Modern pollen from small hollows reflects *Athrotaxis cupressoides* density across a wildfire gradient in subalpine forests of the Central Plateau, Tasmania, Australia

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Abstract
Pollen assemblages from 50 small hollows were used to resolve fire-caused vegetation patterns in a ~2-km^2 subalpine landscape on the Central Plateau of Tasmania, Australia. Sites were characterized by varying abundance of the dominant tree species, *Athrotaxis cupressoides*, reflecting mortality from a wildfire that occurred 53 years prior to sampling. Sites were classified a priori based on fire-related *Athrotaxis* mortality as burned (100% standing dead), unburned (<5% standing dead), and mixed (intermediate proportions). Non-parametric analysis of variance and discriminant analysis were used to quantify the variability in key pollen taxa and pollen ratios among burn classifications. The ratio of *Athrotaxis* to Poaceae pollen was the clearest metric distinguishing among burn classifications. When discriminant analysis was informed with data from the eight most dominant pollen data, samples were classified with high accuracy (0.96–0.98). Macroscopic charcoal concentrations varied widely among sites, but median values were consistent with inferred fire patterns, increasing in abundance from unburned to burned sites. The results support the use of small hollows to resolve fine-scale vegetation patterns (e.g. within 100 m of a site). The discriminant analysis function was also applied to five late-Holocene pollen samples from the study area, to test the potential of these methods to classify samples with unknown group assignments. The posterior probability of assigned group membership ranged from 0.85 to 0.99, demonstrating the similarity of the fossil pollen to the calibration dataset. Our calibration dataset provides a means to classify fossil samples from the region in terms of *Athrotaxis* cover and fire-caused mortality. This approach could be applied to other regions to quantify disturbance-related vegetation patterns or spatial heterogeneity over Holocene timescales.

Introduction

Pollen spectra from small hollows have been widely used to study local-scale vegetation change over Holocene timescales (Bradshaw, 1988; Calcote, 1997; Jackson and Kearsley, 1998; Mitchell, 2005; Sugimura et al., 2008). The vegetation interpretation from pollen records obtained from small-hollow sediments is well supported by theoretical (Sugita, 1994) and empirical studies (Calcote, 1995), which highlight the fidelity of pollen to stand-level vegetation composition (e.g. ≤100 m from a basin). Small-hollow records are also valuable for studying stand-level disturbances, including fire history inferred from macroscopic charcoal (Bradshaw and Lindbladh, 2005; Higuera et al., 2005; Sugimura et al., 2008). Detecting vegetation patterns at fine spatial scales using pollen from lake-sediment records can be challenging (Lynch et al., 2006; Minckley and Long, 2016; Prichard et al., 2009; Sugita et al., 1997) because the assemblages are an integration of the airborne pollen transported from within several kilometers of a site (Sugita, 1994, 2007). Pollen assemblages from small hollows, by contrast, mitigate the mismatch between pollen and patchy vegetation composition because of the local pollen source area; furthermore, by combining multiple small-hollow records, it is possible to reconstruct regional vegetation dynamics with a high degree of spatial precision (Bradshaw and Lindbladh, 2005; Dodson, 1988).

Interpreting vegetation patterns from pollen assemblages in small hollows (as with lake sediments) depends on understanding the relationship between modern pollen spectra and modern vegetation composition. Through the 'modern analog technique' (Gavin et al., 2005; Iglesias et al., 2016; Jackson and Williams, 2004; Williams and Shuman, 2008), fossil pollen samples can be

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qualitatively or quantitatively assigned to modern vegetation types. This approach has been used to reconstruct vegetation history from forest stands (Sugimura et al., 2008) to subcontinental scales (Shuman and Marsicek, 2016). Modern analog approaches could also be used to identify levels of disturbance within a single forest type, provided that (1) the vegetation is significantly altered by the disturbance event in ways that pollen data can detect; (2) the temporal resolution in pollen samples captures post-disturbance vegetation composition, prior to vegetation recovery; and (3) the mechanisms linking vegetation patterns to pollen assemblages do not change through space or time.

