Chapter 2
Millennial-Scale Disturbance History of the Boreal Zone

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Abstract Long-term disturbance histories, reconstructed using diverse paleoecological tools, provide high-quality information about pre-observational periods. These data offer a portrait of past environmental variability for understanding the long-term patterns in climate and disturbance regimes and the forest ecosystem response to these changes. Paleoenvironmental records also provide a longer-term context against which current anthropogenic-related environmental changes can be evaluated. Records of the long-term interactions between disturbances, vegetation, and climate help guide forest management practices that aim to mirror "natural" disturbance regimes. In this chapter, we outline how paleoecologists obtain these long-term data sets and extract paleoenvironmental information from a range of sources. We demonstrate how the reconstruction of key disturbances in the boreal forest, such as fire and insect outbreaks, provides critical long-term views of disturbance-climate-vegetation interactions. Recent developments of novel proxies are highlighted to illustrate advances in reconstructing millennial-scale disturbance-related dynamics and how this new information benefits the sustainable management of boreal forests in a rapidly changing climate.

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2.1 Introduction

Understanding the complex interactions between abiotic and biotic factors and the impact of these factors on the structure of forest communities across space and time is crucial for emulating natural disturbance regimes in sustainable forest management strategies. Disentangling past relationships between biotic and abiotic factors has historically been challenging. Paleoecological and dendroecological approaches serve as the primary means of reconstructing past dynamics, disturbance regimes, and the biotic and abiotic interactions within boreal ecosystems. Tree rings and the preserved accumulations of peat and lake sediments are the main archives that record past environmental conditions within the boreal region. Tree-ring properties and the preserved accumulations of fossil pollen, charcoal, lepidopteran scales, and spores within peat and sediment records serve as proxies of past environmental conditions. Careful interpretation of these proxy tools and their interactions then provides insight into long-term, i.e., the Holocene, patterns of climate, vegetation, and disturbance regimes. All paleoecological approaches and their proxy tools hold intrinsic advantages and disadvantages; combined, however, they offer a powerful tool for building our understanding of boreal ecosystem functioning.

This long-term perspective holds two major advantages. First, rare disturbances or those having a long return interval—relative to the human lifespan and the existing observational record—require a longer reference period to record their occurrence and importance. Second, we are living in a critical, "non-analog" moment in terms of ecology and climate change; therefore, longer time frames offer the possibility of indirectly observing a wider range of climatic conditions and the related response of vegetation and disturbance regimes. Paleoenvironmental data can guide projections of how changing environmental conditions will affect future forest ecology and disturbance regimes.

From the perspective of sustainable forest management, silvicultural interventions can be placed within the same framework as disturbances (see Chap. 1). The consequences of silviculture on forest structures at various spatial scales depend on the characteristics of the given intervention (see Chaps. 13, 16). If we consider that species have adapted to these natural conditions, understanding how past forest structure and composition have responded to specific disturbances can provide insight into how forest management could be improved to maintain those structural and compositional characteristics necessary for preserving biodiversity. In the boreal forest, fire and insect outbreaks, because of their frequency and potential severity, are the major determinants of boreal forest dynamics. Paleoecological methods able to reconstruct this pair of disturbances are now well established and continue to be refined. In this chapter, we provide an overview of the paleoecological approaches able to decipher past records of fire and insect disturbance. This chapter synthesizes the current state of knowledge related to the long-term records of insect and fire disturbances in the boreal forest. We illustrate the potential of new proxies and demonstrate the importance of millennial-scale reconstructions of disturbances for improving our understanding of current and future forest dynamics. Finally, we explain how this knowledge has implications for forest management in the context of future climate change.

2.2 Fire History Reconstruction

Fire is a major disturbance agent in the boreal forest, and future climate warming is projected to increase its frequency and severity in many parts of this biome. Interactions between climate, fire, vegetation, and, in particular, the forest response to changing fire regimes are difficult to predict because of the long timescales associated with these changes. Thus, reconstructing a regional fire—through documentary, observational, and remote-sensing data—becomes essential for extending time series. Fire histories involve the analysis of fire regime characteristics, i.e., fire occurrence, frequency, areal extent, and severity, over the long term. These fire histories also provide a context within which we can evaluate current fire observations. Given the complex interactions between climate, fire, vegetation, and humans, there is increasing recognition by ecologists, restoration planners, and forest managers of the value of the long-term perspectives provided by paleofire records. Understanding the causes and consequences of fire provides a more solid foundation for developing appropriate management guidelines, mitigating the loss of forest ecosystem services, and improving predictions of future fire activity in a changing climate (Waito et al., 2018).

Climate conditions and vegetation characteristics control fires in boreal forests (Girardin & Terrier, 2015; Krawchuk & Cumming, 2011). In the boreal forest, for example, vegetation flammability and fire propagation rates are higher in needleleaf forest stands than in broadleaf forest stands. Needleleaf forest species produce flammable resins and have a lower leaf moisture content. Human-ignited fires have also strongly influenced vegetation dynamics in these forests over thousands of years; this human influence has shaped the current vegetation and fire activity in the boreal zone (Waito et al., 2018). Moreover, active fire suppression policies in populated regions of boreal Canada during the mid to late twentieth century decreased fire activity, leading to accumulations of forest fuel and a higher risk of future catastrophic fires (Parisien et al., 2020).

2.2.1 Studying Fire Histories at Millennial Time Scales

Fire histories are reconstructed using proxies from two main archives: (1) tree ring−based methods, which rely on fire-induced damage in trees and the age of new (even-aged) postfire forest stands; and (2) fire-related charcoal particles deposited onto−and subsequently buried within−soil, peat, or lake sediments.

2.2.1.1 Tree Rings

In general, forest fire reconstructions using tree rings rely on two primary approaches (Niklasson & Granström, 2000), namely using tree rings to date fire scars and examining the age structure of forest stands. Dating fire scars assesses low-intensity fires, which damage the tree cambium without killing the tree. This damage to the cambium leaves a distinct scar; the timing of the related fire event is then determined from the location of the fire scar in the sequence of annual tree rings (Fig. 2.1). When a fire occurs during the growing season, the scar's location within the annual ring can even be used to date the event at a subannual temporal resolution, distinguishing, for instance, early−, late−, and dormant-season fires. An individual tree can hold numerous fire scars and thus record the geographic location and timing of multiple fires. Samples used for dating fire scars are commonly (and preferably) the cross-section of tree stems; however, where possibilities for sampling are limited, such as in strictly protected forests, increment cores extracted from the stem can be used.

Stand initiation dates based on tree rings provide another means of dating forest fires. This approach relies on the premise that a fire event leads to a pulse of regenerating trees. These pulses can often be observed after surface fires in those stands recording fire scars; however, they are particularly useful for dating high-intensity fires in which no trees survive to preserve fire scars. Aging the cohort of postfire regeneration then gives the approximate year of the most recent high-intensity fire.

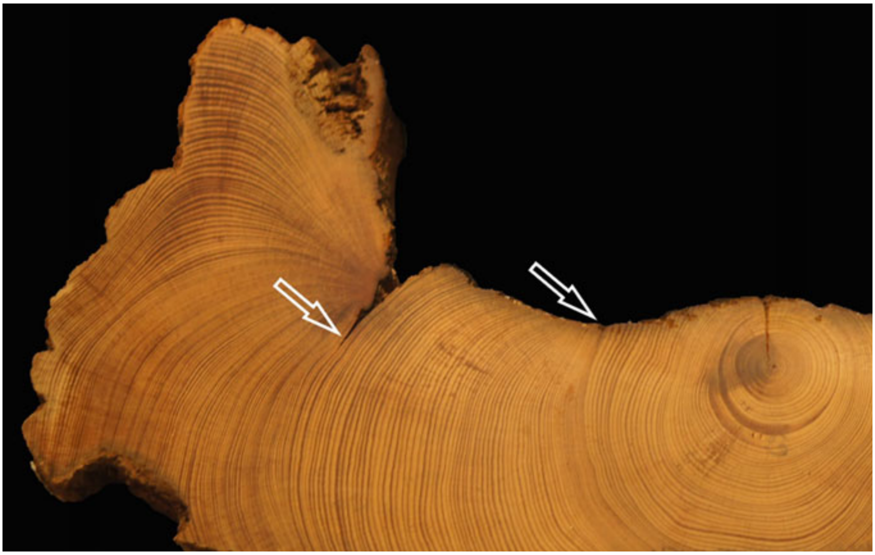

Fig. 2.1 A partial cross-section extracted from a fire-scarred Scots pine (*Pinus sylvestris* L.) collected from northeastern Finland. The *arrows* indicate the locations of fire scars dated dendrochronologically at 1296 and 1227 CE. *Photo credit* Tuomas Aakala

2.2.1.2 Charcoal in Forest Soils

The temporal extent of fire records using stand initiation dates is limited to the most recent fire. This is particularly limiting in locations where the regional fire regime often involves stand-replacing fires. In these conditions, information related to past recurring fires at a given locality can be gained from studying charcoal deposited in forest soils. For this approach, samples of organic matter and mineral soil are collected (Payette et al., 2012). Charcoal fragments greater or equal to 2 mm in diameter are assumed to have been produced in situ; they thus represent local fires (Asselin & Payette, 2005). The fire year is then determined by the radiocarbon dating of a selected number of randomly selected charcoal pieces. Although the temporal resolution of this soil charcoal–based method is rather coarse, it may greatly extend the temporal scale of fire histories initially developed using tree ring–based reconstructions.

