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Historic variability in fire-generated landscape heterogeneity of subalpine forests in the Canadian Rockies

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Climatic variability; Ecosystem management; Fire exclusion; Historical range of variability (HRV); Kootenay National Park (KNP); Natural disturbance; Non-equilibrium systems

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Abstract

Question: This study evaluates historical changes in landscape structure and heterogeneity in subalpine forests. We use response to severe fires in 2001 and 2003, along with historical reconstructions to examine crown-fire effects on landscape heterogeneity and to assess, comparatively, effects of fire exclusion management in the 20th century.

Location: Subalpine forests of Kootenay National Park (KNP), Canadian Rockies.

Methods: Using a landscape-level model based on a fire-origin stand age map, we reconstructed decadal burned areas within the landscape for 1750-2000 (forming reconstructed landscapes). Landscape pattern was analysed for each reconstructed landscape map, and we compared landscape pattern indices (total area, number of patches, mean patch area, patch area variation, largest patch index, edge density, perimeter–area ratio, landscape shape index) with those in 2005 after recent large fires.

Results: After large fires in 1926, connectivity of the KNP landscape increased and its diversity was quite low. After 2001 and 2003 fires, the post-fire landscape of 2005 was highly heterogeneous in terms of size, variation, edge density and perimeter–area ratio of the remnant forest patches. Since the decline in occurrence of large fires after 1926 reflected a period of wet weather, fuel build-up resulting from landscape homogenization within the 20th century landscape could not be attributed solely to fire exclusion. This period without fires greatly enhanced connectivity of late-successional forests that finally burned in 2001/2003, but connectivity was within the historical range for these forests. The gradual increase in stand connectivity before recent large fires may indicate that fire exclusion was less responsible than often believed for fuel build-up in these fire-susceptible older forests.

Conclusions: The large fires at the beginning of the 21st century are within the natural range of disturbances for this landscape, and do not stand out as "human-induced disasters" in their effects on landscape patterns. Such stochastic large disturbances contribute to maintenance of highly heterogeneous landscape structure, which is important for many taxa and natural ecological processes. Identifying future probability of such large disturbances and their ecological roles should be incorporated into management of these dynamic, disturbance-prone systems.

Introduction

All ecosystems undergo changes that are intrinsic and inevitable, and therefore, ecosystem management must be based on an understanding of these changes (White et al. 1999). Natural disturbances can cause sudden and dramatic changes in terrestrial ecosystems (White 1979).

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The importance of natural disturbance regimes has been long identified in various ecological systems (Bormann & Likens 1979; White 1979; Romme 1982; Sprugel 1991; White et al. 1999). Since the 1990s, it has been argued that maintaining ecological integrity and conserving biodiversity in dynamic ecosystems must be based on understanding of disturbance ecology (White et al. 1999; Yaffee 1999; Wallington et al. 2005; Noss et al. 2006). Lindenmayer et al. (2008) stated that failure to acknowledge the dynamic nature of systems would inevitably result in unexpected changes and failure to achieve conservation goals.

Compared to small disturbances, the ecological effects of large, infrequent disturbances on ecosystems and landscapes are less documented because of their unpredictability and rarity and the paucity of long-term data on their outcomes (Turner & Dale 1998; Turner et al. 1998; Kurz et al. 2008). The 1988 fires in Yellowstone National Park, USA, are a well-known example of a large, severe disturbance (Christensen et al. 1989; Turner et al. 2003). They have been shown to be within the historical range of variability (HRV), in terms of their size and ecological effects in the Yellowstone ecosystem (Romme et al. 1998; Turner et al. 2003). However, the sudden occurrence of large disturbances continues to result in public anxiety and people may consider such disturbances to be "disasters" (Romme et al. 1998; Bradstock 2008; Keane et al. 2008). Further study is needed in disturbance-prone forest ecosystems to understand the ecological consequences of large disturbances in order to understand their effects in the context of HRV (e.g. Shinneman & Baker 1997; Ehle & Baker 2003; Veblen 2003).

Several studies have reported that fire exclusion may have affected the length of fire intervals in the subalpine areas of the US Rockies (Kipfmueller & Baker 2000; Howe & Baker 2003). Rollins et al. (2001) further suggested that because of high stand density and fuel build-up across large areas, some subalpine forests in the Rockies are highly susceptible to high-severity crown fires. Excessive ingrowth of forest stands as a consequence of fire exclusion in the 20th century may have resulted in fuel accumulation across large areas (Rollins et al. 2001). On the other hand, current spatially homogeneous landscapes have been reported to be fundamentally consistent with historical fire regimes in some areas (Buechling & Baker 2004; Schoennagel et al. 2004; Sibold et al. 2006). In high-elevation subalpine landscapes of the Rockies, large wildfire activity has increased during the past few decades (Schoennagel et al. 2004; Westerling et al. 2006). Landscapes recently burned by crown fires are expected to differ from pre-fire conditions in spatial structure and heterogeneity (White & Jentsch 2001; Schoennagel et al. 2008) of forest patch structure (Forman 1995). Therefore, potential alternation of the pre-Euro-American landscape structure and fire regimes should be evaluated to assess the effects of the recent large fires on these subalpine forests to clarify whether they can be regarded as within the historic, natural range of disturbance dynamics.

With respect to conservation practices, the term "natural" has complex and frequently vague usage. It often is considered to mean "without human influence" (Hunter 1996). However, this definition may be too stringent because it is impossible to remove all human influences from the ecosystems. Many ecosystems that were presumed to be without human influence have experienced strong influences of people for millennia (e.g. Lepofsky 1999; Heckenberger et al. 2007). Nevertheless, it is necessary to evaluate which anthropogenic modifications of the disturbance regime are critical in order to develop more plausible conservation agendas. Hence, if, for example, fire exclusion has contributed to fuel build-ups and significantly modified fire regimes in subalpine landscapes, recent changes in fire activity in terms of frequency, extent and severity could be regarded as "unnatural" and potentially outside of conservation targets.

