Sensitivity of tropical pendant bryophytes: results from a translocation experiment along an elevation gradient

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We studied growth of three epiphytic bryophyte species in Kenya to determine their sensitivity to environmental changes. Bryophytes collected from a cool and moist upper montane forest were used to prepare 180 pendant transplants. Sixty transplants were placed in their natural habitat while 120 were transferred to two warmer and drier sites in a lower montane forest. After one year, all the transplants recovered from the lower montane forest were transferred back to the upper montane forest. In the third year, half of the remaining transplants were left in their location, and half transferred to an eucalyptus plantation forest, both in the upper montane zone. After each year subsamples were taken from each group for growth measurements. The epiphytic bryophytes demonstrated considerable resilience during the experiment. They clearly suffered from the warm and dry conditions of the lower montane forest, but quickly recovered and then exhibited growth rates comparable to those of the controls. In the third year there was no statistical difference in the growth of transplants in their natural location and in the eucalyptus plantation. This indicates that the lack of suitable substrate is the primary factor limiting bryophyte biomass in plantation forests rather than unsuitable microclimate *per se*.

Introduction

Tropical montane cloud forests are characterized by high density, biomass and diversity of epiphytes, including bryophytes (i.e., mosses, liverworts and hornworts) (Frahm & Gradstein 1991, Wolf 1993, Bruijnzeel *et al.* 2010). Epiphytic bryophytes themselves play an important role in the hydrology and maintenance of cloud forests (Ah-Peng *et al.* 2017). Poikilohydric non-vascular epiphytes absorb water and

dissolved nutrients directly from the air and precipitation through their entire surface (Farmer *et al.* 1992, Gradstein 1992, Löbs *et al.* 2019). Therefore, epiphytes on tree trunks, branches and even on leaves can absorb and temporarily hold large quantities of water and thus help to maintain high atmospheric humidity long after the precipitation has ceased (Pócs 1980, Nadkarni 1984, Frahm 1990, Veneklaas *et al.* 1990, Gradstein 1992, Lawrence & Vandecar 2015, Porada *et al.* 2018). However, many non-vascu-

lar epiphytes in tropical montane cloud forests are sensitive to desiccation and thus vulnerable to changes in forest structure and prevailing climate (Gignac 2001, Jácome *et al.* 2011, Lakatos 2011, Malombe *et al.* 2016).

Very few empirical studies in tropics have explicitly focused on epiphyte resilience despite the predicted sensitivity of this group to global warming (Zotz & Bader 2009). Non-vascular epiphytes (bryophytes, lichens) can be used as sensitive biosensors of environmental conditions and environmental change and have been widely used in air pollution monitoring (Fernández & Carballeira 2000, Nimis *et al.* 2002, Szczepaniak & Biziuk 2003). For example, Jácome *et al.* (2011) found that epiphytic bryophyte transplants placed in a montane cloud forest were highly sensitive to increases in nitrogen deposition and often unable to recover once they had been badly damaged.

Relationships between epiphyte growth and environmental variables have been studied by transplanting bryophytes into habitats and recording their subsequent growth. Transplant studies have been used to obtain information of maximal biomass growth rates under favourable conditions, but also on the negative effects of adverse conditions on bryophyte growth (McCune *et al.* 1996, Bignal *et al.* 2008, Song *et al.* 2014). In our recent study (Stam *et al.* 2017) we found that tropical bryophytes can have growth rates comparable to those of pendant epiphytes in temperate rainforests, with average annual biomass growth rates often between 5% and 40%, and maximal values sometimes exceeding 150%.

Transplant studies have also been used to determine the effect of simulated climate change and the acclimation potential of tropical bryophytes. Song *et al*. (2012) used bryophyte and lichen transplants to study the effects of increased temperature and elevated atmospheric carbon dioxide concentrations on several epiphytic species and predicted a dim future for the epiphytes, especially lichens, in a warming climate. Wagner *et al*. (2014) transplanted ten bryophyte species from high altitudes to lower and warmer altitudes in Panama and studied short-term temperature acclimation of CO_2 exchange for 2.5 months, and survival and growth for 21 months following transplantation. Short-term acclimation was not detected, and final mortality

was high and growth low in the transplanted samples. Interestingly, some transplanted specimens of most species, however, survived and finally had growth rates comparable to controls, suggesting temperature acclimation. The authors concluded that apparent heterogeneity of the acclimation potential within species may allow some populations to adapt locally and avoid being forced uphill under climatic warming.