2.2.1.3 Charcoal in Lake Sediments and Peat

Lake sediments are natural “hard drives” that record the environmental conditions and events affecting the surrounding landscape over time (Dodd & Stanton, 1990). The stored information in this ecological hard drive must be interpreted using proxy indicators found within the sediment record (Bigler & Hall, 2002; Mauquoy & Van Geel, 2007). An effective paleoindicator must be abundant, easy to identify, and well preserved over sufficiently long periods (see Sect. 2.3.1).

Charcoal originating from forest fires can be transported by wind and water to a lake or peat deposit. These pieces then sink and settle onto the bottom of lakes or fall onto the surface of peat. They eventually become buried and preserved in lake sediments and peat accumulations. These sediments archive past fires and can be recovered by extracting a sediment or peat core. For longer lake sediment records, cores are typically extracted from the deepest portion of a lake (Fig. 2.2). More recent sediments, found higher in the sedimentary record, are closer to the water−sediment interface. These less dense sediments have a higher water content and, as they are more easily disturbed, must be collected separately using a free-falling gravity corer, such as the Kajak-Brinkhurst or Willner-type corer. These separate cores are then correlated against one another to produce a composite record using, for instance, ^{210}Pb or the sedimentary properties recorded within each core. The sampling of lakes is conducted in winter using the frozen lake surface as a platform or using a raft during ice-free months. Peat can be sampled from bogs, mires, forested peatlands (Magnan et al., 2018), or small forest hollows (Fig. 2.3), the latter being paludified depressions inside forest stands (Bradshaw, 1988). Peat sequences are usually extracted using a Russian corer or a Wardenaar sampler.

After their extraction and transport to the laboratory, sediment cores are usually sliced into continuous subsamples that are at least 1 cm^3 in volume. In practice, this typically means subsampling at 0.5 or 1 cm intervals along the core. These subsamples are then processed to recover charcoal particles and, often, related proxy tools, e.g., pollen, diatoms, macrofossils, and sediment samples for loss-on-ignition

Fig. 2.2 (*left*) Winter sampling of lake sediments of Lake Huard, Ontario, Canada. Raynald Julien, Adam A. Ali, and Hans Asnong are present in the photo. (*right*) Sediment (gyttja) recovered from Lake Araisu, Latvia, showing varves (annual laminations). *Photo credits* Adam A. Ali (*left*), Normunds Stivrins (*right*)

(LOI) and grain-size analysis (Birks & Birks, 2006). In fire history reconstructions, charcoal pieces are usually categorized according to their size. Charcoal size reflects the distance traveled by a particle from its origin to the sediment archive. In lake sediments, charcoal fragments larger than 160 μm indicate local fires, whereas pieces smaller than 160 μm are sourced from fire events having occurred 0 to 40 km around the sampled lake (Higuera et al., 2010; Oris et al., 2014). A similar particle size–distance interpretation is applied to charcoal recovered from mires and bogs. Charcoal records from small forest hollows, however, usually originate from local fires (<100 s m distant) and are preferably used to reconstruct local or stand-level fire histories (Bradshaw, 1988).

Fire occurrence is typically based on the position of the charcoal layer within the sediment core. Chronological control of the sediment record, and thus the dating of fire events or periods, is commonly through radiocarbon dating of wood charcoal, plant macroremains, or bulk gyttja recovered from the core. The age-depth model derived from the obtained dates then provides an estimated age for each subsample. The temporal resolution of the collected subsample therefore depends on the thickness of the subsample and the sediment deposition rate, i.e., the number of years represented by a 0.5 or 1 cm thick subsample. Sites having a higher sedimentation rate permit a higher resolution of analysis, i.e., fewer years combined within a given sample. The time series of charcoal particle abundance is then typically analyzed

Fig. 2.3 Recovering a peat core from a small forest hollow. (*left*) Richard Bradshaw, Heikki Seppä, and Oleg Kuznetsov working with a Russian corer in the Russian Karelia region. (*right*) Peat core collected with a Russian corer. Charcoal bands are the darker strips observed near the end of the core (toward the bottom of the image). *Photo credits* Niina Kuosmanen

with statistical approaches that aim to distinguish past fire events from background levels of charcoal deposition (Higuera et al., 2010).

Box 2.1 Varved Lake Sediments

Annually laminated lake sediments, also known as varves (Fig. 2.2), are a special, albeit rare, type of lake sediment record. Here, an annual record of sediment deposition is distinguishable, making it possible to date deposited material at an annual and even seasonal resolution, similar to the resolution of tree rings, although varved records can often extend much further back in time. The seasonality within varves is produced by intra-annual changes in the materials deposited from the water column or transported from within the lake catchment area. In addition to a clear seasonality in deposition, other prerequisite conditions include sufficient incoming organic-inorganic material, no disturbance of the deposited material (e.g., through bioturbation), and anoxic conditions at the lake bottom. Once a laminated sequence is determined to represent annual layers (varves), multiple environmental proxies can then be applied, combining the advantages of centennial–millennial length lake records typical to organic sediments with the annual resolution and dating accuracy of tree rings. For fire histories, reconstructions from varved lake sediments have demonstrated the influence of humans and the environment on fire activity over long timescales in boreal Europe (Pitkänen & Huttunen, 1999) and Alaska (Gaglioti et al., 2016). This technique has also been used to validate the use of charcoal in the sediment record in general by comparing the deposition of charcoal in the varves with the fire scar record found in the vicinity of the sampled lake (Clark, 1988).

2.2.2 Limitations and Potential of Fire Reconstruction Methods

Each archive and proxy has its particular advantages and shortcomings; the nature of these depends on the required information or specific question being asked by the researcher (Remy et al., 2018; Waito et al., 2015). Tree-ring analyses remain the most accurate method for reconstructing local- and landscape-scale fire histories; in the boreal forest, however, these reconstructions are limited to the recent past (i.e., <1,000 years; Oris et al., 2014; Wallenius et al., 2010). Tree-ring analyses are also limited in the types of fires that can be dated. Fire scars require that trees survive the fires, and fire scars are also rarely formed in trees that are maladapted to frequent fires. In European boreal forests, for example, Scots pine (*Pinus sylvestris* L.) and Siberian larch (*Larix sibirica* Ledeb.) are useful for dating fires from scars, whereas Norway spruce (*Picea abies* (L.) H. Karst.) and deciduous trees are usually not. In high-intensity and tree-killing fires, stand initiation dates provide valuable information, but the data are limited to the most recent fire (however, see Sect. 2.4 discussing subfossil trees). Finally, although tree-ring records are ubiquitous in boreal forests, forest management based on clear-cutting tends to remove these biological archives in managed areas of boreal forests. Hence, the spatial extent of these reconstructions in such locations is more limited, and the study material is often less available than in unmanaged forest areas.

When fire history is investigated at longer millennial timescales or in regions where tree-ring proxies are unavailable, the selection of archives and proxies depends on the study objectives and the targeted spatiotemporal scale. Charcoal from lake sediments and large peatlands allows the reconstruction of long-term fire histories at a larger spatial scale. Nonetheless, several sites must be analyzed to reliably uncover regional trends in the reconstructions. Furthermore, taphonomic biases specific to each proxy, e.g., effects related to transportation, charcoal mixing, and the quality of charcoal preservation over time, must be minimized. This includes, for instance, avoiding sites showing visible signs of disturbance at the top of the peat (when sampling peatlands) or lakes having a substantial sediment influx. Excluding lakes that contain varved sediment records (Box 2.1), lake sediment–based fire reconstructions identify low-frequency trends rather than individual fire events. This lower-resolution state relates to the dating uncertainty of the age–depth models. This low resolution also occurs as a given charcoal peak within a charcoal series can encompass more than a single fire. Moreover, the low–density nature of the uppermost (i.e., the most recent) lake sediments leads to fewer charcoal fragments being recovered at these shallow depths in the sediment record, leading to a possible underestimation of the number of detected fires in the recent past (Lehman, 1975).

