

BRIEF COMMUNICATION

Novel climates reverse carbon uptake of atmospherically dependent epiphytes: Climatic constraints on the iconic boreal forest lichen *Evernia mesomorpha*

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PREMISE OF THE STUDY: Changing climates are expected to affect the abundance and distribution of global vegetation, especially plants and lichens with an epiphytic lifestyle and direct exposure to atmospheric variation. The study of epiphytes could improve understanding of biological responses to climatic changes, but only if the conditions that elicit physiological performance changes are clearly defined.

METHODS: We evaluated individual growth performance of the epiphytic lichen *Evernia mesomorpha*, an iconic boreal forest indicator species, in the first year of a decade-long experiment featuring whole-ecosystem warming and drying. Field experimental enclosures were located near the southern edge of the species' range.

KEY RESULTS: Mean annual biomass growth of *Evernia* significantly declined 6 percentage points for every +1°C of experimental warming after accounting for interactions with atmospheric drying. Mean annual biomass growth was 14% in ambient treatments, 2% in unheated control treatments, and –9% to –19% (decreases) in energy-added treatments ranging from +2.25 to +9.00°C above ambient temperatures. Warming-induced biomass losses among persistent individuals were suggestive evidence of an extinction debt that could precede further local mortality events.

CONCLUSIONS: Changing patterns of warming and drying would decrease or reverse *Evernia* growth at its southern range margins, with potential consequences for the maintenance of local and regional populations. Negative carbon balances among persisting individuals could physiologically commit these epiphytes to local extinction. Our findings illuminate the processes underlying local extinctions of epiphytes and suggest broader consequences for range shrinkage if dispersal and recruitment rates cannot keep pace.

KEY WORDS biomass accumulation; boreal forests; carbon balance; carbon dioxide enrichment; climate change experiment; epiphytes; extinction debt; growth rates; lichens; whole-ecosystem warming.

The epiphytic habit of growing upon plants has evolved repeatedly among seed-plants, ferns, bryophytes, algae, fungi, and lichens, often concurrently with adaptive radiations and local environmental changes (Hennequin et al., 2008; Givnish et al., 2011; Feldberg et al., 2015). Nonvascular epiphytes (e.g., lichens) are frequent among the world's forest and desert ecosystems, where they modify host

plant physiology by microclimate moisture buffering (Stanton et al., 2014) and regulating canopy heat fluxes (Pypker et al., 2017). Direct exposure to the atmosphere poses a unique set of challenges for sessile photosynthetic organisms that lack roots: they must maintain net positive carbon balance through fluctuations of temperature and moisture or else go locally extinct. Given that atmospheric

conditions limit the physiological performance of nearly all epiphytic vegetation (Palmqvist, 2000; Nadkarni and Solano, 2002; Testo and Watkins, 2012; Chambers et al., 2017), forecasted atmospheric changes may constrain individual growth and biomass accumulation. Quantifying how epiphytes respond to regional warming and drying trends will be critical to refining their use as biological climate indicators.

Organisms are increasingly encountering “no-analog” climates, combinations of climatic conditions never historically observed but which nevertheless shape species’ abundances and distributions (Williams and Jackson, 2007; Mahony et al., 2017). Even when analogous climates do exist for a site, the possibility that a given site could experience “novel” climates unlike any in its recent history suggests unknown consequences for existing vegetation. Rising temperatures, fluctuating moisture conditions, and increasing CO₂ concentrations are expected to alter the growth and composition of forest vegetation in general (Hyvönen et al., 2007), and of forest lichens in particular (Ellis et al., 2017). Epiphytic lichens are fungus–photobiont composite organisms directly exposed to fluctuations in atmospheric conditions. In recent decades, temperate and subtropical lichen species have invaded warming habitats, while many cold-adapted arctic and boreal species have receded to local extinction (Aptroot and van Herk, 2007; Hauck, 2009; Evju and Bruteig, 2013). Likewise, although some lichens can maintain metabolism in the absence of precipitation at relative humidities as low as 75–80% (Lange and Bertsch, 1965; Bertsch, 1966; Lange et al. 1986, 2007; Nash et al., 1990; Gauslaa, 2014), many epiphytic lichens not adapted to drying climates have also disappeared over recent decades (Follmann, 1995). The ability to anticipate shifts in the composition of epiphytic lichen floras depends on quantifying the processes by which novel climates affect individual growth and mortality.

