

An experimental test of niche versus dispersal limitation of the distribution limit of the Ghost Antler Lichen, *Pseudevernia cladonia*, along a temperate–boreal elevation gradient

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Abstract

Understanding the mechanisms underlying species' distribution limits is critical for predicting how species may respond to environmental change. For species restricted to mountain summits, there is concern that climatic changes may result in increasingly restricted distributions. Two central mechanisms govern species distribution limits: (i) niche limitations—environmental conditions beyond distribution limits that are insufficient for survival and reproduction, and (ii) dispersal limitations that prevent colonization of suitable habitat beyond distribution limits. Here, we conducted a transplant experiment to examine the effect of niche versus dispersal limitation on the altitudinal distribution limit of the Ghost Antler Lichen (*Pseudevernia cladonia* (Tuck.) Hale & Culb.) that, within Québec, Canada, is restricted to high-elevation mountain summits in the southeast. Along an elevation gradient, we transplanted individuals into sites *within* its distribution, at the *edge*, and *beyond* its distribution. We observed that survival and performance were greatest within its distribution and decreased markedly beyond its distribution, supporting our prediction that this lichen is niche limited along the elevation gradient. We suggest that cooler and more humid conditions at the summit are important environmental factors for this species' persistence. Our findings suggest that projected climatic changes in these montane habitats may result in less suitable habitat for this species.

Key words: lichen transplants, distribution limits, Ghost Antler Lichen, environmental gradients, mountaintops, boreal forest, *Pseudevernia cladonia* (Tuck.) Hale & Culb.

Introduction

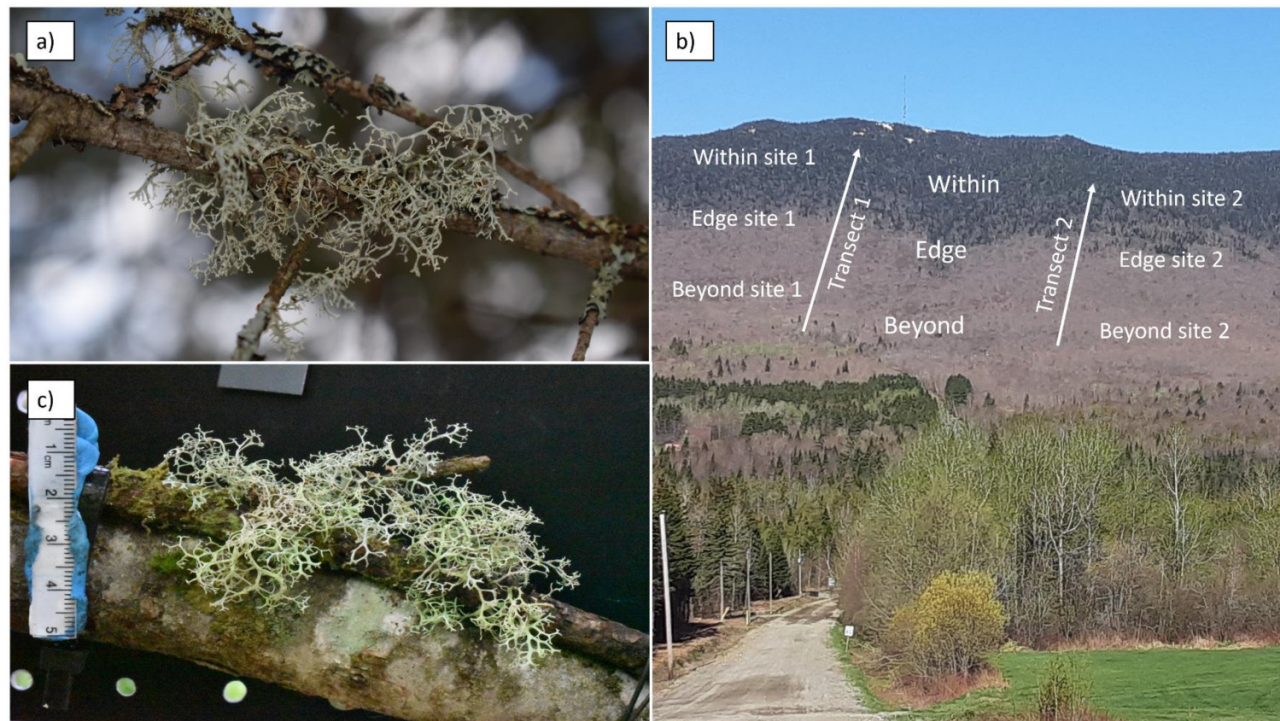
Studies of species distributions are central to the study of ecology, addressing questions concerning the relative role of niches and dispersal in determining range limits (Gaston 2003). For a niche-driven distribution limit along an environmental gradient, a species stops occurring where environmental conditions (such as air temperature) or biotic factors (such as competition) prevent a population from sustaining itself (Holt 2003; DeWalt et al. 2004; Alexander et al. 2022). In contrast, for a dispersal-driven distribution limit, suitable habitat exists for a species beyond its current distribution, but it has not yet colonized the area. A better understanding of the primary driver of a species' distribution is important for predicting a species' response to climatic changes, and whether it may overcome barriers to its distribution limit (Gaston 2003; Holt 2003; Goldberg and Lande 2007; Sexton et al. 2009).

