公益信託エスペック地球環境研究・技術基金 研究成果報告書

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研究テーマ：高標高の森林生態系に与える地球温暖化の影響—大規模な森林火災に注目して—

研究内容の概要：

高標高の山岳域には、原生の古い森林が未だ多く残されている。長い時間を経て形成された、このような老齢原生林も、さまざまな自然現象により破壊されることがある。北米の山岳域の場合、山火事が時に数万・数十万ヘクタールといった規模で森林を焼き尽くすことがある。このような現象は、見た目上は死の山を作ってしまうので、災害であると認識されがちである。しかし、近年の研究により、森林生態系が大規模に破壊されることは、自然のサイクルの中では起こり得る現象であることが分かってきた。さらに、これらの自然現象を人為的に抑制すると、病害や虫害の大発生などの問題を引き起こすことも指摘されている。

本研究の対象は、ユネスコ世界自然遺産のひとつ、カナディアンロッキー山脈自然公園群を形成するクートニー国立公園である。この地域では、 この 10—20 年の間に急速な温暖化に伴い、消雪時期が大幅に早まり、乾燥化が起こっている。その結果として、非常に規模の大きい山火事が起こるようになっている。クートニー国立公園でも、21 世紀に入ってから破壊的規模の火事が頻発している。国立公園の山岳森林景観の半分近くを焼き尽くすほどの山火事は、見た目には空前絶後の大規模な自然災害に思える。実際に、現在国立公園の大半が焼け野原となっており、観光客の数も減少している。しかし、このような自然現象を単に災害として認識することは早計かもしれない。本研究では、世界遺産の生態系に与える地球温暖化の影響を、森林火災に着目して明らかにすることを目的とした。

山火事後に成立した様々な齢の林分が、山岳景観の中に存在する。この林齢マップを基に、地理情報システム(GIS)を用いて、過去 300 年間の山火事の空間的規模と時間的頻度を推定した。その結果、クートニー国立公園の山岳景観において、21 世初頭に発生した山火事は過去 3 世紀間で最大規模の山火事であったが、現在の気候条件下で起こり得る自然撹乱であったことが分かった。このような非常に稀であるが、発生すると規模が非常に大きく、生態系に対するインパクトの大きい自然撹乱としての山火事が、山岳景観の中に多様な森林構造を生み出してきたことが明らかになった。このような景観レベルでの森林パッチ構造の多様性は、結果として、森林に住む様々な生物種にとって、多様なハビタットを提供することからも、非常に重要なイベントである。それゆえ、生態系において将来的に発生し得る大規模自然撹乱を認識し、把握することは今後さらなる重要性を持つと考えられる。

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

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INTRODUCTION

The importance of natural disturbance regimes is now recognised in many forest ecosystems and landscapes (Baker & Kipfmueller, 2001; Łaska, 2001; Seymour *et al*., 2002; Noss *et al*., 2006). This is a remarkable and major conceptual shift towards the non-equilibrium paradigm in modern ecology, which predicts instability and dynamic changes in ecosystems (Levin, 1999; Wimberly & Spies, 2001; Veblen, 2003; Phillips, 2004). In contrast to equilibrium systems, non-equilibrium systems are very heterogeneous and therefore prone to various natural disturbances (Phillips, 2004). Therefore, resource management and biodiversity conservation in these dynamic ecosystems must be based on well-grounded principles of disturbance ecology (Brown & Macleod, 1996; Armstrong *et al*., 2003; Wallington *et al*., 2005).

However, the roles of disturbances with sudden and large-scale occurrences are less well documented. Based on their unpredictability and rarity, it is difficult to evaluate the ecological effects of large-scale and/or high-intensity disturbances (Turner *et al*., 1998). This also results in public anxiety, and people may consider such disturbances as disasters. The 1988 fires in Yellowstone National Park, USA, are some of the best-known examples of large-scale disturbances (Christensen *et al*., 1989; Turner *et al*., 2003). Studies have indicated that even these large-scale fires are within the historical range of fire sizes and ecological effects in the Yellowstone ecosystem (Romme *et al*., 1998; Turner *et al*., 2003). In disturbance-prone forests, because the application of equilibrium-based management may cause considerable deviation from the 'historical range of variability' (HRV) (e.g. Shinneman & Baker, 1997; Baker & Ehle, 2001; Ehle & Baker, 2003; Veblen, 2003; Baker, 2006), further consideration of the non-equilibrium nature existing in these dynamic systems is essential to maintain natural processes and ecological integrity (Armstrong *et al*., 2003).

Because of high stand density and resultant fuel build-up across large areas, many subalpine forests in the Rocky Mountains are at a high risk of high-severity crown fires (Rollins *et al*., 2001). Such landscape structures may have been created by excessive ingrowth as a consequence of fire suppression management imposed in the 20th century (Kipfmueller & Baker, 2000; Howe & Baker, 2001; Rollins *et* *al*., 2001), whereas others argue that spatially homogeneous, current landscapes are fundamentally consistent with historical fire regimes (Buechling & Baker, 2004; Schoennagel *et al*., 2004; Sibold *et al*., 2006). In high-elevation, subalpine forested landscapes in the Rockies, large fire activity has apparently increased during the recent few decades due to climate warming (Schoennagel *et al*., 2004; Westerling *et al*., 2006). Landscapes recently burned by crown fires are expected to be completely different from their pre-fire conditions in terms of spatial structure because disturbances can significantly alter heterogeneity (White & Jentsch, 2001). The possible effects of fire suppression on pre-fire landscape structures should thus be evaluated to understand the causes of recent large fires in these subalpine forests, which can be regarded as 'natural ecological processes' or 'human-induced disasters'.

Landscape heterogeneity, which can be generated by large-scale natural disturbances, is a ubiquitous feature of forested ecosystems (Romme, 1982; Turner *et al*., 1994; Lertzman *et al*., 1998; Howe & Baker, 2003; Lindenmayer *et al*., 2006; Williams & Bradstock, 2008); therefore, we have to maintain ecological integrity of fire-prone systems by acknowledging the ecological consequences of large fires (Bradstock, 2008; Schoennagel *et al*., 2008). However, severe fires that occur due to reasons beyond natural variability may cause landscape homogenization by creating huge single patches and eliminating a large portion of patches of various sizes and ages from a landscape. This is in contrast to the impact of large-scale natural disturbances, which is not uniform but can rather produce heterogeneous patterns throughout a landscape by creating various patches at different seral stages (Tuner & Dale, 1998; Bradstock, 2008). If the recent increased fire activities are considered 'unnatural', it is expected that structures of post-burned landscapes would considerably deviate from their HRVs and a large portion of stands would be converted to the early-seral stage. Fire-related homogeneity is perceived as deleterious, whereas heterogeneity is assumed to be beneficial (Bradstock, 2008). Therefore, the effects of recent high-severity fires on post-burned landscape structures are of concern in terms of their possible homogenising effects.

At the beginning of the 21st century, the high-elevation subalpine landscape of Kootenay National Park (KNP) in the Canadian Rockies experienced large-scale crown fires. The management plan of KNP indicated that decades of effective forest fire suppression had substantially changed the park vegetation; in general, forests were becoming older and less diverse, and several important plant communities were declining as closed canopy forests were becoming established (Parks Canada, 2000). Thus, active management was proposed in the plan, which especially focused on (1) restoring the role of fire as a natural disturbance and (2) perpetuating the natural range of vegetation disturbance (Parks Canada, 2000). Furthermore, in the periodic report on the application of the World Heritage Convention of UNESCO, it was emphasised that due to extensive fire suppression in the past, the vegetation in the Canadian Rocky Mountain Parks and surrounding areas has reduced in natural diversity, resulting in a forest which is more susceptible to large and intense fires (Parks Canada, 2004). Therefore, conservation and restoration of natural ecosystem processes, which shape the unique and diverse natural features of the park, with a particular focus on fire management, are now essential. For this, we need to understand the effects of past fire suppression on the recent large fires and evaluate the fire-generated variability and heterogeneity of landscape structures of this mountain park.