Novel mixtures of warming, drying, and higher CO₂ concentrations may have interacting (or counteracting) effects on growth and carbon exchange of epiphytic vegetation. The climatic dependency of epiphytic lichens stems from their direct physiological reliance on atmospheric temperatures, moisture, and nutrients without recourse to soil reserves. Warming and drying trends lead to performance declines of epiphytic lichens through multiple processes, which include photorespiratory carbon losses (Palmqvist, 2000), chlorophyll degradation (Pisani et al., 2007), oxidative membrane damage (Kranner et al., 2008), photoinhibition during desiccation (Färber et al., 2014), and increased heterotrophic decomposition (Caldiz et al., 2007). These processes and their negative effects on growth can eventually kill individuals, potentially leading to demographic collapses and changes in species’ relative abundances that favor drought-tolerant and warm-temperate species at the expense of cold-adapted boreal species. The expected effects of increasing CO₂ concentrations are less clear, since the supply of sufficient light and moisture under increased CO₂ concentrations can either promote epiphytic lichen growth (Huebert et al., 1985) or inhibit it (Balaguer et al., 1999). Knowing the magnitude of changes required to elicit such responses under climates that are novel to a given site requires an integrated experimental approach.

Here we focus on the climate responses of epiphytic lichenized fungi in the initial year of a 10-year, whole-ecosystem climate manipulation experiment. The purpose of the SPRUCE experiment (“Spruce and Peatland Responses Under Changing Environments”) is to evaluate responses of a northern peatland ecosystem to whole-ecosystem warming, drying, and atmospheric CO₂ addition (ORNL, 2017). Peatlands at the SPRUCE site are important to ecosystem

climate science because large stocks of terrestrial carbon could mobilize as greenhouse gases CO₂ and CH₄. Its location at the southern edge of the western hemisphere’s boreal forest provides potential insight into drivers of ecosystem transitions. While our inferences are site-specific, the experiment also opens the door to understanding how local responses of indicator species might scale to landscapes across the Midwest region.

Our objective was to determine how individual growth of an epiphytic lichen species would respond to experimental whole-ecosystem warming, drying, and CO₂ additions representing novel climates that this site has not experienced at any time in its recent history. We measured responses from in-situ lichen communities and transplants of an archetypal boreal forest lichen, *Evernia mesomorpha* (“*Evernia*” hereafter), at the southern edge of its range. Its geographic distribution is very similar to the iconic boreal forest tree *Picea mariana* (black spruce); therefore, it is indicative of North American boreal forests. Here we report on the individual growth measurements; a follow-up article will report on whole-community composition effects. For our target species *Evernia*, we hypothesized that concurrent warming and drying would reduce growth rates (due to increased respiration rates at higher temperatures, and shortened metabolically active time under drier conditions), while CO₂ additions would increase growth (due to greater photosynthetic efficiency at high CO₂ concentrations). This work provides a basis for ecological forecasting of climate-related effects on focal epiphytic species.

MATERIALS AND METHODS

Experimental site description

The SPRUCE experimental site is an 8.1-ha ombrotrophic *Picea–Sphagnum* peat bog located at Marcell Experimental Forest in northern Minnesota (47.5057°, –93.4534°; 418 m a.s.l.). Organic peat deposits averaging 2.5 m lay atop postglacial ancient lakebed sediments (Sebestyen et al., 2011) in a landscape of rolling uplands, lakes, and low-lying peatlands. The climate is subhumid continental. At Marcell Experimental Forest over the period 1961–2005, mean annual air temperature was 3.3°C (daily mean extremes –38°C and 30°C), with 768 mm of mean annual precipitation falling mostly as warm-season rain. Mean annual air temperatures have increased about 0.4°C per decade over the last 40 years, mostly due to winter increases of about 0.6°C per decade (Sebestyen et al., 2011). Trees in the bog are *Picea mariana* and *Larix laricina* about 5–8 m tall, which have begun to regenerate nearly 50 years after two strip-cut harvests in 1969 and 1974 (Verry and Elling, 1978). Hardwoods, *Populus tremuloides* and *Betula papyrifera*, circle the bog margins. Understory vegetation includes *Sphagnum* mosses (*Sphagnum angustifolium*, *S. capillifolium*, *S. magellanicum*), true mosses (*Aulacomnium palustre*, *Pleurozium schreberi*, *Polytrichum juniperinum*), ericaceous shrubs (*Rhododendron groenlandicum*, *Chamaedaphne calyculata*, *Andromeda polifolia* var. *glaucophylla*) and graminoids (*Carex trisperma*, *Eriophorum spissum*) (Hanson et al., 2012).

Experimental treatments

The SPRUCE experiment consisted of 12 experimental plots distributed along a permanent boardwalk, including ten 8-m tall,

