Combining phytolith analysis with historical ecology to reveal the long-term, local-scale dynamics within a savannah-forest landscape mosaic

Jenny L. McCune · Mark Vellend · Marlow G. Pellatt

J.L. McCune (corresponding author)
The Department of Botany and Biodiversity Research Centre, University of British Columbia,
3529-6270 University Blvd., Vancouver, BC, Canada V6T 1Z4
Current address :
Department of Integrative Biology, University of Guelph
Guelph, ON, Canada N1G 2W1
email: jmccune@uoguelph.ca
phone: 519-824-4120 ext. 52756/ Fax: 519-767-1656

M. Vellend
Département de biologie, Université de Sherbrooke, 2500 boulevard de l'Université, Sherbrooke,
QC, Canada J1K 2R1

M.G. Pellatt
Parks Canada, Natural Resource Conservation, Protected Areas Establishment and Conservation
Directorate, 300-300 West Georgia St., Vancouver, BC, Canada V6B 6B4

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Abstract

An understanding of the historical range of variability of an ecosystem can improve management and restoration activities, but this variability depends on the spatial and temporal scale at which it is measured. We examined the extent of local-scale variation in vegetation prior to European settlement across a savannah-forest landscape mosaic on southeastern Vancouver Island, British Columbia, Canada. We used phytoliths extracted from soil surface samples to calibrate an index that differentiates open savannahs from closed canopy Douglas-fir forests and then examined shifts in this index with soil depth at seven local sites. We tested whether changes with depth aligned with known vegetation changes based on land survey records from the mid-1800s, and then inferred vegetation change prior to European settlement. The log ratio of astrosclereids (phytolith specific to Douglas-fir) and rondels (phytolith specific to grasses) in soil surface samples accurately distinguished between current vegetation types, and shifts in this ratio with depth were sensitive to known historical changes in most of the cores. Some sites have supported open savannah vegetation for at least two thousand years, while others that were formerly open have been filled in by Douglas-fir forest. However, this infilling appears to have begun at different times for different sites. Our findings demonstrate that the degree and timing of historical variation in vegetation can differ between local sites within a broader regional landscape that appears relatively stable.

Keywords British Columbia · Douglas-fir · Garry oak · Historical range of variability · Landscape history · Paleoecology

Introduction

The degree of variation of an ecological system, and the factors driving this variation, depend on the spatial and temporal scale at which the system is observed. For example, the vegetation across a landscape can appear relatively stable, whereas on a patch-level scale there are dynamic changes (Watt 1947; Gillson 2004). Similarly, a system may be considered to be at equilibrium on a temporal scale of centuries although fluctuating from one year to the next (Wiens et al. 2012). Not only does the degree of variation change depending on spatial or temporal scale, but the drivers of ecological patterns can change (Willis and Whittaker 2002). For example, the most important environmental variables predicting species richness have been found to differ depending on spatial resolution (Rahbek and Graves 2001), and the negative relationship between the richness of exotic and native species at a regional scale shifts to a positive relationship at a local scale (Fridley et al. 2007). Therefore, it is essential to consider scale explicitly in all studies of ecological systems, with the goal of determining which factors are most influential in determining ecosystem structure and function at which scales (Willis and Whittaker 2002; Gillson 2004).

The role of scale in understanding ecological processes and patterns has important implications for conservation and restoration. Land managers often use an ecosystem's historical range of variability to provide context for choosing an appropriate restoration goal (Keane et al. 2009; Wiens et al 2012). Clearly, the historical range of variability observed in a system will depend on the spatial and temporal scale at which it is measured (Jackson 2006; Wiens et al. 2012). Taking this into account requires the integration of techniques from historical ecology and paleoecology to bring together lines of evidence with different temporal and spatial scales (Delcourt and Delcourt 1988; Swetnam et al. 1999; McCune et al. 2013). Such studies often show that the system to be restored was not in a state of equilibrium even prior to the dramatic changes initiated by European colonization and/or industrialization over the past few centuries. In some cases, the conditions managers aimed to conserve were actually relatively recent formations resulting from climatic changes within the last millennium (Grimm 1983; Hotchkiss et al. 2007). In others, the changes attributed to recent human disturbance actually had roots in earlier climatic shifts and/or cultural practices (Swetnam et al. 1999).

In this study, we aim to measure the extent of local-scale (1 ha or less) vegetation variation within a landscape mosaic of oak savannah and coniferous forest on southeastern Vancouver Island, British Columbia, Canada. The long-term vegetation history of this region is relatively well-known (McCune et al. 2013). On a regional scale (300-400km^2), pollen records indicate that oak savannahs have been maintained on the landscape at a consistent and relatively low level for approximately the past 3,000 years (Heusser 1983; Pellatt et al. 2001). Work based on land survey records from the mid-1800s has quantified dramatic increases in tree density across the landscape and a decline of open savannah habitats since European settlement in the mid-1800s (Lea 2006; Bjorkman and Vellend 2010). These changes are attributed to the destruction of savannahs to make way for agriculture, and widespread fire suppression (MacDougall et al. 2004; Bjorkman and Vellend 2010). However, the stability of savannahs in the centuries prior to the first land surveys on a local spatial scale is not clear. Was the openness of the landscape at the time of European settlement a relatively stable condition extending back centuries or millennia, or was the vegetation already on a trajectory of increasing tree density due to climatic and/or cultural changes in the centuries before? Did the amount of variation in vegetation before settlement differ between local sites? Our objective was to assess the ability of a novel paleoecological proxy for this region - the soil phytolith record - to answer these questions. The answers are necessary to provide a more thorough understanding of the historical range of variability of these systems on a local scale, and the linkages between climate, land use, and local edaphic conditions in driving vegetation change on this landscape.

Methods

Description of the study area

The study area is located on the southeastern tip of Vancouver Island, between latitude 48°10'N and 49°20'N and longitude 123°W and 124°W (Fig. 1). This region is in the rain shadow of the Olympic and Vancouver Island Mountains, causing drier conditions than those found anywhere else along the coast of British Columbia. The climate is described as sub-Mediterranean, with mild winters and long, dry summers (Meidinger and Pojar 1991) which support dry Coastal Douglas-fir forests and Garry oak savannahs.

Coastal Douglas-fir forests are dominated by Douglas-fir (*Pseudotsuga menziesii*), with components of western red-cedar (*Thuja plicata*), grand fir (*Abies grandis*), red alder (*Alnus rubra*) and bigleaf maple (*Acer macrophyllum*; Egan 1999; Flynn1999). The Garry oak (*Quercus garryana*) is at the northern edge of its range here, and has become the flagship species for a complex of associated vegetation types including savannahs, oak woodlands, and meadows (Fuchs 2001; GOERT 2011). Garry oak savannahs consist of an open canopy of oak with an understory dominated by native wildflowers and grasses. Over 90% of the Garry oak- associated vegetation types present just prior to European settlement have been lost to agricultural or urban land use (Lea 2006). The remnants are highly fragmented, invaded by introduced exotic species, and concentrated in higher elevation, rocky areas (Parks Canada Agency 2006; Vellend et al.