Here, by performing a simple simulation based on a fire origin stand map of the KNP landscape, we estimate historical changes in spatial structures before these recent large-scale fires. Specifically, by comparing landscape structures of the 20th century to those of the 18th and 19th centuries, we examine (1) whether the landscape of KNP has homogenised due to fire suppression in the 20th century; (2) how the estimated variability in landscape structures of KNP co-varied with the fire activity prior to the recent large-scale fires and (3) whether the post-fire landscape of KNP homogenised or heterogenised. Based on this, we discuss the ecological roles of naturally occurring large-scale fires in maintaining the spatial heterogeneity of landscapes.

METHODS

Study area

The study was conducted in KNP, covering the western slopes of the Canadian Rocky Mountains in southern British Columbia, Canada. This park is one of the Canadian Rocky Mountain Parks, which were registered as a World Heritage Site by UNESCO in 1984. The area is about 40 km wide and 82 km long with an elevation of 800–3400 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) 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 0.2–2.0 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. First, a map was created using 1:25,000 aerial photographs to identify forest patch boundaries. The patch age was then estimated based on field censuses that measured the fire scars or the age of the oldest trees in each patch (Masters, 1990) based on previously described methods (McBride, 1983). The 1988 map, which covers a 40.4 km × 82.6 km area (137,092.8 ha), has 117 polygons with dates of fire origins ranging from 1332 to 1984. In this study, the original data were converted into vector data using geographic information system (GIS) software (ESRI ArcInfo 9.2), and the area of each polygon was calculated.

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 represents low-elevation ecosystems, and thus, has a completely different fire regime compared to 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 map with all the fire polygons of each year after 1988, which were estimated from aerial photographs and LANDSAT images, and repeating this procedure until 2000, a stand age map for 2000 was constructed. KNP experienced high-severity crown fires in 2001 (3258 ha) and 2003 (16,376 ha), which burned about 22% of the high-elevation forested areas. The 2000 map can therefore be regarded as the last map of the 'pre-burned landscape'. The current map has been updated using the data of fire polygons from 2001 to 2005. These data mostly comprise large fires in 2001 and 2003 and other small fires until 2005. The resultant map is the 'post-burned landscape', containing current stand origin information.

To estimate historical changes in landscape structures, the simple simulation of Tinker *et al.* (2003), which was estimated based on the 2000 stand age map, was used. In this simulation, an arbitrary assumption of fire interval in the subalpine landscape is required to reconstruct past burned landscapes (Tinker *et al.*, 2003). In the subalpine landscape of Yellowstone National Park, USA, Tinker *et al.* (2003) used a fire interval of 350 years, which is consistent with other data obtained 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, three scenarios of fire intervals (250, 300 and 350 years) were considered in this study. Overall, despite differences in fire intervals, our preliminary analyses showed that the three scenarios generated almost similar results in terms of landscape patterns described later (data not shown). In KNP, Hallett and Hills (2006) estimated a fire interval of 245 ± 87 years based on lake sediment records. In the studied landscape of KNP, the area-weighted mean stand age in the areas burned in 2001 and 2003 ranged from 247 to 251 years. Given these facts, this study deals only with the results based on fire intervals of 250 years. In fact, some of the burned forest stands were younger than 250 years and some were older than 250 years, depending on several factors such as slope aspect and moisture regime of each stand within the studied landscape. Although this assumption of the fire interval would influence the overall results of this study, great differences between the fire scenarios were not observed in the preliminary analyses.

Using the simulation of Tinker *et al.* (2003), the pre-burned landscapes from 1710 to 2000 were generated 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, resulting in a map with the ages of each polygon in 1990. If any of the polygons in the newly created map had a value of zero or less, then these polygons were considered to have been burned between 1990 and 2000, and were assumed to have had a stand age of 250 when they were burned. Based on these assumptions, the stand age of the polygons burned during the previous 10 years was estimated for each of the fire interval scenarios. The stand age maps created were then classified into two categories: burned (grid cells aged < 10 years) and unburned forest (grid cells aged ≥ 10 years).

Burned/unburned forest maps for 2000 and 2005 are shown (Fig. 1). All grid cells in the maps were re-classified into five categories according to their successional stage: early-successional (age < 20 years), young (20 < 80 years), mature (80 < 140 years), early stage of old-growth (140 < 200 years) and late stage of old-growth (≥ 200 years). This classification is based on the structural changes in subalpine forests along a gradient of succession after stand-replacing fires (De Long & Meidinger, 2003; Kashian *et al*., 2005; Sibold *et al*., 2006). In British Columbia, forests older than 140 years are often considered old forests (MacKinnon & Vold, 1998; De Long & Meidinger, 2003; 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 differences in tree density among burned stands converge at around 200 years following fires. In KNP, we have ecological land classification (ELC) data (Achuff *et al*., 1989), which was digitized in 1999. The ELC includes detailed vegetation type information for 1471 polygons throughout the KNP landscape. When we overlayed the original 1988 stand age map with the ELC data, 70.4 % of stands older than 140 years and 80.2 % of stands older than 200 years respectively corresponded to spruce-fir vegetation types, which can be regarded as late-seral stages. Since landscape heterogenization is related to large fire occurrences and older stands differ in terms of fire susceptibility, it is more informative to consider old forests using the two definitions—the early and late stage of old-growth. We therefore used five categories of stand age. The resulting stand maps of the successional status in 2000 and 2005 are shown (Fig. 2). The simulation performed here is based on the assumption that each stand burned only once in the fire interval (Tinker *et al*., 2003). In reality, however, a few stands would have burned more than once, but high-severity crown fire is usually rare in subalpine landscapes, and the areas that were actually burned twice would probably be very small because of the long-term fire intervals in subalpine forests in the Rocky Mountains (Tinker *et al*., 2003; Buechling & Baker, 2004). Tinker *et al*. (2003) suggested that this assumption is valid for reconstruction of past burned landscapes in subalpine areas of the Rockies, where the fire regime is characterised by infrequent high-severity fires.

As a result of the simulation, two landscape maps were created for 1990 based on the 2000 stand age map for each fire interval scenario. Similarly, the 1980 landscape maps were generated based on the 1990 stand age maps, and these procedures were repeated until landscape maps for 1710 were obtained. The other background areas, non-forested areas and a few IDF stands were retained as non-changing areas during the analysis over the three centuries. Furthermore, the post-burned stand age map of 2005 was also used to create two types of landscape maps for each fire interval scenario. All vector data of the pre-burned landscapes (31 maps for the burned/unburned classification and 31 maps for the 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 pre-burned landscapes from 1710 to 2000 (or 1760 to 2000). The ASCII dataset for burned/unburned forests and successional stage classification was used to calculate the parameters of the landscape pattern. This was performed using FRAGSTATS 3.3 (McGarigal *et al*., 2002). For all pre-burned landscape maps, landscape patterns were analysed based on metrics at the class level (burned/unburned class and successional stage class), total area (ha), area percentage within the landscape (%), number of patches, mean patch area (ha), area-weighted mean patch area (ha), coefficient of variation (CV) of patch area, largest patch area percentage within the landscape (%), edge density (m/ha), 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 the landscape consists of a single square or maximally compact patch of the corresponding type; *LSI* increases as the patch type becomes more disaggregated. For the post-burned landscape maps in 2005, the same class level metrics were calculated. These were then compared to those of the pre-burned landscapes between 1710 and 2000.