Landscape heterogeneity is an important feature of forested landscapes (Romme 1982; Turner et al. 1994; Schoennagel et al. 2008) because different species respond differently to the structural diversity, size and spatial arrangement of stand patches (Lindenmayer et al. 2006). It also plays an important role in determining subsequent natural disturbance regimes (Howe & Baker 2003; Kulakowski & Veblen 2007). However, fires of extent and severity beyond the range of natural variability may result in more homogenized landscapes by creating large uniform patches and eliminating a large percentage of small patches of diverse size and age fostered by typical natural fire regimes (Turner & Dale 1998; Bradstock 2008). Fire-related homogeneity is perceived as deleterious (Bradstock 2008) because it can eliminate biological legacies such as seed sources and late seral refugia and seldom leaves patches with diverse shapes, sizes and burn severity, all of which are generally found in heterogeneous landscapes following large natural fires (Schoennagel et al. 2008; Williams & Bradstock 2008). If the recent large fires are considered "unnatural" in this respect (i.e. caused by human-induced excessive fuel build-ups and so more severe and extensive), it is expected that post-fire landscape structures could deviate considerably from their HRV, with most post-fire stands in a uniform, structurally depauperate early seral stage.

At the beginning of the 21st century, in Kootenay National Park (KNP) in the Canadian Rockies, two large crown fires collectively burned 22.5% of the high-elevation subalpine landscape of the park. The management plan for KNP indicated that decades of effective forest fire

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exclusion practiced since 1919 had substantially changed the park vegetation. In general, forests were becoming older and less diverse, and several ecosystems such as grasslands and trembling aspen stands were declining with the development of closed conifer forests (Parks Canada 2000). The Periodic Report on the Application of the UNESCO World Heritage Convention emphasized that due to extensive fire suppression in the past, the biological and structural diversity of the vegetation in the Canadian Rocky Mountain Parks and surrounding areas has been reduced, resulting in forests that are more susceptible to large and intense fires (Parks Canada 2004). Thus, the park's management plan focuses on (1) restoring the role of fire as a natural disturbance and (2) perpetuating the natural range of vegetation disturbance (Parks Canada 2000). This focus further emphasizes the importance of assessing effects of past fire exclusion on the recent large fires and evaluating fire-induced variability and heterogeneity of landscape structure in this mountain park.

We constructed a simple model based on a fire-origin stand map of the KNP landscape to estimate historical changes in spatial structures before and after the recent large fires. By comparing landscape structures of the 20th century to reconstructed landscapes for the 18th and 19th centuries, we assessed (1) whether the KNP landscape was more homogeneous due to fire exclusion in the 20th century; (2) how the estimated variability in landscape structures of KNP co-varied with fire activity prior to the recent large fires; and (3) whether the 21st century landscape structure of KNP is more homogeneous relative to previous time periods. Based on our findings, we discuss the ecological role of naturally occurring large fires in maintaining landscape heterogeneity.

Methods

Study area

The study was conducted in Kootenay National Park (KNP), covering the western slopes of the Canadian Rocky Mountains in southern British Columbia, Canada, and registered as a World Heritage Site by UNESCO in 1984. The study area is about 40-km wide and 82-km long, with an elevation of 800 to 3400 m. According to the biogeoclimatic ecosystem classification system of British Columbia (Meidinger & Pojar 1991), this park has four zones: an interior Douglas-fir zone (IDF), a montane spruce zone (MS), an Engelmann spruce subalpine fir zone (ESSF) and an alpine tundra zone (AT). A large part of the park area can be classified as a high-elevation ecosystem. Forest vegetation mainly consists of lodgepole pine (*Pinus contorta* Loudon var. *latifolia* Engelm.), Douglas-fir (*Pseudotsuga menziesii* Mirb. Franco), white spruce (*Picea glauca* [Moench] Voss), quaking aspen (*Populus tremuloides* Michx.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.). There are many alpine meadows in the alpine areas. The fire season is generally from May to September, with peak ignition activity in July and August. In winter, snow covers most areas, with accumulations of 0.2 to 2.0 m.

Development of landscape maps

The initial map used in this study was obtained from Masters (1990), who developed a stand-origin map of KNP in 1988, using 1:25 000 aerial photographs to identify forest patch boundaries. The patch age was then estimated based on field censuses that used fire scars or the age of the oldest trees in each patch to date stand origin (Masters 1990). The 1988 map covers a 40.4 km × 82.6 km area (137 092.8 ha), and has 117 fire-origin polygons with stand origins from 1332 to 1984. We converted Masters's map into vector format and calculated areas for each polygon using geographic information system (GIS) software (ESRI ArcInfo 9.2).

Non-forested areas, such as alpine meadows, rocks and glaciers, were merged into the background of the 1988 map. Two polygons belonging to the IDF zone were also integrated into the background because this zone includes low-elevation ecosystems with substantially different fire regimes than those of the high-elevation forests (Hallett & Walker 2000). The remaining areas of the map (87 442.7 ha) represent stand age distributions in high-elevation forests of the park in 1988. By overlaying this high-elevation forests map with polygons for fires occurring in each year from 1988 to 2000, estimated from aerial photographs and LANDSAT images, we constructed a stand age map for 2000. High-severity crown fires in 2001 (3258 ha) and 2003 (16 376 ha) burned about 22% of the high-elevation forested areas. We constructed fire polygons for these fires and other small fires until 2005 to produce the most recent (current) map of stand origin.

To estimate historical changes in landscape structures, we used the GIS-based model of Tinker et al. (2003). This model calls for an assumption of uniform fire interval for reconstruction of past burned landscapes. For the subalpine landscape of Yellowstone National Park, USA, Tinker et al. (2003) used a fire interval of 350 years, which is consistent with data on fire rotations in other subalpine forests in Rocky Mountain regions (Veblen et al. 1994; Buechling & Baker 2004). However, several studies have showed that fire intervals in the northern Rocky Mountains are shorter than those in the southern and central Rocky Mountains. Therefore, we calculated the time-since-fire (TSF; Macias Fauria & Johnson 2008) distribution from the stand age map in 2000, and used this distribution to estimate a fire cycle of 244.7 years (Appendix S1). We calculated the area-weighted mean stand age in the areas burned in 2001 and 2003, with resulting values of 247 and 251 years. In KNP, Hallett & Hills (2006) estimated a fire interval of 245 ± 87 years based on lake sediment records. In our models, therefore, we used a fire return interval of 250 years. We recalculated models with fire intervals of 250, 300 and 350 years and did not observe large differences in results.