Understanding the mechanisms behind distribution limits is of particular concern for lichens, as many species are considered sensitive to climate change (Ellis et al. 2007; Vallese et al. 2022). As poikilohydric organisms, lichens' water con-

tent is determined by surrounding environmental conditions (Nash 2008). Many temperate and boreal lichen species obtain most or all their moisture requirements from fog and water vapor under relatively cool temperatures, which favor efficient photosynthesis (Lange et al. 1986; Palmqvist 2008; Gauslaa 2014; Phinney et al. 2019). Studies indicate that climate change is correlated with a loss of diversity and suitable habitat for high-elevation lichens (Allen and Lendemer 2016; Vallese et al. 2022).

The high-elevation forests of Eastern North America are known for their diverse lichen communities, which harbor rare species (Clayden et al. 2011; Rinas and McMullin 2020; Vagle et al. 2024). These forests occur as virtual islands at high elevations on mountaintops along the Appalachian Mountain chain. Within the mountaintop forests of Eastern Canada, moisture input exceeds evaporation and transpiration, resulting in year-round wetness, along with cool temperatures (). Orthographic lift and cooling of air masses results in frequent cloud immersion of higher elevations, which plays an important role in maintaining the humid, cool conditions on the mountaintops in this region (Siccama 1974; Cogbill and

Fig. 1. (a) Naturally occurring *Pseudevernia cladonia* photographed at Mont Mégantic. (b) The study area in spring (before most deciduous trees have leafed out), showing the approximate distribution of *P. cladonia* and our study design: two transects and three transplant locations along each transect within its range, at the edge of its range, and beyond its range. (c) An example of a *P. cladonia* transplant.



White 1991; Vellend et al. 2021). Studies indicate that in these forests, epiphytic lichen diversity on conifer trees is highest at the cooler and more humid high elevations (Rinas et al. 2023).

In the mountains of Southeastern Québec, the arboreal Ghost Antler Lichen (*Pseudevernia cladonia* (Tuck.) Hale & Culb.) (Fig. 1a) has a clearly defined altitudinal distribution limit. It is restricted to high-elevation, humid spruce–fir forests, even though its host trees (fir and spruce) occur at low elevations as well. Its distribution pattern and strong correlation with cool and humid habitats throughout its range in Eastern North American suggest a niche-limited distribution (COSEWIC 2011). However, due to its limited capacity for reproduction, highly clumped and variable distribution within stands, and reported absence from apparently suitable habitat, this species may also be dispersal limited (COSEWIC 2011). Furthermore, on the lower elevation slopes, the Ghost Antler Lichens' coniferous hosts are more widely spaced (Fig. 1b). For this reason, limited dispersal may prevent persistence of a low-elevation metapopulation, despite suitable conditions on individual trees (Holt and Keitt 2000). However, no studies to date have addressed these questions experimentally.

The most direct tests of niche versus dispersal limited distribution limits are experiments that compare the fitness of transplanted individuals within a species' distribution to those beyond the distribution limit (Hargreaves et al. 2013; Lee-Yaw et al. 2016). If transplant fitness diminishes be-

yond the species distribution limit, one can infer that the niche (e.g., environmental factors, which might include biotic factors), determine the species' distribution limit (Fig. S1). However, if transplant fitness does not diminish beyond the species distribution, and is suggestive of population viability, this implies dispersal limitation (Fig. S1; Hargreaves et al. 2013). Many transplant experiments addressing these questions use vascular plants, and most suggest that range limits are caused by the niche (Hargreaves et al. 2013; Lee-Yaw et al. 2016). In a few cases, lichens are also being used in transplant experiments, offering insights into the mechanisms behind their range limits (Mallen-Cooper and Cornwell 2020). Some studies suggest dispersal limitations as transplants of low-elevation species placed outside of their realized niche at mid and high elevations performed well, as did old-growth species transplanted to young forests where they are naturally absent or rare (Sillett et al. 2000; Hilmo 2002; Keon and Muir 2002; Mežaka 2023). Other studies indicated that transplant performance was sensitive to changes in microclimatic conditions and was species-specific, thus indicating some may be limited by the niche (Coxson and Steveson 2007; Steveson and Coxson 2008). Still, the number of studies that directly address the question of niche or dispersal limitation with lichens remains few, and a better understanding of this question is critical for predicting how sensitive species may respond to the changing environment.

In this study, we conducted a transplant experiment to test whether the Ghost Antler Lichen is niche or dispersal lim-

ited along an elevation gradient in Parc National du Mont Mégantic in Southeastern Québec. In addition to addressing a fundamental ecological question, understanding the cause of this lichen's distribution limit is important, given its "sensitive" status in Québec due to likely threats from global climate change and anthropogenic activity (COSEWIC 2011). Furthermore, Parc national du Mont Mégantic is home to a substantial protected population of the Ghost Antler Lichen, and it is hypothesized that that upward shifts of the fog base and warmer, drier conditions predicted in the coming years may reduce its montane habitat (Richardson et al. 2003; Huntington et al. 2009).