Zotz and Bader (2009) identified non-vascular epiphytes of tropical cloud forests as a group which probably is particularly threatened by climate change. Hygrophytic epiphytes are likely to suffer from decreased moisture input but the possible negative effects of rising temperatures on performance are still largely unexplored. Besides climate change, also concurrent changes in land use are predicted to adversely affect cryptogamic epiphytes in tropical montane forests, with the most serious consequences for hygrophilic taxa (Zotz & Bader 2008).

We used a transplant experiment to evaluate the response of epiphytic bryophytes to warmer and drier conditions, and their ability to recover when returned to favorable conditions after one year. To our knowledge, no transplant studies have previously addressed the ability of non-vascular epiphytes to recover from exposure to adverse conditions, which could give valuable insights into their overall resilience when confronted with predicted climate change. After a recovery period of one year we used the same transplants to examine whether, in addition to differences in environmental conditions linked to elevation, also man-induced differences in growth conditions (incl. differences in substrate availability caused by tree species) could have pronounced effects on transplant growth. In total, we measured changes in biomass of 180 transplants of three epiphytic moss species during three years.

Our hypotheses were: (1) Biomass increase of the bryophyte transplants growing in adverse and very adverse conditions during the first year will be markedly smaller than that of the transplants left in their original habitat. (2) In the second year, after being returned to the original habitat some transplants growing in the previous year in adverse and very adverse conditions will recover but will not gain weight as rapidly as those left in their original habitat. (3) By the end

of the third year the effect of the first year's treatment will decrease, and the growth rates of the transplants in all three groups will be the same. (4) Growth of the transplants that spent their third year in the plantation forest will be affected by site, with transplants in the plantation forest growing less than those at the original location.

Methods

Study site

The study was conducted in the Taita Hills located in southeastern Kenya (3°40´S, 38°35´E) that form the northernmost part of the Eastern Arc Mountains. The Eastern Arc Mountains represent a biodiversity hot spot with an exceptionally high number of endemic species (Myers *et al.* 2000) and a rich epiphytic bryophyte flora (Enroth *et al.* 2013, 2019, Malombe *et al.* 2016). However, due to long-lasting and intensive human pressure, the indigenous moist montane forests on the upper slopes of the Taita Hills have been reduced to tiny remnant patches, which threatens the species diversity in the area (Pellikka *et al.* 2009, Aerts *et al.* 2011, Adhikari *et al.* 2017, Pellikka *et al.* 2018).

To study growth of bryophytes at forest sites differing in microclimate (Table 1 and Fig. 1), we selected the following three locations: (1) Mt. Vuria (henceforth V) in the upper montane cloud forest (UMCF), 3°24´S, 38°17´E, 2189 m a.s.l. (the original location from where bryophytes for the study were collected), (2) Ngangao South
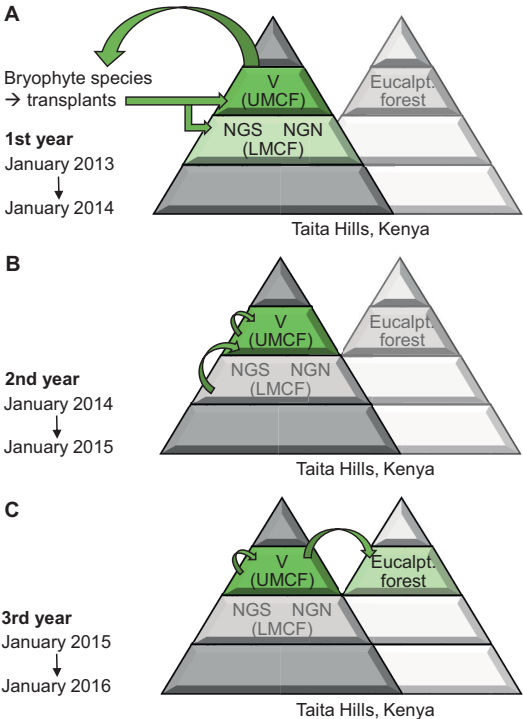
Fig. 1. Experimental setup. — **A**: In the first year, bryophytes were collected from the upper montane cloud forest (UMCF) on Mt. Vuria, and the transplants were prepared. The transplants were then placed at three study sites: one on Mt. Vuria (V) in UMFC, and the two other in the lower montane cloud forest (LMFC) in Ngangao South (NGS) and Ngangao North (NGN). — **B**: In the second year, the transplants from NGS and NGN were returned to their original habitat on Mt. Vuria. — **C**: In the third year, half of the transplants were left on Mt. Vuria, and the other half was placed in a more open and disturbed eucalyptus forest covering the neighboring secondary peak of Mt. Vuria. To assess changes in biomass, the transplants were weighed in the laboratory in December 2012 and after each year of the experiment.