In this study, we characterized the pollen spectra in modern surface-sediment samples from a network of 50 small hollows on the Central Plateau of Tasmania, Australia. The study area burned in the austral summer of 1960–1961 (1960 fire hereinafter), and the vegetation now spans a gradient of post-fire tree mortality and vegetation recovery. Although this fire occurred 53 years prior to sampling, a lack of post-fire *Athrotaxis cupressoides* (pencil pine, *Athrotaxis* hereinafter) recruitment has resulted in distinctly different vegetation composition in burned and unburned sites (Holz et al., 2015). Our goal was to test the utility of small hollows for resolving these fire-caused vegetation patterns and gain insights about the spatial scale represented by the pollen spectra. We expected that sites that experienced high fire-caused tree mortality would be distinguishable from unburned sites as a result of differences in the abundance of *Athrotaxis* pollen, as well as by the presence of pollen taxa that survive or respond positively to fire. We applied statistical classification methods (i.e. non-parametric analysis of variance (ANOVA) and discriminant analysis (DA)) to compare modern pollen spectra among three burn classifications (burned, mixed, and unburned) and then used these relations to classify five fossil samples from the same region.

Study area

The Central Plateau of Tasmania was extensively glaciated during the Pleistocene, and the present-day vegetation communities established at around 3000–4000 years ago (Dodson, 2001; Hopf et al., 2000; Stahle et al., 2016; Thomas and Hope, 1994). Modern vegetation is characterized by spatially heterogeneous patches of eucalypt woodlands at low elevations, coniferous forests and woodlands at higher elevations, and alpine heath above treeline (Jackson, 1972). Pure stands of *Athrotaxis* are characterized by low tree densities, with an understory of grass (e.g. *Poa billardieri*) and *Sphagnum* (Jackson, 1972).

Athrotaxis is a slow-growing conifer with individual trees reaching 1000 years in age (Jackson, 1972). Mature trees are relatively resistant to frost, drought, and surface fire (Holz et al., 2015). European settlement during the 19th and 20th centuries altered the Tasmanian landscape, through forest clearance, introduction of non-native mammals (e.g. sheep and rabbits), and frequent and sometimes severe fires. These land-use changes resulted in a widespread decline of conifer forest cover (Jackson, 1972). During the 1960 fire, three separate human ignitions burned 60% of the Central Plateau, resulting in *Athrotaxis* mortality over 30% of its native range (Corbett, 1996; Johnson and Marsden-Smedley, 2002). Post-fire regeneration of *Athrotaxis* has been extremely slow, as a result of its impoverished seedbanks, poor seed dispersal capabilities, and limited survival in the face of browsing (Holz et al., 2015).

Materials and methods

We use the mortality of *Athrotaxis* from the 1960 fire to identify and categorize 50 sites within our 2-km² study area (Figure 1), based on inferred 'fire severity' at the spatial scale of a forest stand (i.e. 100 m²). Fire severity reflects the impacts of burning on biomass, with % tree mortality commonly used to classify fire severity in forested ecosystems (Keeley, 2009). Tree mortality from the 1960 fire is still clearly evident in the study area, thus providing a robust indicator of fire impacts on tree biomass (Figure 1a–c). Sites with 100% standing dead *Athrotaxis* within a radius of 30–100+ m of the coring site were classified as 'burned' ($n = 17$) and likely experienced high fire severity at the stand scale. Among the burned sites, the median distance to the burn boundary (Figure 1) was 850 m (minimum: 180 m, maximum: 1100 m). Sites with both mature living and dead *Athrotaxis* within a radius of 30 m of the coring site were classified as 'mixed' ($n = 16$) and likely experienced spatially variable burning, with a mix of patches experiencing no/little burning, surface fire, or crown fire. Among mixed sites, the median distance to burn boundary was 230 m (minimum: 30 m, maximum: 800 m). Sites with primarily living mature *Athrotaxis* within a radius of 30 m were classified as 'unburned' ($n = 17$), and the median distance to the burn boundary for these sites was 270 m (minimum: 30 m, maximum: 650 m). At some 'burned' sites, we also observed evidence of soil erosion, which was presumably fire-related and has likely impeded vegetation recovery. Thus, although our a priori classification of 'burned', 'mixed', and 'unburned' primarily reflects the severity of the 1960 fire, variations in present-day vegetation may also reflect site-specific differences and levels of post-fire recovery.

We collected surface-sediment samples at 50 small hollows and ponds in January 2013 (Figure 1). Sites were generally <10 m in diameter with water depths <1 m. For 36 locations, surface sediments were collected from the top 1 cm of sediment using a stainless-steel spoon. The remaining 14 samples were taken from the uppermost 0.5 cm of sediments retrieved with a Russian peat corer (Jowsey, 1966).

Sediment samples of 1 cm³ were processed for pollen following standard laboratory procedures (Faegri and Iversen, 1989). Slide-mounted pollen residues were examined and counted using light microscopy at 500× magnification to a minimum of 300 terrestrial grains, with identification aided by the Australian Pollen and Spore Atlas (APSA Members, 2007). Pollen percentages were calculated based on a sum of total terrestrial pollen; however, because the aim of our study was to use modern pollen assemblages to characterize past vegetation, pollen types from European-introduced species (always <5% of any sample), such as *Acaena* spp. (sheep's burr) and *Pinus radiata* (Monterey pine), were excluded from further analyses. Cupressaceae was assigned to *Athrotaxis cupressoides*, although *Diselma archeri* (dwarf pine) may also have contributed to this pollen type.

