EFFECTS OF INTERACTING DISTURBANCES ON LANDSCAPE PATTERNS: BUDWORM DEFOLIATION AND SALVAGE LOGGING

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Abstract. Prior to European settlement, the 450 000-ha Pine Barrens region in north-western Wisconsin, USA, was characterized by a landscape mosaic of large, open patches, savannas, and closed forest stands of jack pine (*Pinus banksiana*). Crown-fires created large open patches that persisted on the droughty soils, providing important habitat for a number of area-sensitive, open-habitat species. Insect outbreaks may have contributed to periodic fires by increasing the fuel load.

Today, fires are suppressed in the managed landscape, but insect defoliation remains a major disturbance. Salvage logging commonly follows insect outbreaks. Our objective was to evaluate landscape pattern changes caused by this interaction of natural disturbances and forest management. We examined changes in landscape pattern during the most recent (1990–1995) outbreak of jack pine budworm (*Choristoneura pinus pinus*) in northwestern Wisconsin using four Landsat TM satellite images (1987, 1991, 1993, and 1995). The 1987 image provided the basis for a species-level forest classification identifying mature jack pine and open habitat prior to the budworm outbreak. Each subsequent image was used to identify clearcuts in mature jack pine. The 1995 image was also used to classify stand development in the open habitat of the 1987 image so that the overall availability of open habitat in 1995 could be assessed. GIS data layers were used to analyze logging rates and clearcut sizes separately for different classes of land ownership and soils.

Approximately 12 500 ha were salvage logged during the 1990-1995 outbreak. Logging rates were highest on the most infertile soils, and on private, industrial forest land. Annual logging rates of different landowners were 3-6 times higher during the outbreak than previous to it. Salvage cut sizes were larger than clearcuts prior to the outbreak. New cuts were mostly located next to previous cuts, thus increasing the size of openings on the landscape.

Initial survey results by N. Niemuth show that populations of one area-sensitive open-habitat species (Sharp-tailed Grouse, *Tympanuchus phasianellus*) thrive on the salvage cuts. Insect defoliation and subsequent salvage logging did create new habitat for open-habitat species that were declining.

Landscape pattern changes due to multiple interacting disturbances have rarely been studied. The interaction of jack pine budworm defoliation and salvage logging substantially changed landscape pattern in the Pine Barrens. We speculate that interaction between insect defoliation and fire may have significantly shaped the presettlement landscape.

Key words: change detection; clearcut size; fire disturbance; forest; insect defoliation; jack pine budworm (Choristoneura pinus pinus); landscape ecology; pine barrens; Pinus banksiana; remote sensing; salvage logging; spatial pattern; Wisconsin (USA).

Introduction

Habitat loss and fragmentation threaten both biodiversity and ecosystem function (Groombridge 1992, Andrén 1994, Fahrig and Merriam 1994, Fahrig 1997). The effects of landscape patterns on processes and populations have been the subject of many recent studies (e.g., Turner 1989, Kareiva and Wennergren 1995). Disturbances have a strong effect on landscape heterogeneity in unmanaged landscapes (Romme 1982, Tur-

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ner 1987, Turner and Romme 1994). For example, fire has a strong direct effect on landcape pattern, which has been studied in various ecosystems using satellite imagery (Racine et al. 1985, Syrjänen et al. 1994, Turner et al. 1994, Razafimpanilo et al. 1995) and simulated in models of varying realism (Potter and Kessell 1980, Marsden 1983, Baker et al. 1991, Ratz 1995, He and Mladenoff 1999).

Human land use often changes landscape pattern (Mladenoff et al. 1993), both indirectly by altering natural disturbance cycles, for instance by suppressing fire (Baker 1992) and directly, for instance by logging (Ripple et al. 1991, Spies et al. 1994). Effects of logging



Ftg. 1. The Pine Barrens region in northwestern Wisconsin (data courtesy of the ecoregion delineation of the Wisconsin GAP analysis project [Lillesand 1994]).

on landscape pattern have been detected in satellite imagery (Turner et al. 1996, Zheng et al. 1997, Sachs et al. 1998) and forest harvest simulation models demonstrated the severe impact of clearcut patterns on landscape patterns and ecosystem processes (Franklin and Forman 1987, Hansen et al. 1995, Gustafson 1996, Gustafson and Crow 1996).

These studies on the effects of natural and humancaused disturbances have greatly advanced the understanding of the generation of landscape pattern. However, typically only a single disturbance force was examined. For example, forest harvest models commonly assume that harvests are only determined by management decisions and long-term plans. In contrast, multiple, interacting disturbance processes often affect forested ecosystems. For example, in unmanaged forest ecosystems, insect defoliation itself causes tree mortality, but it also increases the likelihood of other types of disturbance (Rykiel et al. 1988). Fires may occur more frequently after insect defoliation because of the increased fuel load (Stocks 1987). In managed forests, widespread salvage logging often follows insect outbreaks. Insect outbreaks change logging schedules and management plans, and salvage cuts can be larger than common clearcuts. Interactions between disturbances are potentially nonlinear, and they might result in landscape patterns that differ from those caused by the disturbance processes individually. This makes it important to study the effect of multiple interacting disturbances on landscape pattern.

The objective of our study was to examine landscape pattern changes due to two interacting disturbances, namely salvage logging following a jack pine budworm outbreak in the northwestern Wisconsin (USA) Pine Barrens region (Fig. 1, Plate 1). Unlike many other forested regions the major conservation concern in the Pine Barrens landscape is not the loss of forest habitat. but rather the increase of forest cover due to fire suppression and afforestation. The Pine Barrens landscape was historically shaped by fire, creating a landscape mosaic with large open patches, savannas, and forested areas on its droughty soils (Murphy 1931, Radeloff et al. 1998), providing favorable conditions for various open habitat species (Niemuth 1995). Current forest management practices decrease the total amount of open-habitat as well as the patch size of openings (Radeloff et al. 1999b). A recent (1990-1995) outbreak of jack pine budworm (Choristoneura pinus pinus) was followed by widespread salvage logging of jack pine (Pinus banksiana) reversing this trend and recreating open habitat.



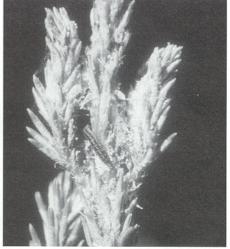


PLATE 1. Left photo, aerial view of some of the salvage cuts that were created in response to the jack pine budworm defoliation. Right photo, feeding jack pine budworm larvae.

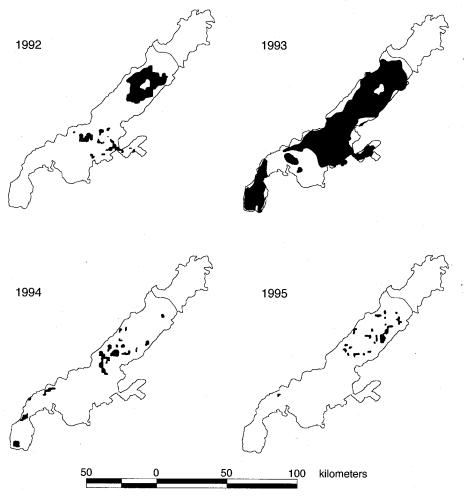


Fig. 2. Defoliation sketch maps for the 1991–1995 outbreak of jack pine budworm. These maps were used to determine the boundary north of which we did not analyze jack pine logging (data courtesy of the Wisconsin Department of Natural Resources).

