Contributed Paper

Defining Historical Baselines for Conservation: Ecological Changes Since European Settlement on Vancouver Island, Canada

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Abstract: *Conservation and restoration goals are often defined by historical baseline conditions that occurred prior to a particular period of human disturbance, such as European settlement in North America. Nevertheless, if ecosystems were heavily influenced by native peoples prior to European settlement, conservation efforts may require active management rather than simple removal of or reductions in recent forms of disturbance. We used pre-European settlement land survey records (1859–1874) and contemporary vegetation surveys to assess changes over the past 150 years in tree species and habitat composition, forest density, and tree size structure on southern Vancouver Island and Saltspring Island, British Columbia, Canada. Several lines of evidence support the hypothesis that frequent historical burning by native peoples, and subsequent fire suppression, have played dominant roles in shaping this landscape. First, the relative frequency of fire-sensitive species (e.g., cedar* [Thuja plicata]*) has increased, whereas fire-tolerant species (e.g., Douglas-fir* [Pseudotsuga menziesii]*) have decreased. Tree density has increased 2-fold, and the proportion of the landscape in forest has greatly increased at the expense of open habitats (plains, savannas), which today contain most of the region's threatened species. Finally, the frequency distribution of tree size has shifted from unimodal to monotonically decreasing, which suggests removal of an important barrier to tree recruitment. In addition, although most of the open habitats are associated with Garry oak* (Quercus garryana) *at present, most of the open habitats prior to European settlement were associated with Douglas-fir, which suggests that the current focus on Garry oak as a flagship for the many rare species in savannas may be misguided. Overall, our results indicate that the maintenance and restoration of open habitats will require active management and that historical records can provide critical guidance to such efforts.*

Keywords: anthropogenic burning, ecological baselines, habitat restoration, historical ecology, land survey records, oak savanna, presettlement vegetation

Definición de Líneas de Base Históricas para la Conservación: Cambios Ecológicos desde el Asentamiento Europeo en la Isla Vancouver, Canadá

Resumen: *Las metas de conservación y restauración a menudo son definidas por condiciones históricas que ocurrieron antes de un período particular de perturbación humana, tal como el asentamiento europeo en América del Norte. Sin embargo, si los ecosistemas fueron influidos severamente por habitantes nativos antes del asentamiento europeo, los esfuerzos de conservación pueden requerir manejo activo en lugar de la simple remoción o reducción de las formas de perturbación recientes. Utilizamos registros de agrimensura previos al asentamiento europeo (1859–1874) y registros de la vegetación contemporánea para evaluar cambios durante los últimos 150 años en la composición de hábitats y de especies de árboles, densidad del bosque y estructura de tamaños de árboles en el sur de la Isla Vancouver y en la Isla Saltspring, Columbia Británica, Canadá. Varias líneas de evidencia soportan la hipótesis de que las quemas frecuentes por habitantes nativos,*

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y la supresión de fuego subsecuente, han jugado papeles dominantes en el modelado de este paisaje. Primero, la frecuencia relativa de las especies sensibles al fuego (e.g., cedro [Thuja plicata]*) ha incrementado, mientras que especies tolerantes al fuego (e.g., abeto Douglas* [Pseudotsuga menziesii]*) han decrecido. La densidad de árboles ha incrementado al doble y la proporción del paisaje con bosque ha incrementado en gran medida a expensas de los hábitats abiertos (llanuras, sabanas), que actualmente contienen la mayoría de las especies amenazadas en la región. Finalmente, la frecuencia de distribución de tamaños de árboles ha cambiado de unimodal a decreciente monotónicamente, lo que sugiere la remoción de una barrera importante para el reclutamiento de árboles. Adicionalmente, aunque la mayoría de los hábitats abiertos están asociados actualmente con roble* (Quercus garryana)*, la mayoría de los hábitats abiertos previos al asentamiento europeo estaban asociados con abeto Douglas, lo que sugiere que el enfoque actual en el roble como un emblema de las muchas especies raras en las sabanas puede estar equivocado. En conjunto, nuestros resultados indican que el mantenimiento y la restauración de los hábitats abiertos requerirán de manejo activo y que los registros históricos pueden proporcionar información crítica para tales esfuerzos.*

Palabras Clave: ecología histórica, incendios antropogénicos, líneas de base ecológicas, registros de agrimensura, restauración de hábitat, sabana de robles, vegetación previa al asentamiento

Introduction

In many parts of the world, conservation and restoration goals are often based on perceptions of ecosystem states prior to intense disturbance by people of European origin (Foster 2000). Although relict patches of relatively undisturbed habitat are often used in studies of the structure and functioning of past ecosytems, such areas may be exceedingly rare and remain only in a highly biased subset of environmental contexts relative to the past (e.g., Vellend et al. 2008) or they may have been influenced in important ways by human activities that are not obvious through observation of their current state (e.g., Dupouey et al. 2002). An alternative is to look directly at historical records, which can provide critical insights into former landscape conditions and processes, and reasons for subsequent changes (Foster 2000; Whitney & DeCant 2005; Rhemtulla et al. 2009).