open-topped enclosures that enveloped the forest canopy (Fig. 1A). Each plot was an unreplicated treatment unit randomly assigned to one of 12 different treatments. Treatments consisted of six levels of warming via energy addition (ambient, enclosed controls, +2.25, +4.50, +6.75, and +9.00°C) factorially crossed with two CO₂ levels (ambient at 450 ppm vs enriched at ~900 ppm). Energy addition was concurrent with relative humidity decreases (ranging from 0–36 percentage points decrease relative to ambient). Air temperature and relative humidity were continuously recorded at half-hour intervals using an HMP-155 Humidity and Temperature Probe (Vaisala Corporation, Helsinki, Finland) mounted 2 m above the bog surface. Treatments represented climates that are novel to this site, although climate analogs may exist elsewhere. All treatments were actively maintained year-round. Ambient plots had no enclosures and no added energy. Control plots also had no energy added, but had full enclosures (structural walls, transparent sheathing, ductwork) installed to assess infrastructure effects. Remaining enclosures had energy added relative to the control plots, with heated air circulated by fans and by underground heaters embedded in the peat layer (Hanson et al., 2017). Construction of the whole-ecosystem experiment was incremental. In the summer of 2013, boardwalks, plumbing, and hydrologic skirts were installed for underground deep peat heating, which began in summer 2014 but did not immediately affect air temperatures (Hanson et al., 2017). Enclosure panels were installed in April 2015, and circulating fans began 24-h operation in July 2015. On 12 August 2015, air-warming treatments began; this date is the initiation point (time zero) for determining warming and drying treatment effects resulting from energy addition. On 16 June 2016, CO₂ addition began. We recorded responses of epiphytic lichens by measuring single-species biomass over each of the 2 years preceding climate treatments (2013–2014 and 2014–2015 baseline periods) and 1 year after treatments (2015–2016 treatment period). Lichens were measured each mid-August from 2013 through 2016.

Epiphyte measurements

In 2013, we installed 322 *Evernia* lichen transplants on *Picea mariana* branches in the plots, about 27 per plot (Fig. 1A, B). In a separate forthcoming study to be reported elsewhere, we also monitored all lichen species in permanent community transects for assessing

community changes. *Evernia mesomorpha* is a fruticose (shrubby) epiphytic lichen species that has a single point of attachment to the substrate, making it conducive for use as a transplant to assess growth. After gathering healthy *Evernia* thalli from the same bog (but outside the boundary of the experiment), we attached them to monofilament line with silicone caulk (McCune et al., 1996). These apparatus materials were inert and did not change over time in preliminary trials. We fixed transplants with removable nylon cable ties to living *Picea* branches 1.5–2.2 m above boardwalks (Fig. 1B), while avoiding dense foliage on younger twigs, avoiding other experimental equipment, and randomizing locations each year among multiple trees within each plot. Transplants were located at least 2 m from any enclosure walls, toward the center of the large, 12-m diameter enclosures. Every August 2013–2016, we temporarily removed transplants, transported them within 2 h to a controlled-environment laboratory, and equilibrated them for 24 h at 20°C and ambient relative humidity before weighing with an analytical balance (precision ± 0.0001 g). To account for potential bias caused by relative humidity fluctuations during weighing, we used the sacrificial method (McCune et al., 1996) in which out-of-sample *Evernia* thalli were collected from nearby, maintained at identical humidity side-by-side with in-sample thalli, and weighed both before and immediately after oven-drying for 1.5 h at 60°C. The air-dried masses of in-sample thalli (minus the mass of the inert apparatus) were multiplied by the ratio of oven-dried to air-dried sacrificial thalli to yield corrected mass. Sacrificial masses remained steady throughout each weighing period, within 0.0005 g of the mean, indicating only minor fluctuations. Annual biomass growth was calculated as percentage change in individuals' dry mass following eq. 4 of McCune et al. (1996).

Statistical models

Computer code for analyses is available in Appendix S1 (see Supplemental Data with this article), and all data are freely available in Appendix S2. All analyses were performed in R version 3.3.1 (R Core Team, 2016). For the temperature variable throughout, we used the actual observed annual mean temperature differentials in each plot (relative to ambient) because actual temperature increases differed slightly from targets. For the moisture variable, we used the actual observed annual mean relative humidity differentials in