Various studies have monitored forest defoliation by insects such as spruce budworm (Nelson 1983, Buchheim et al. 1985, Leckie and Ostaff 1988, Franklin and Raske 1994), jack pine budworm (Radeloff et al. 1999a), gypsy moth (Byrne et al. 1987, Muchoney and Haack 1994), or pine bark beetle (Mukai et al. 1987). Spatial models that predict outbreak dynamics of gypsy moth were developed by Hohn et al. (1993), and Zhou and Liebhold (1995). The individual effects of the disturbance agents we examined—logging and insect defoliation—have been studied before. But the impact of the common combination of insect defoliation and salvage logging on landscape pattern has received less attention. We are not aware of previous studies of landscape pattern changes due to insect defoliation and subsequent salvage logging. The recent (1990-1995) outbreak of jack pine budworm in the northwest Wisconsin Pine Barrens provided an opportunity to examine these interactions (Fig. 2). By 1993, the peak year of the outbreak, "over 90% of the jack pine stands in northwestern Wisconsin were defoliated" (Weber 1995b, pg. 19). Furthermore the widespread outbreak of jack pine budworm was accompanied by localized outbreaks of pine tussock moth (Dasychira pinicola), leading to high mortality rates where both species co-occurred (Weber 1995a). The magnitude of the outbreak, both in extent and in mortality rates, made it likely that this outbreak would have particularly strong effects on forest logging, thus driving our decision to study the interaction of insect defoliation and salvage logging in this landscape. In particular, we examined the amount of open habitat created by salvage logging, and the size of the clearcuts. Each of these two aspects was examined (a) for the total Pine Barrens region affected, (b) separately on different soil types because defoliation differs with soil productivity (McCullough et al 1996), and (c) separately for different land owners (e.g., private industrial forests and county forests) that may have different forest management objectives.

The Pine Barrens region

The Pine Barrens region is located on a glacial outwash plain with coarse, sandy soils and covers about

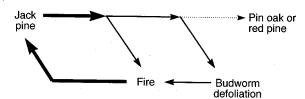


Fig. 3. Disturbance cycles in the Pine Barrens ecosystem before European settlement. Thicker lines indicate higher likelihood of trajectory.

450 000 ha (Fig. 1). Before the arrival of European settlers ~1860, the Pine Barrens landscape was a mosaic of open patches, savannas, and forest stands; dominated by fire-adapted tree species, notably jack pine, red pine (P. resinosa), pin oak (Quercus ellipsoidalis), and burr oak (Q. macrocarpa) (Radeloff et al. 1998). Of these, jack pine is best adapted to a crown-fire disturbance regime due to its serotinous cones. These cones remain closed on the branch until a fire melts the resin and releases the seeds (Johnson and Gutsell 1993). High seed density and exposed mineral soil on burned patches frequently result in dense "dog-haired" stands of jack pine regeneration after a crown fire in a jack pine forest.

Jack pine budworm is the most important insect defoliator of jack pine in our study area (Clancy et al. 1980). Outbreaks appear to be cyclical and occur every 6–10 yr (Volney and McCullough 1994). One result of insect defoliation is an increase in fuel loads (Stocks 1987), and we speculated that the likelihood of a stand-replacing fire may have increased after a jack pine budworm outbreak under pre-European settlement conditions (Fig. 3).

Openings created by stand-replacing fires provided habitat for an array of species in the presettlement land-scape of the Pine Barrens. The patch size of openings is positively correlated with the number of grassland species present, especially for birds. Some species, such as Savannah Sparrow (Passerculus sandwichensis) and Bobolink (Dolichonyx oryzivorus) are found only in patches >1000 ha (Niemuth 1995). Sharp-tailed Grouse (Tympanuchus phasianellus) populations have declined in northwestern Wisconsin due to decreasing amounts of open habitat in this century (Hamerstrom et al. 1952). A Sharp-tailed Grouse population is thought to require open habitat of ≥4000 ha to maintain long-term viability (Temple 1992).

During this century, fire suppression, agriculture, and forestry changed the Pine Barrens landscape and its disturbance regime (Radeloff et al. 1999b). Most forests of the Pine Barrens were logged and farmed after 1860. By 1930 the sandy soils were too depleted of nutrients to sustain farming. Reforestation occurred, either as jack pine plantations or as natural regeneration. At the same time, fire suppression efforts began, initiated by the Wisconsin Department of Conservation in cooperation with the private industrial forests (Vogl

1970). One result of these management practices was a decrease in species adapted to open landscapes created and maintained by wildfire. Large openings resulting from salvage cuts are therefore potentially important for wildlife habitat that would have been previously created by fire.

METHODS

Satellite imagery has been extensively used for land cover change detection (Singh 1989, Hall et al. 1991a, Lambin 1996), because it can cover vast areas repeatedly at relatively low costs. The starting point for our analysis was a species-level forest classification by Wolter et al. (1995) that was based on a Landsat Thematic Mapper (TM) scene from 1987 and multitemporal Landsat Multi-Spectral Scanner (MSS) scenes. The overall accuracy of this classification was 83%. For jack pine, the user's accuracy, or the percentage of the jack pine in the classification which are jack pine on the ground, was 79.5%. The producer's accuracy, the percentage of jack pine on the ground that was identified by the classification, was 91.2% (Wolter et al. 1995). We limited our analysis to the central and southern parts of the Pine Barrens, because defoliation levels in the north were low and had no major effect on jack pine logging. The boundary was determined using jack pine budworm defoliation sketch maps provided by the Wisconsin Department of Natural Resources (DNR) (Fig. 2).

Salvage logging mapping

The mapping of salvage logging combined the species-level forest classification and three subsequent Landsat TM scenes (Fig. 4). The species-level forest classification provided us a map of mature jack pine in 1987. Salvage logging in mature jack pine stands was mapped using three Landsat TM scenes dating from April 1991, August 1993, and October 1995. We derived spectral signatures (the average spectral response of an area measured by the satellite in several wavelength bands) separately for clearcuts and intact forest for each date (Fig. 5). Clearcuts are spectrally distinctive because of their higher spectral response in the near- to mid-infrared part of the spectrum, which is caused by logging slash and exposed mineral soil. Applying a threshold in TM band 5 resulted in maps of clearcuts versus remaining jack pine stands for 1991, 1993, and 1995. No atmospheric correction (Hill et al. 1995) or radiometric rectification (Hall et al. 1991b), of the satellite data was performed, because our approach did not compare the satellite data from different years directly, but rather their classifications. A simple atmospheric correction or radiometric rectification would have applied a linear stretch to the satellite data and thus would not have changed the classification results. The 1991 clearcut map depicts all cuts between 1987 and 1991. These cuts occurred before the jack pine budworm outbreak and offered us a chance to

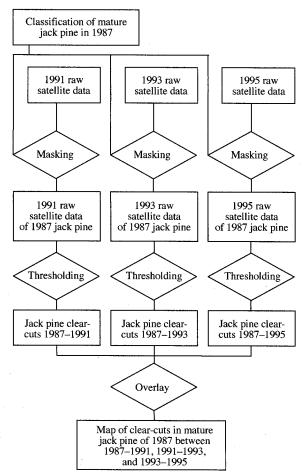


FIG. 4. Satellite data processing steps that combined the species-level forest classification and three subsequent Landsat TM scenes to map salvage logging between 1987 and 1991, 1991 and 1993, and 1993 and 1995.

compare regular logging rates with salvage logging. The 1993 clearcut map covered the first two years of the jack pine budworm outbreak when defoliation was particular strong in the central part of the Pine Barrens. The 1995 clearcut map covered the last two years of the outbreak, when the defoliation was greatest in the southwestern part of the Pine Barrens.

