The changing relation of landscape patterns and jack pine budworm populations during an outbreak

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The influence of landscape patterns on ecological processes is generally acknowledged, but often difficult to quantify. The objective of our study was to quantify the relation of jack pine budworm (*Choristoneura pinus pinus*) population levels to both the abundance of jack pine (*Pinus banksiana*) and of jack pine stand edges in the landscape. The 450000 ha Pine Barrens region, located in northwestern Wisconsin, USA, experienced a severe jack pine budworm outbreak from 1990 to 1995. We calculated landscape indices on a landcover map derived from Landsat TM satellite imagery. Landscape indices were calculated on circular buffers (0.5, 0.75, 1, 1.5, and 2.5 km radius) centered on 143 budworm population sampling points for which annual budworm counts were available. Edge density was normalized for the proportion of jack pine in the landscape using random maps as a standard. Correlations between landscape patterns and budworm populations varied over time: proportion of jack pine showed strongest positive correlation with budworm population levels up to the peak of the outbreak (1993). Edge density exhibited positive correlation up to the peak of the outbreak, but negative correlation in the subsequent years as the outbreak declined. This may suggest that pollen-bearing male cones, which are more abundant along edges, support higher budworm populations in the initial phase of the outbreak, but stronger predation on budworm along edges subsequently reduces populations. We provide insight into previously inconclusive results on the relation of jack pine budworm population density to jack pine stand edges. The effects of landscape patterns, such as edge density, may vary not only in magnitude, but also in direction, being positive and negative during different phases of an insect outbreak. Therefore, caution should be taken in relating landscape patterns to process at either a single scale or point in time.

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The influence of landscape patterns on ecological processes was recognized early in ecology (Leopold 1933, Troll 1939, Watt 1947), and has been an active area of recent research (Turner 1989, Hanski 1994). This research has led to the development of new methods such as the use of indices to quantify landscape patterns (O'Neill et al. 1988, Turner and Gardner 1991, Gustafson 1998). However, quantifying and predicting the effects of landscape patterns on ecological processes remains problematic, due to the complexity of the subject matter (Peterson and Parker 1998) and the difficulty of conducting broad-scale experiments (Kareiva 1990). Landscape indices developed and tested on random maps may have limited explanatory power in real landscapes (McGarigal and McComb 1995, Schumaker 1996); various landscape indices may be highly correlated (Riitters et al. 1995, Hargis et al. 1998), and pattern changes, such as habitat loss and

fragmentation, often co-occur (Fahrig 1997). However, given the profound changes on landscape pattern created by human management in many areas of the world, a better understanding of the effects of landscape pattern on ecological processes, such as population dynamics, is of great importance.

Insect defoliation either by native species, such as western spruce budworm (*Choristoneura occidentalis*), or exotics, such as gypsy moth (*Lymantria dispar*), is a major disturbance in forest ecosystems, and changes landscape patterns (Bonan 1989, Holling 1992, Liebhold et al. 1992, McCullough et al. 1998). Related tree mortality may increase the likelihood and intensity of forest fires (Stocks 1987), resulting in salvage cuttings (Nyrop et al. 1983, Radeloff et al. 2000), and influencing forest planning (Rose 1973). Long-term records showed that insect outbreaks are an intrinsic periodic disturbance force of many ecosystems (Swetnam and Lynch 1993). Duration and intensity of outbreaks appear to be influenced by land management (e.g., spruce budworm outbreaks increased with fire suppression (Blais 1983, Anderson et al. 1987) and jack pine budworm (*Choristoneura pinus pinus*) outbreak frequency increased in the second half of this century (Volney 1988). Wide-spread ecological and economic effects made spruce budworm populations the subject of extensive modeling efforts (Ludwig et al. 1978, 1979, Royama 1984, Holling 1992), but relatively little is known about the relationship between landscape pattern and insect population levels during outbreaks.

Previous studies that examined effects of landscape patterns on forest insects focused on three, related aspects of landscape structure: abundance of host species, edges, and fragmentation. Landscapes with higher abundance of host species were often found to exhibit larger insect populations (Miller and Rusnock 1993, Su et al. 1996, Cappuccino et al. 1998). Possible reasons include greater habitat and food availability, and higher likelihood of successful dispersal (Fahrig and Merriam 1994, Zhou and Liebhold 1995, Gustafson and Gardner 1996, Su et al. 1996).

The effects of edges on animal populations vary. Both positive and negative edge effects have been documented for species in various ecosystems (Leopold 1933, Hansson 1994, Baldi 1996, Sisk et al. 1997), but few general patterns have emerged (Murcia 1995). A study of forest insects showed that birch tube-maker (*Acrobasis betuella*) larvae were more abundant along stand edges (Cappuccino and Martin 1997). Forest tent caterpillars (*Malacosoma disstria*) exhibited lower survival with increasing forest cover due to increased mortality from a virus and a parasitoid assemblage (Rothman and Roland 1998). This was attributed partly to direct effects of edges on populations, such as fine-scale differences in microclimate along edges. In addition, there are indirect edge effects, for instance where parasitoid abundance differs between forest inte-

rior and forest edge (Kulman and Hodson 1961, Cappuccino et al. 1998). Forest tent caterpillar parasitoid populations were higher along edges for three out of four species studied, but parasitism rates were lower (Roland and Taylor 1997). This may explain why fragmentation of forest landscapes in northern Ontario, Canada, altered forest tent caterpillar outbreak duration (Roland 1993).

This study focuses on the correlation of jack pine budworm (*Choristoneura pinus pinus*, Lepidoptera: Tortricidae) population levels with both habitat area and edge density. Previous studies suggested that, among other factors (McCullough et al. 1996), both the abundance of jack pine in the landscape (Weber 1995) and the abundance of jack pine edges affect jack pine budworm populations (Mattson et al. 1968, Mattson 1974, Kouki et al. 1997).

Studies on the effects of jack pine stand edge in the landscape have not been conclusive, reporting both positive and negative effects (Mattson et al. 1968, Mattson 1974, Kouki et al. 1997). Some studies reported that the extent of jack pine stand edges in the landscape was positively correlated with budworm populations, presumably due to higher food abundance (pollen-bearing male cones) along edges (Weber 1995, Kouki et al. 1997). These cones are a limiting feeding factor to budworm populations in spring (Nealis and Lomic 1994). Pollen cone abundance limits second and third instar budworm larvae in spring, because they are more nutritious than needles and they provide protection against predators and late frosts (Nealis 1990, Nealis and Lomic 1994, Nealis et al. 1997). Accordingly, highest jack pine budworm defoliation occurs in mature stands that are adjacent to immature stands (Kouki et al. 1997) and defoliation is highest within 20 m of stand edges (Kulman et al. 1963).

