

Temporal patterns of age-class distributions on foothills landscapes in Alberta

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The strategy of managing for “natural” patterns towards ecological sustainability of forests is currently limited to simple spatial attributes of landscapes. Yet, there is general agreement that landscapes are highly dynamic entities suggesting that temporal patterns may also be important. This study used historical estimates of 20-yr disturbance rates, and a spatially explicit, stochastic landscape model to create multiple possible landscape mosaic scenes for three different landscapes in the foothills of Alberta. The results were summarized as frequency distributions by age-class, and the distributions compared to the percentage of area in the current, and the pre-commercial landscapes. Results indicated that aside from one age-class in one of the landscapes, both current and pre-commercial age-class distributions were well within the historical ranges suggested by the simulations. More generally, the simulations indicated relatively high, but landscape specific, levels of historical temporal variability. This implies that there are patterns to temporal variability which may be captured, quantified, and emulated as alternatives to single age-class management targets. The research also demonstrates a method of assessing age-class distributions within the context of historical ranges of distributions.

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Thirty years ago, the value of forested land was measured largely by the amount of timber it held, or could produce (Zonneveld 1987). Today, forests are also valued for the role they play in regulating water and nutrient flows, fixing atmospheric carbon, influencing climatic patterns, absorbing and transforming atmospheric and water-borne toxins and providing the opportunity for the continued existence and evolution of flora, fauna, and aquatic species (Anon. 1992, Davis 1993). These non-timber functions are often referred to as “biological values” and it is believed they are fundamental to the long-term sustainability of all aspects of forest systems, including the production of timber (Davis 1993).

Providing an ecological basis for forest management is now an explicit goal of many government agencies under the auspices of “ecosystem management” (Anon. 1993, Balsillie 1994, Hamilton 1994). A strategy that

many agencies are now embracing to realize this goal is the emulation of natural landscape structures and patterns (Franklin 1993). By first understanding, and then managing for the natural range in variation of the ecological processes most active on a landscape, the risk of losing biological functions is minimized since the range, type, and frequency of change are familiar (Merriam and Wegner 1992, Noss 1994). This is in sharp contrast to the more traditional species-by-species approach of habitat management.

The success of a management strategy based on natural patterns depends on being able to identify this natural range of variability. Although progress has been made on identifying ranges of disturbance sizes, shapes, and frequencies (Yarie 1981, Eberhart and Woodard 1987, Lorimer et al. 1994, Taylor et al. 1994, Andison 1996, DeLong and Tanner 1996), many natural pattern attributes remain unidentified. This is not

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Table 1. Summary of the major natural sub-region landscapes of the Weldwood FMA.

Type	Natural sub-region				Totals
	Upper Foothills	Lower Foothills	Sub-alpine	Other	
Forested (ha)	569 295	263 073	107 100	11 113	945 158
Non-forested (ha)	59 743	36 789	2375	2741	107 093
Total (ha)	629 038	299 862	109 475	13 854	1 052 251

surprising given the difficulty of finding one or more large, natural landscapes to measure and study. However, because of this difficulty, we are obliged to presume that two mosaic snapshots, spaced several years apart, are sufficient to portray changing landscape patterns (Ripple et al. 1991, Mladenoff et al. 1993a, Wickham and Norton 1994, Luque et al. 1994). This is a dangerous and potentially misleading extrapolation; no matter how representative single snapshots are, we know landscapes to be highly dynamic entities (i.e., Romme and Knight 1982, Forman and Godron 1986, Risser, 1987, Noss 1990, Dunn et al. 1990, Forman 1995).

A case in point is the determination of many land management agencies to manage for "natural" proportions of different seral-stages across landscapes. The perceived value of old-growth forest initiated this desire, but the idea has since matured into recognizing the importance of all stages of forest development. Yet, the manifestation of a seral-stage management strategy has been to define averages, or maximum and minimum percentages of broad age-classes for landscapes. These percentages are generally based loosely on recent historical averages (Anon. 1995). Using such targets may be well intentioned, but a) assumes that change is not an important biological component of natural landscapes, b) continues to encourage maximizing timber productivity, and c) promotes stable forest management ideals. Perhaps of greater consequence, it assumes that single landscape snapshots are representative of long-term averages, and that an average has some biological meaning.

To develop alternatives to managing for static seral-stage targets is challenging, but not beyond our capabilities or our grasp. This paper demonstrates a modelling exercise used to develop ranges of historical seral-stage percentages from existing landscape information. The frequency distributions that are generated allow comparison of existing proportions of areas in different age-classes, as well as provide some indication of the temporal patterns that "natural" landscapes may experience.

