


Standard Paper

Distribution of *Lobaria pulmonaria* (L.) Hoffm. in Mt Kilimanjaro and Mt Meru forests: altitudinal range and specificity to substratum tree species

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Abstract

In this study, we sampled *L. pulmonaria* thalli from Mt Kilimanjaro and Mt Meru, Tanzania. Across all sampled tree species, a range of 1–35 thalli of *L. pulmonaria* were counted per trunk (up to 5 m above ground level), with sampling distributed across 13 (c. 1 ha) plots located in the sub-alpine to montane forest altitudinal gradients of Mt Kilimanjaro and Mt Meru. Descriptive analyses were performed to determine the association of *L. pulmonaria* with particular host trees among the study sites and regions, and linear mixed effects models (LMM) were used to explore relationships with tree-level variables. The analyses showed that most thalli of *L. pulmonaria* were unevenly distributed among the tree species in the montane and sub-alpine forests of Mt Kilimanjaro and Mt Meru. Host tree characteristics such as trunk circumference, height on trunk, bark texture and trunk shape appeared to have an effect on the local population size of *L. pulmonaria* and the frequency of occurrence. Also, the results indicated an effect of trunk circumference and tree bark on the development of *L. pulmonaria* thallus size among the study sites. Furthermore, host tree species, for example, *Hypericum revolutum* and *Rapanea melanophloeos* were important habitats for *L. pulmonaria* on both mountains, whereas *Ilex mitis*, *Bersama abyssinica* and *Hagenia abyssinica* were important only on one mountain. The wider literature on *L. pulmonaria* ecology is also reviewed and it is therefore recommended that for successful conservation of the threatened *L. pulmonaria* in tropical montane forests, strategies should consider the type of the forests, together with the host tree species and their size.

Key words: Africa, conservation, lichen, phorophyte species, tropical tree species

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Introduction

Tropical montane forests contain enormous epiphyte species richness (Pócs 1991; Agrawala *et al.* 2003; Hemp 2005). Most studies have described the forest vegetation of East African mountains based on trees, and also pteridophytes (Hemp 2002) and bryophytes (Pócs 1991; Lovett & Pócs 1993; Mattila & Koponen 1999) including liverworts (Pócs 1991; Lovett & Pócs 1993). Only a few studies have focused on lichen species (Swinscow & Krog 1988; Sipman & Harris 1989; Pócs 1991; Kirika *et al.* 2018). Lichens are mutualistic symbiotic organisms composed of a fungal partner (the mycobiont), and one or more photosynthetic partners (the photobiont), which are either a green alga or a cyanobacterium (Galloway 1992; Scheidegger & Goward 2002; Werth & Scheidegger 2012; Dal Grande *et al.* 2014; Nadyeina *et al.* 2014b). The lichen symbiosis is one of the most successful symbioses known in nature, being found in all parts of the

world, in a vast spectrum of microhabitats and microclimates (Galloway 1992). In most terrestrial ecosystems lichens can survive in situations where higher plants cannot grow (Liska *et al.* 1996). Nevertheless, lichens are among the most neglected taxa in tropical rain forest studies. In addition, lichenological knowledge throughout the African region remains inadequate (Sipman & Harris 1989). A study has shown that the number of lichenologists in Tanzania has been either low or practically non-existent in comparison with the number of scientists specializing in vascular plants, and data on the distribution of lichen species was absent or unpublished (Pócs 1991).

This study investigates the ecology and local population sizes (frequency of occurrence) of the epiphytic macrolichen *Lobaria pulmonaria* (L.) Hoffm. in tropical montane forests on Mt Kilimanjaro and Mt Meru in Tanzania. This species, commonly known as tree lungwort, is an epiphytic foliose tripartite macrolichen species containing fungal (*Ascomycetes*), green-algal (*Symbiochloris reticulata*; Škaloud *et al.* 2016) and cyanobacterial (*Nostoc* sp.) partners (Jordan 1970; Scheidegger *et al.* 1998; Snäll *et al.* 2005; Coxson & Stevenson 2007a; Dal Grande *et al.* 2010; Larsson & Gauslaa 2011; Nadyeina *et al.* 2014b). Due to its wide distribution in humid parts of Europe, Asia, North America and Africa (Liska *et al.* 1996; Scheidegger *et al.* 1998;

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Zoller *et al.* 1999; Walser *et al.* 2001), it is used as an indicator species for rapid assessment of the conservation importance of forests (Nascimbene *et al.* 2007; Nadyeina *et al.* 2014a) and an important model species for studies on the conservation biology of epiphytic lichens (Walser *et al.* 2001, 2003; Scheidegger & Werth 2009; Jüriado *et al.* 2011). Not only is it among the most productive lichens, which provide N-fertilization to forest ecosystems (Campbell & Fredeen 2004; Ellis 2012; Gauslaa & Goward 2012), but also an indicator species for primeval forests (Liska *et al.* 1996; Nadyeina *et al.* 2014a) and often used as a flagship species in practical conservation because it is easily recognized by foresters and naturalists (Scheidegger *et al.* 1998).

Studies have shown that some environmental variables such as forest type and altitude (Liska *et al.* 1996; Gu *et al.* 2001), light regimes (Scheidegger 1995; Gauslaa & Solhaug 2000; Mackenzie *et al.* 2001), and habitat moisture (Liska *et al.* 1996; Gauslaa 2014) may affect the distribution of *L. pulmonaria* (Liska *et al.* 1996; Mackenzie *et al.* 2001). Many studies have also shown that *L. pulmonaria* has a low effective dispersal owing to high juvenile mortality (Walser 2004; Öckinger *et al.* 2005; Werth *et al.* 2006a; Otálora *et al.* 2011). It therefore occupies old-growth forest and occurs most abundantly on large trees (Öckinger *et al.* 2005; Snäll *et al.* 2005), where it is restricted to bark surfaces with relatively high pH between 5.0 and 6.0 (Gauslaa 1985, 1995; Rose 1988; Scheidegger 1995; Kermit & Gauslaa 2001; Carlsson & Nilsson 2009). In recent decades, several studies have documented the loss of populations of *L. pulmonaria* because of air pollution (Rose 1988; Scheidegger 1995; Gu *et al.* 2001) and forest management (Gu *et al.* 2001), and the species is considered as regionally rare and threatened (Nascimbene *et al.* 2007; Carlsson & Nilsson 2009; Catalano *et al.* 2010; Dal Grande *et al.* 2010; Larsson & Gauslaa 2011). As a result, this has led to several studies researching the conservation biology and ecology of the species (Gu *et al.* 2001; Gauslaa *et al.* 2006; Nascimbene *et al.* 2007). Furthermore, *L. pulmonaria* is widely used to evaluate the spatio-temporal continuity of forest cover (Rose 1976) and to assess environmental quality in areas of high biogeographical interest (Catalano *et al.* 2010). However, nothing is known about this species' distribution and ecology in the tropical montane forests of Mt Meru and Mt Kilimanjaro, and a detailed knowledge of the distribution and habitat requirements of *L. pulmonaria* in the tropics remains essential to plan conservation action and develop comprehensive policies for this threatened species and others with a similar ecology.

