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Environmentally biased fragmentation of oak savanna habitat on southeastern Vancouver Island, Canada

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ABSTRACT

Quantifying the degree to which natural or protected areas are representative of a specified baseline provides critical information to conservation prioritization schemes. We report results on southeastern Vancouver Island, Canada, where we compared environmental conditions represented across the entire landscape, in oak savanna habitats prior to European settlement (<1850), and in both protected and unprotected oak savannas in the present-day. In this region, oak savannas represent a rare habitat type, harboring many threatened species. Before European settlement, oak savannas occurred in a distinctly different subset of environmental conditions than they do today. Compared to the entire landscape, oak savannas were historically found predominantly in warm, dry, flat, and low-lying areas, but habitat destruction has left oak savannas in largely the exact opposite set of conditions at present. Thus, the range of conditions in both protected and unprotected oak savannas at present are highly unrepresentative of historical conditions. It appears that fire management by indigenous peoples maintained oak savannas historically across large areas of flat low-lying conditions with deep soils, where succession otherwise produces closed coniferous forest. These areas have since been almost entirely converted to agricultural and urban areas, leaving remnant oak savannas largely on steep, rocky hilltops, where the habitat is maintained by shallow soils. Our results provide quantitative guidance for setting conservation priorities for oak savannas in this region, while highlighting the important general issue of the major role traditional land-use practices can play in shaping landscapes, and therefore in influencing the baselines used to set conservation priorities.

1. Introduction

A central goal of many conservation prioritization schemes is to maximize the "representativeness" of a network of protected areas relative to a specified baseline (World Resources Institute, 1992; Hazen and Anthamatten, 2004). Because ecosystems have been left intact largely in places with limited extractive or commercial value, such as mountainous or arid areas, existing networks of natural or protected areas tend to be highly unrepresentative of their surrounding regions (Pressey, 1994; Margules and Pressey, 2000; Scott et al., 2001; Flinn et al., 2005). Identifying and quantifying such biases provides a critical ingredient to the scientific basis for systematic conservation planning (Margules and Pressey, 2000). Our study focuses on testing for changes since European settlement (~150 years ago) in the environmental conditions represented in

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oak savanna habitats, both protected and unprotected, on southeastern Vancouver Island, Canada, where the predominant natural vegetation is coniferous forest.

A critical first step in any analysis of representativeness involves specification of both the focal sites of interest (e.g., natural or protected areas) and the baseline set of conditions to which the focal sites are being compared (Margules et al., 2002). Since ecological communities change over time even in the absence of anthropogenic disturbance, specifying the baseline conditions one would like to represent is not a trivial matter (Foster, 2000; Egan and Howell, 2001). Using contemporary data on the distributions of species (e.g., Deguise and Kerr, 2005; Kamei and Nakagoshi, 2006) effectively establishes conditions in the present day as the baseline, accepting that species distributions have already been dramatically altered by human activities. Another common basis for assessing biodiversity is a map of potential natural habitat types, which often involves assigning habitat designations to areas already converted to other land uses (e.g., Oldfield et al., 2004). This approach assumes a reliable basis for assessing the natural habitat that would be present in the absence of human disturbance, and implicitly sets the baseline prior to intensive human landscape transformation. In this study we take advantage of an historical reconstruction of the distribution of oak savannas prior to European settlement (Lea, 2006) to establish a pre-settlement baseline of conditions represented in this habitat type.

In North America, an assessment of what the landscape looked like prior to European settlement is often used as an implicit baseline for defining conservation targets (Swetnam et al., 1999; Foster, 2000; Egan and Howell, 2001). Given that the contemporary composition of many North American landscapes has been shaped in large part by land use activities since European settlement, this may often be a reasonable approach. However, it presents the difficult issue of how to establish conservation baselines in landscapes that are known or thought to have been influenced by traditional land-use practices of indigenous peoples prior to European settlement (Gomez-Pompa and Kaus, 1992; MacDougall et al., 2004). Although the paucity of spatially-explicit information on historical land use by indigenous people makes quantitative treatment of this issue difficult, comparing pre-settlement and contemporary data on the distribution of habitat types in relation to environmental conditions may potentially allow some indirect inferences to be made (e.g., Foster et al., 2004).

Another critical step in analyses of representativeness is determining how to represent biodiversity itself, which we assume to be the primary target of conservation efforts. Since data on species distributions and diversity are often not available at the relevant spatial resolution or extent to inform a regional-scale analysis of representativeness, a common proxy for biodiversity is the spatial variability of environmental variables, such as topography, climate, or soil types (Faith and Walker, 1996; Pressey et al., 2000, 2007; Trakhtenbrot and Kadmon, 2005; Sarkar et al., 2006). The assumption is that different combinations of environmental conditions favor different sets of species – an assumption that is well-supported across many different regions and habitat types (Whittaker, 1975), including the focal habitat and region in our study (Roemer, 1972; Lilley, 2007). Using environmental data to assess ecological representativeness is particularly attractive for conservation efforts that wish to take into account changing conditions such as climate, because even as species distributions shift, spatial variability in species composition is likely to remain tightly linked to gradients of environmental conditions such as topography and soils (Sarkar et al., 2006; Pressey et al., 2007).