Furthermore, the patch cohesion index (*PCI*; Gustafson, 1998) of the pre- and post-burned landscapes was calculated to infer how the connectivity of each forest class had varied within the landscape during the last three centuries. *PCI* is defined as

$$PCI = [1-(\sum_{i=1}^{n} P_i / \sum_{i=1}^{n} P_i \sqrt{a_i})][1-1/\sqrt{A}]^{-1} \quad (2),$$

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 focused on 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 (Ernoult *et al*., 2006), which is calculated based on patch size and number in each patch class. The index equals zero when the landscape contains only one patch (i.e. no diversity). The index increases as the number of patches in each different class increases and/or 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 that corresponds to the mosaic of patches representing different forest composition and age classes (Forman, 1995).

Decadal fire-landscape relationships

The relationships of landscape structures with decadal variations in fire activity were assessed. However, the values of both variables cannot satisfy the assumption of independence, since each value may be affected by the preceding values. Therefore, a typical correlation analysis cannot be performed. Fisher's method of randomization allows a modified null hypothesis to be tested 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. Furthermore, we also calculated the 95 % confidence intervals for each correlation using PERASONT 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 have the value of zero (Mudelsee, 2003).

RESULTS

Size distributions of stand polygons

The original pre-burned subalpine map of KNP in 1988 had 95 fire-origin stand polygons. The polygon size of the 1988 landscape showed an inverse J-shaped distribution containing few large polygons and many small polygons (Fig. 3). The post-burned subalpine landscape of 2005 had 119 polygons, and again, had an inverse J-shaped polygon size distribution (Fig. 3). Patches > 5000 ha comprised 45.46% and 45.08% of the studied subalpine landscape in 1988 and 2005, respectively (Fig. 3). However, although the maximum and minimum sizes of the polygons were similar between the two time phases, the mean polygon size decreased significantly from 910.9 ha in 1988 to 712.5 ha in 2005 ($P < 0.01$, Mann–Whitney *U*-test).

Simulated landscape evaluation: burned/unburned forest structures

Based on the burned/unburned forest classification, historical changes in the total area of the burned forest class in KNP have been quite varied during the last three centuries, with values from 8 to 12,668 ha (Table 1; Fig. 4). The CV of stand age in each decade correlated positively with the burned area (Fig. 4), indicating that larger fires can create a landscape with greater stand age variations.

In the post-burned landscape of 2005, most calculated metrics were outside of the simulated historical maximum and minimum values (Table 1). For the burned forest class in 2005, all values, except mean patch area, were beyond the ranges of values in the pre-burned landscapes (Table 1). In 2005, the unburned forest class had lower values of total area, area percentage and mean patch area, and larger values of the number of patches, CV in patch area, edge density and perimeter–area ratio (Table 1). In 2005, the landscape shape index of the unburned forest class reached the maximum value of the simulated historical ranges (Table 1).

During the period studied, the largest patch area percentage of the burned forest class correlated significantly with the total burned area ($r = 0.982$, $P < 0.0001$), indicating the fundamental importance of the largest single patch created by fires. Simulated changes in the largest burned patch area in each decade indicated that this landscape had experienced larger fires in 1770, 1830–40, 1890 and 1930 (Fig. 5). These fires, resulting in a decrease in unburned area, correlated with the decreases in the patch cohesion index of the unburned forest class (Fig. 5). Shannon's diversity index of the landscape also synchronised significantly with the fire activity (Fig. 6). In 2005, the patch cohesion index of the unburned forests decreased markedly (Fig. 5), which reflects the creation of a very large burned patch due to the recent large fires, while landscape-level diversity index increased beyond the simulated historical ranges (Fig. 6).

Simulated landscape evaluation: successional stage structures

For classification based on the successional stage, the post-burned values did not necessarily deviate from the simulated ranges of the pre-burned landscapes (Table 2). In particular, in common with the five successional stage classes, the total area and the area percentage values in 2005 were generally within the range limits of the historical values (Table 2, Fig. 7). In the 2005 landscape, the areas of early and late old-growth forest classes decreased because of the recent large fires, and a large area of early-successional forest class was created (Fig. 7). During the period studied, the estimated decadal burned areas correlated well with the total area value of the oldest growth forest class in the preceding decade ($r = 0.43$, $P < 0.01$), while the burned area did not reflect the pre-burned area value of the early old-growth forest class. Areas of young and mature forest classes did not exhibit much change, even after the large fires (Fig. 7).

The mean patch area in 2005 was also within the range of historical values, except for the older forest classes that showed a smaller value compared to the values in the pre-burned landscape (Table 2). The area-weighted mean patch area was also within the range of historical values, except for the early-successional forest classes that showed a larger value compared to the historical values (Table 2). Values of the largest percentage patch area and edge density in 2005 were also within the range of historical values, except for the early-successional and early old-growth forest classes, respectively (Table 2). However, it is notable that the number of patches increased in 2005 for the early-successional class and the two old-growth classes (Table 2). In all successional stage classes, except for mature forest, the CV in the patch area and perimeter–area ratio also increased in 2005 (Table 2). For the early-successional and early stage of the old-growth forest classes, the landscape shape indices in 2005 were beyond the historical range (Table 2).

The patch cohesion indices for the two classes of old-growth forests have remained variable over the last three centuries. The cohesion index of the old-growth forests showed remarkable decreases in 1770, 1930–40 and 2005, which correspond to the timing of the large fires (Fig. 8). The cohesion index of the early old-growth forests was not significantly related to the largest burned patch area (Fig. 8). Notably, the cohesion index for the two old forest classes increased in the late 20th century, but did not exceed the ranges of the preceding period (Fig. 8). In the post-burned landscape of 2005, these two classes decreased, but remained within the simulated historical ranges (Fig. 8). 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.

Historical changes in the landscape-level diversity index based on the successional stage classification are shown in Fig. 9. The diversity index correlated positively with the largest burned patch area (Fig. 9). In the post-burned landscape of 2005, Shannon's diversity index was 1.594, which slightly exceeded the simulated historical maximum values of 1.592 found in the 1930 landscape.

DISCUSSION

Historic variability of landscape structure

The fire regime of subalpine forests in the Rocky Mountains is characterised by infrequent and large stand-replacing fires that are associated with extreme droughts (Bessie & Johnson, 1995; Kipfmueller & Baker, 2000; Kulakowski & Veblen, 2002; Schoennagel *et al*., 2004; Romme, 2005; Sibold & Veblen, 2006; Sibold *et al*., 2006). The subalpine landscape in KNP contained a few very large stands with numerous smaller stands in both the pre- (1988) and post-burned phases (2005) (Fig. 3), suggesting the fundamental importance and existence of large fires (Baker & Kipfmueller, 2001; Dorner, 2002). A single large burned area evident in the 1770, 1840 and 1930 landscapes remarkably divided the connectivity of the remaining forests (Fig. 5), but consequently enhanced the landscape-level diversity (Fig. 6). These results emphasise that crown fire-induced creation of larger patches has periodically contributed to the enhancement of landscape heterogeneity (Eberhard & Woodard, 1987; Foster *et al*., 1998; Kashian *et al*., 2005).