When using past ecosystem states to define conservation goals in North America, a key debate concerns the degree to which the pre-European settlement (henceforth presettlement) landscape was shaped by natural versus anthropogenic processes (Vale 2002). The pre-1492 landscape is often thought of as a pristine wilderness, where small groups of indigenous people had little ecological impact (Stankey 1989; Gómez-Pompa & Kaus 1992). This view has strongly influenced conservation strategies (Foster 2000; Hobbs & Cramer 2008). Many of these strategies rest on the assumption that removing the human factor will restore pre-European ("natural") conditions (Foster 2000). Other studies suggest, however, that many areas of North America were "cultural landscapes" and as such were heavily influenced by native peoples through land cultivation or prescribed fire (Denevan 1992; Vale 2002). This implies that conservation strategies may need to consider not only current human disturbances, but also the possibility of reinstating cultural practices that were historically important in maintaining ecosystems (Higgs 1997; Anderson & Barbour 2003). Natural and anthropogenic processes have always been temporally dynamic, and both factors have influenced historical vegetation composition in North America (Vale 2002). The primary issue is the scale of anthropogenic impacts: were they highly localized around areas of intense land use (e.g., settlements) or were entire landscapes fundamentally transformed (Whitlock & Knox 2002).

We used data from historical land-survey records (mid-1800s) and contemporary surveys to characterize changes in the landscape and vegetation since European settlement on southeastern Vancouver Island and Saltspring Island, British Columbia, Canada. Land survey records have been used widely for ecological studies in eastern North America (e.g., Radeloff et al. 1999; Whitney & DeCant 2005; Rhemtulla et al. 2009), but seldom in western North America (Galatowitsch 1990). The dominant vegetation in our study region is closed-canopy Douglas-fir forest (*Pseudotsuga menziesii*), but a fragmented network of savanna habitat patches within the forest matrix harbors a rich diversity of native herbaceous plants, including over 100 government-listed threatened species (Fuchs 2001; MacDougall et al. 2004). At present, the savanna trees are largely Garry oak (*Quercus garryana*), and this species is a flagship for regional conservation efforts (e.g., GOERT 2009), where savannas are often called Garry oak ecosystems (Fuchs 2001). The region was settled by Europeans in the mid-1800s, but substantial populations of native peoples have occupied the islands for thousands of years (Suttles 1990). Historical anecdotes suggest savannas were more common historically and were possibly maintained by indigenous burning (Turner 1999; MacDougall et al. 2004). Nevertheless, these qualitative records do not allow quantitative evaluation of the nature or relative abundance of savanna habitats historically and they do not provide an independent test of the fire hypothesis apart from the observed decline in savanna itself. We assessed the degree to which present-day vegetation in undeveloped areas is representative of presettlement vegetation and evaluated the hypothesis that the cultural practices of indigenous peoples heavily influenced the vegetative characteristics of the landscape (Denevan 1992; Anderson & Barbour 2003).

We quantitatively tested four predictions that stem from the hypothesis that frequent prescribed fires shaped vegetation historically, with subsequent changes due largely to fire suppression (MacDougall et al. 2004). (1) Tree species sensitive to fire (e.g., cedar [*Thuja plicata*]) will increase in relative abundance, whereas species resistant to fire (e.g., Douglas-fir) or associated with open habitats in the present-day landscape (e.g., Garry oak) will decrease. With the removal of a key barrier to tree recruitment (i.e., fire), (2) forest density and (3) the proportion of forested landscape will increase. (4) Due to a recruitment barrier from frequent fire in the past but not the present, small trees will have been relatively rare in the past but will be numerically dominant at present. We evaluated these predictions in light of other changes (logging, herbivory, exotic species, and climate change) over the past 150 years, and we discuss the efficacy of current conservation goals in this region.

Methods

Study System

Vancouver and Saltspring islands lie off the southwestern coast of mainland British Columbia. Our study region is in the Coastal Douglas-fir biogeoclimatic zone (Meidinger & Pojar 1991), and it has lower elevations (<150 m), warmer temperatures (~10 °C mean annual temperature), and a drier climate (~650 mm mean annual precipitation due to a rainshadow effect of nearby mountains) than the areas that surround it (Meidinger & Pojar 1991). Outside of areas developed for agricultural or urban uses, closed Douglas-fir forests dominate, interspersed with scattered patches of oak savanna.

Many ongoing management efforts aim to preserve and restore the remaining oak savannas (GOERT 2009; McCoy 2009), but these efforts are hampered by uncertainty concerning the former distribution and composition of savannas and the historical processes that maintained them. Written historical records suggest that fire, likely set by native peoples, may have played an important role in maintaining savannas (Turner 1999; MacDougall et al. 2004), evidence that is corroborated by the oral tradition of native communities (e.g., Turner 1999). Nevertheless, previous studies of fire scars and charcoal deposits in lakes would not have detected the low-intensity, frequent fires thought to have been set by native peoples (Gedalof et al. 2006; McCoy 2006; Pellatt et al. 2007). Relatively infrequent natural fires due to lightning strikes are unlikely to have prevented establishment of closed coniferous forest in this region.