Using the landscape model of Tinker et al. (2003), landscapes from 1750 to 2000 were reconstructed at 10-year intervals. To create the 1990 stand age map, 10 years were subtracted from the age of each polygon in the 2000 stand age map. Polygons in the new map assigned an age of zero or less were considered to have burned between 1990 and 2000, and were assumed to have had a stand age of 250 years when burned. This process was repeated for each earlier decade. This model assumes that each stand burned only once in the fire interval (Tinker et al. 2003). In reality a few stands would have burned more than once, but we assume that areas burned twice would be very small because of the long-term fire intervals in subalpine forests in the Rockies. Tinker et al. (2003) suggested that this assumption is valid for reconstruction of past burned landscapes in subalpine areas of the Rockies with infrequent high-severity fires. Furthermore, in the studied KNP landscape, Hallett et al. (2003) demonstrated that the dates for stand origins, estimated by Masters (1990), were well matched with the timing of both drought and major fire occurrences inferred from lake sediment records. We also looked at the fire history data of Hallett et al. (2003) and the fire-origin stand map of Masters (1990) and no inconsistency in terms of the dates of major fire occurrences was found between the two data sets during the period 1750 to 2000, suggesting that it is unlikely that major fires could not be detected from the Masters' stand map. Therefore, we believe that the assumption that stands were burned twice during identified fire intervals will have minimal impact on the overall results in the fire history reconstruction of this study.

We reconstructed two types of landscape maps from the stand age maps for each period: a burned/unburned map and a successional stage map. To create burned/unburned maps, the stand age maps were classified as either burned (grid cells aged < 10 years) or unburned (grid cells aged ≥ 10 years) forest (e.g. Fig. 1a). All grid cells in the maps were re-classified into five categories according to their successional stage: early-successional (age < 20 years), young (20 to 80 years), mature (80 to 140 years), early old-growth (140 to 200 years) and late old-growth (≥ 200 years). This classification is based on the structural changes in subalpine forests after stand-replacing fires (Kashian et al. 2005; Sibold et al. 2006). In British Columbia, forests older than 140 years are often considered old forests (British Columbia Ministry of Forests 2004; Kopra & Feller 2007; De Long et al. 2008). However, Kashian et al. (2005) showed that in the Yellowstone subalpine landscape of the central Rockies, large

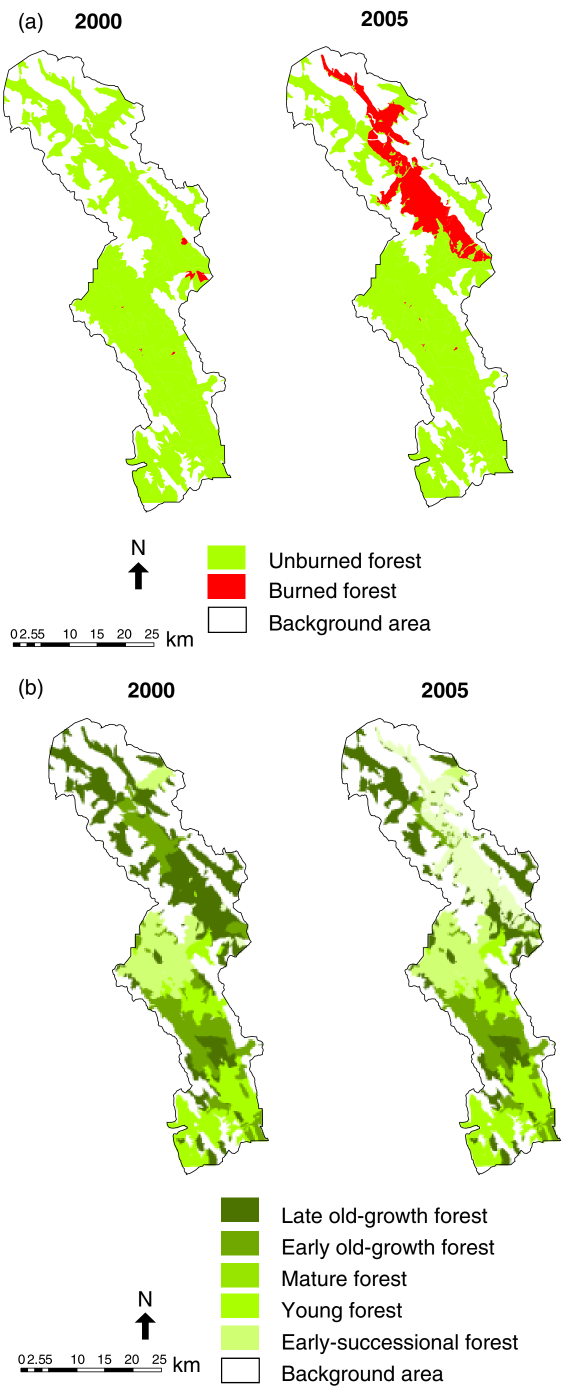

Fig. 1. Subalpine forest structure of Kootenay National Park (KNP) in 2000 and 2005, based on (**a**) burned/unburned classification and (**b**) successional stage classification.

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differences in tree density among burned stands converge at around 200 years following fires. Since landscape heterogenization is related to large fire occurrences and older stands may differ in terms of fire susceptibility, we used two stages of old-growth. We constructed similar maps for 2005 (Fig. 1b). Classified maps for 1750 to 2000 and 2005 (27 each, burned/unburned and successional stage classification) were converted into ASCII format with a 1-ha (100×100 m) resolution for the following analysis of landscape patterns.