The classification of the 1995 image captured not only clearcuts between 1993 and 1995 but also previous cuts since 1987 because the same mask for mature jack pine in 1987 was applied to all three satellite images. We could thereby identify logical errors, such as areas where a clearcut was mapped for 1991, not mapped for 1993, and mapped again for 1995. Examining these logical errors allowed us to assess the accuracy of the clearcut mapping. Furthermore, we compared the effect of majority filtering (Burrough 1986) on the amount of logical errors. This filter smoothed the classification by assigning the class value of the majority of the pixels in a 3×3 window to the pixel in the center of that window. Some of the errors that the majority filter re-

duced were due to problems of slight misregistration of the images (Townshend et al. 1992) and of mixed pixels along forest edges. The filter can be applied (a) before combining the three classifications, (b) after combining the three classifications, or (c) before and after combining the three classifications. We tested all three approaches and compared the remaining error percentages.

Regeneration mapping

Landscape change in the Pine Barrens encompasses not only the creation of new openings due to salvage logging, but also forest regeneration in older openings. We examined regeneration on areas that were mapped as open in the 1987 classification ("shrub and herb," "grass forb," and "cleared forest" classes). We created a mask from the 1987 classification and applied it to the 1995 imagery so that we could examine regrowth on these areas. Spectral signatures between areas that remained open (especially several wildlife management areas that are managed with prescribed burning), and areas where forest canopy closed during those eight years, are not as distinct as the signatures of clearcuts and forest. Therefore, we performed a supervised classification using 39 areas of known vegetation cover as training areas for a maximum likelihood classification algorithm. An accuracy assessment for the regeneration classification was performed by using 87 randomly selected pixels for which we had information regarding their current vegetation cover.

Calculation of logging rates and landscape pattern

Our satellite data analysis resulted in maps of clearcuts between (a) 1987 and 1991, (b) 1991 and 1993,

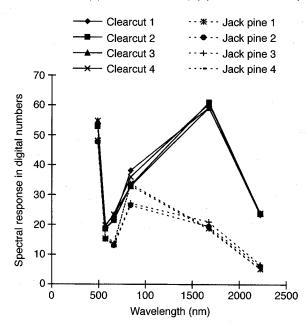


Fig. 5. Spectral signatures of four jack pine stands and four jack pine clearcuts in the Landsat TM image taken in October 1995.

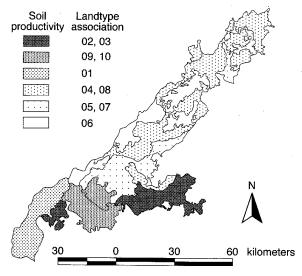


FIG. 6. Landtype association map of the northwestern Wisconsin Pine Barrens region. Soils are ranked according to their productivity, with LTA 06 being lowest (data courtesy of the Wisconsin Department of Natural Resources).

(c) 1993 and 1995, and (d) a map of regeneration on open areas between 1987 and 1995. From these maps we first calculated logging rates and clearcut areas for the Pine Barrens as a whole. Then, we calculated these two parameters separately for different landowners (private industrial forest, county land, state land, national forest, and other private holdings). A digital map coverage containing land ownership information was provided by the Wisconsin DNR. Private industrial forest holdings were added as described by Mladenoff et al. (1995). Next, we calculated the logging rates and clearcut areas separately for the different ecological units (Landtype Associations, LTAs) within the Pine Barrens (Fig. 6). The delineation of LTAs is mainly based on soil types and has been completed for northern Wisconsin by the Wisconsin DNR.

The size of open patches was calculated (a) for each

of the three clearcut maps, (b) for clearcuts during the outbreak (1991–1995), and (c) for the combination of open patches remaining in the regeneration classification and all clearcuts.

We also examined neighborhood associations of clearcuts to identify if they were placed randomly within the area of mature jack pine or if new clearcuts were more likely to occur next to previous cuts. The landscape index used for this analysis was the electivity index (Jacobs 1974, Jenkins 1979) as used by Pastor and Broschart (1990) and Mladenoff et al. (1993). The electivity index ranges from negative infinity for two classes that are never associated with each other to positive infinity for two classes that are always associated with each other.

RESULTS

Extent of salvage cuts

The estimated amount of jack pine logging between 1987 and 1995 depends slightly on the filtering approach applied to the classification (Table 1). When no filter is applied, ~10.6% of the area of mature jack pine in 1987 is classified in the three subsequent clearcut maps in a logically inconsistent manner. An example of these errors is Class 7, which comprises areas mapped as being cut in the 1993 classification but classified as standing timber for 1995. Some of these errors (Classes 5 and 6) could be due to regeneration. Regeneration on clearcuts from 1988 may experience crown closure by 1995, especially where an oak understory remained on a site (V. C. Radeloff, personal observation). We chose a conservative approach and regarded classes 5 and 6 as falsely mapped. By applying a majority filter before and after combining the three classifications, the logical errors were reduced to 4.5%; however, only 88.4% of the original area of mature jack pine remained for further analysis. We chose the approach of applying the majority filter once to each clearcut classification before combining all three.

Table 1. Area (ha) classified as clearcuts and remaining mature jack pine during the outbreak (+, yes; -, no). Results are shown for different majority filtering approaches.

Class number	Jack pine _ in 1987	Cut by			Majority filter before com- bining the	3 2	Majority filter before and after combining the	
		1991	1993	1995	No filter	classifications	classifications	classifications
1	+	_		_	25 202	27 711	23 995	26 553
2	+	+	+	+	5 593	4 079	4 824	3 929
3	+	_	+	+	4816	4 170	4 465	4074
4	+	-	_	+	9 5 2 4	8 451	8 665	8 060
5	+	+	_	_	1 302	755	895	547
6	+	+	+	_	549	202	339	152
7	+	_	+	<u> </u>	1 603	731	1 075	571
8	+	+	_	+	1 907	902	1 321	739
Total area logically correct:				45 134	44 412	41 948	42 616	
Total area logically in error:				5 361	2 591	3 630	2 008	
Percentage logical error:				10.6	5.5	8.0	4.5	
Percentage of area remaining after filtering:				100.0	93.1	90.3	88.4	

Note: Classes 1-4 are assumed to be logically correct; classes 5-8 are assumed to be logically incorrect.

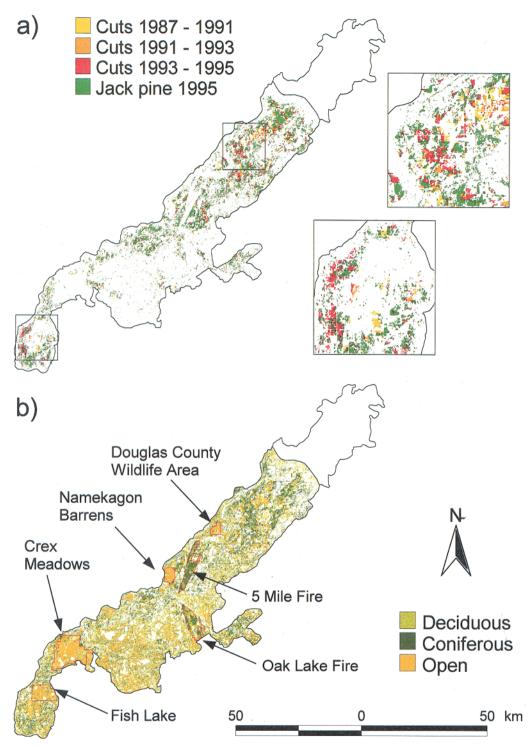


Fig. 7. (a) Mature jack pine in 1987 classified into clearcuts during 1987–1991, 1991–1993, and 1993–1995 and remaining stands of jack pine in 1995 (two areas with particularly high logging rates are magnified so that individual cuts are visible). (b) Succession of open areas between 1987 and 1995; restoration areas and sites of recent major fires are outlined in red.

