Plant Responses to Climate Change and an Elevational Gradient in Mont Mégantic National Park, Québec, Canada

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Abstract - With steep climatic gradients over short distances, montane ecosystems provide exceptional opportunities to study ecological responses to climate and other environmental changes. Here we present a summary and synthesis of 10 years of research on this theme in a protected area in southern Québec, Canada (Parc National du Mont Mégantic), with ecological conditions closely similar to the northern Appalachians. During the ~150 years since European settlement, anthropogenic disturbance has reduced the abundance of certain taxa (e.g., *Picea* [spruce]), while favoring other taxa that thrive during succession (e.g., *Betula* [birch], *Acer* [maple]). In more recent decades, climate warming (~0.21 °C per decade) appears to have prompted upward elevational range shifts for many plant species, although such responses lag behind changes in climate itself. Experimental studies with seeds and seedlings of *Acer saccharum* (Sugar Maple) suggest that upward range expansion might be constrained by non-climatic factors such as belowground properties and seed predators, while escape from insect herbivores might actually accelerate range expansion. Similar studies with understory plants have not revealed clear evidence of non-climatic constraints on range limits, although some preliminary data presented here suggest a possible role of a lack of microsites with rich, moist soil at high elevation. Current studies focus on the lower elevational range limits of species restricted to mountaintops, such as certain lichens. Vegetation and flowering phenology are also sensitive to climate, and we have found that earlier springs are associated with decreased potential gene flow across populations at different elevations; ongoing studies will determine how differential sensitivity of herbs vs. trees might influence the duration of a high light period in spring in the understory. Overall, we have found clear signals of plant responses to long-term anthropogenic disturbances and recent climatic warming, but considerable uncertainty remains about how climatic and non-climatic factors will interact to determine the future of this montane ecosystem.

Introduction

Few ecotones are as visually striking as those between the temperate deciduous forest and the boreal forest along mountainsides in eastern North America (Fig. 1a). Many such mountains can be found in the northern Appalachians of Maine, Vermont, and New Hampshire, but also at several sites in southeastern Canada

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(Cogbill and White 1991). Climate variation clearly plays a key role in driving elevational shifts in vegetation, as evidenced by a steady decline from south to north in the elevational position of the temperate–boreal ecotone, which occurs roughly at the position where mean July temperature is 17 °C (Cogbill and White 1991). As such, ongoing and future climate warming is predicted to prompt northward and upper elevational shifts in plant species distributions, while the northernmost or highest-elevation species should experience range contractions (Berteaux 2014, Evans and Brown 2017, Iverson et al. 2008, Tang and Beckage 2010). At the same time, regardless of distribution shifts, climate warming is also expected to have important effects on individual plants, in particular their phenology (i.e., the timing of yearly events such as flowering or leaf-out), with potentially important impacts on interactions between populations and species (Parmesan 2006, Parmesan and Yohe 2003, Post 2019).

Climate is not the only environmental variable that changes along elevational gradients in this region (Foster and D'Amato 2015). Soils tend to be deep, fine-textured glacial tills at low elevation and are shallower, rockier, and richer in organic matter at high elevation (Demers et al. 1998, Lee et al. 2005). Some studies indicate that the dominant deciduous tree species near the ecotone, *Acer saccharum* Marsh. (Sugar Maple), appears especially sensitive to soil conditions (Leak 1978), such as concentrations of base cations (van Breemen et al. 1997, but see Kellman 2004), and it has been hypothesized that the lack of suitable soil conditions at high eleva-
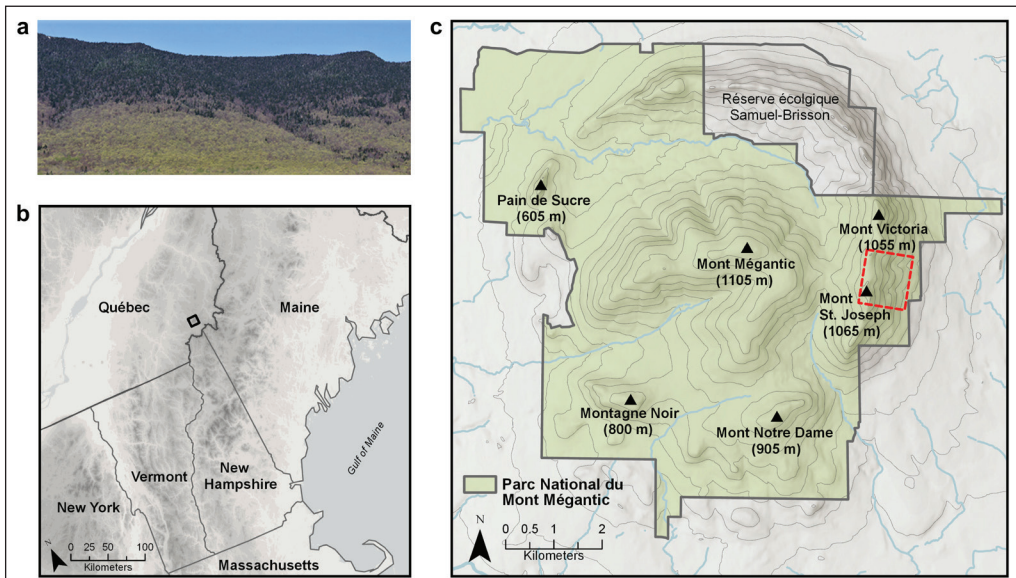

Figure 1. Location and characteristics of the field site. (a) The eastern flank of Mont St-Joseph in spring, showing the Sugar Maple-dominated forest at low elevation (light yellow-green) and fir–spruce forest at high elevation (dark green), with the transition zone at 800–900 m a.s.l. (b) Location of Parc national du Mont Mégantic (black square) in the broader region; (c) Topographic map of the park showing the location of most experimental studies (dashed red rectangle).

tion will limit the capacity of Sugar Maple to colonize sites that become climatically suitable due to warming (Demers et al. 1998, Lee et al. 2005). However, until our recent studies at Mont Mégantic, QC (described in subsequent sections), there were few direct experimental tests of this hypothesis, nor of the broader hypothesis that non-climatic factors in general—such as biotic interactions (HilleRisLambers et al. 2013)—might constrain upper elevational range expansion of Sugar Maple and associated species.

Biotic interactions—between individuals of either the same or different species—can be strongly influenced by phenology (Kharouba et al. 2018, Post 2019), which is itself highly sensitive to climate (Parmesan 2006, Parmesan and Yohe 2003). For example, mating between 2 individuals of the same species (and therefore pollen-mediated gene flow) requires that their flowers are open at the same time, while competition is most direct when individuals are physiologically active at the same time. Consistent with observations in many parts of the world, plants in eastern North American forests generally leaf out and flower earlier in warmer years (Miller-Rushing and Primack 2008, Schwartz and Hanes 2010). Likewise, individuals of a given species tend to flower earlier at low elevation than at high elevation (Lajoie and Vellend 2015, Petrauski et al. 2019). However, little is known about the relative magnitude of climate-driven shifts in phenology at different elevations. If, for example, the relationship between flowering time and temperature is non-linear, then the phenological consequences of a given magnitude of regional warming might vary with elevation. Similarly, when interacting species have different phenological responses to temperature, warming can alter the outcome of interactions (Kharouba et al. 2018, Post 2019). For example, understory plant species that emerge in early spring in low-elevation deciduous forests depend on the short period of high light prior to the leaf-out of deciduous trees such as Sugar Maple (Lapointe 2001), and few studies have asked how climate warming might alter the duration of this period (Heberling et al. 2019).