Background and data

In early 1996, the Foothills Model Forest of Canada, in cooperation with Weldwood of Canada Ltd. in Hinton,

Alberta, and Jasper National Park (JNP), initiated a research program to study natural disturbance patterns. Weldwood was particularly interested in defining the most appropriate seral-stage percentages for long-term management plans. These percentages were ideally to be based on pre-commercial, "natural" levels over an area of ca 1 million ha. As with many North American forest types, the Weldwood Forest Management Area (FMA) landscape mosaic is largely a result of forest fires (Johnson 1992, Sapsis and Martin 1993).

Three major areas with distinctive disturbance behaviour characteristics were identified within the FMA. These areas are associated with the natural sub-region boundaries of the provincial ecological classification system (Beckingham et al. 1996). The Upper Foothills natural sub-region consists of gently rolling tills and is dominated by stands of pure lodgepole pine *Pinus contorta*. The Sub-alpine natural sub-region occurs at steeper, higher elevations, and is dominated by white spruce *Picea glauca*. The third landscape, the Lower Foothills natural sub-region, occurs at lower elevational fluvial areas, and has a mixture of lodgepole pine, white spruce, and trembling aspen *Populus tremuloides* (Table 1).

As part of a larger disturbance dynamics study, extensive spatial datasets were assembled representing two landscape mosaic snapshots: the pre-commercial landscape of 1950, and the current managed landscape from 1995. Although there is evidence that there was some human intervention prior to 1950, this pre-dates both large-scale harvesting and intensive fire control activities in this part of Alberta. Polygon age-classes were cross-referenced using a grid of 2016 permanent sample plots (PSP's) covering the entire FMA. For those polygons with an "older than" (maximum) age, age-classes were estimated by extrapolating the ages measured in the field on 26891 hectares across the entire FMA using methods derived from Arno and Sneek (1977), as well as cross-referencing to the 303 PSP's that fell into this oldest age category. These data were used to calculate the 1995 age-class distribution. The 1950 age-class distribution was then estimated by eliminating the cut-blocks from the spatial database and using the adjacent pre-harvest age-class, and subtracting 45 yr from non-cutblock polygon ages. Since the original time-since-fire mapping was done in the early 1960's, the potential bias of misrepresenting the pre-harvest ages was minimized.

Modelling strategy

The purpose of the modelling exercise was to project estimated spatial variability through time. At the simplest level, the range of area in existing 20-yr age-classes represents variation in historical levels of disturbance rates. However, these data require manipulation to estimate original disturbance rates. The youngest 20-yr age-class is the only class that represents the true amount of disturbance within a 20-yr period. Every other (older) age-class under-represents the actual area disturbed, since more recent disturbances have overlain older ones. Note that this does not imply that the area in the most recent 20-yr age-class is the total area that burnt in that period, only the net amount burnt at the end of 20 yr. Two or more burns within a 20-yr period are possible.

A simple way to estimate the original amount of area disturbed in each 20-yr period is to normalize the areas in each age-class (Murphy 1985). This method involves taking the area in the youngest 20-yr age-class, and distributing it proportionally among the remaining age-classes. Thus, historical age-class distributions are recalculated every 20 yr back in time. At every iteration, the youngest age-class will represent the actual area disturbed. For example, consider a landscape in which the first age-class (0–20 yr) covers 10% of the area, the second (21–40 yr) 20%, and the third (41–60 yr) 5%. To estimate the age-class distribution 20 yr ago, all polygons in age-class 1 would be replaced with age-classes 2, 3, etc. The estimated area of age-class 2 would be $(20 + 20 \times 10\% =)$ 22% and the third age-class $(5 + 5 \times 10\% =)$ 5.5%. The second iteration to calculate the age-class distribution 40 yr ago would distribute the 22% in age-class 2 above, into age-classes 3, 4, etc. in the same manner.

The original area disturbed in the youngest eight 20-yr age-classes were approximated using this method

for each of the three major natural sub-regions (Table 2). As an internal check, the fire cycle was estimated from the average 20-yr burn rates, and compared to the average age estimated from the original age-class distribution. All compared favourably (Table 2). These estimates of disturbance rates were then defined as (three separate) best-fit non-linear functions using SYSTAT (Wilkinson 1988).