The present study examines the target species, *L. pulmonaria*, in terms of population sizes in relation to host tree variables in tropical montane forest landscapes. We hypothesized that: 1) *L. pulmonaria* is associated with large host trees; 2) *L. pulmonaria* forms larger thalli on large and old host trees than on young host trees; 3) factors associated with host trees' microhabitats explain the occurrence of *L. pulmonaria*; 4) *L. pulmonaria* does not occur randomly but only on specific tree species.

Material and Methods

Study area

Mt Kilimanjaro is Africa's highest mountain and was given the status of a Biosphere Reserve and World Heritage Site in 1989 (Noe 2014) It is located 300 km south of the equator in Tanzania on the border with Kenya, between 2°45'–3°25'S and 37°0'–37°43'E (Hemp 2002, 2006). It is 90 km wide from north-

west to south-east (Hemp 2002) and represents an eroded relic of an ancient volcano with three peaks, Kibo, Mawenzi and Shira, that reach altitudes of 5895 m, 5149 m and 3962 m a.s.l., respectively (Agrawala *et al.* 2003; Hemp 2005). Arusha National Park is the core region of Mt Meru located north-east of Arusha town in the Arumeru District of northern Tanzania, at 3°15'S, 36°45'E (Martinoli *et al.* 2006; Giliba *et al.* 2011). It is the African continent's fifth highest mountain (4566 m a.s.l.) and its topography is that of a young volcano of Pleistocene origin (Instituto Oikos 2011).

Climate

Our study focused on the southern part of Mt Kilimanjaro which is characterized as having a typical equatorial climate. The northern slopes, on the lee side of the mountain, receive much less annual rainfall than the southern slopes (Hemp 2002, 2005). The study area has two distinct rainy seasons: the long rains from March to May, and the short rains around November. The annual precipitation reaches its maximum *c.* 3000 mm in the mid-montane zone, between 1800 m and 2400 m (Agrawala *et al.* 2003; Hemp 2005). In the alpine zone, however, the precipitation decreases to *c.* 200 mm (Hemp 2002). The mean annual temperature decreases linearly upslope, with a lapse rate of 0.56 °C per 100 m (Hemp 2005) starting at 23.41 °C at the foothills in Moshi (813 m) and decreasing to –7.11 °C at the top of Kibo (Agrawala *et al.* 2003). The climate on Mt Meru is characterized by two distinct seasonal weather patterns: short rains in November and December, and long rains from mid-March to late May. The southern slopes of Mt Meru receive up to 2000 mm of rainfall per year, with an annual maximum in the montane belt of *c.* 2200 mm. The annual mean temperature is 18.68 °C and the hottest season is between January and February with the temperatures sometimes exceeding 25 °C, while the cold season is from June to August with the temperature at midday just below 16 °C. Furthermore, on the highest parts of Mt Meru, temperatures are lower and frost occurs at night during the cold season. Due to their high elevation, both Mt Kilimanjaro and Mt Meru have a greater orographic influence on the climate and can be considered wet 'islands' in a dry season (Instituto Oikos 2011).

Vegetation

According to Hemp (2005), several bioclimatic belts can be distinguished along the slopes of Mt Kilimanjaro. A dry and hot colline savannah zone surrounds the mountain base between 700 m and 1000 m (mostly farmland, and some intact savannah grassland). The sub-montane belt between 1000 m and 1800 m has been converted to coffee-banana plantations, with montane forests covering an area of *c.* 1000 km² on Mt Kilimanjaro (Hemp 2005). In the western parts of the mountain, the comparatively dry sub-montane forest below 1600 m is dominated by *Olea europaea* ssp. *africana*, *Croton megalocarpus*, *Cassipourea malosana* and *Diospyros abyssinica*. Above 1600 m the most important tree is the camphor-tree *Ocotea usambarensis*. In a lower altitudinal zone, it occurs commonly with *Agauria salicifolia* and *Macaranga kilimandscharica*. In an upper zone it is associated with *Podocarpus latifolius* (Hemp 2002). Similarly, on the drier northern slope, the lower montane zone is dominated by *Croton-Calodendrum* forests. Mid-altitudes there are dominated by *Cassipourea* forests, whereas *Juniperus procera* characterizes