This approach reduces the logical errors to 5.5%, while removing only 6.9% of the area of interest (Table 1).

The percentages of mature jack pine cut after 1987 and before 1995 revealed the extent of the budworm

defoliation and the subsequent salvage logging. In the period before the jack pine budworm outbreak (1987–1991), 8.7% of the mature jack pine was cut. This corresponds to an annual logging rate of 2.2% or a

rotation length of 46 yr, a common management schedule in our study region. Between 1991 and 1993, 6.5% of the mature timber in 1987 was cut. This translates into an annual logging rate of 3.3%. The last phase of the outbreak experienced a total cut of 13.6% and an annual logging rate of 6.8%, about three times higher than before the outbreak.

Spatial distribution of salvage cuts

The spatial distribution of salvage cuts was not uniform across the Pine Barrens (Fig. 7a). Salvage cuts were clustered in the central and in the southwestern portions of the Pine Barrens. Therefore, we examined logging rates separately for different LTAs. Mature jack pine is common only in four LTAs in the Pine Barrens, and results are presented only for those areas (Fig. 8). The LTAs are ranked according to their soil productivity, with LTA 01 being the most productive. The majority of all jack pine in the Pine Barrens occurs in LTAs 04 and 06 and these also have the highest percentage of jack pine out of all land cover classes. Overall logging was highest in LTA 06 where 40.9% of all mature jack pine in 1987 was removed by 1995 (Fig. 8). This LTA also experienced the highest logging rates previous to the outbreak (2.6% annually) and during the first phase of the outbreak (5.7% annually). The highest logging rate during the second phase of the outbreak occurred in LTA 01 (11.7% annually).

The majority of the 45 982 ha of mature jack pine in 1987 was owned by the counties (16 825 ha) and by nonindustrial private landowners (18 460 ha) (Fig. 8). Private industrial forest holdings exhibit the highest percentage of mature jack pine compared to other land cover classes (25.6%). Private industrial forest and county forest land experienced the heaviest overall logging, whereas nonindustrial private land and national forest holdings were least logged (Fig. 9). Highest annual logging before the outbreak occurred on private industrial forest holdings (3.1% annually). National forest land experienced the lowest logging previous to 1991 (1.1% annually, Fig. 10).

When examining differences in logging rates of various ownerships and soil types, it is important to note that not all landowners have holdings in all LTAs. This limits our ability to separate the effects of soil productivity and land ownership on logging rates. However, private industrial forest land in LTA 06 experienced the highest overall logging rate (55%) and the highest logging rate previous to 1991 (4.3% annually). The highest logging rate during the outbreak occurred between 1993 and 1995 in the county forests on LTA 01 (16.5% annually).

The suitability of the Pine Barrens for open-habitat species depends not only on the abundance of open areas, but also on their spatial pattern, especially the size of open-habitat patches. The size of clearcuts increased during the budworm outbreak and they were largest between 1993 and 1995 (Fig. 11). Before the

outbreak, only 28% of the area of all clearcuts occurred in patches >20 ha and only 8.5% in patches >50 ha. Between 1993 and 1995, these percentages increased to 51% and 25% respectively.

The salvage logging map indicated that new cuts were often placed adjacent to previous cuts. This impression was confirmed by calculating the electivity between cuts, remaining jack pine, and other cover types (Table 2). A high electivity value indicates that two land cover classes commonly occur next to each other. The highest electivity value occurred between cuts from 1987 to 1991 and cuts from 1991 to 1993, and the second highest value between cuts from 1991 and 1993 and cuts from 1993 and 1995, indicating that new clearcuts were often extensions of previous clearcuts.

An assessment of open habitat in 1995 requires the examination not only of clearcuts made between 1987 and 1995, but also the fate of open areas in 1987, which might have experienced regeneration by 1995. The limited number of classes (deciduous regrowth, coniferous regrowth, remaining open habitat) for our regeneration classification ensured a high overall classification accuracy of 93% (Table 3). Most regeneration occurred only in small patches, but several large patches stand out (Fig. 7b). Two large patches of regeneration are located on the sites of previous fires. The "5 Mile Fire" occurred in 1977. The site was not regenerated by 1987; however, by 1995 the area was mostly covered by jack pine. The "Oak Lake Fire" occurred in 1980; this site experienced regeneration of both coniferous and deciduous species between 1987 and 1995. The large patches that remained open between 1987 and 1995 are the five wildlife management areas (Fish Lake, Crex. Meadows, Namekagon Barrens, Douglas County Wildlife Area, and Moquah Barrens) which are maintained as open habitat by applying prescribed burning every 5-10 years.

When we count the number of large open patches in the Pine Barrens in 1995, most of them are areas that remained open between 1987 and 1995 (Table 4). There are few large salvage cuts, but they created large open patches by expanding previous smaller openings. This effect is apparent in the map of open patches >100 ha (Fig. 12).

DISCUSSION

Satellite data analysis

The satellite data analysis detected clearcuts with high accuracy (Table 1), but did not provide information on what caused these clearcuts. Some of the logging in mature jack pine between 1991 to 1995 may have not been motivated by insect defoliation. However, the great majority of the logging was directly related to jack pine budworm (S. Weber, personal communication). Most of the salvage logging that we detected occurred in areas that experience multiple years of budworm defoliation (Fig. 2). The extent of the out-

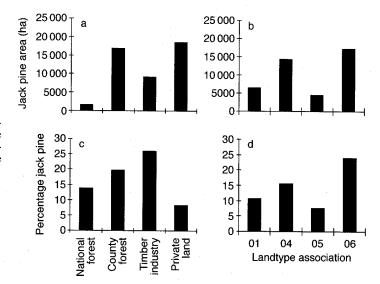


FIG. 8. Jack pine area in 1987 (a) for different land owners and (b) for different landtype associations. Percentage of jack pine (c) for different land owners and (d) for different landtype associations.

break (Fig. 2), and the high levels of mortality (Weber 1995b), led foresters to focus their logging operations on defoliated stands. Jack pine pulpwood is sold by weight; jack pine killed by insect defoliation soon loses value, thus making rapid logging an economic necessity. Furthermore, dead jack pine stands increase the risk of forest fires, thus making salvage logging also important for forest fire prevention.