We used three methods to test whether variability in pollen assemblages could be used to distinguish among burn classification. First, box plots were developed to visualize the distributions of pollen percentages of key taxa and the ratio of *Athrotaxis* to Poaceae pollen (*Athrotaxis*:Poaceae). This ratio was used to emphasize tradeoffs between tree and grass pollen, and it was calculated using pollen counts and the formula $(a − b)/(a + b)$ to standardize values. Second, a Kruskal–Wallis non-parametric ANOVA (with an alpha level of 0.05) was used to test for significant differences among median pollen percentages or ratios. Third, linear DA was employed to corroborate the previous two analyses, provide a tool to apply to fossil (i.e. 'unknown') samples, and evaluate how well linear functions classified pollen assemblages into the three burn categories (Gavin et al., 2005; Liu and Lam, 1985; Lynch, 1996; Sugimura et al., 2008). We evaluated the results of the DA using classification accuracy, defined as $(TP + TN)/(P + N)$, where TP and TN are the number of true positives (TP) and true negatives (TN), and P and N are the total number of positives and negatives for any single classification, respectively. We also evaluated the ability of DA to correctly classify samples not used in creating the discriminant functions through a leave-one-out cross validation.
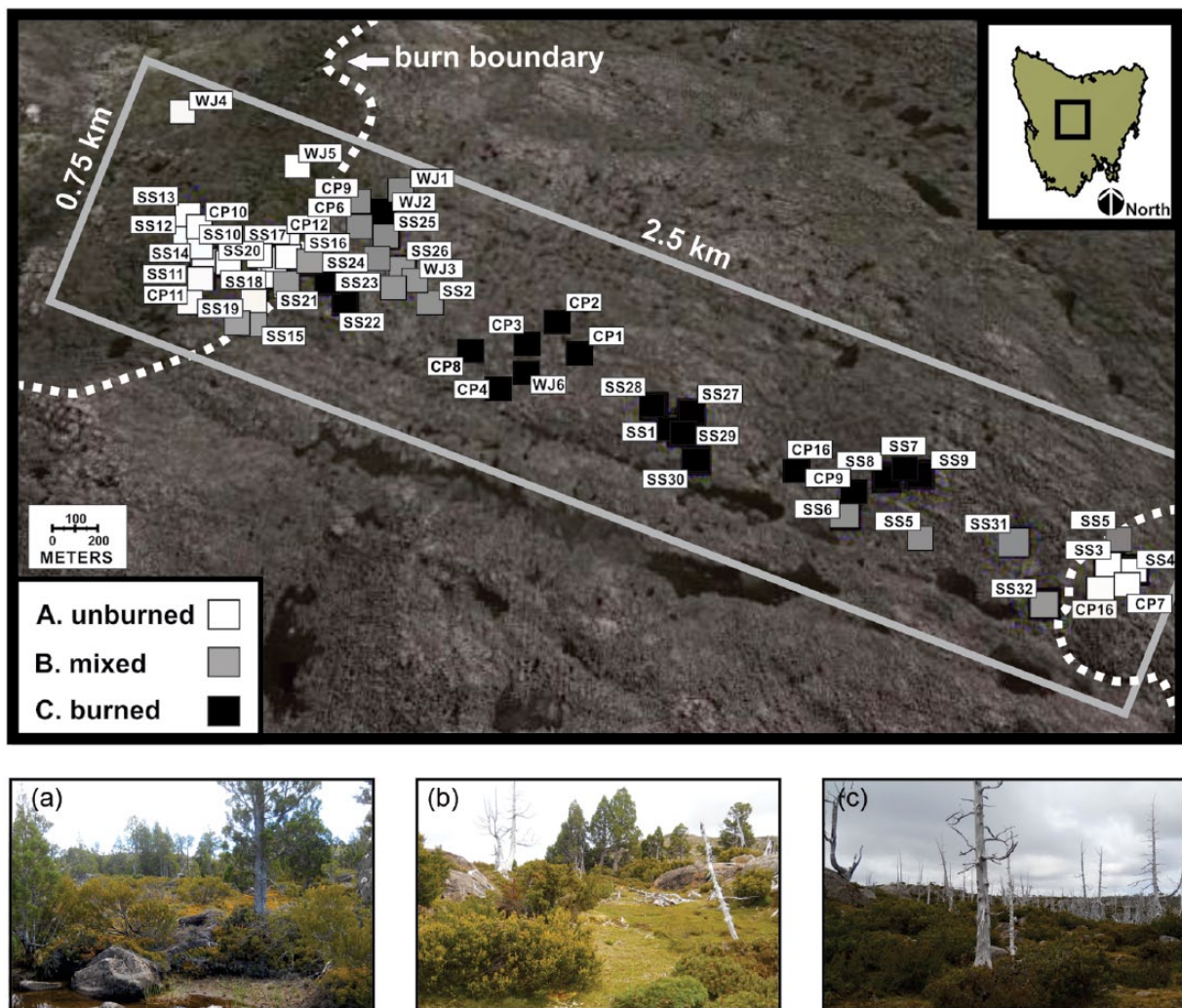
Figure 1. Map depicting the location of pollen surface samples collected in January 2013 on the Central Plateau of Tasmania, Australia: (a) unburned, (b) mixed, and (c) burned. The dashed line represents the approximate boundary of the 1960–1961 fire, and the shaded boxes correspond to fire-related mortality classifications based on *Athrotaxis cupressoides*. Elevations across the study area range from 1290 to 1320 m a.s.l. Photos show representative mortality observed in the field (with a, b, and c corresponding to the map legend).