2008). The few savannahs left on deep soil sites are susceptible to infilling by Douglas-fir in the absence of fire (Fuchs 2001).

This region has a rich human history long before the arrival of Europeans. Indigenous peoples have lived here for at least 5,000 years (Grier et al. 2009). Some Garry oak savannahs were maintained by frequent, low intensity fires set purposely by people (Turner 1999; MacDougall et al. 2004). These fires preserved the open conditions that favoured important food plants like camas (*Cammassia* spp.; Turner and Kuhnlein 1983; Turner 1999). Human management may have contributed to the maintenance of Garry oak savannahs for thousands of years (Pellatt et al. 2001; McCune et al. 2013). However, the decimation of the indigenous population by introduced diseases, and European-enforced fire suppression, put an end to management by fire (Harris 1994; Turner 1999; MacDougall et al. 2004).

The phytolith record as a paleoenvironmental indicator

Phytoliths are silica-based microfossils formed when hydrated silicon dioxide is deposited within and between plant cells (Pearsall 2000). They remain in the soil upon the decay of plant tissue. The use of the soil phytolith record for paleoenvironmental interpretation is still young compared to the use of fossil pollen assemblages from lake or pond sediments (Piperno 1988), and has not yet been utilized in our study region. The phytolith record has the advantage of relatively high spatial resolution due to the limited dispersal of phytoliths (Fredlund 2005). It offers evidence of vegetation change at a finer spatial resolution to compare with what is already known about vegetation change in the broader region based on pollen analysis of sediment from Saanich Inlet and lake cores (e.g. Pellatt et al. 2001; Lucas and Lacourse 2013).

The phytolith record preserved in terrestrial soils is formed via the continuous input of phytoliths to the soil surface combined with organic matter accumulation, weathering of the parent material, translocation of phytoliths and other materials, bioturbation and other soil-forming processes (Alexandre et al. 1999; Targulian and Goryachkin 2004). This gradual but continuous process of phytolith incorporation into the soil profile, called “inheritance” (Fredlund and Tieszen 1994), can document vegetation shifts as long as major erosional events and deep soil mixing can be ruled out. For example, a high concentration of grass-produced phytoliths throughout a soil profile indicates that grasses have formed a significant proportion of the vegetation on the site for a considerable length of time (e.g. Evett et al. 2007). The key to successfully using phytoliths to interpret past vegetation changes is to combine the phytolith record with independent lines of evidence for vegetation shifts derived from historical or other paleoecological data. This way, the sensitivity of the phytolith record to known vegetation changes, and the reliability of various methods for dating these changes, can be tested before interpretations are made at other sites. This strategy has already been used successfully by integrating phytolith studies with legacy data and aerial photographs (McNamee 2013), land survey records (Evett et al. 2012), written and oral records of vegetation change and fire occurrence (Morris et al 2009, 2010), palynological data (Piperno 1985; Alexandre et al. 1999; Okunaka et al. 2012), and data from long-term experiments (Blinnikov et al. 2013).

Site Selection

We took soil samples from 24 sites within the estimated range of Garry oak savannahs in the mid-1800s (Lea 2006; Fig. 1, Table 1). We carefully selected sites to include a wide range of current vegetation types and sites with different histories of post-settlement vegetation change based on the first land survey of the Cowichan Valley (Bjorkman 2008; Bjorkman and Vellend 2010). We included open Garry oak savannahs, “transition” vegetation with oak savannah in various stages of encroachment by Douglas-fir, and closed canopy Douglas-fir forests. We also included two sites that are heavily forested, but with minimal cover by Douglas-fir (plot 16 and COW4, Table 1). We chose some sites which have remained Douglas-fir forest or open savannah since 1859, and some which had a very low density of trees in 1859, but had become forest by 2007 (Table 1). We included deep-soil oak savannahs at two protected locations thought to have been minimally disturbed (e.g. not ploughed) since European settlement: the Somenos Garry Oak Preserve (SOM1) and the Cowichan Garry Oak Preserve (NCC2). The former is adjacent to a significant archaeological site (Brown 1996).

In order to characterize the current vegetation, we set up a 20x20m vegetation plot at each site. Phytoliths are generally deposited in soil less than 100m from their origin (Fredlund and Tieszen 1994; Blinnikov et al. 2002); however Douglas-fir phytoliths are rare or absent in savannah soils 20m distant from the nearest Douglas-fir (McCune and Pellatt 2013). We estimated the percent cover of all vascular plant species present in the plot to the nearest 1%. We took a composite soil surface sample by collecting a small amount of soil from within the top 2 cm (after removing leaf litter) near each of the four corners of the plot. Finally, we extracted a 5cm diameter soil core from within the plot using a multi-stage sediment sampler with a slide hammer (AMS, American Falls, ID, USA). We selected areas for coring that appeared to have minimal soil disturbance, were relatively flat, and free of visible rocks.

We took three cores at the Somenos Garry Oak Preserve (SOM1, SOM2, and SOM3) along a transect proceeding northwards from the open oak savannah at the southern end of the property (SOM1) up to what is now quite a dense Douglas-fir forest (SOM3). SOM2 is currently in an area with a few very large old Garry oak trees that have been completely surrounded by younger Douglas-firs (Fig. 2).

Phytolith extraction, counts and analyses

We chose seven full soil cores to analyze changes in phytolith assemblages with depth (Table 1). We extracted phytoliths from every second 2cm increment starting with the 0-2cm increment, excluding the bottom 3cm, and from our composite surface soil samples. We used a wet oxidation and heavy liquid flotation procedure modified from Pearsall (2000) to extract phytoliths (see McCune and Pellatt 2013 for details). We dried and weighed each sample following removal of organic material to estimate the inorganic fraction.

Based on our reference collection of phytoliths produced by plants in the region (McCune and Pellatt 2013), we counted five phytolith morphotypes: elongates (produced almost exclusively by grasses), rondels and bilobates (produced by grasses only), astrosclereids (sometimes spelled *asterosclereids*; produced by Douglas-fir only) and “other”. The final category included hairbase phytoliths and tracheid phytoliths (produced by multiple species), conical *Carex*-type phytoliths, and various rare unknown phytoliths (McCune and Pellatt 2013). We mounted between 0.5mg and 1.2mg of phytolith extract on a microscope slide in Canada balsam mounting medium. We scanned the entire slide at 200x magnification to count the large astrosclereid phytoliths produced by Douglas-fir. We then counted other phytolith morphotypes at 400x magnification across a transect of 16-18 consecutive microscope fields from the centre of the cover slip to the edge, and used these counts to estimate the number of each morphotype per slide (McCune and Pellatt 2013). We obtained the mean and standard error for the estimated number of each phytolith morphotype per slide, and for the ratio of astrosclereids to rondels, using a bootstrapping procedure with 1000 runs. This provided a measure of the precision of our estimates, which is important when using those estimates to infer vegetation shifts (Strömberg 2009). Bootstrapping was carried out in R (R Core Development Team 2012). We also estimated concentrations of each morphotype per gram of soil.