We limited our satellite data analysis to the detection of changes that can be monitored with high reliability. Clearcuts in jack pine are spectrally distinct compared

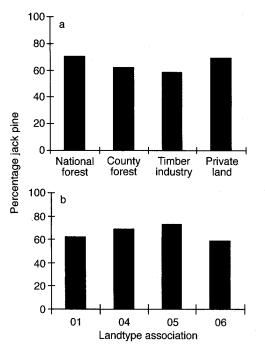


Fig. 9. Percentage of mature jack pine in 1987 that remained jack pine in the 1995 classification (a) for different land owners and (b) for different landtype associations.

to mature jack pine stands, and can thus be classified with high accuracy. Clearcuts in other cover types such as aspen, which are not as different from their previous stands and which regenerate faster, are more difficult to classify. By analyzing logging only in mature jack pine, we potentially missed logging in other cover

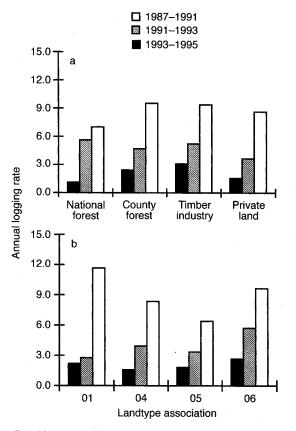


Fig. 10. Annual logging rates (a) for different landowners and (b) for different landtype associations.

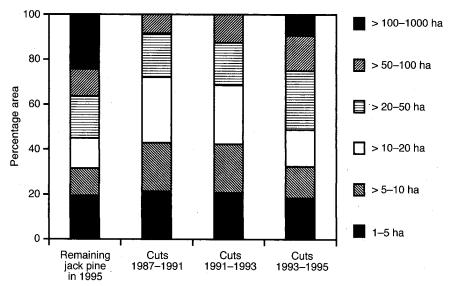


Fig. 11. Percentage of the total area of all patches (>1 ha) separated into different patch size classes.

types. However, forest managers focused their logging on jack pine during the outbreak (S. Weber, personal communication). Furthermore, clearcut patches in other cover types tends to be smaller in size, and thus less important for the creation of large open patches. Our objective was to examine the effect of interacting disturbances, namely jack pine budworm defoliation and logging, on the landscape pattern, and this drove the decision to look only at the logging of mature jack pine, the landscape dominant.

The use of a threshold for Landsat TM band 5 proved to be a reliable method for distinguishing clearcuts from remaining forest. The advantage of this approach was that it was straightforward to apply, and that atmospheric disturbances, such as haze, which particularly affected Landsat TM band 1 and 2 in the 1991 image, did not affect our results. The classification of jack pine salvage cuts was highly accurate (Table 1) which made subsequent clearcut patch size calculations reliable.

"Open habitat" encompasses a variety of land cover classes (e.g., marsh, pasture, clearcut). The habitat requirements for species that depend on large open areas differ and not all of these openings provide suitable

TABLE 2. Electivity between clearcuts, remaining jack pine, and other land cover classes. Higher values indicate higher likelihood that the areas of two classes neighbor each other.

		Remain- ing jack			
Land cover class	1987– 1991	1991– 1993	1993- 1995	pine in 1995	
Other land cover Cuts 1987–1991 Cuts 1991–1993 Cuts 1993–1995	0.09	-0.31 2.79	-0.18 0.80 2.51	0.41 1.30 1.01 2.14	

habitat for all species. The satellite data provided insufficient information for a detailed classification of open habitats. However, it is important to note that the generic class "open habitat" might not be suitable to assess habitat availability for all species adapted to open patches created by fire at presettlement times.

We did not compare overall changes in open habitat between 1987 and 1995. The separation of open habitat depends on the cutoff point along the gradient between open and forested areas. Comparing classified open areas between 1987 and 1995 was not possible because we could not obtain ground-truth data for 1987. Furthermore, the 1987 image was taken in June and the 1995 image in October. Phenological differences (i.e., senescent leaves) would have introduced potential errors.

Regeneration of open areas is a more gradual process than clearcutting and thus more difficult to monitor with satellite imagery (Jakubauskas et al. 1990, Hall et al. 1991a, Fiorella and Ripple 1993, Jakubauskas 1996). We monitored regeneration only for the endpoint of our time series (1995) and we classified only deciduous and coniferous regeneration, not individual tree species. Most classification errors occurred between the two general forest types and between open areas and deciduous regrowth. This was expected due to mixed stands and the gradient between open habitat and deciduous regeneration. By classifying only two broad forest types, we achieved a high classification accuracy (Table 3). This accuracy enabled us to examine landscape pattern in 1995.

Salvage logging rates

The calculation of logging rates before and during the budworm outbreak shows a strong increase during the outbreak due to salvage logging operations (Fig.

TABLE 3. Accuracy assessment for the classification of forest regeneration by 1995 on areas classified as open in the 1987 satellite classification. Comparisons were made of classification results and actual ground cover of 87 randomly selected pixels.

	Land cover type in the regeneration classification					
Land cover type in the ground truth data	Deciduous regrowth	Coniferous regrowth	Remaining open habitat	Row total	User's accuracy (%)	
Deciduous regrowth Coniferous regrowth Remaining open habitat	26 2 2	2 23 0	0 0 32	28 25 34	92.86 92.00 94.12	
Total	30	25	32	87		
Producer's accuracy (%): Overall accuracy (%):	86.67 93.10	92.00	100.00			

10). Out of the different LTAs, LTA 06, with the poorest soils, experienced the highest overall logging rate and the highest salvage logging rate. Jack pine budworm outbreaks in the Pine Barrens occur more frequently on infertile soils (Clancy et al. 1980, Volney and McCullough 1994). Droughts can trigger insect outbreaks (Mattson and Haack 1987) and the low waterholding capacity of LTA 06 may have contributed to the early start of the outbreak in this area. The logging rate previous to the jack pine budworm outbreak was also highest for LTA 06, which was expected because jack pine is managed in shorter rotation cycles on poorer soils. Differences in soil quality did not explain differences in logging rates among the three other LTAs (01, 04, and 05). During the second phase of the outbreak, LTA 01 experienced the highest annual logging rate. The jack pine budworm outbreak peaked on the LTA 04 and 06 in 1991, but did not reach its maximum on LTA 01 until 1994 explaining why salvage cuts occurred later on this LTA.

The ownership pattern in the Pine Barrens is not random with respect to soil quality. For instance, private industrial forest holdings tend to occur on poorer sites because these were the most common "tax delinquent" lands abandoned during the 1930s. These were often subsequently purchased in large blocks by the forest industry. Therefore, ownership pattern and environmental factors have to be examined simultaneously to identify whether both or only one of them best explain logging rates. The highest logging rates pre-

TABLE 4. Number of open-habitat patches in various size classes.

Area (ha)	Openings remaining from 1987	Cuts 1991–1995	Openings as of 1995
>100-250	51	9	54
>250-500	21	1	23
>500~750	7	0	8
>750-1000	2	0	3
>1000-1500	3	0	5
>1500-2000	2	0	4
>2000-4000	2	0	3
>4000	2	0	2

vious to the outbreak and during the outbreak occurred on the private industrial forest holdings on the poorest sites (LTA 06). These logging rates are much higher than private industrial forest logging rates on better sites (LTA 04), and they are higher than those of other land owners on the poorest sites. Also, the logging rates on private lands are highest on the poorest sites. However, the logging rates on county forest land cannot be explained by soil quality. One possible explanation is that differences in forest management between counties are causing the apparent differences in logging rates (e.g., the very high logging rate in LTA 01 between 1993 and 1995). The lack of private industrial forest land or national forest on LTA 01 and 05 limited our ability to separate the relative importance of land ownership and soil quality on logging rates.