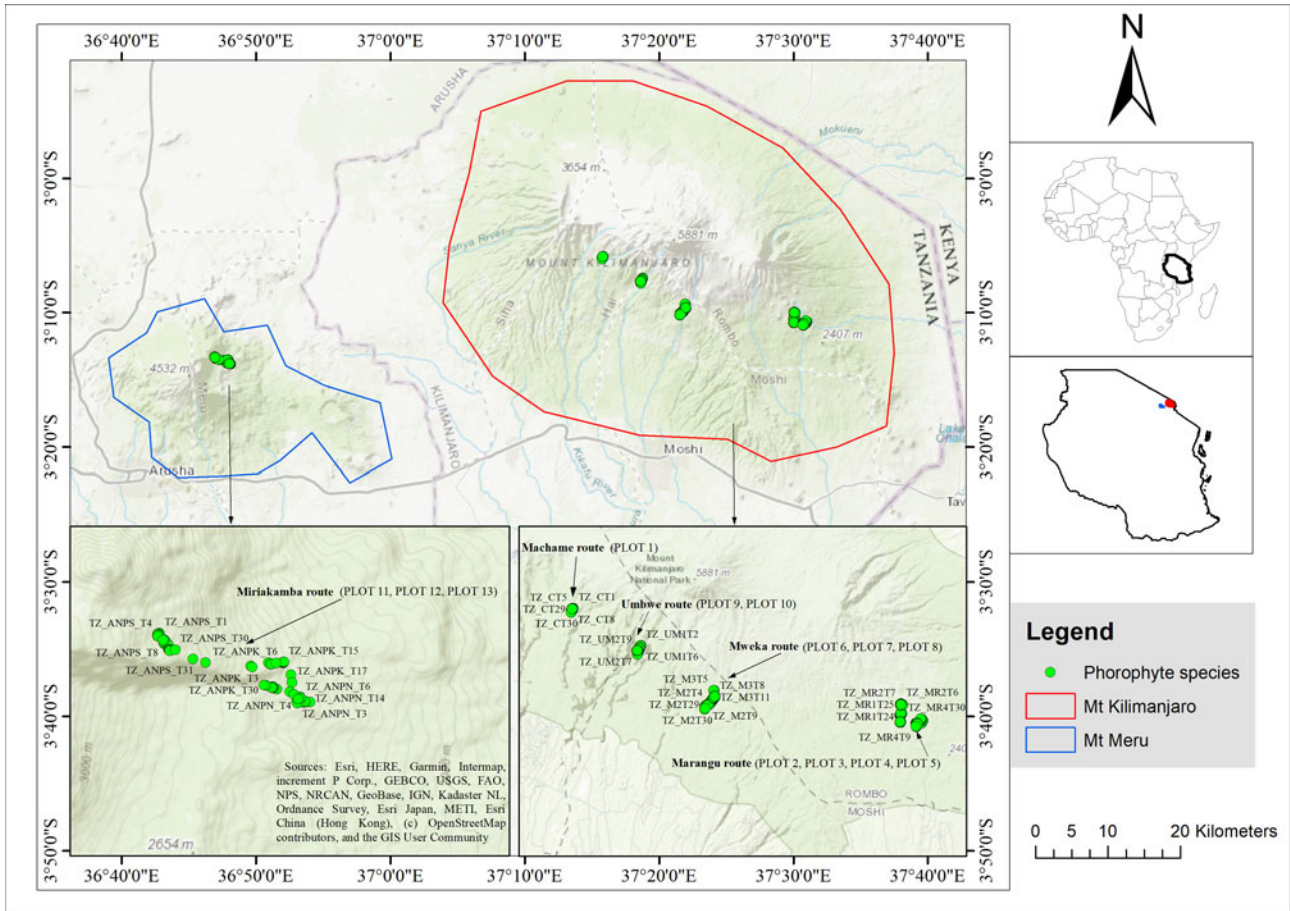


Fig. 1. A map of Mt Kilimanjaro and Mt Meru in Tanzania. Insets show the study sites with a scale provided and annotations which relate to the sampled plots and the phorophytes species (green circles). For further details see Table 3.

the higher altitudes (Hemp 2005). On the southern slope of the mountain, the mature forest reaches a canopy height of up to 40 m or more, is dominated by the camphor-tree *Ocotea usambarensis* and characterized by a high abundance of epiphytes (Schrumpf 2004; Schrumpf et al. 2006). The cloud forest zone is dominated by *Podocarpus latifolius*, *Hagenia abyssinica* and *Erica excelsa*; and above 2800 m *Erica excelsa* is the dominant tree species (Hemp 2005). Above c. 3100 m, these forests have been replaced by *Erica* bush in recent decades; here the species *E. arborea* and *E. trimera*, *Protea kilimandscharica* and *Euryops dacrydioides* cover large areas of the subalpine zone (Hemp & Bayreuth 2001). Around 3900 m elevation, the *Erica* bush grades into *Helichrysum* cushion vegetation with *H. newii* and *H. citrispinum* reaching c. 4500 m, while higher altitudes are poorly vegetated (Hemp 2002, 2005). Moreover, a high number of rare and endemic plants occur on Mt Kilimanjaro, including *Dendrosenecio johnstonii*, *Diospyros kilimandscharica*, *Disperis kerstenii*, *Euphorbia quinquecostata*, *Euryops dacrydioides*, *Gerrardinia eylesiana*, *Helichrysum meyeri-johannis* (decimated along climbing trails), *Impatiens kilimanjari*, *I. digitata*, *I. volkensii*, *Lobelia deckenii*, *Psychotria petiginosa*, *Rubus volkensii* and *Vepris arushensis*. Eleven species of bryophyte are endemic to Mt Kilimanjaro, including *Colura bergheii*, *Pocsiella hydrogonioides* and *Zygodon robustus* (Lovett & Pócs 1993).

According to Instituto Oikos (2011), the vegetation of Mt Meru can be divided into three main zones: the mountain forest

zone (evergreen forest) is dominated by multi-stratified closed evergreen trees with heights up to 30 m or more. It includes the dry montane forests, on the eastern, north-western and northern slopes, between 1500–2600 m elevation, with the threatened *Juniperus procera*, *Olea europaea* ssp. *africana* and *Podocarpus falcatus*; the moist montane forest, on the eastern and western slopes between 1500 and 2400 m elevation, with a great number of broad-leaved hardwood trees; and the upper montane forest between 2300–3000 m elevation, with the bamboo thickets (*Arundinaria alpina*) and *Hagenia abyssinica* forests. The Sub-Afroalpine heath zone (ericaceous zone), between 3000–3600 m elevation, is dominated by arborescent or shrubby species of *Erica* and *Philippia*. The Afroalpine zone, up to the summit at 4560 m, has poor floral species diversity, mainly consisting of open steppe-like communities, dominated by two species of *Pentaschistis* grass.

Sampling design

On Mt Kilimanjaro, *Lobaria pulmonaria* thalli were collected from Marangu, Mweka, Umbwe and Machame between 2700 m and 3100 m elevation (Fig. 1). On Mt Meru, thalli were collected from gradients below the Miriakamba hut, above the Miriakamba hut and below the Saddle hut, between 2100 m and 3300 m elevation (Fig. 1). For each route sampled along the altitudinal gradients, host trees greater than 5 cm in diameter at breast height

were searched for *L. pulmonaria* (Wagner et al. 2005; Öckinger & Nilsson 2010). In total, 1055 thalli of *L. pulmonaria* were sampled and their diameter measured (longest axis), from 389 host trees in forest stands organized as 13 (c. 1-ha) plots (Supplementary Material Table S1, available online). Additionally, a total of 4532 thalli of *L. pulmonaria* were counted on trunks from these sampled host trees up to 5 m above ground level (Nadyeina et al. 2014b). We also recorded other phorophyte variables such as phorophyte species, phorophyte height which was measured with a Blume-Leiss altimeter, phorophyte size (circumference of each sampled phorophyte was measured at breast height, c. 1.3 m above ground level), bark texture (Öckinger et al. 2005; Öckinger & Nilsson 2010) and the diameter of each thallus was measured using a metric ruler. Host tree trunk inclination was estimated and if the trunk was straight up to 2 m height, the host tree was evaluated as straight (Mežaka et al. 2008). Host tree bark samples (0.5 g) were collected from beneath *L. pulmonaria* thalli for pH measurements in the laboratory using standard procedures (Gauslaa 1995). Each host tree was geo-referenced by a hand-held Garmin GPS.