After the large fires were confirmed in the 1930 landscape, the connectivity of this landscape recovered and remained high (Fig. 5), leading to a significant decrease in diversity (Fig. 6). Such a densely stocked, homogeneous landscape structure can lead to a higher risk of large-scale fires (Rollins *et al*., 2001). Hence, at the beginning of the 21st century, high-severity crown fires finally occurred beyond the historical scale (Table 1). The fire-free period during the remainder of the 20th century since ca. 1930 (Fig. 4) was due to a period of wetter climate conditions rather than active fire suppression (Masters, 1990). In adjacent regions, increases in precipitation linked to warming since the 'Little Ice Age' also decreased fire activity in the 20th century (Johnson *et al*., 1990; Johnson & Larsen, 1991). In the US northern Rockies, Morgan *et al*. (2008) also reported the mid-twentieth century gap in regional fire years, which was attributable to broad-scale climate patterns less conductive to large wildfires. Furthermore, at a lake located in this high-elevation landscape of KNP, Hallett *et al*. (2003) demonstrated that the lake-level changes during the previous 1000 years corresponded to a regional climate shift between drought and moist conditions, and most notably, water levels rose from the 1930s to the mid-1970s, reflecting the wetter conditions of this region after the pre-1930 dry period. The decline in large fire occurrences during this wet period in the 20th century (Masters, 1990; Hallett *et al*., 2003) were expected to have caused fuel build-up in the subalpine landscape of KNP (Mori, *in review*). This created homogenised landscape conditions, finally resulting in the high-severity crown fires during extreme fire weather in 2001 and 2003. In the Colorado Rocky Mountains, Buechling and Baker (2004) demonstrated that a recent decline in fire activity, which is seemingly outside HRV, had no direct relationship to fire suppression measures. Based on many studies of fire regimes in the Rocky Mountain region, Schoennagel *et al*. (2004) stated that high density of trees and abundant fuel build-up in high-elevation forests are natural rather than abnormal fuel accumulation events. Because fire suppression over 50 years, at the most, only represents a small portion of the long fire-free intervals of these forests, it has no significant effect in altering the fire regimes (Schoennagel *et al*., 2004, 2005). Accordingly, although the large fires at the beginning of the 21st century were extensive in the subalpine landscape of KNP, the fire suppression management regime has had little effect on the pre-burned landscape structure and the resultant fires.

Older forests contain a relatively higher abundance of large live and dead trees as fuel (Schoennagel *et al*., 2004), and therefore, they are more susceptible to large fires (Rollins *et al*., 2001; Bigler *et al*., 2005; Romme, 2005; Mori, *in review*). The observed correlations of decadal burned area with pre-burned values of total area and connectivity in the oldest forest class also suggest, somewhat, of the need for old-growth forests as loaded fuels, although extreme fire events such as the 1988 Yellowstone fires are known to have little relationship to fuel loading. In Kootenay, although the connectivity of old-growth forests as potential sources of fuel build-up was enhanced during the fire-free period of the 20th century, it did not deviate from the historical range (Fig. 8). This suggests that the observed gradual increase in stand connectivity prior to the large fires in the 21st century was natural and mostly driven by climatic conditions (Mori, *in review*), rather than being the result of an anthropogenic excess fuel build-up. At the beginning of the 21st century, late-successional forests were diminished in the landscape and converted to the early-successional stage (Fig. 7). However, despite the largest scale of the recent fires, the total area and percentage area of all seral stages in the post-burned landscape showed no significant deviation from the simulated ranges of the last three centuries (Table 2). This further indicates that the current landscape characteristics in terms of seral stage composition are within the natural variability.

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

Fire-generated landscape heterogeneity

We hypothesised that if the recent severe fires were a human-induced disaster, the post-burned landscape structures could be homogenised by creation of a very large single burned patch and the resultant reduction of a large portion of a complex mosaic of different patches within the landscape. In reality, the post-burned landscape became highly heterogeneous both in terms of stand age variation (Fig. 4) and landscape structure (Table 1). In the 2005 landscape, many smaller patches were created (Fig. 3), and variation in the patch area, edge density and perimeter–area ratio of the unburned forests had the highest values (Table 1). This emphasises the large magnitude of the recent fires, which left diverse severity patterns with complex structures of patchiness in the post-burned landscape. Although the fires largely disaggregated the remaining unburned patches (Fig. 5), they also enhanced the diversity of the burned/unburned structure (Fig. 6), rather than homogenizing the post-burned landscape. Therefore, we can reject the idea of homogenised post-burned landscape as a basis of the disaster paradigm.

Large patches and complex patch mosaics with various successional stages, which can be observed after the occurrences of large-scale crown fires, provide an important template for subsequent ecological processes in the Rocky Mountain landscape (Schoennagel *et al*., 2004; Baker *et al*., 2007; Lentile *et al*., 2007; Kaene *et al*., 2008; Schoennagel *et al*., 2008). In Kootenay, after the large fires occurred in the 21st century, late successional forests were largely fragmented into numerous smaller patches with more complex shapes and greater size variations (Table 2). The highest landscape shape indices for the late successional classes in the 2005 landscape (Table 2) also demonstrate that these forests became more disaggregated after the recent large fires. In a subalpine landscape of the northern US Rockies, Kaene *et al*. (2008) reported that compared to smaller fires (< 3000 ha), larger fires (> 10,000 ha) can create a more diverse landscape mosaic showing a high landscape shape index. Because the periodic creations of a very large patch by crown fires have contributed to the enhancement of landscape mosaic diversity (Fig. 9), it is not surprising that the landscape of 2005 showed very heterogeneous characteristics. Accordingly, although the spatial scale of the recent large fires was seemingly beyond the historical range (Table 1), these fires should be regarded as natural processes that modulate diverse landscape structures.

Landscape heterogeneity introduced by infrequent large-scale natural disturbances plays an important role in providing diversity and spatial arrangements of habitat patches that are essential for many taxa (Wimberly *et al*., 2000; Lindenmayer *et al*., 2006; Bradstock, 2008; Kaene *et al*., 2008) and affect subsequent diverse natural disturbance regimes (Howe & Baker, 2001; Kulakowski & Veblen, 2002, 2007). Relatively long fire intervals then gradually reduce among-stand variations and homogenise the stand patch mosaic in the landscape (Kashian *et al*., 2005) by the processes of self-thinning in dense stands and infilling in sparse stands. At each stand level, however, high within-stand structural variation can still be maintained and somewhat enhanced, resulting from succession progressing towards old-growth conditions that are very heterogeneous vertically and horizontally (Lindenmayer *et al*., 2006). In this phase, fine-scale disturbances such as gap formations, which are nested within infrequent but predominant large-scale disturbances (Worrall *et al*., 2005), contribute to the enhancement of within-stand structural variation (Kashian *et al*., 2005; Lindenmayer *et al*., 2006). The long-term homogeneous structures of the patch mosaic finally lead to recurrence of catastrophic disruptions in the landscape (Kashian *et al*., 2005). As a consequence of such alternation between homogeneity and heterogeneity, high-elevation forests structured by infrequent large crown fires can show a greater natural variability.

CONCLUSIONS

Our study has demonstrated that the recent high-severity fires in the subalpine forested landscape of KNP are probably natural disturbances rather than human-induced disasters. Unpredictable large-scale disturbance is a primary, essential component in non-equilibrium systems (Shinneman & Baker, 1997; Wallington *et al*., 2005; Mori *et al*., 2007) and/or dynamic equilibrium systems (White & Jentsch, 2001; Rollins *et al*., 2004) that shapes the structures of stands and landscapes, leaving a legacy that can influence ecological processes for a long time (Foster *et al*., 1998; Turner & Dale, 1998; Veblen, 2003; Kashian *et al*., 2005; Kulakowski & Veblen, 2007).