Methods

Study area

We conducted our study on Mont St. Joseph, located within Parc National du Mont Mégantic in southeastern Québec, Canada (hereafter "Mont-Mégantic", Fig. 1b). The park is located at the northern edge of the Appalachian Mountains and has a northern temperate climate (PNdMM 2007). The forests on Mont St. Joseph are typical of the Appalachians with mixed northern hardwood forest at the lower elevations, boreal forest at the higher elevations, and an abrupt transition zone at the mid-elevations (PNdMM 2007; Vellend et al. 2021). In Notre Dame des Bois (567 m), a town close to the park entrance, the weather station reported an annual average temperature for 1980–2010 of 3.9 °C, and precipitation reached up to 980 mm each year (Government du Québec 2021). Along the elevation gradient, precipitation and relative air humidity increase, while temperatures decrease by about 2 °C (PNdMM 2007; Rinas et al. 2023). Disturbances include spruce–budworm outbreaks (1974–1984), ice storm damage (1998), and logging until the 1960s (PNdMM 2007). However, logging likely never occurred at the specific location of the study, or if did, it happened over 100 years ago.

Focal species

The focal species in this study is the arboreal Ghost Antler Lichen (*P. cladonia*; Fig. 1a), a specialist on conifer branches of eastern North America and the Caribbean region. Regionally, this species has a montane–coastal distribution in northeastern North America, with coastal populations in the coniferous forest of Maine, New Brunswick, and Nova Scotia (COSEWIC 2011). Montane populations occur primarily in high-elevation coniferous forests of the Appalachians, from North Carolina to Southeastern Québec (COSEWIC 2011; CNALH 2024). The collection and transplantation of individual Ghost Antler Lichens was approved by the park (authorization no: PNMM-2019-01) as it is abundant in the high-elevation coniferous forest, allowing enough material for transplants without affecting the population. In this park, as in other parts of Canada, this lichen occurs predominately on dead or needle-free twigs and occasionally the trunks of *Abies balsamea* (Linnaeus) Miller. (balsam fir) and *Picea rubens* Sarg. (red spruce) (COSEWIC 2011). The Ghost Antler Lichen reproduces primarily via thallus fragmentation. It does not produce asexual propagules, known in lichens as soredia or

isidia (McMullin and Anderson 2014). Furthermore, apothecia, sexually reproductive fruiting bodies, are extremely rare (COSEWIC 2011; McMullin and Anderson 2014). We have not observed the Ghost Antler Lichen with apothecia at Mont-Mégantic. Little is known about its physiology; therefore, its environmental requirements (cool temperatures and high relative air humidity) are inferred from its habitat (COSEWIC 2011).

Experimental design

We transplanted specimens of Ghost Antler Lichens along two altitudinal transects (experimental "blocks"), with three sites per transect: (i) *within* its distribution (high elevation; average elevation 1031 m on transect 1 and 940 m on transect 2), (ii) at the *edge* of the distribution (mid-elevation, 850 and 888 m), and (iii) *beyond* the lower distribution limit (773 and 781 m; Fig. 1b). Each site was ~2–3 hectares in area. We delineated the distribution of Ghost Antler Lichen (e.g., within, edge, and beyond) starting with habitat descriptions in COSEWIC (2011) and then walking the altitudinal gradient and assessing the lichens' presence and abundance. We selected transplant sites depending on the accessibility of the terrain (e.g., relatively gentle slopes), and whether there were enough balsam fir trees suitable for transplanting (e.g., trees with lower dead branches that were sturdy). Due to steep and difficult-to-access terrain, the "within" site (high elevation) on transect 2 was approximately 90 m lower than the within site on transect 1. At each site, we selected 25 living trees for the transplants (overall, 150 trees with transplants, equally distributed among within, edge, and beyond sites). We selected trees that had a sturdy, dead branch lower than roughly 2.0 m from the ground and that had enough space above the branch to allow us to take photographs. We monitored the fitness of the transplants via semi-annual surveys and photos (described in more detail below).

Collection and treatment of transplants

We collected lichen individuals for transplantation from 4 to 6 June 2019, at five high-elevation locations (~1000 m) spanning the distance between the two high-elevation "within" transplant sites (~1 km). We only collected Ghost Antler Lichen growing on the dead branches of balsam fir, *A. balsamea*. We left each collected lichen attached to the branch it was on, cutting the branch roughly 10–15 cm on either side of the lichen (following Hilmo 2002). We placed each lichen + branch in a paper bag to transport to the lab. For each lichen, we recorded the location, branch height, and aspect of the branch (relative to the trunk). The transplants were collected on branches roughly between 1.2 and 1.9 m from the ground, with the average distance from the trunk ~50 cm.

Photos taken prior to collection indicated that the color of other macrolichens on branches would be difficult to distinguish from the Ghost Antler Lichen when analyzing photos. Therefore, prior to transplantation, we removed all other macrolichens from our transplant branches. We also inspected each transplant under a microscope to ensure that

there were no signs of necrosis. Finally, we stored the transplants in paper bags in cool, dark conditions (recommended by [Duncan 2015](#)), for a period of roughly 1.5 weeks, until reintroducing the lichens back into the field.