We applied the discriminant functions to five fossil samples from core CP13-10, which spanned the last 2000 years (Higuera, unpublished data; Figure 1). DA provides a posterior probability of membership for each category, thereby allowing an analyst to potentially classify unknown samples into groups defined in the modern calibration dataset. For each fossil sample, we assumed a 1/3 prior probability of membership within each burn category (i.e. an uninformed prior). All analyses were done with R (R Development Core Team, 2013), and prior to analyses, pollen percentages were square-root transformed to normalize distributions and downweight abundant taxa. Results, however, were virtually identical when using non-transformed data.

Sediment samples of 1 cm³ volume were processed for macroscopic charcoal at 42 of the surface sample sites. Samples were soaked in an equal solution (9 mL each) of 5% sodium metaphosphate and 6% sodium hypochlorite for 24 h to disaggregate the sediment and remove or lighten non-charcoal organic content. Charcoal particles were counted at 10–40× magnification and quantified as a concentration (particles/cm⁻³). We compared charcoal concentrations among burn categories with box plots and in a non-parametric ANOVA, as with pollen data. We did not include the charcoal data in the DA, for two reasons. First, unlike pollen percentages, charcoal concentrations are sensitive to the amount of time integrated into a surface sample because fire is a discrete event in time, whereas vegetation patterns (e.g. fire-caused tree mortality) persist for decades. The discrete nature of fire motivates

the use of charcoal accumulation rates, but this was not possible in this study in the absence of a chronology. Second, the goal of the DA was to test the ability of pollen to discriminate among burn categories. The charcoal data were used as an additional important proxy to support the fire-related vegetation classification.

Results

Modern pollen assemblages were dominated by six taxa, which averaged >5% across all samples (from most to least abundant): *Athrotaxis*, Poaceae, Cyperaceae, Ericaceae (likely *Richea sprengelioides*), *Eucalyptus* (likely *E. coccifera*), and *Astelia alpina* (Figure 2). *Orites-Bellendena* type (likely *O. revolutus, Orites* hereinafter), *Leptospermum–Baeckea*, and Asteraceae were the three additional taxa that averaged between 2% and 5% across all samples. For quantitative analyses, we excluded Cyperaceae because its abundance varied widely among sites, likely reflecting local moisture levels (e.g. submerged vs dry surfaces). We did include the following six additional taxa for quantitative analyses (for a total of 14), which averaged <2% among all samples but are ecologically relevant in our study area (from most to least abundant): *Juncus, Lomatia, Apium*, Amaranthaceae, *Euphrasia*, and Rhamnaceae (Figure 2).

