

Responses of Terrestrial Mosses to Simulated Climate Change in a Secondary Evergreen Broad-leaved Forest in Southern China

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Research

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Abstract

Tropical regions are biodiversity hotspots and are well suited to explore the potential influence of global climate change on forest ecosystems. Bryophytes have essential ecological functions in tropical forest ecosystems. Knowledge of the potential impact of global warming and possible changes in water availability patterns on terrestrial bryophytes is limited. We transplanted eight moss species from two elevations (900 and 500 m) to warmer and drier elevations (500 and 100 m) during a half-year observation period on Tai Mo Shan, southern China. The simulated climate change resulted in a marked decrease in growth and a negative effect on the health of the transplanted species. Few moss species survived six months after transplanting to the warmer and drier lowlands, and their health status deteriorated severely. Three moss species, *Sematophyllum subhumile*, *Pseudotaxiphyllum pohliaecarpum*, and *Brachythecium buchananii*, were highly susceptible to changes in temperature and moisture and might be used as suitable bioindicators. As the tropics are expected to become hotter and drier, terrestrial mosses might be negatively affected or even be at risk of extinction. The cascading negative effects on the forest ecosystem might be induced by the dying back or even disappearance of terrestrial moss species. Thus, conservation of bryophyte communities is important to sustain and improve the stability and resilience of tropical forest ecosystems to climate change.

Introduction

Tropical regions harbor the highest biodiversity among all terrestrial habitats, as described by the latitudinal diversity gradient theory (Hillebrand 2004; Sahney and Benton 2008; Dowel et al. 2013). More than 40% of bryophytes occur in the tropics (Frahm 2003), which are biodiversity hotspots and well suited to explore the potential influence of global climate change on bryophytes biodiversity (Gaston 2000) based on unexpectedly high rates of habitat degradation and biodiversity loss (Tittensor et al. 2010).

Bryophytes are critical components of tropical forest ecosystems due to their high biodiversity and biomass (Gradstein et al. 2001; Grytnes et al. 2006; Frego 2007; Grau et al. 2007; Glime 2017) and fulfill essential ecological functions (Longino and Nadkani 1990; Nadkani and Longino 1990; Hölscher et al. 2004; Yanoviak et al. 2007; Jeschke et al. 2008; Zhao et al. 2009; Seitz et al. 2017). Bryophytes can reflect climate changes more quickly than vascular plants due to their poikilohydry, which makes them ideal bioindicators for climate monitoring (Markert et al. 2003; Tuba et al. 2011; Ares et al. 2012; Nickel et al. 2018; Wang et al. 2019). They also have a wide geographic distribution, rendering them suitable candidates for both latitudinal and elevational range shift studies, as they are found from the poles to the equator (latitudinal diversity gradient) and from sea level to mountain peaks (elevational diversity gradient) (Andrew et al. 2003; Glime 2017).

The global climate has warmed by approximately 1°C since 1880 (IPCC 2018), resulting in well-documented shifts in species distributions with far-reaching implications for biological communities, yet current international agreements will accept more than double this magnitude of warming compared to pre-industrial levels by 2030 (2°C target according to the Paris Conference of Parties (COP 21)). By the

end of this century, temperature in tropical regions is predicted to increase by about 3°C in the absence of ambitious efforts to combat global warming. Changes in precipitation patterns that are likely linked to increased greenhouse gas concentrations have also been observed on a global scale; these patterns are spatially and temporally heterogeneous, and predictions of future patterns are generally uncertain and often difficult to coherently relate to climate change (Paeth et al. 2008).

Extinction risk related to climate change has been widely studied and scientifically estimated (Malcolm et al. 2006; Maclean et al. 2011; Urban 2015), and species extinction risks for the 21st century are considerable (Pereira et al. 2013). Climate change, mainly global warming, is driving many species towards higher latitudes and elevations (Pecl et al. 2017). Uphill migration allows montane species to search for suitable microclimates and microhabitats, but habitat fragmentation and range contractions sometimes lock species into separated and eventually unsuitable habitats (Dullinger et al. 2012).

Tropical regions have been marginal localities for bryophytes principally because of their negative carbon gain induced by high temperatures (Zotz and Bader 2009; Song et al. 2012). Bryophytes have to equilibrate their daily carbon dioxide acquisition with nightly respiration, especially in warm and humid seasons. Several studies have focused on the ecophysiology of tropical bryophytes (Wagner et al. 2014a), such as desiccation and temperature tolerance (Johnson and Kokila 1970; Zotz and Bader 2009; Song et al. 2012; Bader et al. 2013; Wagner et al. 2014b), photosynthetic light response and related functional traits (Marschall and Proctor 2004; Waite and Sack 2010) and photosynthetic light, water, and temperature responses (Wagner et al. 2013).

However, these empirical studies on the impact of climate change on bryophytes focused mainly on non-vascular epiphytes and even included lichens. Knowledge of the potential influence of global warming and possible changes in water availability patterns on the health, growth, and survival of terrestrial mosses is limited, especially for species inhabiting mountain peaks, as there are no higher elevations to which these species can migrate. In this study, we transplanted eight terrestrial moss species from highland areas to two lower elevations on Tai Mo Shan, Hong Kong, and observed their health condition, growth, and survival rates. During the observation period, Hong Kong experienced the warmest year since records began in 1884; the mean annual temperature was 1.2°C higher than that during the 1981–2010 period (Hong Kong Observatory 2020). The objectives of this study were (1) to explore the potential influence of higher temperatures, lower relative humidity, and rainfall on the health status, growth, and survival rates of eight bryophyte species and (2) to determine whether the selected bryophyte species are ideal bioindicators of climate change.

Materials And Methods

Study area

Hong Kong is situated in the eastern Pearl River Delta of the South China Sea, 22°9' – 22°33' N, 113°50' – 114° 26' E, with a territory of 1104 km². It lies 130 km south of the Tropic of Cancer and features a humid

subtropical climate with distinct hot humid and cool dry seasons. Despite its small area, there are distinct horizontal and vertical climatic gradients in Hong Kong. The primary evergreen or semi-evergreen monsoon forests that used to cover Hong Kong were cleared 400 years ago, except for some tiny, undisturbed patches in elevated, remote, and steep regions (Corlett 1997; Zhuang and Corlett 1997).

Hong Kong is one of the most densely populated places in the world, with less than 25% of the total land area being urbanized. Generally hilly to mountainous terrain with steep slopes occupies approximately 75% of the total land area. Undeveloped land has very few flat areas and consists mostly of secondary forests, grassland, shrubland or farmland (Ashworth et al. 1993; Corlett 2000; Owen and Shaw 2007; Planning Department 2017). About 40% of the undeveloped land area is country parks and nature reserves (Morton and Harper 1995). Despite the small total extent of Hong Kong and massive human disturbance, diverse flora and fauna still survive (Corlett 2000; Dudgeon and Corlett 1994). A diverse ecosystem exists in this region, with more than 3,000 species of vascular plants, of which 300 are endemic to Hong Kong (Hu 2003; Agriculture, Fisheries and Conservation Department 2020). The known bryophyte flora of Hong Kong consists of 372 species from 70 families and 159 genera, of which 238 are mosses and 134 are liverworts and hornworts (Zhang 2003).

Tai Mo Shan is the highest peak in Hong Kong, with an elevation of 957 m. It has an area of 1,440 hectares and is situated in the Tai Mo Shan Country Park in the center of the New Territories, Hong Kong. Due to the height of the mountain, Tai Mo Shan is claimed to be Hong Kong's most misty area, as it is often covered in clouds. It is not uncommon for temperatures to drop below the freezing point during winter (Hong Kong Observatory 2017). Trees planted here are mostly non-native such as *Pinus massoniana*, *Acacia confusa*, *Lophostemon confertus*, and *Melaleuca quinquenervia*. The area has become one of the major forest plantations in Hong Kong. Vegetation types include lowland evergreen broad-leaved forest to grassland with montane forest patches near the peak. Forests are limited to a maximum altitude of 550 m, while the upper slopes are dominated by shrubs and grasses.