Table 1. Climatic differences among the study sites (T_{avg} = average diurnal temperature, T_{min} = average diurnal minimum, T_{max} = average diurnal maximum, RH_{avg} = average diurnal atmospheric humidity, RH_{min} = average diurnal minimum of atmospheric humidity). The temperature and humidity values for Mt. Vuria, Ngangao South, and Ngangao North are based on iButton data collected between May 2013 and March 2014. These data only tentatively characterize climatic conditions under the forest canopy at each site. For comparison, the data from Mwanda, a nearby weather station in open agricultural land near Mt. Vuria, are also given (source: TAITAWATER).

Site	Elevation (m a.s.l.)	T_{avg} (°C)	T_{min} (°C)	T_{max} (°C)	RH_{avg} (%)	RH_{min} (%)	Annual precipitation (mm)
Mt. Vuria	2189	12.28	10.27	14.82	98.61	91.31	1283
Ngangao South	1856	13.97	12.12	16.24	96.99	84.97	963
Ngangao North	1877	14.64	12.27	18.21	93.73	78.94	943
Mwanda	1672	18.28	14.59	25.50	72.92	47.03	807
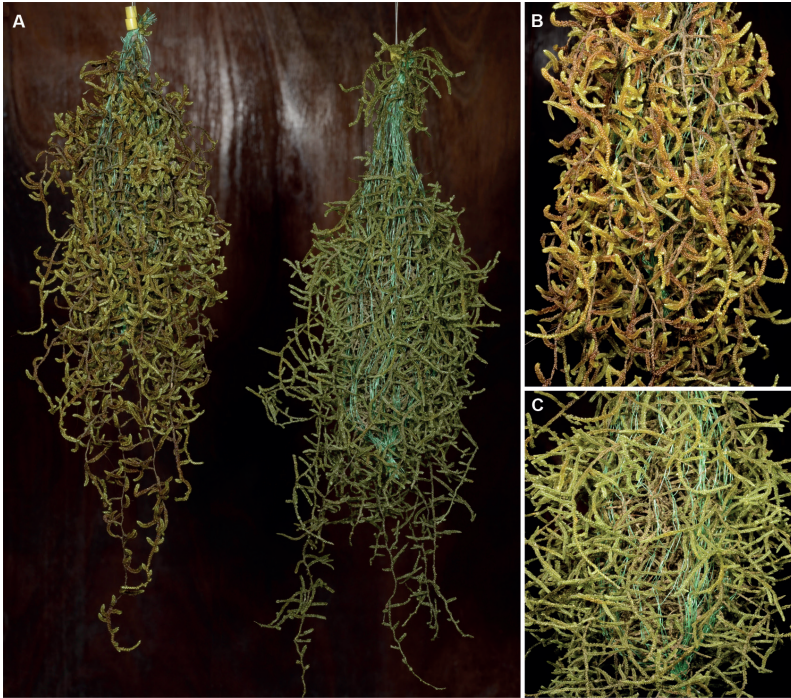
Fig. 2. Examples of well-grown *Orthostichella rigida* transplants retrieved from Mt. Vuria for final weighing in January 2016. — **A**: The transplant on the left spent its last year in the plantation forest (*Eucalyptus*), while the transplant on the right spent the last year at the original location on Mt. Vuria. — **B**: Close-up of a transplant from the plantation forest. — **C**: Close-up of a transplant from the original location on Mt. Vuria.