Historical Data

We used historical land survey records (1859–1874) to reconstruct the landscape of southeastern Vancouver Island and Saltspring Island just prior to European settlement (Fig. 1; original records from the British Columbia Land Title & Survey archives). Surveys were divided into three data sets, each created by a different surveyor in a different location and year. The Cowichan Valley (176 km^2, 225 points) was surveyed in 1859, the Chemainus district (26 km^2, 58 points) in 1864, and Saltspring Island (64 km^2, 145 points) in 1874 (266 km^2 total). Presettlement surveys occurred along east–west (section) and north–south (range) lines, and the resulting survey areas were 1 km × 400 m. At each intersection of the section and range lines, surveyors planted a post, identified and marked the nearest tree (known as a "witness" or "bearing" tree), and measured the distance from the post to the tree (Fig. 1). On Saltspring Island (but not the Cowichan Valley), the diameter of bearing trees was also recorded. We used these data to assess presettlement species composition (species frequencies), forest density (by point-to-tree distances), and size structure (distribution of tree diameters).

Cowichan Valley surveyors reported descriptions of habitat types at each intersection (e.g., "prairie," "open pine and oak plains," "thickly wooded forest."). We identified six reoccurring terms (*forest, open woods, bottom land, swamp, plains*, and *prairie*) that described 155 of 225 historically surveyed points and estimated the proportion of these habitat types across the landscape.

Contemporary Data

In 2007 we collected data at historical survey points using methods similar to those used in the historical surveys. We verified locations of survey points by georeferencing historical maps in ArcGIS (version 9.2; ESRI, Redlands, California). At each point, we recorded the species of, distance to, and diameter at breast height (dbh) (1.3 m from ground) of each of the 10 trees closest to the point. We set a maximum distance of 26 m from point to tree; this was the farthest recorded distance in the historical data (sites with no tree within 26 m were designated as "no bearing tree near"). We recorded only trees with dbh >10 cm, which corresponded to the smallest bearing trees in the historic data and was slightly larger than the 6.35 cm minimum designated in the surveyor instruction manual (Moore 1871). To focus on natural vegetation where there had been some opportunity for recovery from past disturbance, we excluded recently logged areas and urban and agricultural areas (approximately 40% of historically surveyed points).

A criticism of historic tree data is the potential for surveyor bias, which can affect estimated species composition, size structure, and density (Schulte & Mladenoff 2001; Whitney & Decant 2005). We used line tree