In order to find a phytolith-based metric that reliably distinguished between vegetation types, we examined the concentration of the five different phytolith morphotypes and the ratio between astrosclereids and rondels in surface soil samples from the three broad vegetation types. In the complete soil cores we examined the changes in the best phytolith metric and the weight of the inorganic soil fraction with depth.

Radiocarbon dating

Dating vegetation shifts documented in the soil phytolith record is a challenge given the potentially uneven rate of soil formation. It is possible to date small amounts of carbon that are occluded within individual phytoliths, but recent research has shown that young phytoliths can contain astonishingly old carbon (Santos et al. 2010). One alternative is to radiocarbon date bulk soil organic material. Due to the continued movement of younger carbon down in the soil profile, this likely represents a more recent age than the average age of the phytoliths in the same layer (Kerns et al 2001). We decided to radiocarbon date individual macroscopic charcoal or wood. There is some evidence that phytoliths can move downwards in soil more quickly than charcoal due to their smaller size (Alexandre et al. 1999), in which case phytoliths may be younger on average than charcoal in the same soil layer. For this reason, we consider each radiocarbon date to be a very rough estimate of the age of the phytoliths within the same soil layer. We did not attempt to build age-depth relationships given our lack of knowledge about the rate and consistency of soil formation at our study sites. For five of the seven complete soil cores, we obtained radiocarbon dates for 2-3 small pieces of charcoal or wood. Beta Analytic, Ltd. (Miami, Florida) determined accelerator mass spectrometry (AMS) ^{14}C ages. We calibrated the reported conventional radiocarbon ages with the OxCal calibration program using the INTCAL09 calibration curve (OxCal version 4.2; Bronk Ramsey 2009; Reimer et al. 2009; Table 2).

Results

Surface calibration

The concentration of astrosclereid phytoliths differentiated current vegetation type most clearly of all the phytolith types we examined: astrosclereids were almost always absent from surface soils under savannah vegetation, and the distributions of astrosclereid concentration differed significantly between all three vegetation types (Fig. 3; Wilcoxon rank sum tests for pair-wise differences all $p<0.05$). However, the range of overlap in astrosclereid concentration between Douglas-fir forest and "transition" sites was quite large (Fig. 4).

We found that the log ratio of astrosclereids to rondels (ln(A:R)) quite clearly differentiates the three broad vegetation types, with little overlap (Fig. 5a). We determined approximate thresholds between the three vegetation types (Fig. 5). These thresholds correspond to approximate astrosclereid:rondel ratios of less than 1:1250 for savannah vegetation, between 1:1250 and 3:500 for "transition" vegetation, and above 3:500 for Douglas-fir vegetation. The largest astrosclereid to rondel ratio was approximately 1:10 for plot COW1 (Fig. 5b).

Phytoliths can move downwards in the soil profile, the extent of movement being determined by the type of soil, the amount of precipitation, and the size of phytoliths (Alexandre et al. 1999; Fishkis et al. 2010a,b). The ln(A:R) ratio is between a very large phytolith (the astrosclereid, 50-200um) and a very small phytolith (the rondel, 10-20um). Therefore, differential movement of these phytoliths in the soil profile based on size could cause shifts in this ratio independent of vegetation change. Similarly, phytoliths can eventually dissolve in the soil, and larger phytoliths might be expected to dissolve more slowly than smaller ones (Alexandre et al. 1999). However, if these factors were the cause of changes in the ratio, we would not expect to be able to find patterns such as those observed in COW1 and COW14 cores, in which a high ln(A:R) ratio is maintained with depth (see below).

Full core analysis

We assume the average age of the phytolith assemblage is older deeper in the soil cores. The locations of the seven full soil cores are dominated by strongly acidic dystric brunisols (Jungen 1985). We do not have evidence that these soils have been aggrading over time, but we consider the presence of clearly defined soil horizons in five of the seven full cores, and an increase in the inorganic fraction with depth in all cores, to be evidence against significant soil mixing or the presence of buried surface horizons (see Online Resource 1). In addition, in four of the five cores with radiocarbon dates, older charcoal is found below younger charcoal (Table 2). We found a steep decline in phytolith concentration once entering the B horizon of soil cores. This is a common pattern of phytolith distribution in intact soils (Jones and Beavers 1964; Hart and Humphreys 2003).

SOM1 and NCC2, current oak savannah sites, both maintain ln(A:R) ratios in the savannah vegetation range throughout the length of the cores (Fig. 6). The SOM1 core was 59cm in length in total, and the entire length of the core was dark organic soil (we did not reach the B horizon). The NCC2 core was 45cm long with an abrupt change from dark, organic soil to light yellowish, hard clay soil at 12cm. The deepest charcoal sample from SOM1 (34cm) had a calibrated age of 1959 years before present (BP, where “present” is considered the year 1950; Table 2).

SOM2 is less than 200m away from SOM1 and is currently dominated by young (<100 year old) Douglas-firs surrounding a few very old oaks. The core was 49cm long with a dark organic soil from the surface to 14cm, followed by a gradual transition to a yellowish clay horizon that began around 32cm. The ln(A:R) ratio begins in the “transition” vegetation zone near the surface, but then falls below the threshold to savannah levels by 14cm below the surface (Fig. 6). A charcoal sample from 22cm depth had a calibrated age of 2013 years BP (Table 2).

SOM3 and COW14 cores were taken at sites currently dominated by Douglas-fir forests, but described as “oak plains” or “open pine plains” at the time of the first land survey (Table 1). The SOM3 core (total length 63cm) had a very shallow layer of dark organic soil about 6cm deep, followed by a transition to a reddish clay layer from 16-22cm, and then a heavily charred layer of about 4cm containing charcoal and burnt wood. Below the charred layer was an abrupt transition to a yellowish clay horizon at approximately 28cm. The ln(A:R) ratio is well above the threshold of Douglas-fir forest until 16cm below the surface, where it drops down into the “transition” zone (Fig. 6). A charcoal sample from within the charred layer at 24cm depth had a calibrated age of 672 years BP. COW14 also had a shallow layer of dark organic soil for the top

6cm, and then gradually changed to a yellowish clay layer by about 20cm in depth. Unlike SOM3, the ln(A:R) ratio is maintained within the Douglas-fir forest zone (Fig. 6).