(henceforth NGS) in the lower montane forest, 3°22′N, 38°20′E, 1856 m a.s.l., and (3) Ngangao North (henceforth NGN) also in the lower montane forest, 3°21′S, 38°20′E, 1877 m a.s.l. The upper slopes of Mt. Vuria receive abundant moisture from low-lying clouds and fog and are hence wetter than most other forests in the Taita Hills. The two other study sites (NGS, NGN) were in the Ngangao Forest, a somewhat drier, lower montane cloud forest on the steep eastern slope of a north–south oriented mountain ridge, NGN being drier than NGS. Both Ngangao sites represent marginal habitats where bryophyte species occur naturally but are not abundant and are confined to the most favorable microhabitats. The bryophytes used in our study were previously observed to perform poorly at those sites as compared with those at the original location (V) in the upper montane forest (Stam *et al.* 2017). In the third year of the study, one more site was introduced: eucalyptus plantation at roughly the same elevation (2055 m a.s.l.) and having similar microclimatic conditions as the site on Mt. Vuria. For more details on forest structure and climatic conditions, *see* Stam *et al.* (2017) and Räsänen *et al.* (2018).

Transplants

To evaluate growth responses of non-vascular epiphytes to warmer and drier conditions, we selected three easily identifiable pendent moss species (*Orthostichella rigida* 72 transplants, *O. capillicaulis* 54 transplants, *Squamidium brasiliense* 54 transplants) that are common in the epiphyte communities of tree stems and branches in upper montane forests of the study area (Fig. 2).

Bryophyte material (several young shoots) was collected from Mt. Vuria (the highest peak of Taita Hills) in December 2012 and taken to the laboratory where it was air dried in an unheated room. From the material collected we picked several young shoots and weighed them. Based on the previous studies (e.g. McCune *et al.* 1996, Stam *et al*. 2017), the amount of biological material was adjusted so that the air-dry weight of bryophytes in each transplant was about 0.25 g (0.24–0.26 g). After weighing, the transplants were constructed using green plastic (PE) net (mesh size 8 × 8 mm), wrapped around the bryophyte shoots (Fig. 2) and tied at both ends with cable ties. Short (3–5 cm) loops were made of fishing line (tensile strength 11 kg) and

each bag was tied to a loop with a double over-hand knot. The knots were covered with silicone and left to dry indoors (unheated room) for 24 hours. After this, the ends of the knots were trimmed and each rigged pendant was coded for identification with colored plastic beads. Ready transplants were weighed again.

Experimental setup

In January 2013, the transplants of *O. rigida* were placed for one year as follows: 36, 18 and 18 on Mt. Vuria (V), in NGS and in NGN, respectively; and the transplants of *O. capillicaulis* and *S. brasiliense* as follows: 18, 18 and 18 of each species on Mt. Vuria (V), in NGS and in NGN, respectively (*see* Fig. 1). The transplants were attached to ropes at about 40-cm intervals, and then, following Stam *et al.* (2017), the ropes were suspended at the height of 3 meters.

In January 2014, the transplants were collected from the field, brought to the laboratory and weighed after air-drying in an unheated room for 48 hours. We also weighed some reference samples and empty nets to control for changes in weight caused e.g., by humidity. After weighing, all the recovered transplants (including those from NGN and NGS) were placed for one year in their original environment on Mt. Vuria (V). There were 69 transplants of *O. rigida*, 49 transplants of *O. capillicaulis*, and 51 transplants of *S. brasiliense*. All the above was done as quickly as possible (generally within 1 week).

In January 2015, the transplants were again taken to the laboratory, air-dried in an unheated room for 48 hours, and weighed. After that, about half of the remaining transplants were returned to their original environment on Mt. Vuria (V), and the remaining ones were placed in a more open and disturbed eucalyptus forest covering the neighboring secondary peak of Mt. Vuria (2055 m a.s.l.). In total, there were 67 transplants of *O. rigida*, 44 transplants of *O. capillicaulis*, and 47 transplants of *S. brasiliense*.

