forest lichens in Africa. The ongoing identification of these taxa to the species level (e.g., Frisch *et al.* 2014) will likely result in the naming of additional species and the description of new taxa. It is hard to estimate the number of new species, but we speculate that they may amount to over half of the unnamed taxa.

As few studies conducted in a tropical rain forest have examined crustose species, we had few datasets with which to compare our findings regarding species number. We identified 191 lichen species on 276 trees (up to 2 m). Cáceres *et al.* (2007) reported 150 species from the lower trunks of 47 trees in a 50 ha Atlantic rain forest in the Northeast region of Brazil, in sample plots of 60 cm × 20 cm. A study conducted in a 1.5 ha plot in a Venezuelan lowland rain forest reported 250 species on nine trees, but this study examined all parts of the trees (Komposch & Hafellner 2000). Crustose lichens contributed about 70 percent of all the lichen species we recorded in Bwindi, similar to the 73 percent reported in Cáceres *et al.* (2007). Most of the about 60 recorded macrolichens found in Bwindi were foliose species, while only 10 were fruticose. However, the abundance of macrolichens was much lower than suggested by total species

numbers. Of the 27 lichen species with more than 10 occurrences on the inventoried trees, only five were macrolichens, and the six most abundant species in our dataset were crustose species.

Crustose lichen taxa associated with humid microclimatic conditions were abundant (e.g., *Lepraria*, *Herpothallon*, *Cryptothelia*, *Chrysothrix candelaris*, and *Dichosporidium brunthaleri*). This likely resulted from our sampling method, as the lower 2 m of tree trunks is often shaded and unfavorable for macrolichens. Our informal field observations suggest that macrolichens commonly occur on higher tree branches in and around Bwindi. Although studies of epiphytic lichen ecology commonly include only the lowest parts of trunks, this may have distorted our findings, as different species assemblages may occur higher on trunks, in the crown, and on branches. For example, for lowland rain forest, Komposch and Hafellner (2000) claimed that studies limited to the lower part of the trunk may miss 80–90 percent of the total species number. In the future, advanced methods like drone-technology may enable routine sampling higher up on trees.

An average of five lichen species per trunk is also low. For instance, Cáceres *et al.* (2007) in their relatively small trunk sample plot found an average of about nine species per tree. We observed many bryophytes on tree trunks during our fieldwork, and this may have caused the low species number, as many epiphytic lichens are sensitive to competition from bryophytes (e.g., Kantvilas & Minchin 1989). Many of the tree species with few lichen occurrences were located in the darkest forest plots in valley bottoms, often along streams. In this habitat, large proportions of the sampled tree trunks supported bryophytes and epiphytic ferns.

CONCLUSIONS

We have made the first detailed ecological study of forest lichens in Africa, focusing on epiphytes in a montane rain forest in a national park in Uganda. In contrast to earlier ecological studies on lichens growing on tree trunks, we examined all growth forms, including crustose lichens, a hitherto neglected group. Although large gaps remain in the knowledge of lichen taxonomy in the tropics, we were able to record near complete species lists from tree trunks, using a mixture of specimens identified to species, and distinct, unidentified species. This work shows that studies of epiphytic lichen ecology in other humid forests in Africa are possible. As elevation drove tree species composition, and tree species composition determined lichen species composition, we conclude that both abiotic and biotic factors influence species assembly processes. One way to better separate the effect of tree species and elevation (and thus climate) would be to analyze lichen species composition on individual tree species that occur over large elevation ranges.

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Conservation) for help with fieldwork, including tree species identification.

SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

FIGURE S1. Map of Africa, showing the location of the Bwindi National Park in SW Uganda and the five study areas, located within three sectors of the park.

APPENDIX S1. *Lichen taxa found in the 14 transects within the five study areas of Buboma, Byumba, Center, Rubija, and Rusbaga.*

APPENDIX S2. *Tree species found in the 14 transects within the five study areas of Buboma, Byumba, Center, Rubija, and Rusbaga.*

LITERATURE CITED

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