In this paper, we present an overview and synthesis of 10 years of research concerning how plants respond to environmental variation over space and time in Parc National du Mont Mégantic, QC, which lies roughly 15 km north of where the borders of Maine and New Hampshire meet Canada (Fig. 1b). Geologically, Mont Mégantic and surrounding peaks are the easternmost Monteregian Hills, but ecologically these mountains bear a much closer resemblance to the northern Appalachians, with temperate deciduous forest dominated by Sugar Maple at low elevation giving way to boreal forest on the peaks (Hall 1998, Marcotte and Grandtner 1974). As for other mountains in this biogeographic region, the steep climatic gradients over short distances provide exceptional opportunities to study spatial shifts in species distributions, and other possible responses to climate change, in the 2 dominant biomes of eastern North America. The studies we reviewed from Mont Mégantic, both observational and experimental, focus on historical changes in tree abundance, upward elevational range expansion of Sugar Maple and several understory plants, phenology of flowering and leaf emergence, and consequences for mountaintop species and communities.

Field-site Description

Parc National du Mont Mégantic is a 55-km^2 protected area in southeastern Québec, Canada (Fig. 1b–c). The park encompasses the Mégantic Massif, with Mont Mégantic itself (1105 m a.s.l.) in the center, surrounded by a ring of peripheral peaks. Mont St-Joseph is the second highest peak (1065 m a.s.l.), sitting along an arcing ridge, the eastern slope of which is the focal area of much of the ecological research within the park (Fig. 1c). For convenience, we use "Mont Mégantic" to refer to the entire park, with particular peaks (e.g., Mont St-Joseph) mentioned as appropriate. The climate in the region is characterized by warm, wet summers and cold winters with abundant snowfall (PNMM 2007). Mean annual temperature is ~4 °C at low elevation, with a decline of 0.64 °C for every 100 m of increase in elevation, and an average total annual precipitation of >1000 mm (PNMM 2007). Soils in the park are classified as humo-ferric and ferro-humic shallow podzols (Marcotte and Grantner 1974), and soil properties are correlated with elevation: the top layer of boreal soils is more acidic and has greater C:N ratios and lower nutrient availability compared to temperate forest soils (Carteron et al. 2020).

Northern deciduous forest is the most widespread vegetation type in the park, with the canopy dominated by Sugar Maple, and to a lesser extent *Betula alleghaniensis* Britton (Yellow Birch) and *Fagus grandifolia* Ehrh. (American Beech). In the ecotone between the deciduous and coniferous forests, the dominant canopy species are Yellow Birch, *Abies balsamea* (L.) Mill. (Balsam Fir), *Picea rubens* Sarg. (Red Spruce), and *Betula papyrifera* Marshall (Paper Birch). Just beyond this ecotone are the upper elevational limits of Sugar Maple and several associated understory species such as *Trillium erectum* L. (Red Trillium), *Claytonia caroliniana* Michx. (Spring Beauty), and *Streptopus lanceolatus* (Aiton) Reveal (Rose Twisted Stalk). Limited to high elevation (>900 m a.s.l.), the boreal forest is dominated by Balsam Fir, which frequently grows with Red Spruce, Paper Birch, and *Sorbus americana* Marshall (American Mountain Ash). At the highest summits, the canopy is almost exclusively composed of stunted Balsam Fir, where individuals rarely exceed 10 m in height and standing dead individuals are common due to insect outbreaks (Filion et al. 1998). In essence, Mont Mégantic represents the middle portion of the generic elevational gradient described for eastern North American mountains by Cogbill and White (1991), with species from the both the warmest end (e.g., *Tilia americana* L. [American Basswood], *Quercus rubra* L. [Red Oak]) and the coldest end (alpine tundra) largely rare or absent.

The current mix of tree species has been present in the region for roughly the past 8000 years, prior to which boreal and tundra vegetation had been dominant since the melting of glaciers ca. 11,500 years ago (Kesterman et al. 1998, PNMM 2007). Native peoples have been present in the broader region essentially since the retreat of the glaciers, with Iroquois and Abenaki peoples using the areas around, and including, Mont Mégantic for hunting, fishing, and collecting plants, although there is no evidence yet of permanent settlements nearby (Kesterman et al. 1998). People of European origin began settling the broader region (the Eastern Townships of Québec) in the late 1700s, while the area in the close vicinity of Mont Mégantic

was not colonized until the late 1800s. Agricultural land use has been modest in the vicinity of Mont Mégantic, although forestry has been widespread.

Parc National du Mont Mégantic, a provincial park, was established in 1994, although planning (and therefore a degree of protection) began in the 1970s. Prior to park planning, there was a long history of logging within the current park boundaries, with extensive partial logging in the 1960s (PNMM 2007). Areas that were not logged in the 1960s, including the eastern slope of Mont St-Joseph, have either never been logged (a few areas restricted to high-elevation peaks), or have not experienced logging for more than a century (PNMM 2007). Natural disturbances in this region include windfall, ice-storm damage, and outbreaks of *Choristoneura fumiferana* (Clemens) (Spruce Budworm) (Fisher et al. 2013). Additionally, since 1950, the mean annual temperature in southern Québec has increased by ~2 °C, and the region is projected to continue to warm by 1.7–4.6 °C by 2050 (Ouranos 2015). Models specifically for this site indicate an average increase of 0.21 °C per decade since 1970 (Fig. 2).

Long-term Vegetation Change

Vegetation change since European settlement

Early European land surveys combined with modern forest plots provide a unique opportunity to characterize changes over the past ~150 years, a period of
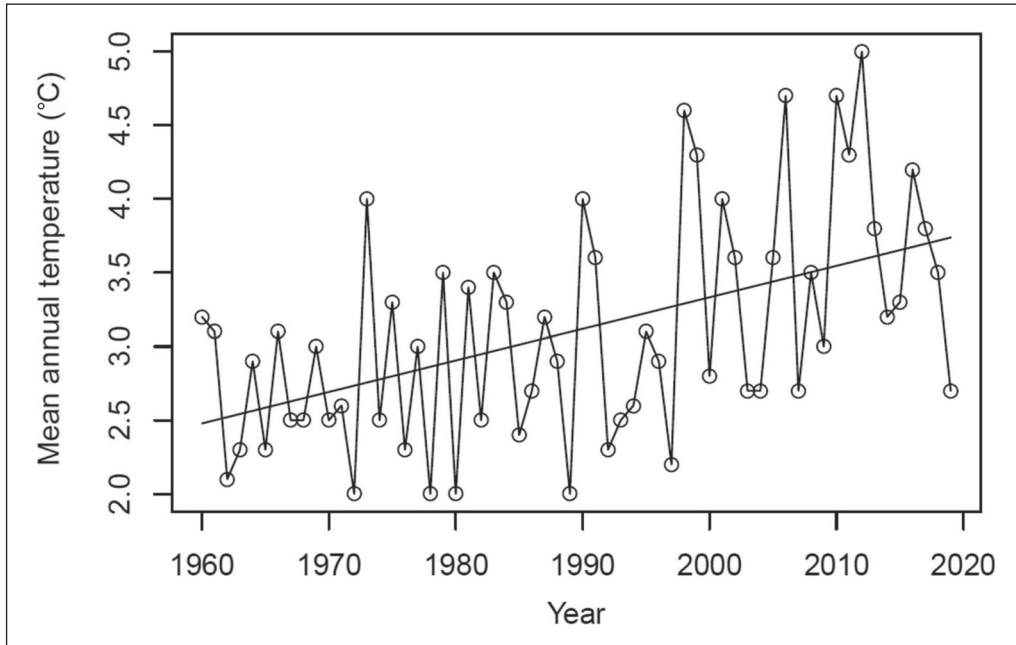

Figure 2. Change in mean annual temperature over time estimated for 700 m elevation in Parc national du Mont Mégantic, using the ClimateNA model (Wang et al. 2019). Output from this model is highly correlated with local weather station data (results not shown), for which we do not have continuous temporal coverage. Linear regression model: Mean annual temperature = -39.36 + 0.0214 × Year.