The soil at COW1 was extremely rocky, and we were unable to extract more than 28cm of soil. Throughout this core, the ln(A:R) ratio is maintained well into the forest zone (Fig. 6). The COW2 core had a shallow dark organic layer to 6-8cm below the surface, followed by a reddish hard clay horizon from 8cm to about 36cm, and then a yellowish clay layer. The ln(A:R) ratio in the top 6cm was well above the forest threshold, but then declined into the "transition" zone (Fig. 6).

Discussion

Despite the regional-scale maintenance of significant grass and oak pollen over the past 3,000 years, our results suggest that the landscape was not in equilibrium at the time of European settlement on a local scale. The two deep-soil sites currently under oak savannahs show no evidence of Douglas-fir presence for at least the last 2,000 years (SOM1 and NCC2; Fig. 6). However, three of the five sites now dominated by Douglas-fir show evidence of being more open in the past, and the increase in Douglas-fir at two of these sites may have predated the arrival of Europeans.

The profile for SOM2, just uphill from SOM1, matches expectations for a savannah recently filled in with Douglas-fir. The crossing of the ln(A:R) ratio into the "transition" zone coincides with a charcoal sample dated 181±98 calibrated years BP. If the charcoal age accurately estimates the average phytolith age, this shift occurred approximately at the time of European settlement, or just before (1671-1867AD; Table 2). This timeframe overlaps with a particularly wet period that occurred on southern Vancouver Island from the 1560s to the 1760s, at the end of the cold period known as the Little Ice Age (Zhang and Hebda 2005). Dendroecological studies have documented pulses of oak and Douglas-fir recruitment at various sites in the region in the early- to mid-1800s, and attribute these pulses to fire suppression, climatic changes, changes in herbivory levels, or a combination of these factors (Gedalof et al. 2006; Dunwiddie et al. 2011). The coincidence of the wet period with changes in human management due to the population decline of indigenous peoples and land appropriation by Europeans make it difficult to disentangle which was responsible for the infilling of the savannah at SOM2. This is a challenge in other areas of North America as well (e.g. Millar and Woolfenden 1999).

The SOM3 site is currently a Douglas-fir forest with little grass cover, which is reflected in the high ln(A:R) ratio in the surface soil. However, by 16cm below the soil surface, the ratio has dropped into the "transition" zone (Fig. 6). The shift occurs above a charcoal fragment dated at 672 calibrated years BP (1250-1306AD), but below charcoal dated at 119 calibrated years BP (1751-1911AD; Table 2). This indicates that the transition may have happened well before European settlement in the region, possibly triggered by the onset of the Little Ice Age climate anomaly, which brought higher precipitation and lower growing season temperatures from approximately 1400AD (Mann et al 2009). Several charcoal and tree ring-based studies have found reduced fire frequencies in the region during this time (e.g. Brown and Hebda 2002; Lucas and Lacourse 2013), which would favour increased recruitment of Douglas-firs. It is curious that the entire landscape east of Somenos Lake is described as "oak plains" on the 1859 map given this potential increase in Douglas-fir at SOM3 well before the original surveys (Fig. 2). However, the bearing tree for the gridline intersection nearest SOM3 was a Douglas-fir, as was the bearing tree for the next three intersections heading north. The surveyor's description at the intersection less than 500m north of SOM3 reads: "oak and pine plains, excellent land". It is clear that there was a significant presence of Douglas-fir in this area at the time.

The COW14 core was taken from a site described as "open pine plains" in 1859, which now has a forest density of over 1300 trees/ha (Table 1). However, the ln(A:R) ratio remains at a high level throughout the depth of this core (Fig. 6). This suggests Douglas-fir forest has existed here for many centuries, which does not match with historical descriptions of a "pine plain" in 1859. These "pine plains" were described by a surveyor as "land of the best quality, open, and little wood upon it, which usually grows in clumps with an occasional isolated tree" (Bjorkman 2008). It is possible that long-term "pine plains" can produce ln(A:R) ratios as high as Douglas-fir forests, but "pine plains" are practically nonexistent on the landscape in the present. They represent a sort of no-analog community, for which we do not have a contemporary example with which to calibrate the surface soil phytolith ratio (Williams and Jackson 2007).

The COW1 core had the highest level of astrosclereids of all samples, and maintains a ln(A:R) ratio well into the forest zone throughout its length (Figs. 4,6). We consider this evidence that this site has been dominated by Douglas-fir since well before European settlement. COW2, on the other hand, shows a decline in the ln(A:R) ratio into the "transition" zone by 8cm below the surface (Fig. 6). The charcoal sample at 12cm yielded a radiocarbon date older than one near the base of the core (Table 2), indicating potential soil mixing, so we cannot estimate when this more open phase in the history of COW2 occurred. However, this site is on the western boundary of the estimated historical range of Garry oak savannah (Fig. 1), and it is quite possible that this now forested location was more open before the surveyors came through, and may have begun filling in with Douglas-fir due to climatic change centuries before, as observed for SOM3.

We suggest that a high concentration of astrosclereids sustained deeper in the soil profile indicates a longer time period of Douglas-fir presence. This explains mismatches observed between the ln(A:R) ratio in soil surface samples and current vegetation. For example, sites like COW12, currently dominated by Douglas-fir but with a surface ln(A:R) ratio in the transition zone, are likely actually "transition" sites that have been filled in by Douglas-fir relatively recently (Fig. 5b). The concentration of astrosclereids in the soil surface seems to correspond well with the relative length of time of Douglas-fir dominance of a site (compare Figs. 4 and 6).

Conclusions

Our results echo many other studies that have found that the North American landscape was not in a stable equilibrium prior to European settlement (e.g. Sprugel 1991; Lynch 1998; Hotchkiss et al. 2007). The trends we observed in the phytolith record are consistent with the idea that the extensive open landscape documented in the first European land surveys was not a long-term stable condition, but had already begun to see an increase in Douglas-fir density at some sites prior to those surveys. European settlement brought about a dramatic acceleration of this trend, leading to the current high levels of endangerment for species adapted to open conditions.

Swetnam et al. (1999) cautioned that the vegetation history of specific locations and ecosystems often cannot be extrapolated from broader scale regions. Our findings exemplify this, showing that the amount of variation in vegetation before settlement differs depending on which local site was examined. On a local spatial scale different sites show different histories in terms of the balance and timing of shifts between savannah and Douglas-fir forest. In addition, changes on a local scale at one site are not always synchronous with other sites (Delcourt and Delcourt 1988; Lynch 1998; Hotchkiss et al. 2007). Further work with phytoliths in this region could solidify the relationship between the concentration of astrosclereids in the surface soil and the relative timing of Douglas-fir infilling. We can then test for links between the timing of afforestation and landscape factors, such as soil depth, elevation, slope, and proximity to important indigenous villages or harvesting grounds. This will make it possible to understand what has driven the historical variability in vegetation on this landscape at a local scale, and perhaps direct restoration activities towards sites that have been transformed most recently.