Statistical analyses

Data were analyzed using R v. 4.1.0 (R Core Team 2021). We performed two types of analyses. Firstly, the statistical tests were treated in a preliminary and descriptive manner to discriminate between relevant and uninteresting results and determine the association of *L. pulmonaria* with host trees among the study sites and regions. Secondly, linear mixed-effects models (LME) were used to determine the relationship of host tree variables, and, as response variables i) the diameter of *L. pulmonaria* thalli sampled per host tree, ii) the number of *L. pulmonaria* thalli counted per host tree. The analyses were performed with two datasets. The dataset with 4532 *L. pulmonaria* thalli that were counted from the trunks of respective host trees ($n = 389$) (combined over the altitudinal gradients on Mt Kilimanjaro and Mt Meru), and another dataset with 1055 *L. pulmonaria* thalli that were sampled from respective host trees (combined over the plots on Mt Meru and Mt Kilimanjaro). Relationships between host tree variables and the number of *L. pulmonaria* thalli were tested with LME fitted by restricted maximum likelihood (REML). The number and size of thalli were log-transformed to obtain the normal distribution of residuals. The model selection was then carried out using an automated stepwise selection procedure based on Akaike's information criterion (AIC) to find an optimal model according to predictive power and to avoid overparameterization (Shao 1997; Jürriado et al. 2012). The 'stepAIC' function was performed in the MASS package (Venables & Ripley 2002). To check for heteroscedasticity (Kormann et al. 2015), models with and without a variance function were implemented using restricted maximum likelihood. AIC values indicated that the model without a variance function considerably improved the model fit for the number of thalli in

Table 1. Sequential analysis of variance for the effects of height and circumference on the number of *Lobaria pulmonaria* thalli per phorophyte (linear mixed effect model).

Parameter	DF	F	P
(Intercept)	375	14.4232	< 0.0001
Phorophyte height (m)	375	19.7213	< 0.0001
Phorophyte circumference (cm)	375	2.93831	0.0873

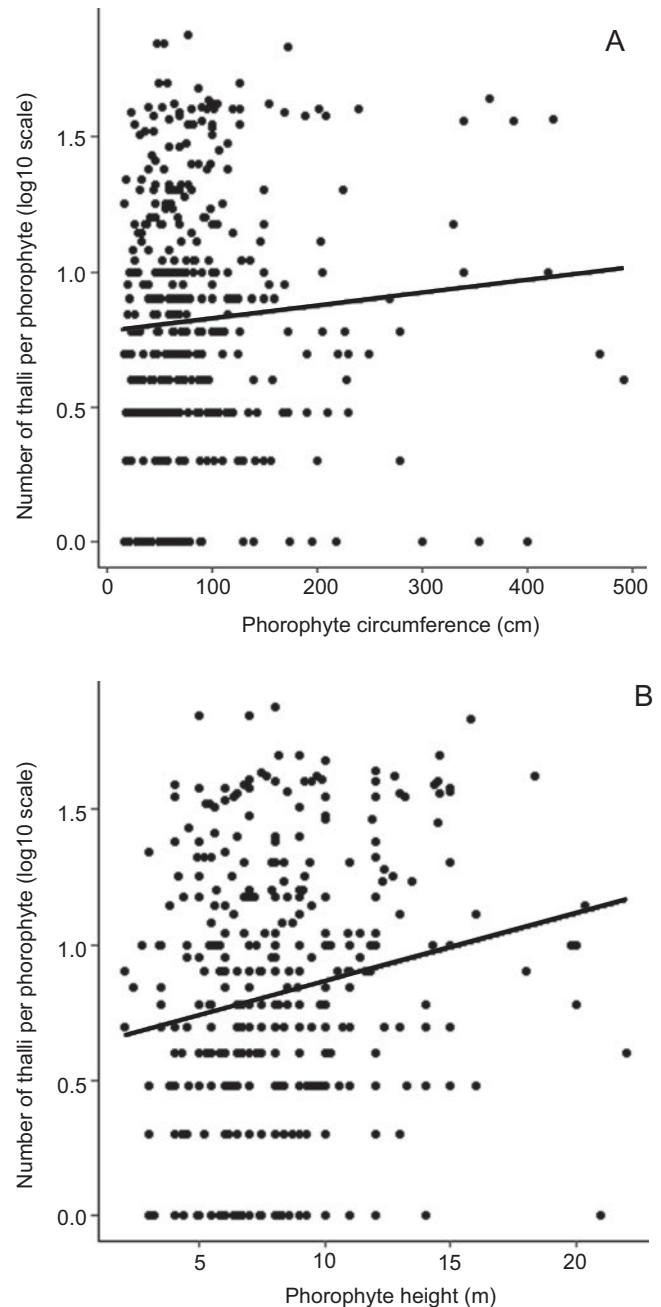


Fig. 2. Relationship between the number of thalli of *Lobaria pulmonaria* counted per trunk and phorophyte circumference (A) and height (B), in the forests of Mt Kilimanjaro and Mt Meru in Tanzania. These two host tree variables were the best predictors of the number of thalli counted per trunk in the data set analyzed by the linear-mixed effects models.

relation to the host tree. The *ggplot2* package (Wickham 2009) was used to display the graphical distribution of *L. pulmonaria* thalli number and size with host trees among the study sites and regions.

Results

Distribution of *Lobaria pulmonaria* with host tree size

In the first data set, analyzed by the linear-mixed effects models using the 'stepAIC' function, two host tree variables (i.e. circumference (Fig. 2A) with AIC = 300.30 and height (Fig. 2B) with

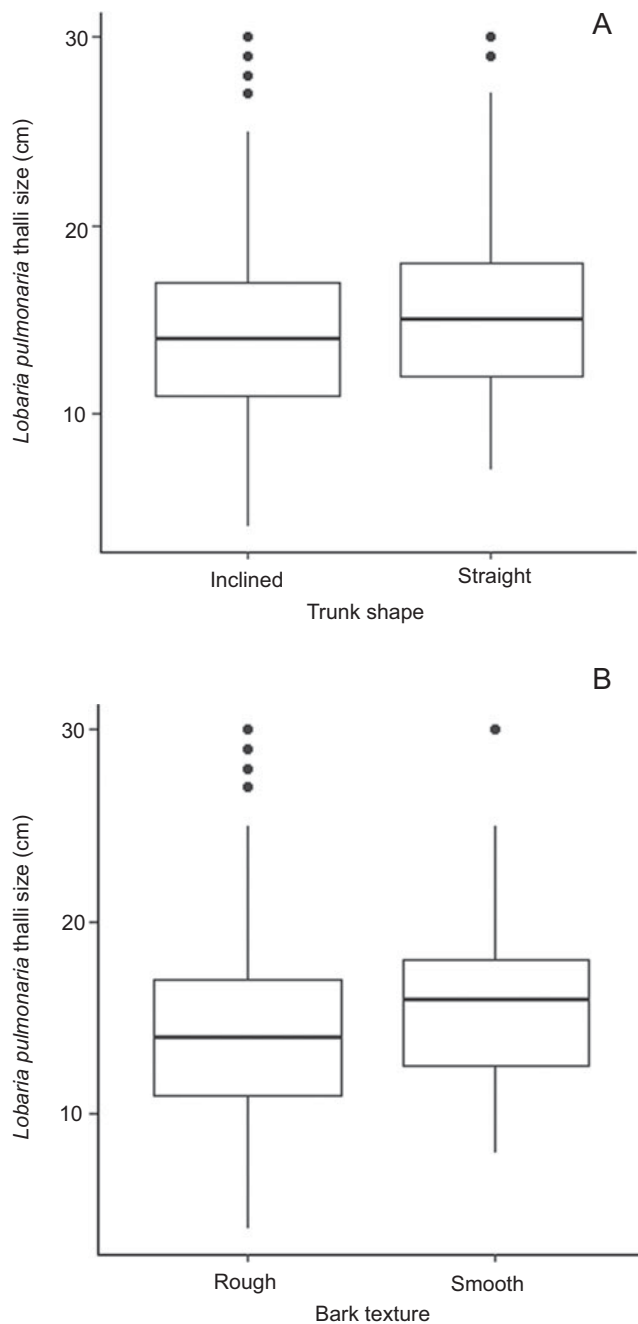


Fig. 3. Relationship between *Lobaria pulmonaria* thallus diameter, and phorophyte trunk shape (A) and bark texture (B) in the forests of Mt Kilimanjaro and Mt Meru in Tanzania. In this analysis linear mixed-effects models were used to determine the relationship of the host tree variables, with the diameter of *L. pulmonaria* thalli sampled per host tree as a response variable.