Experiment design and measurement

Eight terrestrial moss species from two elevations (six species from 900 m, two species from 500 m) were selected from the northern part of Tai Mo Shan (Table 1). All eight species were common at the original elevation, and a few or no species were found at the three other altitudes. In April 2019, fresh and healthy samples of the moss species were collected and air-dried for 24 h to a constant weight in the laboratory, and litter and non-target species were removed from each sample. A total of 198 bags were used for the treatments (3 elevations \times 6 species \times 3 replicates \times 3 observation times + 2 elevations \times 2 species \times 3 replicates \times 3 observation times). Samples (1.0 ± 0.01 g for each treatment) were prepared and placed in 5 cm \times 5 cm stretchy plastic bags.

Table 1

Terrestrial moss species from 2 elevations for being used in the transplanting experiment (listed in descending order of their relative field abundance)

Location	Altitude (m asl)	Species	Family	Life form
Summit	900	<i>Hypnum plumaeforme</i>	Hypnaceae	Weft
		<i>Brachythecium buchananii</i>	Brachytheciaceae	Mat
		<i>Thuidium glaucinoides</i>	Thuidiaceae	Mat
		<i>Anomobryum julaceum</i>	Bryaceae	Cushion
		<i>Pterobryopsis crassicaulis</i>	Pterobryaceae	Mat
		<i>Pseudosymblepharis angustata</i>	Pottiaceae	Cushion
Waterfall path	500	<i>Sematophyllum subhumile</i>	Sematophyllaceae	Mat
		<i>Pseudotaxiphyllum pohliaecarpum</i>	Hypnaceae	Mat

On the first day of May 2019, samples were transplanted to the various elevations, and the original elevation served as the control (six species from 900 m to 500 m and 100 m, two species from 500 m to 100 m). Before the samples were randomly planted or placed in each plot, the litter layer and other bryophytes were removed to make sure that each sample was in direct contact with the mineral soil. The plots at each site were fenced by a plastic board to make sure the samples were not washed away by moving water caused by heavy rain. After placement, the samples were moistened to their normal state.

Twenty-four sacrificial samples were placed in a 60°C oven for 24 h and reweighed. The health status, survival rate, and growth of all study species both in situ and after transplanting were monitored. Samples were collected for analysis after two, four, and six months. In total, 66 treatments were collected into plastic bags and transported to the laboratory at each observation time. The health status of all samples at each elevation was assessed at the study sites. In the laboratory, treatments were air-dried for 24 h to a constant weight, and litter and non-target species were removed for biomass measurements.

Table 2
Criteria for assessing the overall health status of each sample

Thallus color	Score
Completely brown or dead looking \approx 90%	0
Yellowish or mostly brown patches \approx 70%	1
More than half brown or dying back \approx 50%	2
Most healthy and active green \approx 30%	3
Very healthy and active green \approx 10%	4
Completely healthy and active green \approx 10%	5

We modified the method developed by Rosso et al. (2001) to assess the overall health condition of all samples according to their thallus color, using a scale of 0–5, with 0 indicating completely brown or dead-looking and 5 representing active green thalli (Table 2). We recorded moss biomass accumulation over a 6-month period after transplanting during the growing season from the end of April to the end of October in 2019. Biomass accumulation rates were measured as biomass changes relative to the initial biomass over the experimental period. Through biomass accumulation measurements, we assessed the net result of growth and decomposition, especially the acclimation to lower elevations. The weight of each sample was corrected to the oven dry weight using sacrificial standards. We assumed that the difference in the relative humidity of the laboratory at various times would not influence the results.

Environmental and climatic factors

Environmental and climate indices, including air temperature, dew point, relative humidity, and rainfall at each elevation, were obtained from a local weather station if possible. Weather data were not available for the northerly-aspect 500 m asl elevation sites, and climate parameters were instead measured at the self-deployed mini weather stations or were estimated according to the nearest meteorological station. Two mini weather stations were set up at this elevation to collect air temperature, dew point, relative humidity, and rainfall data.

Statistical analysis

All environmental variables were averaged for each elevation. All statistical tests were performed using SPSS (version 26.0; IBM). Data were checked for deviations from normality and homogeneity of variance before statistical analysis. ANOVAs with Tukey's post hoc tests were performed to assess significant differences between different elevations and observation times. Differences in the health status, growth, and environmental factors among different elevations and sampling periods were analyzed using multi-way ANOVAs. Differences in growth among different elevations within each observation period were analyzed with one-way ANOVA.

Results

Environmental factors during measuring periods

Multi-way ANOVAs showed significant effects of elevation on air temperature, dew point, relative humidity, and rainfall during the observation period (Table 3). The mean air temperature at 900 m asl was 21.2°C, which was significantly lower than that at 500 (24.0°C) and 100 m asl (27.1°C). The mean dew point showed a trend similar to that observed for air temperature, with mean values of 20.0, 22.2, and 23.6 °C at 900, 500, and 100 m asl, respectively. The relative humidity, however, showed a reverse trend compared with air temperature, with mean values of 94.4%, 91.9%, and 84.4% at 900, 500, and 100 m asl, respectively. Mean rainfall at 900 m asl (642 mm) was significantly higher than at the two other elevations. Multi-way ANOVAs showed significant effects of measuring time (July, September, and November) on air temperature, dew point, relative humidity, and rainfall (Table 3). The dynamics of air temperature, dew point, relative humidity, and rainfall followed similar seasonal patterns among the three elevations. The highest air temperature, dew point, and rainfall occurred in August, the highest relative humidity in June, and the lowest air temperature, dew point, relative humidity, and rainfall in October (Fig. 1). In addition, significant interaction effects of elevation and observation time were observed for air temperature, dew point, and rainfall, but not relative humidity (Table 3).

Table 3
Results of multi-way ANOVAs for environmental factors of the three elevations during the observation periods (n = 3)

Measure	df	F	p
Air temperature			
Elevation	2	4337.703	< 0.001
Time	2	611.618	< 0.001
Elevation x time	4	12.057	< 0.001
Dew point			
Elevation	2	1233.369	< 0.001
Time	2	1441.816	< 0.001
Elevation x time	4	1.580	0.222
Relative humidity			
Elevation	2	464.321	< 0.001
Time	2	566.547	< 0.001
Elevation x time	4	2.491	0.080
Rainfall			
Elevation	2	428.101	< 0.001
Time	2	23775.025	< 0.001
Elevation x time	4	143.758	< 0.001

Health status of terrestrial mosses

The initial *Hypnum plumaeforme* samples from the three elevations were completely healthy with active green thalli. The health status of *H. plumaeforme* differed significantly among the three elevations four (F = 40.939, P < 0.001) and six (F = 14.837, P < 0.01) months after transplanting. The health status of samples at 100 m asl deteriorated markedly, with parts of the transplants turning brown or dying back four months after transplanting (Fig. 2). Multi-way ANOVAs showed that the effect of measuring time on the health status of all six moss species from 900 m asl was significant, similar to the effect of elevation (Table 4).

The initial *Brachythecium buchananii* samples from the three elevations were completely healthy with active green thalli. The health status of *B. buchananii* differed significantly among the three elevations two months after transplanting (F = 40.939, P < 0.001). The health status of samples at 500 and 100 m

asl deteriorated obviously, with parts of the transplants turning brown or dying back four months after transplanting (Fig. 2). Samples at 100 m asl turned completely brown and died back.

