



Pollen whiskers, rational limits and cryptic refugia: Determining the local presence of spruce on lateglacial landscapes of eastern Canada



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ABSTRACT

The 20% spruce isopoll has traditionally been used to identify the range limit of spruce in eastern North America. Using plant macrofossils and stomates in a network of 25 lateglacial-aged sites throughout Nova Scotia, we identified sites where spruce was locally present but contributed as little as 4% to the pollen rain. Our data suggest that 8% pollen abundance is a more reasonable limit that consistently indicates the local presence of trees. Using 8% to define the presence of spruce, we find that the number of sites likely to contain spruce increases from 3 to 11 as compared to using the 20% isopoll. The resulting increase in the estimated distribution of spruce leads to a reduction in the apparent migration lags and migration rates of spruce into the region. Reducing the error in distribution histories will provide better-constrained estimates of climate change and its impact on the local vegetation.

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1. Introduction

Identifying the point at which trees are first present on the landscape in the paleovegetation record is important for several reasons. These trees may represent the earliest arrivals, marking the onset of conditions suitable to support those trees and help define the climate of the time. Determining with greater precision when the first migrants arrived can reduce the apparent migration lag between trees and climate, a critical step for understanding the effect of climate on the movement of trees (Webb, 1986; Latałowa and van der Knaap, 2006). Of similar importance are the trees surviving in suitable microhabitats within an otherwise inhospitable landscape. In some cases, environmental conditions may not be conducive to sexual reproduction and trees will persist in a vegetative state. These trees, undetectable in the pollen record (Hicks, 2006), can rapidly begin seed production when conditions improve. Persisting in cryptic refugia, surviving trees can explain rapid recolonization rates found after the retreat of glaciers; missing them results in unrealistic migration and colonization rates (Payette et al., 1985; Bennett et al., 1986; Kullman, 2002; Latałowa and van der Knaap, 2006; Kullman, 2008; Ammann et al., 2014). When conditions deteriorate, small numbers of trees can mark the limits of suitable shrinking habitat (Cwynar and Spear, 1991) and constrain the timing of apparent

climate change. Furthermore, trees themselves can significantly affect climate by changing the albedo of the landscape, so knowing when trees are present and physically modifying the landscape is important for climate modelers (Bonan, 2008).

Unfortunately, identifying isolated groups and individual trees is difficult using traditional pollen analysis. Pollen has evolved to be dispersed in two main ways. Insect-pollinated trees produce sticky pollen that is poorly dispersed and therefore seldom deposited in lakes, the most commonly studied repository of pollen. Wind-pollinated taxa have evolved to be easily dispersed over large distances, even into areas where they do not occur. Their pollen may be deposited in advance of a migrating front of trees and appear in a pollen diagram as a whisker that is indistinguishable from pollen deposited by small numbers of local trees (Davis et al., 1991; Moore et al., 1991). Larger numbers of local trees can also create an apparent whisker in the sediment record if they are poor pollen producers. Pollen production varies between taxa by several orders of magnitude (Birks and Birks, 1980; Fægri et al., 1989; Moore et al., 1991; David, 1997).

Trees migrate slowly and may take decades to reach sexual maturity. Consequently, a considerable lag may occur between the earliest arrival of trees on the landscape and the first detectable occurrence of their pollen in lake sediments, although the lag may be small relative to radiocarbon dating errors (Webb, 1986; Williams et al., 2002). Considering delayed reproduction, variation in pollen production and widespread dispersal of pollen into sites that do not contain trees, the question then becomes, "How much pollen must be present at a site in order to conclude that a taxon was actually growing there?"

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1.1. Pollen limits

Since the 1940s, palynologists have been trying to identify the point in the pollen record that indicates a tree is present on the landscape. Different techniques have yielded mixed results that were often later rejected. A thorough history of the presence/absence challenge has been presented by Ammann et al. (2014) and includes the use of the “rational limit”, a term discussed as early as 1949 by Firbas and later defined by Smith and Pilcher (1972) as “the point at which the pollen curve begins to rise to sustained values” indicating the arrival of trees. Although the rational limit is often a good reference for the arrival of trees, early colonizing trees living near their physiological limits can occur in very small numbers and be indistinguishable from the whisker preceding the arrival of trees. By the time the “rational limit” has been reached, some trees have arguably been present for a long time (Bennett, 1985; Kullman, 2008). For some moderate pollen producers, the beginning of the continuous pollen curve (the empirical limit) has been suggested (Ammann et al., 2014) as indicative of the arrival of a species at a site.

In other studies, a numerical limit has been set to indicate the presence of trees. MacDonald and Cwynar (1985) used abundances increasing through 15%, rather than the attainment of “sustained values”, to mark the arrival of lodgepole pine (*Pinus contorta* ssp. *latifolia*) in Yukon Territory. This value has since been refined to 5%, resulting in arrival estimates ~500–2500 years earlier than previously suggested (Strong and Hills, 2013). In the Northwest Territories, Ritchie (1974) found that spruce contributed >15% to the pollen spectra of lake sediments in the forest tundra and 10–14% in the tundra. Spruce (*Picea* spp.) tree line in eastern North America has been shown to correlate with the 20% isopoll (Anderson et al., 1991). This work was based on a 100 km grid using pollen from lakes that reflect regional vegetation (Jacobson and Bradshaw, 1981). Although the 20% limit conforms well to the general position of treeline, itself a broad area (up to 100 km wide) of fluctuating tree abundance, it cannot resolve the limits of individual trees or isolated stands on the landscape. To determine if trees were present on the local (100's of meters or less) landscape scale, we must look to evidence that is locally sourced, such as plant macrofossils and stomates.

