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Using lake sediment records to reconstruct bark beetle disturbances in western North America

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Abstract. The recent outbreak of native bark beetles in western North America is unprecedented in severity and scale, at least during the historical period. The aim of this work is to develop a proxy-based methodology to understand how bark beetle disturbances are recorded in lake sediments. Three hypotheses are tested to determine how the ecological impacts of severe spruce beetle (Dendroctonus rufipennis) disturbances are recorded following mortality of Engelmann spruce (Picea engelmannii). Outbreaks are hypothesized to: (1) decrease the ratio of spruce to fir pollen; (2) increase soil erosion and mobilize terrestrial C; and (3) leach foliar N, enhancing algal productivity. To test these hypotheses, sediment cores from spruce beetle-affected basins were analyzed for pollen, insect remains, organic and minerogenic content, and isotopic and elemental concentrations. The dataset was tested statistically using generalized linear mixed models (GLMMs) to determine if the response variables differed significantly between outbreak and non-outbreak periods.

Keywords. bark beetles, climate warming, Dendroctonus, disturbance, subalpine forests

Introduction

The ongoing native bark beetle outbreak in western North America has affected over 47,000,000 ha of coniferous forest (Raffa et al. 2008). The social, aesthetic, and economic losses combined exceed those of wildfire and other forest disturbances (Logan et al. 2003). Warming temperatures are implicated in driving the outbreak in two significant ways: mediating shifts in beetle reproductive behavior (Hansen et al. 2001), and mitigating cold-induced mortality of overwintering beetles (Bentz et al. 2010). In addition to climate warming, landscape and land use history are also important in explaining the intensity of the recent outbreaks (J.L. Morris, unpubl. data). Model forecasts indicate that prolonged warming during the 21st century will enable irruptive beetle populations in ecosystems where they previously were limited by climate (Bentz et al. 2010).

As poikilotherms, spruce beetle (Dendroctonus rufipennis) reproductive cycles are responsive to temperature changes. During cool climate periods, two–three year reproductive cycles are common whereas the species may produce one generation per year in response to warm climate conditions (Hansen et al. 2001). In the Rocky Mountains, mature spruce beetles emerge to seek host trees when daily maximum temperature reaches 16 °C (Dyer 1969). Once the temperature threshold for beetle emergence is surpassed, attacking beetles select host trees based on chemical cues emitted by other colonizing beetles. Upon selection of a suitable host tree, beetles aggressively chew through the outer bark to access phloem tissue, generating large quantities of boring dust and excrement (frass) (Schmid and Frye 1977, Morris et al. 2013). Trees defend against invading bark beetles by flushing attack sites with volatile-rich sap, resulting in the formation of pitch tubes. If a host tree is moisture stressed, it produces less sap with which to repel invading beetles. However, during severe outbreaks, the quantity of attacking beetles is sufficient to overwhelm even healthy, vigorous trees. The trajectory of a watershed-scale spruce beetle disturbance is conceptualized in Figure 1.

The scale and severity of the bark beetle episode in western North America is believed to be unprecedented, at least during the 19th and 20th centuries (Raffa et al. 2008). Our current un-
Understanding of ‘precedence’ has been established using tree rings and historical reports (e.g., Veblen et al. 1994, Hebertson and Jenkins 2008). However, these records encompass the last several centuries and are reflective of a climate transition period between the cool and dry Little Ice Age and the anthropogenic warming period (Morris and Brunelle 2012). Further, climate conditions more analogous to the late 20th and those forecasted for the 21st century are potentially more similar to the conditions of the middle Holocene (8,000–4,000 cal yr BP) (Wanner et al. 2008). Sediment-based environmental reconstructions are vital for understanding past disturbance regimes (e.g., Davis 1981, Power et al. 2008) and can potentially provide long-term information on beetle disturbance dynamics. The aim of this research is to study the ecological outcomes of recent beetle outbreaks as recorded in lake sediments to develop an approach for reconstructing these important disturbance events during the Holocene (or last 11,700 years).