We randomly assigned each experimental lichen to a transplant location (within, at the edge, or beyond its natural distribution) and placed them in the field between 18 and 21 June 2019 (Figs. 1b and 1c). We used plastic zip ties and wire to attach each branch + transplant to a low, dead branch of *A. balsamea* (1.2–1.9 m above the ground)—i.e., the same height from which lichens were collected. However, we were unable to match the average distance from the trunk (50 cm) as the dead branches further from the trunk were small and brittle and photographing at the same distance was not feasible. We placed each transplant ~6–19 cm from the branch's attachment to the trunk, where the branch was most stable and likely to hold for the duration of the experiment. We monitored the transplants five times over a period of 2 years, with the first monitoring period from 30 June to 4 July 2019, and the final one from 31 July 2021 to 8 August 2021.

We took repeated photos of each transplant with a Nikon 3500 DSLR camera equipped with a level and mounted to a wooden strip and attached to a surveyor's tripod (Fig. S2). On the end of the wooden strip opposite the camera was a black background and compass. This apparatus allowed us to photograph transplants at the same height and distance each time, from three different angles. We placed a ruler on the branch next to the transplant before taking photographs to permit later spatial calibration. Secondly, we inspected each transplant for qualitative signs of distress (discoloration, broken branches, detaching from transplant branch, and downturned; Fig. S3).

Measures of transplant fitness

We measured transplant fitness/performance by (i) its presence (survival) or absence (mortality), and (ii) the change in size (described below) over the course of the experiment, quantified as the relative growth rate. During three of the monitoring periods (summer 2019, 2020, and 2021), we took a set of three photos of each transplant, one photo from each of three different angles (0, 45, and 135 from horizontal) to analyze changes in size of the transplants. Because lichens can change size throughout a single day as they gain or lose water, we took measures to ensure that the lichens were photographed in the same state. First, we waited for dry conditions with no rain for two days prior to photographing. Finally, to account for any humidity differences resulting from microclimate, we sprayed each transplant 15 times with deionized water from a spray bottle to standardize the degree of hydration of the transplants. Preliminary measurements on lichens outside of the experiment indicated that 15 sprays was sufficient for hydration and attainment of a stable wet weight.

Transplant survival

To test for effects of transplant site location on the survival of the lichen transplants, we used a generalized lin-

ear model (GLM) with the binomial family of link functions (function `glmmTMB`; package `glmmTMB`; v. 1.0.2.1; [Brooks et al. 2023](#)) and tested the significance of each predictor with an Analysis of variance (ANOVA). Lastly, we evaluated the fit of each model using the `simulatedResiduals` function in `DHARMA`, an R package for residual diagnostics of GLMs ([Hartig 2016](#)).

Prior to this analysis, we removed one transplant because the branch it was on broke. Presence (1) or absence (0) of a transplant was the response variable in the model. We included the location of the transplant site (within, edge, or beyond) and the time after transplantation (expressed as days after start of the experiment) as predictor variables. The raw data revealed a potential effect of transect on transplant survival at the edge locations, thus “transect” was included as a covariate (Fig. 2a).

Image analysis (relative growth rate)

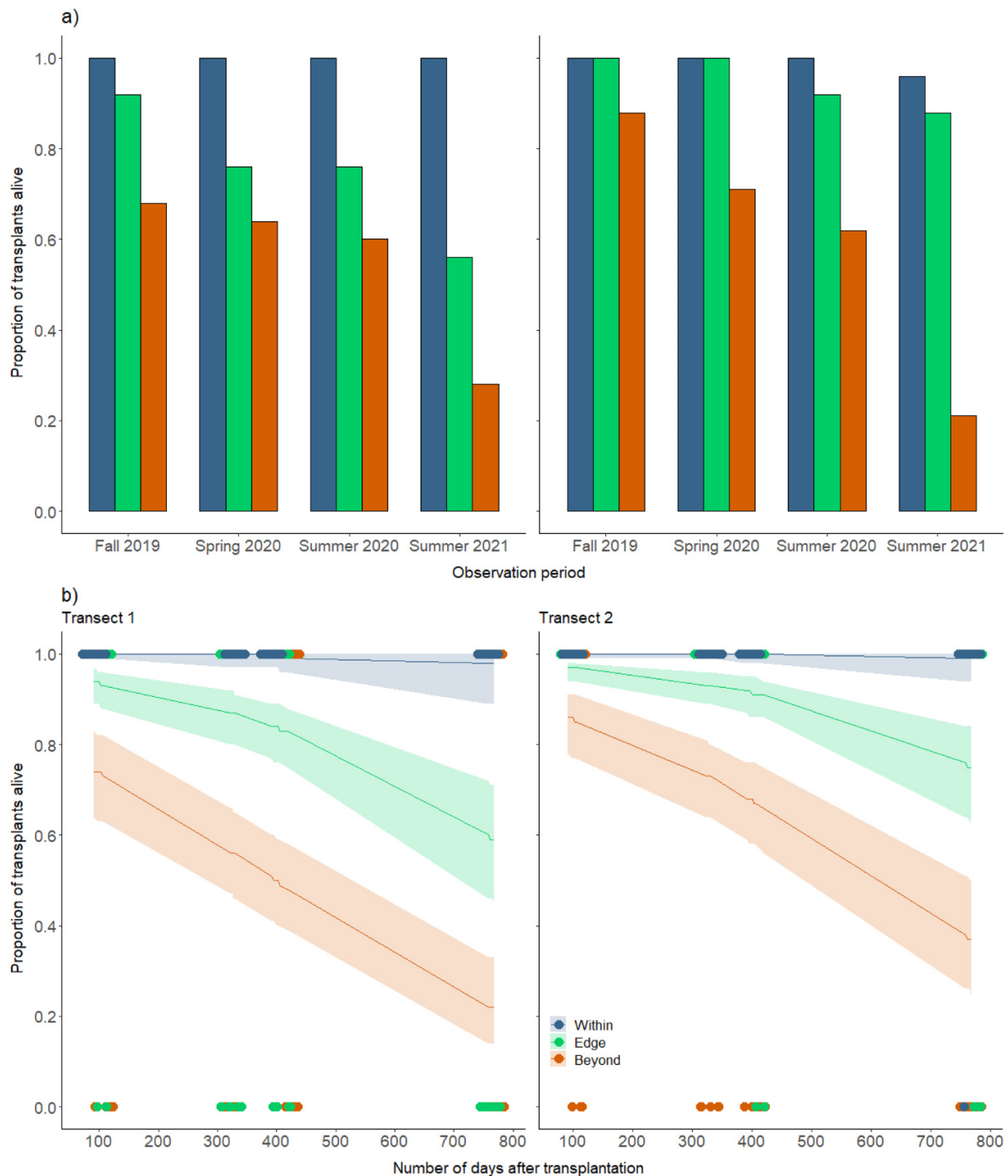
We used `ImageJ` software (version 1.53q) to quantify changes in the size of the transplants over the 2-year period. Prior to this analysis, we removed six transplants from the data set because they had either fallen over backwards and the photos could not be taken in a comparable way between time periods, or because the branch on which the transplant was placed broke. Our methodology for size estimation resembled a digital point frame, mimicking point frames used to estimate percent cover in vegetation plots. We used the ruler in each photo of a transplant to create and overlay a 0.5 cm² grid of open circles (each with a diameter 0.1 cm) on each photo (Fig. S4). Each 0.1 cm circle in which any part of the transplant was present was counted as a “hit”. We estimated size as the total number of hits, averaged across the three photos. We calculated the change in size of transplants as the relative growth rate, by taking the log ratio of the size at a given time (mean across the three photos) and size at the start of the experiment. We calculated the relative growth rate separately for 2019–2020 and 2020–2021, due to different sample sizes given mortality between years. We then used linear models to investigate whether the relative growth rates differed among site locations. We created a different model for each period, including the relative growth rate as the response variable, and site location and transect as the predictor variables; we tested the significance of each predictor with an ANOVA.