The disturbance rates in Table 2 were then fit to an equation, and projected through time stochastically using a spatially explicit, raster-based, disturbance model (LANDMINE) developed to test the sensitivity of various disturbance regime parameters on pattern (Andison 1996). LANDMINE is based on the original cellular automaton model formulation of Clarke et al. (1994), and is very similar to the models of both Baker et al. (1991) and Mladenoff et al. (1993b). The model "grows" disturbances over large areas consistent with observed patch-sizes and shapes, using the function of the 20-yr disturbance rates (Andison 1996).

To avoid bias associated with starting LANDMINE at any single landscape, 50 model runs were competed in 20-yr time-steps on a blank landscape of a single age before pattern measurements were taken. For brevity, the original 20-yr classes were grouped into six broad age categories: 0–40, 41–100, 101–140, 140–200, 210–300, and > 300 yr. For the next 50 model runs, the percent area in each of the six age-classes was recorded at the end of each 20-yr period. This generated 50 different possible age-class distributions under three different disturbance regimes.

The results from the 50 model runs were summarized using the range of observed (simulated) percentages in each age-class. The percentages of each age-class as of 1950 and 1995 were then compared to the simulated ranges for each natural sub-region.

Results

Simulated frequency distributions for the first five age-class percentages were compared to the pre-commercial (1950) and current (1995) age-class percentages for the Upper Foothills landscape. The simulation produced only a very small amount of area in the oldest age-class beyond 300 yr, and there were insignificant areas of forest older than 300 yr in 1950 or 1995, so this age-class was not included in the results. Of the five age-classes compared, all were well within the range of the simulation output (Figs 1a–e).

More generally, it is interesting to note how wide the range of "possible" age-class percentages was for the simulated landscapes. This is particularly true of the frequency distribution of the younger age-classes, which are wide and flat. The lack of a central tendency in the first two age-class frequencies suggests that there is an

Table 2. Normalized estimates of historical 20 yr disturbance rates for each of the natural sub-regions of the Weldwood FMA.

Period	Estimated original area burnt (percent of landscape)		
	Lower Foothills	Upper Foothills	Sub-alpine
1930–1950	1	2	<1
1910–1919	10	8	14
1890–1909	14	21	36
1870–1889	47	46	35
1850–1869	51	28	<1
1830–1849	60	39	26
1810–1829	10	1	2
1790–1809	7	13	18
Average	25	20	16
Fire cycle est.	80 yr	100 yr	125 yr
Average age	80 yr	101 yr	123 yr

equal probability of between 0 and 70% of the Upper Foothills landscape being occupied by either of these two age-classes (Figs 1a and b). The older age-classes show narrower distributions of simulated percentages, and also demonstrate an increasing negative bias. The oldest age-class has the strongest tendency towards small percentages, although it still shows the (rare)