Charcoal records from soil and peat deposits in small forest hollows provide information on past fires at the local scale, and charcoal layers in peat sediments offer a reliable record of in situ fires within a single forest stand. However, these peat records of fire events suffer from the same limitations in temporal resolution as lake sediments. Furthermore, fire events can also consume/destroy the uppermost peat layers during exceptional droughts.

Paleofire studies continue to pursue novel methodological advances to refine current proxy tools and to develop new avenues. Recent studies have used charcoal morphology (morphotypes) to identify the fuel type–herbs, grass, wood, leaves (broadleaf versus coniferous)–and determine the material burned in a given fire, thereby providing a more complete portrait of the reconstructed fire regime. Stivrins et al. (2019) recently used *Neurospora* fungal spores to complement the charcoal-based fire record. *Neurospora* spp. produce spores after forest fires, and these spores can be identified within the sediment sequence.

Fire reconstructions are also being improved by integrating a wider set of data derived from various proxies of past fire and environmental conditions. A fire history, combined with detailed descriptions of past vegetation changes inferred from pollen and macrofossil records from the same sediment cores (Colombaroli et al., 2009), provides an ecosystem-level assessment of the effects of fire. Moreover, combining this paleofire and paleoecological information with multiproxy, high-resolution centennial- to millennial-scale climate reconstructions–including both temperature and precipitation–and modern observational data can offer details regarding the long-term trajectories in fire activity and identify the associated drivers (Girardin et al., 2013b, 2019).

2.2.3 Fire in the North American Boreal Forest

The fire history in the boreal region of eastern North America has been particularly well documented (Fig. 2.4). The regional Holocene fire history can be divided into four periods. The earliest period (ca. 10,000–8,000 ± 500 years BP) corresponds to the *afforestation phase* during which fire activity began to increase owing to the progressive regeneration of vegetation following the retreat of the Laurentide ice sheet (Dyke, 2004; Liu, 1990). Between ca. 7,500 and 3,500 years BP, the

Holocene thermal maximum (also called Holocene climatic optimum) was characterized by hotter and drier conditions, which favored an increase in fire activity (Viau & Gajewski, 2009). A colder and moister climatic phase, the *neoglacial period*, then followed, lasting until the last two centuries, during which fire activity was relatively reduced in boreal forests (Cayer & Bhiry, 2014; Viau & Gajewski, 2009). The most recent *industrial period* (starting ca. AD 1850), marked by anthropogenic warming, has generally witnessed an increase in fire activity (De Groot et al., 2013; Krawchuk et al., 2009). Nonetheless, a decreased fire frequency observed in some regions (Drobyshev et al., 2014; Larsen, 1996) underlines the spatial heterogeneity of fire activity across North American boreal forests related to regional and local abiotic and biotic conditions (Remy et al., 2017b).

Stand composition has also altered the Holocene fire regimes in eastern boreal North America (Fig. 2.5). The early Holocene *afforestation phase* was characterized by more frequent and larger fires in the temperate deciduous forest than those within the boreal coniferous forest owing to the earlier retreat of the ice sheet in southern latitudes (Blarquez et al., 2015). During the *Holocene thermal maximum*, fire frequency and, to a lesser extent, the amount of biomass burned were greater in the coniferous forest than in the deciduous forest because of the higher abundance of fire-prone species in the former (Gaboriau et al., 2020; Girardin et al., 2013a). This relatively higher fire activity in coniferous forests decreased slightly during the neoglacial period to reach levels similar to those within the deciduous forest. This neoglacial shift is best explained by a shorter fire season in the coniferous forest related to the cooler conditions and the larger amount of precipitation falling as snow during this period (Ali et al., 2012; Remy et al., 2017a; Turetsky et al., 2011). In deciduous forests, the amount of biomass burned increased slightly during the neoglacial period, and fire frequency reached its Holocene maximum for deciduous forests at this time. A higher abundance of fire-prone coniferous forest species colonizing from higher latitudes—resulting from colder and moister conditions—can explain this increased fire activity (Blarquez et al., 2015; Girardin et al., 2013a; Remy et al., 2019). An absence of a large increase in fire activity over the last centuries in eastern boreal North America in both coniferous and deciduous forests results from a combination of a less favorable climate for fire and anthropogenic fire suppression (Bergeron & Archambault, 1993; Bergeron et al., 2001; Blarquez et al., 2015).

Interregional comparisons of fire reconstructions improve our understanding of the mechanisms leading to long-term changes in fire activity, especially when the sites vary in their environmental characteristics. Nonetheless, interactions between climate changes and vegetation dynamics behind the extreme fire events experienced over the past two decades and their consequences on forest regeneration remain poorly understood. Thus, a new challenge in paleoecology is detecting and focusing on past extreme fire events to understand their causes and consequences to improve predictions and mitigate future risks. Several studies have begun to address this issue and have highlighted the *Medieval Warm Period*, a period characterized by particularly warm temperatures during which unusual peaks of fire activity occurred within various regions of the boreal forest (Girardin et al., 2019). Further studies

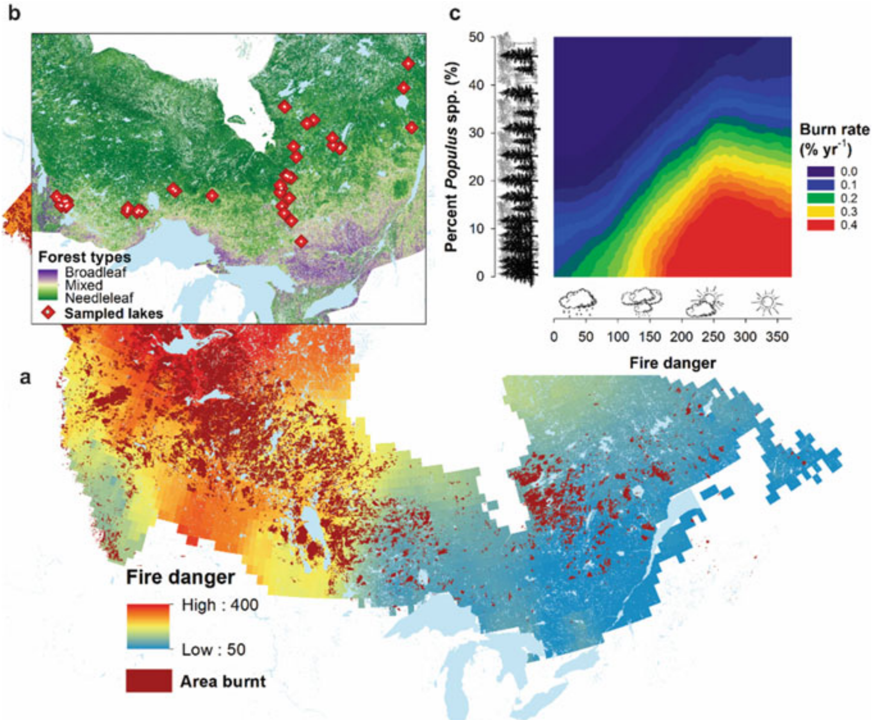

Fig. 2.4 Simplified representation of interactions between fire, vegetation, and climate within Canadian forests. **a** Mean seasonal fire danger across Canada for the 1900–2017 period and areas burned 1981–2017 (*dark red*). Fire danger includes the additive effects of seasonal drought severity and the duration of the snow-free period (equivalent to the fire season length), with higher values reflecting a greater seasonal fire danger. **b** The dominance of needleleaf trees in northern Ontario and northwestern Québec, Canada. Data was obtained from Beaudoin et al. (2014) at 250 m resolution land cover classes. The dimensionless scale covers needleleaf-dominated (*dark green*) to broadleaf-dominated (*dark brown*) areas, with lakes sampled for fire history reconstruction using charcoal records (*red diamonds*). **c** An empirical model of the burn rate, i.e., percentage of burned area per year for a given region, as a function of fire danger (in **a**) and percentage cover of broadleaf *Populus* species **b**. Fire-prone conditions exist when the fire danger is high and the percentage of *Populus* spp. in the regional landscapes is less than 30%. Adapted by permission from Springer Nature from Girardin and Terrier (2015)

focusing on this warm period at multiple locations in the boreal forest could improve our understanding of the environmental processes involved in extreme fires.