Environmental variables

Given the Ghost Antler Lichen's strong correlation with cool and humid habitats, we took hourly air temperature and relative air humidity measurements using Hobo data loggers (HOBO pro v2 Temp/RH; Onset Corporation) during the duration of our experiment, from 4 July 2019 to 8 August 2021, at each transplant site. We placed 2–3 loggers at each site. Prior to analysis, we calculated the daily averages for the within, edge, and beyond locations on each transect (e.g., one daily average for the beyond sites on transect 1 and one for the beyond sites on transect 2, etc.)

We used a linear model to assess temperature patterns among sites. In the model, we included location (within,

Fig. 2. (a) The proportion of transplants alive across locations and transects for each observation period. (b) Logistic regressions showing the relationship between the probabilities of survival of a transplant over time in different locations and transects. Intervals represent 1 standard error above and below the mean.



edge, and beyond sites on each transect), transect (either transect 1 or 2), and season as predictor variables. We defined winter as December–February; spring as March–May, summer as June–August, and fall as September–November. To model

relative air humidity, we used a generalized linear mixed effects models with the beta family of link functions (function `glmmTMB`; package `glmmTMB`; v. 1.0.2.1; Brooks et al. 2023), with the logit transformation, which is recommended for

Table 1. Model results for transplant survival (generalized linear model) and the relative growth rate for 2019–2020 and 2020–2021 (linear models).

Transplant survival, 2019–2021			
Predictor variable	χ^2	Df	<i>p</i>
Site location	57.1	2	<0.001
Days after initial transplant	38.9	1	<0.001
Transect	8.5	1	0.004
Transplant relative growth rate, 2019–2020			
Predictor variable	<i>F</i>	Df	<i>p</i>
Site location	18.59	2	<0.001
Transect	0.007	1	0.93
Transplant relative growth rate, 2020–2021			
Predictor variable	<i>F</i>	Df	<i>p</i>
Site location	7.32	2	0.001
Transect	0.15	1	0.7

continuous proportion data (Warton and Hui 2011; Douma and Weedon 2019).