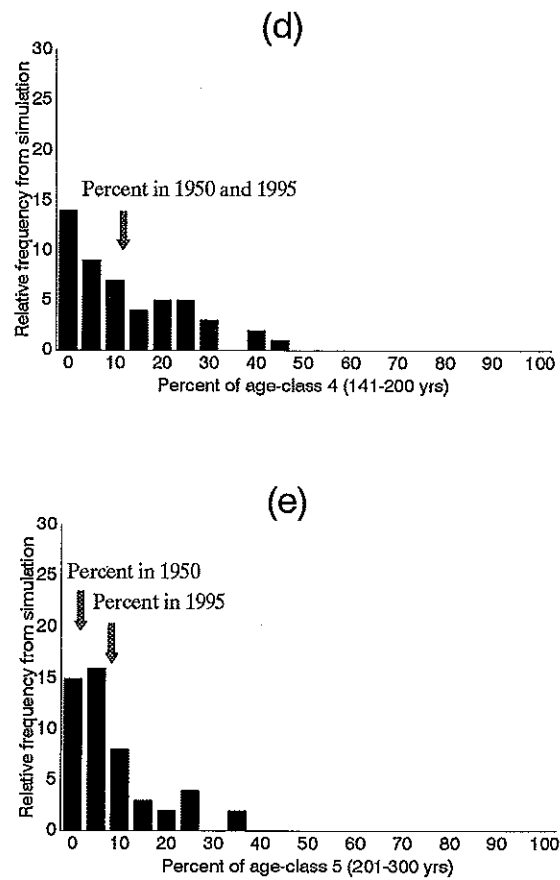
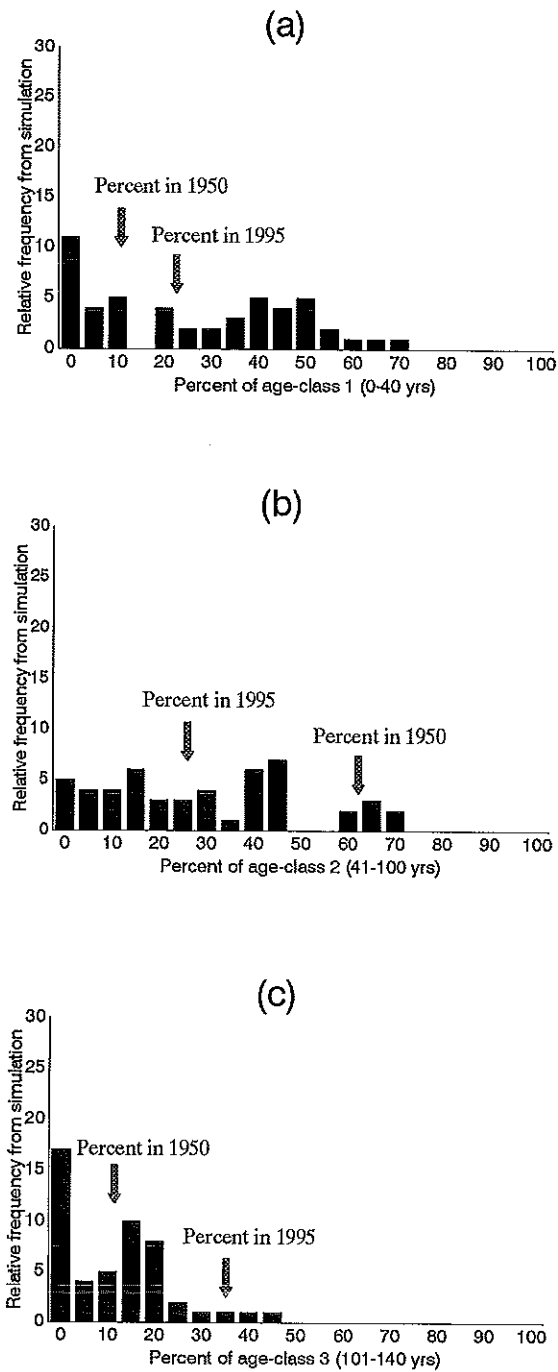


Fig. 1. Frequency distributions of percentages of age-class 1 a), 2 b), 3 c), 4 d), and 5 e) created from simulation for the Upper Foothills natural sub-region of the Weldwood FMA, compared to the actual percentages from 1950 and 1995.

potential for comprising 20% or even 30% of the landscape area (Fig. 1e).

The same comparison for the Lower Foothills age-class percentages included only the first three age-classes (Fig. 2). Beyond 140 yr, the percentages of areas from the simulations were very small, and highly negatively skewed. According to Fig. 2, the Lower Foothills 1995 and 1950 age-class percentages for the first two age-classes are well within the simulated range. In fact, it would be difficult for a percentage of age-class 1 or 2 not to be within this range. The Lower Foothills displayed the widest range of disturbance activity. It is interesting to note that the youngest age-class frequency distribution suggests bi-modal behaviour of either very low or very high fire activity in any given 20-yr period. The trend can also be seen in the disturbance rate estimates for the Lower Foothills (Table 2). On the other hand, the 1995 percentage of age-class 3 is well beyond the range predicted by the simulations. In other words, the simulations suggest that the amount of

forest currently beyond 100 yr of age in the Lower Foothills may be unusually high (Fig. 2c).

The age-class comparison for the Sub-alpine natural sub-region included only age-classes 1, 3, and 5 for brevity. The age-class distribution of age-class 2 was much like that of age-class 1, and age-class 4 was much

like that of age-class 5. Comparisons to all age-classes for the sub-alpine landscape showed that age-class percentages from both 1950 and 1995 were well within simulated limits (Figs 3a–c). It is also interesting that the frequency distributions for the Sub-alpine suggest a central tendency, unlike the results from the other two landscapes. The range of possible percentages for the youngest age-class is also much narrower than that of either the Upper Foothills or Lower Foothills natural sub-regions (Fig. 3).

Discussion

Based on the simulated range of age-class landscape behaviour, neither the 1950 nor the 1995 distributions can be identified as being more appropriate, or “natural”, than the other for the Upper Foothills landscape and the sub-alpine landscape. All observed percentages, at both times, were within the simulated ranges.