In this paper we analyze the distributions of biotically important environmental variables in different subsets of the Saanich Peninsula on Vancouver Island, Canada, with a focus on oak savanna habitats. Oak savannas represent the most threatened habitat type in this region (Fuchs, 2001), and their extent has declined dramatically since European settlement (Lea, 2006). Prior to European settlement, fire management by indigenous peoples is thought to have played a role in the maintenance of oak savannas (Pellatt et al., 2007). Based on environmental data (topography and climate), and both historical and contemporary maps of oak savanna habitats across this region, we assessed changes in the relationship between the distribution of oak savannas and environmental conditions over the past ~150 years. We further evaluate the degree to which the present-day network of remnant oak savanna habitats (protected or not) is representative of oak savanna habitats in the pre-settlement landscape, and also the degree to which protected oak savanna habitats are representative of the larger set of oak savannas across the contemporary landscape.

2. Methods

2.1. Study area

The Saanich Peninsula occupies ~340 km^2 at the southeastern end of Vancouver Island, Canada (Fig. 1). Climate in the region is sub-mediterranean, with cool, wet winters and dry, fairly hot summers (Roemer, 1972; Fuchs, 2001). Summers typically include a significant drought period, as a result of the region lying with a rain shadow of mountains on the Olympic Peninsula (Washington State, USA) and the central spine of Vancouver Island.

Elevation varies from sea level to about 400 m, and soils are largely post-glacial, relatively infertile and shallow (Roemer, 1972). The study area falls within the Coastal Douglas Fir zone according to the British Columbia Biogeoclimatic Ecosystem Classification (Meidinger and Pojar, 1991), where the dominant natural vegetation is comprised of Douglas fir-dominated coniferous forests. Oak savannas – grasslands with scattered Garry oak (*Quercus garryana*) trees – are relatively rare, but disproportionately important in regional conservation efforts as they harbor many habitat-specific species, including 61 plant species considered "at risk" in Canada (Fuchs, 2001).

Humans have had an impact on the landscape in a variety of ways. Prior to European settlement in the mid 19th century, indigenous peoples influenced the landscape via establishment of villages and cultivation of food plants such as *Camassia* species, likely involving fire management to maintain relatively open habitats (Pellatt et al., 2007). The city of Victoria (population ~330,000) occupies the southern end of the Peninsula, though there are many natural areas within the