Thuidium glaucinoides, *Anomobryum julaceum*, *Pterobryopsis crassicaulis*, and *Pseudosymblepharis angustata* showed similar trends as those observed for *B. buchananii*. Significant differences among the three elevations in the health status of *T. glaucinoides*, *A. julaceum*, *P. crassicaulis*, and *P. angustata* occurred two months after transplanting (Fig. 2). The overall health of samples at 100 m was significantly worse than at the original elevation.

Table 4
Results of multi-way ANOVAs for the health status of six terrestrial moss species from 900 m asl during the observation periods (n = 3)

Measure	df	F	p
<i>Hypnum plumaeforme</i>			
Elevation	2	39.306	< 0.001
Time	3	104.617	< 0.001
<i>Brachythecium buchananii</i>			
Elevation	2	94.596	< 0.001
Time	3	245.263	< 0.001
<i>Thuidium glaucinoides</i>			
Elevation	2	62.791	< 0.001
Time	3	250.920	< 0.001
<i>Anomobryum julaceum</i>			
Elevation	2	54.973	< 0.001
Time	3	316.529	< 0.001
<i>Pterobryopsis crassicaulis</i>			
Elevation	2	40.258	< 0.001
Time	3	264.387	< 0.001
<i>Pseudosymblepharis angustata</i>			
Elevation	2	91.806	< 0.001
Time	3	496.970	< 0.001

Sematophyllum subhumile and *Pseudotaxiphyllum pohliaecarpum* from 500 m asl responded to the simulated climate change in a similar way as samples of these species from 900 m asl. The health

status of the two species differed significantly between 500 and 100 m asl two months after transplanting ($P < 0.001$). Samples at 100 m asl turned brown and died back four months after transplanting (Fig. 3). The effect of time on the health status was significant, as was the effect of elevation (Table 5).

Table 5
Results of multi-way ANOVAs for the health status of two terrestrial moss species from 500 m asl during the observation periods ($n = 3$)

Measure	df	F	p
<i>Sematophyllum subhumile</i>			
Elevation	1	973.345	< 0.001
Time	3	374.448	< 0.001
<i>Pseudotaxiphyllum pohliaecarpum</i>			
Elevation	1	1863.758	< 0.001
Time	3	1174.182	< 0.001

Response of the growth condition of terrestrial mosses

Multi-way ANOVAs showed that effect of time on the growth of all six moss species was significant, as was the effect of elevation (Table 6). No significant differences in the initial biomass of the six moss species were detected among the different elevations (Fig. 4).

Significant differences in *H. plumaeforme* biomass were measured among the three elevations after transplanting. *H. plumaeforme* grew fastest at 900 m and slowest at 100 m, and the differences between 500 and 100 m asl were not statistically significant (Fig. 4). The mean biomass of *H. plumaeforme* at the lower elevations was significantly lower than that at 900 m after transplanting (Fig. 4). Samples at all sites exhibited a negative growth rate from July to October 2019 (Fig. 4).

B. buchananii responded to the simulated climate change in a similar way as *H. plumaeforme*, but transplants at the low elevation exhibited little growth after transplanting, and the mean biomass accumulation of *B. buchananii* at the low elevation was 0 g six months after transplanting due to the dying back of this species (Fig. 4).

T. glaucinoides samples grew best at the high elevation followed medium elevation. No significant differences were measured in the first two months after transplanting. Samples at all sites exhibited a negative growth rate from July to October 2019 (Fig. 4).

A. julaceum, *P. crassicaulis*, and *P. angustata* responded to the simulated climate change in a similar manner to *B. buchananii*. We observed no significant differences in *P. angustata* among the three elevations four months after transplanting. The biomass of *A. julaceum* and *P. crassicaulis* differed significantly among different elevations after transplanting; these species grew better at high elevation

than at 500 and 100 m asl, and no significant differences were observed between the two lower elevations.

Table 6
Results of multi-way ANOVAs for the growth condition of six terrestrial moss species from 900 m asl during the observation periods (n = 3)

Measure	df	F	p
<i>Hypnum plumaeforme</i>			
Elevation	2	17.387	< 0.001
Time	3	52.377	< 0.001
<i>Brachythecium buehneri</i>			
Elevation	2	170.709	< 0.001
Time	3	191.275	< 0.001
<i>Thuidium glaucinoides</i>			
Elevation	2	22.191	< 0.001
Time	3	77.452	< 0.001
<i>Anomobryum julaceum</i>			
Elevation	2	67.331	< 0.001
Time	3	87.601	< 0.001
<i>Pterobryopsis crassicaulis</i>			
Elevation	2	40.640	< 0.001
Time	3	139.736	< 0.001
<i>Pseudosymblypharis angustata</i>			
Elevation	2	30.442	< 0.001
Time	3	61.004	< 0.001

S. subhumile and *P. pohliaecarpum* from 500 m asl responded to the simulated climate change in a similar manner as observed for these species from 900 m asl. The growth of these species differed significantly between the two elevations two months after transplanting ($P < 0.001$). Samples at 100 m asl completely died back four months after transplanting (Fig. 5). The effect of observation time on growth was significant, as was the effect of elevation (Table 7).

Table 7
Results of multi-way ANOVAs for the health status of two terrestrial moss species from 500 m asl during the observation period (n = 3)

Measure	df	F	p
<i>Sematophyllum subhumile</i>			
Elevation	1	1259.959	< 0.001
Time	3	318.464	< 0.001
<i>Pseudotaxiphyllum pohliaecarpum</i>			
Elevation	1	433.581	< 0.001
Time	3	121.486	< 0.001

Discussion

The results indicate that habitat temperature decreased but water availability increased with increasing altitude. During the observation period, the mean air temperature increased by 5.9°C, the dew point increased by 3.6°C, relative humidity decreased by 10%, and rainfall decreased by 84 mm in the lowland area compared with the high elevation. Under rapid and persistent global warming and a likely declining trend of relative humidity and rainfall (Hijmans et al. 2005; Ramirez and Jarvis 2008), the relocation of terrestrial mosses from high to low elevations can be used to estimate the impacts of future global climate change in the study area.

The most marked result of this study is that only a few moss species survived six months after transplanting to the warmer and drier lowlands, and even in these species the health status deteriorated severely (Figs. 2 and 4). We did not detect a positive growth rate after June at lower elevations, so survival might be pro-acclimated to warmer and drier lowlands. The simulated climate change significantly negatively affected the growth and health of most moss species studied in the six-month period (Figs. 2–5). Similar results were obtained in our laboratory study: as the temperature increases, the health status, photosynthetic activities, and biomass gains decline sharply (JW. Hao, unpubl. data). Song et al. (2014) also observed markedly declined growth rates and a negative effect on the health of transplanted epiphytes within two years. In addition, Wagner et al. (2014b) found that no short-term acclimation existed, and that a temperature increase led to poorer health and eventually high mortality of transplanted bryophytes. The relative abundance of species in the field changed significantly with a 1.5–2.5 °C temperature increase over two years (Jácome et al. 2011).

These results can be explained in two ways. First, high respiratory carbon losses and a shorter period of photosynthetic activities induced by increased temperature contributed to the decline of growth gains (Proctor 2011; Wagner et al. 2013). Second, mosses are poikilohydric, rapidly losing water and thus photosynthetic capacity when the relative humidity decreases, with photosynthetic capacity resuming only if they are rehydrated (Sillett and Antoine 2004). Wagner et al. (2013) suggested that the timing and

duration of wetting rather than the water content were the main drivers in this respect, and temperature-dependent metabolism is limited with increasing evaporation rates, restricting the period for net photosynthesis. This situation was exacerbated by wet and warm nights. Consequently, the mosses were incapable of the high photosynthetic rates needed to counteract the respiratory carbon losses in warmer and drier lowland areas.

