CAUSES AND CONSEQUENCES OF DEER BROWSING ON RED TRILLIUM
(TRILLIUM ERECTUM) ALONG AN ELEVATIONAL GRADIENT

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Abstract

Models of ecological responses to climate warming predict species’ migration towards higher latitudes or elevations. However, models often neglect non-climatic factors, such as herbivory, that could slow down or prevent geographic range expansion. A previous study in Mont Mégantic National Park (Québec) found that in one year (2016) white-tailed deer browsing of *Trillium erectum* was substantially higher at high elevation than low elevation. Under the hypothesis that deer herbivory could limit upper elevational range expansion of *T. erectum*, here we ask whether (i) herbivory increases with elevation in two additional years (2017-18), (ii) the rate of deer visitation increases with elevation, and (iii) the effect of herbivory on relative growth rates increases with elevation. Contrary to the earlier study, we did not find a significant trend of herbivory with elevation, although there was a weak positive relationship between deer visitation and elevation. We found a strong negative impact of browsing on relative growth rates, but the magnitude of this effect did not vary with elevation. Our results thus do not support the hypothesis that herbivory limits the range of *T. erectum* at high elevation, but herbivory could have a negative impact on populations in general if browsing rate remains high.

**Key words:** distribution limit, prey-predator relationship, altitudinal range, herbivory, population growth, climate change
Résumé

Les modèles de réponses au réchauffement climatique prédisent la migration des espèces vers des altitudes ou latitudes plus élevées, négligeant souvent les facteurs non-climatiques, comme l’herbivorie, qui pourraient ralentir ou empêcher leur migration. Une précédente recherche au parc national du Mont-Mégantic (Québec, 2016) a détecté que l’herbivorie de *Trillium erectum* par le cerf était plus élevé à haute qu’à basse élévation. Notre hypothèse étant que l’herbivorie par le cerf pourrait limiter l’expansion de *T. erectum*, nous cherchons si (i) l’herbivorie augmente avec l’élévation pendant deux années (2017-18), (ii) le taux de visitation du cerf augmente avec l’élévation, et (iii) l’effet de l’herbivorie sur le taux de croissance relatif augmente avec l’élévation. Contrairement à la précédente recherche, nous n’avons pas détecté une tendance significative entre l’herbivorie et l’élévation, bien qu’il y ait une faible relation positive entre le taux de visitation du cerf et l’élévation. Nous avons détecté un fort impact négatif de l’herbivorie sur le taux de croissance relative, sans variation de magnitude avec l’élévation. Nos résultats ne supportent pas l’hypothèse que l’herbivorie limite la distribution de *T. erectum* à haute élévation, mais l’herbivorie pourrait avoir un impact négatif sur les populations en général si le taux d’herbivorie reste haut.

**Mots-clés** : gradient altitudinal, limite de distribution, relation prédateur-proie, herbivorie, taux de croissance, réchauffement climatique
Introduction

One of the many effects of climate warming on plant species is a shift of geographic ranges towards poleward latitudes or higher altitudes (Thuiller et al. 2005; Parmesan 2006; Damschen et al. 2010; Bertrand et al. 2011; Savage and Vellend 2015). However, there is substantial variability in migration rates among species, populations and habitats, suggesting that factors other than warming effects on performance could be playing a role (Barbier et al. 2008; Chen et al. 2011; Brown and Vellend 2014). Such non-climatic factors, such as soil properties, light availability, predation or competition, may need to be considered when predicting responses to climate change, as they could speed up, slow down or even reverse predicted migration rates (Lafleur et al. 2010; HilleRisLambers et al. 2013).

The contribution of abiotic factors in setting cold range limits has been widely studied, often under the assumption that, at high altitude or latitude, abiotic factors are the main drivers of range limits, with biotic factors playing a minor role (Benton 2009; Louthan et al. 2015). Thus, many models predicting range shifts use only climate data (temperature and precipitation), neglecting biotic factors in the models (Brown 1984; Walther 2003; Engelbrecht et al. 2007; Morin et al. 2007; McKenney et al. 2007; Mendoza-González et al. 2013).