In January 2016, the transplants were taken to the laboratory for final weighing after air-drying in an unheated room for 48 hours.

Statistical analyses

Statistical analyses of the effect of microclimate (site) on growth were conducted in two ways: (1) separately for each year, and (2) for the entire study period. Annual increase in biomass was calculated as the relative weight change in the year as follows: change in biomass = $(W_{year} - W_{year-1})/W_{year-1}$, where W is the weight (g). Note that annual change in biomass is unlimited and values above 1 (biomass more than doubled) as well as negative ones (i.e., decrease in biomass) are possible. Indeed in 2014, the mean biomass for all species slightly decreased. The differences were tested with ANOVA and Tukey's HSD *post hoc* test. Normality of residuals was visually confirmed.

The effect of microclimate (site) on overall growth (between 2013 and 2016) was approximated with the linear regression (weight$_{year}$ = $a \times$ year + b) whose slopes (a) were used as dependent variables in ANOVA. Further differences were analysed with Tukey's HSD *post hoc* test. Lastly, a mixed effects model was used to examine the overall effects of different years and microclimates (sites) on growth. The intention here was mainly to check the robustness of the results obtained from the two main statistical approaches, and to provide further insight into differences between subsequent years.

All statistical analyses were conducted in the R ver. 3.5.3 (http://www.R-project.org/). Mixed effects models were fitted using the *nlme* package.

Results

General patterns

The biomass of the transplants growing on Mt. Vuria during all three years increased the most, regardless of the forest type (original *vs.* eucalyptus) during the final year (Fig. 3 and Table 2). However, the difference in growth between the transplants that spent one year in NGN and NGS and then were returned to Mt. Vuria (V) and those left on Mt. Vuria (V) for the duration of the study was still statistically significant after the third year, even though the transplants from NGN and NGS had two years to recover on Mt. Vuria.
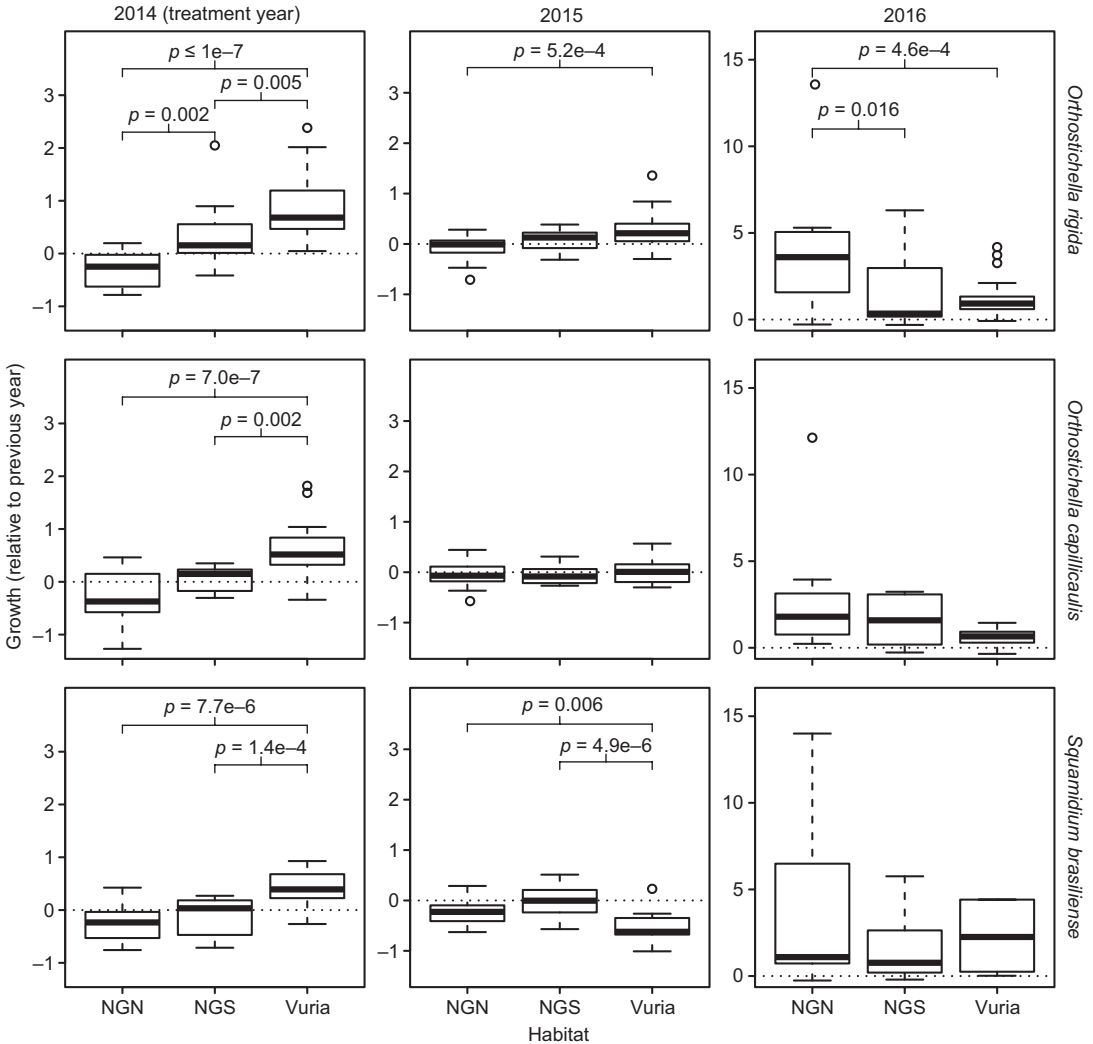
Fig. 3. Proportional change in biomass (± SD) of transplants after first (2014), second (2015) and third (2016) years in different habitats. The change in biomass was calculated as the weight difference between the current and the previous years, divided by the previous year's biomass (*see* Methods for details). Significant differences in biomass change (Tukey's HSD test) are shown with horizontal brackets and *p* values. NGN = Ngangao North, NGS = Ngangao South. Bottom and top edges of a box show the first and third quartiles around the median (thick horizontal line), respectively, and the whiskers show the greatest/smallest value that is within 1.5 times the box height from the box edge. Extreme values outside this range are shown with circles.