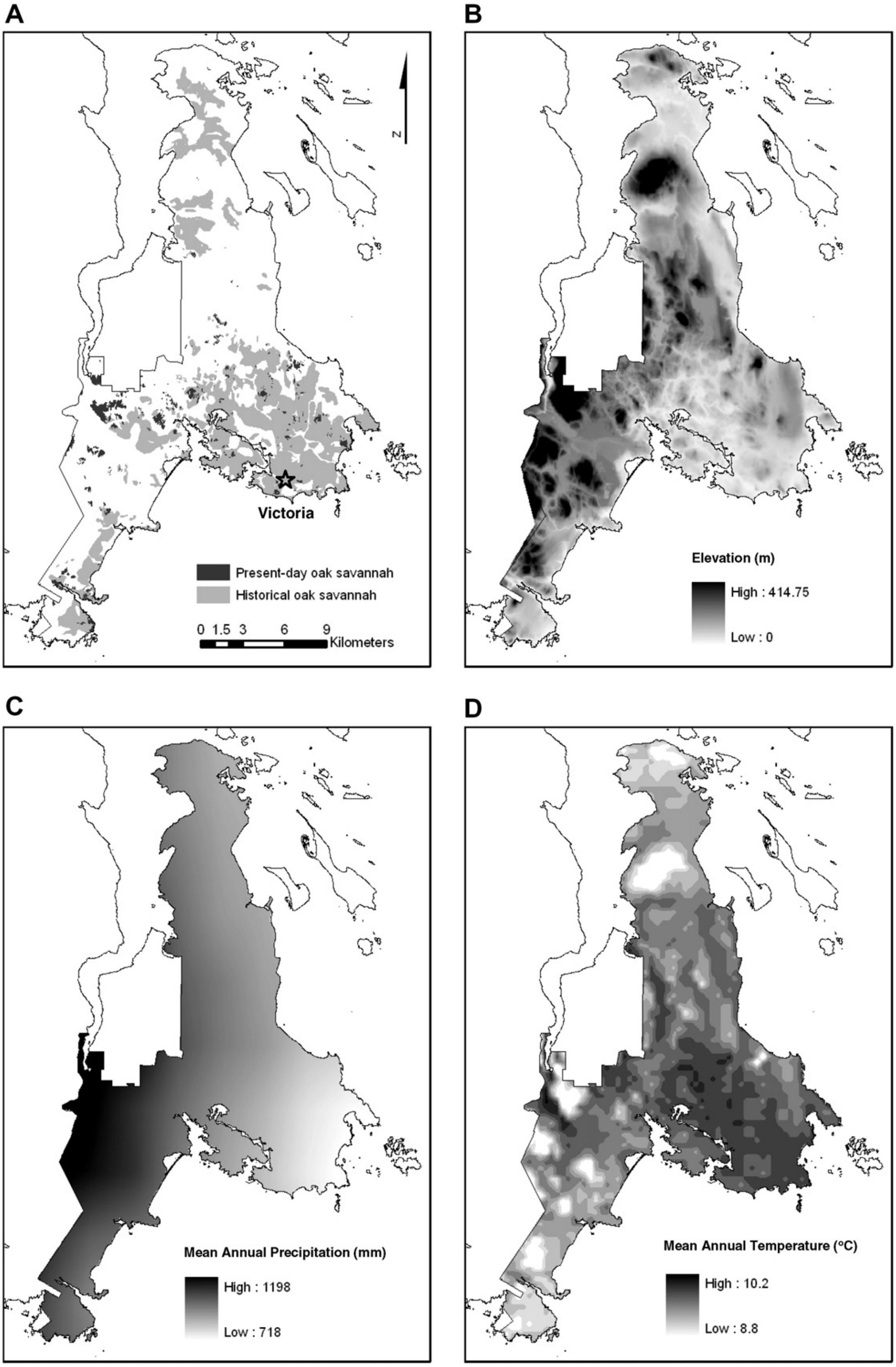

Fig. 1 – Maps of the study area, Saanich Peninsula, Vancouver Island, British Columbia, Canada, illustrating (A) historical (<1850) and present-day oak savanna habitat distribution, (B) elevation above sea level, (C) mean annual precipitation, and (D) mean annual temperature. No information on historical oak savannas was available for the central-western portion of the Saanich Peninsula, so it was not part of the study area.

metropolitan Victoria area. The entire Peninsula has been heavily influenced by residential and industrial development, agriculture, and forestry. Roemer (1972) provides a detailed account of the ecology of this region.

2.2. GIS maps: oak savanna distribution

All data were derived from digital maps overlaid in ArcGIS 9.2 (ESRI, Redlands, CA). We analyzed environmental conditions in a nested set of four portions of the landscape: the entire landscape, historical oak savannas, present-day oak savannas, and present-day oak savannas within protected areas (see Fig. 2).

Lea (2006) reconstructed the historical distribution of oak savanna habitats (<1850, prior to European settlement) based on a combination of original European surveyor notes and maps from the 1850s and 1860s, remnant Garry oak trees in the landscape today, historical photographs and paintings, and expert advice. For some portions of the Saanich Peninsula historical reconstruction was not possible; these areas appear as sections of the Peninsula that were not included in our study area (Fig. 1). Present-day oak savanna habitats were mapped using the regional Sensitive Ecosystems Inventory (SEI; Ward et al., 1998), updated in 2004. The SEI recognizes a variety of community types, three of which potentially represent oak savanna: “woodland”, “coastal bluff”, and “tall herbaceous”. Included in our map were any polygons assigned to one of the three habitat types listed above, and for which Q. *garryana* was listed as one of the dominant trees based on field observations conducted as part of the SEI. After extracting these polygons, 231 polygons remained within one of the three habitat types but for which there was no information, or ambiguous information, on whether or not the site was an oak savanna. For example, some woodland sites are riparian poplar forests, and some tall herbaceous sites are beach strands. We examined the areas within these 231 polygons individually on high-resolution (0.5 m) aerial photographs provided by the Capital Regional District (Victoria, British Columbia) to determine whether or not to include them in the present-day oak savanna map. Any present-day oak savanna site was assumed to also have been an oak savanna site in the historical period.

