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Thaw circles around tree trunks provide spring ephemeral plants with a big head start on the growing season

Where winter lasts half the year, naturalists rejoice at the sight of early spring plants emerging from the cold and damp forest floor: the first sign of the imminent and long-awaited eruption of life from above and below. In temperate deciduous forests across the globe, a set of plants known as "spring ephemerals" emerges upon the melting of snow, and immediately enters a race against time. Spring ephemerals in northeastern North America, such as spring beauties (*Claytonia caroliniana* Michx.) and trout lilies (*Erythronium americanum* Ker-Gawl.), have only a month or so of high light during which to complete all or nearly all of their yearly photosynthesis, before the leaf-out of canopy trees cuts off their light supply. Extending or contracting this brief window of opportunity by even just a week would, therefore, represent a substantial change to the length of their growing season (Lapointe 2001).

On 19 April 2017, we walked with snowshoes on top of about 50–70 cm of snow to the prospective location of a new field experiment in Parc national du Mont Mégantic, a protected area in southern Quebec, Canada, about 15 km north of the border with New Hampshire and Maine, USA. The low-elevation forest here is dominated by sugar maple (*Acer saccharum* Marsh.), with minor components of American beech (*Fagus grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britt.). Upon entering the forest, we were immediately struck by circles of bare ground extending about one trunk's width out from the edges of most medium-sized to large trees. Interestingly, the depth of snow did not increase gradually with distance from the trunk; rather, snow-free ground abutted up against near-vertical walls of snow upward of 50 cm high. More importantly for this story, plants of several species, including spring beauty, trout lily, and red trillium (*Trillium erectum* L.), the latter of which emerges in early spring but with leaves that remain green through midsummer, were emerging in these "thaw circles" (a term we borrow from Veblen et al. [1977]). We returned to the site five days later for some high-quality photos (Fig. 1).

During the transition from winter to spring, tree trunks receive direct sunlight, become considerably warmer than the surrounding air, and contribute to relatively early snowmelt in the vicinity of the trunk (Fig. 1; Geiger 1965). Thaw circles have thus been described previously, and the potential impact on the microsite-scale growing season noted (e.g., Brooke et al. 1970). To our knowledge, however, the potentially major impact of thaw circles on the phenology and distribution of spring ephemeral plants has not been studied. Having returned to our field site every few days after the initial visit, we estimate that the onset of the growing season for spring ephemerals (i.e., the time of snowmelt) occurred about a week earlier in thaw circles than in microsites just 1 or 2