massive changes in land use, including forest exploitation, in Québec. Danney-rolles et al. (2019) used these data to study temporal vegetation change across all of southern Québec. For the present paper, we compiled data from Danneyrolles et al. (2019) and Savage and Vellend (2015), for an area covering Parc National du Mont Mégantic plus a surrounding buffer out to 6 km, on the presence–absence of tree taxa at survey points prior to 1900 (mostly 1850–1870) and in modern inventory plots (late 1980s–2012). We standardized the number of taxa per observation following methods described in Danneyrolles et al. (2019) and focused on 2 elevational bands that cover most of the park: 500–700 m (*n* = 172 historical points, 130 modern) and >700 m (*n* = 30 historical, 22 modern). Some data are at the species level, while others are at the genus level (e.g., *Acer*, *Picea*)

The most prominent changes over the past ~140 years, in both elevational bands, have been a decline in spruce and an increase in Paper Birch (Fig. 3). Red Spruce and White Spruce have declined throughout much of northeastern North America, including Québec, in recent centuries due to a combination of heavy logging (the timber is prized) and pollution, while Paper Birch is a well-known colonizer following disturbances (Danneyrolles et al. 2020, Dumais and Prévost 2007). At lower elevations, we also see a decline in beech and an increase in maples, which is consistent with trends in the broader region of southern Québec (Danneyrolles et al.
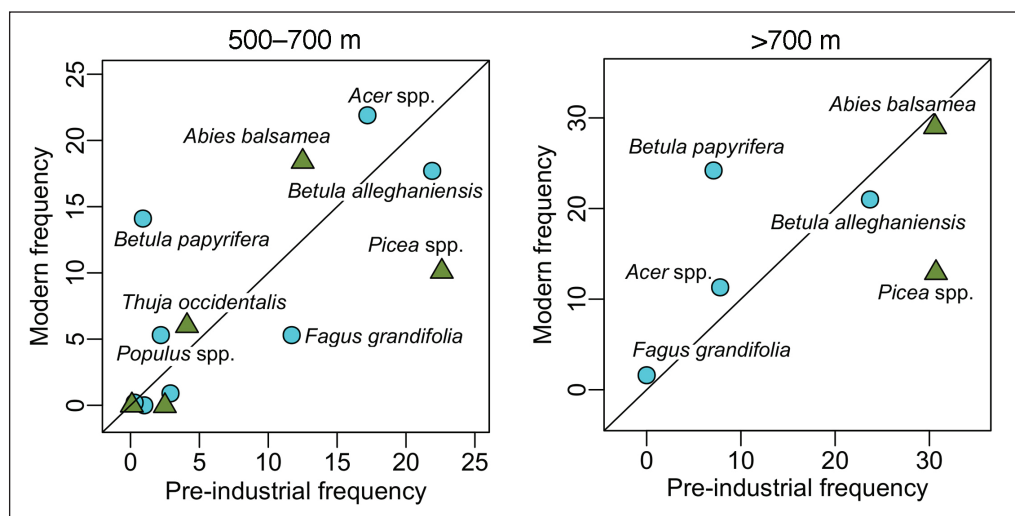

Figure 3. Changes in the frequency of tree taxa over the past ~150 years in Parc National du Mont Mégantic and nearby areas. Pre-industrial data are prior to 1900 (mostly 1850–1870) and modern data are from the late 1980s to 2012. Conifers are shown with green triangles, broad-leaved species with blue circles. The unlabelled species at lower elevation with frequency <5% in both time periods are *Ostrya virginiana* (Mill.) K. Koch (Hophornbeam), American Basswood, *Ulmus americana* L. (American Elm), *Tsuga canadensis* (L.) Carrière (Eastern Hemlock), and *Larix laricina* (Du Roi) K. Koch (Eastern Larch). *T*-tests performed on bootstrapped distributions of preindustrial and modern taxon frequency (99 random samplings with replacement) showed that changes were significant (*P* < 0.01) for all taxa except American Basswood at lower elevation (500–700 m) and Balsam Fir at >700 m. See Danneyrolles et al. (2020) for bootstrapping method.

2019, 2020) and in the northeastern United States, most likely due to disturbance history but possibly to beech bark disease as well (Thompson et al. 2013). While Balsam Fir has also increased at lower elevations, our field observations suggest that this trend is true largely in terms of frequency (i.e., presence of at least 1 individual in a plot), but not local abundance (e.g., total basal area), in that this species is often present but rarely abundant at lower elevations.

Climate warming during recent decades

One of the motivating factors in deciding to set up a research program at Mont Mégantic in 2011 was the availability of historical, georeferenced data on the composition of the vegetation circa 1970 (Marcotte and Grandtner 1974). Forest plants—trees, shrubs, and herbs alike—are almost all long-lived (Whigham 2004), such that responses to environmental change are likely to occur over many decades. But, without the ability to travel in time, in order to assess long-term vegetation change one must rely opportunistically on whatever historical data exist (Vellend et al. 2013). Marcotte and Grandtner (1974) surveyed the vegetation in 94 plots (400 m^2 in coniferous forest, 800 m^2 in deciduous forest), 48 of which fall within current park boundaries, and were re-surveyed in 2012 by Savage and Vellend (2015). The initial vegetation survey focused primarily on undisturbed forest stands, and so we did not expect a strong impact of succession on temporal changes. Our core hypothesis was that vegetation change has been influenced by climate warming, in particular given an especially pronounced upward temperature trend during the period 1970–2010 (Fig. 2).

The core prediction that species distributions have shifted upslope was clearly supported: across species, the abundance-weighted mean elevation of occurrences has shifted upslope by 35.7 ± 6.9 m (Savage and Vellend 2015). The interpretation that these changes are due to climate warming was strengthened by the absence of such elevational shifts in coastal Québec where the warming trend has been weaker (Becker-Scarpitta et al. 2019). That said, distribution shifts have been minimal compared to what warming might predict. Specifically, with temperature declining 0.64 °C per 100 m elevation, these distribution shifts correspond to a change of only ~0.24 °C along the elevational gradient, while the regional climate has warmed by ~0.90 °C. In other words, temperature isotherms (lines connecting points with the same temperature) have likely moved upslope ~140 m, while species distributions have shifted only about a quarter of that distance. One possible hypothesis to explain this difference is simple time lags, given the longevity of forest plants. A second, non-mutually exclusive hypothesis is that there are non-climatic factors (e.g., soil or biotic interactions) that systematically slow or prevent upslope migration of some species. The latter hypothesis has been the focus of several experimental studies described in the next section.

Overall, it is clear that anthropogenic disturbances—logging in particular—have had a major impact on long-term vegetation change by altering the relative abundances of some species, although for the most part, the more common species are still relatively common, and the rarer species are still relatively uncommon

(Fig. 3). Echoing the conclusions of Thompson et al. (2013) concerning forests in the northeastern US, the vegetation has changed considerably while also staying much the same, depending on how the data is evaluated. In recent decades, we see clear evidence of the impacts of climate warming, although shifts in species distributions are not keeping pace with the shift in actual climatic conditions.

Constraints on Upward Elevational Range Expansion

Sugar Maple

If plant distributions are determined by climatic conditions, warming should cause range shifts upward in elevation and poleward (Berteaux et al. 2014, Iverson et al. 2008, McKenney et al. 2007, Tang and Beckage 2010). For plants in northeastern North America, some evidence supports this prediction both for latitudinal (Boisvert-Marsh et al. 2014, Evans and Brown 2017, Sittaro et al. 2017) and elevational gradients (Savage and Vellend 2015), with other studies showing minimal changes over multi-decadal periods (Foster and D'Amato 2015, Leak and Yamaska 2012). However, as described above, the magnitude of plant range shifts—when observed at all—generally appears to lag well behind climate change itself (Boisvert-Marsh et al. 2014, Evans and Brown 2017, Sittaro et al. 2017, Talluto et al. 2017). A major axis of research at Mont Mégantic has addressed the hypothesis that non-climatic factors limit upward elevational range expansion, with a particular focus on the dominant low-elevation tree species, Sugar Maple (Fig. 1a). Along the elevational gradient, experimental sites have been set up within the core of Sugar Maple's distribution (~600–700 m elevation), at the edge of the distribution (~800 m), and just beyond the range edge (~900 m) (Fig. 4).