Enhanced fire activity is projected for the twenty-first century as temperatures rise (Flannigan et al., 2009; Jolly et al., 2015). Anticipated consequences from the increased fire activity include changes to wildlife habitat, increased carbon emissions, heightened threats to human safety and infrastructure (e.g., injury, death, property loss, reduced clean air and water supplies), and greater economic losses for the forestry sector, losses that may include fewer commercial products and timber supplies (Brecka et al., 2018; Gauthier et al., 2015; Walker et al., 2018).

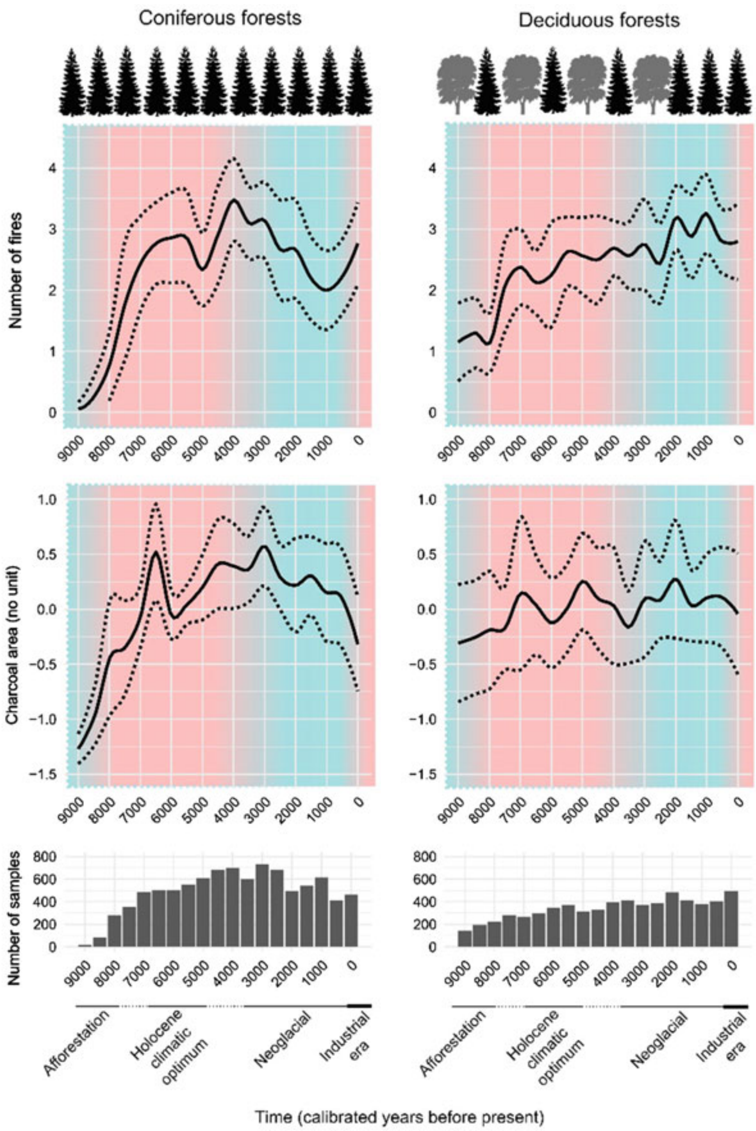

Fig. 2.5 The reconstructed Holocene fire regime history of the boreal deciduous and coniferous forests of eastern Canada as derived from the analysis of lacustrine charcoal deposits. Plots of the number of fires and the charcoal areas indicate the fire occurrence and the area burned, respectively. General temperature patterns over the Holocene include cooler (*light blue*) and warmer (*light red*) periods. The trees illustrate the most abundant species over the Holocene in terms of deciduous (*gray*) or coniferous (*black*) trees

2.2.4 Fire in the European Boreal Forest

Studies of past fires in European boreal forests have revealed a complex, mixed-severity fire regime that varies in both time and space and is influenced by climate, vegetation, landscape structure, and human activities. Fire histories are particularly well studied in regions within the western portions of European boreal forests, particularly on the Fennoscandian Shield. Here, fire shows several broad-scale patterns during the Holocene. The analysis of 69 individual fire records recovered from lake sediments spread across Fennoscandia revealed that early Holocene fire frequencies peaked 8,500 to 6,000 years BP. Fire frequency then declined until starting a rising trend ca. 4,000 years BP (Molinari et al., 2020). This early Holocene pattern reflects the well-resolved climate variability over similar time frames showing that the warmest part of the Holocene, the Holocene thermal maximum, and the changes in fire activity coincide very well. The trend of more frequent fires in the region over the last 4,000 years is driven by an increased human influence related to greater human population densities and changes in forest use.

In addition to the climate-driven patterns in fire occurrence, millennial fire history reconstructions illustrate a long-term interaction between vegetation and fire. After the Holocene thermal maximum, the most conspicuous change in forest composition in the boreal forest in Europe involved the expansion of spruce, which began in eastern Fennoscandia ca. 6,500 years BP and has continued in western Fennoscandia over the last two millennia. Paleoecological records of charcoal in organic sediments from remote sites having limited human influence demonstrated that the expansion of spruce coincided with a marked decrease in fire occurrence (Ohlson et al., 2011). Nonetheless, it remains unclear whether the expansion of spruce represented the cause or the consequence—a changing microclimate or fuel type and distribution—of reduced fire activity (Ohlson et al., 2011).

In the more southern hemiboreal and boreonemoral zones, the emerging picture of the Holocene fire trends similarly differs from the expected pattern of a climate-only forcing; the observed pattern confirms the importance of interactions with vegetation. A detailed lake sediment record from this zone showed that fire frequency was relatively high 9,500 to 8,000 years BP (Fig. 2.6). As the climate became warmer and drier around 8,000 years BP, fire frequency decreased notably. This observation contrasts with the expected causal link between the climate and fire frequency in the boreal zone; however, it may be explained by a change in the vegetation and fuel type (Feurdean et al., 2017). During the warm and dry period, 8,000 to 5,000 years BP, the populations of temperate deciduous broadleaf tree species (e.g., hazel, oak, lime, and elm) in the southern part of the boreal zone increased and replaced the boreal tree species. This major shift in forest composition reduced the regional fire frequency because these deciduous species are less flammable than conifers. It is also possible that greater shade in the dense deciduous forest and the higher moisture content of the leaves favored a reduced fire frequency (Feurdean et al., 2017), similar to the effects of spruce expansion in more northern regions (Ohlson et al., 2011).

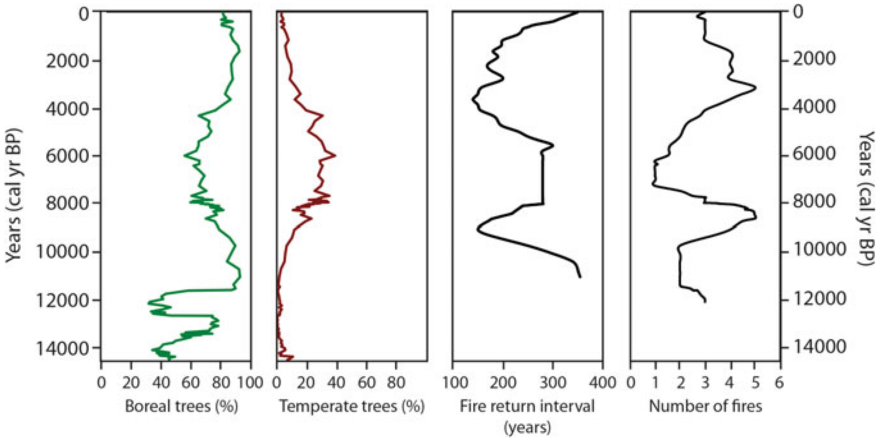

Fig. 2.6 Vegetation and fire frequency in the southernmost edges of the European boreal forest; fire return intervals increased, and the number of fires decreased as vegetation shifted toward a greater presence of temperate trees during the Holocene thermal maximum, despite the climate being warmer and drier. Figure redrawn from Feurdean et al. (2017) with permission from Elsevier

Approaching the modern period, the human influence on forests and the fire regime becomes increasingly evident within the sediment record (Molinari et al., 2020); this pattern is also observed in tree ring–based records where the longest reconstructions extend 700 to 1,000 years BP (Niklasson & Granström, 2000; Rolstad et al., 2017; Wallenius et al., 2010). The timing of this increased human influence varies between regions, very much related to human settlement and lifestyle changes (Wallenius, 2011). In particular, the increase and eventual decline in slash-and-burn agriculture, widely practiced over much of Finland, has been identified as a driver of the onset and cessation of high fire activity; similar patterns have been identified across the region, from southeastern Norway in the west (Rolstad et al., 2017) to the Komi Republic in the east (Drobyshev et al., 2004). This anthropogenic influence is reflected by increased fire frequencies, smaller fire sizes, and a greater number of early−season fires (Niklasson & Granström, 2000; Rolstad et al., 2017). Climate continues to be a driver, in particular during exceptionally dry years and periods when Fennoscandian forests experience a greater area of forest burned (Aakala et al., 2018; Drobyshev et al., 2016). In most of Fennoscandia, this period of human-induced high fire activity has receded over the past 100 to 250 years because of changes in forest use, land tenure, and, more recently, the greater development of infrastructure and fire suppression (Rolstad et al., 2017; Wallenius, 2011), giving way to the modern fire regime (see Chap. 3).