Another striking result was that net growth rates were found only in the first observation period irrespective of whether mosses were transplanted to lower elevations. We cannot differentiate whether the reduced growth rate was caused by the warmest year since records began in 1884 or whether this represents a seasonal phenomenon. A possible explanation for the positive growth rates in the first measurement period is that the highest relative humidity occurred in the first two months. Wet and warm nights might be the possible reasons for negative growth rates recorded in the subsequent measurement periods because the highest air temperature, dew point, and rainfall occurred in August.

Other studies have also documented the responses of bryophytes to climate change, and even slight shifts in climate conditions may have negative consequences. Range shifts of vascular plants induced by higher temperatures in high-latitude ecosystems led to a reduction in bryophyte cover (Tømmervik et al. 2004; Guglielmin et al. 2014; Royles and Griffiths 2014). Bjerke et al. (2011) suggested that a warm winter had negative effects on the photosynthetic activities and growth rates of moss species in sub-arctic heathlands. Furthermore, the range for many European bryophyte species has contracted whereas range expansions for other species have occurred at their northern limits (Bergamini et al. 2009; Désamoré et al. 2012; Hodd et al. 2014).

Bryophytes, especially epiphytes, have long been used as excellent indicators to monitor climate change (Gignac 2001). *S. subhumile* and *P. pohliaecarpum* showed the most significant and substantial differences in growth and health four months after being exposed to warmer and drier environments. Therefore, *S. subhumile* and *P. pohliaecarpum* could be employed as potential climate change indicators in the marginal tropics. A significant negative effect of relocation to lowland areas on the health and biomass of *B. buchananii* was detected six months after transplanting. These results indicate that *B. buchananii* is susceptible to climate change. The five other moss species survived the experiment even though they experienced severely deteriorated health and reduced growth rates. This implies that these species are not good indicators of climate change, and might indicate that even warmer and drier sites are suitable for some species due to their phenotypic plasticity (Bradshaw 1965; Callahan et al. 1997). Why these five species were unsuccessful in establishing in lowland areas remains unresolved. All species have limitations to their capacity for adaptive response to changing environments (Williams et al. 2008), and these limits are unlikely to increase for species already experiencing warm temperatures close to their tolerance limits (Araújo et al. 2013).

Implications for conservation

To understand the rapid, persistent impact of climate change, we generally need several decades of data to rigorously assess pre- and post-climate change trends at the level of species and ecosystems (Brown et al. 2016); however, such long-term data sets are rare for biological systems (Laurance et al. 2011). In this study, we attempted to assess the possible short-term impact of climate change on the health status, growth, and survival rate of terrestrial moss species. These species were susceptible to simulated climate change and may be more vulnerable than vascular species. This study fills the gap in empirical evidence on the sensitivity of terrestrial moss species to climate change. As climate conditions in the tropics are expected to become hotter and drier (Ramirez and Jarvis 2008; Lewis et al. 2011), many moss species might be negatively affected or even at the risk of extinction. The bryophyte communities in the tropics might be one of the best biological populations to reflect the direct impact of climate change and provide an early warning of biological outcomes induced by ongoing climate change, even though we cannot predict the long-term influence of climate change from the present study.

Because bryophytes have essential ecological functions in land ecosystems, the adverse effects of climate change on moss species cannot be considered in isolation (Zotz and Bader 2009). The dying back and even disappearance of terrestrial moss species related to climate change may have cascading negative effects on the whole forest ecosystem. Thus, conservation efforts to sustain and improve the stability and resiliency of tropical forest ecosystems to climate change should include bryophyte communities.

Although there is an enormous body of basic research on climate change, few long-term conclusions can be drawn about future consequences. Local adaptation due to phenotypic plasticity may be overestimated due to current climatic conditions. However, as the rate of future climate change will likely outweigh the potential acclimation of many species, in addition to human-induced habitat loss and habitat fragmentation, the challenges of moss species redistribution induced by climate change may not occur.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and materials

The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

J.H. and L.M.C. conceived the ideas. J.H. carried out the fieldwork and sample collection, laboratory procedures, and data analyses. J.H. led the writing, and J.H. and L.M.C. edited and approved the final manuscript.

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References

1. Agriculture, Fisheries and Conservation Department (2020) Hong Kong biodiversity database: The Natural Environment, Plants & Animals in Hong Kong.
<https://www.afcd.gov.hk/english/conservation/hkbiodiversity/hkbiodiversity.html>
2. Andrew NR, Rodgeron L, Dunlop M (2003) Variation in invertebrate-bryophyte community structure at different spatial scales along altitudinal gradients. *J Biogeogr* 30:731–746.
<https://doi.org/10.1046/j.1365-2699.2003.00849.x>
3. Araújo Miguel B, Ferri-Yáñez F, Bozinovic F, Marquet PA, Valladares F, Chown SL (2013) Heat freezes niche evolution. *Ecol Lett* 16:1206–1219. <https://doi.org/10.1111/ele.12155>
4. Ares A, Aboal JR, Carballeira A, Giordano S, Adamo P, Fernández JA (2012) Moss bag biomonitoring: a methodological review. *Science of Total Environment* 432:143–158.
<https://doi.org/10.1016/j.scitotenv.2012.05.087>
5. Ashworth JM, Corlett RT, Dudgeon D, Melville DS, Tang WSM (1993) Hong Kong ecological database. World Wide Fund for Nature, Hong Kong
6. Bader MY, Reich T, Wagner S, González González AS, Zotz G (2013) Differences in desiccation tolerance do not explain altitudinal distribution patterns of tropical bryophytes. *Journal of Bryology* 35:47–56. <https://doi.org/10.1179/1743282012Y.0000000033>
7. Bergamini A, Ungricht S, Hofmann H (2009) An elevational shift of cryophilous bryophytes in the last century – an effect of climate warming? *Diversity Distribution* 15:871–879.
<https://doi.org/10.1111/j.1472-4642.2009.00595.x>

8. Bjerke JW, Bokhorst S, Zielke M, Callaghan TV, Bowles FW, Phoenix GK (2011) Contrasting sensitivity to extreme winter warming events of dominant sub-Arctic heathland bryophyte and lichen species. *J Ecol* 99:1481–1488. <https://doi.org/10.1111/j.1365-2745.2011.01859.x>
9. Bradshaw AD (1965) Evolutionary significance of phenotypic plasticity in plants. *Adv Genet* 13:115–155. [https://doi.org/10.1016/S0065-2660\(08\)60048-6](https://doi.org/10.1016/S0065-2660(08)60048-6)
10. Brown CJ, O'Connor MI, Poloczanska ES et al (2016) Ecological and methodological drivers of species' distribution and phenology responses to climate change. *Glob Change Biol* 22:1548–1560. <https://doi.org/10.1111/gcb.13184>
11. Callahan HS, Pigliucci P, Schlichting CD (1997) Developmental phenotypic plasticity: where ecology and evolution meet molecular biology. *BioEssays* 19:519–525. <https://doi.org/10.1002/bies.950190611>
12. Climatological normals for the reference period of 1981–2010 are available at: <https://www.hko.gov.hk/en/wxinfo/pastwx/2019/ywx2019.htm>
13. Corlett RT (1997) Human impact on the flora of Hong Kong Island. In: Jablonski N (ed) *The Changing Face of East Asia during Tertiary and Quaternary*. Center of Asian Research, Hong Kong, pp 400–412
14. Corlett RT (2000) Environmental heterogeneity and species survival in degraded tropical landscapes. In: Hutchings MJ, John EA, Stewart A (eds) *The Ecological Consequences of Environmental Heterogeneity*. Blackwell Science, Oxford, pp 333–355
15. Désamoré A, Laenen B, Stech M, Papp B, Hedenäs L, Mateo RG, Vanderpoorten A (2012) How do temperate bryophytes face the challenge of a changing environment? Lessons from the past and predictions for the future. *Glob Change Biol* 18:2915–2924. <https://doi.org/10.1111/j.1365-2486.2012.02752.x>
16. Dowle EJ, Morgan-Richards M, Trewick SA (2013) Molecular evolution and the latitudinal biodiversity gradient. *Heredity* 110:501–510. <https://doi.org/10.1038/hdy.2013.4>
17. Dudgeon D, Corlett RT (1994) *Hills and Streams: An Ecology of Hong Kong*. Hong Kong University Press, Hong Kong
18. Dullinger S, Gattlinger A, Thuiller W et al (2012) Extinction debt of high-mountain plants under twenty-first century climate change. *Nature Climate Change* 2:619–622. <https://doi.org/10.1038/nclimate1514>
19. Frahm J-P (2003) Diversity of bryophyte species in the tropics. *Tropical Bryology* 23:13–21
20. Frego KA (2007) Bryophytes as potential indicators of forest integrity. *For Ecol Manage* 242:65–75
21. Gaston KJ (2000) Global patterns in biodiversity. *Nature* 405:220–227. <https://doi.org/10.1038/35012228>
22. Gignac LD (2001) Bryophytes as Indicators of climate change. *Bryologist* 104:410–420
23. Glime JM (2017) Introduction. In: Glime JM (ed) *Bryophyte ecology*. Michigan Tech Open Access Publications, Houghton, Michigan, pp 1–10