Perhaps the most obvious non-climatic factor correlated with the elevational shift from Sugar Maple-dominated forest to Balsam Fir-dominated forest is soil. As mentioned in the Introduction and Field-Site Description, high-elevation soils are shallower, rockier, more acidic, with higher C:N ratios and lower cation exchange capacities (a measure of soil fertility) than low-elevation soils (Carteron et al. 2020, Demers et al. 1998, Leak 1978, Lee et al. 2005); in addition, high-elevation conifers are ectomycorrhizal, whereas Sugar Maple is arbuscular mycorrhizal (Carteron et al. 2020). Two experiments have directly tested the effects of these soil differences on Sugar Maple recruitment. First, Brown and Vellend (2014) transplanted 2-L volumes of soil among sites, so that all combinations of soil origin and location (within, edge, and beyond for both) were represented. Sugar Maple seeds planted at the beyond site almost all failed to produce seedlings (more on this below), but at the within and edge sites, there was a significant effect of soil origin, with lower regeneration on soils from beyond the range edge than on soils from within the range.

In a second experiment, after bringing field-collected soils into the greenhouse, Carteron et al. (2020) also found reduced seedling performance in high-elevation soils and went further to disentangle the effects of abiotic vs. biotic soil properties. Adding soil microbes from within Sugar Maple's range to sterilized soils from beyond the range increased seedling performance (indicating a biotic effect), but the

highest performance was found on soils from within the range with their "home" microbes (indicating an abiotic effect). Overall, it appears that the ability of Sugar Maple to regenerate in the high-elevation boreal forest is limited both by non-optimal abiotic soil conditions such as low cation availability, in addition to reduced opportunities for the formation of arbuscular mycorrhizal symbioses (Carteron et al. 2020, Cleavitt et al. 2014, Collin et al. 2017).

Three observations made during the initial experiment reported in Brown and Vellend (2014) pointed to a possible role of biotic interactions (other than mycorrhizae). First, in many of the high-elevation plots, we found the wings of the Sugar Maple samaras we had planted, but not the portions containing the seed. In a follow-up experiment using cages to protect seeds from seed predators (most likely *Myodes gapperi* (Vigors) [Red-Backed Vole]), protective cages allowed almost all seeds to germinate and establish beyond the range edge, whereas almost no regeneration resulted from unprotected seeds (effects of protection were modest within the range and at the edge) (Brown and Vellend 2014). Second, observations of fungal pathogens on the radicle and stem of seedling were more frequent at higher elevation. Third, overall regeneration appeared to be somewhat higher at the range edge than within the range, suggesting some unidentified factor reducing regeneration at the lowest-elevation sites.
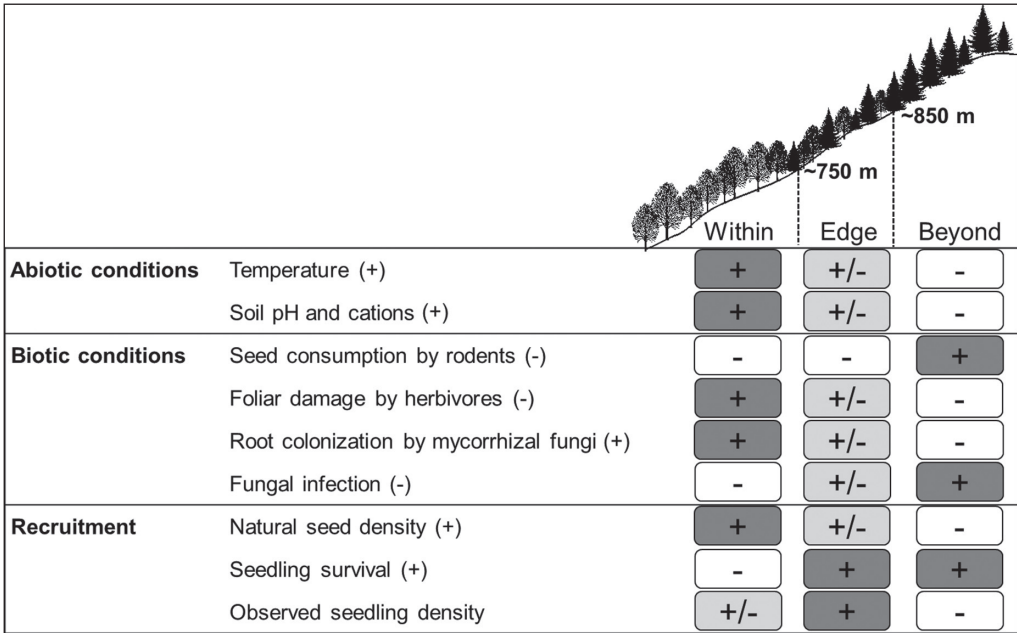
		Within	Edge	Beyond
Abiotic conditions	Temperature (+)	+	+/-	-
	Soil pH and cations (+)	+	+/-	-
Biotic conditions	Seed consumption by rodents (-)	-	-	+
	Foliar damage by herbivores (-)	+	+/-	-
	Root colonization by mycorrhizal fungi (+)	+	+/-	-
	Fungal infection (-)	-	+/-	+
Recruitment	Natural seed density (+)	+	+/-	-
	Seedling survival (+)	-	+	+
	Observed seedling density	+/-	+	-

Figure 4. Variation in abiotic and biotic variables along the elevational gradient of Mont St-Joseph, at sites within Sugar Maple's elevational range, at the edge of the range, and beyond the range. The expected direction of effect of each variable on Sugar Maple recruitment (+ or -) is shown in parentheses. Relative variation for a given variable along the gradient is indicated by darker shades (and the + symbol) for higher values, and lighter shades (and the - symbol) for lower values. Results are from Brown and Vellend (2014), Urli et al. (2016), and Carteron et al. (2020).

Using a combination of observations and experiments, Urli et al. (2016) confirmed the peak in Sugar Maple seedling survival at the range edge, a pattern dubbed "the happy edge". Sugar Maple shows highly episodic seed production (Cleavitt and Fahey 2017, Houle 1999), allowing us to follow discrete cohorts of seeds and seedlings. For 2011 and 2013 ("mast" years), seed density declined monotonically with elevation, but after 2 years (e.g., the 2011 cohort in 2013), the density of seedlings was highest at the range edge. So, what is killing seedlings at low elevation? Inspired by the related ideas of reduced regeneration near established adults due to enemy pressure (Connell 1970, Janzen 1970) and the enemy-release hypothesis used to explain non-native species colonization (Keane and Crawley 2002), Urli et al. (2016) provided support for the hypothesis that insect herbivores contribute to this higher mortality at low elevation, finding that protection (using nets with a smaller mesh size than the cages discussed above) had the greatest positive effect on seedling survival at these sites. However, even protected seedlings showed lower survival within the range than in the other 2 zones, suggesting an additional factor increasing seedling mortality at low elevation. In addition, seedling survival was highest beyond the range edge, suggesting the possibility of accelerated range expansion if individuals can make it beyond the seed-to-seedling transition.

Overall, these results paint a complex picture of the potential for Sugar Maple to expand its range to higher elevations (Fig. 4). Constraints on upward elevational range expansion appear to include abiotic soil properties, a lack of appropriate mycorrhizal fungi, seed predators, and possibly fungal pathogens. In contrast, a release from enemy pressure (e.g., herbivorous insects) might promote range expansion, as should a warming climate. The 2 results most challenging to reconcile are (i) high seedling survival beyond the range edge in the field (whether protected from insects or not), and (ii) low seedling survival and growth in the greenhouse on soils from beyond the range edge, despite overall positive effects of soil microbes (seedling performance was lowest in sterilized soils). Differences in light—year-round shade at high elevation, seasonally high light at low elevation—seem unlikely to explain higher mortality at low elevation, given that high spring light is favorable to seedling performance (Kwit et al. 2010). Are there soil pathogens reducing survival at low elevation in the field whose effects do not manifest in the greenhouse? Microbes growing on Sugar Maple seedlings vary across the elevational gradient (Wallace et al. 2018), but the ecological significance of this trend is unclear. These questions and many others await future studies.