Several recent studies emphasize the potential importance of biotic factors in determining species distributions, even at higher elevations and latitudes, and thus the importance of including them in distribution models (Sexton et al. 2009; Speed and Austrheim 2017; Boulangeat et al. 2018; Staniczenko et al. 2018; Benning et al. 2019). Furthermore, studies on the impacts of biotic factors on range limits have focused most often on competition, whereas
predation (and thus herbivory) has been less studied (Sexton et al. 2009). In recent years, some research has focused on predation or herbivory at range limits, but usually via conceptual models and hypotheses (Shevtsov et al. 2013; HilleRisLambers et al. 2013; D’Amen et al. 2018). Empirical data on the topic are sparse (Bruelheide and Scheidel 1999; Maron and Crone 2006). Herbivory (predation of plants) can lead to plant mortality, reduced reproduction or reduced growth (Howe 1990; Knight 2004), such that in a climate change context, herbivory could counter or slow down the colonization of species at the limit of their range (Cairns and Moen 2004; Fagan et al. 2005; Maron and Crone 2006).

Here we report a study of spatial patterns of herbivory by white-tailed deer (*Odocoileus virginianus* Zimmermann) on red trillium (*Trillium erectum* L.) along an elevational gradient up to *T. erectum*’s upper elevational range limit, including tests of potential causes and demographic consequences of the pattern of herbivory. In a recent study at our field site (Mont Mégantic National Park), Rivest and Vellend (2018) observed rates of browsing by white-tailed deer on *T. erectum* varying from <10% at low elevation, up to more than 60% at high elevation (the range limit of the species). Because deer target large *Trillium* plants, and because *Trillium* population growth rates are most sensitive to the survival and growth (or lack thereof) of large plants, such high herbivore pressure at high elevation could potentially lead to important consequences for long-term population growth (Knight 2004; Kalisz et al. 2014), and thus on colonization potential at the range limit of *T. erectum*. In this study, we extend the one-year observations of herbivory patterns in Rivest and Vellend (2018) to two additional years, in addition to assessing the visitation frequency of deer along the gradient, and the consequences of browsing for *T. erectum* growth rates. We studied populations at the low elevation “core” of
Trillium erectum’s distribution and at its upper elevational range limit, where climate change is predicted to permit range expansion.

Trillium erectum is a slow-growing long-lived species (Lamoureux et al. 2002). At our field site, it is one of the most abundant understory plants at low elevation in the deciduous forest, and its abundance declines until sparse at the limit of its distribution, at roughly 900-950 meters elevation a.s.l. (above sea level), in the coniferous forest (Savage and Vellend 2015; Lajoie and Vellend 2015; Rivest and Vellend 2018). The highest peaks within the park are at ~1100 meters.

Intensive browsing by deer can reduce the growth rates and survival of many forest plant species (Russell et al. 2001; Côté et al. 2004). For plants targeted preferentially by deer, including Trillium spp. (Augustine and Frelich 1998), browsing can severely limit regeneration or population growth. As such, if the level of herbivory – or the negative impact of a given level of herbivory – are especially high at the limit of T. erectum’s distribution at high elevation, this could slow or prevent population migration into new sites that have otherwise become climatically well suited for the species. Since the 1960s, deer populations in North America have increased sharply, reaching unprecedented densities in some areas (Lesage et al. 2001; Russell et al. 2001; Côté et al. 2004).

Our main objective was to test whether the magnitude or consequences of herbivory by deer on T. erectum increase with elevation, and thus whether herbivory might influence the species’ upper elevational range limit. At the population level (for plants), deer browsing could have a greater negative impact in two ways. First, assuming a negative effect of herbivory on population growth, the level of herbivory itself might be greater at high elevation (as observed
in one year by Rivest and Vellend 2018), either because deer visitation rates are higher at high elevation, or because deer target *T. erectum* to a greater degree at high elevation. Second, even if the level of herbivory is similar at different elevations, the effect of herbivory on plant growth rates might be greater at high elevation under more challenging growth conditions.