Apparently contradictory evidence demonstrates higher rates of avian predation (Mattson et al. 1968, Mattson 1974) and parasitism (Kulman and Hodson 1961) on jack pine budworm along stand edges (i.e., lower jack pine budworm populations in landscapes with higher edge density). Jack pine monocultures themselves contain low avian densities and avian predation is concentrated along stand edges and in small stands (Mattson et al. 1968). However, the effect of bird populations on jack pine budworm populations appeared to be low and only of importance when population levels were low (Mattson 1974). Exclosure experiments showed that for the closely related western spruce budworm, bird predation had strong effects on population levels (Torgersen and Campbell 1982, Campbell et al. 1983, Torgersen et al. 1990). Models also support this finding (Holling 1988). Generalist parasitoids may also have stronger impact along edges (Kulman and Hodson 1961, Su et al. 1996, Cappuccino et al. 1998).

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The objective of our study was to examine the relationship between jack pine budworm population levels and landscape patterns, namely, jack pine abundance and jack pine stand edge in the landscape, through a recent outbreak of jack pine budworm in the northwest Wisconsin Pine Barrens. In this study, we present an attempt to resolve the inconclusive evidence presented in the literature on the relationship between budworm population levels and jack pine edge.

Methods

Study area

Our study area was the northwest Wisconsin sand plains or pine barrens region (hereafter referred to as the Pine Barrens). The Pine Barrens are located on a sandy outwash plain covering approximately 450000 ha (Fig. 1). Nutrient-poor soils with low water-holding capacity create xeric conditions. Forest fires occurred frequently before European settlement around 1860 (Murphy 1931). The landscape structure resulting from this disturbance regime was a mosaic of open areas, scattered trees and dense regenerating patches. After a fire, these open patches regenerated and converted to stands of jack pine. Red and white pine (*P. resinosa* and *P. strobus*) also occurred less frequently, under varying fire frequency and intensity (Radeloff et al. 1999). The

southern part of the Barrens contained areas of northern pin and bur oak savannas (*Quercus ellipsoidalis* and *Q. macrocarpa*) suggesting more frequent, but less intense, ground fires (Radeloff et al. 1998).

Beginning around 1860, European settlement brought widespread logging and farming until 1930 (Murphy 1931). Since then, reforestation, mainly with jack and red pine, and fire suppression have changed the landscape structure of the Pine Barrens (Vogl 1964). The major conservation concern here is not forest habitat fragmentation, but rather the loss of large open patches (Radeloff et al. 1998).

Budworm population sampling

Historically, the Pine Barrens have been affected by a sequence of budworm outbreaks (Clancy et al. 1980, Volney and McCullough 1994). Jack pine budworm outbreaks were most likely also part of the Pine Barrens ecosystem before European settlement, but no data exist for this period. Since 1952, the Wisconsin Department of Natural Resources (WDNR) has monitored budworm densities at 143 sampling locations throughout the Pine Barrens landscape (Fig. 1). The last outbreak in this region occurred between 1990 and 1995, and we examined budworm populations only during these years. Annual surveys included early larvae, late larvae, pupae, and egg masses. We used only the early
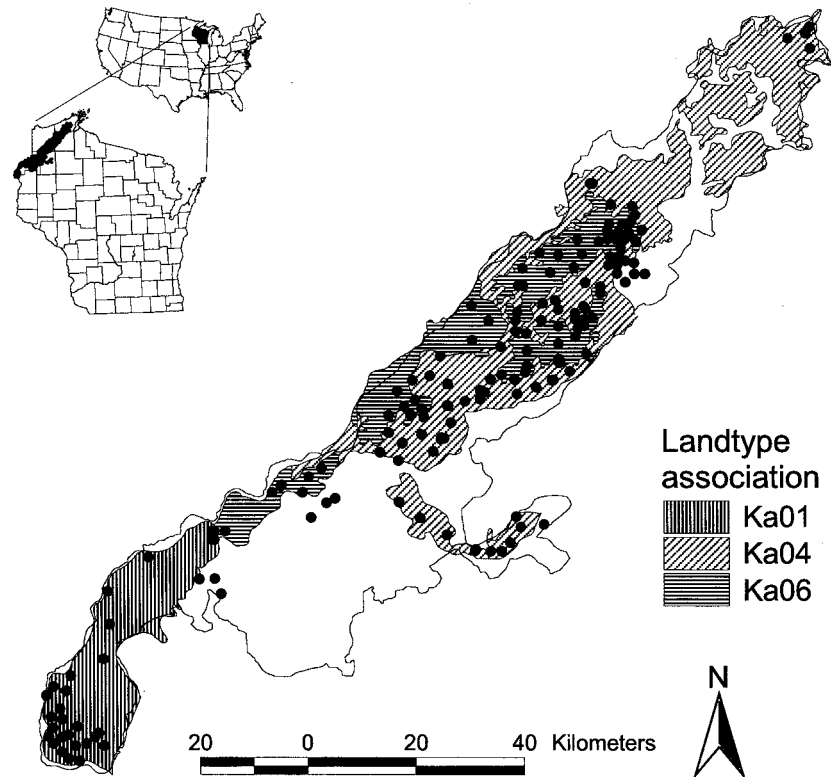

Fig. 1. Location of the northwest Wisconsin Pine Barrens and jack pine budworm sampling points. Land type association (LTA) boundaries used for stratifying the sampling points are superimposed; boundaries of other LTAs are not shown.

Landtype association
Ka01
Ka04
Ka06

N

20   0   20   40 Kilometers

larval counts to construct our database because this was the most complete data set. Early larval counts were conducted in spring, prior to mid-June, and consisted mainly of 2nd through 4th instar budworm larvae. The numbers of larvae on 30 shoots per sampling plot were counted (Clancy et al. 1980). The sampling unit is number of larvae per sampling locations. Shoots were collected from the middle part of the crown. Some sampling locations shifted small distances between years (up to 100 m).