24. Gradstein SR, Churchill SP, Salazar N (2001) Guide to the bryophytes of tropical America. *Memoirs of New York Botanical Garden* 86:1–577
25. Grau O, Grytnes J, Birks HJB (2007) A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. *J Biogeogr* 34:1907–1915. <https://doi.org/10.1111/j.1365-2699.2007.01745.x>
26. Goffinet B, Shaw AJ (2009) Physiological ecology. In: Proctor MCF (ed) *Bryophyte Biology*. Cambridge University Press, Cambridge, pp 237–295. <https://doi.org/10.1093/aob/mcp109>
27. Green TGA, Lange OL (1994) Photosynthesis in poikilohydric plants: a comparison of lichens and bryophytes. In: Schulze ED, Caldwell MM (eds) *Ecophysiology of Photosynthesis*. Springer, Berlin, pp 319–341. https://doi.org/10.1007/978-3-642-79354-7_16
28. Grytnes JA, Heegaard E, Ihlen PG (2006) Species richness of vascular plants, bryophytes and lichens along an altitudinal gradient in western Norway. *Acta Oecol* 29:241–246. <https://doi.org/10.1016/j.actao.2005.10.007>
29. Guglielmin M, Dalle Fratte M, Cannone N (2014) Permafrost warming and vegetation changes in continental Antarctica. *Environmental Research Letters* 9:045001. <https://doi.org/10.1088/1748-9326/9/4/045001>
30. Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978. <https://doi.org/10.1002/joc.1276>
31. Hillebrand H (2004) On the generality of the latitudinal diversity gradient. *Am Nat* 163:192–211. <https://doi.org/10.1086/381004>
32. Hodd RL, Bourke D, Skeffington MS (2014) Projected range contractions of European protected oceanic Montane plant communities: focus on climate change impacts is essential for their future conservation. *PLOS ONE* 9:e95147. <https://doi.org/10.1371/journal.pone.0095147>
33. Hölscher D, Köhler L, van Dijk A, Bruijnzeel LA (2004) The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. *J Hydrol* 292:308–322. <https://doi.org/10.1016/j.jhydrol.2004.01.015>
34. Hong Kong Observatory (2017) Monthly Means of Meteorological Elements for Tai Mo Shan, 1997–2016: Cold/Hot Weather and Rainfall statistics. <https://www.hko.gov.hk/en/wxinfo/pastwx/mws2016/mws201601.htm>
35. Hu Q-M (2003) Preface: Rare and Precious Plants of Hong Kong. Agriculture, Fisheries and Conservation Department, Hong Kong SAR Government
36. IPCC (2018) Summary for Policymakers. In: Masson-Delmotte V, Zhai P, Pörtner H-O (eds) *Global Warming of 1.5°C: An IPCC Special Report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty*. World Meteorological Organization, Geneva, p 32

37. Jácome J, Gradstein SR, Kessler M (2011) Responses of epiphytic bryophyte communities to simulated climate change in the tropics. In: Slack N, Tuba Z, Stark LR (eds) *Bryophyte Ecology and Climate Change*. Cambridge University Press, Cambridge, pp 191–210
38. Jeschke M, Kiehl K (2008) Effects of a dense moss layer on germination and establishment of vascular plants in newly created calcareous grasslands. *Flora* 203:557–566. <https://doi.org/10.1016/j.flora.2007.09.006>
39. Johnson A, Kokila P (1970) The resistance to desiccation of ten species of tropical mosses. *Bryologist* 73:682–686. <https://doi.org/10.2307/3241280>
40. Laurance WF, Carolina Useche D, Shoo LP et al (2011) Global warming, elevational ranges and the vulnerability of tropical biota. *Biol Cons* 144:548–557. <https://doi.org/10.1016/j.biocon.2010.10.010>
41. Lewis SL, Brando PM, Phillips OL, van der Heijden GMF, Nepstad D (2011) The 2010 Amazon drought. *Science* 331:554–554. <https://doi.org/10.1126/science.1200807>
42. Longino JL, Nadkarni NM (1990) A Comparison of Ground and Canopy Leaf Litter Ants (Hymenoptera: Formicidae) in a Neotropical Montane Forest. *Psyche: A Journal of Entomology* 97: 81–93. <https://doi.org/10.1155/1990/36505>
43. Maclean IMD, Wilson RJ (2011) Recent ecological responses to climate change support predictions of high extinction risk. *PNAS* 108:12337–12342. <https://doi.org/10.1073/pnas.1017352108>
44. Malcolm JR, Liu C, Neilson RP, Hansen L, Hannah L (2006) Global warming and extinctions of endemic species from biodiversity hotspots. *Conserv Biol* 20:538–548. <https://doi.org/10.1111/j.1523-1739.2006.00364.x>
45. Marchall M, Proctor MCF (2004) Are bryophytes shade plants? Photosynthetic light responses and proportions of chlorophyll a, chlorophyll b and total carotenoids. *Ann Bot* 94:593–603. <https://doi.org/10.1093/aob/mch178>
46. Markert BA, Breure AM, Zechmeister HG (2003) *Bioindicators & bio-monitors: Principles, concepts, and applications*. Elsevier, Amsterdam, pp 329–375
47. Morton B, Harper E (1995) *An Introduction to the Cape d'Aguilar Marine Reserve*. Hong Kong University Press, Hong Kong
48. Nadkarni NM, Longino JL (1990) Invertebrates in canopy and ground organic matter in a Neotropical Montane Forest, Costa Rica. *Biotropica* 22:286–289. <https://doi.org/10.2307/2388539>
49. Nickel S, Schröder W, Schmalfuss R et al (2018) Modelling spatial patterns of correlations between concentrations of heavy metals in mosses and atmospheric deposition in 2010 across Europe. *Environmental sciences Europe* 30:53. <https://doi.org/10.1186/s12302-018-0183-8>
50. Owen B, Shaw R (2007) *Hong Kong Landscapes: Shaping the Barren Rock*. Hong Kong University Press, Hong Kong
51. Paeth H, Scholten A, Friederichs P, Hense A (2008) Uncertainties in climate change predictions: El Nino southern Oscillation and monsoons. *Global Planet Change* 60:265–288. <https://doi.org/10.1016/j.gloplacha.2007.03.002>