Salvage logging patterns

The size class analysis for clearcuts before and during the budworm outbreak indicates a strong increase in clearcut size during the outbreak (Fig. 11). This

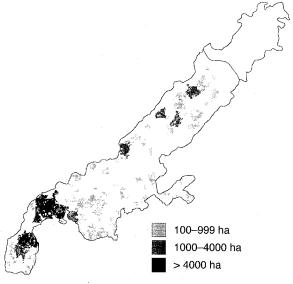


Fig. 12. Large open patches in 1995, classified according to their size.

increase began between 1991 and 1993, when the relative area of cuts between 10 and 20 ha decreased and cuts between 20 and 100 ha became more dominant. This trend continued between 1993 and 1995 and was also exaggerated by an increase of very large clearcuts (>100 ha).

The increase in clearcut size during the budworm outbreak (Fig. 11) and the fact that many of these clearcuts occurred next to previous openings (Table 3) resulted in an increase of large, open areas, especially in the central part of the Pine Barrens (Table 4, Fig. 12). Some of these openings were surveyed by the Wisconsin Sharp-tailed Grouse Society. In the spring of 1997, 213 males were counted at leks, the dancing grounds where Sharp-tailed Grouse gather and mate during spring (N. Niemuth, unpublished data). To put this number in perspective, it is noteworthy that it is higher than the total of all males counted on the wildlife management areas in the Barrens (198 total; 117 at Crex Meadows, 55 at the Namekagon Barrens, 9 at the Douglas County Wildlife Area, and 17 at the Moquah Barrens). There are no survey results for other species available, but the Sharp-tailed Grouse survey indicates that the salvage cuts are providing habitat for species adapted to openings previously caused by fire. More surveys are needed to determine to what extent salvage cuts are suitable habitat for other species adapted to openings that would have been typically caused by fire.

When calculating clearcut patch sizes, we assumed that only pixels that have at least one common edge are neighbors. Furthermore, the resolution of the satellite data $(28.5 \times 28.5 \text{ m})$ determined that two patches were mapped as separated when a strip >28.5 m wide ran between them. The definition of neighborhood is partly dependent on the species of interest and on its dispersal capabilities. Our definitions represent a conservative approach. However, we are aware that many bird species might perceive several medium sized open patches which we mapped as separated, as one large, open area.

Salvage logging versus wildfire

Salvage logging has largely replaced fire in the disturbance cycle of the Pine Barrens ecosystem as a followup to jack pine budworm defoliation (Fig. 3). This has many consequences on different scales. Fire has unique effects on forest floor nutrient dynamics (Weber 1987, Stergas and Adams 1989). Microbial diversity differs in harvested jack pine stands when compared with wildfires (Staddon et al. 1998), and carabid assemblages vary with disturbance type, and regeneration technique employed (Beaudry et al. 1997). Herbaceous prairie species depend on fire to maintain their competitive advantage over other herbaceous species (Leach and Givnish 1996, Whittle et al. 1997). Also, fires leave abundant coarse woody debris and snags, which are valuable, for instance, for cavity nesters, but most logging does not (Niemuth 1998), and decay rates

of coarse woody debris are higher on harvested sites (Wei et al. 1997). We did not compare these differences in detail, but further research is required to understand the extent to which clearcuts can replace wildfires to maintain open habitat in managed landscapes (Hunter 1993, Attiwill 1994, Schulte and Niemi 1998).

In the context of our study, the more general question was whether salvage logging could be a suitable substitute for fire in its effect on open-habitat patterns on the landscapes. This question cannot be fully answered, because of the lack of data to analyze landscape pattern at presettlement times with the required spatial resolution. However, we speculate that fire and insect defoliation may have interacted to shape landscape patterns of the presettlement landscape (Fig. 3). Salvage cuts are similar to fire in that they may both occur subsequent to jack pine budworm attacks, and both remove dead jack pine. However, fire affects not only mature jack pine stands, but can spread over very large areas. In the Pine Barrens, the three largest recorded fires in recent times covered 7150, 5450, and 4700 ha (West Marshland fire in 1959, 5 Mile Fire in 1977, and Oak Lake Fire in 1980). Salvage logging between 1991 and 1995 did not create openings of this magnitude.

Jack pine budworm outbreaks in the Pine Barrens occur in cycles of 6-10 yr (Volney and McCullough 1994). We did not examine landscape pattern changes due to previous outbreaks, but it is likely that the most recent outbreak had particularly strong effects. The outbreak examined in our study extended over 400 000 ha, only 50 000 ha in the northeastern Pine Barrens experienced no defoliation. A large age cohort of jack pine originating from the reforestation efforts in the 1930s had reached its peak susceptibility to jack pine budworm attacks in the 1980s. The landscape pattern changes described here probably represent the maximum changes that can be expected in the current managed landscape. However, the area dominated by jack pine was higher at presettlement times than today (Radeloff et al. 1999b). Jack pine budworm outbreaks followed by wildfires may have had even stronger impact on landscape structure at that time.

Conclusion

The 1991–1995 jack pine budworm outbreak in the northwestern Wisconsin Pine Barrens was followed by salvage logging on 27% (12 700 ha) of the area of mature jack pine. This logging altered the landscape pattern, particularly in the central Pine Barrens. Logging rates were highest on poorest sites and on private, industrial forest holdings. Salvage cuts were larger than preoutbreak clearcuts and they tended to be located next to previous openings, thus recreating large (100–1000 ha) open-habitat patches. Such patches provide habitat for open-habitat species. For instance, survey data indicated that the large salvage cuts harbored substantial Sharp-tailed Grouse populations.

The replacement of fires with clearcuts is often con-

sidered when managing fire-adapted ecosystems (e.g., Hunter 1993). Fire was the dominant disturbance in the Pine Barrens ecosystem before European settlement. Salvage cuts resemble fire in that they are considerably larger than regular clearcuts, and in that they follow jack pine budworm defoliation. However, salvage cuts are limited to mature jack pine stands, whereas fires can spread into stands of younger jack pine and other tree species. Salvage cuts alone did not create very large open patches (>4000 ha) equal to those that were created by fires in the Pine Barrens during this century. Furthermore, logging differs from fire, for instance, in its effects on soil nutrients (Weber 1987), carabid assemblages (Beaudry et al. 1997), and surface vegetation (Whittle et al. 1997). We do not suggest that salvage logging can fully replace fire, but we suggest that its effect on landscape pattern might be comparable in that it provides habitat attributes important to a large group of vertebrates.

Understanding the interaction of disturbances is crucial when ecosystem management is attempted. We examined landscape changes caused by salvage logging after a jack pine budworm outbreak. Insect defoliation and fire are major disturbances in many forested ecosystems. Salvage logging is a common management response to current defoliation events. Our results indicate that salvage cuts can substantially alter the landscape pattern, because of their larger size, and because of their proximity to previous openings. Whether or not these effects are desirable will depend on the ecosystem under consideration, and especially how these effects resemble the patch size distribution caused by natural disturbance regimes.