For the Lower Foothills landscape, the 1995 area in the 101–140 yr age-class is over 15% beyond the maximum amount determined by the simulations. This suggests that the area in forest over 100 yr of age is beyond that observed historically, and that disturbance may be overdue. This is consistent with observed stand dynamics in the Lower Foothills area. Recall that this particular landscape is mixedwood dominated, consisting of aspen, white spruce, and lodgepole pine (Beckingham et al. 1996). The combination of intensive fire control and lack of harvesting in this area has allowed many stands to reach advanced stages of development. It is not uncommon to see declining aspen and invading all-aged spruce, essentially converting mixedwood stands to conifer dominated ones (Pojar et al. 1984, Clark 1994).

Overall, the simulated frequencies suggest that variation in disturbance rates allows for a highly dynamic landscape. This is consistent with what is known of fire-dominated landscape behaviour (Romme 1982, Romme and Knight 1982, Baker 1989, Turner and Dale 1991, Antonovski et al. 1992). The percentages of very young forest (0–40 yr) for each landscape were particularly agile, covering between 0 and > 50% of the landscape, and often higher. The breadth of percentages of older age-classes was less, as one would expect.

The bi-modal distribution of the youngest age-class of the Lower Foothills is particularly notable in that it indicates either very high or very low levels of disturbance. One can imagine mixedwood areas experiencing very high levels of disturbance only when infrequent spring fires occur, prior to hardwood leaf-out when fuel moisture is at its lowest (Bradley et al. 1992). However, when spring fires do not occur, fires cannot spread easily through mixedwood in full leaf even when burning indices are quite high, creating low levels of disturbance. Intermediate levels of disturbance are thus not common.

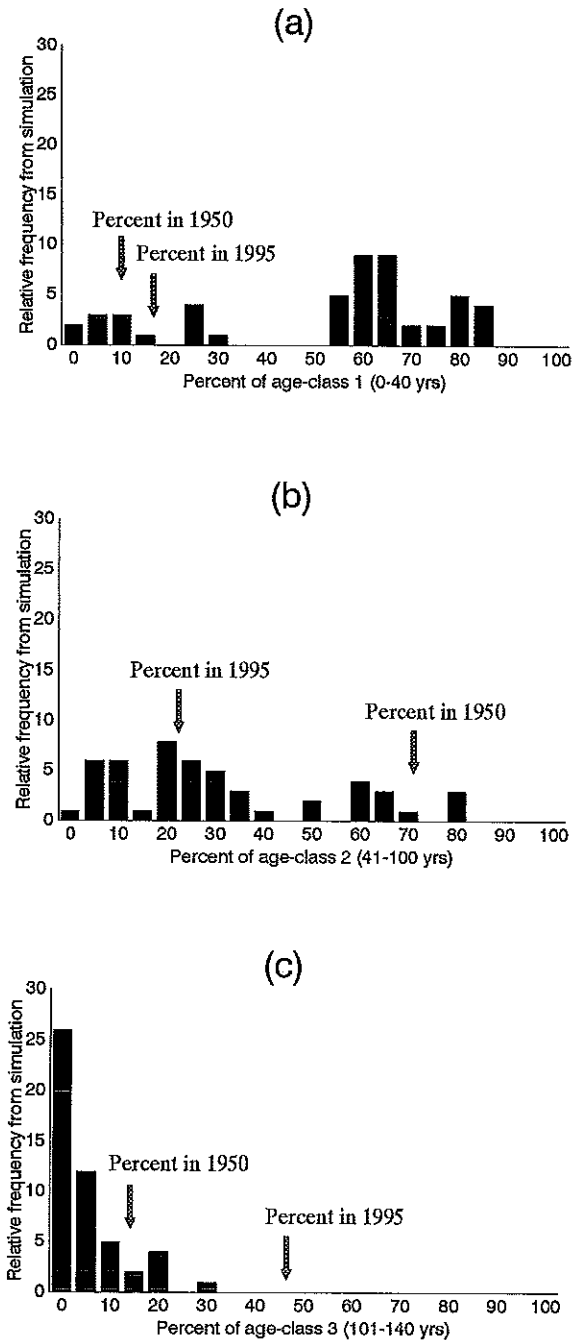


Fig. 2. Frequency distribution of age-class 1 a), 2 b), and 3 c) for the Lower Foothills natural sub-region of the Weldwood FMA from simulation, compared to the actual percentages from 1950 and 1995.