52. Pecl GT, Araujo MB, Bell JD et al (2017) Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* 355:1389–1399.
<https://doi.org/10.1126/science.aai9214>
53. Pereira HM, Ferrier S, Walters M et al (2013) Essential biodiversity variables. *Science* 339:277–278.
<https://doi.org/10.1126/science.1229931>
54. Planning Department (2017) Land Use in Hong Kong. Retrieved 1 September 2018.
https://www.pland.gov.hk/pland_en/info_serv/statistic/landu.html
55. Proctor MCF (2011) Climate responses and limits of bryophytes: comparisons and contrasts with vascular plants. In: Slack N, Tuba Z, Stark LR (eds) *Bryophyte Ecology and Climate Change*. Cambridge University Press, Cambridge, pp 35–54. <https://doi.org/10.1111/j.1442-9993.2012.02409.x>
56. Ramirez J, Jarvis A (2008) High Resolution Statistically Downscaled Future Climate Surfaces. International Center for Tropical Agriculture (CIAT), CGIAR Research Program on Climate Change, Agriculture and Food Security (CCAFS). Cali, Colombia
57. Rosso AL, Muir PS, Rambo TR (2001) Using transplants to measure accumulation rates of epiphytic bryophytes in forests of western Oregon. *The Bryologist* 104:430–439.
<https://www.jstor.org/stable/3244776>
58. Royles J, Griffiths H (2014) Invited review: climate change impacts in polar regions: lessons from Antarctic moss bank archives. *Glob Change Biol* 21:1041–1057. <https://doi.org/10.1111/gcb.12774>
59. Sahney S, Benton MJ (2008) Recovery from the most profound mass extinction of all time. *Proceedings of the Royal Society B: Biological Sciences* 275: 759–765.
<https://doi.org/10.1098/rspb.2007.1370>
60. Seitz S, Nebel M, Goebes P, Käppeler K, Schmidt K, Shi X, Song Z, Webber CL, Weber B, Scholten T (2017) Bryophyte-dominated biological soil crusts mitigate soil erosion in an early successional Chinese subtropical forest. *Biogeosciences* 14:5775–5788. <https://doi.org/10.5194/bg-14-5775-2017>
61. Sillett SC, Antoine ME (2004) Lichens and bryophytes in forest canopies. In: Lowman MD, Nadkarni NM (eds) *Forest Canopies*. Elsevier Academic Press, Amsterdam, pp 151–174
62. Song L, Liu WY, Nadkarni NM (2012) Response of non-vascular epiphytes to simulated climate change in a montane moist evergreen broad-leaved forest in southwest China. *Biol Cons* 152:127–135. <https://doi.org/10.1016/j.biocon.2012.04.002>
63. Tittensor DP, Mora C, Jetz W, Lotze HK, Ricard D, Berghe EV, Worm B (2010) Global patterns and predictors of marine biodiversity across taxa. *Nature* 466:1098–1101.
<https://doi.org/10.1038/nature09329>
64. Tømmervik H, Johansen B, Tombre I, Thannheiser D, Høgda KA, Gaare E, Wielgolaski FE (2004) Vegetation changes in the mountain birch forests: the influence of grazing and climate. *Arctic Antarctic Alpine Research* 36:322–331. DOI:10.1657/1523-0430(2004)036[0323:VCITNM]2.0.CO;2

65. Tuba Z, Slack NG, Stark LR (2011) *Bryophyte Ecology and Climate Change*, 1st eds. Cambridge University Press, Cambridge. <https://doi.org/10.1111/j.1442-9993.2012.02409.x>
66. Urban MC (2015) Accelerating extinction risk from climate change. *Science* 348:571–573
67. <https://doi.org/10.1126/science.aaa4984>
68. Wagner S, Zotz G, Allen NS, Bader MY (2013) Altitudinal changes in temperature responses of net photosynthesis and dark respiration in tropical bryophytes. *Ann Bot* 111:455–465. <https://doi.org/10.1093/aob/mcs267>
69. Wagner S, Zotz G, Bader MY (2014a) The temperature acclimation potential of tropical bryophytes. *Plant Biol* 16:117–124. <https://doi.org/10.1111/plb.12037>
70. Wagner S, Bader MY, Zotz G (2014b) Physiological ecology of tropical bryophytes. In: Hanson D, Rice S (eds) *Photosynthesis in Bryophytes and Early Land Plants, Advances in Photosynthesis and Respiration*. Springer, Dordrecht, pp 269–289. https://doi.org/10.1007/978-94-007-6988-5_15
71. Waite M, Sack L (2010) How does moss photosynthesis relate to leaf and canopy structure? Trait relationships for 10 Hawaiian species of contrasting light habitats. *New Phytol* 185:156–172. <https://doi.org/10.1111/j.1469-8137.2009.03061.x>
72. Wang Z-M, Ye W, Xing F-W (2019) Bryophyte diversity on a tropical continental island (Hainan, China): potential vulnerable species and environmental indicators. *Journal of Bryology* 41:350–360. <https://doi.org/10.1080/03736687.2019.1653557>
73. Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G (2008) Towards an Integrated Framework for Assessing the Vulnerability of Species to Climate Change. *PLOS Biology* 6:e325. <https://doi.org/10.1371/journal.pbio.0060325>
74. Yanoviak SP, Nadkarni NM, Solano JR (2007) Arthropod Assemblages in Epiphyte Mats of Costa Rican Cloud Forests. *Biotropica* 39:202–210. <https://doi.org/10.1111/j.1744-7429.2006.00261.x>
75. Zhang L (2003) An updated and annotated inventory of Hong Kong Bryophytes. *Memoirs of the Hong Kong Natural History Society* 26:1–133
76. Zhao J, Zheng Y, Zhang B, Chen Y, Zhang Y (2009) Progress in the study of algae and mosses in biological soil crusts. *Frontiers of Biology in China* 4:143–150. <https://doi.org/10.1007/s11515-008-0104-0>
77. Zhuang XY, Corlett RT (1997) Forest and forest succession in Hong Kong. *J Trop Ecol* 14:857–866. doi:10.1017/S0266467400011032
78. Zotz G, Bader M (2009) Epiphytic plants in a changing world: global change effects on vascular and nonvascular epiphytes. *Progress in Botany* 70:147–170. https://doi.org/10.1007/978-3-540-68421-3_7