Landscape pattern analysis

To estimate past variability of the subalpine landscape of KNP, landscape patterns were analysed based on the reconstructed maps from 1750 to 2000 and the 2005 landscape. The ASCII dataset for burned/unburned forests and successional stage classification was used to calculate landscape parameters using FRAGSTATS 3.3 (McGarigal et al. 2002). For each landscape map, landscape patterns were assessed using metrics defined at the class level (burned/unburned class and successional stage class), including total area (ha), number of patches, mean patch area (ha), coefficient of variation (CV) of patch area, largest patch index (area percentage within the landscape; %), edge density (m ha^{-1}), perimeter–area ratio and landscape shape index. The landscape shape index (*LSI*) (Milne 1991; Bogaert et al. 2000) is defined as

$$LSI = e_i/e_{\min}, \quad (1)$$

where e_i is the total length of the edge (or perimeter) of class *i* including all landscape boundary and background edge segments involving class *I*, and $e_{\min}$ is the minimum possible total length of the edge (or perimeter) of class *i*, which is achieved when class *i* is maximally clumped into a single compact patch. $LSI = 1$ when a type consists of a single maximally compact patch and increases as the patch type becomes more disaggregated. We also calculated the patch cohesion index (*PCI*; Gustafson 1998) to assess how the connectivity of each forest class varied within the landscape during the studied period. *PCI* is defined as

$$\mathrm{PCI} = \left[1 - \left(\sum_{i=1}^{n} Pi \Big/ \sum_{i=1}^{n} Pi\sqrt{ai}\right)\right]\left[1 - 1/\sqrt{A}\right]^{-1}, \quad (2)$$

where P_i is the perimeter of patch *i*, a_i is area of patch *i* and *A* is the total area of the landscape. *PCI* increases as the proportion of the landscape comprising the focal class increases and becomes physically connected. This is calculated for the unburned forest class and the late-successional forest classes because we were specifically interested in whether the connectivity of unburned forests, especially older forests, had increased before the high-severity crown fires in the 21st century.

In this study, to estimate historical changes in landscape heterogeneity, we used Shannon's diversity index, which is calculated based on the number of different patch classes and the proportional area distribution among patch classes. The index equals zero when the landscape contains only one patch (i.e. no diversity) and increases with the number of patches of different classes and as the proportional distribution of area among patch classes approaches equity. This is not a class-level metric but a landscape-level metric that evaluates patch richness within the landscape (McGarigal et al. 2002). Based on the diversity index, we evaluated how the recent large fires have altered the landscape heterogeneity.

Decadal fire–landscape relationships

In assessing relationships between landscape structure and decadal variation in fire activity, standard correlation analyses are inappropriate, as values of both variables cannot satisfy the assumption of independence, since each value may be affected by the preceding values. Fisher's method of randomization allows tests of a modified null hypothesis when observations are not independent. In this study, the null distributions of the correlation coefficient (*R*) were generated by 5000 randomizations. The observed *r*-value was then compared to the null distributions to determine significance. We calculated the 95% confidence intervals for each correlation using the PEARSONT program (Mudelsee 2003), which accounts for the presence of serial correlation in the time series. In the PEARSONT analysis, coefficients are significant at $P < 0.05$ when the associated 95% confidence interval does not include the value of zero.

Results

Size distributions of stand polygons

The subalpine map of KNP for the year 2000, prior to the recent large fires, had 103 fire-origin stand polygons. The polygon sizes of the 2000 landscape showed an inverse *J*-shaped distribution, with few large polygons and many small polygons (Appendix S2). In 2005, following the recent large fires, the landscape included 119 polygons and also had an inverse *J*-shaped polygon size distribution (Appendix S2). Patches > 5000 ha in area comprised 45.16% and 45.08% of the studied subalpine landscape in 2000 and 2005, respectively. However, although the maximum and minimum sizes of the polygons were similar between the two years, the mean polygon size decreased significantly from 837.4 ha in 2000 to 712.5 ha in 2005 ($P < 0.01$, Mann-Whitney *U*-test).

Simulated landscape evaluation: burned/unburned forest structures

Area of the "burned forest" class in simulated landscapes varied from 8 to 12 668 ha during 1750-2000 (Appendix S3). Total area of the burned forest class in 2005 was 16 231 ha. The CV of stand age in each decade correlated positively with the burned area (Appendix S3), suggesting that more extensive fires can create a landscape with greater variation in stand age.

In the post-fire landscape of 2005, most calculated metrics were outside of the simulated historical maximum and minimum values (Fig. 2). For the burned forest class in 2005, all values, except mean patch area, were beyond the ranges of values in the past landscapes (Fig. 2). In 2005, the unburned forest class had lower values of total area and mean patch area, and larger values of the number of patches, CV in patch area, edge density and perimeter–area ratio (Fig. 2), while, the