In addition to this temporal variability, long-term fire reconstructions have demonstrated a latitudinal gradient of more frequent fires in the south to less frequent fires in the north (Drobyshev et al., 2014). This gradient has a climatic origin (Larjavaara et al., 2005); however, except for the mountainous areas, the fire gradient also follows a population density gradient over much of the region. In the southern areas, characterized by warmer and drier conditions in the summer and a greater human influence, the estimated mean fire interval over the past several millennia has varied between 70 and 95 years, as determined from charcoal records from varved lake sediments (Pitkänen & Huttunen, 1999; Tolonen, 1978). In northern Sweden, a fire interval about of about 80 years has been obtained from tree rings (Zackrisson, 1977), and a millennium-long tree-ring reconstruction in northern boreal Finland found a mean fire cycle−time required to burn an area equal to the area studied—of 350 years (Wallenius et al., 2010). The Finnish site has a less fire-conducive climate and lower population density than more southern, fire-prone sites. Within forested landscapes, characteristics such as fire breaks, topography, and differences in soil hydrology produce a within-landscape variability in the Holocene fire record. In southern Fennoscandian and western Russian boreal forests, for example, the sediment charcoal–based fire return interval ranges from 109 to 237 years during the last 11,000 years (Stivrins et al., 2019), whereas nearby sites are without any evidence of fires (Kuosmanen et al., 2014). A similar type of spatial variability in fire history is recorded in the eastern parts of the European boreal forests in the Ural Mountains (Barhoumi et al., 2020). Tree ring−based reconstructions tell a similar story with substantially different fire return intervals in various parts of a landscape, depending on soil hydrology (Aakala, 2018).

2.3 Millennial Insect Outbreak History

The detailed patterns of fire history described in the preceding sections reflect the predominance of wildfire as the most commonly studied disturbance in boreal paleoenvironmental research (Bergeron et al., 2010; Flannigan et al., 2001). Our understanding of millennial-scale natural disturbances has traditionally revolved around the role of fire in influencing forest dynamics, despite an understanding that disturbances interact and operate at multiple scales and that in many locations, insect outbreaks, rather than wildfires, are the major drivers of forest landscapes. Over the short term, insect outbreaks and plant diseases can damage extensive areas of forest and produce significant economic losses. Insect outbreaks are one of the most influential factors shaping modern boreal forest diversity (McCullough et al., 1998). As with fire, insects contribute to the regeneration of the forest mosaic. In contrast to fire, however, insects affect stands selectively by, for example, targeting old and vulnerable trees.

Various insect defoliators, composed mainly of lepidopterans, affect boreal stands. These defoliators include the forest tent caterpillar, *Malacosoma disstria* (Hübner), the hemlock looper, *Lambdina fiscellaria* (Guénée), and the spruce budworm (SBW), *Choristoneura fumiferana* (Clemens). The latter has the greatest influence within the boreal region owing to its very extensive distribution and marked effect on North American boreal forests. SBW is a defoliating lepidopteran native to coniferous forests in Canada and the northeastern United States. This species is responsible for the largest area of damage in the North American boreal forest for insect defoliators. Its primary hosts are balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), and, to a lesser extent, red spruce (*Picea rubens* Sarg.) and black spruce (*Picea mariana* (Mill.) BSP). The univoltine cycle of this moth consists of an egg stage, diapause, six larval instars, pupation, and an adult stage (moth). This last stage is relatively short (two weeks), during which the insect spends all its time looking for a mate. If successful in finding a mate, the females then lay their eggs. Balsam fir may die after three or four consecutive years of severe defoliation (Bergeron et al., 1995; MacLean, 1984), whereas secondary hosts suffer crown and branch mortality and growth reduction of up to 75% (MacLean, 1984; Nealis & Régnière, 2004). In the province of Québec (Canada), the forest surface affected by this species of Lepidoptera over the last century is twice the size of the state of California (Navarro et al., 2018c). SBW outbreaks have major ecological effects and result in important economic consequences through the loss of forest productivity (Shorohova et al., 2011).

Despite the scale and significance of this natural disturbance agent, we remain limited in our knowledge regarding the frequency and severity of SBW outbreaks at a multimillennial scale and understanding how these outbreaks relate to climate and other disturbances, such as fire. Given that variations in temperature and precipitation affect an organism's survival, reproduction cycle, and spatial dispersion (Dale et al., 2001), it is critical to understand the links between SBW outbreaks and climate to better understand the potential of SBW outbreaks under future climate change scenarios (Klapwijk et al., 2013; Volney & Fleming, 2000). Paleoenvironmental records of these insect outbreaks can therefore offer a long-term perspective of SBW outbreaks and shed light on the periodicity, synchronicity, and consequences of past insect outbreaks improve our understanding of the spatiotemporal patterns of SBW in relation to climate (Berguet et al., 2021; Jardon et al., 2003; Navarro et al., 2018a). Until recently, however, the lack of effective proxies and methods for reconstructing insect-related disturbances led to a severely neglected and oversimplified understanding of the frequency, intensity, and impacts of past insect outbreaks on the forest landscape. In the following section, we summarize recent advances in the paleoenvironmental reconstruction of past insect outbreaks, specifically those of SBW, in the boreal forest.

2.3.1 Insect Outbreak Reconstruction

2.3.1.1 Dendrochronology

Dendroecological approaches have been applied to the reconstruction of past insect outbreaks. Tree rings provide indirect measurements of insect activity; years of unusually narrow or otherwise anatomically abnormal tree rings can be related to insect outbreaks. These tree ring–based approaches have helped reconstruct outbreaks of numerous insects, including outbreaks of the forest tent caterpillar

(Cooke & Roland, 2000; Sutton & Tardif, 2007), the larch sawfly (*Pristiphora erichsonii* (Htg.); Jardon et al., 1994; Girardin et al., 2001, 2002; Nehemy & Laroque, 2018), the larch budmoth (*Zeiraphera diniana* Gn.; Weber, 1997; Rolland et al., 2001), the western and eastern spruce budworm (Boulanger et al., 2012; De Grandpré et al., 2019; Flower et al., 2014; Krause, 1997; Morin & Laprise, 1990; Navarro et al., 2018c; Swetnam & Lynch, 1993), and the jack pine budworm (*Choristoneura pinus* Free; Volney, 1988), as well as outbreaks of the geometrid moths *Epirrita autumnata* Borkh (Babst et al., 2010) and *Operophtera brumata* L. (Hoogesteger, 2006; Tikkanen & Roininen, 2001; Young et al., 2014).

The reconstruction of insect outbreak regimes at the landscape scale is a major challenge, as aerial surveys of defoliation have been available only since the 1960s—covering only one major outbreak in the last century—and are concentrated mainly in the balsam fir area; thus, the use of dendrochronological approaches becomes essential. Similar to tree ring–based studies of fire history, a major limitation in dendrochronological reconstructions of insect outbreaks is the maximum age of host trees. This is particularly true for trees affected by eastern spruce budworm, as this insect often kills its host. Cross-dating has been helpful when using dead trees, found either in the field or as lumber in old buildings, to extend tree-ring chronologies (Boulanger & Arseneault, 2004; Boulanger et al., 2012; Krause, 1997); in North America, however, there are few historical buildings, which limits the longest chronologies to the last 400 years. The available tree-ring series for extensive areas of the eastern Canadian boreal forest extend only to the early twentieth century (Navarro et al., 2018c). Subfossil trees, buried stems recovered from peatlands or lakes, can extend dendrochronological records further back in time. Simard et al. (2002), for example, studied a small peat bog surrounded by host trees of spruce budworm and found evidence of outbreaks between 4,170 and 4,740 years BP. A more extensive use of subfossil trees from lakes appears promising, as highlighted by a recently published 800-year chronology of SBW outbreaks relying on subfossil stems (Morin et al., 2020). Nonetheless, long-term local and regional chronologies remain unavailable for extensive areas.