We addressed the three following questions: (i) Does the rate of deer browsing increase with elevation up to *T. erectum’s* range limit? (ii) Does the rate of deer visitation increase with elevation? (iii) Does browsing have a negative impact on *T. erectum* growth rates, and is this impact greater at high elevation than at low elevation? To answer these questions, we collected data in 2017 and 2018 on the size, reproductive status, and browsing of individually marked *Trillium* plants, as well as deer visitation frequency, at three different elevations. These data allowed us to calculate individual relative growth rates, and to test the relationship between browsing and relative growth rate.

**Methods**

**Study site**

Field data were collected in 2017 and 2018 on the east-facing slope of Mont Saint-Joseph (Latitude: 45.45, Longitude: -71.12), an area without trails in the eastern portion of Mont-Mégantic National Park (southern Québec), which is protected by the Société des établissements de plein air du Québec (SÉPAQ). The park is surrounded by forests (mostly deciduous and mixed), agricultural fields and villages. Low elevation forests in the park are dominated by deciduous tree species, predominantly sugar maple (*Acer saccharum* Marshall) and also beech
(Fagus grandifolia Ehrhart). At high elevation, the forest is boreal, dominated by balsam fir (Abies balsamea (Linnaeus) Miller), white birch (Betula papyrifera Marshall), mountain birch (Betula cordifolia Regel), and red spruce (Picea rubens Sargent). Between roughly 800 to 850 m elevation, the ecotone is characterized by a mix of boreal and deciduous forests, with a high abundance of yellow birch (Betula alleghaniensis Britton).

*Trillium erectum*

Red trillium (*Trillium erectum* L.) is a perennial plant from the Melanthiaceae family, abundant in the understory of maple forests in southern Quebec (the northern portion of its distribution), and with a geographic range in eastern North America extending to the deciduous forests of the southeastern United States. It has multiple growth stages, starting as one-leaved plants, then three-leaved non-reproductive plants, and finally reproductive three-leaved plants, after multiple growing seasons (Lamoureux et al. 2002). Empirical studies of *T. erectum* have not found reproductive plants younger than 11 years old (approximate ages can be determined using annual leaf scars on the rhizome), which is probably an underestimate of minimum age at reproduction since the oldest sections of *Trillium* rhizomes begin to deteriorate within a decade (Davis 1981; Lamoureux et al. 2002; Broyles et al. 2013). *Trillium erectum* flowers in spring, and its leaves usually wither in August (Lamoureux et al. 2002). Yearly photosynthesis (carbon gain) occurs largely during the first 2-5 weeks of the growing season, before the deciduous canopy has formed (Lapointe 2001). Resources are stored overwinter in a rhizome and used for plant growth the subsequent year (Routhier and Lapointe 2002). If a growing season is interrupted by browsing (typically removal of all three leaves) the likelihood of reproduction
the next year is reduced (Knight 2004; Kalisz et al. 2014). The species has a widespread distribution within Mont-Mégantic National Park. Abundant at low elevations, its abundance declines up to ~900-950 m, beyond which it is absent (the peak is at ~1100 m) (Hall 1998; Rivest and Vellend 2018).

Trillium measurements

We established three plots in the deciduous forest (low-elevation plots, from south to north: 730 m, 714 m, 713 m), three in the mixed forest (mid-elevation plots: 878 m, 801 m, 855 m) and three in the boreal forest (high-elevation plots: 952 m, 897 m, 898 m). The lateral distance between plots at a given elevation was roughly 800-1000 m, and the plots are thus arranged roughly in a 3×3 grid. We refer to each trio of low-mid-high plots as being located in a different “sector”: south, central, and north. In each sector, the elevation of a plot of a given forest type was not fixed in advance, with plots selected according to forest conditions rather than elevation per se. As such, elevation was treated as a categorical variable (low, mid, high) rather than as a continuous variable in the analyses.