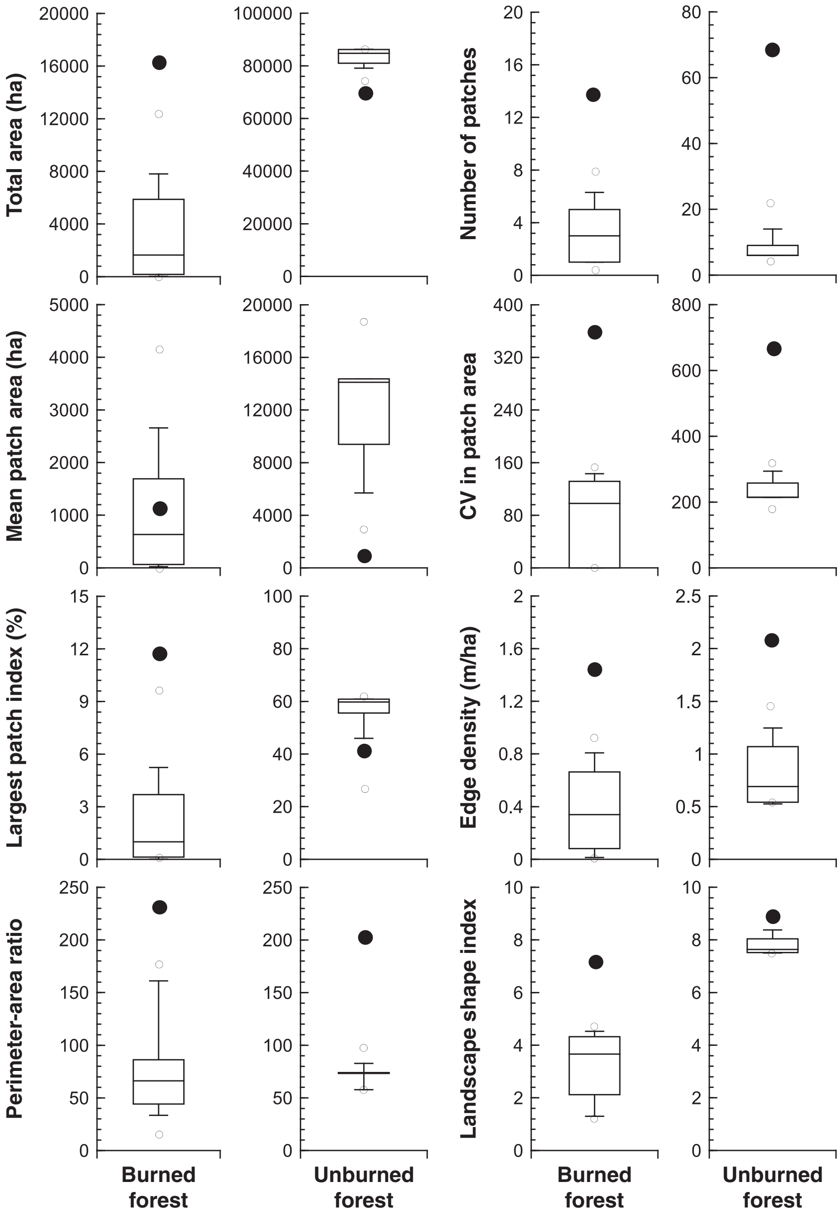

Fig. 2. Landscape patterns of the burned and the unburned forest classes in the subalpine landscape of KNP. Box plots show 10, 25, 50, 75 and 90 percentile values for calculated landscape indices for the period 1750 to 2000. Maximum and minimum values of each landscape index are shown with open circles. Solid black circles indicate values in the post-burned landscape of 2005. Note that the landscape shape index of the unburned forest class in 2005 was the same as the historical maximum value.

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landscape shape index matched the maximum value of the simulated historical range (Fig. 2).

During the period studied, the largest patch index of the burned forest class correlated significantly with the total burned area ($r = 0.98$, $P < 0.0001$). Simulated changes in the largest burned patch area suggested large fires in 1770, 1830-1840, 1890 and 1930 (Fig. 3), and largest burned patch correlated significantly with decreases in the patch cohesion index of the unburned forest class (Fig. 3). Shannon's diversity index for the landscape also correlated significantly with fire activity (Fig. 4). In 2005, the patch cohesion index of the unburned forests decreased (Fig. 3), reflecting creation of a very large burned patch due to the recent large fires, while the landscape-level diversity index increased beyond the simulated historical ranges (Fig. 4).

Simulated landscape evaluation: successional stage structures

In the 2005 landscape, the areas of early and late old-growth forest classes decreased relative to the 2000 landscape because of the recent large fires, and a proportionately larger area of early-successional forest class was created (Appendix S4); nevertheless, total areas for all five successional stage classes were within the range limits of the historical values (Fig. 5). Over the period studied, the estimated decadal burned areas correlated well with the total area of the oldest growth forest class in the preceding decade ($r = 0.43$, $P < 0.01$), but not with the previous decade's area for the early old-growth forest class. Areas of young and mature forest classes exhibited less change, even after the recent large fires (Appendix S4).

In 2005, the number of patches of both the early-successional forest class and the two old-growth forest classes increased (Fig. 5). The oldest two successional forest classes in 2005 had mean patch areas smaller than the historical values, while those for the earlier three successional forest classes in 2005 were within their historical range (Fig. 5). The largest patch index and edge density in 2005 were within the range of historical values, except for the early-successional and early old-growth forest classes, respectively (Fig. 5). In all successional stage classes, except for mature forest, the CV for patch area and perimeter–area ratio in 2005 were larger than the historical ranges (Fig. 5). For the early-successional and old-growth forest classes, the landscape shape indices in 2005 were larger than the historical range (Fig. 5), indicating that these forests became more disaggregated after the recent large fires.

In simulated landscapes, the patch cohesion indices for late old-growth forests showed sharp decreases in 1770, 1830, 1930 and 2005, corresponding to the timing of the large fires (Fig. 6). The cohesion index of the early old-growth forests was not significantly related to the largest burned patch area (Fig. 6). The cohesion index for the two old forest classes increased in the late 20th century, but did not exceed historic ranges (Fig. 6). In the post-fire landscape of 2005, these two classes decreased, but remained within

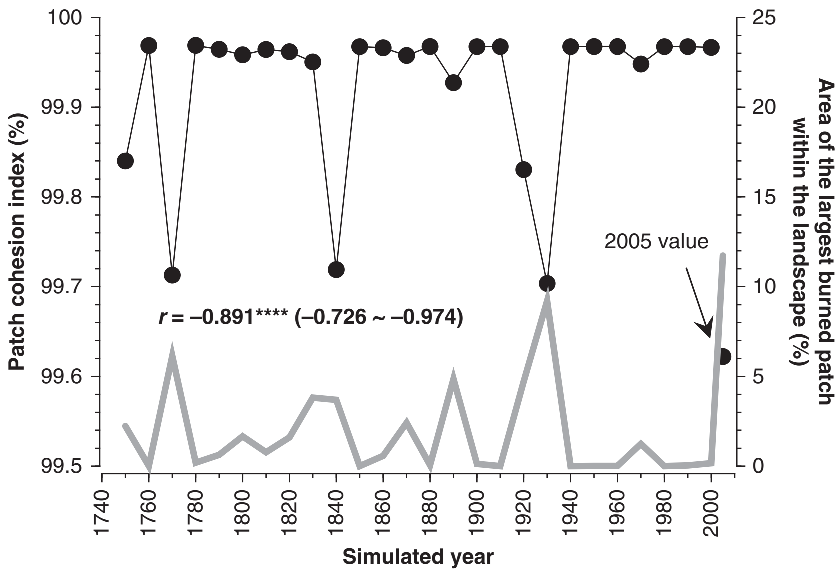

Fig. 3. Historical changes in the patch cohesion index of the unburned forest class within the subalpine landscape of KNP between 1750 and 2000, and in 2005. Solid black circles indicate the patch cohesion index. Grey line shows the decadal changes in the largest burned patch area. Correlation coefficient (r) is shown, and **** indicates $P < 0.0001$. The statistical significance of the relationship was calculated with 5000 randomizations. The 95% confidence interval calculated by the PEARSONT is also shown in parenthesis.