2.3.1.2 Macrofossils

Macrofossils are plants and animal parts preserved in the sediment record and are visible without using a microscope; they include cones, leaves, seeds, stems, exoskeletons, teeth, and bones. These indicators confirm the nearby presence of these organisms and are powerful tools for reconstructing insect outbreaks. Head capsules, pupae, and other insect remains preserved in the sedimentary record can serve as proxies of past SBW (and other species) outbreaks (Bhiry & Filion, 1996; Davis & Anderson, 1980). Most body parts of the caterpillar or butterfly stage are nonetheless fragile and often recycled very rapidly within the soil humus layer (Potelle, 1995). SBW feces (frass pellets), however, are well-preserved macrofossils (Fig. 2.7). During heavy budworm infestations, fecal pellets can rain down continuously from infested trees to the ground. The feces can be identified to the species level, and parts of balsam fir needles within the fecal matrixes remain identifiable (Potelle, 1995).

At present, the longest budworm macrofossil profile covers more than 8,200 calibrated (cal.) years BP (Simard et al., 2006). Spruce budworm feces began accumulating at the study site around 8,240 cal. years BP and were observed throughout the profile. Budworm feces peaks occur at ca. 6,775 cal. years BP and 6,550 cal. years BP. Three other sampled bogs from the same region also demonstrate two or three periods of higher feces abundance during the Holocene (Simard et al., 2011); however, these periods of higher insect macrofossil abundance are not synchronized, indicating that episodes of high spruce budworm abundance varied between locations. This initial evidence also suggested that peaks of high spruce budworm abundance were rare over the course of the Holocene. Although Simard et al. (2006, 2011) found only a few peaks of spruce budworm feces during the Holocene, these were the first studies to identify budworm outbreaks over the Holocene.

Macrofossils as indicators of insect outbreaks have some significant limitations. Similar to the lake- or peat-based paleoecological methods presented above, macrofossils collected from sedimentary records do not provide high-resolution reconstructions; identified periods of high budworm populations can encompass several outbreaks. Furthermore, questions have been raised regarding feces preservation over time owing to greater decomposition with age, biasing against older outbreaks. Moreover, insect macrofossils represent only a local signal, and study sites are limited to

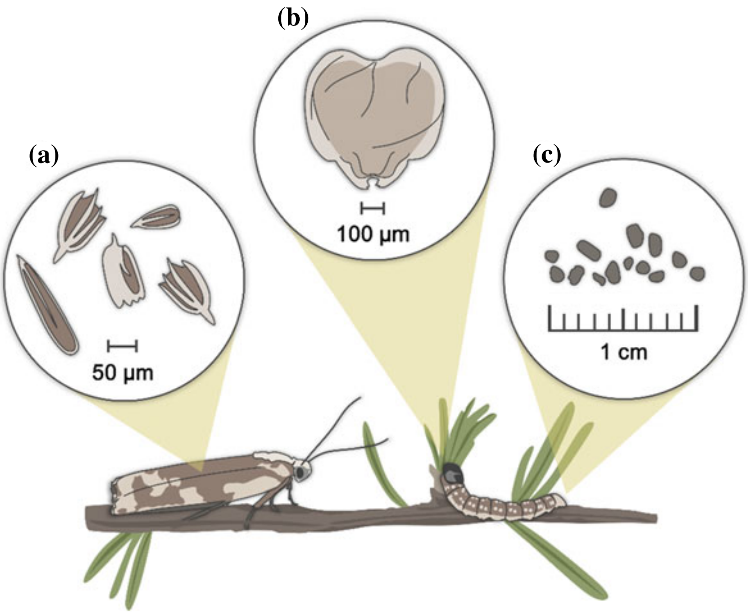

Fig. 2.7 Proxies from lepidopterans used to reconstruct insect outbreaks; **a** wing scales, **b** cephalic capsules, and **c** feces

the few, sporadically scattered locations where balsam fir, the preferred host of the spruce budworm, grow near the sampled peat bogs and lakes. Finally, this approach requires a sizable amount of sample material, and the extraction of macrofossils is a very laborious manual task.

2.3.1.3 Microfossils: Lepidopteran Scales as a Novel Paleoindicator

The lack of robust, abundant, and nondecomposing proxies has limited previous paleoecological reconstructions of SBW outbreaks. During the current SBW infestation in the Saguenay-Lac-Saint-Jean region (Québec), however, large quantities of adult moth scales were observed in the water column of regional lakes. These lepidopteran scales are released as an individual moth dies (around 150,000 scales per insect). These scales, transported by the wind and water, land on the lake surface and eventually settle onto the lake bottom to become part of the sediment record. The chitinous composition of these scales favors their preservation in the sediment, and their abundance in the sediment indicates the relative timing and intensity of the outbreaks (Montoro Girona et al., 2018b).

There are several advantages to this new proxy. The identification of spruce budworm scales is less problematic than that of spruce budworm feces, as the scales are chitinous, and their long-term preservation in lake sediments is excellent. Numerous lakes, and their sediment archives, dot the boreal forest landscape; thus, it is possible to produce a large-scale portrait of insect outbreaks. Moreover, only a small amount of material is required for sample preparation and analysis (1 cm^3), and lepidopteran scale analysis can be combined with charcoal and pollen analyses from the same sample. This innovative methodology to extract lepidopteran scales (Montoro Girona et al., 2018b; Navarro et al., 2018b) from the sediment samples circumvents some of the limitations of the feces-based approach.

Distinct scale morphologies among lepidopteran taxa permit taxonomic identification of the scale to the species level (Fig. 2.8). Given that billions of spruce budworm individuals live during an outbreak, significant peaks in the number of scales within a lake core should indicate outbreak events. Preliminary work using sediment traps and short cores demonstrated that the relative and absolute abundances of scales in the traps and sediment are proportional to the intensity of the annual defoliation of the surrounding forest and that the transfer of the scales from the lake surface to the lake bottom occurs over a few days, generally less than a week. Moreover, the stratigraphic position of scales within a well-dated sediment record matched the timing of known outbreaks (Navarro et al., 2018b). This series of tests confirmed the potential for a scale-based reconstruction of lepidopteran outbreaks from the sediment record.

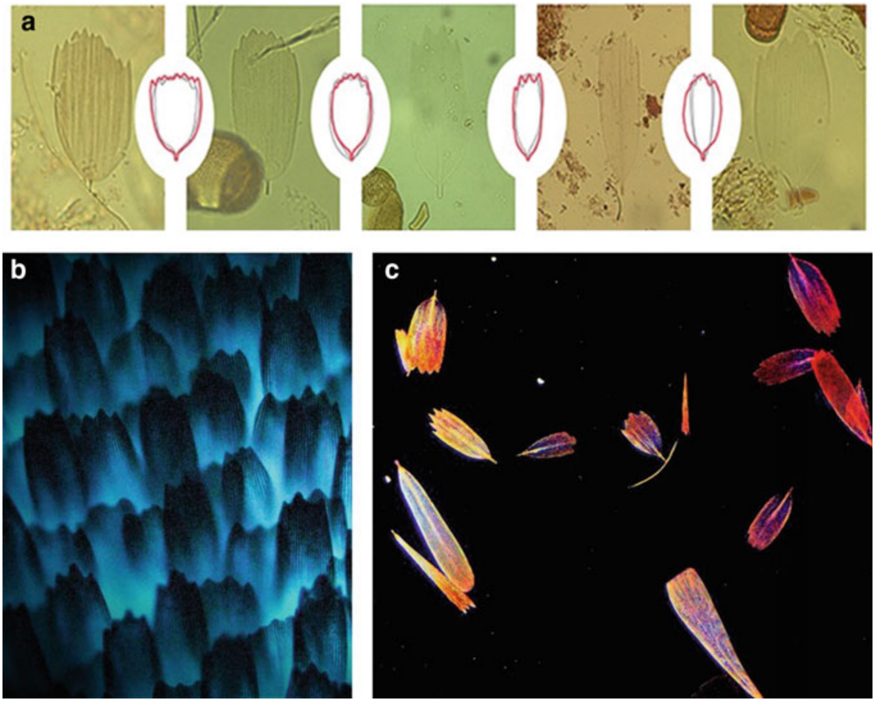

Fig. 2.8 Potential of lepidopteran scales as a paleoindicator of insect outbreaks. Scales are composed by chitin and are thus difficult to degrade. **a** Comparison of four well-preserved scales extracted from a lake sediment core with spruce budworm (SBW) morphotypes generated through shape measurements of thousands of SBW specimen scales. **b** Wing scales organized like roof tiles. **c** Diversity of wing scale morphotypes. *Photo credits* **a** Montoro Girona et al. (2018b; CC BY 4.0); **b**, **c** Emy Tremblay and Miguel Montoro Girona

2.3.2 Holocene History of Insect Outbreaks and Consequences for Understanding Outbreak-Fire-Climate-Vegetation Interactions

Navarro et al. (2018c) identified 87 significant peaks in scale abundance over the last 8,000 years. These results contrasted markedly with those of the SBW feces–based record, which recorded few events over the Holocene. The lepidopteran scale record indicates a pattern of highly variable but consistently present budworm populations over the Holocene. Pairing the scale record with microcharcoal and pollen records revealed that the frequency of outbreak events was inversely correlated with the frequency of fire events (Fig. 2.9). When the periods of high budworm populations in the four feces diagrams produced by Simard et al. (2011) are combined, the frequency of outbreaks produces an inverse relationship with published fire frequency events. Therefore, the spruce budworm feces record recovered from peat deposits did not contain all outbreaks that occurred at the sampling site; this absence from the peat record likely relates to the easily degradable nature of the SBW feces in the peat archive.