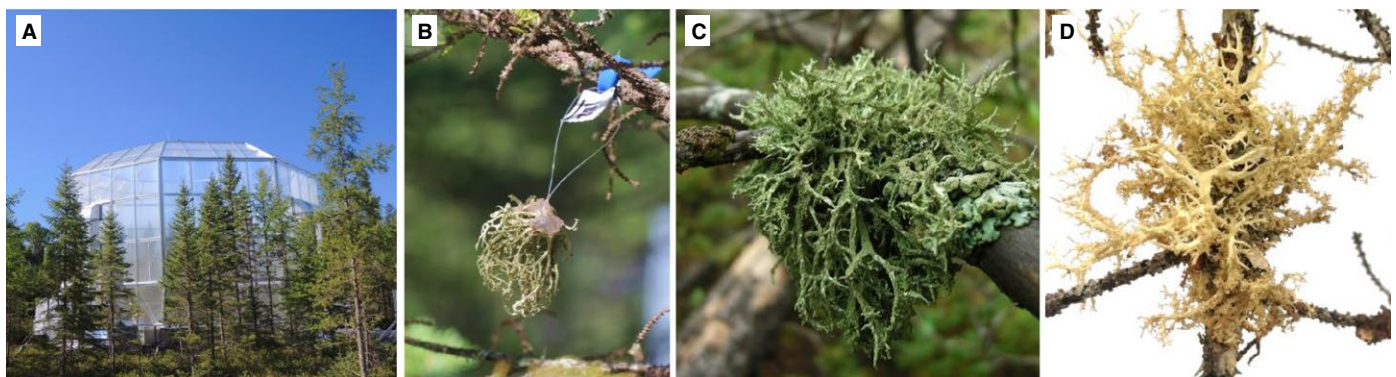


FIGURE 1. Overview of the SPRUCE experiment. (A) Twelve plots installed at the SPRUCE experiment site in a northern Minnesota peat bog. Each 8-m tall, open-topped enclosure is dynamically maintained in reference to ambient temperatures and CO₂ concentrations. (B) Example of a single *Evernia mesomorpha* transplant hung with monofilament from *Picea mariana*. (C) Healthy *Evernia mesomorpha* in ambient conditions. (D) Bleached or failing *Evernia mesomorpha* tended to persist on *Picea* branches in the energy-added treatments.

each plot (relative to ambient). We determined the proportion of transplants that were lost, visibly fragmented, or not recorded in all four annual sampling events, and excluded these from further analyses. We also excluded any individuals with annual biomass losses greater than 2.5 standard deviations below each treatment mean because such drastic changes were likely due to unseen fragmentation rather than climate-related growth declines (only seven individuals met this criterion). For each of the three sampling periods (two pretreatments and one posttreatment), we then used a fixed-effects linear model to test the null hypothesis of no difference in mean annual biomass growth among climate treatments. We began with full models including coefficients for effects of CO₂ addition, warming temperature, drying relative humidity, and all higher-order interactions. On the basis of a preliminary analysis of the full models (Appendix S3), we removed the CO₂ coefficients in reduced models for final interpretation. This final linear model can be written as $Y_i = \beta_0 + \beta_1 W_i + \beta_2 D_i + \beta_3 (WD)_i + \varepsilon_i$, where Y_i is the average annual biomass growth rate of transplants in plot i over a 1-year sampling period, β_0 is the mean annual biomass growth rate at ambient temperatures and ambient relative humidity, β_1 is the incremental effect of a 1°C increase in warming on the mean annual biomass growth rate, β_2 is the incremental effect of a 1 percentage-point decrease in relative humidity on the mean annual biomass growth rate, β_3 is the further incremental effect of both a 1°C increase in warming and a 1 percentage-point decrease in relative humidity on the mean annual biomass growth rate, W_i is the amount of warming (°C) in plot i relative to ambient, D_i is the amount of drying (relative humidity percentage points) in plot i relative to ambient, ε_i is the random error term for the i th plot, $\varepsilon_i \sim N(0, \sigma^2)$, and errors ε_i are independent. Each of the models were fit using the base function “lm” in R version 3.3.1 (R Core Team, 2016). After model fitting, we checked the assumptions that errors were symmetrically distributed by inspecting a QQ plot and a plot of the model residuals vs. fitted values. Upon verifying that assumptions were reasonably met, we performed an F -test of the null hypothesis that the interaction and main-effect coefficients did not differ from zero. The F -tests used type III sums of squares to evaluate the effect of each coefficient after accounting for the effects of all others.

Representativeness of climate treatments

To assess representativeness of the climate treatments, we examined how actual conditions in the SPRUCE experiment corresponded to current and potential future climates across the central United States and Canada. First, we quantified actual conditions in each SPRUCE plot as the annual mean differentials of temperature and relative humidity (relative to ambient) based on the half-hourly measurements taken 2 m above the bog surface. These measurements effectively gave the climate conditions that epiphytes actually experienced, rather than assuming target values. We compared these with values extracted from the ClimateNA database (Wang et al., 2016) for central United States and Canada sites. Current-day values from the database were 30-year normals (1981–2010). Potential future values were from a pessimistic ensemble model scenario (CMIP5-RCP8.5) that assumed emissions would increase through the 21st century until 2085 (IPCC, 2014), although this scenario may or may not simulate a realistic outcome. We selected the pessimistic scenario only for illustration purposes, without making claims about the chances of it actually occurring. We then determined which geographic locations were similar to the unique combinations of temperature and

relative humidity that epiphytic lichens actually experienced in each SPRUCE plot.

RESULTS

Overall, we found that 1 year of experimental whole-ecosystem warming and drying caused significant biomass losses of a boreal epiphytic lichen species, but 2 months of CO₂ addition had no significant effect. Of 322 original *Evernia* transplants, 280 remained 3 years later (13% loss of individuals). Transplants in ambient treatments (Fig. 1C) were green and healthy as before the treatments, but transplants in all energy-added plots were visibly discolored and chlorotic (Fig. 1D). For each pretreatment period before the experimental energy additions, mean annual biomass growth did not significantly differ among plots (Appendix S3; Fig. 2A, B), although we did observe interannual variation consistent across all plots. Specifically, growth declined (mean −31.5%, sample standard deviation ± 15.8%; Fig. 2A) in the first annual pretreatment period across all plots, which corresponded to very harsh ambient winter conditions. In the following year, moderate positive growth across all plots in the second annual pretreatment period (15.3% ± 17.8%; Fig. 2B) corresponded to milder ambient winter conditions.