AIC = 305.94) were the best predictors of the number of thalli counted per trunk. Whereas in the second data set, the analysis retained trunk shape (Fig. 3A) with AIC = 2225.3, bark texture (Fig. 3B) with AIC = 2225.0, trunk circumference (Fig. 4A) with AIC = 2225.2 and bark pH (Fig. 4B) with AIC = 2229.2 as the best predictors for maximum thallus size of *L. pulmonaria*. The results for the first data set (Table 1) indicate a significant effect of host tree height on the distribution of *L. pulmonaria* species among the study sites and across the regions (DF = 375, $P < 0.0001$). Also, there is weak evidence that trunk circumference

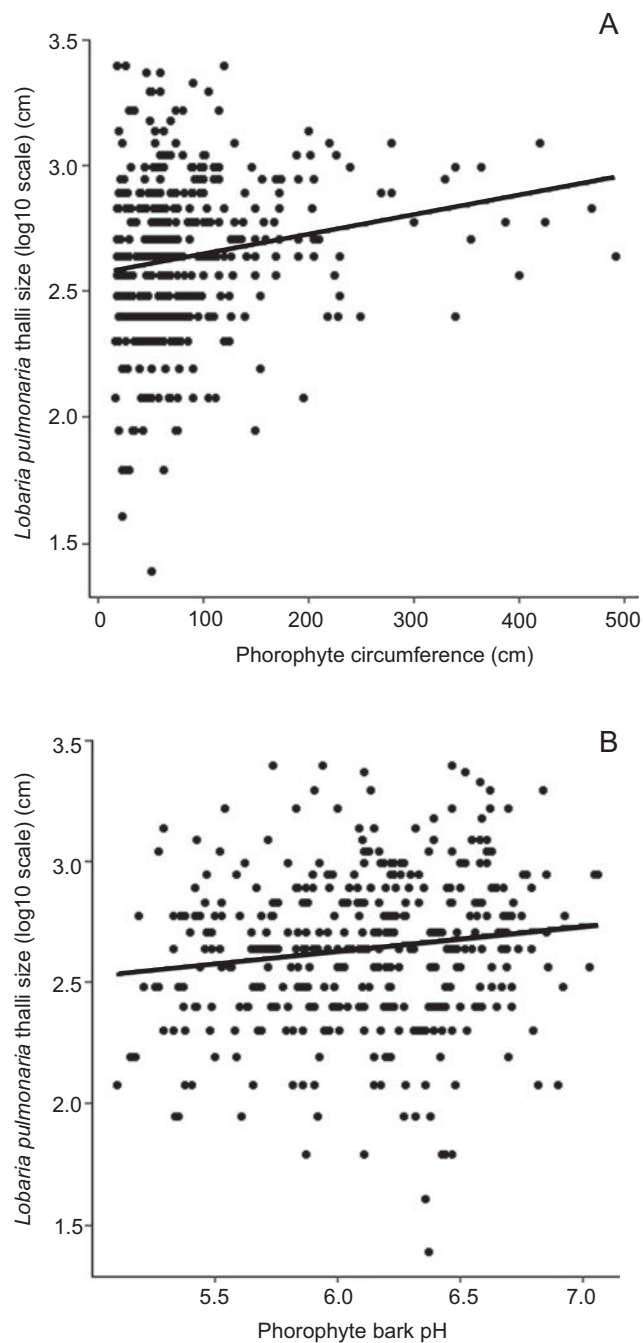


Fig. 4. Relationship between *Lobaria pulmonaria* thallus diameter, and phorophyte circumference (A) and bark pH (B) in the forests of Mt Kilimanjaro and Mt Meru in Tanzania. In this analysis linear mixed-effects models were used to determine the relationship of the host tree variables, with the diameter of *L. pulmonaria* thalli sampled per host tree as a response variable.

may influence *L. pulmonaria* species in occupying the host trees ($P = 0.0873$). The results of the second data set (Table 2) indicate a significant effect of trunk circumference ($P = 0.0299$) on *Lobaria pulmonaria* thallus size among the study sites and across the regions. Also, there is strong evidence that host tree bark pH ($P = 0.0123$) influences the *L. pulmonaria* thallus size but weak evidence was found for the influence of trunk shape ($P = 0.1896$) and bark texture ($P = 0.1881$) on *L. pulmonaria* thallus size among the study sites and across the regions.

Table 2. Sequential analysis of variance for the effects of phorophyte bark texture, circumference, trunk shape and bark pH on the size of *Lobaria pulmonaria* thalli per phorophyte (linear mixed effect model).

Parameter	DF	F	P
(Intercept)	371	531.2287	< 0.0001
Phorophyte bark texture	371	1.7388	0.1881
Phorophyte circumference (cm)	371	4.7493	0.0299
Phorophyte trunk shape	371	1.7269	0.1896
Phorophyte bark pH	371	6.3341	0.0123