Understory plants

Trees provide the most visually striking evidence of vegetation change along the elevational gradient (Fig. 1a), but a great many understory plants also show clear elevational distribution patterns. Without any true alpine tundra in the park, all common plant species at high elevation (e.g., *Oxalis montana* Raf. [Woodsorrel], *Coptis trifolia* (L.) Salisb. [Threeleaf Goldthread], *Cornus canadensis* L. [Bunchberry]) are also present at least occasionally at even the lowest elevations. In contrast, many of the understory plants common at low elevations have range edges that stop short of the summits. Of special interest has been the group of plants active

in deciduous forests during the ~4-week period of high light in the understory, after the melting of snow and before leaf-out of canopy trees, given their potential sensitivity to changes in tree phenology (Lapointe 2001). At Mont Mégantic, these species include Red Trillium (whose leaves persist into late summer), and the spring ephemerals Spring Beauty, *Erythronium americanum* Ker Gawl. (Trout Lily), and *Dicentra cucullaria* (L.) Bernh. (Dutchman's Breeches), whose leaves wither shortly after the tree canopy fills in. Do non-climatic factors also influence the range edges of these species?

Unlike most tree species in the region whose pollen travels by wind, most understory plants are insect pollinated. With a shortened growing season and sparsely spaced individuals at higher elevations, Rivest and Vellend (2018) hypothesized that reduced seed set due to insufficient pollen quantity or quality ("pollen limitation"; Knight et al. 2005) might constrain population growth and therefore the potential for upward elevational range shifts. As predicted, experimental pollen supplementation increased seed set for Red Trillium at the range edge (by ~30%) but not at lower elevations, although natural seed set declined with elevation only in 1 of 2 years, and then only by a relatively small amount (~20%). No pollen limitation was observed for Trout Lily at any elevation. Combined with the fact that small changes in fecundity are expected to have only minimal effects on population growth in long-lived herbs such as Red Trillium (Knight 2004), we do not have clear evidence that population growth at or beyond the range edge is likely to be strongly constrained by pollen limitation.

By monitoring individual plants frequently during 1 growing season, Rivest and Vellend (2018) observed herbivory, which—surprisingly—was found to increase sharply with elevation for Red Trillium: from <10% at low elevation to >60% at the range edge. The dominant large herbivores are *Odocoileus virginianus* (Zimmermann) (Whitetailed Deer) and *Alces alces* (L.) (Moose), and by targeting larger individuals, such herbivory can have a strong negative impact on population growth in species such as Red Trillium (Kalisz et al. 2014, Knight 2004), which is a preferred browse species for Whitetailed Deer in particular (Auberson-Lavoie and Vellend 2020). Herbivory on Trout Lily was <10% at all elevations (Rivest and Vellend 2018). Subsequently, Auberson-Lavoie and Vellend (2020) monitored a larger number of Red Trillium plants across elevations for 2 additional years but did not see the same elevational trend in herbivory. Video observations made with camera traps confirmed that Whitetailed Deer were the dominant herbivores of Red Trillium, and herbivory had a clear negative effect on individual plant growth, consistent with other studies (e.g., Kalisz et al. 2014). Most surprisingly, individual growth rates actually increased with elevation, for reasons we do not yet understand.

To date, we have not found strong evidence for stronger or weaker biotic interactions at understory species' elevational range edges, but we now have ongoing studies testing the potential importance of edaphic factors, which we know to vary along the elevational gradient (see previous section; Carteron et al. 2020). Many understory plants show patterns of distribution and abundance that are strongly correlated with soil microsite factors (Gilliam 2014), and species in the genera

Trillium, *Dicentra*, *Erythronium*, and *Claytonia* are sometimes associated with relatively rich soils (Horsley et al. 2008). At Mont Mégantic, informal field observations suggest that spring understory plants are especially common in wet areas such as seeps and creek sides, which are also likely to be rich in nutrients. Such areas are relatively common at low elevations and rare to absent at the highest elevations, and thus might play a role in defining upper elevational range limits. Wet microsites might be favorable due to direct effects of increased water and nutrient availability, or due to indirect effects on snowmelt, which happens earlier in such wet areas (Vellend et al. 2017:appendix S3). As an initial exploratory analysis using 359 presence–absence records for Red Trillium in the park at >600 m elevation (Hall 1998), we found that species' presence was more likely in wet areas (as determined by indicator species) overall, and that the difference was especially large towards the range edge (Vellend et al. 2017:appendix S4).

In the springs of 2018 and 2019, we began a pilot study to explore the hypothesis that upper elevational range limits of spring plants are limited by the availability of suitable edaphic microsites. Along each of 2 creeks on the eastern flank of Mont St-Joseph, as well as along 2 nearby elevational transects away from the creeks, we recorded the approximate abundances of 4 species (Spring Beauty, Dutchman's Breeches, Trout Lily, Red Trillium) in a contiguous set of transect segments, each ~12 m long and 3 m wide.

Among the 4 species, Dutchman's Breeches appears most strongly influenced by creeks across the entire elevational gradient (Fig. 5b), with occurrences along creeks at elevations ≥100 m higher than areas away from creeks. Spring Beauty shows some tendency for increased abundance along creeks at higher elevations (Fig. 5a), while abundance is clearly lower along creeks for Trout Lily across most of the elevational gradient (Fig. 5c). The data suggest no difference for Red Trillium (Fig. 5d). Perhaps most strikingly, these surveys turned up a large wet area at the source of a creek at ~1000 m elevation where all 4 species were present, sometimes at high density. This is a notable outlier in terms of the elevational gradient, and assuming that climatic conditions are typical of that elevation (nothing about the site stands out except the wetness), it does point to the possibility that soil properties rather than climate per se represent an important constraint on upper elevational range limits. More detailed observational studies and possibly experiments are currently being designed to test this hypothesis.

Overall, we have made some progress in understanding some of the factors that might influence the elevational range limits of forest understory plants. We have not found any clear evidence of biotic interactions constraining these range limits, but the possibility that edaphic constraints play an important role is a hypothesis worth pursuing further.

Phenology

Probably the best-documented ecological responses to climate warming have involved the timing of yearly life-cycle events (phenology). For example, climatic warming has led to earlier returns of migratory birds to their breeding grounds in