After 1 year of applied climate treatments, short-term CO₂ addition (2 months) had no significant effect on mean annual biomass growth, either alone or by interaction with other effects in the full models (Appendix S3); the final reduced models therefore included only warming and drying effects. As expected given the humidity decreases that accompanied energy additions, there was a significant interactive effect of warming and drying ($F_{1,8} = 20.65$, $P = 0.0019$, Fig. 2D). Drying had no significant effect ($F_{1,8} = 0.001$, $P = 0.97$) after accounting for the effects of warming and the warming–drying interaction. In contrast, warming significantly decreased growth after accounting for the effects of drying and the warming–drying interaction ($F_{1,8} = 11.64$, $P = 0.0092$). Specifically, mean annual biomass growth decreased 6.2 percentage points (95% CI: −10.4 to −2.0; Fig. 2C) for every 1°C increase, after accounting for the effects of drying and the warming–drying interaction. Plots exhibited a range of mean annual growth rates that progressively declined from 14% in ambient treatments, to 2% in control treatments with no energy added, to a range of −9% to −19% (decreases) across energy-added treatments (Table 1). Actual temperature differentials differed slightly from targets (Table 1). Temperatures increased and relative humidities decreased with progressive energy additions.

Based on local measurements, ambient plots and enclosed control plots had temperatures, precipitation inputs, and relative humidity conditions that were quantitatively similar to other locations along the southern edge of the North American boreal coniferous forest, and therefore did not represent novel climates for this site. As expected, the energy-added treatments had warmer temperatures and reduced relative humidity when compared to ambient conditions. The representativeness analysis revealed that the energy-added treatments represented current modern conditions at locations trending southwesterly across the western Great Plains toward the Rocky Mountain Front (Fig. 3), and therefore represented climates that are novel to this site. These geographic trends were similar for projected future climates given IPCC (2014) emissions scenarios. Energy-added treatments represented realistic potential future warming (projected 5.9°C increase) expected for