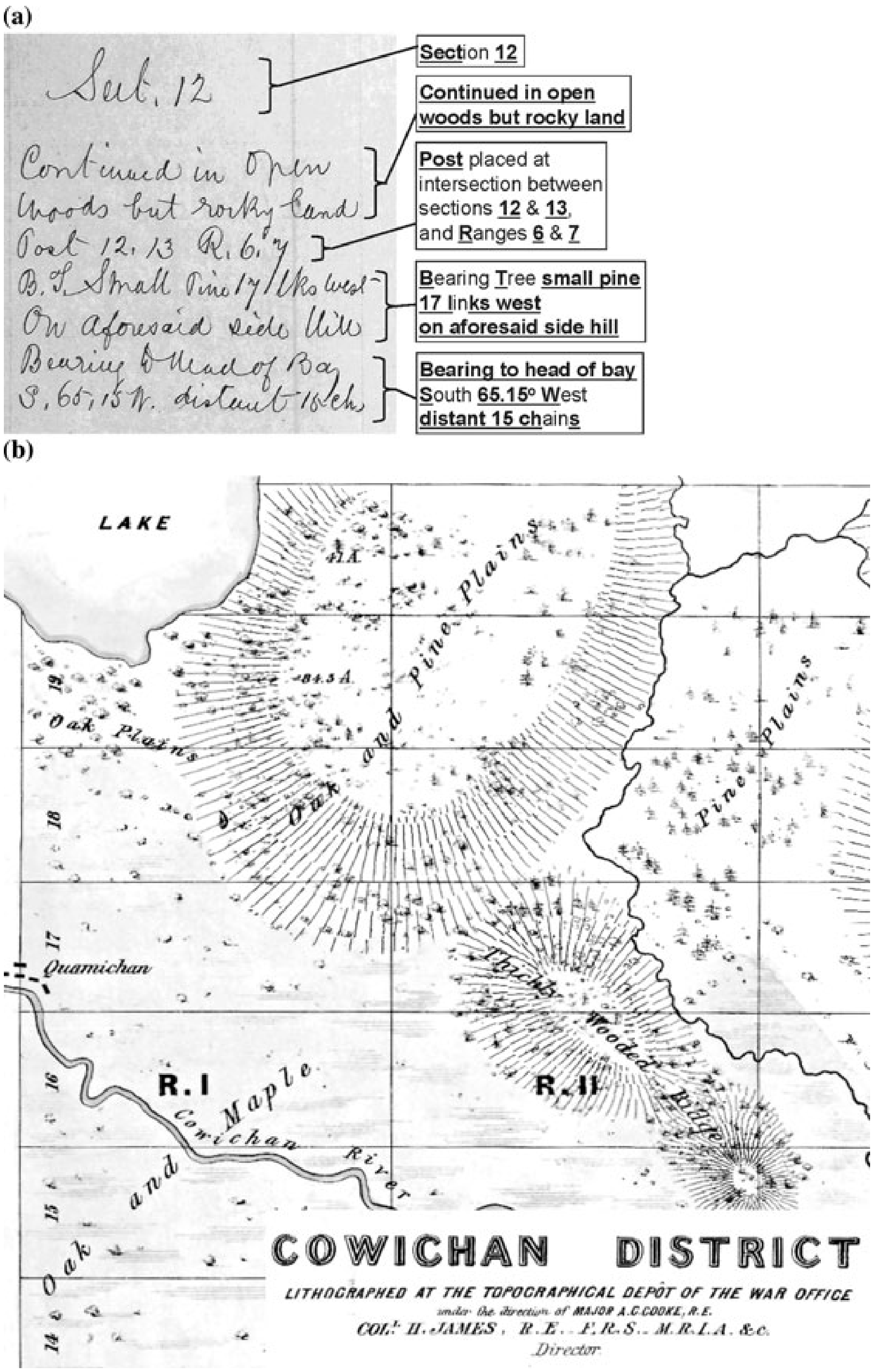

Figure 1. (a) A sample of the notes and (b) section of a map from the original 1859 survey of the Cowichan Valley, Vancouver Island. Our interpretations of the survey notes are shown in boxes in which letters from the original notes are underlined and in bold type and additional text is provided for clarity. Lines on the map represent divisions between "sections" (horizontal lines) and "ranges" (vertical lines) defined by the survey. Bearing trees were marked and recorded at every intersection of these section and range lines. Section numbers are listed along the far left edge of the map (sections 14–19 shown here), and ranges are identified by the letter "R" and a roman numeral (ranges I–III shown here). Each rectangle is 400 × 1000 m. The historical survey notes and maps are available at the British Columbia Land Title & Survey office in Victoria, British Columbia, Canada.

data from Saltspring Island to test for bias in tree species composition or diameter. Line trees were marked and recorded every time the survey line intersected a tree larger than the minimum (6.35 cm dbh), irrespective of species (Moore 1871). Therefore, these data allow unbiased estimation of species composition and diameter because line trees were not selected to serve any particular purpose (Whitney & Decant 2005).

Chi-square analyses (SAS version 9.1; SAS Institute, Cary, North Carolina) were used to test for changes in species frequencies from past to present across all points, and rare species were lumped together for analysis. The 1859 Cowichan Valley surveys did not distinguish between hemlock (*Tsuga heterophylla*) and Douglas-fir, and referred to both species as "pine"; thus, we grouped these two species in the Cowichan Valley for both time periods. We used only points with data for both time periods in our analyses.

We calculated forest density in the Cowichan Valley and Saltspring Island data sets with two estimators that are based on the distances from each point to the center of the *n*th closest tree and that allow for variable tree density across the landscape. The GamPoi estimator explicitly accounts for variable densities and performs well on simulated data sets (Magnussen et al. 2008), although it cannot accommodate variable values of *n* across sample points (i.e., points with <10 trees within 26 m) or where the surveyed area is <360° around each point (i.e., sites at habitat edges). Therefore, GamPoi was only applied to the subset of points entirely surrounded by natural habitat (360° points) and with $n = 10$. For the complete set of present-day sites, we estimated density ($\hat{\Theta}$) with an equation introduced by Morisita (1957) and later revised by Keuls et al. (1963),

$$\hat{\Theta} = \frac{10000}{t} \sum \frac{(n-1)}{A},$$

with a variance adapted from Cochran (1977),

$$\mathrm{Var}(\hat{\Theta}) = \sum \left[\frac{10000}{t} \times (n-1) \right]^2 \times \frac{1}{t(t-1)} \left[\frac{1}{A} - \left(\frac{\bar{1}}{A} \right) \right]^2,$$

where t is the number of points, n is for the nth closest tree, the summation is across points, and A is the area within which trees were recorded around that point (for 360° sites, this is equivalent to πr^2, and for points on habitat edges this is the portion of πr^2 in which natural habitat occurs). This method allows density to vary from point to point, assuming a negative binomial (clumped) distribution of trees (Bouldin 2008). Because the same density estimation methods could not be used on the entire set of both presettlement and present-day sites, we also analyzed a subset of suitable sites ($n = 10$ and 360°) using both estimation methods to assess potential differences between them.

We calculated tree density (GamPoi estimator) for the historical Cowichan Valley data within the four described habitat types that had a sufficiently large sample size ($n \geq 20$): prairie, plains, open woods, and forest. To provide a rough assessment of the representation of comparable habitat types in the present day, we calculated the number of 2007 sites within density ranges defined by the approximate midpoints between the density estimates of two consecutive presettlement habitat types. Contemporary density was calculated at each point by dividing the number of trees (generally, $n = 10$) by the area within which trees were recorded.