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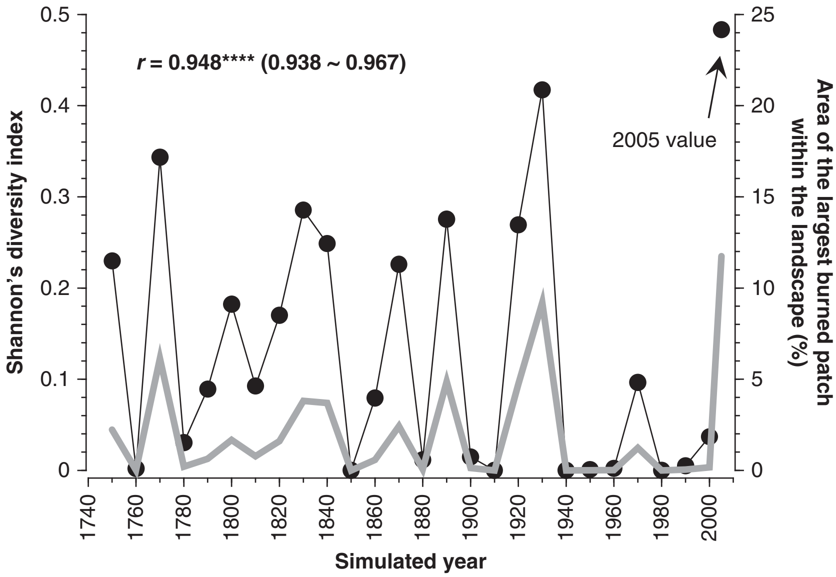

Fig. 4. Historical changes in Shannon's diversity index of the subalpine landscape in KNP between 1750 and 2000, and in 2005. Results are based on burned/unburned forest-classified landscapes. Solid black circles indicate the diversity index. Grey line shows the decadal changes in the largest burned patch area. Correlation coefficient (*r*) is shown, and **** indicates $P < 0.0001$. The statistical significance of the relationship was calculated with 5000 randomizations. The 95% confidence interval calculated by the PEARSONT is also shown in parenthesis.

the simulated historical ranges (Fig. 6). During the period studied, the estimated decadal burned areas correlated significantly with the cohesion index of the oldest growth forests in the preceding decade ($r = 0.47$, $P < 0.01$); this correlation was not significant for the early old-growth forest class.

Over the study period, the landscape-level diversity index based on successional stage correlated positively with the largest burned patch area (Fig. 7). In the 2005 landscape, Shannon's diversity index was 1.594, barely exceeding the simulated historical maximum values of 1.592 found in the 1930 landscape.

Discussion

Historic variability of landscape structure

The fire regime in subalpine forests of the Rockies is characterized by infrequent and sometimes large stand-replacing fires associated with severe drought (Bessie & Johnson 1995; Kipfmueller & Baker 2000; Schoennagel et al. 2004). The subalpine landscape of KNP contained a few very large stands with numerous smaller stands in both pre-fire (2000) and post-fire (2005) phases (Appendix S2), suggesting the dominant role of large fires (Baker & Kipfmueller 2001; Dorner 2002). A single large burned area evident in the 1770, 1840 and 1930 landscapes caused significant reduction in connectivity of the remaining forest patches (Fig. 3), but consequently enhanced the landscape-level diversity (Fig. 4). Elsewhere, large crown fire-induced patches have periodically contributed to the enhancement of landscape heterogeneity (Eberhard & Woodard 1987; Foster et al. 1998; Kashian et al. 2005).

After the 1930s, landscape connectivity remained high (Fig. 3), associated with a significant decrease in diversity (Fig. 4). Such a homogeneous landscape structure can lead to a higher risk of large-scale fires (Rollins et al. 2001). At the beginning of the 21st century, high-severity crown fires occurred with properties beyond the HRV (Fig. 2).

The long fire-free period following the fires ca. 1930 has been attributed to wetter climate conditions rather than fire exclusion (Masters 1990). In the US northern Rockies, Morgan et al. (2008) reported a mid-20th century gap in regional fire years, and attributed it to broad-scale climate patterns less conducive to large wildfires, namely resulting from a long period of the negative phase of the Pacific Decadal Oscillation (Appendix S5). Furthermore, at a high-elevation lake at KNP, Hallett et al. (2003) found that the lake-level changes during the last 1000 years corresponded to a regional climate shift between drought and moist conditions; notably, water levels rose from the 1930s to the mid-1970s, reflecting the wetter conditions of this region after the pre-1930 dry period (Hallett et al. 2003). The decline in large fire occurrences during this wet period (Masters 1990; Hallett et al. 2003;