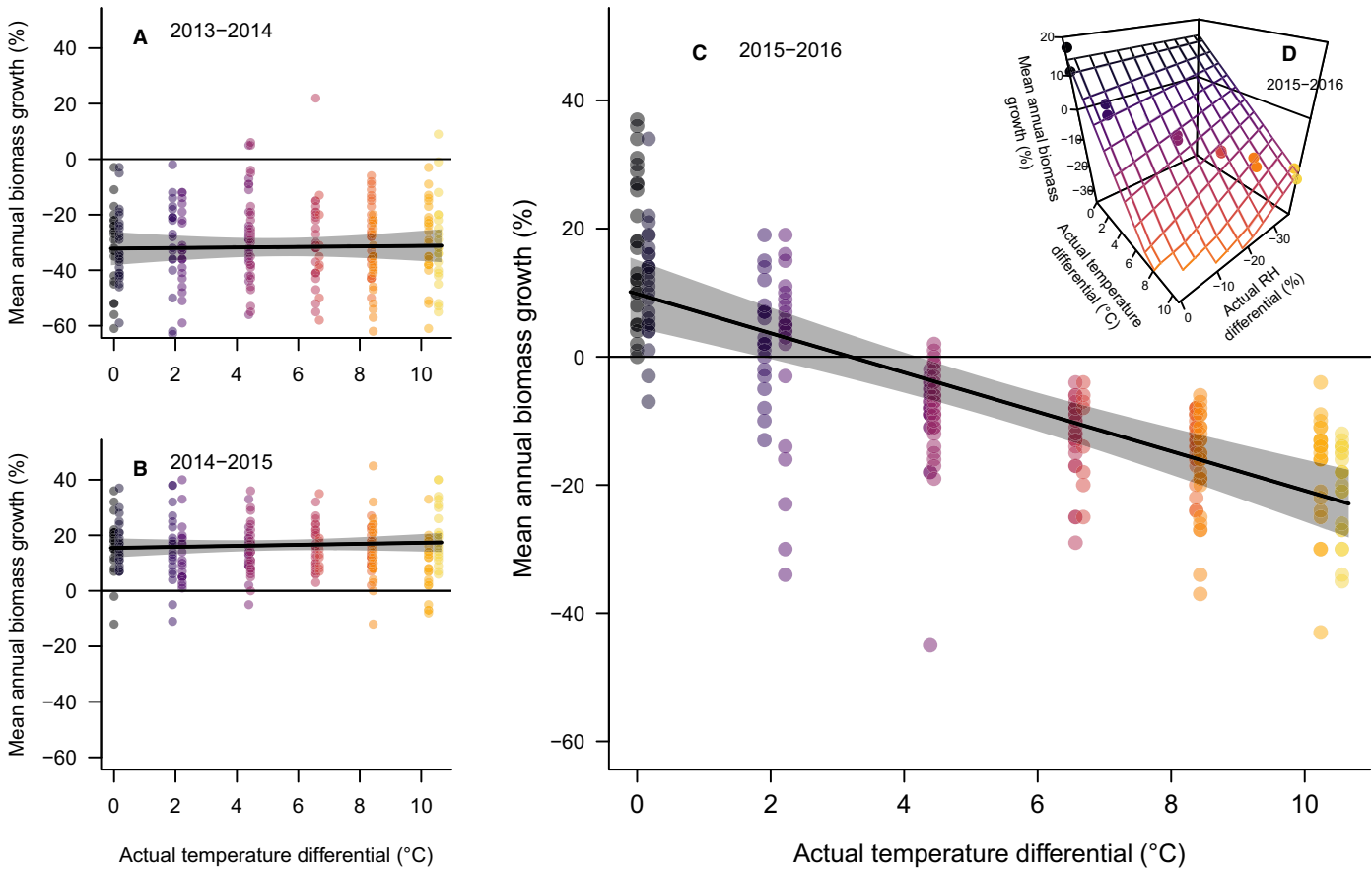


FIGURE 2. Annual biomass growth rates of *Evernia mesomorpha* transplants at the SPRUCE experimental site in northern Minnesota. Each symbol is the annual biomass growth rate for one transplanted lichen thallus. Growth rates are for each pretreatment year (A, B) and in the first year of whole-ecosystem warming and drying (C, D). Slope of regression lines (A, B, C) are the estimated incremental effect of a 1°C increase in warming on the mean annual biomass growth rate, and shaded areas around lines are 95% confidence intervals of the estimated mean. In the first year of whole-ecosystem warming and drying, mean growth significantly decreased 6.2 percentage points for every 1°C increase in warming (95% CI: –10.4 to –2.0 percentage points) after accounting for potential effects of drying (not significant, not shown) and the drying-warming interaction (regression surface in D). RH: relative humidity.

TABLE 1. Mean annual biomass growth of *Evernia mesomorpha* transplants at the SPRUCE experiment in Minnesota. Measurements were in 12 experimental plots at the SPRUCE experiment over the first year of whole-ecosystem warming, drying, and CO₂ addition. Transplant numbers are unbalanced because of incomplete measurements or losses over time. Rows are sorted by actual temperature differentials (relative to ambient) as measured at 2 m above the bog surface.

Target temperature differential (°C)	Actual temperature differential (°C)	Actual relative humidity differential (percentage points)	CO ₂ treatment (ppm)	N transplants	Annual biomass growth (mean ± SD, %)	Net effect 2015–2016
ambient	0.0	0.0	450	25	17.4 ± 11.8	+
ambient	0.2	0.5	450	25	11.3 ± 8.7	+
control	1.9	–3.7	900	21	3.0 ± 8.3	+
control	2.2	–3.2	450	22	0.4 ± 14.6	+
2.25	4.4	–16.5	900	24	–9.5 ± 8.5	–
2.25	4.4	–16.3	450	25	–7.6 ± 5.9	–
4.50	6.6	–23.8	900	25	–12.4 ± 6.3	–
4.50	6.7	–23.6	450	8	–12.8 ± 7.6	–
6.75	8.4	–28.4	450	27	–13.4 ± 4.7	–
6.75	8.4	–29.7	900	26	–17.2 ± 8.1	–
9.00	10.2	–36.3	900	23	–17.3 ± 8.6	–
9.00	10.6	–36.4	450	22	–20.5 ± 7.2	–

the SPRUCE site in the year 2085. The treatments had a less distinct match to potential changes in average relative humidity (projected 3 percentage-point increase), although average moisture changes are

also expected to be accompanied by a larger range of variability at the northern Minnesota SPRUCE site based on comparison to forecast data (IPCC, 2014; Dunn et al., 2017).