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LITERATURE CITED

- Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355-366.
- Attiwill, P. M. 1994. The disturbance of forest ecosystems: the ecological basis for conservative management. Forest Ecology and Management **63**:247–300.
- Baker, W. L. 1992. Effects of settlement and fire suppression on landscape structure. Ecology 73:1879–1887.
- Baker, W. L., S. L. Egbert, and G. F. Frazier. 1991. A spatial model for studying the effects of landscapes subject to large disturbances. Ecological Modelling 56:109–125.
- Beaudry, S., L. C. Duchesne, and B. Côté. 1997. Short-term effects of three forestry practics on carabid assemblages in

- a jack pine forest. Canadian Journal of Forest Research 27: 2065–2071.
- Buchheim, M. P., A. L. Maclean, and T. M. Lillesand. 1985. Forest cover type mapping and spruce budworm defoliation detection using simulated SPOT imagery. Photogrammetric Engineering & Remote Sensing 51:1115-1122.
- Burrough, P. A. 1986. Principles of geographical information systems for land resources assessment. Clarendon. Oxford, New York, USA.
- Byrne, S. V., M. M. Wehrle, M. A. Keller, and J. F. Reynolds. 1987. Impact of gypsy moth infestation on forest succession in the North Carolina piedmont: a simulation study. Ecological Modelling 35:63–84.
- Clancy, K. M., R. L. Giese, and D. M. Benjamin. 1980. Predicting jack-pine budworm infestations in northwestern Wisconsin. Environmental Entomology 9:743-751.
- Fahrig, L. 1997. Relative effects of habitat loss and fragmentation on population extinction. Journal of Wildlife Management 61:603-610.
- Fahrig, L., and G. Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8:50-59.
- Fiorella, M., and W. J. Ripple. 1993. Analysis of conifer forest regeneration using Landsat Thematic Mapper data. Photogrammetric Engineering & Remote Sensing 59:1383– 1388.
- Franklin, J. F., and R. T. T. Forman. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecology 1:5–18.
- Franklin, S. E., and A. G. Raske. 1994. Satellite remote sensing of spruce budworm forest defoliation in western Newfoundland. Canadian Journal of Remote Sensing 20: 37–48.
- Groombridge, B., editor. 1992. Global biodiversity: state of the earth's living resources. Chapman and Hall, New York, New York, USA.
- Gustafson, E. J. 1996. Expanding the scale of forest management: allocating timber harvest in space and time. Forest Ecology and Management 87:27–39.
- Gustafson, E. J., and T. R. Crow. 1996. Simulating the effects of alternative forest management strategies on landscape structure. Journal of Environmental Management 46:77–94
- Hall, F. G., D. B. Botkin, D. E. Strebel, K. L. Woods, and S. J. Goetz. 1991a. Large-scale patterns of forest succession as determined by remote sensing. Ecology 72:628-640.
- Hall, F. G., D. E. Strebel, J. E. Nickeson, and S. J. Goetz. 1991b. Radiometric Rectification: Toward a common radiometric response among multidate, multisensor images. Remote Sensing of Environment 35:11-27.
- Hamerstrom, F., F. Hamerstrom, and D. E. Matson. 1952. Sharptails into the shadows. Wisconsin Conservation Department. Madison, Wisconsin, USA.
- Hansen, A. J., S. L. Garman, J. F. Weigand, D. L. Urban, W. C. McComb, and M. G. Raphael. 1995. Alternative silvicultural regimes in the Pacific Northwest: simulations of ecological and economic effects. Ecological Applications 5:535-554.
- He, H. S., and D. J. Mladenoff. 1999. Spatially explicit and stochastic simulation of forest landscape fire disturbance and succession. Ecology 80:81–99.
- Hill, J., W. Mehl, and V. C. Radeloff. 1995. Improved forest mapping by combining corrections of atmospheric and topographic effects in Landsat TM imagery. Pages 143–151 in J. Askne, editor. Sensors and environmental applications of remote sensing. Balkema, Rotterdam, The Netherlands.
- Hohn, M. E., A. M. Liebhold, and L. S. Gribko. 1993. Geostatistical model for forecasting spatial dynamics of defoliation caused by the gypsy moth (Lepidoptera: Lymantriidae). Environmental Entomology 22:1066–1075.
- Hunter, M. L. 1993. Natural fire regimes as spatial models

- for managing boreal forests. Biological Conservation **65**: 115–120.
- Jacobs, J. 1974. Quantitative measurement of food selection: a modification of the forage ratio and Ivlev's electivity index. Oecologia 14:413-417.
- Jakubauskas, M. E., K. P. Lulla, and P. W. Muasel. 1990. Assessment of vegetation change in a fire-altered forest landscape. Photogrammetric Engineering & Remote Sensing 56:371-377.
- Jakubauskas, M. E. 1996. Thematic Mapper characterization of lodgepole pine seral stages in Yellowstone National Park, USA. Remote Sensing of Environment 56:118-132.
- Jenkins, S. H. 1979. Seasonal and year to year differences in food selection by beavers. Oecologia 44:112-116.
- Johnson, E. A., and S. L. Gutsell. 1993. Heat budget and fire behaviour associated with the opening of serotinous cones in two *Pinus* species. Journal of Vegetation Science 4:745-750.
- Kareiva, P., and U. Wennegren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373:299-302.
- Lambin, E. F. 1996. Change detection at multiple temporal scales: seasonal and annual variations in landscape variables. Photogrammetric Engineering & Remote Sensing 62: 931–938.
- Leach, M. K., and T. J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. Science 273: 1555-1558.
- Leckie, D. G., and D. G. Ostaff. 1988. Classification of airborne multispectral scanner data for mapping current defoliation caused by the spruce budworm. Forest Science 34:259-275.
- Lillesand, T. M. 1994. Strategies for improving the accuracy and specificity of large-area, satellite-based land cover inventories. Pages 23–30 in Proceedings, Symposium on Mapping and Geographic Information Systems (May 31 1994–June 3 1994). Center for Remote Sensing and Mapping Science. Athens, Georgia, USA.
- Marsden, M. A. 1983. Modeling the effect of wildfire frequency on forest structure and succession in the northern Rocky Mountains. Journal of Environmental Management 16:45-62.
- Mattson, W. J., and R. A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. BioScience 37:110–118.
- McCullough, D. G., L. D. Marshal, L. J. Buss, and J. Kouki. 1996. Relating jack pine budworm damage to stand inventory variables in northern Michigan. Canadian Journal of Forest Research 26:2180–2190.
- Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern great lakes region. Conservation Biology 9:279–294.
- Mladenoff, D. J., M. A. White, J. Pastor, and T. R. Crow. 1993. Comparing spatial pattern in unaltered old-growth and disturbed forest landscapes. Ecological Applications 3: 294–306.
- Muchoney, D. M., and B. N. Haack. 1994. Change detection for monitoring forest defoliation. Photogrammetric Engineering & Remote Sensing 60:1243-1251.
- Mukai, Y., T. Sugimura, H. Watanabe, and K. Wakamori. 1987. Extraction of areas infested by pine bark beetle using Landsat MSS data. Photogrammetric Engineering & Remote Sensing 53:77-81.
- Murphy, R. E. 1931. Geography of northwestern pine barrens of Wisconsin. Transactions of the Wisconsin Academy of Science, Arts and Letters **26**:96–120.
- Nelson, R. F. 1983. Detecting forest canopy change due to insect activity using Landsat MSS. Photogrammetric Engineering & Remote Sensing 49:1303-1314.