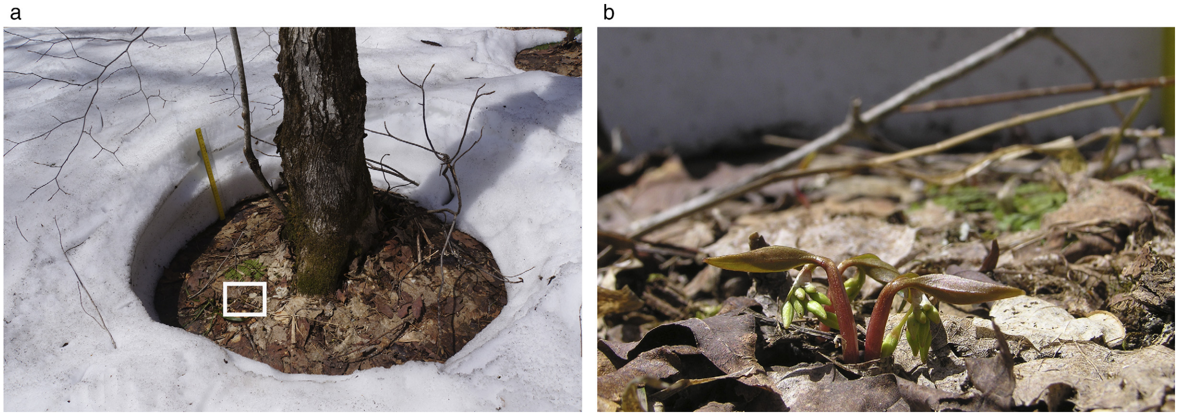

Fig. 1. A thaw circle with emerging spring ephemeral plants. (a) An area free of snow (thaw circle) around the trunk of a sugar maple (*Acer saccharum*) tree and (b) two reproductive shoots of spring beauty (*Claytonia caroliniana*) growing within the thaw circle. The photo in panel b is of a plant growing within the white rectangle drawn on the photo in panel a. The ruler in panel a is 30 cm long. Photos were taken in Parc national du Mont Mégantic, Quebec, Canada on 24 April 2017.

m away, and at least two weeks earlier than in the scattered depressions where >10 cm of snow remained until the first week of May. The canopy surpassed ~50% closure by about 25 May, such that thaw circles appear to have provided an extension of at least ~20% to the growing season for the lucky plants that inhabit them.

One of the species most strongly influenced by thaw circles at this site is likely spring beauty. Its leaves emerge earliest upon snowmelt (synchronous with trout lily while red trillium leaves mostly emerge a few days later). The leaves of spring beauty are withered and its seeds are dispersed just a week after canopy closure (Vezina and Grandtner 1965). In our region, it is frequently more abundant near tree trunks than elsewhere (Fig. 2; see also Appendix S2). Compared to summer-green species, spring beauty and other spring ephemerals are clearly adapted to growing under a leafless canopy because they require higher light levels for photosynthesis to exceed respiration and they have higher maximum photosynthetic rates in high light (Sparling 1967). For later emerging species, the most abundant of which at our field site include blue bead lily (*Clintonia borealis* (Aiton) Rafinesque) and whorled wood aster (*Oclemena acuminata* (Michaux) Greene), the period of photosynthetic activity occurs almost entirely after canopy closure and lasts several months. Consequently, we do not expect a major influence of one week's difference in the timing of snowmelt for emergence of these species.

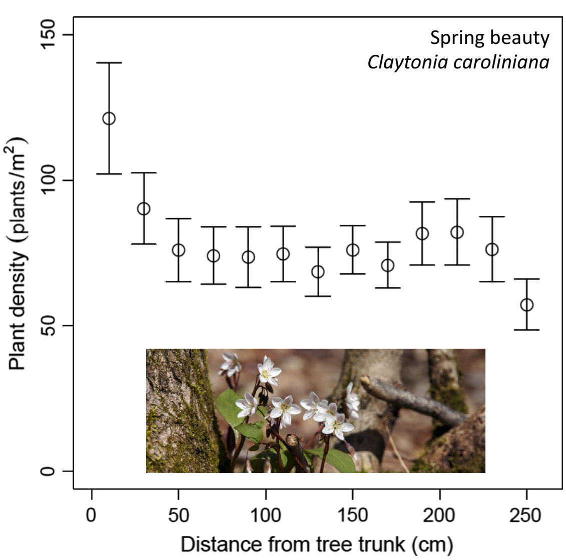

FIG. 2. Density (mean ± SE) of shoots of spring beauty (*Claytonia caroliniana*) in 20-cm segments of belt transects (N = 100), each 50 cm wide and 2.6 m long. Each transect started at the trunk of a different haphazardly chosen tree of at least 10 cm diameter at breast height, extending in a randomly chosen azimuth. Trees were located at elevations between roughly 650 and 750 m above sea level on the east-facing slope of Mont St-Joseph in Parc national du Mont Mégantic, Quebec, Canada. Data were collected during May 2017, after all plants had emerged but before senescence.