1.2. Macrofossils

Size and fragility prevent macrofossils from being transported far from their source (Birks, 1980; Birks and Birks, 1980), except in rare instances of transport by forest fire convection (Pisaric, 2002) or in mountainous regions with open vegetation that permits transport by wind (Glaser, 1981). Plant macrofossils have been used to improve vegetation reconstructions on the local scale, often at treeline, minimizing apparent migration lags found in the pollen data alone (MacDonald and Ritchie, 1986; Peteet, 1986; Davis et al., 1991; Peteet, 1991; Prentice et al., 1991; Clayden et al., 1996; Kullman, 1996, 1998; Pisaric et al., 2000; Gervais and MacDonald, 2001; Ali et al., 2003; Pisaric et al., 2003; Tinner and Theurillat, 2003; Leitner and Gajewski, 2004). For example, Kullman (1995, 2001) dated fossil spruce wood at 2 sites in the Scandes Mountains and found it to be 2000 and 5000 years older than previous estimates for spruce arrival based on pollen. Lodgepole pine macrofossils have been found with 2% pine pollen in southeastern Alaska (Peteet, 1991), suggesting that pine may be present at pollen values significantly below the 15% proposed by MacDonald and Cwynar (1985). *Larix* and *Pinus* plant imprints were found at a high altitude travertine site in the French Alps 100 m higher than previous estimates for treeline history and 2600 years prior to estimates based on pollen evidence (Ali et al., 2003).

1.3. Stomates

Despite the reliability of macrofossils as indicators of the local presence of trees, macrofossils are often absent or rare in lake sediments

(McLachlan and Clark, 2004; Ammann et al., 2014). The absence of a macrofossil is negative evidence that is subject to several interpretations (Ammann et al., 2014); the taxon may indeed have been locally absent; the taxon was present but no plant macrofossil reached the coring site, or the taxon was present and its macrofossils reached the core location but were destroyed by insects or decomposition. The addition of stomate analysis can often fill in the gaps where macrofossils are absent (Gervais et al., 2002). Stomates are generally found in large numbers on the surface of leaves. The lignified guard cells of conifer stomates preserve well, even after the needle from which they came has been degraded, making them potentially more abundant than fossil leaves — the same is not true for the unlignified stomates of deciduous, broadleaved trees. Limited by the same dispersal factors as leaves (a plant macrofossil), stomates provide strong evidence that the source plant was locally present (Hansen, 1995; Clayden et al., 1996; Clayden et al., 1997), although stomates have been found beyond treeline in situations where reworking of older sediments is possible (Leitner and Gajewski, 2004; Clayden et al., 1996). Despite the relative abundance of stomates compared to macrofossils, the interpretation of negative stomate evidence can also be ambiguous and should be approached with caution (Gervais and MacDonald, 2001; Pisaric et al., 2001; Leitner and Gajewski, 2004; Ammann et al., 2014).

1.4. Spruce in Nova Scotia

Black and white spruce (*Picea mariana*, Britton, Sterns and Poggenburg, *Picea glauca* (Moench) respectively) are found throughout present day Nova Scotia whereas red spruce (*Picea rubens* Sargent), is limited to lowland regions. Spruce was among the first trees on the landscape after deglaciation (Mott et al., 1986; Jetté and Mott, 1989; Mayle and Cwynar, 1995).

The 20% spruce isopoll applied to lateglacial Nova Scotia sites suggests that spruce trees were present in central Nova Scotia (Stea and Mott, 1989; Mayle and Cwynar, 1995) during the last few centuries before the onset of the Younger Dryas (12,700 cal BP) with limited northern expansion immediately before Younger Dryas cooling began (Jetté and Mott, 1989). This distribution is very restricted, given that ice had been absent from most of the province since 14,000 cal. BP (Shaw et al., 2006), and may be a minimal distribution considering that spruce macrofossils have been found in the area associated with pollen values <15% (Mayle and Cwynar, 1995).

As part of a larger study examining the distribution of spruce during the lateglacial period, we sought to refine the limits of spruce distribution in Nova Scotia prior to the onset of the Younger Dryas. Here we present data that support the use of plant macrofossils and stomates as a means to refine significantly the pollen limit for the presence of spruce on the local landscape in lateglacial Nova Scotia. These results also confirm that spruce can be present while contributing surprisingly small amounts of pollen to the local pollen rain.

2. Methods

2.1. Field methods

Twenty-five lakes, evenly spaced throughout Nova Scotia, were selected for this study (Fig. 1, Table 1). Small lakes (~200 m diameter) without inflowing streams were selected to ensure the pollen input is dominated by local sources within several hundred meters of the site (Jacobson and Bradshaw, 1981). The Cape Breton Highlands were not sampled because ice covered this region until the end of the Younger Dryas (Stea and Mott, 1998).

All sites were cored using a modified Livingstone piston sampler (Wright, 1967). Cores were taken from the deepest part of each lake for maximum sediment recovery with the exception of Skating Bench Pond and Brier Island Bog; they were cored from the bog surface after sounding for bedrock or clay with coring rods to determine the deepest

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