For low- and mid-elevations, plots were rectangular, 30 to 50 m long (along elevation contours) and 20 m wide. Sample size in terms of the number of plants (and thus plot size) was determined according to preliminary data. Because Rivest and Vellend (2018) found that fewer plants were browsed at lower elevations, in order to achieve at least ~10 browsed plants per plot (~30 per elevation), we aimed to sample at least 300 Trillium plants in each low elevation plot and at least 250 in each mid-elevation plot. At high elevation, Trillium populations are patchy and sparse, such that we established several subplots (respectively 7, 3 and 2) in any areas where
*Trillium* was present (i.e., not only in particular microsites) within an area of roughly 120 meters horizontally (along elevational contours) and 50 meters vertically. Sample sizes per plot at high elevation were 135, 147 and 147 plants, respectively.

For each plant in each plot, we placed a metal tag tied to a 15 cm long nail 5-10 cm from the stem, allowing us to track individuals among years. Each plot was visited every two weeks during the growing seasons of 2017 (8 May – 21 September) and 2018 (10 May – 5 September), with each plant classified as one of the following during each visit:

- Emerging: in early spring, when the plant has started to emerge out of the soil, but leaves are still curled together
- Expanded: plant with fully expanded and undamaged leaves
- Broken: with the stem broken (but leaves not removed)
- Browsed: leaves consumed by an animal; recognizable by a cut stem with no sign of the leaves nearby
- Senesced: withered leaves
- Disappeared: no stem or leaf material found near the tag
- Not found: the tag itself not found
- Failed to emerge: only in 2018, for plants that did not emerge

The two-week interval permitted detection of these differences (e.g., personal observations indicate that it takes more than two weeks for a browsed stem to disappear), while maximizing sample size given logistic constraints. At three time points during the growing season, we...
measured the maximum length and width of one leaf of each plant (allowing estimation of leaf area; see below), and we noted presence or absence of a flower bud at the first time point.

Estimating deer visitation

In order to estimate the frequency of deer visitation, we placed a camera “trap” near each of our nine plots. In order to minimize our own presence near the cameras, they were not set up to view our *Trillium* measurement plots; rather, they were set up within 100 m in closely comparable habitat conditions. We used Spypoint SOLAR Trail Cameras (GG Telecom, Victoriaville, Québec, Canada), which minimize the need for battery changes given a solar panel mounted on the camera itself. The cameras were in place from May to September each year, with installation dates varying among sites according to the timing of *Trillium* emergence (i.e., just after snowmelt). For optimal visibility of the forest understory, cameras were mounted on tree trunks 1.0-1.5 m from the ground, depending on topography and visual obstructions. Cameras were set on high motion sensitivity, taking three photos each time movement was detected, with no lag period between triggers. Presence of an animal in any string of photos (taken back-to-back) was considered as a single occurrence, with more than one occurrence (i.e., multiple animals) in a single photo possible. We used a minimum delay of 5 minutes between photos before we considered an animal in view as a new occurrence. Other studies have used comparable delays (e.g., four minutes in Koerth and Kroll 2000), and in any case 10 minutes was the minimum time we observed between occurrences. We placed ten bamboo poles (1.8 m tall), spaced 2.5 meters apart, along the center line of the field of view of each camera, in order to evaluate the distance between the camera and a given animal. We alternated orange and red duct tape on the
tips of the bamboo poles, with small offsets from the center line, to better distinguish poles. Every 2-3 weeks we downloaded pictures and verified proper camera functioning.

In order to gather qualitative information on the identity of browsing animals and browsing behaviour, nine additional cameras (one within ~200m of each plot) were set up in 2018, in video mode. Cameras were mounted ~30 cm from the ground, in front of a *Trillium* patch. If a patch of *Trillium* was heavily browsed, the camera was moved into a new spot with *Trillium*. Cameras took 30 seconds of video when triggered by a movement, with no lag period between triggers. Cameras were visited every two weeks to upload videos and verify camera functioning.