Our observations provide a plausible alternative hypothesis to explain results showing altered plant species' abundances in the close vicinity of tree trunks in temperate deciduous forests, as we have observed qualitatively (Appendix S2) and quantitatively (Fig. 2) for spring beauties. In a beech–oak–maple forest in Ohio, Crozier and Boerner (1984) found several plant species to be most abundant within a meter of tree trunks, most notably several species in the early-emerging genera *Claytonia*, *Viola*, and *Hepatica*. In the Great Smoky Mountains of Tennessee, Bratton (1976) also observed increased abundances of two spring *Dicentra* species in the vicinity of trunks of a diverse mix of deciduous tree species. In a deciduous forest in New Jersey, Collins et al. (1984) found increased leaf area and flowering, but not density, of *Erythronium americanum* near tree trunks. In all three papers, the authors considered the potential roles of soil nutrients or water availability, in some cases enhanced at the base of trees via water flow down the trunk ("stem flow"), as potential factors influencing plant distributions and composition. While we don't doubt the possibility that soil properties help explain the observed patterns, we can now offer an entirely different explanatory hypothesis, based on the timing of snowmelt. This hypothesis is testable in a straightforward way via removal and addition of snow to microsites near and far from tree trunks. One could also install dark-colored vertical pipes (and light-colored controls), which should alter the timing of snowmelt via local heating without a major influence on moisture, given the absence of branches from which water is channeled down the trunk (stem flow).

Tree trunks are not the only type of microsite on the forest floor where snow melts unusually early. Many forest herb distributions are influenced by microtopographic "mounds" (small elevations) and "pits" (depressions), which vary according to several environmental parameters, including the timing of snowmelt (earlier on mounds; Beatty 1984). In addition, along the edges of creeks and in small seeps (the latter typically 10–30 m^2 on Mont Mégantic), the presence of liquid water in early spring can melt the snow from below earlier than in surrounding areas (Geiger 1965). At the same time that we observed spring ephemerals emerging in thaw circles, we also found them emerging in such wet microsites (Appendix S3). This realization has generated a novel hypothesis to explain a preliminary observation from Mont Mégantic suggesting that red trillium is more closely associated with wet microsites at its upper elevational range limit (900–950 m above sea level, where it is found infrequently) than it is at lower elevations (600–700 m above sea level, where it is very common; see Appendix S4). To date, we have operated under the working hypothesis that soil moisture itself is the causal, non-climatic factor somehow implicated in defining *T. erectum*'s range limit (see also

Brown and Vellend 2014). It now seems at least as likely that the length of the growing season (a factor most often considered "climatic") is limiting at and beyond the range edge, with wet microsites providing a small but crucial advancement of the snow-free period. This hypothesis is also testable via snow manipulation.

Absorption of solar energy by tree trunks is not the only way in which trees can influence the timing of snowmelt. Evergreen trees have a major effect on the spatial distribution of snowpack development in a forest, reducing snow depth under tree canopies and therefore advancing the timing of complete snowmelt (Brooke et al. 1970, Veblen et al. 1977, Ettinger and HilleRisLambers 2017). Thaw circles under evergreen canopies tend to be larger than those around deciduous tree trunks (Veblen et al. 1977), they are produced largely via a different mechanism, and evergreen forests do not contain light-demanding spring ephemeral plants. Nonetheless, many evergreen forests occur in cold environments where the length of the growing season is limiting for plants (Brooke et al. 1970, Holtmeier and Broll 2010), such that microclimatic variation induced by individual trees is likely to have an important impact in a range of different forest types.

In sum, our natural history observations indicate that the mere physical presence of tree trunks has a major impact on the phenology of spring ephemeral plants. We can further hypothesize that the micro-scale influence of tree trunks and wet areas on growing season length might help to explain plant distribution patterns within forest stands, and potentially even along broader elevational or latitudinal gradients. More generally, it is clear that the temperature and moisture conditions experienced by organisms vary across distances several orders of magnitude smaller than the typical grain size of the climate maps used to model biotic responses to climate change (Potter et al. 2013). Future modeling studies may need to take into account the extent to which habitat features such as thaw circles influence broad-scale species distributions via their effects on microclimate.

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