Distribution of *Lobaria pulmonaria* with tree species

In total there were 301 host trees associated with the 10 populations of *L. pulmonaria* recorded in the forests of Mt Kilimanjaro and 88 host trees among three populations in the forests of Mt Meru (Table 3, Fig. 5A & B). Among the host tree species that were surveyed in the forests of Mt Kilimanjaro, there were five which appeared to host a greater number of *L. pulmonaria* thalli, including *Ilex mitis* with 0.26 frequency of occurrence, *Podocarpus latifolius* (0.18), *Senecio* sp. (0.16), *Prunus africana* (0.11) and *Rapanea melanophloeos* (0.09). On Mt Meru, as shown in Table 3 and Fig. 5B, the occurrence of *L. pulmonaria* was overall less frequent; however, among the host trees that were surveyed, there were also five tree species which appeared to host a relatively high number of *L. pulmonaria* thalli, including *Bersama abyssinica* with 0.33 frequency of occurrence, *Hypericum revolutum* (0.27), *Hagenia abyssinica* (0.14), *Rapanea melanophloeos* (0.10) and *Olea capensis* (0.07). It was found that there were more host tree species associated with *L. pulmonaria* in the forests of Mt Kilimanjaro, including *Catha edulis*, *Erica arborea*, *E. excelsa*, *Hypericum revolutum*, *Ilex mitis*, *Macaranga capensis*, *Maytenus acuminata*, *Ocotea usambarensis*, *Podocarpus latifolius*, *Prunus africana*, *Rapanea melanophloeos*, *Rhamnus prinoides*, *Senecio subsessilis* and *Senecio* sp., than on Mt Meru which had fewer host tree species including *Bersama abyssinica*, *Catha edulis*, *Clematis* sp. (climber), *Hagenia abyssinica*, *Hypericum revolutum*, *Mystroxydon aethiopicum*, *Olea capensis*, *Podocarpus latifolius*, *Prunus africana* and *Rapanea melanophloeos*. Among the 14 host tree species where *L. pulmonaria* was recorded on Mt Kilimanjaro, thalli were more frequent on both small to medium sized and large old-growth host trees of *Ilex mitis* and *Podocarpus latifolius* than on any other host tree. While the results from Mt Meru indicated that *L. pulmonaria* thalli were more frequent on small to medium sized *Bersama abyssinica* than other host trees. Furthermore, the information given in Supplementary Material Table S1 (available online) and Table 3 indicated that *L. pulmonaria* was unevenly distributed elevationally among the sub-alpine to montane forest altitudinal gradients of Mt Kilimanjaro and Mt Meru.

Discussion

Distribution of *Lobaria pulmonaria* with tree size

In this study, data collected from high elevation tropical forests, between 2500 m and 3200 m elevation on Mt Kilimanjaro, have indicated that *L. pulmonaria* occurs most frequently on *Ilex mitis* and *Podocarpus latifolius* (Fig. 5A). Also, it often occurred on small sized host trees such as *Senecio* sp. However,

Macaranga capensis is one of the largest old-growth host trees and an important habitat of *L. pulmonaria* species, though was present only in one locality (MR4). These findings for Mt Kilimanjaro differ from the observations in the forest of Mt Meru, where *L. pulmonaria* occurred most frequently on *Bersama abyssinica* and *Hypericum revolutum* (shrub) (Fig. 5B). These host trees were small to medium sized in terms of height and circumference. Also, *Hagenia abyssinica*, a large old-growth host tree and a supposed important habitat of *L. pulmonaria* species on Mt Meru, had a few individual thalli which appeared to occur in only a small elevational range between 2570 m and 3220 m above Miriakamba hut. Comparatively, Scheidegger et al. (1998) indicated that colonization by *L. pulmonaria* significantly increased with a tree's circumference, and that small trees with a circumference less than 47 cm were not colonised with *L. pulmonaria*. On the contrary, the results of this project have shown that, in tropical mountain forests, *L. pulmonaria* formed a large number of thalli even on small sized, young host trees with a circumference of c. 20 cm, with larger thalli on host trees with a circumference between 50 cm and 100 cm. Moreover, large thalli of *L. pulmonaria* were present, but only on a few thicker, old-growth host trees with a circumference over 300 cm. A possible explanation is that lichen fragments falling off nearby large old-growth hardwood host trees continue to grow on branches of small sized host trees in their vicinity. It would be interesting to conduct another study on the effect of distance between putative old-growth and young host trees in relation to the number and size of *L. pulmonaria* thallus per host tree.

Previous literature has demonstrated that old-growth forests are key reservoirs of epiphytic lichen species (Neitlich & McCune 1997; Scheidegger et al. 1998; Sillett et al. 2000; Bosch et al. 2013). Furthermore, cyanolichens and tripartite lichens such as *L. pulmonaria* are often categorized as old growth-dependent species (Muir et al. 1997; Öckinger et al. 2005; Snäll et al. 2005; Coxson & Stevenson 2007b). In wider relation to this, Lie et al. (2009) has shown that there is a relationship between tree size and lichen epiphytic diversity patterns, while Nadyeina et al. (2014a) and Liska et al. (1996) have also shown that *L. pulmonaria* prefers old-growth forests. Gauslaa (1995) and Jürriado & Liira (2010) have discussed the characteristic feature of the species which is considered to be a representative of a climax lichen community on mature hardwood trees in old forests. Meanwhile, other studies (Gu et al. 2001; Kalwij et al. 2005; Öckinger et al. 2005; Edman et al. 2008) have clearly shown that in a forested landscape, the occurrence of *L. pulmonaria* within a stand is dependent on the diameter of host trees. Under optimal climate and habitat conditions where *L. pulmonaria* is abundant, the species can grow on various trees, even those with small diameters (Carlsson & Nilsson 2009; Jürriado et al. 2012). Edman et al. (2008) have reported a strong relationship between tree size and the abundance of lichens, indicating the importance of large trees in forest ecosystems. Therefore, our results concur with most of the above studies, while suggesting that there is a strong increase in the number of *L. pulmonaria* thalli with increasing host tree size.

Furthermore, our results indicate that many trees, regardless of their size, being small, medium sized to large old-growth trees, were potential habitats for a considerable number of *L. pulmonaria* thalli, including such shrubby host trees as *Hypericum revolutum*. Although the results have indicated that *L. pulmonaria* thalli were largely associated with young host trees, these findings do not invalidate suggestions that protecting old-growth host trees

Table 3. Frequency of phorophyte species recorded with *Lobaria pulmonaria* from the 13 sampled populations (plots) on Mt Kilimanjaro and Mt Meru in Tanzania.