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Figure Captions

Fig.1 Location of southeastern Vancouver Island, including the Cowichan Valley and the Saanich Peninsula, on the west coast of North America (inset). The shaded area indicates the range of savannah vegetation as quantified from the first land surveys. Symbols indicate the locations of 24 soil samples. Sites where full soil cores were analyzed are labelled

Fig. 2 Location of soil cores taken from the Somenos Garry Oak Preserve. The left panel shows the landscape in a map drawn in 1859, and the right panel shows the landscape as seen in a recent aerial photo. The description on the 1859 map to the East of Somenos Lake reads “Oak Plains”. Non-marshy sites that are currently still naturally vegetated have mostly become filled in with thick Douglas-fir forest (darkest areas in right panel)

Fig. 3 Differences in total phytoliths per gram of surface soil estimated for each phytolith morphotype by vegetation type: Douglas-fir dominated forest (“forest”), “transition” or “other” vegetation types (“trans/oth”), and Garry oak savannah (“savannah”). Note that the scale of the y axis differs for each plot. Different letters above the boxes indicate significantly different distributions according to pairwise Wilcoxon rank sum tests

Fig. 4 The number of astrosclereid phytoliths (thousands per gram of soil) in soil surface samples plotted against the difference between the total percentage cover of Douglas-fir and the total percentage cover of all grasses within each 20x20m plot. Sites where full soil cores were analyzed are labelled

Fig. 5 (a) The log ratio of astrosclereid to rondel phytoliths in surface samples by vegetation type: Douglas-fir dominated forest (“forest”), “transition” or “other” vegetation (“trans/oth”), and Garry oak savannah (“savannah”) (b) The log ratio of astrosclereid to rondel phytoliths in surface soil samples plotted against the difference between the total percentage cover of Douglas-fir and the total percentage cover of all grasses within the plot. Dotted lines are the estimated thresholds between vegetation types. Error bars show ± the bootstrapped standard error. Samples have more than one estimate if their composite surface soil sample and the 0-2cm increment of the soil core were both analyzed

Fig. 6 Change with depth below the soil surface in the log of the ratio of astrosclereid to rondel phytoliths in the seven soil cores. Dotted lines indicate the estimated thresholds between savannah vegetation (below lowest line), “transition” vegetation (between the two lines), and Douglas-fir forest (above the top line). Symbols indicate the present vegetation type of the plot from which each core was taken. Error bars are ± the bootstrapped standard error. Samples have more than one estimate at 0cm if the composite surface soil sample and the 0-2cm increment of the soil core were both analyzed. The phytolith ratio is not plotted past the point where phytolith concentration declined below 500,000 phytoliths per gram of soil, as estimates become less accurate. Depth below surface should not be considered a surrogate for time before present, as the length of cores and the depth at which phytolith concentration tapered off differ for each core