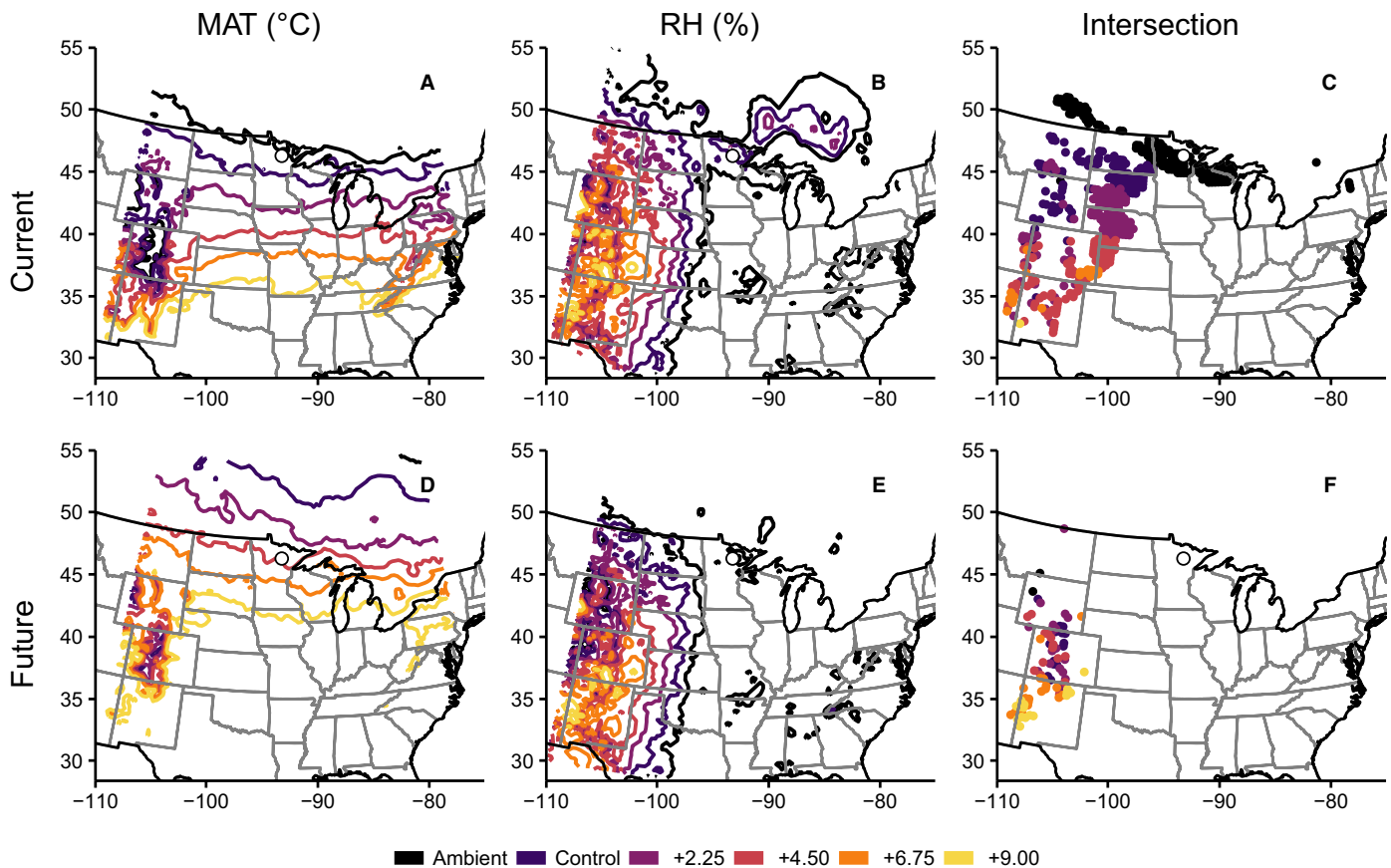


FIGURE 3. Representativeness of SPRUCE experimental treatment conditions. Representativeness is measured relative to current-day climate (A, B, C) and potential future climate (D, E, F) across the central United States and Canada. Each isoline corresponds to conditions in experimental treatments. Mean annual temperature (MAT; A, D) increases under the potential future scenario, with little change in mean annual relative humidity (RH; B, E). Combinations of temperature and humidity in treatments were similar to current-day conditions at locations along the western Great Plains and Rocky Mountain Front (C, F). Current climate data are from Wang et al. (2016), future climate data from IPCC (2014).

DISCUSSION

Anticipating future ecological changes requires knowing the magnitude of atmospheric changes required to affect individual growth and species membership in local communities. Here, we identified the short-term effects of warming and drying on individual growth of the boreal epiphytic lichen species *Evernia mesomorpha* at a northern Minnesota peat bog, finding significant growth decreases as warming and drying increased. We interpret these negative growth trends as a reversal of carbon uptake induced by novel climates, which this site has not experienced in its recent history. During pretreatment baseline periods, we found that growth varied among years but not among plots, allowing us to assess subsequent growth declines as a function of treatment effects against the background of yearly variation. Observed annual biomass growth (+14%) in ambient treatments corresponded very well with *Evernia* growth in unharvested boreal forests in western Quebec, Canada (Boudreault et al., 2013). Significant observed biomass decreases (−9% to −19% annually) in our energy-added treatments suggest that persistent warming and drying beyond the historical range of variability at this site could lead to population declines. Our findings are consistent with climate-driven individual growth declines and mortality observed among other experimental transplants of

vascular and nonvascular epiphytes (Nadkarni and Solano, 2002; Song et al., 2012).

Our finding of no short-term CO₂ effect on growth was initially surprising, given prior evidence that net photosynthesis of *Evernia mesomorpha* increases monotonically with CO₂ concentrations in the range of 100–460 ppm when moisture and light are not limiting (Huebert et al., 1985). One likely explanation is that warming and drying curtailed carbon uptake in photosynthesis such that CO₂ addition had no stimulating effect. Indeed, no CO₂ fertilization effect would be expected if atmospheric carbon were not the most limiting resource in lichen photosynthesis. For example, moisture limitation could decrease photosynthetic efficiency (Huebert et al., 1985) and extreme desiccation could lead to photoinhibitory damage (Färber et al., 2014). Another possible explanation is that CO₂ fertilization effects would require more time to develop, since CO₂ addition was delayed relative to energy additions. A potential delayed effect of CO₂ is a hypothesis addressed by ongoing monitoring at the SPRUCE site.