Phorophytes	Frequency	Altitudinal range	pH range	Mt Kilimanjaro (n = 301)										Mt Meru (n = 88)			Np	
				Machame		Marangu			Mweka			Umbwe		Miriakamba hut		Saddle hut		
				Plot 1	Plot 2	Plot 3	Plot 4	Plot 5	Plot 6	Plot 7	Plot 8	Plot 9	Plot 10	Plot 11	Plot 12	Plot 13		
<i>Catha edulis</i>	0.00	2943	5.9	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Erica arborea</i>	0.01	2828–2840	5.2–5.8	0	0	0	3	0	0	0	0	0	0	0	0	0	0	3
<i>E. excelsa</i>	0.04	2963–3083	5.5–6.5	0	0	2	0	0	0	0	4	5	1	0	0	0	0	12
<i>Hypericum revolutum</i>	0.03	2754–3009	5.5–6.5	0	5	0	0	2	0	0	2	0	0	0	0	0	0	9
<i>Ilex mitis</i>	0.26	2804–3087	5.7–6.9	17	0	0	3	0	11	20	2	11	14	0	0	0	0	78
<i>Macaranga capensis</i>	0.05	2708–2798	5.9–6.8	0	0	0	0	15	0	0	0	0	0	0	0	0	0	15
<i>Maytenus acuminata</i>	0.02	2827–2908	5.9–6.2	0	0	0	0	0	2	5	0	0	0	0	0	0	0	7
<i>Ocotea usambarensis</i>	0.01	2835–2916	5.7–6.0	0	0	0	0	0	0	2	0	0	1	0	0	0	0	3
<i>Podocarpus latifolius</i>	0.18	2753–3036	5.4–6.7	6	3	0	8	2	8	3	2	14	7	0	0	0	0	53
<i>Prunus africana</i>	0.11	2707–3033	5.5–7.1	1	6	5	6	11	1	0	3	0	0	0	0	0	0	33
<i>Rapanea melanophloeos</i>	0.09	2829–3034	5.4–6.7	6	4	2	3	0	3	0	6	2	1	0	0	0	0	27
<i>Rhamnus prinoides</i>	0.00	2935	6.0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>Senecio subsessilis</i>	0.04	2823–3076	5.9–7.1	0	1	3	5	0	0	0	0	3	0	0	0	0	0	12
<i>Senecio</i> sp.	0.16	2821–3049	5.2–6.7	0	11	18	2	0	5	0	11	0	0	0	0	0	0	47
<i>Bersama abyssinica</i>	0.33	2449–2669	5.1–6.8	0	0	0	0	0	0	0	0	0	0	18	11	0	0	29
<i>Catha edulis</i>	0.01	2555	6.4	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
<i>Clematis</i> sp.	0.02	2574	6.5–6.6	0	0	0	0	0	0	0	0	0	0	0	1	1	0	2
<i>Hagenia abyssinica</i>	0.14	2565–3216	5.4–7.0	0	0	0	0	0	0	0	0	0	0	0	8	4	0	12
<i>Hypericum revolutum</i>	0.27	2466–3245	5.2–6.0	0	0	0	0	0	0	0	0	0	0	1	5	18	0	24
<i>Mystroxydon aethiopicum</i>	0.02	2460–2497	6.0–6.8	0	0	0	0	0	0	0	0	0	0	2	0	0	0	2
<i>Olea capensis</i>	0.07	2463–2545	6.3–6.9	0	0	0	0	0	0	0	0	0	0	4	2	0	0	6
<i>Podocarpus latifolius</i>	0.01	2459	6.2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
<i>Prunus africana</i>	0.02	2683–2692	6.5–6.7	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
<i>Rapanea melanophloeos</i>	0.10	3175–3237	5.3–6.0	0	0	0	0	0	0	0	0	0	0	0	1	8	0	9
			Ns	30	32	30	30	30	30	30	30	35	24	26	31	31	389	

n = number of host trees recorded

pH range = pH of sampled bark of host trees recorded

Np = number of phorophytes recorded with *Lobaria pulmonaria*

Ns = number of phorophytes sampled per study site

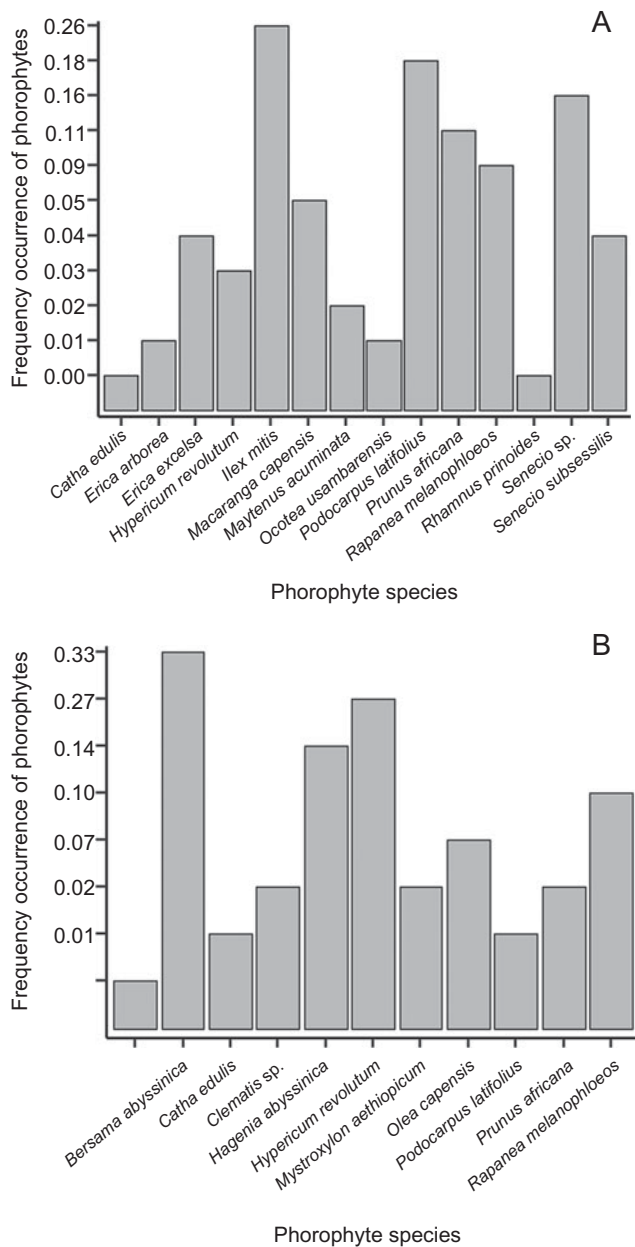


Fig. 5. Frequency of occurrence of phorophytes with *Lobaria pulmonaria* in the 13 sampled populations from the forests of Mt Kilimanjaro (A) and Mt Meru (B).

is of paramount importance for preserving biodiversity (Muir et al. 1997). In essence, the key challenge of relying on lichen communities associated with young host trees is that after catastrophic disturbance such as frequent fires, which are often re-occurring on Mt Kilimanjaro (Hemp 2001; personal field observation) and Mt Meru (personal field observation), the rate of recovery of epiphytes may depend on old-growth remnants beyond the reach of fire as propagule sources for recovery into in young forests (Nascimbene et al. 2007).