Figures

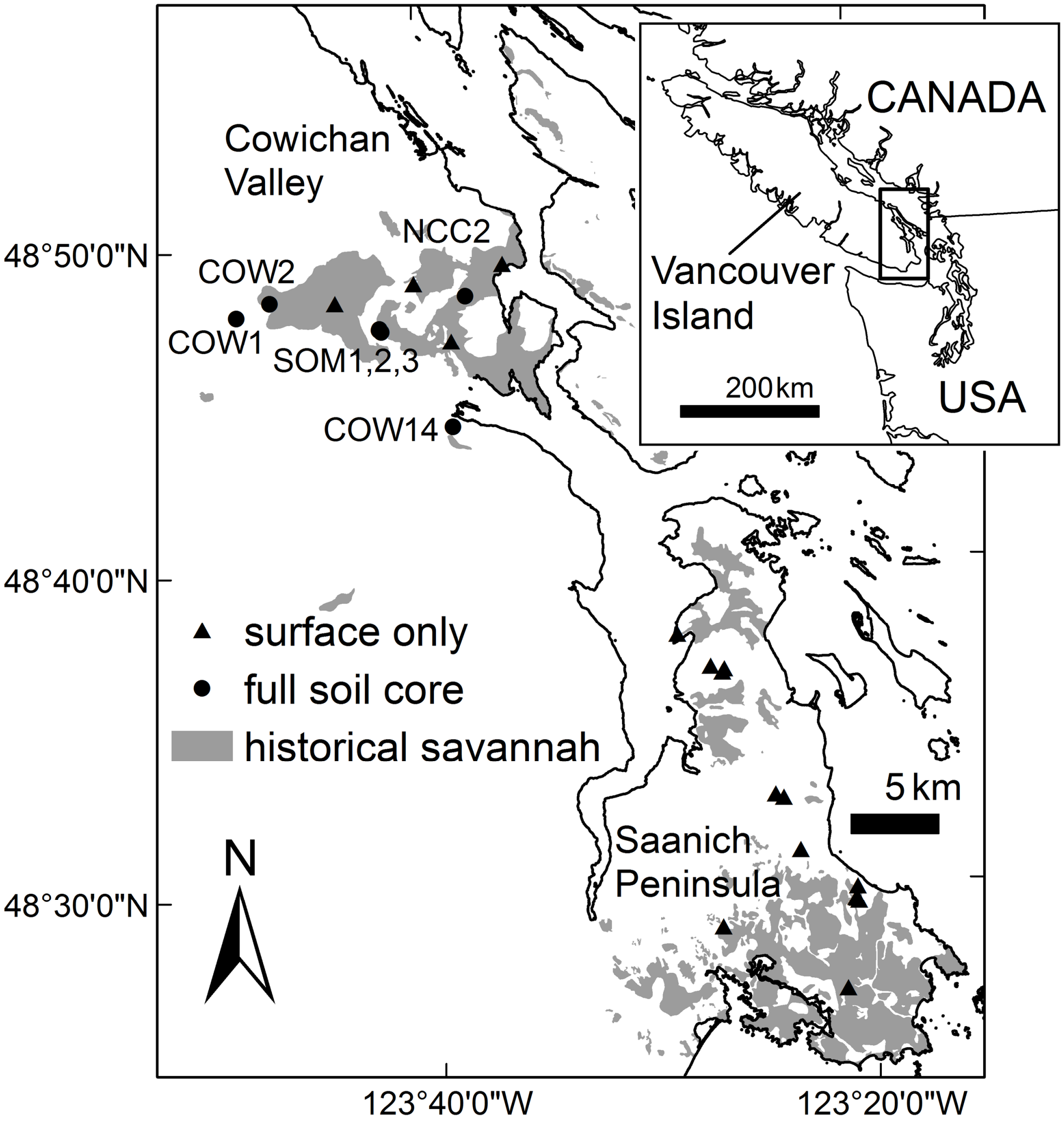


Figure 1

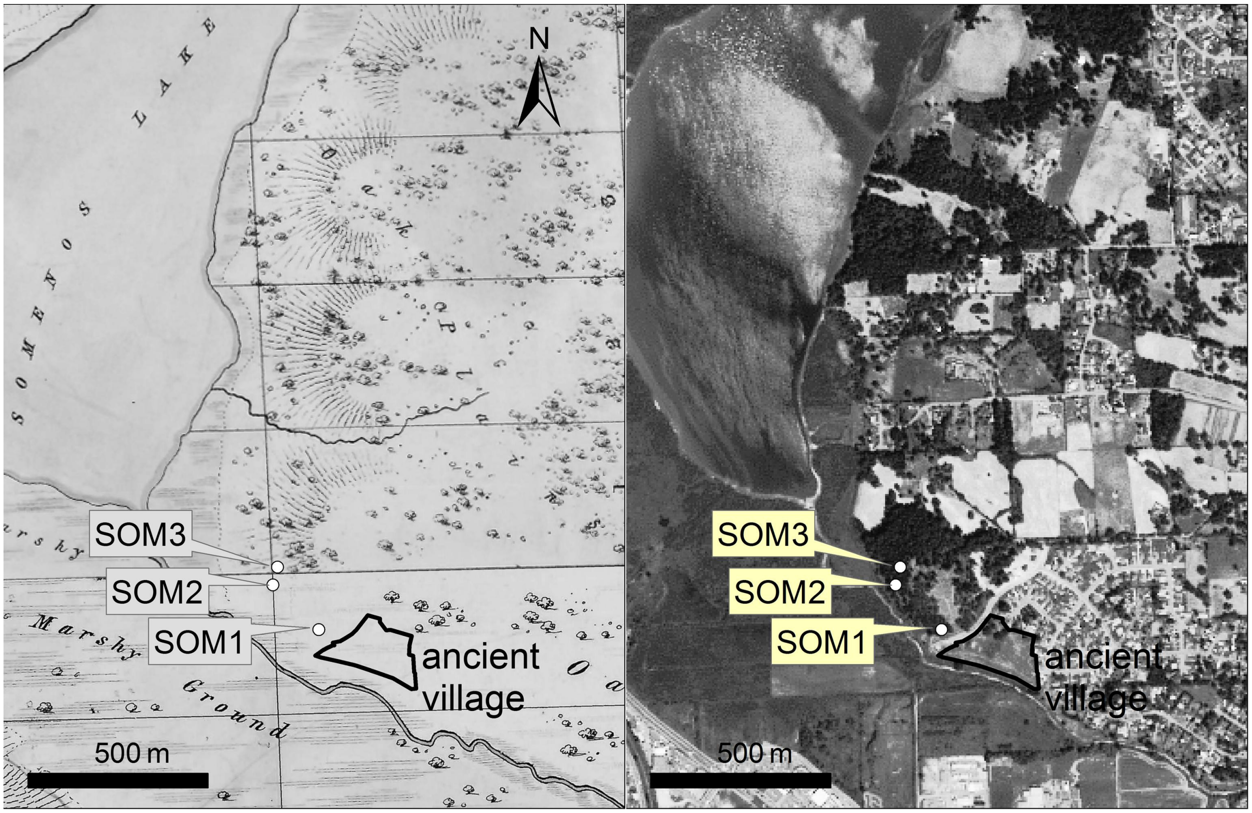

N
SOMENOS LAKE
Marshy Ground
SOM3
SOM2
SOM1
ancient village
500 m
SOM3
SOM2
SOM1
ancient village
500 m

Figure 2

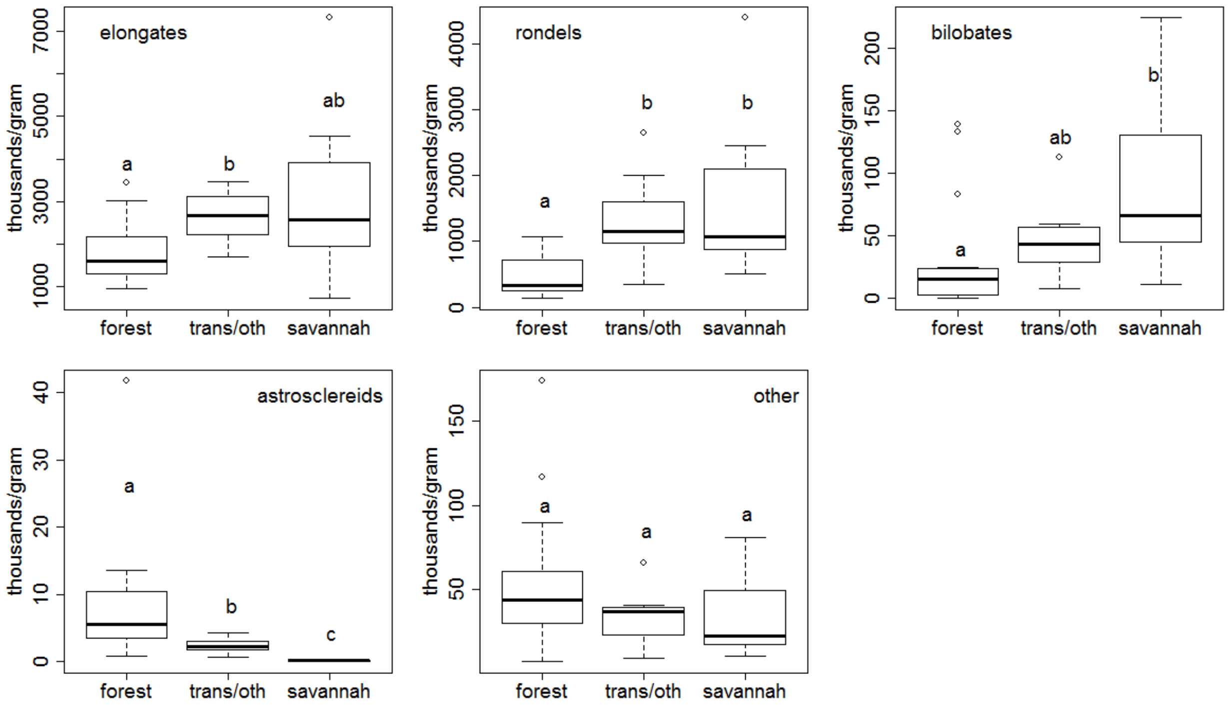

elongates
rondels
bilobates
astrosclereids
other
thousands/gram
forest
trans/oth
savannah
a
b
ab
c
1000
3000
5000
7000
0
1000
2000
3000
4000
0
50
100
150
200
0
10
20
30
40
50
100
150