Satellite classification

Our analysis of the landscape patterns was based on a species-level forest classification derived from multi-temporal Landsat satellite imagery with a spatial resolution of 28.5×28.5 m (Wolter et al. 1995). Phenological differences among tree species throughout the growing season allowed differentiation of tree species (Wolter et al. 1995). Overall accuracy of forest and landcover classes was 83%. User's accuracy for jack pine (the percentage of all classified jack pine that were also jack pine on the ground) was 79.5%. Producer's accuracy for jack pine (the percentage of jack pine on the ground correctly identified in the classification) was 91.2% (Wolter et al. 1995). The class jack pine contains only mature stands older than 15–25 yr. Younger stands do not exhibit crown closure and are classified as 'open forest' or 'brush'. We updated the classification of Wolter et al. (1995), using a 1991 Landsat TM scene. Change detection analysis revealed jack pine stands harvested between 1987 and the first year of the jack pine budworm outbreak, 1991 (Radeloff et al. 2000). Our landscape pattern analysis was thus based on a map of mature jack pine in 1991.

Landscape indices

The selection of landscape indices for this study was based on previous research suggesting that both the proportion of jack pine and jack pine edge density influence jack pine budworm population levels (Kulman and Hodson 1961, Mattson et al. 1968, Weber 1995, Su et al. 1996, Kouki et al. 1997).

The percentage, PC_i, of a landcover class i is defined as the ratio of the area of the landcover class divided by the area of the landscape A_L multiplied by 100.

The abundance of edge is often loosely defined in the jack pine budworm literature (Kulman et al. 1963) and it was unclear if authors referred to the abundance of edge in the landscape (i.e., edge density) or abundance of edge in relation to a given area of jack pine (i.e., perimeter/area ratio). We calculated three edge related indices (edge density, mean perimeter/area ratio and corrected mean perimeter/area ratio) to capture differ-

ent aspects of edge in relationship to landscape area and jack pine area.

Edge density (ED) is defined as the perimeter of class i divided by the total area of the landscape (Eq. 1).

$$ED_i = \frac{P_i}{A_L} \tag{1}$$

where ED_i is the edge density of landcover class i (m/ha), P_i is the total perimeter of landcover class i (m), and A_L is the total area of the landscape (ha).

The mean perimeter/area ratio, PA_i, is the sum of the ratio of perimeter and of all patches of class i divided by the number of patches (Eq. 2).

$$PA_i = \frac{\sum_{j=1}^{n_i} \frac{P_{i,j}}{A_{i,j}}}{n_i} \tag{2}$$

where PA_i is the mean perimeter/area ratio of landcover class i (m/ha), n_i is the number of patches of landcover class i, $P_{i,j}$ is the perimeter of patch j of landcover class i (m), and $A_{i,j}$ is the area of patch j of landcover class i (ha).

The corrected mean perimeter/area ratio (CPA_i) standardizes PA_i so that the value becomes 1.0 for a circle and 1.1 for a square (Eq. 3).

$$CPA_i = \frac{\sum_{j=1}^{n_i} \frac{P_{i,j}}{\sqrt{4\pi \cdot A_{i,j}}}}{n_i} \tag{3}$$

All indices were calculated using APACK 2.00 (DeZonia and Mladenoff 1997) a software package designed to rapidly compute landscape indices from large raster maps. We assumed an 'eight pixel neighborhood' such that pixels with at least one common corner belonged to the same patch. The edge of the buffer was assumed to be also the edge of the patch.

The calculation of landscape indices depends on the scale chosen for the analysis. Scale can be separated into two components: grain, the smallest spatial resolution, and extent of the area under investigation (Turner and Gardner 1991). The resolution of the Landsat TM5 satellite sensor determined the grain in our study (28.5×28.5 m). The scales at which jack pine budworm populations are affected by habitat heterogeneity are unknown. To our knowledge, no a priori information exists about the scales at which jack pine budworm populations respond to landscape structure. We therefore calculated circular buffers of 0.5, 0.75, 1.0, 1.5, and 2.5 km radius around each of the 143 sampling points and calculated the landscape indices for each of the 715 buffers. We did not analyze buffers smaller than 0.5 km because the calculation of landscape indices such as average patch size becomes unreliable when the number of patches within a sampling area becomes too small.
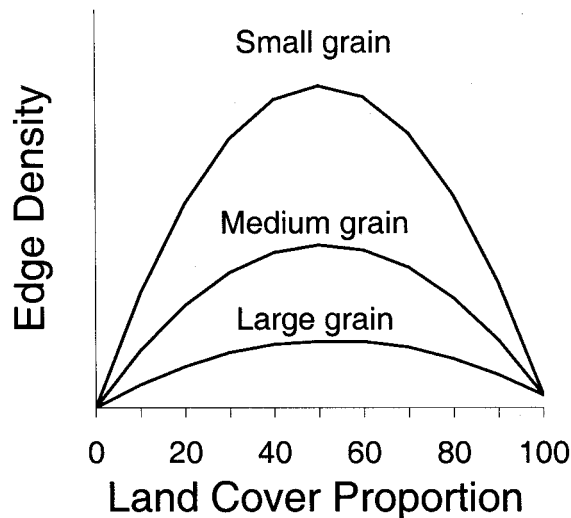
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Fig. 2. Theoretical relationship between edge density and grain sizes derived from random maps with varying proportions of the map covered by a certain landcover type.

Normalized edge density

The problem of correlation among landscape indices (Gustafson and Parker 1992, Riitters et al. 1995, Hargis et al. 1998) was addressed by normalizing the measured edge density using edge density calculated from random maps as a standard (Fig. 2).

The edge density of a cover type in a random landscape is 0 at 0% landcover and peaks at 50% (Gardner et al. 1987). It decreases beyond 50% landcover, but does not reach 0 at 100% landcover when map edge is assumed to be patch edge. The grain size of the analysis determines the maximum edge density at 50% landcover; smaller grain sizes exhibit higher maxima (Fig. 2). We used the edge density of random maps for comparison with the edge densities measured in our data by deriving mean edge density from 30 random maps for each of the 143 values of PC_i as found in the buffers surrounding the budworm population sampling plots. This procedure was performed separately for each of the five buffer sizes because PC_i varied with buffer size. Edge density was measured on a total of 21450 random maps (143 plots × 30 random maps × 5 buffer sizes).

The shape of the curve that describes the relationship between edge density and PC_i is independent of grain size. Curves of one grain size can be transformed into curves of other grain sizes by multiplying them by a constant. The actual grain size of jack pine in our study area was unknown because the minimum size of jack pine patches varied among buffers and may be affected by the grain size of the satellite imagery on which the classification was based. We used single Landsat TM pixels as the smallest spatial unit and applied a constant c to fit the edge density curve from the random maps through the edge density cloud measured in our buffers.