Infrequent large-scale natural disturbances are unpredictable (Turner *et al*., 1998), and thus, their effects on ecological processes and outcomes remain highly uncertain (Kurz *et al*., 2008). In addition to wildfires, actual subalpine landscape is also shaped by other major events such as insect outbreaks, making it spatially and temporally varied and complex. Furthermore, Kaene *et al*. (2008) pointed out that historical spatial distributions of large fire severity are unknown because of the lack of spatially explicit legacy field data, causing difficulties in comparing today's fire severity patterns with historical patterns. In this study, because the landscape simulation was solely based on the recent stand age map, available data regarding fires and simple assumptions of fire regimes, the historical variability of the metrics generated by the simulation can be changed depending on the model's assumptions. Thus, further study, such as a detailed model approach including the possibility of fire recurrence within the fire interval and the effects of other types of major disturbances, could enhance our understanding of largely fluctuating landscape structures that have been shaped by infrequent but predominant natural disturbances.

In the present simulation of KNP landscape, the crown fires that occurred at the beginning of the 21st century should be regarded as natural disturbances. This implies that the variability expected from the last three centuries after Euro-American settlement is not necessarily a paramount reference point. Jackson (2006) suggested that this tended to focus on the last 200–300 years in assessing historical variability and that this narrow time span may underestimate the range of variation within which an ecosystem is sustainable. The current forest vegetation in this landscape of KNP, which is of a relatively wet type, was created around 6–7 centuries ago (Hallett & Walker, 2000; Hallett *et al*., 2006), and therefore, the fire regime during the last three centuries is only a part of the larger variability. At present, we would expect a shift in the fire regime and more stand-replacing fires in this park (Hallett *et al*., 2006), such as those that occurred at the beginning of the 21st century. Further consideration of climatic variability is thus required to evaluate natural disturbance regimes under the changing climate.

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Table 1. Landscape patterns of burned and unburned forest classes for the pre-burned landscapes (1710–2000) and the post-burned landscape (2005). Maximum and minimum values of class-level metrics for the period 1710–2000 are shown.

Forest type	Class-level metrics	Pre-burned landscapes		Post-burned landscapes
		Max	Min	
Burned forest	Total area (ha)	12668	8	16213
	Area percentage within the landscape (%)	9.24	0.01	11.82
	Number of patches	8	1	14
	Mean patch area (ha)	4222.67	8.00	1158.07
	Area-weighted mean patch area (ha)	12558.36	8.00	15979.96
	CV in patch area	154.19	0.00	357.75
	Largest patch area percentage within landscape (%)	9.20	0.01	11.74
	Edge density (m/ha)	0.96	0.00	1.55
	Perimeter–area ratio	175.00	20.80	234.60
	Landscape shape index	4.61	1.17	6.98
Unburned forest	Total area (ha)	86250	73582	70037
	Area percentage within the landscape (%)	62.91	53.67	51.08
	Number of patches	22	5	69
	Mean patch area (ha)	17246.40	3344.64	1015.03
	Largest patch area percentage within landscape (%)	80888.09	32585.44	44571.17
	CV in patch area	314.24	191.87	655.07
	Largest patch area percentage within landscape (%)	60.82	25.67	40.17
	Edge density (m/ha)	1.44	0.52	2.07
	Perimeter–area ratio	99.06	54.29	202.35
	Landscape shape index	8.99	7.24	8.99

Table 2. Landscape patterns of each forest classified by successional stage for the pre-burned landscapes (1710–2000) and the post-burned landscape (2005). Maximum and minimum values of class-level metrics for a period 1710–2000 are shown.

Successional stage	Class-level metrics	Pre-burned landscape		Post-burned landscape
		Max	Min	
Early	Total area (ha)	19237	8	16578
	Area percentage within the landscape (%)	14.03	0.01	12.09
	Number of patches	16	1	17
	Mean patch area (ha)	4222.67	8.00	975.18
	Area-weighted mean patch area (ha)	12558.36	8.00	15632.36
	CV in patch area	223.53	0.00	387.69
	Largest patch area percentage within landscape (%)	9.26	0.01	11.74
	Edge density (m/ha)	1.72	0.01	1.65
	Perimeter–area ratio	175.00	20.80	223.27
	Landscape shape index	6.16	1.17	7.28
Young	Total area (ha)	29627	7891	13483
	Area percentage within the landscape (%)	21.61	5.76	9.83
	Number of patches	23	6	11
	Mean patch area (ha)	3761.57	526.1	1225.73
	Area-weighted mean patch area (ha)	12800.94	1201.06	11806.84
	CV in patch area	272.62	113.27	293.81
	Largest patch area percentage within landscape (%)	10.39	1.23	9.19
	Edge density (m/ha)	2.20	0.50	1.16
	Perimeter–area ratio	106.60	46.60	164.83
	Landscape shape index	8.57	4.26	4.44

Table 2. Continued.				
Mature	Total area (ha)	30325	7891	18791
	Area percentage within the landscape (%)	22.12	5.76	13.71
	Number of patches	23	10	10
	Mean patch area (ha)	2693.36	526.07	1879.10
	Area-weighted mean patch area (ha)	12377.04	1201.06	10051.70
	CV in patch area	272.62	113.27	208.55
	Largest patch area percentage within landscape (%)	10.45	1.23	9.63
	Edge density (m/ha)	2.31	0.50	1.90
	Perimeter–area ratio	106.65	46.60	69.07
	Landscape shape index	8.57	5.27	7.06
Early old-growth	Total area (ha)	30325	7891	15161
	Area percentage within the landscape (%)	22.12	5.76	11.06
	Number of patches	25	11	33
	Mean patch area (ha)	2693.36	526.07	459.42
	Area-weighted mean patch area (ha)	12377.04	1201.06	6030.76
	CV in patch area	272.62	113.27	348.23
	Largest patch area percentage within landscape (%)	10.45	1.23	6.79
	Edge density (m/ha)	2.79	1.08	3.30
	Perimeter–area ratio	106.65	46.60	150.30
	Landscape shape index	8.56	6.06	8.57
Old-growth	Total area (ha)	33033	13009	22237
	Area percentage within the landscape (%)	24.09	9.49	16.22
	Number of patches	37	15	84
	Mean patch area (ha)	2178.73	479.17	264.72
	Area-weighted mean patch area (ha)	11662.88	1349.84	2797.24
	CV in patch area	284.21	132.95	309.30
	Largest patch area percentage within landscape (%)	10.45	1.57	4.35
	Edge density (m/ha)	2.22	0.65	1.23
	Perimeter–area ratio	97.51	55.12	171.12
	Landscape shape index	10.73	6.46	12.24