Pollen assemblages from unburned, mixed, and burned sites showed significant differences among median pollen percentages ($n = 6$) and pollen ratios ($n = 1$), integrating information
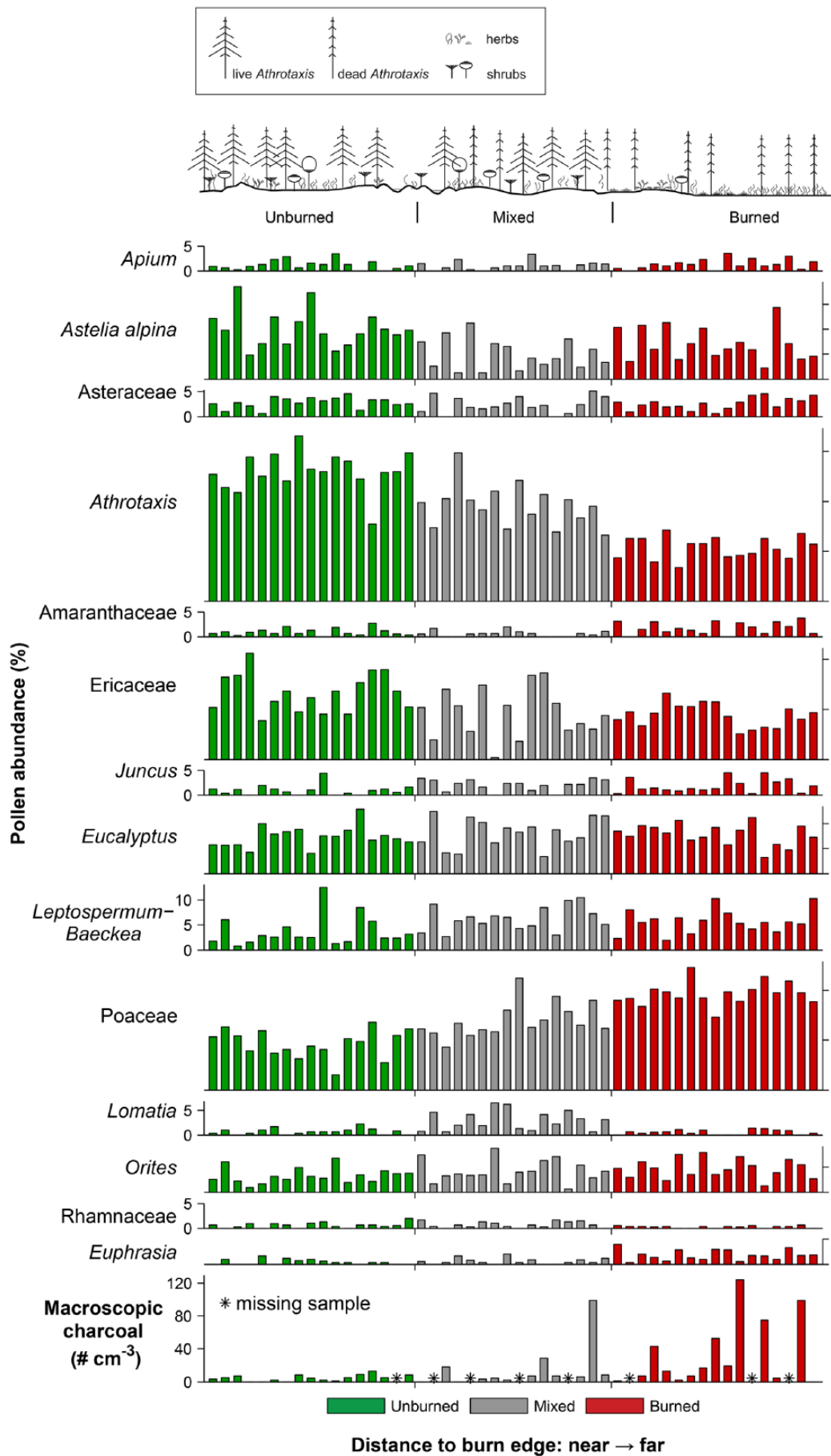
Figure 2. Relative abundance plots and charcoal concentration from surface samples from 50 small hollows from the Central Plateau of Tasmania, Australia. Within each category, samples are ordered by distance to burn edge, from left (closest) to right (farthest; see 'Materials and methods' for distance values for each category). For a color version of this figure, see the online version of this paper.
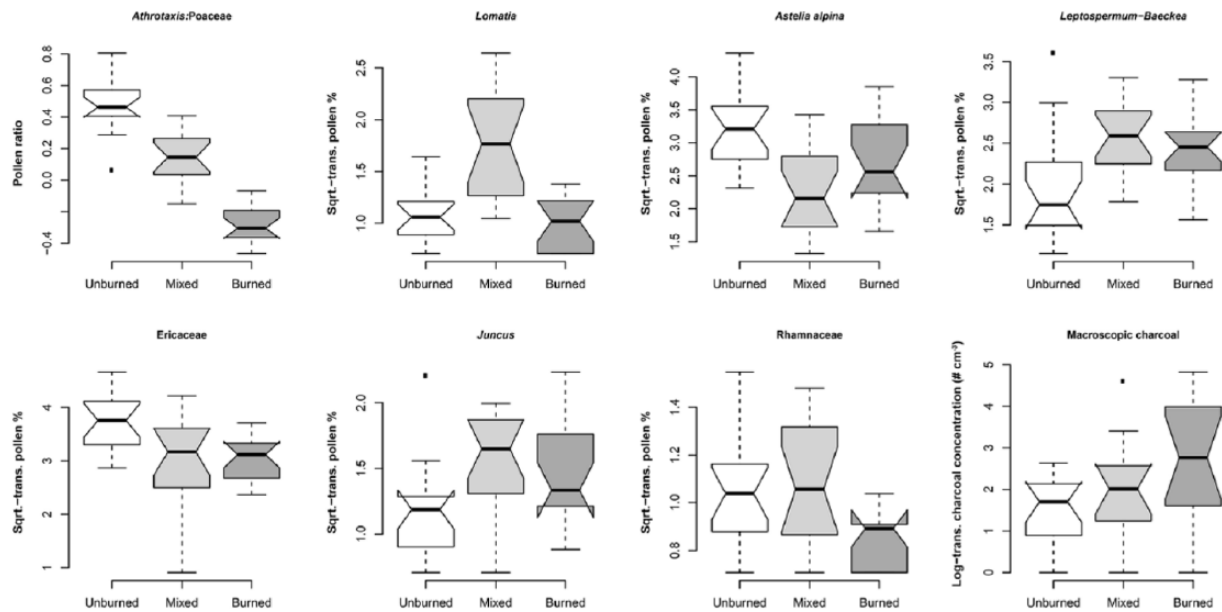
Figure 3. Distribution of key pollen ratios and taxa among the three burn classifications. Boxes outline 25th and 75th percentiles, with notches approximating 90% confidence intervals around the 50th percentile (median, dark horizontal line). Whiskers identify the 10th and 90th percentiles, and dots identify outliers. All taxa or ratios had significantly different median values among burn classifications, as indicated by a Kruskal–Wallis non-parametric ANOVA ($p < 0.05$), whereas charcoal concentrations yielded a p value of 0.061. Taxa are ordered from upper left to lower right by the p value from the Kruskal–Wallis test (from low to high). Note that charcoal concentrations are displayed as log-transformed values (with 1 added to 0 values to accommodate transformation), but this does not affect the non-parametric ANOVA results.