Results

Survival of transplants

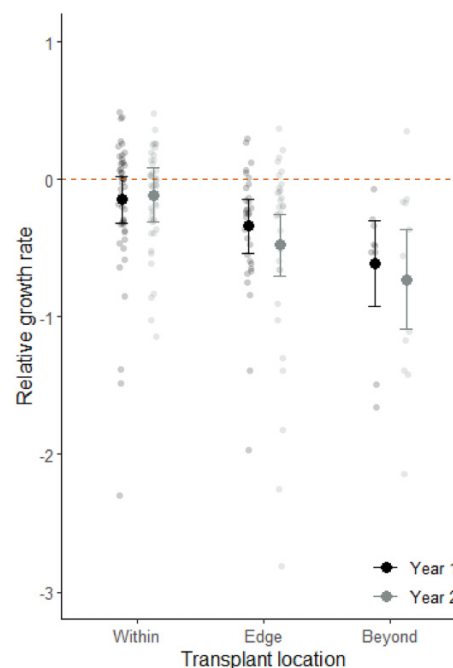
Our GLM (Fig. 2b; Table 1) revealed a clear decline in Ghost Antler Lichen transplant survival moving from within its range at the high elevations to beyond its range at the low elevations. The location of the transplant site (within, edge, and beyond), time after initial transplantation, and transect were significant predictors of transplant survival. At the end of the experiment, 98% of the transplants at the within sites were still present, 72% for the edge, and 24% for beyond. Finally, the effect of transect was most apparent on the survival of the transplants at the edge sites, with 56% of the edge transplants present at the end of the experiment on transect 1, and 88% of the edge transplants present at the end of the experiment on transect 2 (Fig. 2a).

Relative growth rate of transplants

Our linear models (Fig. 3; Table 1) revealed a clear decline in the relative growth rate moving from within the range to beyond for both periods (2019–2020 and 2020–2021). The location of the transplant site was a significant predictor of the relative growth rate of transplants but transect was not. The effect of the location of the transplant site had a greater effect on the relative growth rate from 2019 to 2020 than from 2020 to 2021 (Fig. 3; Table 1).

Site level environmental variables

Air temperature decreased significantly with elevation (Fig. 4a; Table 2). Overall, the annual average difference in temperature between the beyond locations (773 and 781 m) and the within locations (1031 and 940 m) was 1.7 °C. The annual average difference in temperature between the beyond site and edge site (0.7 °C; 850 and 888 m) was roughly 0.3 degrees

Fig. 3. The relative growth rate of transplants in different locations during year 1 of the experiment (2019–2020; black) and year 2 (2020–2021; gray). The bars represent 95% confidence intervals, the points represent the raw data, and the dashed red line represents no growth.

smaller than the average difference in temperature between the edge site and the within site (1.0 °C). Temperature did not vary significantly among similar locations on different transects (e.g., there was no difference in temperature between the beyond sites on transect 1 and 2, etc.) (Fig. 4a; Table 2).

For relative air humidity, we found a significant interaction between season and transplant location, revealing that relative humidity was highest at the within site and lowest at the beyond site for all seasons but the summer (Fig. 4b). Second, we observed a significant difference among transects, with the relative humidity lower on transect 1 than on transect 2 (Fig. 4b). During the spring, both beyond sites had significantly lower average air humidity than the edge and within transplant locations (Fig. 2b). Finally, over the course of the experiment, the within site had 101 (transect 1) and 77 (transect 2) more days with an average RH over 82% (the approximate amount of humidity in the air when chlorolichens—which includes the Ghost Antler Lichen—can activate photosynthesis; Phinney et al. 2019) than the beyond locations (Table 3).

Discussion

We tested hypotheses concerning whether the Ghost Antler Lichen is niche- or dispersal-limited along an elevation gradient in Mont-Mégantic in Southeastern Québec. Our results support a niche-limited distribution for this population as both survival and the relative growth rate of transplants declined markedly from within its high-elevation distribu-

Fig. 4. Modeled average temperature (a) and air relative humidity (b) (error bars show 95% confidence intervals) by transplant location and season for 4 July 2019–8 August 2021. The dashed line at 0.82 in (b) represents the point where studies have indicated (Phinney et al. 2019) that the air is humid enough for chlorolichens (which includes *Pseudevernia cladonia*) to use the moisture for photosynthesis.