Best fit was obtained when the sum of all differences between the mean edge density of 30 random maps $ED_{y,p}$ and the measured edge density in a buffer $ED_{y,m}$ over 143 sampling plots y became zero.

$$\sum_{y=1}^{143} (ED_{y,m} - c \cdot ED_{y,p}) = 0 \qquad (4)$$

Using this fit, c was employed to derive normalized edge density ED_n for each buffer.

$$ED_n = ED_m - c \cdot ED_p \qquad (5)$$

Conceptually, ED_n can be compared to regression residuals. It assumes positive values when edge density in the real landscape is higher than predicted from random maps.

Regression analyses

Linear regression analyses were used to examine the relationships between landscape patterns and budworm population levels. We employed a square root transformation of the budworm data to achieve normal distribution prior to analysis. Each landscape index was regressed against budworm population data for each single year of the outbreak (1990–1995), and against the six-year mean budworm population levels. In the following, we will present the correlation coefficient (r) resulting from our regression analyses, instead of the r^2, to show the sign of the regression slope.

We grouped sampling points based on a land type associations (LTA) map of the Pine Barrens (WDNR, unpublished data), to permit analyze on a sub-region level in our study area (Fig. 1). Three LTAs contained sufficient sampling points to perform separate linear regressions (Ka01: $n = 26$; Ka04: $n = 56$; Ka06: $n = 46$).

Correlation analyses were performed among single year budworm population data (e.g., 1991 vs 1992). We also calculated correlations between different landscape indices at the same buffer radius, and between values for a single landscape index calculated with different buffer radii.

Spatial autocorrelation in the budworm population data (the dependent variable) was of concern in our analyses because it may have artificially raised the degrees of freedom thus leading to potentially unwarranted detection of significance. The common procedure to test if autocorrelation in the data affects a regression analysis is to examine autocorrelation in the regression residuals (Upton and Fingleton 1985, Haining 1990, Cressie 1993). Autocorrelation in the residuals would indicate a falsely raised regression coefficient that would need to be accounted for before applying significance tests (Cressie 1993). We calculated correlograms on the residuals of significant regressions. The
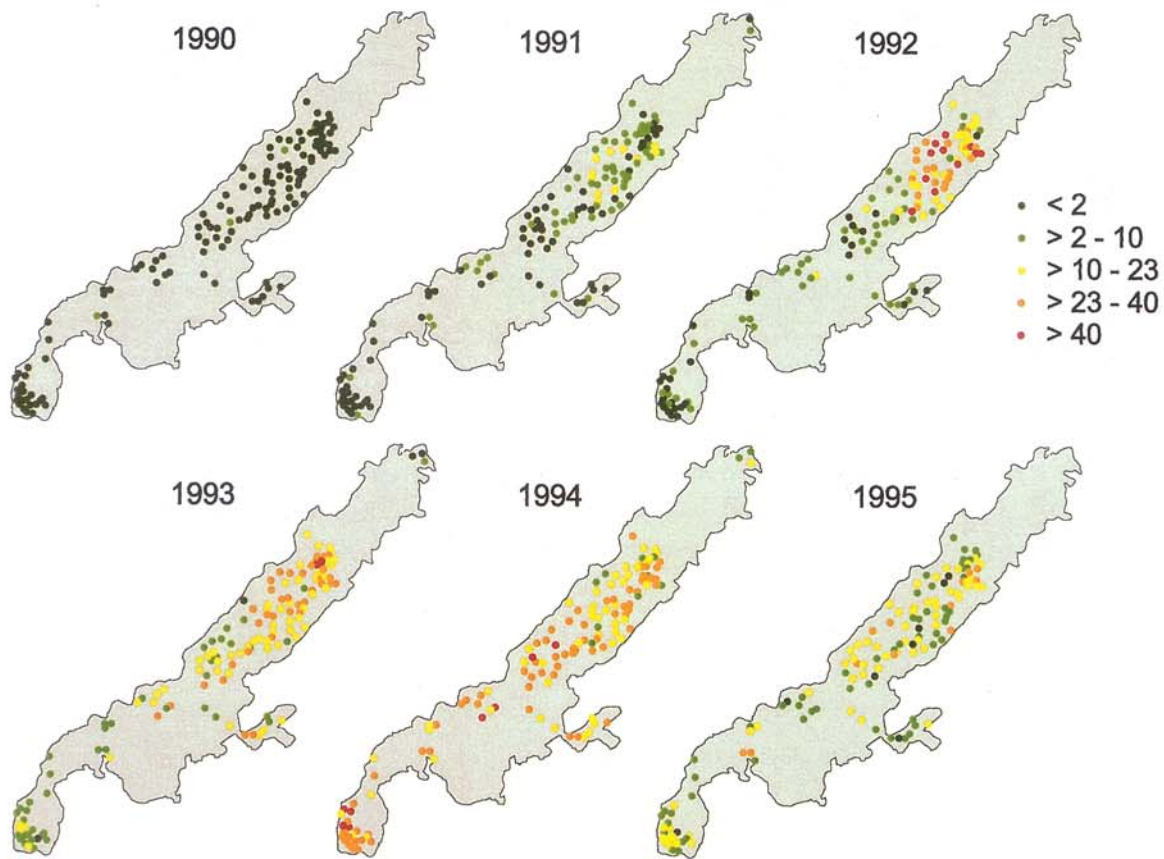
Fig. 3. Number of jack pine budworm early larvae (instars 2–4) at each of the 143 sampling locations during the recent outbreak (1990–1995).

use of correlograms allowed testing the significance of the autocorrelation in the residuals (Rossi et al. 1992). Significance levels for autocorrelation values in the correlograms ($p < 0.05$) were derived based on the number of distance pairs within distance classes (Clayton and Hudelson 1995).

Results

Jack pine budworm populations

The jack pine budworm population showed spatially varying densities in the different years during the last outbreak (1990–1995, Fig. 3). Budworm population levels first increased in the north-central Pine Barrens, and peaked in 1992–1993. However, the outbreak occurred later in the southern Pine Barrens, peaking in 1994. Single year budworm population levels exhibited significant ($p < 0.05$) correlation between years (Table 1). Years preceding 1993 exhibited significant positive correlation among themselves, while years after 1993 exhibited lower correlations, and 1994 populations showed significant negative correlations with 1991 and 1992 population levels.