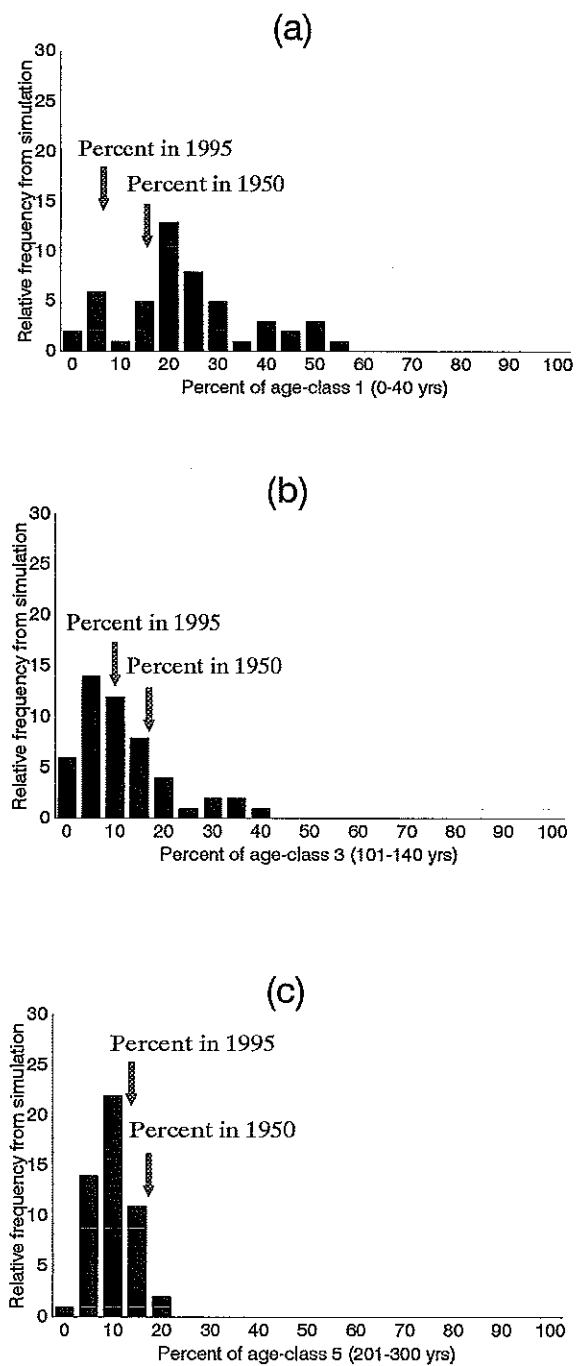


Fig. 3. Frequency distributions of age-class 1 a), 3 b), and 5 c) for the Sub-alpine natural sub-region of the Weldwood FMA from simulation, compared to the actual percentages from 1950 and 1995.

The age-class frequency distributions did not suggest a single "average" rate of disturbance, except for the oldest age categories. In fact, for most of the younger age-classes, simulated frequency distributions were quite flat, indicating that any percentage of young

forest would be equally representative. This raises two important questions. First, what is the point in defining average age-class targets for management if any single number is arbitrary? At the very least, upper and lower limits of age-class percentages should be defined as a sort of confidence interval. Situations such as the excessive area in the 100–140 yr age-class in the Lower Foothills landscape could be anticipated and avoided using such limits. Note that this solution still limits the "natural" behavioural range to the most recent historical range.

The second question raised by these simulations is whether we should be looking closer at temporal aspects of pattern, rather than focusing on spatial ones. Whether or not there are biological functions associated with temporal variability is unknown, but there is agreement that ecological phenomena respond to both spatial heterogeneity and changes over time in the number and type of organisms, and nutrients, water, and energy availability (Romme and Knight 1982, Pickett and Cadenasso 1995). For example, Holling (1996) suggests that it is the change itself (i.e., the movement between states) that maintains the structure and diversity allowing species to co-exist. In any case, to question the validity of maintaining temporal variability on the basis of a lack of proof of ecological relevance is antithetic to the concept of pattern and structure approximation under the auspices of ecosystem management. Given the tremendous levels of change suggested by the simulations, this variation needs to be studied, quantified, and included as an integral part of natural pattern emulation through management planning.

Conclusions

This landscape simulation exercise was valuable for identifying where age-class percentages for at least one area of a landscape in the foothills of Alberta may be beyond historical limits. Independent field evidence corroborates this suspicion, warranting further investigation and consideration. The simulations also suggest that the historical natural range of variability of the area in younger age-classes is far greater than that of older age-classes. This may be interpreted to mean that younger forest areas allow greater levels of management flexibility.

More generally, the simulation exercise implies that change is a regular part of the pattern of these landscapes. Furthermore, the imposition of any age-class percentage target is, at best arbitrary and, at worst, perilous. Change is an important element of both ecological and evolutionary processes.