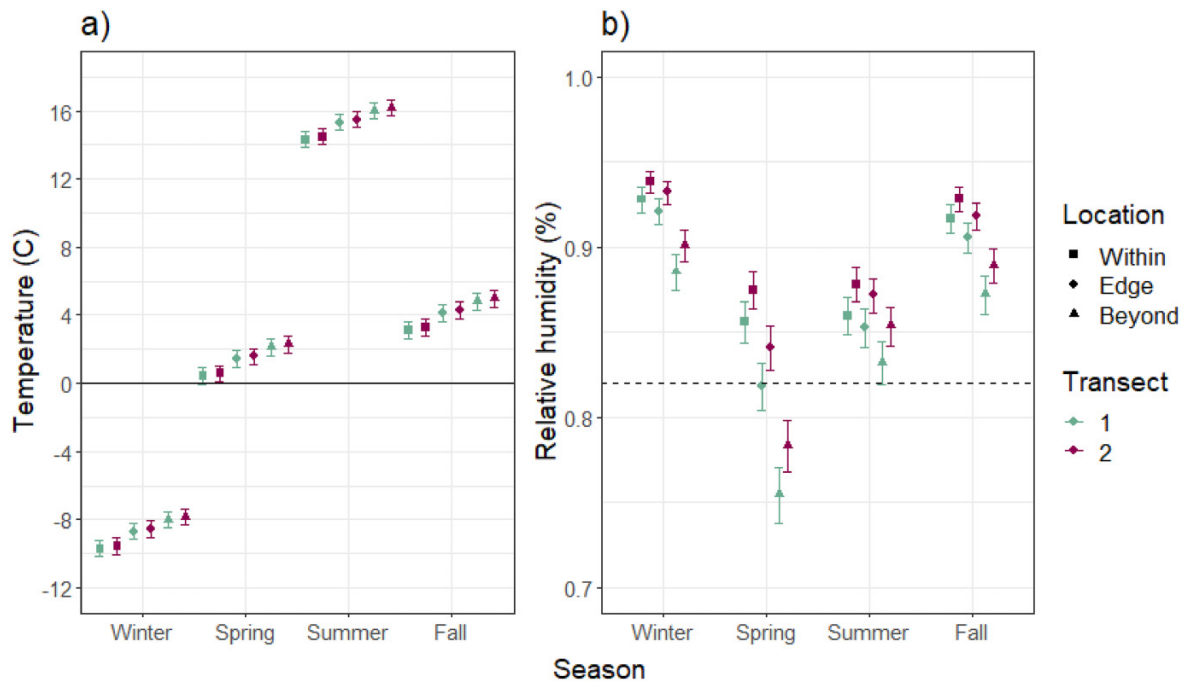


Table 2. Analysis of variance results of linear mixed-effect models (package LMER, F statistics) and generalized linear mixed-effect models (package glmmTMB, χ^2 statistics) predicting site level temperature and relative humidity by transplant location (beyond, edge, and within), season (winter, spring, summer, and fall), and transect (1 and 2).

Model	Effect	df	F	p
Air temperature	Location	2	28.69	<0.001
	Season	3	3002.39	<0.001
	Transect	1	0.7	0.4
		df	x2	p
Air relative humidity	Location	2	195.38	<0.001
	Season	3	643.04	<0.001
	Transect	1	35.53	<0.001
	Location:Season	6	28.72	<0.001

tion, to the edge, and beyond its distribution (Figs. 2 and 3; Table 1). These results suggest that environmental conditions within its high-elevation mountaintop habitat are the key to understanding the distribution limits of this species.

The Ghost Antler Lichen is strongly associated with cool, humid habitats, and our climatic data confirms that its high-elevation habitat at Mont-Mégantic is cooler and has a higher relative air humidity during most of the year than the edge and beyond sites (COSEWIC 2011) (Figs. 4a and 4b). The Ghost Antler Lichen is a “shrubby” fruticose lichen with a trebouxoid green-algae photobiont (COSEWIC 2011). Typically,

lichens with these characteristics are efficient at utilizing water vapor from the air at high relative humidity (Lange et al. 1986; Gauslaa 2014) and in cool conditions, which reduce respiration relative to photosynthesis (Palmqvist 2008). More specifically, many lichens with a green algae photosymbiont activate photosynthesis at ~82% relative humidity, and ~95% relative humidity is particularly important for full photosynthetic activation of shrubby fruticose growth forms (Phinney et al. 2019).

Assessing how growth rates vary across seasons could yield insights into potential future consequences of climate change. Studies have indicated that growth rate does vary according to changing environmental conditions related to the season for some foliose lichen species (Benedict 1990; Muir et al. 1997). For lichens, light availability during humid conditions is important for photosynthesis and growth (Palmqvist 2008). However, too much solar radiation can lower air humidity (Gauslaa 2014), which poses a limitation for the Ghost Antler Lichen. We propose that springtime may be an important period of growth for this lichen, as temperatures are cooler than the summer, and relative air humidity at the within sites and at the edge site on transect 2 is well above 82%, whereas the beyond site is much lower (Fig. 2b). The overall lower relative humidity on transect 1, especially during the springtime, could have contributed to the lower survival of transplants at the edge site on this transect (Figs. 2a and 2b).

As the Ghost Antler Lichen is a mountaintop specialist in Québec closely associated with cool, humid forests, its greatest immediate threat is likely climatic changes affecting its

Table 3. The number of days when the average relative humidity in different seasons and elevations was 82% or higher for each transplant location (beyond, edge, and within) and across transects (1 and 2) (time range: 4 July 2019–8 August 2022; 676 days in total).

Location	Beyond 1	Beyond 2	Edge 1	Edge 2	Within 1	Within 2
Elevation (m)	773	781	850	888	1031	940
Winter	168	169	179	177	181	180
Spring	76	81	85	91	109	112
Summer	138	148	147	145	158	161
Fall	132	139	151	150	167	161
Total	514	537	562	563	615	614

habitat. Studies show that the cloud base is shifting upwards along the Appalachian chain, likely due to global climate change (Richardson et al. 2003). A shift in the altitude of the cloud base could result in increasingly warmer and drier conditions due to reduced moisture input and increasing evapotranspiration (COSEWIC 2011). While these conditions may be favorable to warm-adapted lichens, they will likely have a negative impact on boreal-montane species (van Herk et al. 2002; Aptroot et al. 2021). Although the exact effects on the Ghost Antler Lichen are unknown, experiments with *Evernia mesomorpha*, another shrubby fruticose lichen, showed that increased temperature and reduced humidity was associated with negative impacts, such as loss of mass and physiological functions (Meyer et al. 2023). Moving species to establish, re-establish, or augment populations has been proposed as a means to mitigate threatened and sensitive species faced with declining habitat due to anthropogenic changes (Brichieri-Colombi and Moehrensclager 2016). Our study raises the question of how practical it might be to transplant Ghost Antler Lichens for the population to persist. Transplant experiments of old-growth lichens with dispersal limitations show that they can survive in younger forests (Sillett et al. 2000; Hilmo 2002). A second study of terricolous *Cladonia* lichens transplanted to restore caribou habitat also showed positive results, with the transplants surviving and displaying no or minimal signs of stress 5–6 years after transplantation (Rapai et al. 2023). Our data suggest that transplants can survive if environmental conditions are appropriate (i.e., transplant shock is not a major barrier). However, transplanting niche-limited lichens depends on suitable environmental conditions, which may not exist outside of the current distribution. Furthermore, microclimatic conditions also play a role for species, and considering these conditions is also important for successfully identifying appropriate conditions for transplantation (Brooker et al. 2018). For example, while Ghost Antler Lichen is more strongly associated with northern aspects, it was also found growing at its lower elevation limit in mossy, cool microhabitats on southern aspects (COSEWIC 2011). Detailed measurements of both macro- and microscale climatic factors will be important for any future translocation efforts.