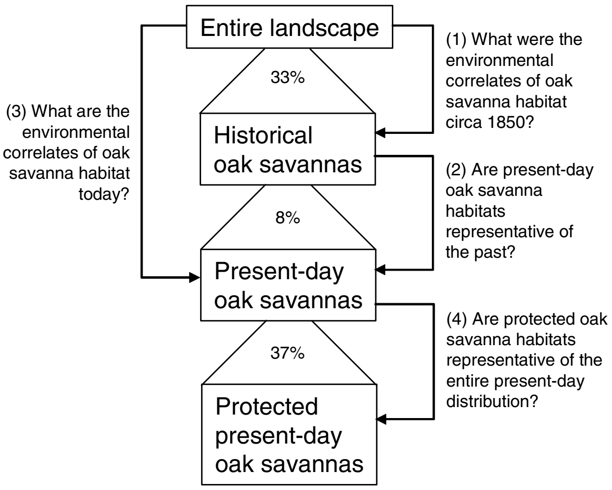

Fig. 2 – Illustration of the four nested portions of the landscape considered in this study, with the four specific questions addressed by asking whether environmental conditions in a data subset (at the ends of the arrows) are significantly different from conditions in the reference data set (at the source of the arrows). The percentage of each reference data set that each data subset represents is shown between boxes.

To map the portion of present-day oak savannas in our study area that fall within a protected area of some kind, we used a map of all provincial, regional, and municipal parks, as well as National Historic Sites, within our study. This map layer is part of the Natural Areas Atlas of the Capital Regional District (http://www.crd.bc.ca/maps/natural/), which encompasses Victoria and its surrounding municipalities.

2.3. GIS maps: environmental variables

Maps were constructed for the following environmental variables across our study region: aspect, slope, elevation, mean annual temperature, and mean annual precipitation. These variables represent the dominant predictors of plant community composition in this region (Roemer, 1972; Lilley, 2007). Originally we also extracted information on soil acidity and drainage from a regional soils map (Jungen, 1985), but these were ultimately excluded from analysis for several reasons. The soils map did not include the greater Victoria area (an area with a concentration of oak savanna habitat historically); the acidity and drainage scores were quite coarse (2 and 6 categories, respectively); and these scores were correlated with the other environmental variables, and therefore did not contribute new information to the results.

Aspect, slope and elevation were mapped by first using a 25 m-grid digital elevation model (DEM) from the British Columbia Terrain Resource Information Management data source, provided by the Province of British Columbia. The 25 m DEM was aggregated up to a 50 m grid in order to reduce some minor artifacts in the original data, such as faint ridges along roads. This aggregation visibly reduced the artifacts in the original DEM. The 50 m DEM was then used to generate raster maps for aspect and slope angle at the same resolution. Aspect was expressed as degrees from north to reflect growing conditions in terms of solar radiation, and to remove the circularity from the scale of this variable.

Mean annual temperature (°C) and precipitation (mm) were derived from pre-calculated rasters (ClimateBC Program, Hamann and Wang, 2005). The underlying data represent climate normals for all weather stations in British Columbia for the years 1961–1990, interpolated into a raster which incorporates topography in order to accurately model temperature and precipitation. The available rasters were at 400 m resolution, and we resampled these rasters using bilinear interpolation to align them to the same grid and projection as the DEM raster.

In addition to conducting analyses of each environmental variable separately, we explored principal component analysis (PCA) on the five variables together. This did not reveal any ecological inferences distinct from those derived in the univariate analyses, so the results are not shown here. The two variables showing the greatest differences among data sets were slope and aspect; these variables were correlated across the entire landscape ($r = 0.49$) and their means showed the same ordering across data sets. To characterize a joint slope-elevation axis, we conducted a PCA on these two variables and used the scores on the first PCA axis in the same set of analyses as the other variables (described below).

2.4. Data extraction and analysis

We compared the distributions of environmental variables in four circumscribed areas: the entire study area, historical oak savannas, present-day oak savannas, and present-day oak savannas within protected areas. For the entire study area and historical oak savannas, each of which occupy substantial portions of the landscape (Fig. 1), we extracted environmental data at 2000 points selected randomly, with the restriction that no two points be closer than 150 m apart (three times the dimensions of a single map pixel in raster maps). There are 238 discrete present-day patches (polygons) of oak savanna habitat in our study area, 234 of which can be sampled without falling within 150 m of another patch. We extracted data from one randomly selected point within each of these 234 patches to represent the present-day oak savanna habitats, and extracted in a separate data set the 73 of these 234 points that fell within protected areas.

The degree to which a data subset (e.g., present-day oak savannas) is representative of a reference data set (e.g., historical oak savanna) may be reflected not only in differences between means, but in other parameters of the distributions as well, such as variance and extreme values. For example, the present-day and historical sites might have the same mean elevation, but there may be very few present-day sites at very high or low elevation where ecological conditions are most distinct. As such, we characterized each environmental distribution in each of the four data sets by calculating the following eight parameters: mean, median, coefficient of variation, lower and upper 95th percentiles, and lower and upper 75th percentiles.