The use of lepidopteran scales has heightened our ability to understand outbreak dynamics during the Holocene and their relationship to fire, climate, and forest structure across the landscape. We are currently sampling several lakes in the mixed forest—the current center of SBW distribution—and the black spruce forest—the modern northern distribution of the insect—to better understand the links between SBW outbreaks and forest structure. Balsam fir abundance fluctuates in relation to other species, and these fluctuations relate mainly to climate and fire as indicated by the fluctuations of fire-adapted species, such as jack pine, and charcoal abundance over the Holocene (Bergeron & Leduc, 1998). Our initial results support the earlier finding of an inverse relationship between outbreak frequency and fire (Fig. 2.9). A drier climate appears to induce a higher fire frequency. This shift favors the installation of fire-adapted species (e.g., jack pine) that are not hosts of budworm. The frequency of detectable outbreaks therefore decreases. In contrast, a more humid climate—most likely a warmer humid climate—leads to a lower fire occurrence, thereby favoring the maturing of forests where SBW host trees, such as balsam fir

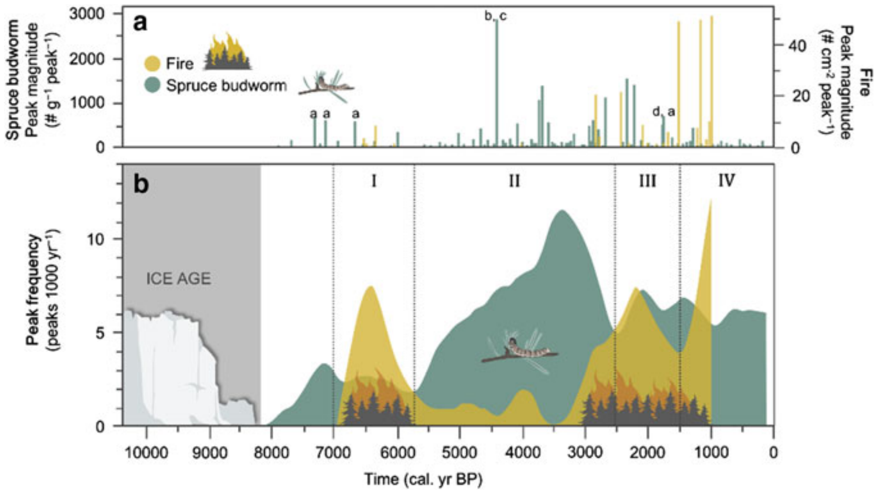

Fig. 2.9 Interactions between fire and insect outbreaks over the Holocene in the province of Québec, Canada. **a** Magnitude of fire and lepidopteran scale peaks (#·cm^{-2}·peak^{-1}). Letters correspond to peaks identified from other proxy records; *a* Simard et al. (2006), *b* Anderson et al. (1986), *c* Bhiry and Filion (1996), and *d* Jasinski and Payette (2007). **b** The frequency of fire and SBW outbreaks (peaks·1,000·yr^{-1}). To extract fire events from the charcoal stratigraphy, we defined a background component (C_{back}) using a Lowess smoothing that was robust to outliers and with a 500-year smoothing window. C_{back} was extracted from the interpolated series of raw data (C_{int}) to define a peak series (C_{peak}) as a residual of $C_{int} - C_{back.}$ Each peak exceeds the 99th percentile threshold of the residual of $C_{int} - C_{back}$. Roman numbers correspond to the disturbance interaction steps during the Holocene: *I* and *IV* represent periods where fire was the dominant disturbance; *II* (6,200–2,500 cal. yr BP) had insect outbreaks as the main disturbance, and period *III* experienced fire and outbreaks at a similar frequency

and white spruce, proliferate. Thus, this specific forest composition leads to periods of higher SBW abundance.

The recent dynamics of SBW outbreaks and the observed changes to fire regimes reflect millennia of interactions between the insects and their environment. Thus, understanding these complex dynamics requires that we use approaches such as dendrochronology and paleoecology to improve our understanding of the frequency and severity of epidemic periods over the longest possible period. Some studies have demonstrated that SBW was already present and abundant in stands lacking balsam fir, suggesting a high SBW activity on this insect's secondary host, namely black spruce (Simard et al., 2006). Moreover, this high abundance was observed during a relatively warm period of the Holocene (7,000–6,000 cal. yr BP), suggesting a phenological synchronization between insect and host (Fig. 2.9).

Using periods of growth suppression in dendroecological series, Navarro et al. (2018a) identified three insect outbreaks in eastern Canadian forests over the last century; these outbreaks differed in their respective spatiotemporal pattern, duration, and severity. The first outbreak (AD 1905–1930) affected up to 40% of the studied trees, initially synchronizing from local infestations and then migrating to more northern stands. The second outbreak (AD 1935–1965) was the longest lasting, although the least severe, with only up to 30% of trees affected by SBW activity. The third event (AD 1968–1988) was the shortest; however, it was also the most severe and extensive, affecting nearly 50% of trees and 70% of the study area. This most recent event was identified for the first time at the limit of the commercial forest, illustrating a northward shift of the SBW distribution area during the twentieth century. This observation provided the first documented evidence of how climate change influences the current spatiotemporal patterns of SBW outbreaks (Navarro et al., 2018c).

However, dendroecological reconstructions of past outbreaks have assumed that only defoliation is responsible for the sustained growth suppression in the host trees. Recent work illustrates that periods of climate-related growth suppressions can precede or co-occur with insect disturbances (De Grandpré et al., 2019). It is therefore possible that some of these reconstructed outbreak periods are, in fact, confounding effects of climatic periods unfavorable for growth (Gennaretti et al., 2018; Girardin et al., 2014, 2019). More research must be carried out to differentiate the effect of defoliation and climate-related growth suppressions in dendroecological series to improve reconstructions of the spatial and temporal dynamics of past insect outbreaks.

Outbreak reconstructions provide strong support for the hypothesis that SBW has been present and influencing forest dynamics in the boreal forest Québec throughout the Holocene (Simard et al., 2006). SBW abundance and outbreaks are strongly correlated with the presence of its primary hosts; this presence is itself influenced by climatic variations and fire regimes. This information will be essential for building predictive models of SBW outbreaks in the face of climate change. The early and late Holocene were characterized by a relatively high fire frequency; the greater number of fires may have restricted the development of severe epidemics by reducing the number of mature hosts in the landscape. These results also suggest that epidemics would have been much more frequent and possibly more severe in the mid-Holocene when fires had less (or more local) influence on the landscape, highlighting the importance of intermediate severity disturbances in the forest landscape and providing insight for ecosystem-based management to adapt the silvicultural practices to this type of disturbance, e.g., applying partial harvest in locations having longer fire intervals (Bose et al., 2014; Martin et al., 2020; Montoro Girona et al., 2016; Moussaoui et al., 2020).

2.4 An Archive of Boreal Forest Dynamics: Subfossil Trees

Subfossil trees, where available, offer another means of reconstructing disturbance histories at an annual resolution. The potential information preserved in the tree-ring records of subfossil trees includes the temporal patterns of tree recruitment and mortality, the occurrence and timing of forest disturbances, and the interannual variations in forest productivity and climate over timescales ranging from centuries to a few millennia (Gennaretti et al., 2014b). Subfossil trees provide information mainly in terms of local stand-scale forest dynamics; however, their tree-ring patterns may also be imprinted by regional- and hemispheric-scale climate signals, thereby allowing reconstructions of past climate variability and the influence of main climate forcing agents, e.g., solar, orbital, and volcanic influences; see Gennaretti et al. (2014a). The varying ages of the preserved subfossil trees can also extend the regional tree-ring records beyond the period covered by living trees.