Growth in the year 2014

The weight increase of transplants in 2014 was the highest on Mt. Vuria and the lowest in NGN (Vuria > NGS > NGN) (Table 2 and Fig. 3). The biomass of transplants of *O. rigida*, *O. capillicaulis* and *S. brasiliense* on Mt. Vuria increased by 86%, 61% and 46%, respectively, whereas in the driest NGN site decreased by 30%, 29% and 23%, respectively (*see* Table 2).

Growth in the years 2015 and 2016

In 2015 (in January, the transplants recovered from NGN and NGS were returned to Mt. Vuria), the microclimate (site) in which the transplants of *O. rigida* and *S. brasiliense* were kept in 2014 still had an effect on their growth in 2015 (Table 2). Interestingly, the effects were different. For *O. rigida*, the highest biomass increase was recorded for transplants that had spent the

first year on Mt. Vuria (Vuria +25% > NGS +7% > NGN –8%), whereas for *S. brasiliense* these had the lowest growth (NGS –2% > NGN –24% > Vuria –51%) (Fig. 3). In 2015, growth of *O. capillicaulis* was close to zero, regardless of where the transplants were in 2014.

In 2016, half of the remaining transplants were placed in the eucalyptus plantation on the secondary peak of Mt. Vuria. According to ANOVA, the forest type did not have a significant effect on growth of any of the three bryophyte species. Growth conditions still had a measurable effect on the growth of *O. rigida*, but not on the growth of the other two species (Table 2). Interestingly, during the third year the *O. rigida* transplants that had spent their first year in NGN increased in weight more (+498%) than the transplants that had been in NGS (+156%) or on Mt. Vuria (+116%).

Three-year growth

The environmental conditions of the sites where the transplants were growing during the first year had a significant effect on the growth of *O. rigida* (Table 2). *Post hoc* analysis identified clear differences in bryophyte growth between Mt. Vuria and NGN ($p = 8.2e–3$), as well as Mt. Vuria and NGS ($p = 5.1e–4$), but not between NGN and NGS. For the other two bryophyte species, the overall effects of the treatments on their three-year growth were not significant.