Statistical analyses were complicated by the fact that the four statistical "populations" were perfectly nested: protected oak savannas within present-day oak savannas, present-day within historical oak savannas, and historical oak savannas within the entire landscape (Fig. 2). As such, we used iterative resampling techniques to pose four specific questions for each distribution parameter (questions paraphrased in Fig. 2). (1) Did the environmental conditions in historical oak savanna sites represent a significantly biased subset of conditions across the entire landscape? (2) Do the environmental conditions in present-day oak savannas represent a significantly biased subset of the conditions in historical oak savannas? (3) Do the environmental conditions in present-day oak savannas represent a significantly biased subset of the conditions across the entire landscape? (4) Do the environmental conditions within protected oak savannas represent a significantly biased subset of conditions in present-day oak savanna sites? In the first three cases, the reference distribution (i.e., the second listed under each question) was re-sampled 1000 times, each time drawing 234 data points at random with replacement. For question 4, we drew 1000 random samples of 73 points with replacement from the present-day sites. From these simulations, for each distribution parameter we then calculated the proportion of simulations giving values greater or less than that in the data set being evaluated (i.e., the first listed under each question). These proportions represent p-values of two separate one-tailed tests that the parameter value in the subset of data is less than or greater than, respectively, the value in the reference data set. All analyses were conducted using code written in MATLAB version R2007b (MathWorks Inc., Natick, MA).

3. Results

3.1. Question 1: Historical oak savannas vs. the entire landscape

Prior to European settlement, oak savannas occurred in a distinct subset of environmental conditions across the landscape. In terms of variable means, oak savannas were found under relatively warm and dry climatic conditions, at low elevation sites with shallow slope angles (Table 1, Fig. 3). Differences in the same direction between historical oak savannas and the entire landscape were found for lower and upper 75th percentiles for most of the same variables, but the extent of variation within data sets (standard deviation, CV) did not tend to differ significantly (Table 1). The distribution of aspects across the two data sets did not differ significantly in any respect (Table 1, Fig. 3).

3.2. Question 2: Present-day oak savannas vs. historical oak savannas

Oak savannas in the present-day landscape occur under a very different set of environmental conditions than they did prior to European settlement. Present-day oak savannas are found in a relatively cool, wet, steep, and high-elevation subset of the conditions under which oak savannas were found in the past (Fig. 3, Table 1). This is reflected in mean differences for all four of these variables, in differences of lower and upper 75th and 95th percentiles for slope and elevation, and in some of the extreme percentiles of the climatic variables (Table 1). The difference is most distinct at the lower end of the combined slope-elevation axis (Fig. 3F), where fully 29% of conditions in historical oak savanna sites fall below the lower 95th percentile of conditions in present-day oak savannas. The coefficient of variation for temperature was slightly higher, and for slope slightly lower, in present-day than historical oak savannas (Table 1).

3.3. Question 3: Present-day oak savannas vs. the entire landscape

Compared to the landscape as a whole, present-day oak savannas occur under similar climatic conditions, but at relatively high elevations and on steep slopes (Fig. 3, Table 1). These differences are reflected in mean values, and also in the 75th and 95th percentiles (Table 1). Interestingly, these differences are in exactly the opposite direction as those between historical oak savannas and the entire landscape.

Table 1 – Estimated parameters of environmental variable distributions at points randomly selected across the landscape (Entire), within the historical range of oak savannas (Historical), within the present-day range of oak savanna (Present), or in present-day protected oak savannas (Protected)

Parameter	Portion of landscape	Mean annual temperature (°C)	Mean annual precipitation (mm)	Aspect (degrees from N)	Slope (degrees)	Elevation (m)	PCA1 (slope & elevation)
Mean	Entire	9.78^{a}	920^{b}	94^{a}	5.3^{b}	60^{b}	0.11^{b}
	Historical	9.83^{b}	879^{a}	98^{a}	4.3^{a}	48^{a}	-0.20^{a}
	Present	9.80^{a}	922^{b}	100^{a}	8.6^{c}	81^{c}	0.76^{c}
	Protected	9.82	899	87^{*}	9.2	83	0.82
Median	Entire	9.80^{a}	916^{b}	94^{a}	3.8^{b}	51^{b}	-0.04^{b}
	Historical	9.90^{b}	879^{a}	102^{a}	2.9^{a}	38^{a}	-0.37^{a}
	Present	9.90^{b}	929^{b}	104^{a}	7.3^{c}	65^{c}	0.58^{c}
	Protected	9.90	900	88	7.2	67	0.62
Coefficient of variation	Entire	$0.018^{a,b}$	0.10^{a}	0.52^{a}	0.92^{b}	0.75^{a}	NA
	Historical	0.017^{a}	$0.10^{a,b}$	0.50^{a}	1.02^{b}	0.89^{b}	NA
	Present	0.019^{b}	0.11^{b}	0.49^{a}	0.76^{a}	$0.71^{a,b}$	NA
	Protected	0.023	0.12	0.54	0.87	0.76	NA
Lower 95th percentile	Entire	$9.50^{a,b}$	759^{a}	13^{a}	0.5^{a}	10^{a}	-1.24^{a}
	Historical	9.50^{b}	740^{a}	12^{a}	0.5^{a}	10^{a}	-1.26^{a}
	Present	9.40^{a}	746^{a}	11^{a}	1.1^{b}	17^{b}	-0.71^{b}
	Protected	9.30	744	12	1.0	18	−0.74
Upper 95th percentile	Entire	10.00^{a}	1100^{b}	170^{a}	14.7^{a}	145^{a}	2.00^{a}
	Historical	10.00^{a}	1050^{a}	171^{a}	12.3^{a}	129^{a}	1.88^{a}
	Present	10.00^{a}	1091^{b}	172^{a}	19.9^{b}	205^{b}	2.71^{b}
	Protected	10.00	1082	170	24.0	204	2.94
Lower 75th percentile	Entire	9.70^{a}	865^{c}	55^{a}	1.9^{b}	26^{a}	-0.61^{b}
	Historical	9.70^{a}	805^{a}	$60^{a,b}$	1.5^{a}	23^{a}	-0.80^{a}
	Present	9.70^{a}	849^{b}	68^{b}	3.7^{c}	42^{b}	-0.13^{c}
	Protected	9.72	804^{*}	43	3.5	46	−0.20
Upper 75th percentile	Entire	9.90^{a}	972^{b}	135^{a}	7.2^{b}	81^{b}	0.65^{b}
	Historical	10.00^{b}	937^{a}	140^{a}	5.5^{a}	60^{a}	0.11^{a}
	Present	$9.90^{a,b}$	988^{b}	137^{a}	12.2^{c}	106^{c}	1.61^{c}
	Protected	9.90	978	117^{*}	12.0	97	1.12