Figures

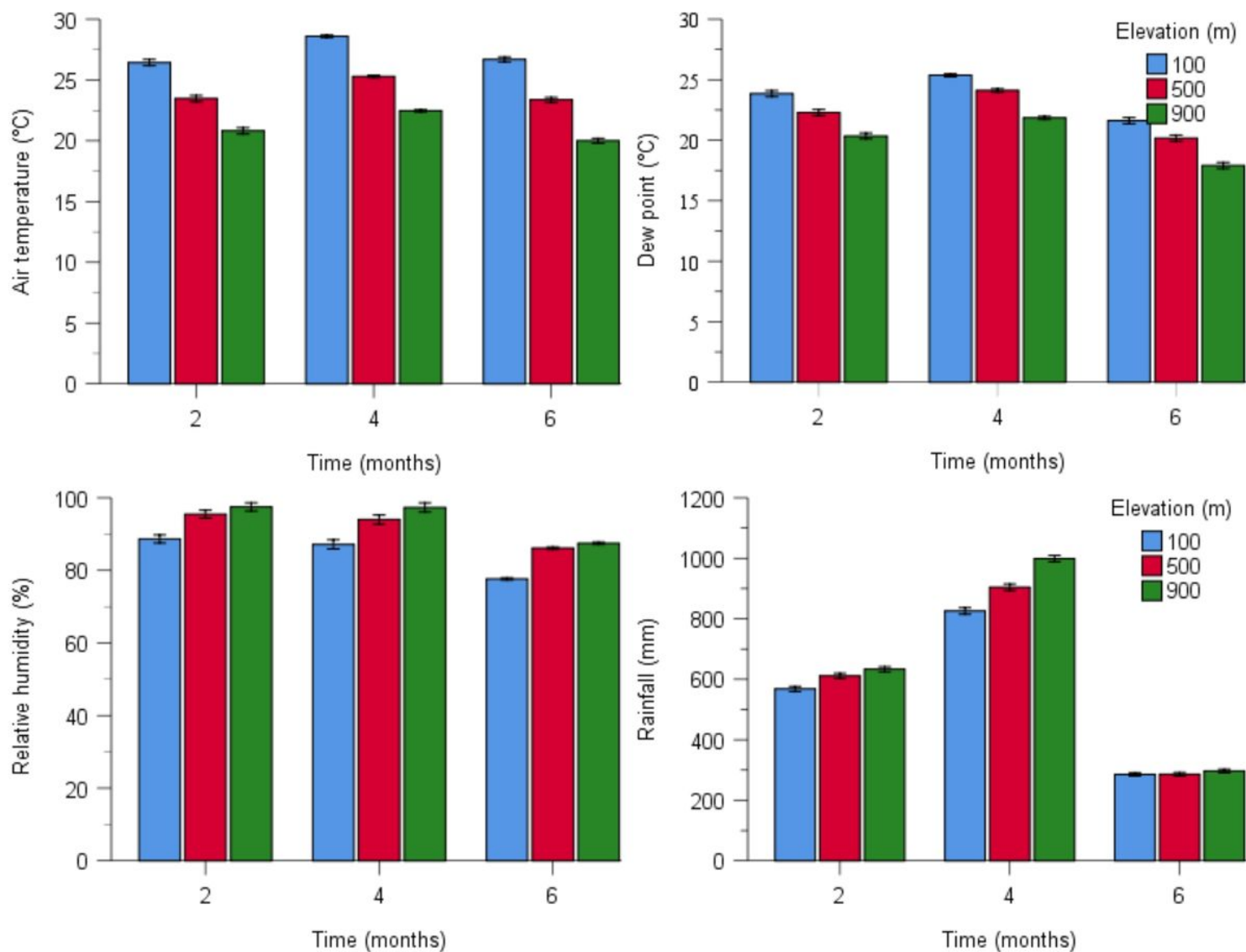


Figure 1

Comparison of mean air temperature, dew point, relative humidity, and rainfall among different elevations during the observation period. Error bars indicate the 95% confidence interval (n = 3).

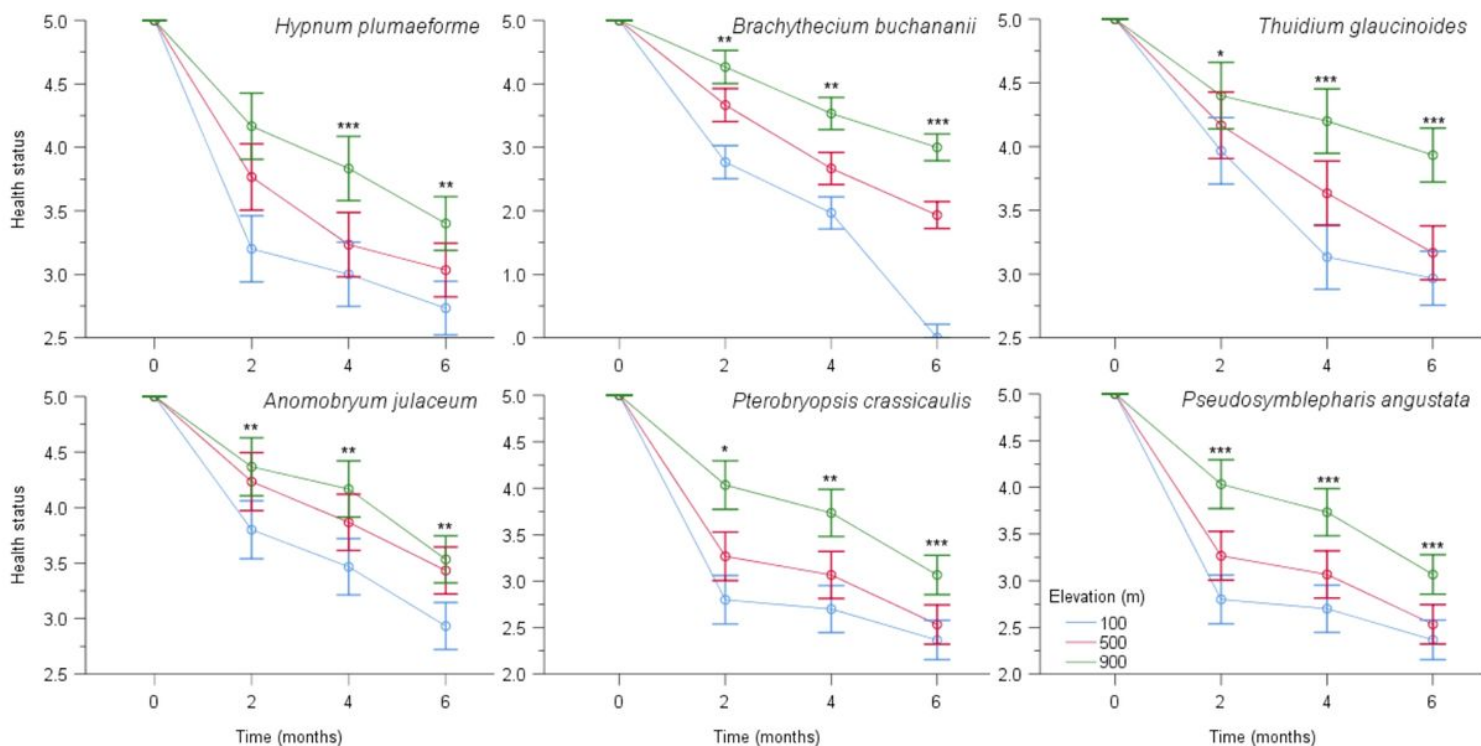


Figure 2

Effect of simulated climate change on the health of six terrestrial moss species from 900 m asl. Error bars indicate the 95% confidence interval (n = 3). *** significant at the 0.001 level; ** significant at the 0.01 level; * significant at the 0.05 level.

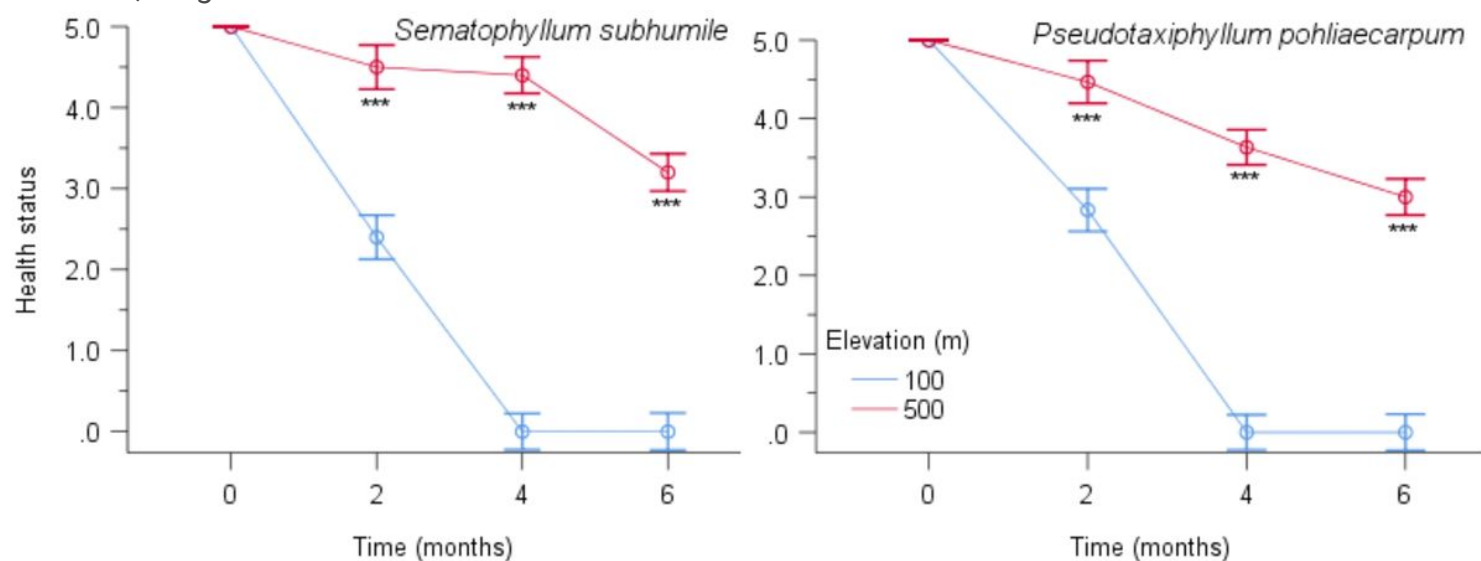


Figure 3

Effect of simulated climate change on the health of two terrestrial moss species from 500 m asl. Error bars indicate the 95% confidence interval (n = 3). *** significant at the 0.001 level; ** significant at the 0.01 level; * significant at the 0.05 level.