Mixed-effects

Differences in transplant growth were analyzed by fitting a variable intercept (mixed-effect) model with annual growth as the dependent variable, year and treatment year conditions as fixed effects, and species as a random effect. This model identified growth in the final year (2016) as significantly different from the previous years ($p < 1.0e–3$), with an approximately tenfold growth as compared with that in the first year. The variable intercept model did not identify treatment year conditions as a significant factor, most likely because its effect was different between years and species. However, the interaction (treatment year condition × year) was highly significant ($p = 2.2e–13$), confirming that conditions experienced

Table 2. Relative changes in biomass (SD, number of transplants) of *Orthostichella rigida*, *O. capillicaulis* and *Squamidium brasiliense* transplants in each study. ANOVA results are shown for each species × year combination (for results of the *post hoc* analysis *see* Fig. 3). The change in biomass was calculated as the biomass difference between the current and the previous years biomass divided by the previous year's biomass (*see* Methods for details). The values for 2016 were pooled as forest type (on Mt. Vuria and eucalyptus plantation) did not have a significant effect on transplant growth. The values presented in the last column are the slopes (*a*) of the regression (*see* Methods for details), with SD and number of transplants given in parentheses.

Species	Site	2014	2015	2016	2014–2016
O. rigida	Vuria	0.86 (0.57, 36)	0.25 (0.32, 35)	1.16 (0.92, 34)	0.29 (0.13, 34)
	NGS	0.35 (0.57, 16)	0.07 (0.22, 15)	1.56 (2.26, 10)	0.10 (0.09, 10)
	NGN	–0.30 (0.33, 17)	–0.08 (0.27, 17)	4.98 (5.55, 12)	0.15 (0.15, 12)
O. capillicaulis	Vuria	0.61 (0.52, 18)	0.03 (0.24, 14)	0.61 (0.55, 8)	0.12 (0.12, 8)
	NGS	0.06 (0.24, 15)	–0.04 (0.20, 14)	1.57 (1.54, 6)	0.11 (0.13, 6)
	NGN	–0.29 (0.47, 16)	–0.04 (0.27, 16)	2.02 (4.22, 12)	0.08 (0.09, 12)
S. brasiliense	Vuria	0.41 (0.32, 18)	–0.51 (0.25, 15)	1.84 (1.82, 5)	0.00 (0.05, 5)
	NGS	–0.14 (0.37, 16)	–0.02 (0.32, 16)	1.71 (2.03, 9)	0.04 (0.06, 9)
	NGN	–0.23 (0.39, 17)	–0.24 (0.24, 16)	3.71 (4.49, 13)	0.04 (0.06, 13)
ANOVA	*O. rigida*	$F_{2,66} = 28.86$, $p = 9.9e–10$	$F_{2,64} = 8.34$, $p = 0.0006$	$F_{2,53} = 8.46$, $p = 0.00065$	$F_{2,53} = 10.56$, $p = 1.4e–4$
	O. capillicaulis	$F_{2,46} = 18.75$, $p = 1.1e–6$	$F_{2,41} = 0.41$, $p = 0.67$	$F_{2,23} = 0.53$, $p = 0.6$	$F_{2,23} = 0.41$, $p = 0.67$
	S. brasiliense	$F_{2,48} = 16.57$, $p = 3.4e–6$	$F_{2,46} = 15.32$, $p = 8.0e–6$	$F_{2,25} = 1.47$, $p = 0.25$	$F_{2,25} = 0.93$, $p = 0.41$

by the transplants in the treatment year affected their growth during the three-year period.

Discussion

Together with human activities (e.g., land-use changes and deforestation), climate change has been identified as a major driver of biodiversity changes (Sala *et al.* 2000, Gradstein & Sporn 2010, Koren *et al.* 2014, Löbs *et al.* 2019) and may become the principal cause of species extinctions in tropical ecosystems (Malcolm *et al.* 2006, He *et al.* 2019). Because of steep environmental gradients, narrow thermal tolerances of species, and the expected increase of the average altitude of cloud formations, montane tropics may be threatened by even slight increases in air temperature (Foster 2001, Corlett 2011, Laurance *et al.* 2011). Global warming may thus eventually lead to an upward shift in the altitudinal zones of forest vegetation and associated biota (La Sorte & Jetz 2010, Corlett 2011, Krishnaswamy *et al.* 2014).