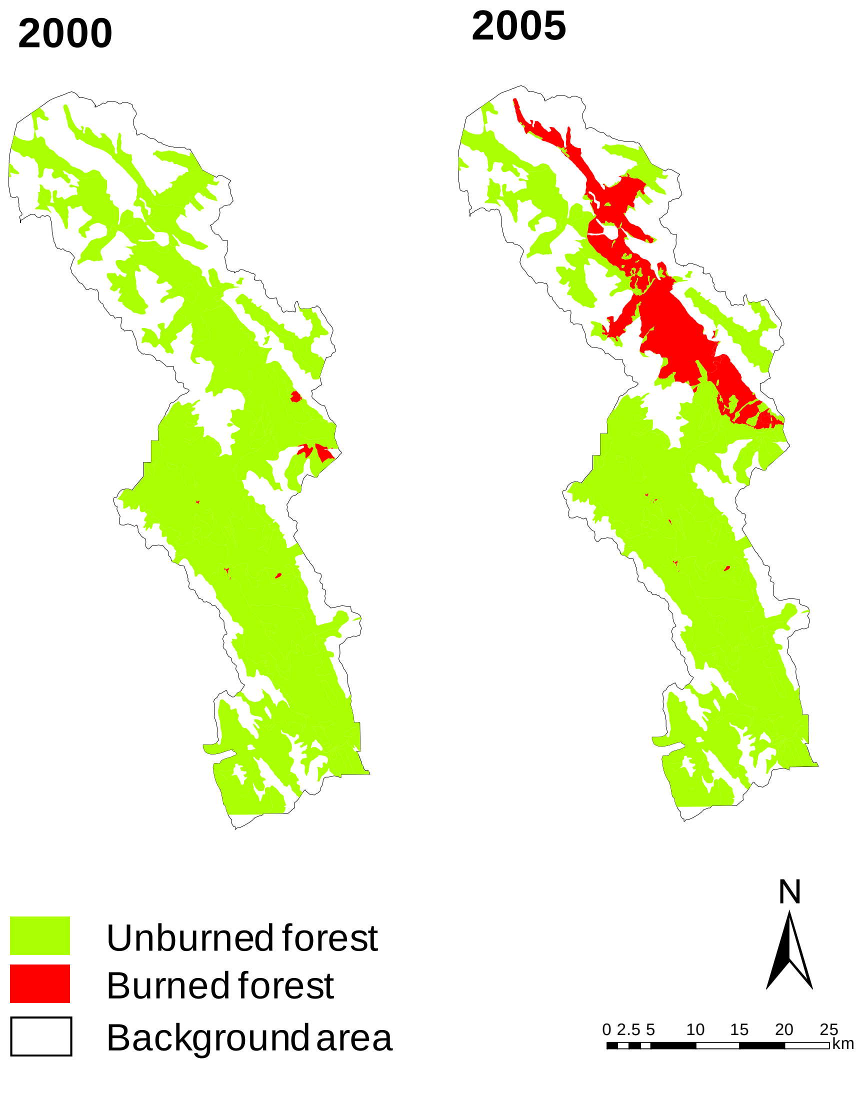

Fig. 1 Subalpine forest structure of Kootenay National Park (KNP) in the pre-burned (2000) and post-burned (2005) phases, based on burned/unburned classification.

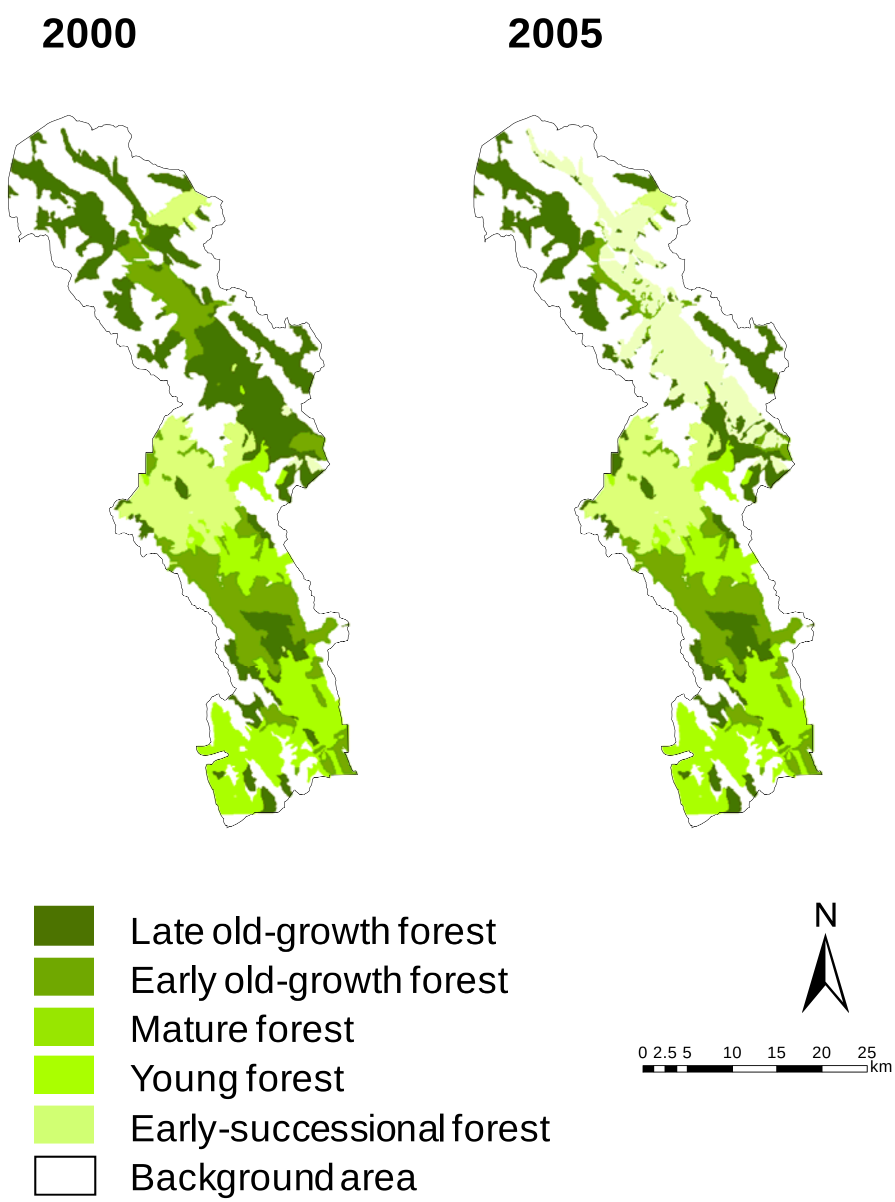

Fig. 2 Subalpine forest structure of KNP in the pre-burned (2000) and post-burned (2005) phases, based on successional stage classification.