*Data processing*

Prior to analysis, we removed observations with uncertain status with respect to the contrast in year-over-year growth between browsed and non-browsed plants (the focus of analyses). *Trillium* aerial parts can senesce prematurely for several reasons other than being browsed (e.g., disease, physical damage), and we removed from the dataset such plants that were not available for browsing for the duration of the growing season. However, we included plants that were broken later in season, assuming that they had closely approached their full photosynthetic period for the season. We set a threshold between “early” and “late” season as the date when ≥10% of plants had died at a given elevation (see Supplementary Data Table S1 for date of senescence by site). Following this logic, we excluded any plant categorized as “Disappeared”, “Not found”, or “Broken” early in the season at a given site. Plants that failed to emerge in 2018 were also excluded, given that dormancy and mortality were both possible. From the initial sample, 583 plants were removed in 2017 and 221 in 2018, for a final sample size of 1531 in
2017 and 1896 in 2018. For the RGR (relative growth rate) analysis, we could only use plants retained in both years, such that the final sample size for this analysis was 1250 plants.

**Analysis**

All analyses were performed in R version 3.5.1, using the following packages and versions:
- lme4 1.1-20
- mrds 2.2.0
- ggplot2 3.1.0
- gridExtra 2.3
-plyr 1.8.4
- dplyr 0.7.8
- ggeffects 0.7.0
- mosaic 1.2-14
- car 3.0-2

**Trillium data**

One of our core analyses focused on relative growth rates (RGR) of individual plants and the effect of browsing on RGR. RGR was calculated as log(maximum size 2018) – log(maximum size 2017), with maximum sizes calculated or estimated as follows.

First, as a metric of size, we calculated total leaf area as the product of maximum leaf length and maximum leaf width, multiplied by 1.53, based on an empirical regression model \( r^2 = 0.98 \) developed by Rivest and Vellend (2018). For all plants in the analyses, we had an estimate of the “initial area” for both 2017 and 2018, based on the first measurements taken on leaves after expansion. “Maximal area” refers to the largest area recorded for a given plant in a given year, most often the third of three measurements. For plants browsed prior to the third measurement in a given year (173/1250 plants in 2017; 307/1250 in 2018), we do not have a direct measure of maximal area for that year, but given very strong correlations between initial and maximal area we were able to estimate the maximal area a plant would have achieved had it not been browsed. For all plants with both initial and maximal area measurements, we created a linear
model predicting the log of maximal area based on log initial area, plot identity, year, and all two-way and the three-way interactions between the three variables ($r^2 = 0.74$). Using estimates of the residual variance and of the other parameters from this model allowed us to simulate observations of maximal leaf area for each plant browsed before the third measurement, as described in the next paragraph.

To test the influence of browsing and elevation on RGR, we used linear mixed models (lme4 package in R; Bates et al. 2015) with RGR as the response variable, and with 2017 browsing (binary: yes or no), elevation, and their interaction as predictors; plot was included as a random factor. Average leaf area (across the two years) was included as a variable to take into account the fact that larger *Trillium* plants tend to be preferred by deer and that there were fewer large *Trillium* plants at high elevation. In order to incorporate both the uncertainty associated with the missing maximum leaf area values and the uncertainty associated with parameter estimates in the RGR model, we used a two-step procedure. We first simulated observations for plants with missing maximal leaf area using the maximal leaf area model described previously; each simulated observation was a random draw from a normal distribution with mean equal to the model prediction and variance equal to the model’s residual variance. This formed a complete dataset with the observed values and the added simulated values. We then used a bootstrap approach where we sampled with replacement this complete dataset to estimate parameters in the RGR model. This two-step procedure was repeated 1000 times to derive a distribution of values for each parameter. Significance of each effect was assessed by determining whether 0 was excluded from the 95% equal-tailed confidence interval of each parameter distribution. We also report results from one model using the mean predicted value for plants without direct
observations, with $P$-values calculated according to a type 3 Wald chisquare anova in the car package.