The preservation of these paleoenvironmental archives requires exceptional depositional conditions for the trees to experience minimal decay (Fig. 2.10 a, b). These settings include anoxic sediments (peat, lake, and river sediments) or in sites where arid or cold conditions limit insect and microbial activity on the dead tree trunks (Eronen et al., 2002; Gennaretti et al., 2014b; Hantemirov & Shiyatov, 2002; Spurk et al., 2002). Subfossil trees can sometimes be dated from their depositional context with variable precision, although the main interest in their use stems from the analysis of their tree rings to determine the exact calendar years of ring formation through the dendrochronological cross-dating of ring-width patterns against a "master chronology" (see Box 2.2 on master chronologies).

The systematic or exhaustive sampling of subfossil stems at a single site can reveal several tree generations of stand-scale forest dynamics acting in response to local disturbances (Fig. 2.10). Subfossil tree records collected from peatlands, lakes, and rivers in the eastern Canadian boreal forest highlight the long-lasting consequences of individual fire events (Arseneault & Payette, 1997; Arseneault & Sirois, 2004; Arseneault et al., 2007; Gennaretti et al., 2014c). These effects include shifts to treeless environments, changes in stem density, and the exclusion of fire-sensitive tree species. The sampling of subfossil logs from several sites across a relatively broad region allows large-scale patterns and processes to be documented, including latitudinal or altitudinal shifts of tree line (Helama et al., 2005; Kullman, 1995) and

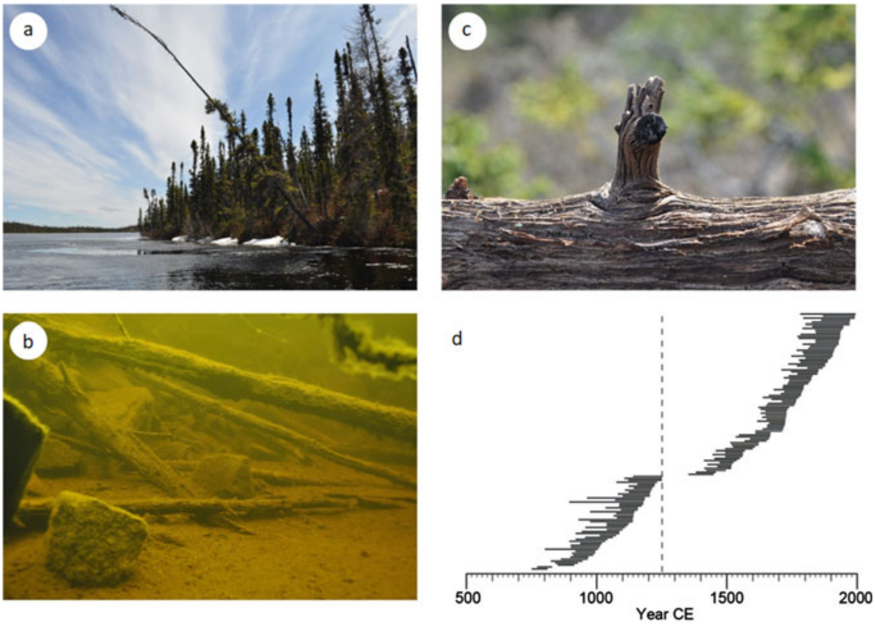

Fig. 2.10 Typical examples of subfossil trees in lakes of the eastern Canadian boreal forest. **a** A dominant living tree prone to be recruited as a dead tree in the littoral zone of a small lake surrounded by an old-growth black spruce forest. This tree fell into the lake two years after this picture was taken. **b** A dense accumulation of subfossil trees in the littoral zone of the same lake as **a**. The subfossil stems in the photo have been accumulating continuously over the last two millennia. **c** A charred lateral branch of a cross-dated tree indicates that the corresponding tree died during a fire several centuries ago. **d** Impact of a stand-killing fire (*vertical dashed line*) on the recruitment of individual subfossil stems (*horizontal bars*). More than a century is generally needed for the postfire recovery of the lakeshore forest and subsequent inputs of new tree trunks into the littoral zone. Subfossils recruited before the fire event must be cross dated using subfossil trees from another shore segment or nearby lake. Such fire-induced recruitment gaps often limit the development of millennial master chronologies for the North American boreal forest. *Photo credits* **a–c** Dominique Arsenault **d** Modified permission from John Wiley & Sons, Inc. (Journal of Ecology © 2013 British Ecological Society) from Gennaretti et al. (2014b)

long-term reconstructions of defoliating-insect outbreaks (Esper et al., 2007). At a more local scale, sunken cut logs, deposited in river sediments during the timber-driving era in eastern Canada, provide evidence of the nineteenth and twentieth-century logging history in the corresponding watershed. Information obtained from these sunken logs testifies to the progressive changes in logging activities from the preferential cutting of large pine and spruce stems in the nineteenth century to a more generalized exploitation of all conifer species following the development of the pulp and paper industry at the turn of the twentieth century (Boucher et al., 2009).

Box 2.2 Master Chronologies

Developing a long "master chronology" from subfossil trees is a long, difficult, and expensive task, requiring the analysis of several hundred to thousands of trees and their respective tree-ring records. Master chronologies longer than 7,000 years have been developed from subfossil stems recovered from lakes in northern Fennoscandia by sampling about 1,000 Scots pine (Eronen et al., 2002; Grudd et al., 2002), and more than 2,000 black spruce were needed to develop a 1,300-year master chronology for the eastern Canadian boreal forest (Gennaretti et al., 2014b). The general idea is to use these hundreds of overlapping tree-ring records to produce an average characteristic tree-ring sequence for a region. Undated tree-ring records of an individual tree or a group of trees ("floating" tree-ring series) can then be matched to the patterns of the master chronology to obtain a precise dating (cross-dating process) of the individual records. Successive dating of older trees permits the temporal extension of the master chronology. The challenge of developing a master chronology in the boreal forest stems from the high frequency of stand-killing forest fires, which limits the temporal continuity of tree-ring chronologies in this fire-prone region (Fig. 2.10c; Arseneault et al., 2013; Gennaretti et al., 2014c). Thus, many trees and sites are required to build a long, boreal master chronology that extends through periods where severe stand-killing fires burned specific stands, but not all sites.

2.5 Looking Toward the Future

Anthropogenic environmental changes are pushing global forest ecosystems toward *non-analog* states, including disturbance regimes not previously encountered in the period of recorded human history. The use of the various environmental signals stored in biological archives, such as tree rings and lake and peat sediments, can provide critical information on past changes in environmental conditions, the associated changes in disturbances, and how forest ecosystems have responded to these shifts. This multiproxy paleoenvironmental approach is particularly important for slowly occurring processes, which require centennial- to millennial-scale measurements to be noted and assessed. Paleoecological information provides a long-term context for the observed changes and a means of testing models and simulations that fall beyond environmental conditions observed in recorded history. Paleoecology can also explain how the current ecosystem structures have developed, e.g., the long-term patterns of fire occurrence related to human activities. Combining paleoenvironmental approaches at sites within the boreal forest has improved our understanding of the interactions between various disturbances over the Holocene, the role of insect outbreaks on landscape dynamics, and the interactions between climate, vegetation, fire, and insects over the short term, i.e., last 200 years, and plurimillennial scales.

The development of alternative paleoenvironmental proxy indicators remains active, including the use of fungal spores for reconstructing the occurrence of pathogenic fungi, the recovery of insect remains other than the abovementioned lepidopteran scales (Schafstall et al., 2020), and the application of ancient DNA and molecular biomarker analyses to the sedimentary record (Crump, 2021; Dubois & Jacob, 2016). Specific proxy records may serve complementary and related purposes. Living and subfossil tree-ring chronologies hold information on long-term forest disturbances at an annual resolution and may also be used to study climate variability over the chronological coverage. Subfossil samples could also potentially improve our understanding of climate-related changes in forest productivity in commercial forests by providing information related to past tree growth, an element needed to improve the forecasts of future forest productivity under climate warming. Finally, the long-term patterns of forest response to natural disturbances can help develop more sustainable forest management strategies. Central to this framework is that harvest methods should emulate patterns of natural disturbance to thereby minimize the differences between managed and natural forests (Kuuluvainen, 2002; Montoro Girona et al., 2018a). The development of these management methods requires a thorough understanding of patterns, consequences, and long-term variability of fire, insect outbreaks, and other natural disturbances to adapt silvicultural practices to future shifts in climate.

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