- Niemuth, N. D. 1995. Avian ecology in Wisconsin pine barrens. Dissertation. University of Wyoming, Laramie, Wyoming. USA.
- Niemuth, N. D., and M. S. Boyce. 1998. Disturbance in Wisconsin pine barrens: implications for management. Transaction of the Wisconsin Academy of Sciences, Arts and Letters 86:167–176.
- Pastor, J., and M. Broschart. 1990. The spatial pattern of a northern conifer-hardwood landscape. Landscape Ecology 4:55-68.
- Potter, M. W., and S. R. Kessell. 1980. Predicting mosaics and wildlife diversity resulting from fire disturbance to a forest ecosystem. Environmental Management 4:247–254.
- Racine, C. H., J. G. Dennis, and W. A. Patterson. 1985. Tundra fire regimes in the Novak River Watershed, Alaska (USA): 1956–1983. Arctic 38:194–200.
- Radeloff, V. C., D. J. Mladenoff, and M. S. Boyce. 1999a. Detecting jack pine budworm defoliation using spectral mixture analysis: separating effects from determinants. Remote Sensing of Environment 69:156–169.
- Radeloff, V. C., D. J. Mladenoff, H. S. He, and M. S. Boyce. 1999b. Forest landscape change: The northwest Wisconsin Pine Barrens before European settlement and today. Canadian Journal of Forest Research, in press.
- Radeloff, V. C., D. J. Mladenoff, K. L. Manies, and M. S. Boyce. 1998. Analyzing forest landscape restoration potential: Pre-settlement and current distribution of oak in the northwest Wisconsin Pine Barrens. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 86:189–205.
- Ratz, A. 1995. Long-term spatial patterns created by fire: a model oriented towards boreal forests. International Journal of Wildland Fire 5:25-34.
- Razafimpanilo, H., R. Frouin, S. F. Iacobellis, and R. C. J. Somerville. 1995. Methodology for estimating burned area from AVHRR reflectance data. Remote Sensing of Environment 54:273–289.
- Ripple, W. J., G. A. Bradshaw, and T. A. Spies. 1991. Measuring forest landscape patterns in the Cascade range of Oregon, USA. Biological Conservation 57:73-88.
- Romme, W. H. 1982. Fire and landscape diversity in subalpine forests of Yellowstone National Park. Ecological Monographs **52**:199–221.
- Rykiel, E. J., R. N. Coulson, P. J. H. Sharpe, T. F. H. Allen, and R. O. Flamm. 1988. Disturbance propagation by bark beetles as an episodic landscape phenomena. Landscape Ecology 1:129–139.
- Sachs, D. L., P. Sollins, and W. B. Cohen. 1998. Detecting landscape changes in the interior of British Columbia from 1975–1992 using satellite imagery. Canadian Journal of Forest Research 28:23–36.
- Schulte, L. A., and G. J. Niemi. 1998. Bird communities of early successional burned and logged forest. Journal of Wildlife Management **62**:1418–1429.
- Singh, A. 1989. Digital change detection techniques using remotely-sensed data. International Journal of Remote Sensing 10:989-1003.
- Spies, T. A., W. J. Ripple, and G. A. Bradshaw. 1994. Dynamics and pattern of a managed coniferous forest landscape in Oregon. Ecological Applications 4:555-568.
- Staddon, W. J., L. C. Duchesne, and J. T. Trevors. 1998. Impact of clear-cutting and prescribed burning on microbial diversity and community structure in a Jack pine (*Pinus banksiana* Lamb.) clear-cut using Biolog Gram-negative microplates. World Journal of Microbiology & Biotechnology 14:119–123.
- Stergas, R. L., and K. B. Adams. 1989. Jack pine barrens in northeastern New York: postfire macronutrient concentrations, heat content, and understory biomass. Canadian Journal of Forest Research 19:904–910.
- Stocks, B. J. 1987. Fire potential in the spruce budworm-

- damaged forests of Ontario. The Forestry Chronicle 63:8-14.
- Syrjänen, K., R. Kalliola, A. Puolasmaa, and J. Mattson. 1994. Landscape structure and forest dynamics in subcontinental Russian european taiga. Annales Zoologici Fennici 31:19-34.
- Temple, S. A. 1992. Population viability analysis of a sharp-tailed grouse metapopulation in Wisconsin. Pages 750–758 in D. R. McCullough and R. H. Barrett, editors. Wildlife 2001: populations. Elsevier Applied Science. London UK.
- Townshend, J. R., C. O. Justice, C. Gurney, and J. McManus. 1992. The impact of misregistration on change detection. IEEE Transactions on Geoscience and Remote Sensing 30: 1054–1060.
- Turner, M. G. 1987. Landscape heterogeneity and disturbance. Springer-Verlag, New York, New York, USA.
- Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics. **20**:171–197.
- Turner, M. G., W. W. Hargrove, R. H. Gardner, and W. H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone National Park. Journal of Vegetation Science 5:731-742.
- Turner, M. G., and W. H. Romme. 1994. Landscape dynamics in crown-fire ecosystems. Landscape Ecology 9:59-77.
- Turner, M. G., D. N. Wear, and R. O. Flamm. 1996. Land ownership and land-cover change in the southern Appalachian Highlands and the Olympic Peninsula. Ecological Applications 6:1150-1172.
- Vogl, R. J. 1970. Fire and the northern Wisconsin pine barrens. Pages 175–209 in Proceedings of the 10th Annual Tall Timbers Fire Ecology. Los Angelos, California, USA.
- Volney, W. J. A., and D. G. McCullough. 1994. Jack pine budworm population behaviour in northwestern Wisconsin. Canadian Journal of Forest Research 24:502-510.
- Weber, M. G. 1987. Decomposition, litter fall, and forest

- floor nutrient dynamics in relation to fire in eastern Ontario jack pine ecosystems. Canadian Journal of Forest Research 17:1496–1506.
- Weber, S. D. 1995a. Jack pine budworm and the Wisconsin Pine Barrens. Page 8 in E. A. Borgerding, G. A. Bartelt, and W. M. McCown, editors. The future of pine barrens in northwest Wisconsin: a workshop summary, Solon Springs, Wisconsin, September 21–23 1993. Wisconsin Department of Natural Resources. Madison, Wisconsin, USA.
- Weber, S. D. 1995b. Integrating budworm into jack pine silviculture in northwest Wisconsin. Pages 19-24 in W. J. A. Volney, V. G. Nealis, G. M. Howse, A. R. Westwood, D. G. McCullough, and B. L. Laishley, editors. Proceedings of the Jack Pine Budworm Symposium (Winnipeg 1995), Canadian Forest Service, Northwest Region, Edmonton, Alberta, Canada.
- Wei, X., J. P. Kimmins, K. Peel, and O. Steen. 1997. Mass and nutrients in woody debris in harvested and wildfirekilled lodgepole pine forests in the central interior of British Columbia. Canadian Journal of Forest Research 27:148–155.
- Whittle, C. A., L. C. Duchesne, and T. Needham. 1997. The impact of broadcast burning and fire severity on species composition and abundance of surface vegetation in a jack pine (*Pinus banksiana*) clear-cut. Forest Ecology and Management **94**:141–148.
- Wolter, P. T., D. J. Mladenoff, G. E. Host, and T. R. Crow. 1995. Improved forest classification in the northern Lake States using multi-temporal landsat imagery. Photogrammetric Engineering & Remote Sensing 61:1129–1143.
- Zheng, D. L., D. O. Wallin, and Z. Q. Hao. 1997. Rates and patterns of landscape change between 1972 and 1988 in the Changbai Mountain area of China and North Korea. Landscape Ecology 12:241–254.
- Zhou, G., and A. M. Liebhold. 1995. Forecasting the spatial dynamics of gypsy moth outbreaks using cellular transition models. Landscape Ecology 10:177-189.