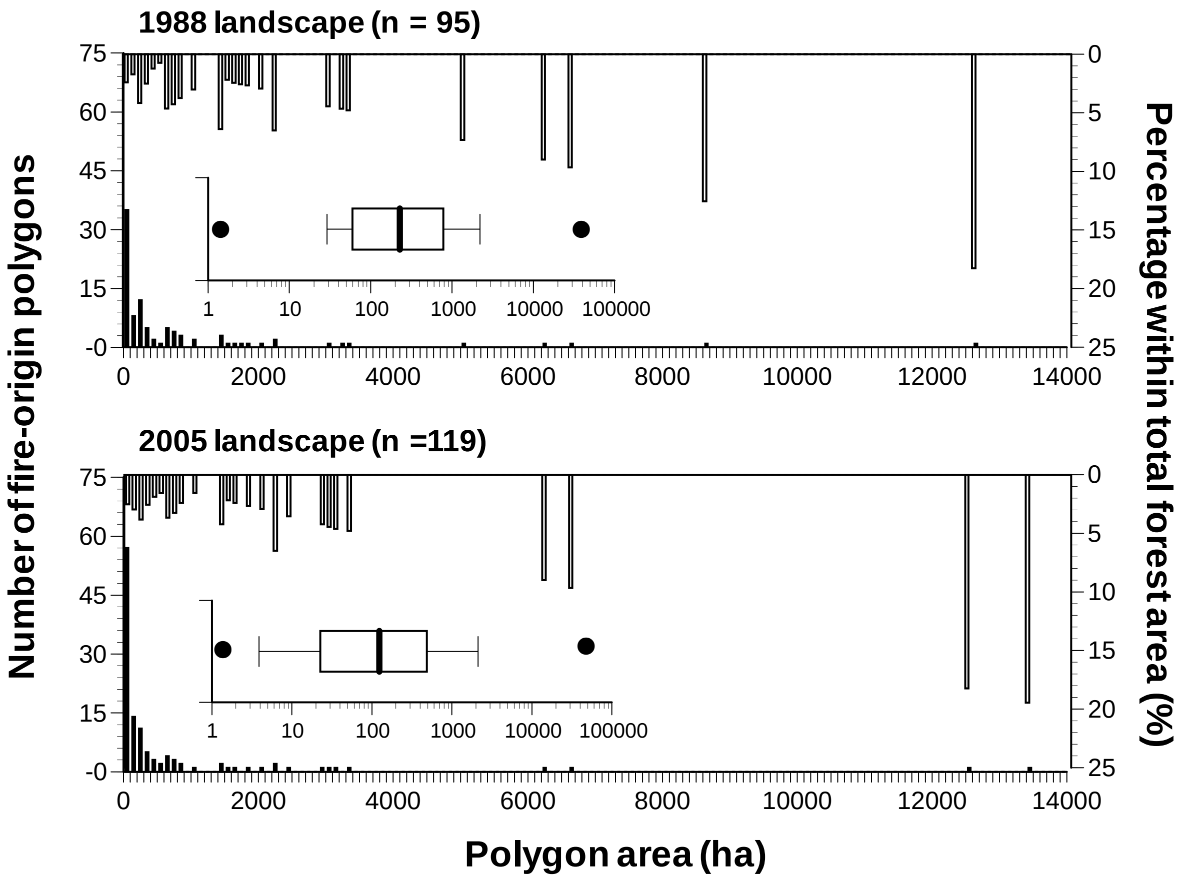

Fig. 3 Patch size distributions within the subalpine landscape of KNP in the initial census of 1988 (Masters, 1990) and in the post-burned phase of 2005. Solid bars show number of polygons and open bars indicate total area percentage within total forest area of the studied landscape. Each box plot represents the smallest value, lower quartile, median, upper quartile and the largest value.

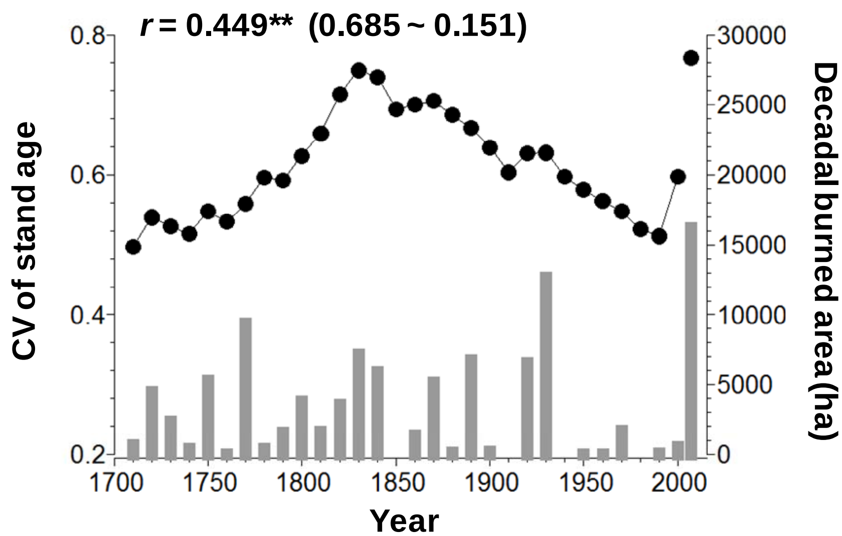

Fig. 4 Historical changes in coefficient of variation (CV) in stand age and reconstructed decadal burned area of the subalpine landscape in KNP between 1710 and 2000, and in 2005. Solid black circles indicate the CV of stand age and grey bars show the decadal burned area. Burned area in 2005 includes that of 1996–2005. Correlation coefficient (*r*) is shown, and ** indicates $P < 0.01$ calculated based on the 5000 randomizations. The 95 % confidence interval calculated by the PEARSONT is also shown in parenthesis.

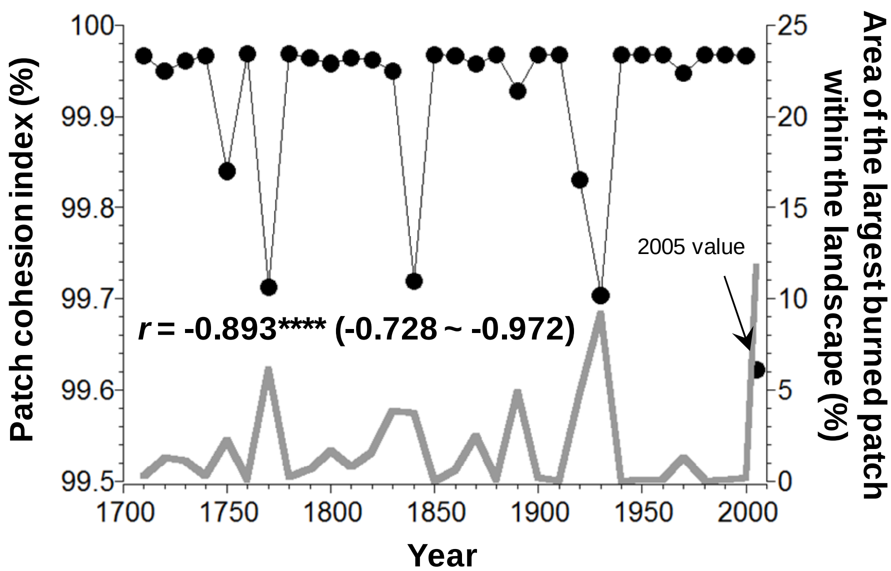

Fig. 5 Historical changes in the patch cohesion index of the unburned forest class within the subalpine landscape of KNP between 1710 and 2000, and in 2005. Solid black circles indicate the patch cohesion index. Grey line shows the decadal changes in the largest burned patch area. Correlation coefficient (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.

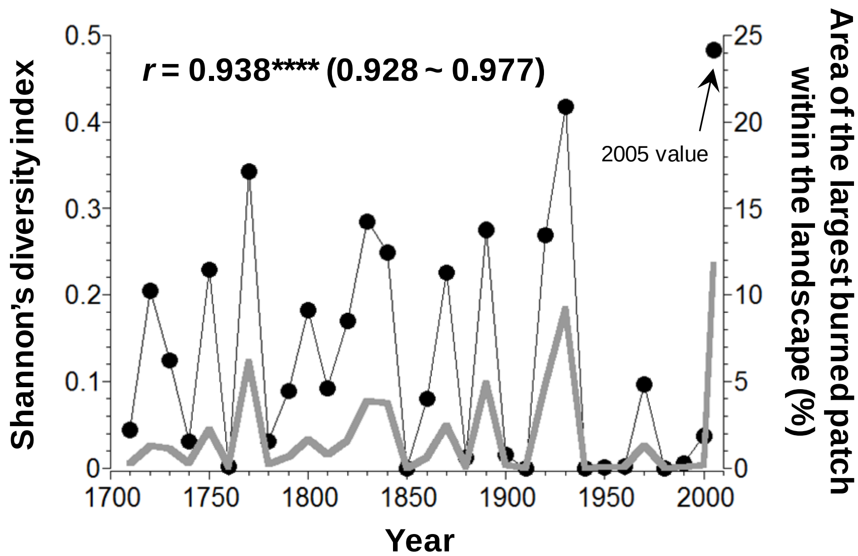

Fig. 6 Historical changes in Shannon's diversity index of the subalpine landscape in KNP between 1710 and 2000, and in 2005. Results are based on burned/unburned forest-classified landscapes. Solid black circles indicate the diversity index. Grey line shows the decadal changes in the largest burned patch 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.