In relatively low tropical mountains, such as the Taita Hills, the future climatic conditions of upper montane forests may closely approach those currently present in lower montane forests (Foster 2001). As the epiphytic bryophytes and other biota of upper montane forests of low mountains cannot migrate to higher elevations, they must confront warming and drying in their present location. Indeed, if global temperatures continue to rise as predicted for the coming decades, the organisms adapted to high-elevation conditions in the tropics may end up being among the most endangered species on Earth (Williams *et al.* 2007, Jácome *et al.* 2011, Laurance *et al.* 2011, Tuba *et al.* 2011). While a comparatively sheltered forest environment of epiphytic bryophytes may not totally disappear, the epiphytes must be able to withstand higher maximum temperatures and extended dry periods. In such a situation, their resilience, i.e., the ability to first survive adverse conditions and then quickly recover, is crucial.

The results of this study demonstrate that tropical epiphytic bryophytes respond to climatic changes but can also be quite resilient. On the other hand, the effects of adverse conditions

can be seen in the growth rate of bryophytes even several years after they were exposed to a period of heat and drought. Naturally, a short-term study does not necessarily allow to predict all effects of and long-term responses to climate change (Hollister *et al.* 2005). The conditions experienced by our bryophyte transplants during the first year had a significant effect on their subsequent growth, however, with notable differences among species (Table 2 and Fig. 3). This indicates that adverse conditions may cause long-term effects on growth for some but not all epiphytic bryophyte species. After returning the transplants to the favorable environment, the first year's treatment still had a statistically significant effect on growth, but only when the most favorable and the least favorable sites were compared. This indicates that even short-term exposure to adverse conditions can in some cases have significant long-term effects, but there are major differences in the responses of different bryophyte species. Data on the ecophysiology of pendent bryophytes is still too sparse, especially regarding tropical epiphytes, as to allow a true analysis of reasons between such species-specific differences.

As expected, by the end of the third year the effect of the initial conditions on growth had largely decreased with all groups growing at roughly the same rate.

On average, the annual biomass increase was markedly higher in the third year than in any previous year. This could probably be attributed to particularly favorable weather conditions during that year, but it is also possible that there was a lag phase of slow growth in freshly constructed transplants at the beginning of the study.

Interestingly, there were no significant differences in growth of bryophyte transplants between original location on Mt. Vuria and eucalyptus plantation, both sites at the same favorable elevation. Many previous studies demonstrated that species diversity and abundance of bryophytes tends to be higher in natural forests than in plantation forests (Pócs 1980, 1982, Gradstein 1992). Natural forests often have significantly older trees and more dead wood, which may partly explain their higher biodiversity (e.g., Pharo *et al.* 2004, Löhmus *et al.* 2007). Other explanations have included dispersal inefficiency (Sillett & McCune

1998, Pharo & Zartman 2007) and/or the strict microclimatic constraints (Humphrey *et al.* 2002).

Our results clearly demonstrate that mature pendant bryophytes can survive and even grow well in exotic plantation forests, therefore, their very sparse presence in eucalyptus stands must be related to dispersal limitation or a lack of suitable substrate. Mota de Oliveira *et al.* (2009) studied differences in species composition of bryophyte communities in different height zones in Neotropical lowland forests and concluded that niche assembly, rather than dispersal limitation predominantly affected species composition in the communities studied. Also, in the plantation forests of the Taita Hills, the upright branches and rapidly peeling bark of eucalyptus can explain the scarcity of pendant bryophytes in these forests, as these characteristics effectively hinder the establishment of many cryptogamic epiphytes, including pendant bryophytes.

To conclude, we detected and documented considerable resilience and recovery capacity in tropical epiphytic bryophytes. These organisms are especially promising indicators of climatic change as without rooting systems they both acquire and loose water through their entire surface. Therefore, monitoring changes in bryophyte community composition and species distributions can offer practical and cost-effective ways of monitoring impending changes in different forest ecosystems (Gignac 2001, Jácome *et al.* 2011, He *et al.* 2016).

Acknowledgements

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