from 8 of the 14 taxa used in our analyses (Figure 3). Burned sites were characterized by low *Athrotaxis* pollen (average ~10%) and high Poaceae pollen percentages (average ~20%). The *Athrotaxis*:Poaceae ratio clearly distinguished all three categories, with high median values in unburned sites (0.48) and lower values in mixed (0.18) and burned (−0.31) sites (Figure 3). A number of other pollen types showed significant but not unidirectional differences among burn categories, including *Lomatia, Astelia alpina, Leptospermum–Baeckea*, Ericaceae, *Juncus*, and Rhamnaceae (Figure 3). For example, the median value of *Lomatia* was significantly higher from mixed sites, compared with the median value from unburned or burned sites. Median values of *Leptospermum–Baeckea* and *Juncus* were significantly higher in mixed and burned sites, compared with unburned sites (Figures 2 and 3). In contrast, Ericaceae pollen percentages were higher in unburned compared with mixed or burned sites (Figure 3).

Macroscopic charcoal concentrations varied from 0 to 124 particles cm^{-3} in surface samples from unburned, mixed, and burned sites, with high variability within each category (Figure 2). Median charcoal concentrations increased from unburned to mixed to burned sites, from 4.5 to 6.5 to 15 particles cm^{-3}, respectively (Figure 3). The non-parametric ANOVA comparing median values yielded a p value of 0.061, not significantly different at alpha = 0.05 but significantly different at alpha = 0.10 level.

A DA, which was based on the six pollen types and one ratio (*Athrotaxis*:Poaceae) that varied significantly among burn categories (i.e. listed in Figure 3), accurately classified samples from unburned (0.98), mixed (0.96), and burned (0.98) sites (Figure 4). These results were robust to leave-one-out cross validation, with accuracy decreasing to 0.94 for unburned, 0.90 for mixed, and 0.96 for burned sites. Discriminant axis 1 explained 79% of the variability among pollen spectra, clearly separating burned (high values) and unburned sites (low values), with mixed sites with intermediate axis 1 values. The most influential taxa along axis 1 were *Athrotaxis* and Poaceae (as represented by their ratio), with high ratios associated with low axis 1 values

(Figure 4). Axis 2 explained the remaining 21% of variability, with high values associated with unburned sites and low values associated with mixed sites. The most influential taxa along axis 2 were *Lomatia*, Rhamnaceae, and *Astelia alpina*, with the former two associated with mixed sites and the latter indicative of unburned sites (Figure 4).