Figure 3

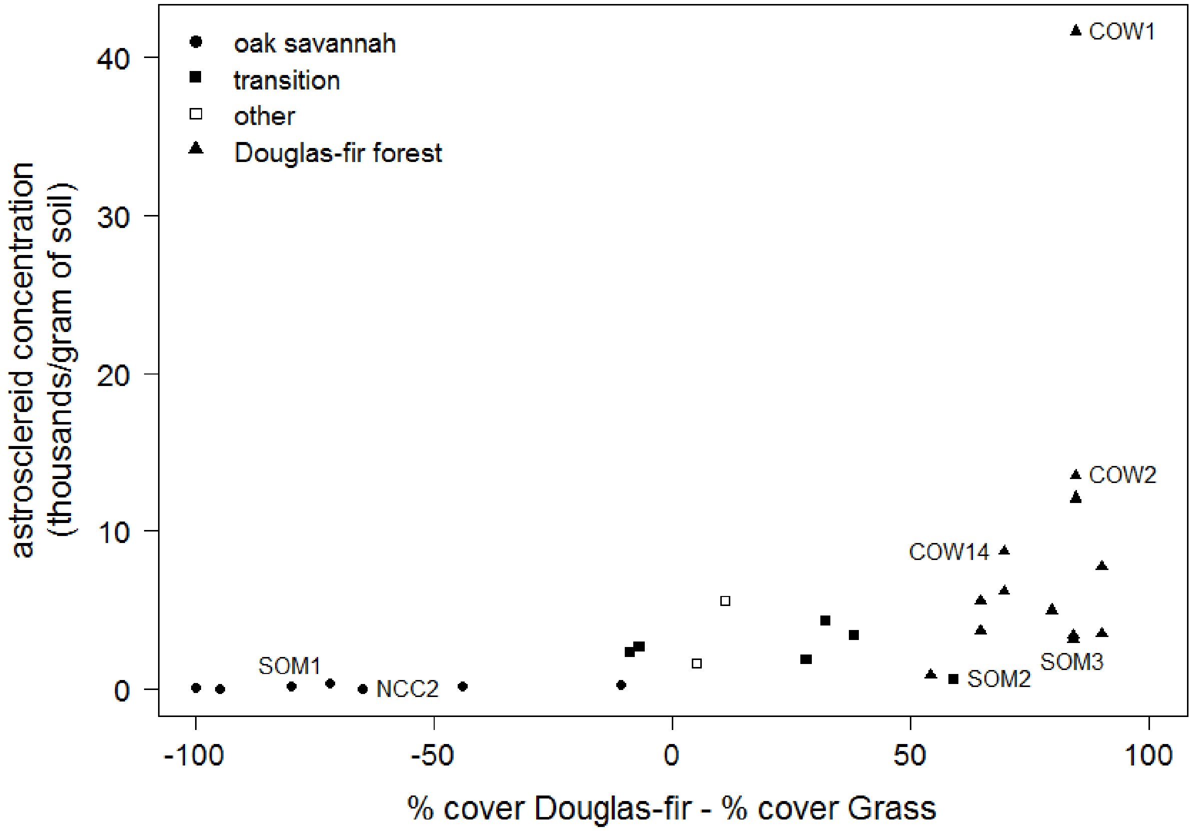

● oak savannah
■ transition
□ other
▲ Douglas-fir forest
astrosclereid concentration (thousands/gram of soil)
40
30
20
10
0
-100
-50
0
50
100
% cover Douglas-fir - % cover Grass
COW1
COW2
COW14
SOM1
NCC2
SOM2
SOM3

Figure 4

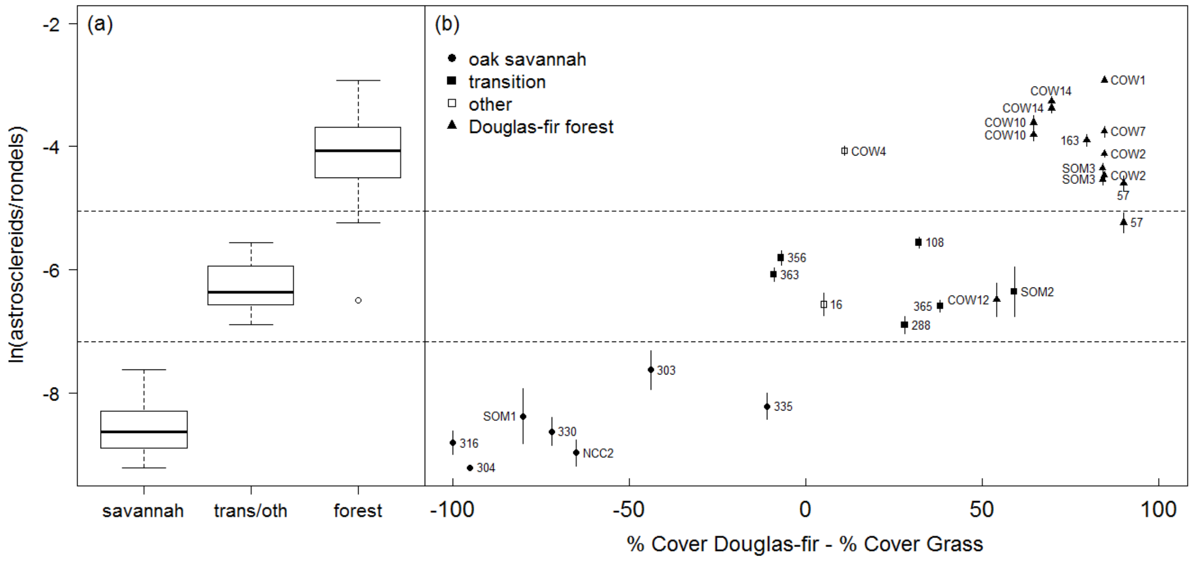
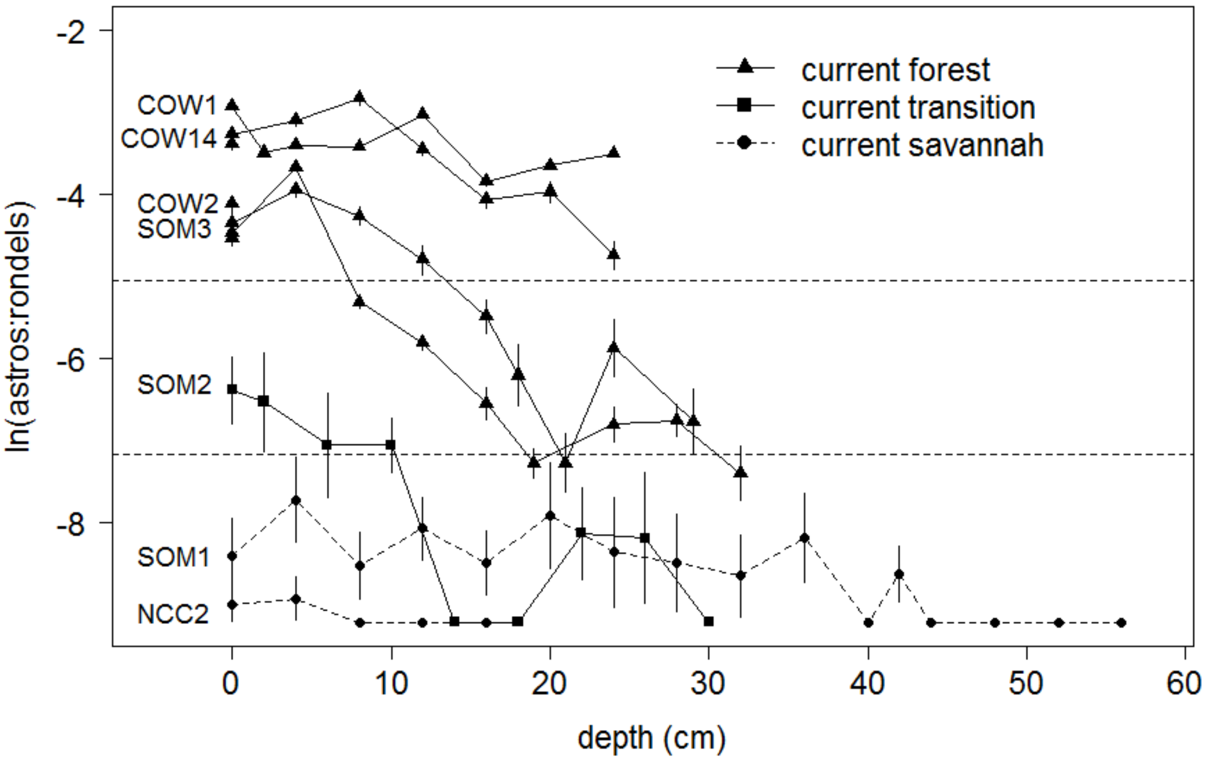