Landscape indices

The values calculated for the five landscape indices differed according to buffer radii and these differences were not consistent between indices (Table 2). The mean proportion of jack pine, PC, was almost constant for 0.5 to 1.0 km buffer radius and declined with larger radii. The measured mean edge density, ED_m, was highest for the smallest buffer radius and declined steadily for larger radii. This was due to the assumption that the map boundary is counted as edge; the smallest buffers exhibited the largest ratio between buffer perimeter and buffer area. The mean normalized edge

Table 1. Correlation coefficients (Pearson's r) between budworm population levels across sites in single years and mean population levels. An asterisk indicates statistically significant correlations ($p < 0.05$, $n = 143$).

	1990	1991	1992	1993	1994
1991	0.08				
1992	0.15	0.70*			
1993	0.14	0.47*	0.61*		
1994	−0.09	−0.34*	−0.38*	−0.16*	
1995	−0.14	−0.03	−0.01	−0.04	0.28*

Table 2. Mean, minima, and maxima of the different landscape indices when calculated using buffers of different radii.

		Buffer radius (m)				
		500	750	1000	1500	2500
PC	Min.	0	0	0	0:01	0:02
	Mean	0:23	0:23	0:23	0:22	0:21
	Max.	0:83	0:81	0:80	0:74	0:61
PA	Min.	0	0	510	627	790
	Mean	831	884	907	926	932
	Max.	1228	1241	1123	1112	1082
CPA	Min.	0.0	0.0	1.4	1.4	1.5
	Mean	1.7	1.7	1.7	1.7	1.7
	Max.	2.6	2.6	2.4	2.3	2.1
ED_m	Min.	0	0	2	4	8
	Mean	85	80	76	72	67
	Max.	177	155	146	131	111
ED_n	Min.	−44	−36	−43	−33	−21
	Mean	0	0	0	0	0
	Max.	65	51	43	43	29

density, ED_n, was by definition zero independent of the buffer size; minima and maxima decreased with larger buffer size. The mean values for perimeter/area ratio, PA, and its corrected form, CPA, remained almost constant over the range of different buffer radii, but the range from minima to maxima decreased sharply with larger buffer sizes.

Landscape indices also changed spatially with increasing buffer radii (Fig. 4). Larger buffer radii tended to smooth the spatial variation, but this effect was not consistent throughout the Pine Barrens. For example, PC calculated with a 0.5 km buffer radius exhibited maxima in the north-central and southwestern Pine Barrens. At the 2.5 km buffer radius, only the central part of the Pine Barrens contains high values of PC (Fig. 4).

The landscape indices calculated with different buffer radii exhibited correlation among scales (Table 3). Correlations among different scales were strongest between the smaller buffer radii (0.75–1 km) but significant even between smallest (0.5 km) and largest (2.5 km) buffer ($p < 0.01$). Correlations among scales for other landscape indices (not shown) were comparable to PC.

The various landscape pattern indices were also correlated (Table 4). Commonly used landscape indices depicting edge exhibited significant correlation with PC at all scales thus introducing problems of collinearity among independent variables. Our procedure to derive a normalized edge density was successful in that the correlation between PC and ED_n was considerably below the correlation of any other edge related landscape index, thus removing potential collinearity between variables.

Regression analyses

First, we examined the relationship between landscape patterns and mean jack pine budworm populations over the entire outbreak. The five landscape indices and mean budworm populations were significantly ($p < 0.05$) correlated at all scales (Table 5), but PC exhibited the highest r of all indices. ED_n exhibited the lowest r and significant relationships only at the smaller buffer sizes. When comparing results for the entire Pine Barrens region with those calculated for subregions, we found similar values of r for mean population levels calculated over the two northern Landtype Associations (LTA's Ka04 and 06, not shown). The southwestern LTA, Ka01, exhibited higher r (Table 5), but the threshold for significant relationships was also higher due to fewer sampling points (26 versus 143). The most important difference between LTA Ka01 and the entire Pine Barrens was that ED_n did not exhibit any significant correlations and that the non-significant correlation coefficients were negative.

Second, we performed regression analyses for single years of the outbreak and found strong temporal patterns (Fig. 5). The relationship with PC, when calculated for the entire Pine Barrens, exhibited significant and increasing r between 1991 and 1993, but no significant r afterwards (Fig. 5a). Within 1991, the highest r occurred at 0.75 km buffer size ($r = 0.35$); in 1993, 2.5 km buffer exhibited the highest r ($r = 0.46$). The regression analyses with ED_n resulted in similar positive r from 1991 to 1993, and also a shift of higher r from smallest buffer size in 1991 (0.5 km: $r = 0.25$) to largest buffer size in 1993 (2.5 km, $r = 0.30$; Fig. 5b). Markedly different from these positive correlations were the significant ($p < 0.05$) negative r for 1994, the highest one occurring at 0.5 km buffer size ($r = −0.20$).

Results for PC in LTA Ka01 for single years also showed increasing r over time, but the peak occurred one year later (1994: $r = 0.73$, buffer radius 0.75 km), and remained significant and positive in 1995 (Fig. 5c). Single year results were not calculated for 1990 for LTA Ka01, because only 5 out of 26 sampling points

Buffer radii

| 500 m | 1 km | 2.5 km |

Percent Jack pine

- 0 - 8.8
- > 8.8 - 19.7
- > 19.7 - 29.3
- > 29.3 - 43.7
- > 43.7 - 82.6

Normalized edge density (m/ha)