Different letter superscripts indicate significant pairwise differences between the Entire, Historical, and Present categories; asterisks indicate when the Protected value was significantly different than the Present value ($p < 0.01$). PCA1 takes negative values, so calculating the coefficient of variation is inappropriate.

3.4. *Question 4: Protected oak savannas vs. all present-day oak savannas*

In the present-day landscape, protected areas encompass a set of oak savannas that occur under a very similar set of environmental conditions as the entire set of oak savanna sites in the region (Fig. 3, Table 1). There was a slightly reduced tendency for protected sites to occur on south-facing slopes, and also a reduced lower 75th percentile for precipitation, compared to the full set of present-day oak savanna sites (Table 1).

4. Discussion

The most striking result of this study was that both past and present oak savanna distributions, relative to the entire landscape, could be predicted based on environmental conditions, but in exactly opposite directions in the past vs. the present. On average, oak savannas circa 1850 occurred on shallow slopes at low elevation, and under dry, warm climatic conditions, while present-day oak savannas occupy sites in precisely the opposite set of conditions. As such, present-day oak savannas are highly unrepresentative of historical oak savannas – biased towards cool, wet, steep, and high elevation areas. This pattern is particularly strong at the lower end of slope-elevation gradient, where a large proportion of conditions represented in the pre-settlement landscape are almost completely missing from remnant oak savannas in the present day (Fig. 3F). Oak savannas in protected areas are largely representative of the broader set of oak savannas in the present-day landscape (protected + unprotected), and therefore highly unrepresentative of historical conditions as well.

In southwestern British Columbia, oak savannas represent a relatively rare habitat type (Ward et al., 1998; Lea, 2006). The predominant natural vegetation in the broader coastal region consists of coniferous forests dominated by Douglas fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*), and western hemlock (*Tsuga heterophylla*) (Meidinger and Pojar, 1991). Within this broader region, oak savannas occur only on southeastern Vancouver Island and the adjacent Southern Gulf Islands – the driest and warmest parts of the broader region – such that the wet and cool conditions in present-day oak savannas relative to the Saanich Peninsula as a whole are still relatively dry and warm compared to the broader region. In addition to the low summer rainfall in our study area, two main factors are thought to have maintained the open conditions of oak savanna habitats historically. First, very shallow soils, which are found most commonly on steep