Historical tree size structure was estimated from the diameter measurements of bearing trees on Saltspring Island. We assessed differences between 1874 and 2007 with a Kolmogorov-Smirnov test. We also compared the 1874 bearing tree and line tree data to test for size bias in the former. To create size-frequency distributions, each line tree was weighted by the inverse of its diameter because the probability of a straight line intersecting a tree is proportional to the tree's diameter.

Results

Of 428 historic survey points, we resurveyed 263 (61%) in 2007. Changes in species frequencies over time were significant in all data sets ($p < 0.0001$ Cowichan Valley; $p = 0.0022$ Chemainus; $p = 0.0001$ Saltspring Island; Fig. 2). There was no significant difference in species frequencies between line trees and bearing trees ($p = 0.7416$), which indicates there was negligible surveyor bias. In all data sets the abundance of maple (*Acer macrophyllum*) and cedar increased and the abundance of Douglas-fir decreased. Other minor changes in species composition were not uniform across data sets.

All estimates of tree density increased approximately 2-fold from presettlement to the present (Fig. 3). Confidence intervals (95%) did not overlap in any of the past-present comparisons, which indicates a significant increase in mean forest density. The GamPoi and Morisita-Keuls methods produced nearly identical density estimates for the data subsets, indicating that the results of the two methods can be compared directly.

The 1859 notes revealed a landscape mosaic of prairie, plains, open woods, and forest. Of the 155 historical points with habitat descriptors, more than two-thirds were described as prairie, plains or open woods, with the remainder as forest, swamp, or bottom land (Table 1). Most plains were described as "pine plains," indicating that Douglas-fir was the main tree species in these habitats. Density estimates within habitat categories corresponded closely to expectations; density decreased from prairies to plains to open woods to forest. After defining density ranges corresponding to these descriptors, the majority of 2007 points (79%) were classified as forest and only 3% as prairies or plains (Table 1). The density estimate for historically undescribed points corresponded most closely to the forest category (Table 1). Even if all undescribed areas were forests, however, the proportion of the landscape in forest still roughly doubled over the past 150 years, whereas the proportion of prairies or plains declined precipitously.

The distribution of tree sizes changed significantly from past to present (Kolmogorov-Smirnov, $p < 0.0001$). In 1874 the size distribution was unimodal (few small trees, many large trees), and in 2007 it was monotonically decreasing (many small trees, few large trees; Fig. 4). The same pattern occurred both for bearing and