- > 23 - 44
- > 7 - 23
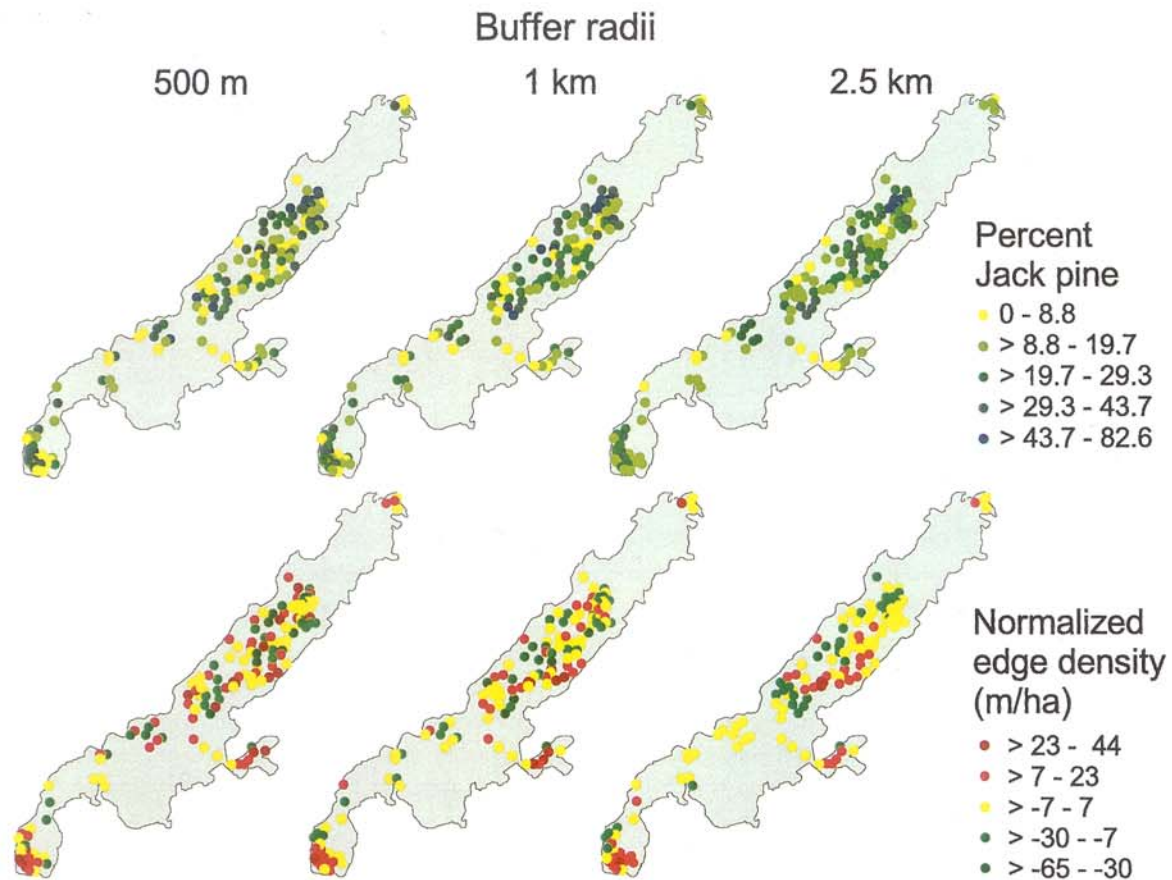- > -7 - 7
- > -30 - -7
- > -65 - -30

Fig. 4. Spatial variation of proportion of jack pine and normalized edge density calculated in buffers of different radii surrounding the 143 sampling locations.

had population levels > 0. ED_n did not show a positive r up to the peak of the outbreak, but was negative in the year subsequent to the peak (1995: $r = -0.58$, buffer radius 1 km; Fig. 5c).

Correlograms calculated from the residuals of significant regressions exhibited no significant ($p < 0.05$) spatial autocorrelation. Examples are presented for the two regressions with the highest r for PC and ED_n (Fig. 6). Only one distance class in the two examples showed autocorrelation beyond the 95% confidence limits. Variation did not decrease with increasing distance, which would be expected if autocorrelation were present. The regression residual analysis showed no evidence for artificially raised regression coefficient due to autocorrelation in the data.

Discussion

Effect of landscape patterns

We found statistically significant relationships between landscape pattern, namely the abundance of jack pine

and jack pine stand edge in the landscape, and jack pine budworm populations. Our most important finding suggests that the relationship between landscape patterns and jack pine budworm populations may change over time during an outbreak. Both the abundance of jack pine and the abundance of jack pine edge showed markedly different correlations with budworm populations over the duration of the outbreak. The proportion of jack pine (PC) had the highest positive relationship with jack pine budworm population density in the peak year of the outbreak (Fig. 5), but no significant relationship thereafter. This may indicate that dispersal of female jack pine budworm moths and

Table 3. Correlation coefficients (Pearson's r) between percent jack pine calculated with buffers of different radii. All correlations are statistically significant ($p < 0.05$, $n = 143$).

Buffer radius (km)	0.5	0.75	1	1.5
0.75	0.95			
1	0.88	0.97		
1.5	0.78	0.88	0.94	
2.5	0.65	0.73	0.79	0.90

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Table 4. Correlation coefficients (Pearson's r) between percent jack pine and different indices capturing jack pine stand edge calculated with buffers of different radii. All correlations are statistically significant ($p < 0.05$, $n = 143$).

Buffer radius (km)	PA	CPA	ED_m	ED_n
0.50	−0.34	0.58	0.81	0.23
0.75	−0.40	0.57	0.78	0.26
1.00	−0.48	0.57	0.75	0.26
1.50	−0.51	0.65	0.74	0.33
2.50	−0.50	0.72	0.79	0.40

larvae is only of importance in determining budworm population levels while an outbreak increases.

Normalized edge density (ED_n) in the entire study area correlated positively with budworm populations up to the peak of the outbreak (Fig. 5). This pattern is most likely related to the larger abundance of pollen cones along edges, which provide more abundant food and result in higher defoliation in such locations (Kouki et al. 1997). Pollen bearing male cones along edges decrease during outbreaks as a result of budworm feeding, and this has been suggested as an explanation for the delayed density dependence apparent in budworm populations (Nealis and Lomic 1994, Volney and McCullough 1994). In the year subsequent to the peak, ED_n exhibited a negative r. This pattern was observed in both the entire study area and the southwestern part, where the peak of the outbreak was delayed one year. Other studies found higher avian predation along edges (Mattson et al. 1968), and the primary wasp parasitoid (*Itoplectis conquisitor*) is an also an edge species (Kulman and Hodson 1961). We speculate that avian predators and/or parasitoids will have the largest effect on budworm numbers in edge habitats where birds and parasitoids are most abundant.

Our analysis focused on the correlation between landscape pattern and budworm population. One limitation of such an approach is that correlation does not equal causation, and our interpretation concerning causal relationship remains speculative. We recognize that the temporal patterns revealed here suggest further time series analysis. Such analysis should examine, for

instance, the presence of population fluctuations that indicate direct density dependence versus those that indicate indirect density dependence, potentially caused by avian predators and/or parasitoids. We are currently conducting this analysis; however, it was not the objective of this study.