Fossil pollen spectra from the five samples in core CP13-10 were composed primarily of *Athrotaxis, Astelia*, and Poaceae (all taxa 10–20%) and to a lesser degree Asteraceae, Ericaceae, and *Eucalyptus* (all taxa 5–10%). The composition of fossil samples broadly matched pollen assemblages from the modern samples, reflecting subalpine vegetation communities observed across our study area. When applied to these fossil samples, the discriminant functions yielded high posterior probabilities of burn-category membership, ranging from 0.85 to 0.99. Based on the highest probability of group membership, two samples were classified as similar to modern samples from 'unburned' sites, one was classified as most similar to 'mixed' sites, and two were most similar to modern samples from 'burned' sites (Figure 4).

Discussion

This study adds support for the use of pollen from small hollows as a tool for detecting stand-level vegetation heterogeneity, regardless of cause, and it provides the first application of these methods to subalpine forests in Tasmania. Pollen spectra from the 50 surface samples accurately placed samples within three predefined categories of *Athrotaxis* abundance, even though the majority of burned sites were relatively close (<850 m) to unburned forest. Even the five unburned sites within 100 m of the burn edge were correctly classified (e.g. those along the border of the 1960 fire; Figures 1 and 4), indicating that small hollows can resolve vegetation patterns within <100 m of a site. The ability to resolve this fine-scale spatial variability stems from the small basin size of the study sites and thus their local pollen source area (Bradshaw, 1988; Calcote, 1997; Jackson and Kearsley, 1998; Parshall, 1999; Sugimura et al., 2008). Additionally, by aggregating multiple, locally sensitive small-hollow
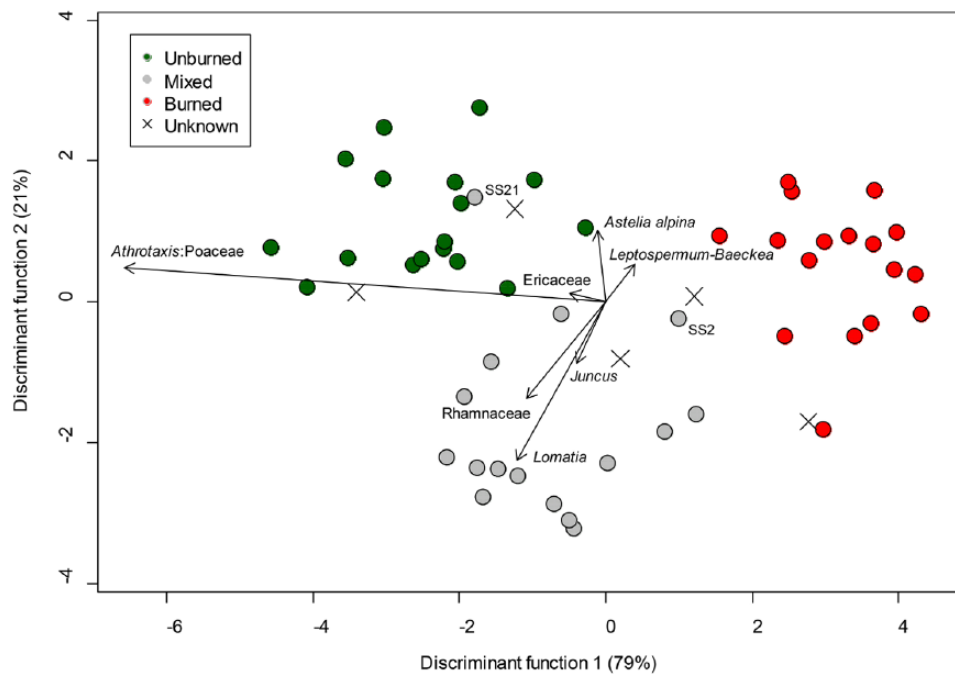
Figure 4. Discriminant analysis results. The two discriminant functions accurately classified samples into unburned, mixed, and burned classes, with classification accuracy of 0.98, 0.96, and 0.98, respectively. Discriminant function 1 was most strongly influenced by the ratio of *Athrotaxis* to Poaceae (negative values), while discriminant function 2 was most strongly influenced by *Lomatia* (negative values) and *Astelia alpina* (positive values). The two misclassified samples were both from mixed sites, each identified by the site name: SS21 was misclassified as 'low', and SS2 was misclassified as 'high'. Fossil samples ('Unknown') were classified as unburned ($n = 2$), mixed ($n = 1$), and burned ($n = 2$). For a color version of this figure, see the online version of this paper.

sites, we were able to detect landscape-scale fire-caused vegetation patterns. The charcoal data also show higher concentrations of charcoal in sites that burned compared with mixed or unburned sites, supporting inferences of a small source area (e.g. within 100 m) of macroscopic charcoal in small-hollow systems (Higuera et al., 2005).