spring, and earlier emergence and flowering of plants following winter dormancy (Parmesan 2006, Parmesan and Yohe 2003). Despite the general tendency for phenology to respond to climate in predictable directions, individual species and populations vary greatly in the magnitude and sometimes even the direction of their responses (Post 2019), thus prompting considerable interest in how climate warming will impact interactions among species and populations. Our phenological research focuses on the timing of flowering and of leaf-out across the elevation gradient and among different years.
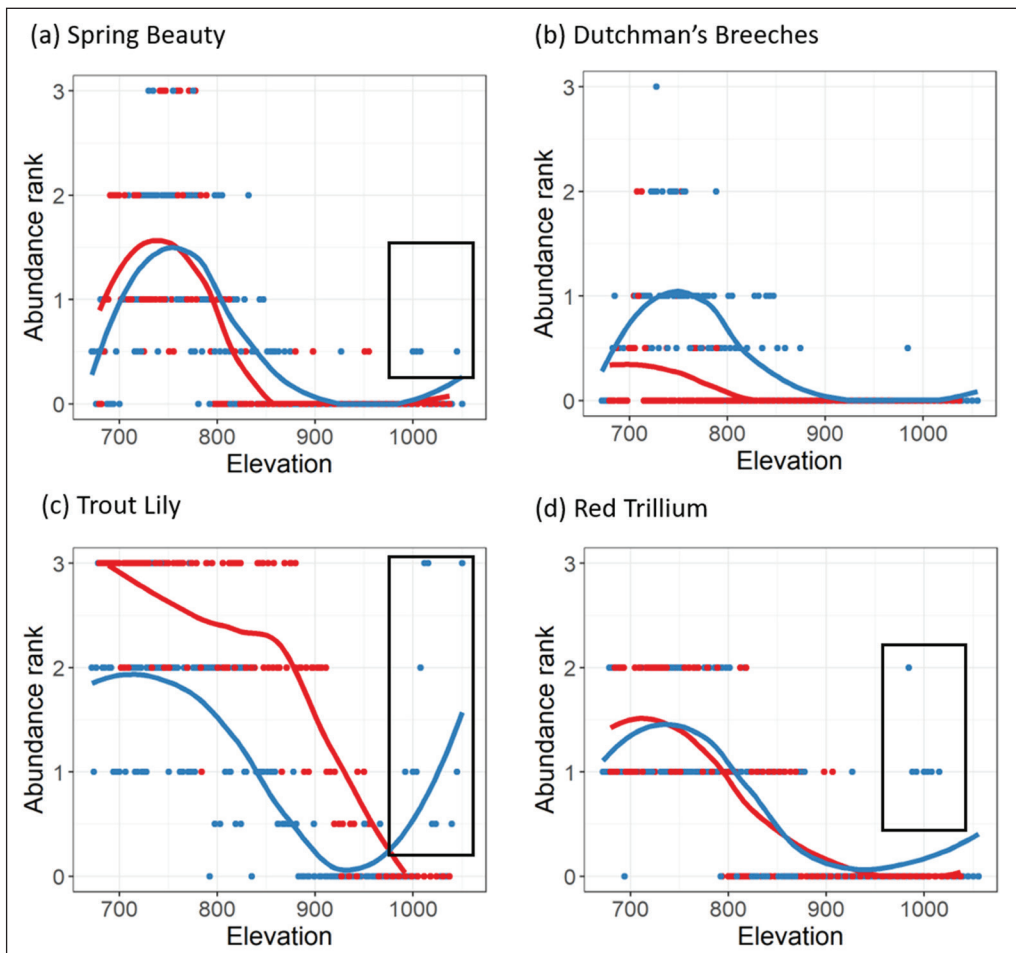
Figure 5. The abundance of 4 understory plant species along the elevational gradient on Mont St-Joseph: Spring Beauty, Dutchman's Breeches, Trout Lily, and Red Trillium. Blue points indicate the observations made along creeks; red points indicate the observations on transects away from creeks. Each data point represents an area of ~12 m long and 3 m wide, and abundance classes were as follows: 0 = 0 individuals; 0.5 = 1–10; 1 = 10–100; 2 = 100–1000; 3 = >1000. For Trout Lily, which grows at high densities, the boundary between abundance categories 1 and 2 was ~500. Lines show locally estimated scatterplot smoothing (LOESS) curves for each relationship (span = 0.75, polynomial = 2; Wickham 2016). Black boxes indicate an unusual wet area at high elevation.

The timing of flowering across space and time

Since 2013, we have monitored plant flowering along the elevational gradient every year, between the start of spring and late summer, roughly twice per week (we do not observe later flowering species, e.g., in the Asteraceae). Our monitoring began to estimate flowering time as a functional trait (Lajoie and Vellend 2015) and has continued in order to test the relative sensitivity of different populations and species to climate change. Along 2 elevational transects, we have recorded the number of flowers of each understory species in 6 plots (104 m^2) along each transect (Rivest et al. 2021). Within a given species, if populations at low vs. high elevation are differentially sensitive to temperature, warming could either cause convergence in flowering times across elevation (thus increasing potential gene flow) or divergence in flowering times (decreasing potential gene flow). This question is of interest given that gene flow is expected to have a major impact on the potential for range-edge populations to adapt to changing conditions (Garant et al. 2007, Kirkpatrick and Barton 1997). For example, if populations at the range edge experience warmer conditions, gene flow from low-elevation populations (where conditions are warmer) could accelerate adaptation.

Using data through 2018, Rivest et al. (2021) found that potential gene flow among populations of Red Trillium was reduced in warmer years (Fig. 6), while no
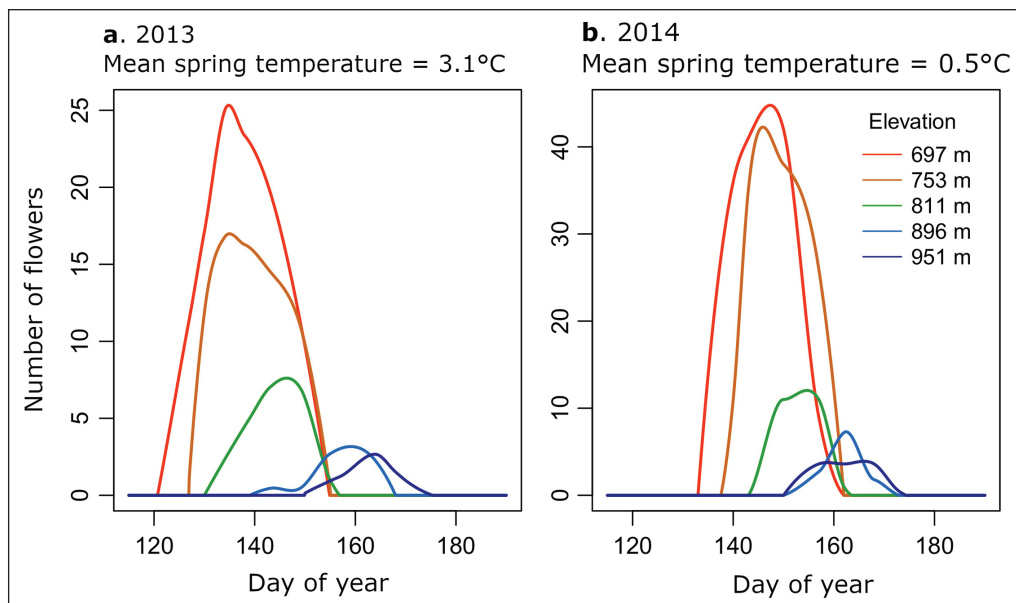

Figure 6. Estimated number of flowers of Red Trillium in 5 long-term phenology plots at different elevations for 2 years with contrasting mean spring (March–May) temperatures for (a) a relative warm/early year (2013) and (b) a relatively cool/late year (2014). Curves were estimated using locally weighted scatterplot smoothing, as described in Rivest et al. (2021), from which we modified panel a. Potential gene flow between low and high elevation populations, estimated based on overlap between flowering curves, was lower in relatively early, warm springs (as in panel a). Temperature estimates come from the same model used for Figure 2.

tendency was found for Trout Lily. For this study, Rivest et al. (2021) developed a new index of potential gene flow that depends not only on the difference in mean flowering times between populations, but also on population sizes and variation within populations, which affect overlap between them (Fig. 6). Assuming random mating on any given day among all the flowering individuals in a pair of populations, the index of potential gene flow for a given population is the estimated proportion of pollination events involving pollen coming from individuals in the other population. The same qualitative result of reduced potential gene flow in years in which plant activity starts relatively early was found using a purely statistical descriptor of overlap, which has been used in other studies of phenological overlap (e.g., Fox 2003). The results suggest that warming will decrease gene flow among Red Trillium populations, potentially impeding adaptation to warming in the highest-elevation populations, to the extent that gene flow from warmer populations could accelerate this process (Garant et al. 2007).

A comprehensive analysis of the best correlates of flowering time, and of variation across populations and species, awaits more years of data, but we can already see clear sensitivity of flowering times to spring temperature (M. Vellend et al., unpubl. data), similar to results for plants elsewhere in the broader region (e.g., McDonough MacKenzie et al. 2019, Miller-Rushing and Primack 2008). Given that temperature over the past 7 years has actually declined on average (it was highest in 2013 and lowest in 2019; Fig. 2), we have not seen the expected advancement of flowering dates over time.