Random maps and normalized edge density

Collinearity problems became apparent when commonly used landscape indices measuring edge were correlated with the proportion of jack pine (Table 4). This made separating the effects of these two aspects of landscape patterns problematic. Correlation coefficients for ED_m, PA, and PAC in relation to the budworm data were significant (Table 5), but their correlation coefficients were similar to the correlation coefficients between these indices and PC (Table 4). These problems required normalizing edge density for the proportion of jack pine using mean values of random maps as a standard, which effectively minimized correlation between PC and ED_n. Random maps have previously been used as neutral models to determine if observed spatial patterns differ from random (Gardner et al. 1987, Gardner and O'Neill 1991), to analyze the sensitivity of landscape indices to different landscape pattern (Gustafson and Parker 1992) and to predict critical thresholds at which landscape-level processes such as dispersal change abruptly (Andrén 1994, With and Crist 1995, With and King 1997, With et al. 1997). However, to our knowledge this is the first study to use random maps to normalize landscape indices and minimize correlations among them.

Potential error sources

Our regression analyses revealed significant relationships between landscape patterns and budworm populations ($p < 0.05$) but the majority of the variance in the budworm data remained unexplained. There are several

Table 5. Correlation coefficients (Pearson's r) between average jack pine budworm population densities and various landscape indices calculated with buffers of different radii. An asterisk indicates statistically significant correlations ($p < 0.05$, $n = 143$ for the entire study area, $n = 26$ for LTA Ka01).

	Buffer radius (km)	PA	CPA	ED_m	ED_n	PC
Entire Pine Barrens study area	0.5	−0.02	0.34*	0.26*	0.24*	0.37*
	0.75	−0.12	0.18*	0.25*	0.18*	0.35*
	1	−0.17*	0.23*	0.26*	0.13	0.33*
	1.5	−0.26*	0.26*	0.25*	0.09	0.30*
	2.5	−0.11	0.17*	0.25*	0.09	0.28*
Only for LTA Ka01	0.5	0.06	0.67*	0.65*	−0.27	0.64*
	0.75	−0.25	0.57*	0.77*	−0.29	0.73*
	1	−0.24	0.51*	0.77*	−0.35	0.72*
	1.5	−0.27	0.58*	0.77*	−0.33	0.70*
	2.5	−0.15	0.45*	0.74*	−0.26	0.66*

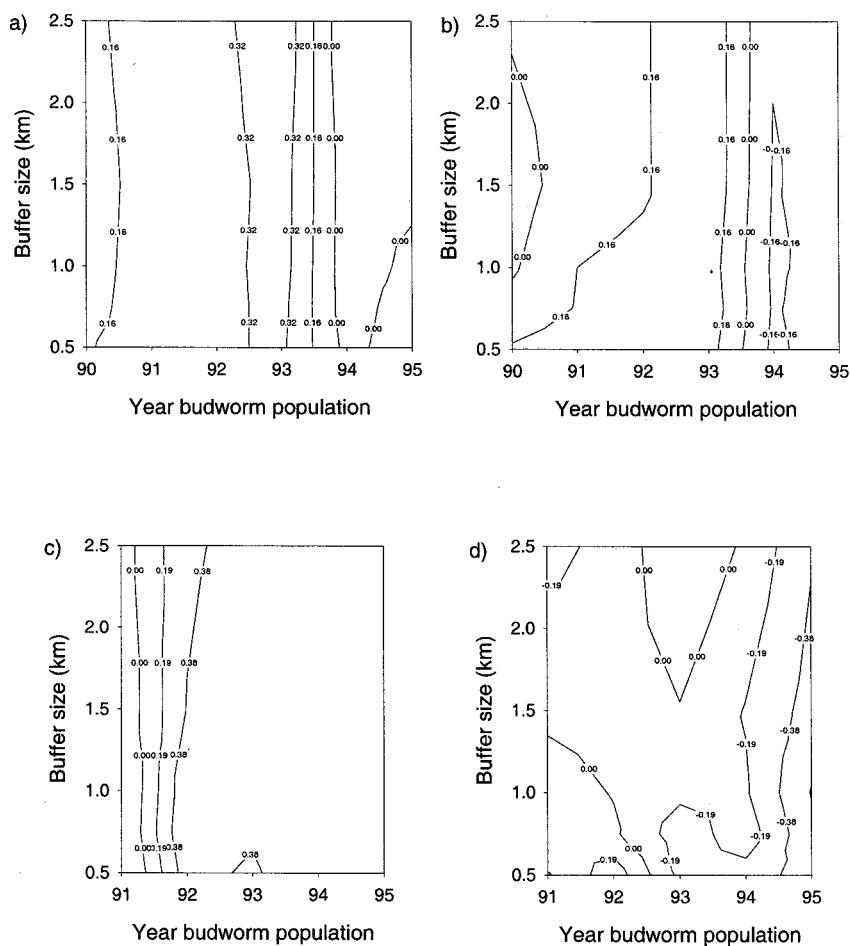Fig. 5. Correlation coefficients (r) of the regression analysis between single year budworm population and proportion of jack pine (a, c) and normalized edge density (b, d) at different buffer sizes for the entire Pine barrens (a, b) and the southwestern Landtype Association Ka01 (c, d). Values between full years and buffer radii are interpolated. In a) and b), correlation coefficients are significant ($p < 0.05$) if > 0.16 or < -0.16. In c) and d), correlation coefficients are significant ($p < 0.05$) if > 0.38 or < -0.38. Contour line intervals were selected so that these cut-off points can be easily identified.

potential sources of error in our analysis that may have decreased correlation coefficients.

The grain of the satellite data and the limited accuracy of the budworm sampling point locations on the satellite map prevented us from analyzing smaller scales (i.e. < 0.5 km). We may have missed the scale at which jack pine budworm correlates most strongly to landscape patterns.

The satellite classification contained errors that propagated into the landscape indices calculated (Wickham et al. 1997). Salvage logging occurred during the outbreak, thus changing landscape patterns. Also, we treated all jack pine edges equally but edges along openings might fulfill different ecological functions than edge along hardwood stands (Kouki et al. 1997), and the function of edges may change as stands mature. The effects of these errors on our regression analyses are difficult to estimate, but may have decreased the resulting correlation coefficients.

We performed numerous regressions and 5% of these are expected to be statistically significant by chance when a p-value of 0.05 is applied. However, 50% of all relationships between single year budworm data and

the various landscape indices were significant (Fig. 5). Furthermore, the regression analyses for different years and scales showed consistent pattern (e.g., the increasing regression coefficients for the analysis between proportion of jack pine and budworm population up to the peak of the outbreak). Such patterns were unlikely to occur if the results of our regressions were driven by chance only.

In summary, several error sources may have decreased the reported correlation coefficients, but it is unlikely that the significant results presented in this study are the result of these errors.