The amount and timing of moisture availability should have strong effects on *Evernia* metabolism. Pearson (1969) considered *Evernia mesomorpha* as a moisture indicator species that requires alternating wet–dry cycles, implying that prolonged dry (or prolonged wet) periods are detrimental. Warming in the SPRUCE

experiment was accompanied by proportional decreases in relative humidity as a product of the experimental design (Hanson et al., 2017), including a reduction in the potential for dew formation. Moisture reductions ranging from mild to drastic are projected for the Midwest region of the United States given plausible carbon emissions and atmospheric scenarios (Dunn et al., 2017), which could severely impact photosynthesis and biomass accumulation of poikilohydric epiphytes that rely on dew and humid air as sources of moisture instead of liquid rain (Lange et al., 2007; Gauslaa, 2014). Dew occurs at relative humidity approaching 100% and can thus be viewed as one point along an atmospheric moisture continuum (humid air < dew < liquid rain). While *Evernia* species can maintain a positive carbon balance at relative humidities near 80% (Bertsch, 1966), moisture in the form of dew may be essential to many other species (Gauslaa, 2014). Our experimental approach allowed us to assess the joint influence of warming and drying together, rather than making assumptions of independence. The energy-added treatments were representative of existing thermal and moisture combinations currently found in mesic and submesic portions of the United States, which would represent novel climates for this site. These combinations are indicative of the kinds of future climates that epiphytic lichens might realistically experience, although caution should be exercised in forecasting species' responses due to inherent uncertainty in climatological forecasts.

Local extinctions at southern margins would shrink the range sizes of boreal epiphytes unless compensated by expansion elsewhere. Yet we do not know enough about dispersal and colonization probabilities for most epiphytic species to accurately predict how fast migration could happen. For *Evernia mesomorpha* and similar species, rates of colonization may be limited by dispersal, and by the ecophysiological tolerances of the algal photobiont partner during establishment (Piercey-Normore, 2006; Werth and Sork, 2014). Average colonization rate of the closely related congener *Evernia prunastri* was approximately 30 m yr⁻¹, with fewer than 1% of diaspores dispersing over 100 m yr⁻¹ (Tapper, 1976), although rare long-distance dispersal events could permit range expansion. Considering rates of dispersal, colonization, persistence, and extinction across environmental gradients will help in building process-based species distribution models (Evans et al., 2016), toward accurately forecasting future range shifts.

The apparent population- and community-level effects of warming and drying may lag well behind their effects on individuals, leading to extinction debts at the trailing edges of species' ranges (Svenning and Sandel, 2013). Our observation that individual thalli persisted on *Picea* branches despite clearly negative growth rates suggests that individuals may remain structurally intact (at least temporarily) even while they are functionally moribund. Lichen thalli at our site may die yet remain intact on tree branches for several months to years if decomposition and mechanical disturbances are slow. The lag between the physiological decline of individuals and their eventual disappearance suggests the possibility of an extinction debt, wherein some epiphytic species may be committed to local extinction even as individuals persist (Öckinger and Nilsson, 2010). Lagged extinctions of "patch-tracking" epiphytes depend in part on the availability of suitable host trees in suitable environments (Johansson et al., 2013), which suggests that epiphyte persistence is constrained not only by climate but also by the dynamics of the trees on which they grow (Snäll et al., 2005; Belinchon et al., 2017). Extinction debts may be greater among rooted plants than among epiphytic lichens

because the latter are directly exposed to the atmosphere, they lack specialized perennating organs, and they generally have a more rapid life cycle than the host plants that they inhabit. The possibility of extinction debts among any vegetation group suggests that extrapolating species distribution models into novel climate spaces would be most effective only when accounting for lags between physiological and whole-organism responses.

Aside from the direct effects of climate, its effects on future interactions with host trees and other epiphytes may change epiphytic communities in unexpected ways. For example, foliage loss (from drought-stressed host trees) or foliage gains (from increased tree vigor) would alter subcanopy light availability that could differentially affect lichen species based on differing light tolerances. Therefore, outcomes depend not only on abiotic conditions, but also on biotic processes mediated by light tolerance and other evolved traits. Continued monitoring of single species and communities over the next decade will reveal long-term outcomes of biotic interactions as the SPRUCE experiment proceeds. The next challenge will be to model expectations for focal species, and for many species together across large landscapes, based on demographic measures and environmental constraints. Novel combinations of experimentation and modeling will help link local species responses to landscape levels and will allow forecasts of range shifts among vulnerable forest epiphytes exposed to warming and drying trends that may exceed historical ranges of variability.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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