Figure 1. Conceptual diagram of the progression of a spruce beetle (Dendroctonus rufipennis) disturbance from endemic (Panel A), incipient or attack phase (Panel B), red or epidemic phase (Panel C), and grey or collapse phase (Panel D).
Recent work using lake sediments from the northern Rocky Mountains suggests that bark beetle exoskeletons preserved in sediments may provide a useful indicator of past beetle disturbances (Brunelle et al. 2008). A macrofossil-based approach is credible because historical reports document drifts of “beetles 6 inches (15 cm) deep and 6 feet (1.8 m) or more wide ... for more than 1 mile (1.6 km)” along a lakeshore in a beetle-affected watershed in Colorado (Schmid and Frye 1977). Understanding the taphonomic processes of environmental indicators is an essential, if not vital, foundation of paleoecology (Jackson 2012). One primary aim of my research was to test whether the findings of Brunelle et al. (2008) were repeatable and to gain a better understanding of how bark beetle remains might become entrained in lacustrine deposits.

A second aim was to develop a proxy-based strategy for reconstructing outbreaks. This hypothesis-based approach focused on predicting how observed changes to stand conditions would be reflected in the sedimentary profile. Emphasis was placed on the relationship between the canopy dominant host Engelmann spruce (Picea engelmannii) and the co-dominant non-host subalpine fir (Abies lasiocarpa) (see Veblen et al. 1994). Given the mortality level of canopy-dominant host trees observed in recent outbreaks (>90%), a biogeochemical response also would be expected. To assess the ecological and biogeochemical outcomes of spruce beetle outbreaks, I formulated three hypotheses: (1) that the loss of mature spruce across a landscape after an outbreak results in a significant decrease in the ratio of spruce to fir pollen; (2) that reduced canopy interception of precipitation following needlefall increases soil erosion and/or the mobilization of terrestrial C, i.e., woody litter, needles, frass, and boring dust; and (3) that needlefall will cause leaching of foliar N that will increase algal productivity and sedimentary N.

Methods

Site selection

South-central Utah was selected for this study because the region experienced severe bark beetle outbreaks on the Wasatch Plateau during the 1990s (Dymerski et al. 2001), Markagunt Plateau during the 1990s (DeRose and Long 2007), and the Aquarius Plateau during the 1930s (Morris and Brunelle 2012; Figure 2). Information regarding bark beetle outbreaks is inherently qualitative, even during the historical period. Unlike fire, modern detection of the onset and collapse of bark beetle eruptions are often difficult to pinpoint (Hebertson and Jenkins 2008). Characteristics of lakes selected for this study included USDA Forest Service documentation of a severe 20th century spruce beetle outbreak (Hebertson and Jenkins 2008), the presence of spruce-fir forest with visually detectable beetle-caused mortality, basins with limited man-made impoundments and surface water inflow/outflow, absence of stand-replacing wildfire during the 20th century, and no evidence of large-scale salvage logging to remove beetle-killed trees (Morris and Brunelle 2012). Based on these criteria, six basins were selected and cored using modified piston devices between 2005 and 2009 (Wright 1967).

Analysis of lake sediments

Six short sediment cores (two from each plateau) were dated using 210Pb/137Cs analysis (Morris and Brunelle 2012). Sedimentary pollen was isolated using standard methods and marker grains were introduced to calculate pollen accumulation rates (i.e. influx, grains/cm²/yr) (Fægri et al. 1989). Pollen subsamples were identified using laboratory reference material and relevant literature (citations provided in Morris and Brunelle 2012). Relative abundance (%), influx (grains/cm²/yr), and ratios were calculated for each pollen sequence (Morris and Brunelle 2012). Macrofossils were disaggregated from the sediment matrix with sodium hexametaphosphate [(NaPO3)6] and then screened through nested sieves (125, 250 μm) to isolate insect remains. Residues were examined using light microscopy and potential Dendroctonus spp. elytra and head capsules were submitted to a coleopteran taxonomist for identification (Morris and Brunelle 2012). Twenty-four additional undated cores were collected and screened for insect macrofossils. Continuous sediment sub-
samples were collected for each historic core for magnetic susceptibility, loss-on-ignition, and geochemical indicators, including stable light isotopes (δ¹⁵N and δ¹³C) and elemental concentration analysis (%C, %N, C/N ratio) (Morris et al. 2013). Due to the complexity of this dataset, the results were tested with generalized linear mixed model (GLMMs) using R software (Zuur et al. 2009).

Results

Macrofossils

No diagnostic remains for spruce beetle were found in correspondence to the historic outbreaks in any of the thirty short sediment cores (see Morris and Brunelle 2012).