Leaf emergence in the understory and overstory

Understory plants whose leaves emerge early in spring in deciduous forests depend on the brief window of time prior to canopy closure to complete most, if not all, of their yearly photosynthesis (Lapointe 2001). As such, there is considerable interest in the question of whether climate warming will have an influence on the duration of this period. If the vegetative phenology of spring herbs is more sensitive to warming than the phenology of canopy leaf emergence, then warming is expected to increase the duration of the period of high spring light. In contrast, if canopy leaf emergence is more sensitive, warming should decrease the duration of the period of high light. In one of the few empirical studies on this issue, Heberling et al. (2019) used historical records and modern observations in Massachusetts to suggest that tree phenology had advanced to a greater degree than understory plant phenology, thus indicating a reduction in the duration of the period of high light in the understory. However, most understory species in this analysis were not among those active in early spring, and estimates of vegetative phenology relied on an assumption of fixed delays between leaf-out and flowering (historical observations were available only for flowering). Later springs can be associated with more rapid development (Klosterman et al. 2018, Lambert et al. 2010), which could have biased results in the direction found in the analyses. In short, we consider this an open question.

In 2017, we set up a network of cameras in or near our flowering phenology plots to monitor vegetative phenology of 2 understory plants, Red Trillium and Trout Lily, and the canopy trees above them. For understory plants, we have used these

images to measure the relative size of the leaves of individual plants daily in order to characterize emergence and growth, and thus the timing of leaf expansion (e.g., the date at which leaves reached 50% of their maximum area; Fig. 7). Similarly, we have extracted an index of greenness from images of canopy trees to estimate the timing of understory shading, which allows us to directly test whether warming will have an influence on the duration of the high light period for spring ephemeral plants.

The Status of Mountaintop Forests and Associated Species

Most of the research described so far has concerned deciduous forest plants, with a particular focus on how climate warming might prompt expanding distributions.
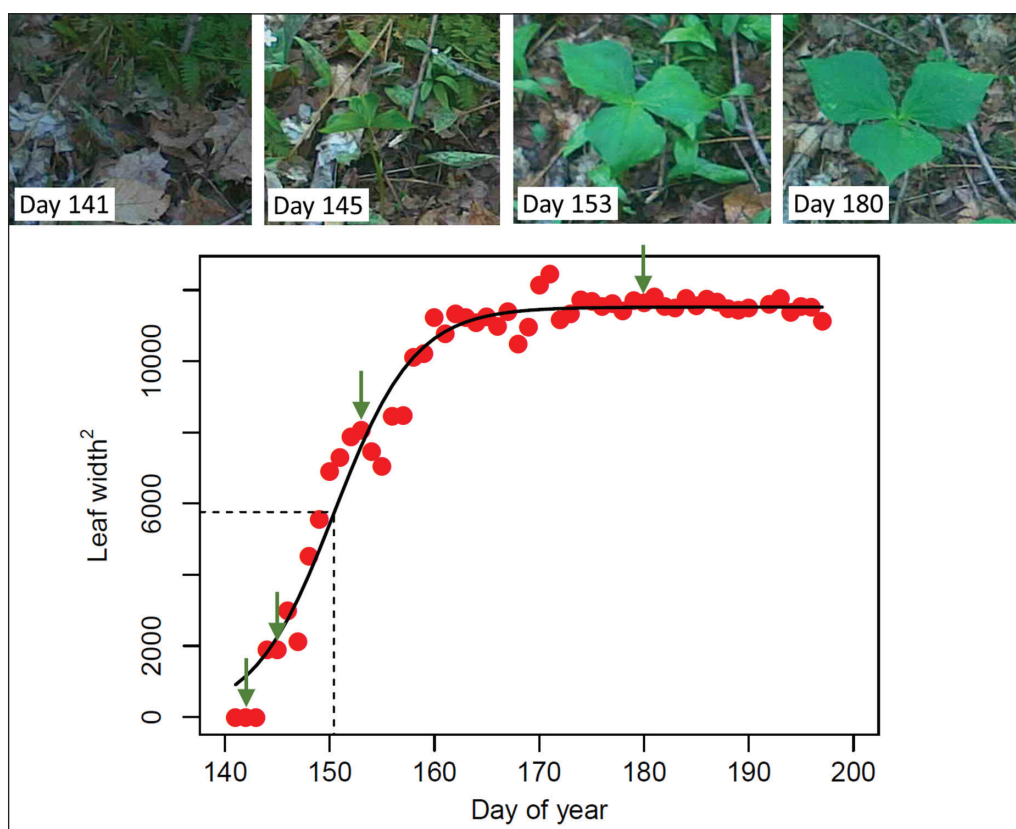

Figure 7. Using size measurements from photographs to estimate the timing of leaf emergence in Red Trillium. Photos were taken using a Link-Evo camera from Spypoint (Victoriaville, QC, Canada); small, cropped sections of 4 photos are shown here, with each photo corresponding to a green arrow in the graph (ordered left to right; note that the plant had not yet emerged on day 141). Using the ImageJ software (Schneider et al. 2012), we measured the width of 1 leaf in each image in arbitrary units (doubling the value of a half-width if the full leaf was not visible) and used width^2 as a size estimate proportional to leaf area. A sigmoid logistic function was fit to the data: Leaf width^2 ~ 11,520/(1 + exp[-0.261 × (Day of year - 150.4)]). The dotted lines show the estimate of the day of year at which leaf area had reached 50% (this is also the third estimated parameter in the model, 150.4).

For species restricted to the mountaintops, however, climate warming might have just the opposite effect: increasingly restricted distributions. In a regional context, the high-elevation fir–spruce forest is unique in climate and structure. Orographic lift causes unusually high precipitation at Mont Mégantic, and as for other sites in the northern Appalachians (Cogbill and White 1991, Siccama 1974), a cloud base often enshrouds the summits (Fig. 8a). The resulting forest type is referred to as "perhumid boreal", which is found on high mountaintops in the Appalachians and along portions of coastal eastern Canada and the northeastern US where there is substantial fog input (Clayden et al. 2011).

Many of the mountaintop forests at Mont Mégantic escaped logging, and due to their rarity, old-growth status, and importance for other species, 2 stand types within the park's high elevation coniferous forests have been classified as "exceptional forest ecosystems" (in French: écosystème forestier exceptional; Forêts, Fauna, et Parcs Québec 2020, PNMM 2007). One is the fir-dominated forest type with a high abundance of Woodsorrel in the understory (Sapinière à oxalide des montagnes), and the other is the mix of Balsam Fir and Red Spruce on steep rocky slopes (Sapinière à épinette rouge montagnarde). These forests are the only places in the region where one can find *Catharus bicknelli* (Ridgway) (Bicknell's Thrush), one of the rarest birds in North America (Connolly et al. 2002). Additionally, although few vascular plant species have distributions restricted to the summits within the park, there are a few mountaintop specialists (*Juncus trifidus* L. [Highland Rush],
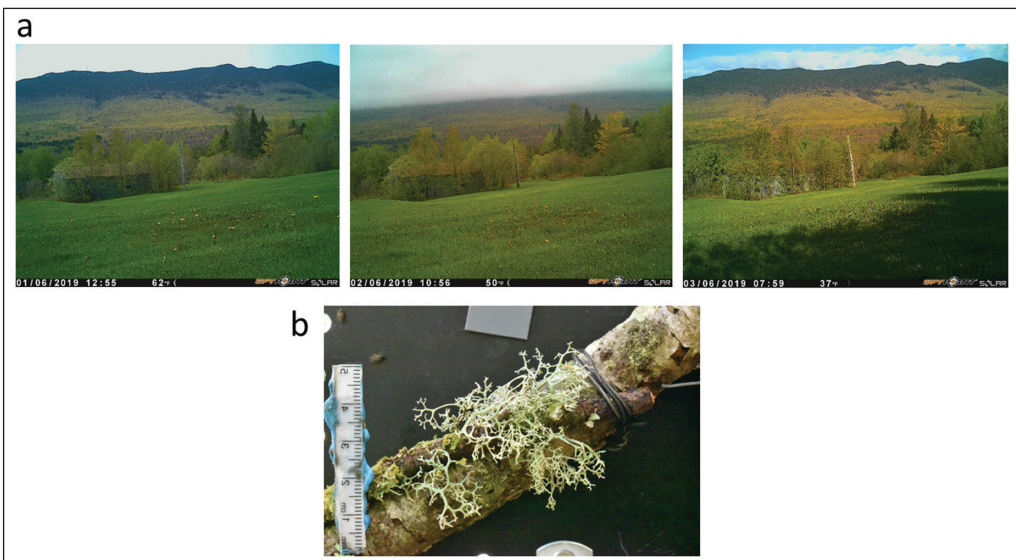