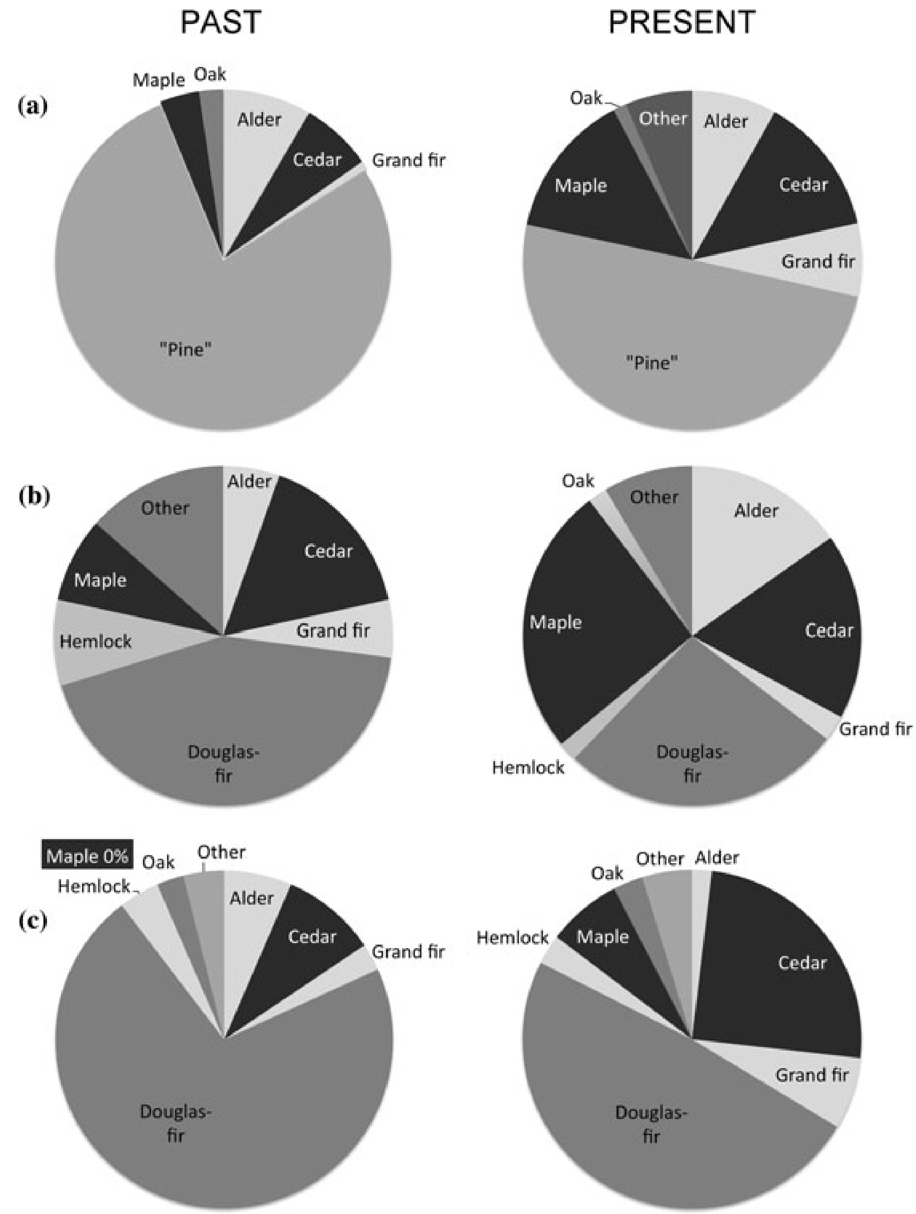

Figure 2. Proportions of tree species in the past and present: (a) Cowichan Valley, (b) Chemainus district, (c) Saltspring Island. "Pine" in the Cowichan Valley refers to Douglas-fir (Pseudotsuga menziesii) *and hemlock* (Tsuga heterophylla) *combined. The category "other" includes apple* (Malus fusca), *cottonwood* (Populus balsamifera), *arbutus* (Arbutus menziesii), *yew* (Taxus brevifolia), *and willow (*Salix *spp.), which occurred at very low frequencies.*

line trees ($p = 0.5775$), which suggests the bearing-tree data were not highly size biased.

Discussion

The composition, density, and size distributions of trees and proportions of habitat type changed tremendously over the past 150 years on southeastern Vancouver Island and Saltspring Island. Although the most visually obvious landscape change has been the conversion of natural habitat to urban development and agriculture (~40% of the landscape), even areas of "natural" habitat have been profoundly altered. Attributes of the present-day landscape are clearly a poor guide to understanding the structure of ecosystems prior to European settlement. The changes we observed were largely consistent with the hypothesis that frequent prescribed fires in the past and fire suppression since European settlement have been dominant forces in shaping the vegetation and landscape of this region. Logging since European settlement has likely been an important contributing factor to some, but not all, of the changes we observed.

Other factors that may have large impacts on ecosystems in this region besides fire and logging include exotic species, climate change, and herbivory (Hamann & Wang 2006; Gonzales & Arcese 2008; Lilley & Vellend 2009). These factors, however, are unlikely to have caused the substantial changes in species composition, tree density, and size structure we observed. There are very few invasive tree species in natural habitats in this region, so any substantial influence of exotics on tree species

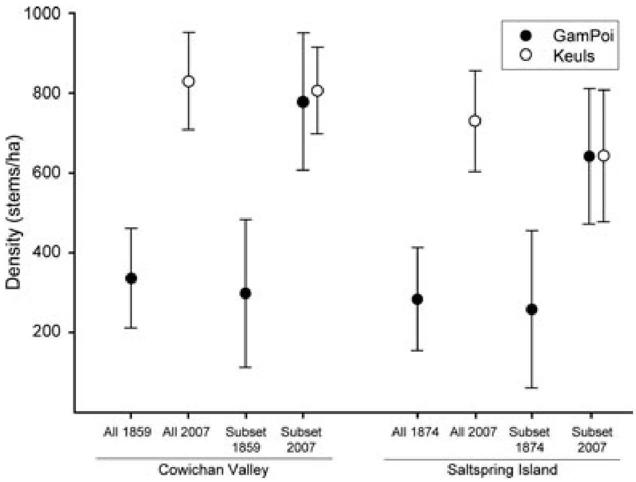

Figure 3. Changes in density (95% CI) of trees over time in the Cowichan Valley and on Saltspring Island. Density estimators are the GamPoi method (Magnussen et al. 2008) and Keuls' et al. (1963) equation. Subsets of the full data set were used to test the similarity of the two estimation methods.