Clearly, sustaining biological values through emulating "natural" patterns entails much more than first anticipated. Aside from many of the details of spatial

pattern that we have yet to understand and quantify, there is a prominent temporal aspect to pattern. Until now, ignorance has given us the luxury of overlooking the temporal dimension of landscape pattern and variability. However, conducting simple simulations through extrapolation of existing spatial information through time is within our capabilities, technically and intellectually. Given this ability, we are obliged by the ideals of ecosystem management to investigate these patterns further.

This exercise was not necessary to prove that artificial stabilization of large forested areas is an unnatural phenomenon. It is well accepted that fire-dominated landscapes do not experience age-class stability. However, the simulation was useful for drawing attention to ways and means of beginning to understand and deal with temporal variability on large scales.

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References

- Anderson, D. W. 1996. Managing for landscape patterns in the sub-boreal forests of British Columbia. – Ph.D. thesis, For. Manage. Dept, Univ. of British Columbia, Vancouver, B.C.
- Anon. 1992. Global biodiversity strategy. – World Conserv. Union, U.N. Environ. Prog., Food and Agric. Organ. and U.N. Educ., Sci. and Cult. Organ.
- Anon. 1993. Task force report on sustaining long-term forest health and productivity. – Bethesda, Maryland.
- Anon. 1995. Forest practices code of British Columbia biodiversity guidebook. – B.C. Min. of For., Victoria, B.C.
- Antonovski, M. Y., Ter-Mikaelian, M. T. and Furyaev, V. V. 1992. A spatial model of long-term forest fire dynamics and its applications to forests in western Siberia. – In: Shugart, H. H., Leemans, R. and Bonan, G. B. (eds), A systems analysis of the global boreal forest. Univ. Press, Cambridge, pp. 373–403.
- Arno, S. F. and Sneek, K. M. 1977. A method for determining fire history in coniferous forests of the mountain west. – USDA For. Serv. Gen. Tech. Rep. INT 42.
- Baker, W. L. 1989. Effect of scale and spatial heterogeneity on fire-interval distributions. – Can. J. For. Res. 19: 700–706.
- Baker, W. L., Egbert, S. L. and Frazier, G. F. 1991. A spatial model for studying the effects of climatic change on the structure of landscapes subject to large disturbances. – Ecol. Modell. 56: 109–125.
- Balsillie, D. 1994. Applying the ecosystem approach to resource management in Ontario. – In: Jordan, J. K. and Uhlig, P. W. C. (eds), Ecosystem management strategies for the Lake Superior Region. A conference and workshop in Deluth, Mn. 16–19 May 1994, pp. 8–11.
- Beckingham, J. D., Corns, I. G. W. and Archibald, J. H. 1996. Field guide to ecotones of west-central Alberta. – Northern For. Cent., CFS, Edmonton, Alta. Special Report 9.
- Bradley, A. F., Fischer, W. C. and Noste, N. V. 1992. Fire ecology of the forest habitat types of eastern Idaho and western Wyoming. – USDA For. Serv. Gen. Tech. Rep. INT–290.
- Clark, D. F. 1994. Post-fire succession in the sub-boreal spruce forests of the Nechako Plateau, central British Columbia. – M.Sc. thesis, Univ. Vic., Victoria, B.C., Canada.
- Clarke, K. C., Brass, J. A. and Riggan, P. J. 1994. A cellular automaton model of wildfire propagation and extinction. – Photo. Eng. and Remote Sensing 60: 1355–1367.
- Davis, W. 1993. The global implications of biodiversity. – In: Fenger, M. A. et al. (eds), Our living legacy. Proc. Symp. Biological Diversity, Victoria, B.C, pp. 23–46.
- DeLong, S. C. and Tanner, D. 1996. Managing the pattern of forest harvest: Lessons from wildfire. – Biodiversity and Conserv. 5: 1191–1205.
- Dunn, C. P. et al. 1990. – In: Turner, M. G. and Gardner, R. H. (eds), Quantitative methods in landscape ecology. In: Ecol. Stud, Vol. 82, Springer, pp. 173–198.
- Eberhart, K. E. and Woodard, P. M. 1987. Distribution of residual vegetation associated with large fires in Alberta. – Vegetatio 4: 412–417.
- Forman, R. T. T. 1995. Some general principles of landscape and regional ecology. – Landscape Ecol. 10: 133–142.
- Forman, R. T. T. and Godron, M. 1986. Landscape ecology. – J. Wiley and Sons.
- Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes? – Ecol. Appl. 3: 202–205.
- Hamilton, E. H. 1994. Biodiversity research and extension strategy. – B.C. Min. For., Victoria, B.C.
- Holling, C. S. 1996. Surprise for science, resilience for ecosystems, and incentives for people. – Ecol. Appl. 6: 733–735.
- Johnson, E. A. 1992. Fire and vegetation dynamics: Studies from the North American boreal forest. – Cambridge Univ. Press.
- Lorimer, N. D., Haught, R. G. and Leary, R. A. 1994. The fractal forest: Fractal geometry and applications in forest science. – USDA For. Serv. NC For. Exp. Stn. Gen. Tech. Rep. NC-170. St. Paul, Minn.
- Luque, S. S., Lathrop, R. G. and Bognar, J. A. 1994. Temporal and spatial changes in an area of the New Jersey Pine Barrens landscape. – Landscape Ecol. 9: 287–300.
- Merriam, G. and Wegner, J. 1992. Local extinctions, habitat fragmentation, and ecotones. – In: Hansen, A. J. and Di Castri, F. (eds), Landscape boundaries: Consequences for biological diversity and ecological flows. In: Ecol. Stud, Vol. 92. Springer, pp. 150–169.
- Mladenoff, D. J., White, M. A. and Pastor, J. 1993a. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. – Ecol. Appl. 3: 294–306.
- Mladenoff, D. J. et al. 1993b. LANDIS: A spatial model of forest landscape disturbance, succession, and management. – Sec. Int. Conf. on Integrating Modelling and GIS. NC-GIA, Santa Barbara, Calif.
- Murphy, P. J. 1985. Methods for evaluating the effects of forest fire management in Alberta. – Ph.D. thesis, Dept. of Forestry, Univ. of Alberta, Edmonton, Alta.
- Noss, R. F. 1990. Can we maintain biological and ecological integrity? – Conserv. Biol. 4: 241–243.
- Noss, R. F. 1994. At what scale should we manage biodiversity? – Oregon State Univ., Corvallis, Or.
- Pickett, S. T. A. and Cadenasso, M. L. 1995. Landscape ecology: Spatial heterogeneity in ecological systems. – Science 269: 331–334.
- Pojar, J., Trowbridge, R. and Coates, D. 1984. Ecosystem classification and interpretation of the sub-boreal spruce zone, Prince Rupert Forest Region, British Columbia. – B.C. Min. For. Land Manage. Rep. no. 17.
- Ripple, W. J., Bradshaw, G. A. and Spies, T. A. 1991. Measuring forest landscape patterns in the Cascade Range or Oregon, USA. – Biol. Conserv. 57: 73–88.
- Risser, P. G. 1987. Landscape ecology: State of the art. – In: Goigci-Turner, M. (ed.), Landscape heterogeneity and disturbance. In: Ecol. Stud, Vol. 64. Springer, pp. 3–14.
- Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. – Ecol. Monogr. 52: 199–221.
- Romme, W. H. and Knight, D. H. 1982. Landscape diversity: the concept applied to Yellowstone Park. – BioScience 32: 664–670.