Pollen

Morris and Brunelle (2012) found that the relationship between the host pollen (spruce) and non-host pollen (fir) tracked stand conditions. At all six sites, spruce pollen declined by an average of 86% during the outbreak while fir pollen increased by an average 25% (Figure 3). All pollen ratios moved from positive to negative values following the onset of the outbreak (Morris and Brunelle 2012; Figure 4). The spruce/fir pollen ratio is a statistically robust response variable (fixed effect = 0.50 ± 0.10 SE, random effect = 0.23, p < 0.001), shifting by a factor of -0.45 ± 0.06 SE between non-outbreak (1950–1985) and outbreak (1985–2000) status (Table 1; Morris et al. 2013).

Figure 2. (A) Map depicting the location of six subalpine lakes located on the Wasatch Plateau, Aquarius Plateau, and Markagunt Plateau. (B) Photographs of ‘ghost forests’ on the Wasatch, Markagunt, and Aquarius plateaus resulting from spruce beetle (Dendroctonus rufipennis) infestation of Engelmann spruce (Picea engelmannii) following outbreaks that occurred in 20th century. Living trees are subalpine fir (Abies lasiocarpa). Photo of the Aquarius Plateau provided by A. Steve Munson, United States Forest Service.
Geochemical

The geochemical, elemental, and organic responses to the historic outbreaks are heterogeneous across the six sites (Morris et al. 2013). In general, the magnetic susceptibility and CaCO₃ content of the sediments decreased significantly in response to the outbreak (p < 0.002, p < 0.0036, respectively; Table 1), although the variability among sites was considerable for both parameters. The δ¹⁵N, δ¹³C, and %C profiles generally declined (e.g., δ¹⁵N -0.18 ± 0.11) in response to the outbreak, however not at a statistically significant level across (e.g., δ¹⁵N p < 0.106; Morris et al. 2013). However, %N increased following outbreaks at some sites while at other sites no response was detected (e.g., increased at Emerald Lake, decreased at Aquarius Plateau lakes; Table 1; Morris et al. 2013).

Discussion

Despite reports of successful recovery of bark beetle macrofossils from lake sediments coincident with historic bark beetle epidemic (Brunelle et al. 2008), no bark beetle remains were found in the cores analyzed for this study. Morris et al. (2010) determined that the diagnostic features of bark beetles may be lost in certain chemical environments. Morris and Brunelle (2012) point out that for insect remains to be deposited in lake sediments, adult beetles must come in contact with surface water. They argue that it is probably a rare occurrence because bark beetles spend the majority of their life in subcortical chambers of their host trees and emerge only briefly for flight (about a week) during their 1–2 year lifespan. In the US Rocky Mountains, spruce beetle flight typically occurs in June (Dyer 1969). The National Climate Data Center reports that June 1949, the month when Schmid and Frye (1977) chronicled the extensive beetle carcass drifts, was the single wettest June during the 20th century (National Climate Data Center 2010); heavy precipitation during peak beetle emergence may have adversely affected flight and contributed to the re-

Figure 3. Summary of changes in the relative abundance of subalpine forest taxa during severe spruce beetle (Dendroctonus rufipennis) infestations in central and southern Utah (Morris and Brunelle 2012).
reconstructing bark beetle disturbances

Table 1. Results of GLMMs analyses examining the effects of spruce beetle (*Dendroctonus rufipennis*) population status (fixed effect) and sites (random effect). Beetle population status assigned to non-outbreak (e.g., Wasatch Plateau 1950–1985) and outbreak years (e.g., Wasatch Plateau 1985–2000). All intercepts are significantly different from zero (Morris et al. 2013).

<table>
<thead>
<tr>
<th>Response variable</th>
<th>Intercept (Estimate ±SE)</th>
<th>Fixed effects Beetle status (Estimate ±SE)</th>
<th>p</th>
<th>Random effect (variability among sites)</th>
</tr>
</thead>
<tbody>
<tr>
<td>spruce/fir ratio</td>
<td>0.50 ± 0.10</td>
<td>-0.45 ± 0.06</td>
<td>&lt;0.001</td>
<td>0.23</td>
</tr>
<tr>
<td>MS</td>
<td>1.34 ± 0.58</td>
<td>-0.52 ± 0.17</td>
<td>0.002</td>
<td>1.40</td>
</tr>
<tr>
<td>carbonate</td>
<td>10.91 ± 4.37</td>
<td>-0.88 ± 0.42</td>
<td>0.036</td>
<td>10.60</td>
</tr>
<tr>
<td>%N</td>
<td>1.30 ± 0.15</td>
<td>0.11 ± 0.06</td>
<td>0.071</td>
<td>0.36</td>
</tr>
<tr>
<td>δ¹⁵N</td>
<td>0.87 ± 0.26</td>
<td>-0.18 ± 0.11</td>
<td>0.106</td>
<td>0.62</td>
</tr>
<tr>
<td>C/N ratio</td>
<td>12.12 ± 1.10</td>
<td>-0.36 ± 0.34</td>
<td>0.295</td>
<td>2.64</td>
</tr>
<tr>
<td>δ¹³C</td>
<td>-18.25 ± 5.22</td>
<td>-0.23 ± 0.33</td>
<td>0.476</td>
<td>12.66</td>
</tr>
</tbody>
</table>