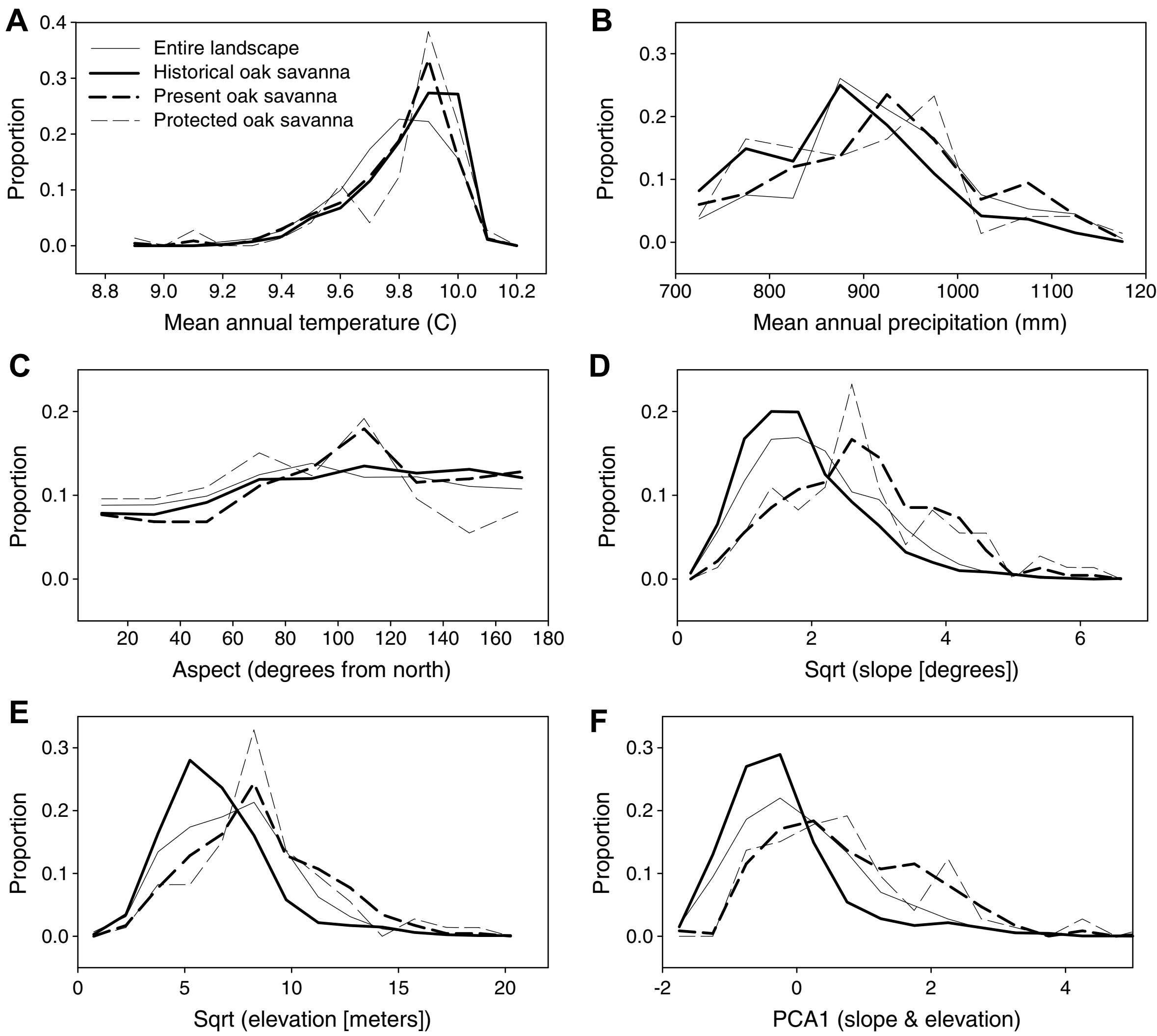

Fig. 3 – Histograms of environmental conditions across the entire landscape (thin solid line), in historical oak savannas (thick solid line), in present-day oak savannas (thick dashed line), and in protected present-day oak savannas (thin dashed line). For simplicity of presentation, histograms are shown by connecting the peaks of bars with lines, rather than showing the bars themselves.

rocky hilltops at higher elevations, as well as in coastal bluffs, can prevent establishment of coniferous trees and thereby maintain open savanna conditions (Scholes and Archer, 1997). Second, periodic fires can also prevent the establishment of coniferous trees and maintain open conditions (Pellatt et al., 2007). The encroachment of Douglas fir into oak savanna sites on deeper soils (Gedalof et al., 2006) suggests that fire is in fact necessary for the maintenance of oak savannas under such soil conditions. Although natural fires do occur in the region (Pellatt et al. 2007), a major agent of burning in the pre-settlement landscape was indigenous use of fire to enhance production of food plants such as camas bulbs (*Camassia* spp.) and bracken fern (*Pteridium aquilinum*) (Turner, 1999). Active fire suppression and the cessation of indigenous fire management since European settlement have essentially eliminated fire as an important agent of ecological change in the region (MacDougall et al., 2004). Although herbivores, such as native black-tailed deer or introduced goats and sheep, may have strong effects on oak savanna vegetation (Gonzales, 2008), there is no evidence to suggest that the distribution of oak savannas across the landscape is related to variability from place to place in herbivore pressure.