- Sapsis, D. B. and Martin, R. E. 1993. Fire, the landscape, and diversity. A theoretical framework for managing wildlands. – 12th Conf. on Fire and For. Meteorol., Oct. 26–28, 1993, Jekyll Is. GA, pp. 270–278.
- Taylor, S. W. et al. 1994. Wild fire frequency in Yukon ecoregions. – For. Can., Victoria, B.C.
- Turner, M. G. and Dale, V. H. 1991. Modelling landscape disturbance. – In: Turner, M. G. and Gardner, R. H. (eds), Quantitative methods in landscape ecology. In: *Ecol. Studies*, Vol. 82. Springer, pp. 322–351.
- Wickham, J. D. and Norton, D. J. 1994. Mapping and analyzing landscape patterns. – *Landscape Ecol.* 9: 7–24.
- Wilkinson, L. 1988. SYSTAT: The system for statistics. – Evanston, IL, SYSTAT Inc.
- Yarie, J. 1981. Forest fire cycles and life tables: a case study from interior Alaska. – *Can. J. For. Res.* 11: 554–562.
- Zonneveld, I. S. 1987. Landscape ecology and its application. – In: Moss, M. R. (ed.), *Landscape ecology and management. Proc. of the First Symp. of the Can. Soc. for Land. Ecol. and Manage.* Univ. of Guelph, pp. 3–16.