Management implications

The role of mixed-species composition of forests in reducing the impact of pest outbreaks, both on the stand and landscape level, has been discussed for at least seven decades (Miller and Rusnock 1993). In the case of jack pine budworm, management for a diverse age distribution across the landscape may also limit outbreaks because of the greater susceptibility of older

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jack pine stands (Weber 1995, Kouki et al. 1997). Defoliator populations cause higher tree mortality where host species are more abundant (Bergeron et al. 1995, Su et al. 1996, Cappuccino et al. 1998), and rates of parasitism on defoliating insects are often higher in more complex landscapes (Marino and Landis 1996, Cappuccino and Martin 1997). The logical management recommendation to limit future outbreaks is to increase tree species diversity and reduce the percentage of jack pine in the landscape (Miller and Rusnock 1993). Forest management can have a strong effect on landscape patterns and could potentially achieve such goals (Franklin and Forman 1987, Gustafson 1996).

Should limiting jack pine budworm populations be a management goal? Limiting defoliation may be crucial where timber production is at stake, but jack pine budworm is an important element in the Pine Barrens' disturbance cycle. Fire suppression during this century may have interrupted this cycle, and forest management altered tree species composition and landscape patterns (Mladenoff et al. 1993). The pre-settlement Pine Barrens were dominated by *Pinus* spp. and contained a

landscape mosaic of large open patches, savannas, and forests (Radeloff et al. 1998). In 1855, about 55% of the Pine Barrens area was dominated by pine, compared to only 38% in 1987 (Radeloff et al. 1999). Fire suppression and resource management increased hardwood abundance, and decreased the availability of open habitat; crucial, for instance, for grassland birds. One effect of the jack pine budworm outbreak studied here was that logging rates increased due to salvage operations, thus creating large patches of open habitat (Radeloff et al. 2000). We caution against concluding from this study that managers should suppress insect outbreaks by further decreasing jack pine abundance in the landscape; such decisions require examining possible effects on the entire ecosystem.

Conclusions

We investigated the relation of landscape patterns (proportion of jack pine and jack pine edge) on jack pine budworm population levels during an outbreak. Previous studies reported a positive relation between proportion of jack pine and jack pine budworm populations because of increased moth dispersal success (Su et al. 1996), but the effect of edge was unclear. Some suggested that more abundant male cones along edges provide better food habitat, thus concluding that edge had a positive effect on budworm populations (Kulman et al. 1963, Kouki et al. 1997). Others found higher numbers of avian predators along edges (Mattson et al. 1968) and suggested that birds and parasitoids decrease budworm populations where high amount of edge habitat facilitates predator access into stands (Su et al. 1996); however, it remained unclear to what extent bird populations can affect budworm populations (Mattson 1974, Torgersen and Campbell 1982).

Our results agreed with previous studies, but found changing correlations between landscape patterns and budworm populations during different phases of the outbreak. Correlation coefficients were significant ($p < 0.05$) at a range of scales and for various years during the outbreak. However, landscape patterns explained only a minor part of the variation in the budworm data.

Proportion of jack pine in the landscape was positively correlated with jack pine budworm population levels, but only up to the peak of the outbreak. Edge density was positively correlated up to the peak of the outbreak, thus possibly supporting the hypothesis that pollen cones along edge provide better food habitat. After the outbreak peak, edge density was negatively correlated. The decrease of pollen cones during outbreaks suggests that their effect should diminish (Nealis 1995). Predator populations often respond with a time lag to more abundant prey, possibly indicating that the
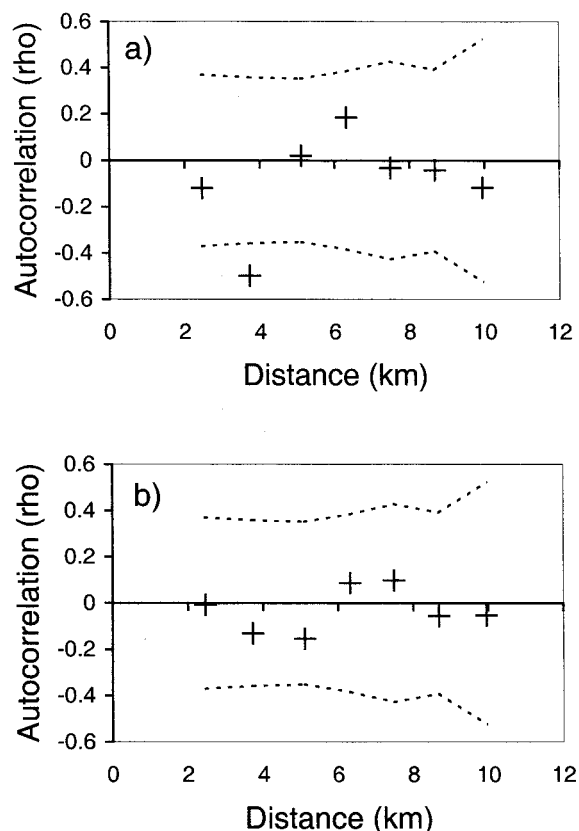

Fig. 6. Correlograms for the residuals of the regression between budworm population in LTA Ka01: a) 1994 versus proportion of jack pine (0.75-km radius circles), and b) 1995 versus normalized edge density (1-km radius circles). Values between the dotted lines are not significant autocorrelation ($p < 0.05$).

effects of birds and parasitoids may be strongest when outbreaks decline. Consistently, edge was not significantly related to mean budworm populations; its positive and negative effects seemed to counteract each other.

Landscape ecology strives to relate landscape patterns to processes. Insect populations may offer a fruitful path for future studies in landscape ecology, both because longterm data sets are available (Liebhold et al. 1992, Sharov et al. 1997) and because of the spatial scales at which insects operate (Wiens and Milne 1989, With and Crist 1995, Jonsen and Fahrig 1997, Wiens et al. 1997). Recent studies on the effects of edges, tree species diversity, forest fragmentation, and patch isolation on forest defoliators (Roland 1993, Bergeron et al. 1995, Su et al. 1996, Cappuccino and Martin 1997) and their parasitoids (Marino and Landis 1996, Cappuccino and Martin 1997, Roland and Taylor 1997), revealed fascinating but highly complex dynamics and interactions. This study suggests that edges have opposing effects before and after the peak of jack pine budworm outbreaks. Future research that combines spatial and temporal patterns of insect outbreaks over a range of scales is needed.

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