Figure 4. Summary diagram of spruce/fir pollen ratio for six replicate sites in southern and central Utah, USA. At all sites, the ratio shifts negative during historically documented spruce beetle (*Dendroctonus rufipennis*) disturbances, which are outlined in gray boxes.

ported carcass drifts.

The six pollen records summarized here reflect known ecological responses to severe spruce beetle disturbances. At all sites decreases in spruce pollen are accompanied by concurrent increases in fir pollen in response to outbreaks (Figure 3). In Figure 4, the spruce/fir pollen ratio is plotted against the mean 20th century ratio average for each site; the negative ratio shifts are significant across all sites (Table 1). At Banana Lake, which experienced an outbreak during the 1930s, the spruce/fir ratio remains low for several decades following the outbreak.

The geochemical and elemental analyses
indicate that post-outbreak alterations to nutrient cycling, hydrologic fluctuations, and canopy interception are not predictable indicators for reconstructing outbreaks. Changes to erosion and groundwater hydrology as assessed by magnetic susceptibility and CaCO₃ of sediments were significant but exhibited considerable variability among sites and therefore are not broadly applicable. Based on the work of Morehouse et al. (2008), we expected that post-needlefall, the C/N ratio would decrease from leaching of foliar N and enhanced algal productivity. However, our results indicate that in general, δ¹⁵N, %N, δ¹³C, and the C/N ratio did not differ at a statistically significant level between non-outbreak and outbreak periods (Table 1; Morris et al. 2013). It is possible that these lakes are receiving N contributions from salmonid fish stocking and atmospheric deposition from fossil fuel combustion (Wolfe et al. 2003, Morris et al. 2013). Alternatively, Rhodes et al. (2013) found that nitrate in surface water was lower than expected following outbreaks, which they attribute to N uptake by residual vegetation. More geochemical work is needed to improve our understanding of ecosystem nutrient cycling in response to beetle outbreaks.

Conclusions

Despite their obvious ecological and economic significance, surprisingly little is known about the recurrence and ecological role of native bark beetles prior to recent centuries. This is because, unlike fire disturbances, bark beetle outbreaks do not predictably deposit unequivocal evidence in sedimentary environments (e.g., charcoal produced by fire). In the thirty sediment cores that were screened for bark beetle remains, no elytra or head capsules were recovered in correspondence with documented outbreaks. Observations of ecological outcomes of beetle disturbances include reorganization of the terrestrial nutrient pool, relocation of terrestrial organic material, and increased surface and groundwater availability (e.g., Morehouse et al. 2008). I expected to see evidence of similar changes recorded in elemental, organic, and mineral constituents in the lake sediment deposits. However, my analysis suggests that basin-specific controls and anthropogenic activity confound the geochemical and elemental signal of recent outbreaks, despite similar forest composition and host tree mortality across sites. The ratio of spruce to fir pollen (host to non-host) responded most clearly and consistently to spruce beetle disturbances. My findings demonstrates that high-resolution pollen analysis is required to detect bark beetle disturbance, which may not be practical considering time and budgetary constraints of many research projects. Further, other non-fire disturbances such as windthrow and avalanches could influence the spruce/fir pollen ratio similarly. Efforts to reconstruct beetle disturbances would benefit from supporting lines of evidence, such as ancient DNA, biomarkers, and/or preserved insect remains. Success using pollen analysis may be limited to ecosystems where a canopy co-dominant host/non-host relationship exists. Because tree-ring studies have successfully reconstructed bark beetle disturbances prior to the historic period (e.g., Veblen et al. 1994), overlapping high-resolution pollen analysis with tree ring studies may offer more temporally extensive datasets that would facilitate rigorous statistical testing of pollen time series data and also provide information about landscape susceptibility to outbreaks (J.L. Morris, R.J. DeRose, & A.R. Brunelle, unpubl. data).

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