We tested whether browsing varied with elevation using a binomial mixed model with browsing (yes, no) as response variable, elevation, year, and maximal leaf area as predictors, and plot as random effect.

*Frequency of deer visitation*

In order to test the relationship between deer visitation and elevation, we first calculated an index of visitation frequency using counts of the number of deer that passed in front of each camera, the time the camera was active, and an estimate of the detection distance of the camera. We first calculated the effective distance detection (EDD) of each camera, which is defined as “the distance at which the number of animals detected further away equals the number of animals missed nearer by” (Hofmeester et al. 2017). Following the methods of Hofmeester et al. (2017), four models were fit to describe the relationship between the number of deer detected and the distance from the camera (half-normal model without cosine adjustment, half-normal model with cosine adjustment, hazard-rate model without cosine adjustment, and hazard rate model with cosine adjustment) using the mrds package (see Hofmeester et al. 2017). Given comparable fits of the four models, we used the mean predictions across the four models to calculate EDD. The index of deer visitation frequency is the total number of deer counted on a camera, divided by the product of the number of hours the camera was on and the EDD (Hofmeester et al. 2017). We analyzed this index using a linear mixed model (lme4 package) with elevation and year as fixed predictor variables, and plot as a random effect. We compared
this model to a null model (the same model without elevation) with anova. $P$-values were extracted with a type 2 Wald Chi-square anova from the car package.

We also tested if deer visitation was correlated with browsing using a binomial mixed model (lme4 package) with browsing (yes/no) as the response variable, the index of deer visitation and year as predictors, and plot as random factor.

**Results**

Overall, across years and sites, 19.2% of *Trillium* plants were browsed prior to the onset of senescence (Supplementary Data Table S1), and it is likely that white-tailed deer accounted for the vast majority of browsing. In our videos, the majority of *Trillium* plants eaten were browsed by white-tailed deer (a total of 25 *Trilliums* were eaten by deer; 3 by a groundhog, *Marmota monax* (Linnaeus); Supplementary Data Table S2). However, in contrast to the earlier results of Rivest and Vellend (2018), browsing was not significantly related to elevation in our data ($\chi^2 = 1.23, p = 0.53$), although the probability of being browsed varied significantly between the two years ($\chi^2 = 42.34, p < 0.01$) (Fig. 1, Supplementary Data Table S3, S4). In 2017, the central sector had the highest browsing rate while in 2018 it was the north sector.

Browsing had a significant negative effect on the relative growth rate of *Trillium* plants, with browsed plants having a lower relative growth rate than unbrowsed plants (Fig. 2, Table 1, Table 2). On average, unbrowsed plants had positive RGRs while browsed plants had negative RGRs, indicating that browsed *Trillium* tend to decline in size the year after browsing, while unbrowsed
plants tend to increase in size. Unexpectedly, elevation had a significant positive effect on RGR, with no significant interaction between browsing and elevation (Fig. 2).

The deer visitation index was found to be positively, albeit weakly, correlated with elevation when comparing the full model with the model excluding elevation ($\chi^2 = 6.09, p = 0.047$, Supplementary Data Table S5) or when using the type II Wald chisquare anova test ($\chi^2 = 5.96, p = 0.051$) (Fig. 3, Supplementary Data Table S6). This relationship was strongly influenced by a single (but different) plot in each year where visitation was especially high; the central-sector high elevation plot in 2017 and the north-sector high elevation plot in 2018. In each year, the two other high elevation plots had similar browsing rates as the mid and low elevation plots (Fig. 3).

Browsing was weakly positively correlated with deer visitation rate (slope = 0.057, $p < 0.01$), and as for the main model of browsing (Supplementary Data Table S3), this model detected a significant difference between years (Fig. 4, Supplementary Data Table S7).