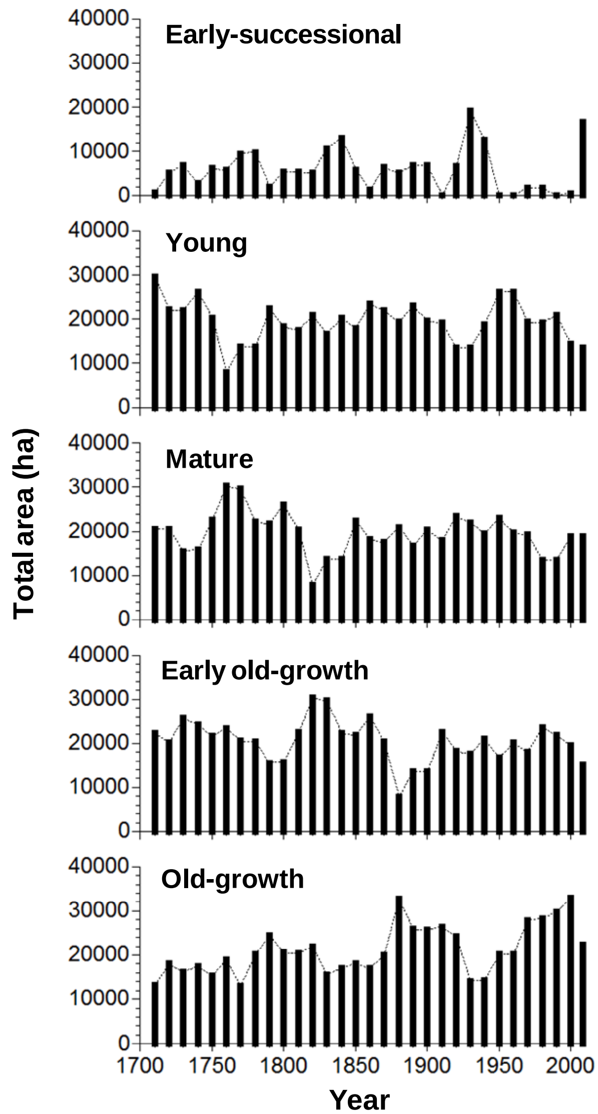

Fig. 7 Historical changes in the patch cohesion index of late-successional forest classes within the subalpine landscape of KNP between 1710 and 2000, and in 2005. Solid black circles indicate the patch cohesion index. Grey lines show the decadal changes in the largest burned patch area.

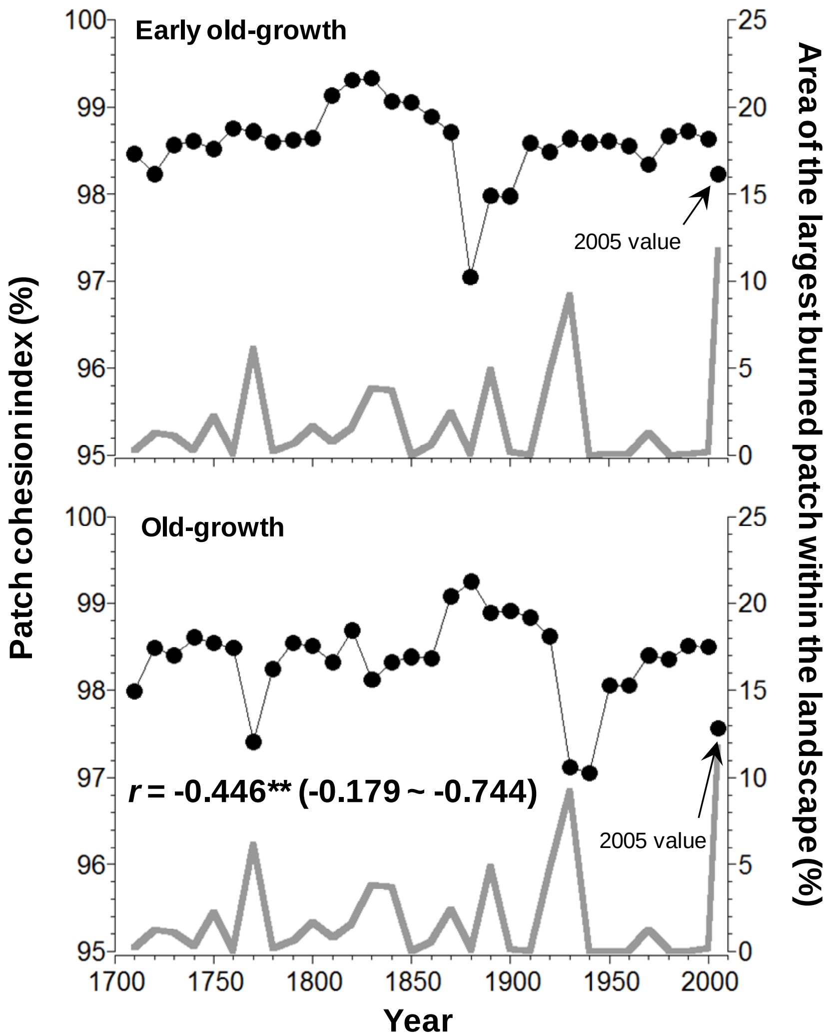

Fig. 8 Historical changes in Shannon's diversity index of the subalpine landscape in KNP between 1710 and 2000, and in 2005. Solid black circles indicate the diversity index. Grey line shows the decadal changes in the largest burned patch area. Correlation coefficient (r) is shown, and ** indicates $P < 0.01$. The statistical significance of the relationship was calculated with 5000 randomizations. The 95 % confidence interval calculated by the PEARSONT is also shown in parenthesis.

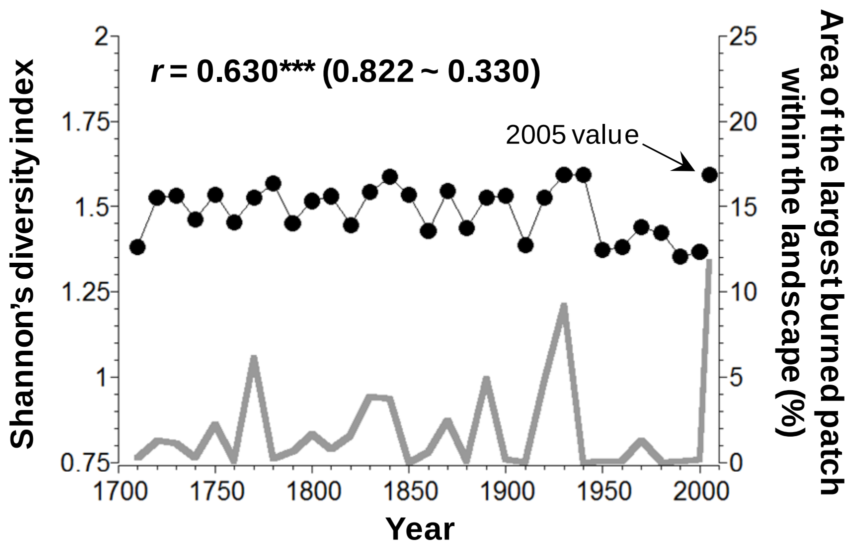

Fig. 9 Historical changes in total area (ha) of each successional stage class within the subalpine landscape of KNP from 1710 to 2005. The last values in each sub-figure are each area within the 2005 landscape map. Correlation coefficient (*r*) is shown, and *** indicates $P < 0.001$. The statistical significance of the relationship was calculated with 5000 randomizations. The 95 % confidence interval calculated by the PEARSONT is also shown in parenthesis.