(a)
(b)
ln(astrosclereids/rondels)
-2
-4
-6
-8
savannah
trans/oth
forest
● oak savannah
■ transition
□ other
▲ Douglas-fir forest
COW1
COW14
COW14
COW10
COW10
COW7
163
COW4
COW2
SOM3
SOM3
COW2
57
57
108
356
363
16
365
COW12
SOM2
288
303
335
SOM1
316
330
NCC2
304
-100
-50
0
50
100
% Cover Douglas-fir - % Cover Grass

Figure 5



current forest
current transition
current savannah
COW1
COW14
COW2
SOM3
SOM2
SOM1
NCC2
ln(astros:rondels)
-2
-4
-6
-8
depth (cm)
0
10
20
30
40
50
60

Figure 6

Tables

Table 1: Site location and characteristics of the 24 sampled sites, ordered from open savannah sites through closed canopy Douglas-fir sites. Sites in bold are cores for which sub-surface soil layers were analyzed. The 1859 and 2007 descriptions and tree density are shown when available for full cores only, as determined by Bjorkman (2008)

Site name	Location (Latitude/Longitude, decimal degrees)	Percent cover grasses	Percent cover Douglas-fir	Percent cover Garry oak	Current vegetation type	1859 Surveyor Description	2007 Description
316	48.491426/-123.346108	100	0	55	savannah		
304	48.491758/-123.346873	95	0	85	savannah		
SOM1	**48.790096/-123.697797**	**80**	**0**	**80**	**savannah**	**oak plains (<102 trees/ha)**	**open savannah**
330	48.445731/-123.355471	72	0	40	savannah		
NCC2	**48.807193/-123.632094**	**65**	**0**	**90**	**savannah**	**rich oak plains (<102 trees/ha)**	**open savannah**
303	48.490301/-123.34473	44	0	85	savannah		
335	48.546421/-123.40583	11	0	25	savannah		
363	48.610067/-123.443593	44	35	35	transition		
356	48.611696/-123.441934	17	10	32	transition		
16	48.497894/-123.345376	0	5	0	other[a]		
COW4	48.805237/-123.732968	1	12	0	other[a]		
288	48.544552/-123.399784	42	70	0.5	transition		
108	48.47925/-123.449628	8	40	20	transition		
365	48.613227/-123.45248	17	55	0.5	transition		

COW12	48.822967/-123.602714	1	55	0	forest		
SOM2	**48.791246/-123.699469**	**1**	**60**	**3**	**transition**	**oak plains (< 102 trees/ha)**	**young Douglas-fir (232 trees/ha)**
COW10	48.784177/-123.644108	0.5	65	0	forest		
COW14	**48.740475/-123.644616**	**0.5**	**70**	**0**	**forest**	**open pine plains[b] (<102 trees/ha)**	**dense Douglas-fir (1369 trees/ha)**
163	48.630271/-123.477194	0.5	80	0	forest		
SOM3	**48.791687/-123.699275**	**1**	**85**	**0**	**forest**	**oak plains (<102 trees/ha)**	**open Douglas-fir**
COW7	48.814114/-123.671741	0.5	85	0	forest		
COW2	**48.806341/-123.783417**	**0.5**	**85**	**0**	**forest**	**heavily timbered (405-700 trees/ha)**	**open Douglas-fir (378 trees/ha)**
COW1	**48.799319/-123.809655**	**0.5**	**85**	**0**	**forest**	**thick heavy timber (405-700 trees/ha)**	**dense Douglas-fir (1297 trees/ha)**
57	48.517584/-123.388316	0	90	0	forest		

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[a] "other" plots are forest plots not dominated by Douglas-fir. COW4 is dominated by bigleaf maple, and plot 16 is dominated by grand fir.

[b] Note that the 1859 land surveyors used the term "pine plains" to describe open grasslands dotted with a low density of Douglas-fir trees; they referred to Douglas-fir as a "pine" (Bjorkman and Vellend 2010).

Table 2: AMS (accelerator mass spectrometry) radiocarbon and calibrated calendar ages of charcoal or wood samples from soil cores

Core	Depth below surface (cm)	Lab number	Material	Radiocarbon age (^{14}C years BP ± 1σ)	Calendar age (cal years BP)[a]
SOM1	12	Beta-322820	charred material	60 ± 30	93 ± 77
SOM1	34	Beta-327609	charred material	2010 ± 30	1959 ± 38
SOM2	10	Beta-322821	wood	220 ± 30	181 ± 98
SOM2	22	Beta-322822	charred material	2050 ± 30	2013 ± 48
SOM3	4	Beta-327610	charred material	120 ± 30	119 ± 80
SOM3	24	Beta-322824	charred material	720 ± 30	672 ± 28
COW2	12	Beta-351518	charred material	3269 ± 30	3480 ± 44
COW2	24	Beta-350718	charred material	2390 ± 30	2417 ± 78
COW2	48	Beta-350719	charred material	3280 ± 30	3509 ± 40
COW14	16	Beta-350720	charred material	1850 ± 30	1784 ± 43
COW14	24	Beta-350721	charred material	2860 ± 30	2978 ± 53

[a] shown is the median age ± 1σ with 95.4% probability as calibrated by OxCal (Bronk Ramsey 2009).