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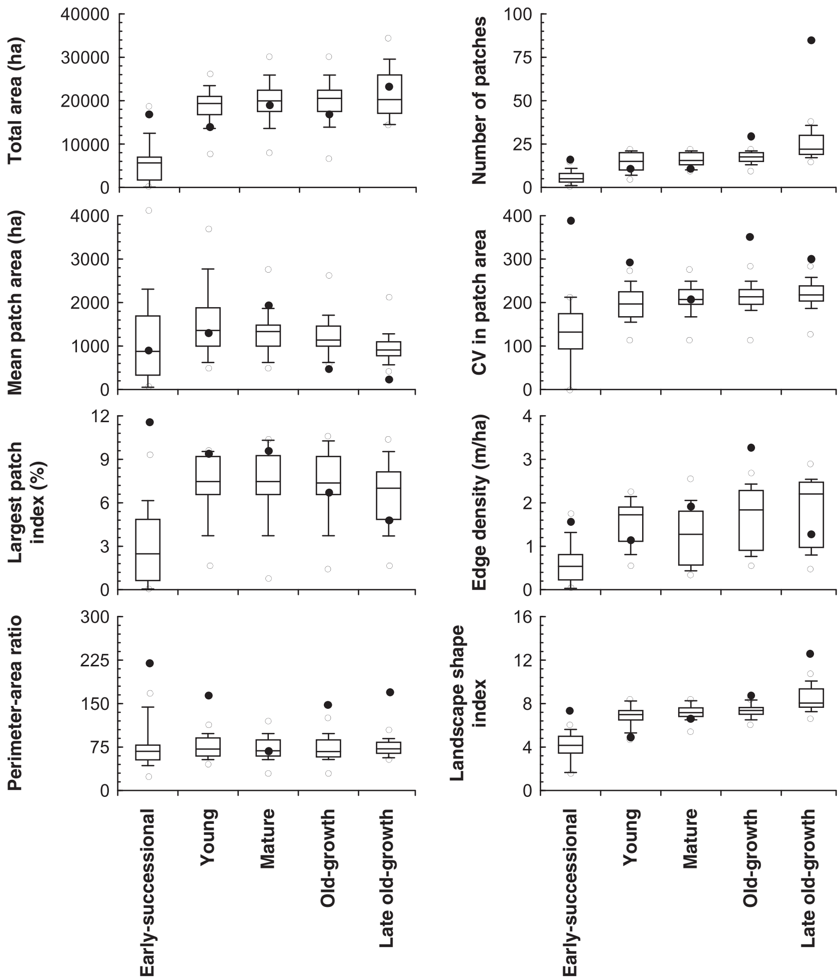

Fig. 5. Landscape patterns of each successional-stage class in the subalpine landscape of KNP. Box plots show 10, 25, 50, 75 and 90 percentile values for calculated landscape indices for the period 1750 to 2000. Maximum and minimum values of each landscape index are shown with open circles. Solid black circles indicate values in the post-burned landscape of 2005.

Appendix S5) would predictably cause fuel build-up in the subalpine landscape of KNP (Mori, unpublished data), creating homogenized landscape conditions and finally contributing to the high-severity crown fires during extreme fire weather in 2001 and 2003. In the Colorado Rockies, Buechling & Baker (2004) argued that a recent decline in fire activity, which was seemingly outside HRV, had no direct relationship with fire exclusion measures. Based on several reports of fire regimes in the Rockies, Schoennagel et al. (2004) concluded that high tree density and abundant fuel build-up are generally natural in high-elevation forest stands; because fire exclusion practices over 50 years represent only a small portion of the typical long fire-free intervals of these forests. Thus, although the large fires at the beginning of 21st century were unusually extensive in the subalpine landscape of KNP, we do not see strong support for the idea that relative homogeneity of pre-fire landscape structure can be attributed to fire exclusion management.

The relation between seral stage distribution, landscape characteristics and fuel load is complex. The correlations we observed between area burned per decade and pre-burn landscape character (e.g. values of total area and connectivity in the oldest forest class) are consistent with heavy fuel loads in older forests, although extreme fire events such as the 1988 Yellowstone fires are known to have little relationship with fuel loading (Turner et al. 2003). In Kootenay, the landscape-level connectivity of old-growth forest stands was enhanced during the fire-free period of the 20th century (Fig. 6), suggesting increased fuel loading at a landscape scale. However, despite the large scale of the recent fires (Fig. 2), values for total area of each seral stage in the post-fire landscape in 2005 were within the range of historical variability

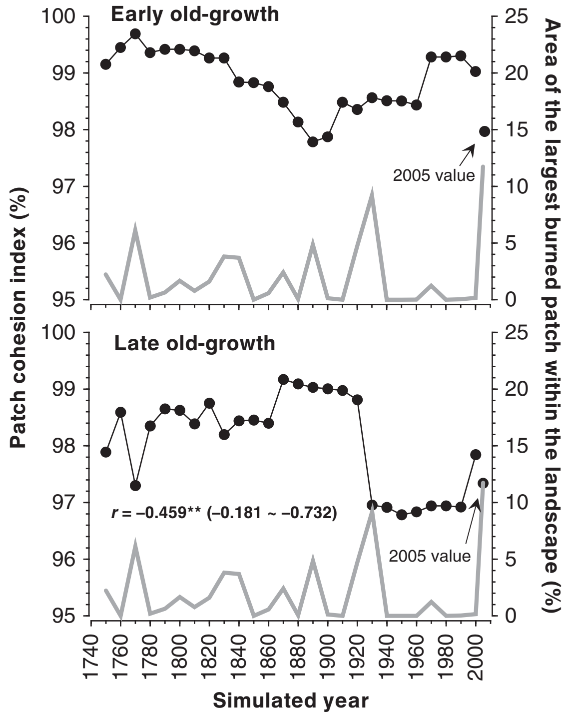

Fig. 6. Historical changes in Shannon's diversity index of the subalpine landscape in KNP between 1750 and 2000, and in 2005. Solid black circles indicate the diversity index. Grey line shows the decadal changes in the largest burned patch area. Correlation coefficient (*r*) is shown, and ** indicates $P < 0.01$. The statistical significance of the relationship was calculated with 5000 randomizations. The 95% confidence interval calculated by the PEARSONT is also shown in parenthesis.

(Appendix S4). Thus, the pre- and post-fire landscape characteristics were not exceptional, at least in terms of seral stage composition.

Fire-generated landscape heterogeneity

We hypothesized that if the recent severe fires were uniquely severe due to human activities, the subsequent landscape structure would be unusually homogeneous, composed of fewer, larger burned patches, with a reduced diversity overall of the mosaic of landscape patches. In reality, the 2005 landscape was very heterogeneous in terms of both stand age (Appendix S3) and landscape structure (Fig. 2). It contained many smaller patches, with high variation in patch area, edge density and perimeter–area ratio of unburned forests (Fig. 2). This emphasizes the large extent of the recent fires, which resulted in diverse spatial patterns of burn severity and complex structures of patchiness in the 2005 landscape. Although the fires largely disaggregated the remaining unburned patches (Fig. 3), they enhanced the diversity of burned/unburned structures (Fig. 4) rather than homogenizing the post-burned landscape. Therefore, we can reject the idea of a homogenized landscape as a basis for the disaster paradigm.