In light of our knowledge of how oak savannas are maintained, our results can be most parsimoniously interpreted as follows. First, the predominance of oak savanna habitats in flat, low elevation, warm and dry areas prior to European settlement, was likely a result of the large indigenous population in the area now occupied by the city of Victoria (Fig. 1; Turner, 1999; Lea, 2006), and traditional management of the landscape in this area using fire. Historically, oak savannas were also present on steep, rocky hilltops at higher elevations, but these comprised a relatively small proportion of the larger extent of oak savanna habitats (Fig. 3). European settlement brought the decimation of indigenous populations, and therefore their traditional land-use practices, as well as active fire suppression, and development of land for agriculture, urban development, and forestry (MacDougall et al., 2004). Low-lying areas on deeper soils, without a dense cover of coniferous trees, were ideally suited for conversion to intensive agriculture and for establishment of the city of Victoria by European settlers (MacDougall et al., 2004). As such, the vast majority of oak savanna habitats under such conditions have been destroyed, leaving as remnants the subset of sites on steep, rocky terrain at high elevations. This heavy bias in which sites were destroyed or left more-or-less intact has resulted in a present-day set of oak savannas that is highly unrepresentative of historical conditions. An ecologist predicting the environments under which oak savannas could be found in 1850 would have come up with the exact opposite prediction as an ecologist working in the contemporary landscape.

Although there is no detailed information on how all of the protected areas in the region were established, it seems clear that to a certain a degree the process was *ad hoc* (sensu Pressey, 1994), in that areas were protected where competing interests (e.g., agriculture) were limited, and where there were opportunities for recreation and scenery, rather than where biodiversity goals could be met (Pressey, 1994). Protected areas in the region fall under the management of a variety of agencies, including the Canadian federal government (National Historic Sites, Department of National Defense lands), the Province of British Columbia (Provincial Parks), the Capital Regional District (Regional Parks), and individual municipalities (municipal parks). To our knowledge there is no systematic co-ordination among these agencies to achieve representation across the region. However, because new subdivisions often require the establishment of parkland locally (e.g., District of Saanich, 2007), protected areas are fairly evenly distributed across the region, and because remnant oak savannas occur predominantly in steep, rocky sites, those that are protected are largely representative of the broader network of oak savannas, protected and otherwise. We can speculate that the small bias towards north-facing slopes in protected areas (Table 1) is due to the desirability of south-facing slopes for real estate development, which represents the main agent of habitat destruction at present.

Our results are in line with those from many other regions, where remnant natural or protected areas are located largely where conditions are unsuitable for competing land uses, resulting in relatively poor representation of broad-scale or historical ecological conditions (Pressey, 1994; Margules and Pressey, 2000; Scott et al., 2001). The main conservation implication in such cases is that the top priority for the establishment of new protected areas should be on sites with conditions that are underrepresented in the current network of protected areas. In our case, this would be warm, dry sites on level terrain at low elevations, where soils are generally relatively deep. However, there seems to be strong evidence that oak savanna habitats were maintained historically under such conditions largely due to indigenous fire management (MacDougall et al., 2004; Pellatt et al., 2007), which no longer occurs, and is not feasible for widespread use as a management tool today given the high population density in the region. As such, prioritizing conservation of oak savannas under these underrepresented conditions implies acceptance of a culturally modified landscape as an appropriate conservation baseline – a contentious issue in conservation biology (Phillips, 1998; MacDougall et al., 2004). It also presents a challenge to managers with respect to how (or if) to maintain such sites as oak savannas. One of the few flat, low-lying, deep-soil oak savannas in the region occurs in the Cowichan Garry Oak Preserve, owned by the Nature Conservancy of Canada, ~10 km northwest of the Saanich Peninsula. Colonizing Douglas fir trees are being actively removed from this site in order to maintain its integrity as an oak savanna (Andrew MacDougall, personal communication). Carefully-timed mowing is another management tool that may contribute to the maintenance of oak savanna habitats at sites otherwise susceptible to natural succession to Douglas fir forest (MacDougall and Turkington, 2007).

Finally, the role of indigenous cultural practices in shaping the landscape of southeastern Vancouver Island (Turner, 1999; MacDougall et al., 2004), and indeed many landscapes around the world (Denevan, 1992; Gomez-Pompa and Kaus, 1992), needs to be explicitly recognized in prioritization schemes for habitat conservation and restoration. However, depending on one's view of the role that traditional land-use practices should play in establishing baselines for conservation, the remnant oak savannas of the Saanich Peninsula could either be considered largely representative of the conditions under which oak savanna habitats could be expected to occur in the absence of human influence (steep, rocky hilltops), or highly unrepresentative of historical conditions (flat, low-lying areas). Accepting the latter argument, our results provide quantitative support for the prioritization of flat, low-lying, deep-soil sites for efforts to conserve oak savanna habitats and their many regionally-unique species, although management of such sites presents considerable challenges. Our study provides a unique perspective on the very general issues of how to establish targets for conservation, and the roles of historical data and traditional land-use practices in conservation prioritization.

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