Distribution of *Lobaria pulmonaria* with the type of host tree species

Our survey along altitudinal gradients in the tropical montane forests of Mt Kilimanjaro and Mt Meru, indicated that *L.*

pulmonaria thalli were unevenly distributed among the sub-alpine and montane forests and we found that the species occurred in patches along the hills and valleys (observational data, unpublished). Similar findings were reported by McCune et al. (1996) who observed the occurrence of *L. pulmonaria* along valleys, but also on hills (Rose 1988; Liska et al. 1996) and otherwise in patches (Nascimbene et al. 2007). Furthermore, host tree distribution can cause patterns to emerge. It was observed that, in the mountains of Kilimanjaro, *L. pulmonaria* most frequently occurred on *Hypericum revolutum* (shrub), *Ilex mitis*, *Podocarpus latifolius* and *Rapanea melanophloeos* host trees, and less frequently on others including *Catha edulis*, *Erica arborea*, *E. excelsa*, *Macaranga capensis*, *Maytenus acuminata*, *Ocotea usambarensis*, *Prunus africana*, *Rhamnus prinoides*, *Senecio subsessilis* and *Senecio* sp. On Mt Meru, *L. pulmonaria* was mainly growing on *Bersama abyssinica* and *Hypericum revolutum* host trees and less frequently on *Catha edulis*, *Clematis* sp. (climber), *Hagenia abyssinica*, *Myroxylon aethiopicum*, *Olea capensis*, *Podocarpus latifolius*, *Prunus africana* and *Rapanea melanophloeos*. In some instances, host tree species such as *Hypericum revolutum* and *Rapanea melanophloeos* were important habitats on both of the mountains while other host trees species such as *Bersama abyssinica*, *Hagenia abyssinica* and *Ilex mitis* were a good substratum host on one mountain only. The distribution of epiphytic lichens has been described at different spatial scales ranging from the single tree scale, to the forest stand and landscape scales, up to the regional scale (Lie et al. 2009). Many studies combined indicate that *L. pulmonaria* does not have a specific preference for certain type of forests; for example, in European countries *L. pulmonaria* is found in different forest types, the most important being beech forests (Nadyeina et al. 2014a), coniferous montane forests, chestnut forests and oak forests (Nascimbene et al. 2010). In Finland, Gu et al. (2001) and Nadyeina et al. (2014a) have reported that *L. pulmonaria* occurs throughout the country and has greatly declined but is not yet considered as a threatened species because it is still fairly common in the remaining eastern-central old-growth forests, especially on *Populus tremula*, *Salix caprea* and *Sorbus aucuparia*. In humid forests, *L. pulmonaria* has also been found on other tree species such as the lower branches of old spruce trees (*Picea abies*) and on vertical cliffs. The studies carried out by Walser (2004), Werth et al. (2006b) together with Werth & Scheidegger (2012) have shown that the distribution of *L. pulmonaria* along the pasture-woodland landscape of the Jura Mountains in Switzerland was most frequent on host trees of sycamore maple (*Acer pseudoplatanus*) and beech (*Fagus sylvatica*); both host trees were scattered throughout their study area. Clearly, *L. pulmonaria* can grow in a range of situations, though its actual distribution in Tanzania is not well known and documented (Pócs 1991).

Nevertheless, in many Central European regions, *L. pulmonaria* is often restricted to single trees due to increased anthropogenic interference at the tree and stand levels (Scheidegger et al. 1998). In addition, existing literature indicates that *L. pulmonaria* is an indicator species for long ecological continuity in forest ecosystems (Gauslaa & Solhaug 2000). However, the presence of only three host trees of *Ocotea usambarensis*, which is a commercially important hardwood species in the montane forest on the southern slopes of Mt Kilimanjaro (Pócs 1991; Nsolomo & Venn 2000), is explained by extensive exploitation in the past for timber (Misana 1991). A similar situation was observed on Mt Meru, where *L. pulmonaria* was found on only one *Podocarpus latifolius* among the few specimens of this species that were observed in the study sites, and which are

commercially important hardwood species (Misana 1991). The scarcity of these commercially valuable tree species reflects human-induced disturbance, such as over exploitation of timber, firewood and charcoal (Giliba *et al.* 2011), and deliberate fire setting (field personal observation).

Association of *Lobaria pulmonaria* with host tree variables

The results of this study suggest that host trees in sub-alpine and montane forests of Mt Kilimanjaro and Mt Meru host the largest thalli on larger, smooth bark surfaces and straight trunks. This may imply that the further colonization and occurrence of small thallus diameters on large trunks is interrupted by features associated with the wide host trees circumference such as a rapid growth of the crown, resulting in a fluctuating light (Scheidegger 1995; Gauslaa & Solhaug 2000; MacKenzie *et al.* 2001). There are other potentially important factors. Sillett *et al.* (2000) reported that small thalli were found frequently establishing on moss-free bark, and often found vigorous thalli of old-growth associated species on smooth-barked twigs and branches. Other studies have similarly reported that several microhabitat factors such as the height of the trunk, bark slope and bark moisture (Bates 1992), and bark roughness, tree age and size (Ellis 2012) have an important role in determining the establishment and distribution of epiphytic lichen species in forest ecosystems (Mistry & Berardi 2005; Mežaka *et al.* 2008; Ellis 2012). Also, the physical and chemical quality of the host trees' bark structure which changes through time may enhance an old host tree in providing a different substratum than the young host tree (Lie *et al.* 2009). Furthermore, it has been reported that colonization of macrolichens is often restricted to the rough branch scars as opposed to adjoining smooth bark. This is because the young bark is relatively smooth, resinous, non-absorbent and moss-free compared to the old-bark surfaces which become rough, less resinous, more porous, absorbent and moss-covered; the latter type of bark surface stores water, accumulates humus and forms a spongy surface that could either promote or inhibit lichen thallus development (Sillett *et al.* 2000). In this study, we observed an enormous quantity of bryophyte mats on host trees associated with the occurrence of *L. pulmonaria* on both smooth and rough barked trunks. The presence of a large quantity of bryophyte mats on some host trees such as *Erica excelsa*, *Ilex mitis*, *Rapanea melanophloeos* and *Senecio* sp. in montane and sub-alpine forests suggests they might be an optimal substratum for the establishment and growth of large thalli.

Studies have found out that *L. pulmonaria* is restricted to bark that is not strongly buffered, with a relatively high pH (5.0–6.0) (Gauslaa 1985; Rose 1988; Scheidegger 1995). Rose (1988) discovered that rain of low pH, contaminated by sulphuric and nitric acids of industrial or automobile origin, acidifies bark and may have a negative effect on thallus development. Rose (1988) further reported that trees with bark of higher pH (above *c.* 5.0) hosted *L. pulmonaria*, and those with low pH bark did not. This study found a high buffer capacity of bark pH between 5.1 and 7.1 and this phenomenon corresponded to some host trees such as *Hagenia abyssinica* having a high cover of *L. pulmonaria*. However, the occurrence of *H. abyssinica* was restricted only to Mt Meru and it was not recorded in the forests of Mt Kilimanjaro. Further investigation on the effect of bark pH, amount of moisture and mineral content as important factors for the occurrence and absence of *L. pulmonaria* on tree species needs to be conducted.

Conclusion and implications for lichen conservation

The nature of the present study on macrolichen species in tropical montane forests demonstrates the importance of conservation management systems that ensure forest stand continuity for lichen conservation. Based on the findings of this and related studies discussed above, it can be concluded that the current forest fire activity in protected areas may lead to the decline of regionally rare and threatened populations of *L. pulmonaria*. The largest trees host the largest, remnant thalli. Therefore, conservation programmes in tropical montane forests should improve fire prevention regimes and establish a monitoring programme to preserve viable populations of the target species in the protected areas.

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