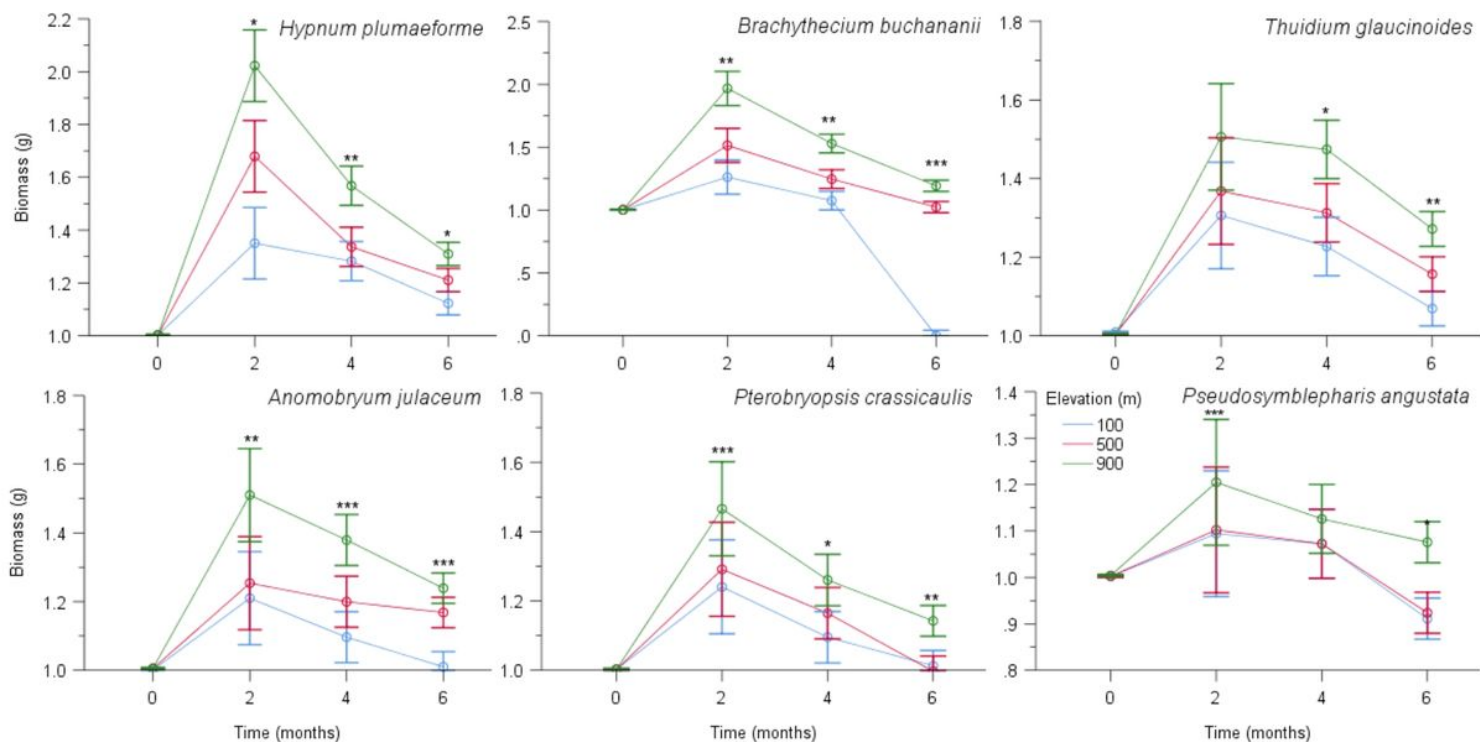


Figure 4

Effect of simulated climate change on the growth condition of six terrestrial moss species from 900 m asl. Error bars indicate the 95% confidence interval (n = 3). *** significant at the 0.001 level; ** significant at the 0.01 level; * significant at the 0.05 level.

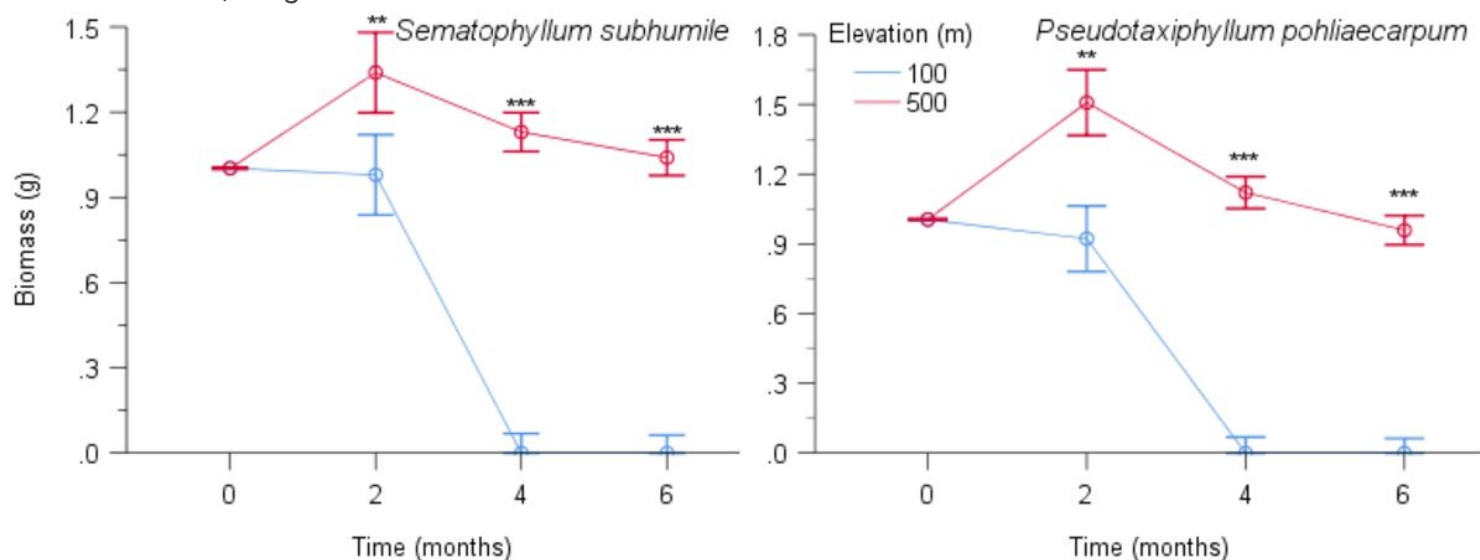


Figure 5

Effect of simulated climate change on the growth condition of two terrestrial moss species from 500 m asl. Error bars indicate the 95% confidence interval (n = 3). *** significant at the 0.001 level; ** significant at the 0.01 level; * significant at the 0.05 level.