**Discussion**

The initial motivation for this study was to evaluate if herbivory by white-tailed deer could impact the upper elevational distribution limit of *Trillium erectum*. If the demographic impact of deer is strongest at high elevation, herbivory could constrain upper elevational range expansion, which is otherwise expected due to rising temperatures. Greater overall deer impacts at high elevation could result either from more intense deer herbivory (as observed in 2016;
Rivest and Vellend 2018), or from stronger effects on performance of a given level of herbivory. Our results did not clearly support either of these possibilities.

First, we found that Trillium plants were not more likely to be browsed at higher elevations (Fig. 1), despite some evidence that deer visitation is more frequent at high elevation (Fig. 3). Second, the effect of browsing on RGR was not stronger at high elevation. Since population growth rates of Trillium and other long-lived species are most sensitive to the growth and survival of established individuals (Silvertown et al. 1993; Knight 2004), we interpret RGR as having important demographic consequences.

Our results suggest that the magnitude of the demographic impacts of browsing on Trillium (RGR specifically) is not related to elevation, such that this study does not support the hypothesis that deer browsing influences the distribution limit of T. erectum at this site. However, a more definitive test of this hypothesis might require many years of data. We found a significant (if weak) positive relationship between browsing and the deer visitation index (Fig. 4), and between deer visitation and elevation (Fig. 3). Thus, one might have expected to find a positive relationship between browsing and elevation. It is possible that the relatively small sample size of plots (N = 9), despite having observed >1000 individual plants, and the high interannual and spatial variability in herbivory, prevented us from detecting what is a real relationship. Moreover, we have data for three years (2016 in Rivest and Vellend (2018), 2017 and 2018 in this study), and in one year (2016) we found a 60% browsing rate at high elevation on reproductive plants (<35% at mid-elevation; <10% at low elevation) (Rivest and Vellend 2018). Speculatively, it is possible that years with higher browsing rates at high elevation
happen often enough to cause any nascent populations beyond the range edge to decline. A study of *Trillium grandiflorum*, a species very similar to *T. erectum*, demonstrated that with 50% browsing on reproductive plants, populations would decline 3% yearly (Knight 2004). Similarly, Kalisz et al. (2014) showed that protecting plants from deer, which browsed 26% of plants on average in their study, increased the proportion of reproductive plants.

Nevertheless, deer browsing impacts *T. erectum* growth quite strongly, with browsed *Trillium* showing negative relative growth rates (Fig. 2). This result is consistent with several others and indicates strong evidence for a negative effect of deer browsing on *Trillium* growth (Anderson 1994; Augustine 1997; Rooney and Gross 2003; Knight 2003; Kalisz et al. 2014). Due to our supplementary cameras set in video mode in 2018, we were able to determine that the majority of *Trillium* browsing was caused by deer, and that deer often browse many *Trillium* plants in a patch on a single occasion. We also observed that *Trillium* browsing varied strongly over time: all of the browsing events caught on video occurred in the spring and early summer. When *Trillium* plants began to show signs of withering (normally coincident with fruit formation), plants were typically ignored by passing deer, who were observed browsing on ferns and young maple trees at this time. Across our three years of data available (2016, 2017 and 2018), an average of 25% of reproductive *Trillium* were browsed, and the proportion of browsed plants varied significantly among years and sites. Consequences for population dynamics over the long term are not known, but there is a risk that browsing could lead to population decline at this site, especially if deer density remains high in the region, or if the interannual variation in browsing rate remains high, given that high variation in browsing itself can lead to population decline (Anderson 1994; Beissinger and Westphal 1998; Knight 2003; Huot and Lebel 2012).
An unexpected result of our study was the positive association of elevation with relative growth rates (Fig. 2), despite a marked decline in the density of *T. erectum* with elevation (Rivest and Vellend 2018). We can only speculate on the causes of this result, but it points to some intriguing hypotheses. One possibility could be that low-density populations at high elevation are to some degree released from pressure from enemies (e.g., insects or pathogens), as Urli et al. (2016) found for seedlings of the dominant tree, sugar maple, at the same site. As *Trillium* population density declines with elevation, so might the presence or abundance of enemies, such that plants – once established at high elevation – have better growth than plants at low elevation, where enemy pressure is stronger (Engelkes et al. 2008; van Grunsven et al. 2010). Another hypothesis is that climate warming has already shifted optimal *T. erectum* habitat upslope, with population size and density simply lagging behind. Savage and Vellend (2015) have observed upward elevational shifts of species distributions at this site over the past 40 years, but the magnitude of such shifts (~35m on average) are far smaller than shifts in isotherms. These hypotheses remain to be tested.