Figure 8. (a) The eastern flank of Mont St-Joseph over three days in early June 2019, showing the common occurrence of a cloud cap covering the summit, roughly down to the deciduous–coniferous ecotone. Photos were taken with a Solar camera (Spypoint, Victoriaville, QC, Canada). (b) An experimental individual of *Pseudevernia cladonia* (Ghost Antler Lichen) which occurs naturally only at the highest elevations; the branch on which the individual was growing was attached to a branch at the transplant site; size changes will be measured using digital image analysis.

Gentianella amarella (L.) Börner [Autumn Dwarf Gentian], *Epilobium hornemannii* Rchb. [Hornemann's Willowherb]; PNMM 2007).

   Importantly, these forests are a refuge for lichens. Many lichens are able to obtain most or all of their moisture needs from fog and air humidity (Nash 2008), which are elevated on mountaintops of the region, in part due to the frequent presence of a cloud cap (Fig. 8a; Cogbill and White 1991, Siccama 1974). Recently, a rare lichen, *Alectoria sorediosa* (Lång ex Räsänen) McMullin & Lendemer, was observed on the summit of Mont St-Joseph (Rinas and McMullin 2020). Lichens have not been well-studied at Mont Mégantic, and we are currently examining their patterns of distribution and diversity. Preliminary results indicate that arboreal lichen diversity in coniferous forests increases with elevation (C. Rinas, unpubl. data). Mountaintop forests are a refuge for some species, such as *Pseudevernia cladonia* (Tuck.) Hale & Culb. (Ghost Antler Lichen; Fig. 8b), which has a disjunct distribution, found in coniferous forests at high elevation in the Appalachians and at low elevation along the coast in maritime Canada and Maine, where air humidity is also high due to coastal fog (COSEWIC 2011). Reversing the direction of our experiments with Sugar Maple, we have initiated experiments at Mont Mégantic with the Ghost Antler Lichen, transplanting individuals to sites within the current mountaintop range and below the lower elevational range limit (Fig. 8b). We hypothesize that the elevated fog and humidity at high elevation restricts the lower elevational range limit, and future studies in which moisture is manipulated directly will be needed to test this hypothesis. Climate warming is expected to raise the base of the frequent cloud cap (Fig. 8a; Richardson et al. 2003), and experimental studies like this can help predict potential consequences with respect to shrinking species ranges.

Synthesis and Projections

   Empirical research necessarily focuses on the past and present, but ultimately we would like to predict what might happen in the future. Will plant species from the deciduous forest continue to migrate towards the summit, pushing boreal-forest species towards local extinction? Or will the thin, rocky soils on the mountaintops continue to support a coniferous forest for many centuries to come? Will the responses of plants to climate warming be gradual and linear, or will changes ultimately accelerate or decelerate? Our research to date provides some clues as to the answers to these questions, while new studies will be needed to improve predictions and to characterize long-term changes in the future.

   Our results indicate that the upward elevational shifts in plant species' distributions lag behind climate warming itself, and it seems likely that part of this lag involves an unavoidable consequence of the long life spans and typically short-distance dispersal of many forest plants (Talluto et al. 2017, Whigham 2004). That is, we might expect continued range shifts even in the absence of further warming. However, our results also point to non-climatic factors that can constrain upward elevational range expansion, such as soil properties or seed predators (Fig. 4). Some of these factors (e.g., mycorrhizae and soil acidity) are clearly influenced by the

dominant trees themselves. If, for example, the effect of soil microbes on Sugar Maple regeneration eventually switches from negative to positive, we might see an acceleration of vegetation changes at high elevation as deciduous tree species begin to increase in abundance. To the extent that the pace of major forest transitions is limited by the low mortality rates of long-established adult trees, we might expect such vegetation changes to also be accelerated by disturbance (Evans and Brown 2017, Svenning and Sandel 2013). Indeed, across a latitudinal gradient in Québec, moderate disturbance appears to accelerate transitions from mixed deciduous–coniferous forest to deciduous forest (Brice et al. 2020), perhaps due to a "short cut" around the purely demographic lags (i.e., by increasing mortality of canopy trees). Experimental disturbances or alterations of forest composition could more directly test these ideas, although this would have to be done outside of a protected area (i.e., not at Mont Mégantic itself).

Changes in the composition of trees are also likely to have an important impact on the understory community (Gilliam and Roberts 2003). Such impacts might be mediated by effects of trees on soil properties or on the light regime. A transition from coniferous to deciduous forest would introduce a period of high light in early spring, thus potentially favoring colonization by spring ephemerals (Lapointe 2001). However, the duration of the high light period will depend on the dominant tree species. At a given elevation, Yellow Birch leaves emerge later than Sugar Maple leaves, such that a transition from dominance of Yellow Birch (more common at high elevations) to dominance of maple (more common at low elevations) would reduce the period of high light. At the same time, under the canopy of a given species, climate warming itself might increase or decrease the duration of the high light period (or have no effect). Continued monitoring of phenology and vegetation change will allow us to test these ideas.

If climate warming permits upper elevational range expansion of species from the deciduous forest, the future of the unique high-elevation habitats and associated species might be in jeopardy (Iverson et al. 2008, Tang and Beckage 2010). However, although we have seen upward elevational range shifts at Mont Mégantic, these shifts have been of modest magnitude and do not directly indicate a contraction of the high-elevation fir–spruce forest. In addition, across many sites in the northern Appalachians, the temperate–boreal ecotone does not appear to have shifted systematically upward in recent decades, with downslope shifts actually as prevalent as the opposite (Foster and D'Amato 2015). There is considerable uncertainty regarding the future position of the temperate–boreal ecotone on mountainsides in this region.

Simply monitoring vegetation changes over time with sufficient spatial coverage to quantify the magnitude of distribution shifts is a major challenge. With roughly 50 plots of 400–800 m^2, we were able to detect an average upward elevation shift across species of the central tendencies of their distributions (Savage and Vellend 2015). However, if a species is present in 15–20 plots in each of 2 time periods, this is not a large enough sample size to allow quantification of the position of the range edge itself. Even estimates of the central tendency (an abundance-weighted

average elevation) come with considerable uncertainty. At least for canopy trees, remote sensing—specifically hyperspectral imagery—is now being used as part of the Canadian Airborne Biodiversity Observatory (https://www.caboscience.org/) to characterize vegetation in the entire park at high resolution (~1–2 m²). This effort will provide a baseline with an exceptional combination of spatial coverage and resolution for monitoring future changes in tree species distributions.

In sum, it is clear that environmental changes of various types—climate warming in particular—have had, and will continue to have, important impacts on the forest ecosystems of Mont Mégantic and other mountains in the region. Some changes are predictable, such as the upslope movement of species' ranges and earlier timing of phenological events like leaf-out and flowering. However, there remains considerable uncertainty concerning the trajectories of individual species, as well as the magnitude and timing of future changes. Continued monitoring and experimentation can help to solve some of the remaining puzzles concerning the patterns and mechanisms of ecological response to environmental change.

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