For a translocation effort to achieve long-term success, individuals need not only grow but also reproduce (Allen 2017). Our results indicate that the mean relative growth rate of the transplants at the within site declined the least, but the

average was still slightly negative (Table 1; Fig. 3). This tendency may be due to the slow growth rate and recovery of lichens after transplant shock (for the transplants that survived the first year of the experiment, we observed some form of stress, either discoloration or sections of thallus detaching, on about half of them). A similar phenomenon was seen with transplants of a red-listed lichen, for which shock was most severe during the first year but leveled off afterwards (Bjelland 2023). At the end of our experiment, we observed that at within sites the thalli of 35 transplants (out of 50 total) were attached onto branches of the host tree (i.e., not part of the branch transplant with the lichen). In contrast, we observed this phenomenon on only 17 transplants at the edge sites and 3 at the beyond sites. These observations suggest that despite the shock of transplanting, when the conditions are favorable, the Ghost Antler Lichen can re-establish itself. However, longer term studies are needed to assess reproduction (i.e., establishment of new individuals), and full reestablishment may take many years.

Our study had some limitations. First, we placed our transplants about 30–40 cm closer to the trunk than from where we collected them (~50 cm). Different microclimatic conditions closer to the trunk may have affected the fitness of the transplants. We also removed other lichens and occasionally bryophytes from our transplant branches, which may have altered interactions that influenced the microclimate of the transplants. Finally, balsam firs at lower elevations may also have different exposure to sun and different bark pH, as they are mostly surrounded by deciduous trees rather than other conifers, which may have had an influence on the transplants.

Other mechanisms not addressed here should be addressed in future distribution studies of the Ghost Antler Lichen and other high-elevation specialists. We did not address the influence of biotic interactions on range limits; however, a meta-analysis of transplant studies (mostly of vascular plants) along elevation gradients noted that biotic interactions may be more influential on a species' range limit at the more species-rich lower elevations than higher elevations (Hargreaves et al. 2013). For example, competition from a dominant competitor may influence a species' performance at the range edge (HilleRisLambers et al. 2013). Observations suggest that the Ghost Antler Lichen might be a weak competitor, as few other lichens are present on twigs colonized by the Ghost Antler Lichen; perhaps it tolerates a character-

istic of the twig microhabitat that is unfavorable for other lichens (COSEWIC 2011). Future studies addressing the role of interspecific and (or) intraspecific competition could advance our understanding of the Ghost Antler Lichen's within-tree and altitudinal distribution limits. In Québec, the Ghost Antler Lichen is principally limited to mature forest stands (COSEWIC 2011), thus forest stand age may play a role in determining its distribution in other sites. Finally, the possibility of an interaction between the niche and dispersal limitations warrants attention. There are several disjunct subpopulations of the Ghost Antler Lichen throughout the Appalachian Mountains, and it has been observed as far south as the Caribbean (COSEWIC 2011; CNALH 2024). It is possible that subpopulations of the Ghost Antler Lichen are restricted locally by climate and regionally by dispersal limitations. Specifically, it is possible that southern populations could be better adapted to the lower elevation condition at Mont-Mégantic than the norther, high-elevation populations.

Conclusion

In this first experimental study analyzing the altitudinal distribution limits of the Ghost Antler Lichen, we have demonstrated that this species is likely niche limited along altitudinal gradients. Its high-elevation distribution seems mostly likely due to the cooler and more humid conditions, though factors such as competition and herbivory may also play a role in determining its distribution and should be considered in future studies. Our findings suggest that climatic changes resulting in warmer and drier conditions in these montane habitats may result in less suitable habitat area for this species. For niche-limited species such as the Ghost Antler Lichen, translocations present a particular difficulty of selecting sites with suitable environmental conditions. However, our study suggests that in favorable conditions, the Ghost Antler Lichen can re-establish itself. In a regional context, high-elevation, humid forest habitats are uncommon in southeastern Québec and our study site, Parc National du Mont Mégantic, is home to a substantial protected population of the Ghost Antler Lichen.

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Data availability

The datasets used for this study are available in the supplementary information. Data were analyzed in R and the code is available on request. You may contact us via GitHub (clrin44) or via email (christina.rinas@usherbrooke.ca or mark.vellend@usherbrooke.ca).

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Competing interests

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjb-2024-0004>.

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