In conclusion, we tentatively reject the hypothesis that browsing by white-tailed deer affects *T. erectum* populations disproportionately at the limit of their elevational range on Mont Saint-Joseph, while recognizing the possibility that long-term data might change this conclusion. Considerable uncertainty remains concerning the factors influencing the response of this species and others to climate warming.

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References


Table 1. Median coefficients (with 95% confidence limits) from 1000 runs of a mixed model predicting *T. erectum* relative growth rate as a function of elevation and browsing (with plot as a random effect). Mid and high elevations were tested against low elevations.

<table>
<thead>
<tr>
<th>Variable tested</th>
<th>2.5%</th>
<th>median</th>
<th>97.5%</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Browsing</td>
<td>-0.427</td>
<td>-0.255</td>
<td>-0.085</td>
<td>*</td>
</tr>
<tr>
<td>Mid elevation</td>
<td>0.041</td>
<td>0.117</td>
<td>0.188</td>
<td>*</td>
</tr>
<tr>
<td>High elevation</td>
<td>0.122</td>
<td>0.211</td>
<td>0.305</td>
<td>*</td>
</tr>
<tr>
<td>Browsing×mid elevation</td>
<td>-0.322</td>
<td>-0.082</td>
<td>0.183</td>
<td></td>
</tr>
<tr>
<td>Browsing×high elevation</td>
<td>-0.333</td>
<td>-0.064</td>
<td>0.191</td>
<td></td>
</tr>
<tr>
<td>Mean leaf area</td>
<td>-0.916</td>
<td>-0.113</td>
<td>0.063</td>
<td></td>
</tr>
</tbody>
</table>

* = confidence intervals do not overlap zero.
Table 2. Results from a linear mixed model testing how browsing and elevation influence *Trillium erectum* relative growth rates (see Table 1), using the mean predicted value of leaf area for plants without direct observations.

<table>
<thead>
<tr>
<th></th>
<th>$x^2$</th>
<th>df</th>
<th>$P$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Browsed</td>
<td>91.70</td>
<td>1</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Elevation</td>
<td>10.01</td>
<td>2</td>
<td>0.007</td>
</tr>
<tr>
<td>Mean area</td>
<td>0.07</td>
<td>1</td>
<td>0.790</td>
</tr>
<tr>
<td>Browsed×elevation</td>
<td>0.94</td>
<td>2</td>
<td>0.626</td>
</tr>
</tbody>
</table>
**Figure captions**

**Fig. 1.** Variation in the proportion of browsed *Trillium erectum* plants among elevations and sectors on Mont St-Joseph in 2017 and 2018.

**Fig. 2.** Impact of elevation (low, mid, high) and browsing (yes = yellow/light grey, no = red/dark grey) on relative growth rates (RGR) of *Trillium erectum*. Standard deviations are shown in black, standard errors in light red/grey (extremely small given large sample sizes).

**Fig. 3.** Top: Effect of elevation and year on deer visitation, averaged across sectors. Bottom: Effect of elevation and year on deer visitation in different sectors and years.

**Fig. 4.** Relationship between deer visitation and the proportion of browsed *Trillium erectum* plants in each plot, for the years 2017 and 2018.
The figure shows the deer visitation index at different elevations and sectors for the years 2017 and 2018. The elevations are categorized as Low, Mid, and High, and the sectors are South, Center, and North. The data is represented using bar charts, where the y-axis indicates the deer visitation index and the x-axis shows the elevation levels.