Large patches with complex patch mosaics at various successional stages provide an important template for post-fire ecological processes in the Rockies landscape (Schoennagel et al. 2004, 2008; Keane et al. 2008). After the large fires in Kootenay, late seral forests were fragmented into numerous smaller patches with more complex shapes, greater size variations and high landscape shape index (Fig. 5). Similarly, in a subalpine landscape of the northern US Rockies, Keane et al. (2008) reported that compared to smaller fires (< 3000 ha), larger fires (> 10 000 ha) produced a more diverse landscape mosaic with a high landscape shape index. The periodic formation of very large patches by crown fires can enhance landscape mosaic diversity (Fig. 7). In these kinds of systems, after the introduction of heterogeneity by infrequent large natural fires, relatively long fire intervals gradually reduce between-stand variation and homogenize the stand patch mosaic by the processes of self-thinning in dense stands and infilling in sparse stands, finally leading to recurrences of larger-scale, high severity disturbances (Kashian et al. 2005). As a consequence of such alternation between relative homogeneity and heterogeneity, high-elevation forests regulated by infrequent large crown fires can show great natural variability over the long term.

Climatic variability

Westerling et al. (2006) and Morgan et al. (2008) reported that in the northern Rockies, the earlier warmer spring and longer dry summer seasons since the mid-1980s have drastically increased the occurrence of wildfires. This dry period is consistent with the decrease in the pattern of lake levels observed in the high-elevation landscape of KNP (Hallett et al. 2003). Furthermore, paleoenvironmental studies conducted in KNP have predicted that ongoing global warming and Holocene climate variability will produce drier conditions leading to more stand-replacing fires (Hallett & Walker 2000; Hallett & Hills 2006). This climatic shift towards more fire-vulnerable conditions may have triggered the recent large and severe fires in the late-successional forests.

While we did not observe marked deviation from the historic range of variability and unnatural homogenization of landscape structure prior to the recent drought-induced large fires, we did find that the landscape was increased in homogeneity during the wetter climate period that caused the mid-20th century fire gap (Figs 4 and 7). Large fires in the 1770, 1840 and 1930 landscapes also coincided with drier periods following periods of

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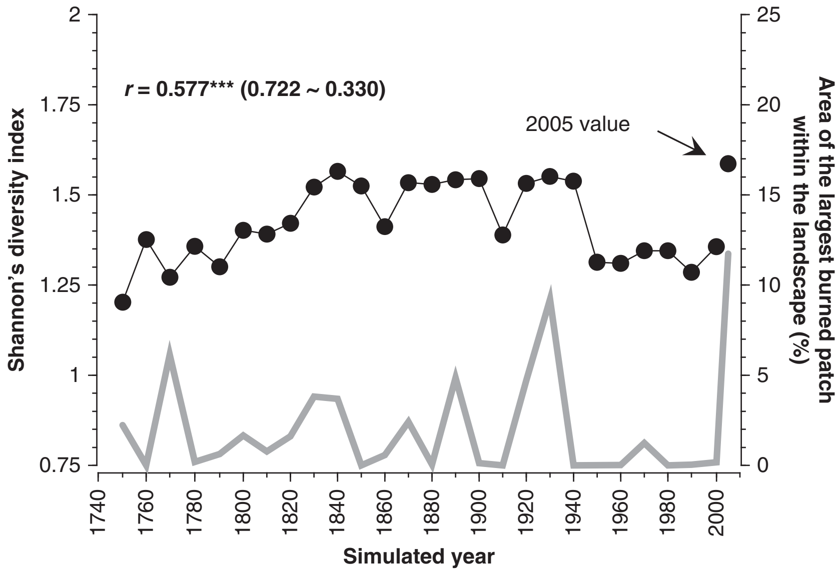

Fig. 7. Historical changes in the patch cohesion index of late-successional forest classes within the subalpine landscape of KNP between 1750 and 2000, and in 2005. Solid black circles indicate the patch cohesion index. Grey lines show the decadal changes in the largest burned patch area.

wetter conditions (Hallett et al. 2003). Patch mosaic diversity at the landscape level has been largely regulated by the extent of fires (Figs 4 and 7), indicating that prolonged wet periods with reduced fire occurrence can homogenize the landscape and cause fuel build-up. This predisposes the landscape to extensive fires in subsequent incidents of extreme drought – which can eventually lead to increased landscape-level heterogeneity. Thus homogenization and heterogenization over time of the KNP subalpine landscape are processes inherently linked to climatic variability.

In KNP, the crown fires that occurred at the beginning of the 21st century were more extensive than the HRV but are best explained as a response to patterns of drier and wetter periods in 20th and 21st century climate. We thus regard them as natural events that introduced a high landscape-level heterogeneity. Such unpredictable large natural disturbances are a primary driver of non-equilibrium systems (Shinneman & Baker 1997; Wallington et al. 2005; Mori et al. 2007). Here, it is notable that the variability expected from the last several centuries after Euro-American settlement is not necessarily a useful reference point. Jackson (2006) suggested that this led to focusing solely on the last 200 to 300 years for assessing HRV, and that this narrow time span may underestimate the range of variation within which an ecosystem is sustainable. The current forest vegetation in the KNP landscape, which is of a relatively wet type, was created around six to seven centuries ago (Hallett & Walker 2000; Hallett & Hills 2006), and therefore, the fire regime during the last two to three centuries is only a part of a larger variability. Like many other areas, because we now expect a shift in the fire regime towards more stand-replacing fires in this park (Hallett & Walker 2000; Hallett & Hills 2006), further consideration of climatic variability is required to evaluate natural disturbance regimes under an expectation of changing climate.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. The figure shows the time-since-fire (TSF) distribution estimate based on the subalpine landscape map of Kootenay National Park (KNP) in the year 2000.

Appendix S2. Patch size distributions within the subalpine landscape of KNP in the initial census of 1988 and in the post-burned phase of 2005.

Appendix S3. Historical changes in coefficient of variation (CV) in stand age and reconstructed decadal burned area of the subalpine landscape in KNP between 1750 and 2000, and in 2005.

Appendix S4. Historical changes in total area (ha) of each successional stage class within the subalpine landscape of KNP from 1750 to 2005.

Appendix S5. The figures show the historical changes in climate indices and simulated burned areas in the subalpine landscape map of Kootenay National Park (KNP).

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