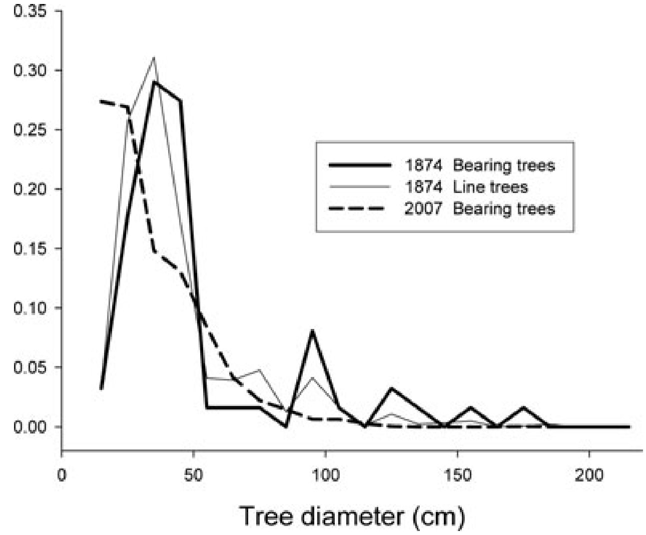

Figure 4. Tree size frequency for Saltspring Island (thick black line, bearing tree data from 1874; thin black line, diameters of line trees weighted by inverse diameter in 1874; dashed line, bearing tree data from 2007) (single closest tree at each site).

composition is unlikely. Intense herbivory can have effects similar to that of fire—reducing the cover of shrubs and trees and causing episodic recruitment (van Langevelde et al. 2003)—but due to the extirpation of natural predators, current abundances of herbivores, especially deer, are likely higher now than at any time over the past two centuries (MacDougall 2008). Finally, although there have been modest increases in mean annual temperature (~0.7 °C) and precipitation (13%) over the past century (Mote 2003; Hamann & Wang 2006), these changes are predicted to cause an expansion of the coastal Douglas-fir zone (Hamann & Wang 2006) and an *increase* in open habitats (Hebda 1997), rather than the dramatic decline in open habitats we observed.

Table 1. Estimated tree density at points defined by different habitat descriptors in the historical Cowichan Valley survey notes, and the percentage of the landscape, past and present, within each habitat and tree-density category.

Habitat descriptor	*Density (stems/ha) (±95% CI)*	*Percentage 1859**	*Percentage 2007*
Forest	404 (296)	9 (15)	79
Open woods	227 (187)	15 (26)	18
Plains	61 (41)	23 (39)	2
Prairie	8 (3)	12 (20)	1
Swamp + bottom land	not measured	11	N/A
Undescribed	394 (167)	30	N/A

**Numbers in parentheses indicate percentages within the set of points described as forest, open woods, plains, or prairie.*

Logging and Fire

Intensive logging since European settlement can help explain some, but not all, the changes we observed. Logging of old-growth forests was likely an important factor leading to the decrease in Douglas-fir—a valuable timber species—and the increase in early-successional species such as big-leaf maple. Maple is commonly found in disturbed areas due to its rapid growth and ability to sprout from stumps after logging (Uchytil 1989). Logging likely also influenced the increases in forest density and decreases in tree size because forests of low density with large trees are replaced by forests with many smaller trees (Kaufmann et al. 2000).

Changes in the fire regime appear to have had a large effect on ecosystems in our study region. Several lines of evidence strongly suggest that frequent, low-intensity fires greatly affected the presettlement landscape and that subsequent fire suppression may have led to many of the observed changes. Fire suppression has been linked to shifts in species composition in many areas of the world (Agee 1993; Radeloff et al. 1999). In our study, the increase in cedar—despite the fact that cedar is prized for timber—could be partly a consequence of fire suppression because cedar trees have thin bark and shallow roots and are highly susceptible to fire (Agee 1993). Thus, frequent fires likely restricted the range of cedar to wet areas less prone to fire historically, which reduced its abundance overall. In contrast, Douglas-fir has thick bark that is unlikely to be penetrated by low-intensity ground fires (Uchytil 1991). Fire, therefore, may have played a role in favoring Douglas-fir over other species historically.

Finally, the increase in forest cover with fire suppression may have further favored shade-tolerant cedar over shade-intolerant Douglas-fir (Uchytil 1991; Agee 1993).

The shift in forest structure from a low to high frequency of the smallest trees is difficult to explain without invoking a shift in the fire regime. A unimodal distribution of tree sizes (as we observed) arises with frequent fires (at least once every four years) as a result of episodic seedling recruitment (Fule & Covington 1994; Peterson & Reich 2001; Zenner 2005). Conversely, most old-growth forests and forests subject to infrequent, small-scale disturbances display a monotonically decreasing or "inverse-J" distribution of tree sizes (e.g., Peterson & Reich 2001; Westphal et al. 2006), as we found for present-day forests. Although a stand-replacing fire can also create a unimodal distribution by producing an even-aged, postfire cohort that later shades out new saplings (Zenner 2005), this is unlikely to be a factor in our region due to the relatively open canopy historically (i.e., insufficient shade to prevent recruitment), the rarity of such stand-replacing fires (Lertzman et al. 2002), and the large size of our study area over which such a fire would have to occur to produce the observed pattern. Thus, the unimodal size distribution appears to be a likely indicator of a frequent fire regime in the presettlement landscape.