Our study also provides information about the pollen composition of post-fire vegetation communities in the Central Plateau region of Tasmania, and the potential of DA to classify fossil pollen samples into fire-related categories. DA distinguished present-day samples from burned and unburned sites with near perfect accuracy. Sites from mixed burns with intermediate levels of *Athrotaxis* mortality were more difficult to classify. They were characterized by intermediate levels of the dominant taxa (e.g. *Athrotaxis* and Poaceae) and also featured high percentages of *Lomatia* pollen not found in either burned or unburned sites. The high abundance of *Lomatia* in mixed sites may reflect its ability to resprout from lignotubers after low and intermediate levels of burning, and its tendency to grow in semi-shaded environments (Dickinson and Kirkpatrick, 1987). *Lomatia* is also relatively unpalatable to non-native and native browsers (Jackson, 1972). The low abundance of *Lomatia* in burned sites may reflect heat-caused mortality of belowground biomass or loss of soil organic matter from fire-caused erosion, both of which would favor herbaceous colonization over resprouting shrubs. Variability among site classifications in other pollen taxa may additionally reflect both pre-fire environmental conditions and fire-caused vegetation change. For example, *Astelia alpina* prefers mesic sites and grows near perennially wet areas (Dickinson and Kirkpatrick, 1987), conditions that would reduce the probability of burning. With only a snapshot in time from the surface sample dataset, we are unable to infer the degree to which the consistently high *Astelia alpina* pollen in unburned sites reflects pre-fire environmental condition versus fire-caused vegetation patterns.

The use of small-hollow pollen assemblages to reconstruct disturbance-related vegetation patterns comes with three important limitations. First, the ability to detect differences in pollen spectra from our sites stems in part from site selection that emphasized distinct differences in the canopy dominance of a single species (*Athrotaxis*), forming the basis of our a priori classification of fire-caused mortality. If *Athrotaxis* were less abundant and/or Poaceae more abundant in space or time (and pollen from these taxa scaled accordingly), the discriminant function developed here could incorrectly classify samples as similar to 'burned' sites, regardless of disturbance history. Thus, without complementary evidence for fire (e.g. macroscopic charcoal), we advise against using pollen alone to infer disturbance history.

Second, local vegetation patterns could be distinguished in the pollen data because post-fire recovery rates of the dominant pollen contributors (e.g. *Athrotaxis*) were relatively slow. This situation is also true for other subalpine species in this region, which require decades to centuries to return to pre-disturbance abundances (e.g. Fletcher et al., 2014). In other regions and other study areas, detecting fire-related vegetation change from pollen data would be possible only if the temporal sampling resolution is shorter than the time it takes for vegetation to return to pre-fire states.

Third, our sites occur within a small area (~2 km²) of subalpine vegetation on the Central Plateau. Although we sampled 50 sites, this aspect of our study increases the risk of encountering a 'no-analog' scenario, wherein a fossil ('unknown') sample is a poor match to any modern samples (Jackson and Williams, 2004). However, a key advantage of the DA used in this study is that group membership is based on posterior probability, thus helping identify no-analog scenarios. For example, when applied to the five fossil samples from a sediment core in our study area, the lowest posterior probability of group assignment was high (0.81), suggesting a relatively strong match to samples from the calibration dataset. A low posterior probability (e.g. 0.10) would indicate a no-analog scenario, in which classification is not possible based on the modern calibration dataset.

Conclusion

The calibration dataset developed here and its application to fossil samples provide a quantitative approach for interpreting fossil pollen spectra in the context of modern vegetation characteristics. Despite the small spatial extent of the study area, significant differences in the *Athrotaxis*:Poaceae ratio observed here are likely applicable in other pollen assemblages on the Central Plateau (in space or time) because pollen ratios are less sensitive than pollen percentages to pollen rain from other taxa. Our data suggest that high *Athrotaxis*:Poaceae ratios are a strong indicator *Athrotaxis* woodlands, which are unlikely to occur with frequent high-severity events such as the 1960 fire. Our approach also provides a framework for pollen-based reconstructions of spatially heterogeneous vegetation, irrespective of cause. Applying these techniques to other region-specific calibration datasets would facilitate insights into disturbance-mediated vegetation change and help assess the magnitude of modern disturbance impacts in the context of the long-term paleoecological record.

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