Fire suppression is likely implicated in the increase in forest density (Agee 1993; Covington & Moore 1994). Encroachment of forest into prairie following fire suppression has been documented widely (Agee 1993), including in a few localities on Vancouver Island (Gedalof et al. 2006; Pellatt et al. 2007). Thus, fire suppression can increase tree density within existing forests and contribute to the conversion of prairie to forest. Estimates of the density of trees within habitat types indicate that more than one-third of the historical landscape (prairie and plains) averaged <100 stems/ha—considerably less than in contemporary old-growth forests (250–500 stems/ha; Spies & Franklin 1991). In contrast, only 3% of the current landscape has a density <100 stems/ha. This result is consistent with a regime of frequent fire in the past, which would have maintained open habitats.

Finally, although frequent fires do not necessarily imply an anthropogenic cause, our results do indicate that the fire regime was influenced by native peoples. The observed patterns are characteristic of landscapes prone to more frequent fires than expected by lightning strikes. Experiments suggest that the unimodal tree size distribution observed on Saltspring Island occurs at a fire interval of <5 years (Fule & Covington 1994; Peterson & Reich 2001). In contrast, a study in the Douglas-fir forests of Vancouver Island estimated a fire cycle of 5700 years, on the basis of the frequency of lightning strikes between 1950 and 1992 (Pew & Larsen 2001). A more localized study of charcoal in lake sediments (Cowichan Valley), which would not have detected low-intensity grassland fires, estimated a fire-return interval of 27–41 years, although it was difficult to detect distinct fire events relative to the background level of charcoal (McCoy 2006; Pellatt et al. 2007). These results suggest fires were more frequent than expected given the natural fire-return interval and were therefore likely related to anthropogenic activity (Turner 1999; MacDougall et al. 2004).

Indicator and Flagship Species in Savannas

Our results broaden and challenge commonly held views of presettlement conditions on Vancouver Island. In particular, pine plains (i.e., Douglas-fir plains), which made up a substantial portion of the presettlement landscape, are virtually nonexistent today and, prior to this study, were not known to exist historically in this region. This is in marked contrast to present-day savannas where oaks predominate. In addition, current conservation efforts emphasize the role of Garry oak in prairie and savanna restoration (Hosten et al. 2006). Nevertheless, our data show that the proportion of Garry oak trees relative to other species has changed little over time, even though the proportion of open habitats, which currently harbor most of the region's species at risk (Fuchs 2001), has declined dramatically. Thus, the emphasis on conservation of Garry oak trees per se may be misdirected because historically these habitat types were as likely to be associated with Douglas-fir (or with no trees at all) as with oak. Given the low density of trees, many of the threatened herbaceous species currently associated with savannas likely grew in both prairie and open pine plains historically. This highlights the broader issue of the potential pitfall in assuming that the presence of a particular species represents the status of an entire habitat type or community, when in fact the species–habitat association may be without historical precedent (e.g., Sinclair et al. 2007) or the flagship species is not representative of species diversity more broadly (e.g., Williams et al. 2000).

Conclusions

Our results have important implications for the development of a perspective on historical human impacts in the New World that is more balanced than the simple dichotomy of landscapes as either humanized or pristine (Vale 2002). Ambiguities concerning the intensity, spatial extent, and timing of anthropogenic impacts were identified by Vale (2002) as being in great need of clarification in order to reconcile opposing viewpoints. Most of our study region appears to represent an intermediate level of intensity of historical landscape modification—less intense than within the confines of a densely populated village, but of sufficient intensity to have modified vegetation structure relative to what one would expect in the absence of humans. In terms of space, the presence of both forested and open habitats historically suggests considerable spatial variability in the magnitude of human impacts, with prescribed fire likely to have maintained at least half of the landscape as open habitat (Table 1). In terms of time, the duration of impacts has likely varied across the landscape, with sites on relatively deep soils filling in rapidly with forest and sites on shallower soils remaining as open habitats to the present day (Vellend et al. 2008). Our results support the viewpoint that for the conservation implications of historical human impacts to be fully appreciated, conservation professionals need to abandon the simple yes–no dichotomy and embrace the reality of continuous variation in the intensity, spatial extent, and duration of such impacts.

Restoration efforts are often prone to uncertainty about target conditions (Higgs 1997; Hobbs & Cramer 2008), especially in areas with no appropriate reference sites to help define historical conditions. Land managers often follow a do-nothing approach and allow land to return to its "natural" state (Hobbs & Cramer 2008). Nevertheless, our study indicates that the open nature of the endangered savannas on Vancouver Island was likely maintained by fires purposefully set by native peoples. Thus, restoration of these habitats to their pre-European state cannot be accomplished simply by removing human influences. Achieving the goal of maintaining open savannas would almost certainly need to involve active removal of encroaching trees and shrubs, either through burning or alternative strategies (e.g., mowing, tree removal) (MacDougall et al. 2004; Gedalof et al. 2006). Ideally such measures should be implemented in controlled experiments (i.e., through adaptive management; Walters 1986). Furthermore, the tree species currently most closely associated with savannas (Garry oak) does not appear—in a historical context—to be an appropriate flagship for savannas in general or their rich diversity of associated species. This highlights the necessity of understanding and preserving ecosystem processes, rather than patterns only, and emphasizes the need for active management to achieve conservation and restoration goals in many ecosystems.

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