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Forest fragmentation and duration of forest tent caterpillar (*Malacosoma disstria* Hübner) outbreaks in northern hardwood forests

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ABSTRACT

In northern forests dominated by aspen (*Populus* spp.), the duration of outbreaks of forest tent caterpillar (*Malacosoma disstria* Hübner) has been reported to increase with forest fragmentation. This relationship has not been tested in other forest types affected by this widespread native defoliator. From 2002 to 2007, a large-scale outbreak of this insect in the northeastern United States defoliated millions of hectares, with sugar maple (*Acer saccharum* Marsh.) the primary host. We used digital defoliation maps generated from aerial surveys and national land cover data to assess the effect of fragmentation on outbreak duration in areas of NY, MA, VT, and NH. We found that outbreak duration increased with forest cover and decreased with the forest edge, in opposition to the pattern previously reported for aspen-dominated forests in Canada. This pattern was significant from plot sizes ranging from 100 m to 1000 m in radius. The relationship between FTC and its natural enemies, which was postulated to underlie the effect of fragmentation on outbreaks in aspen forests, may be affected differently in northern hardwood forests, or other factors may be more important in determining outbreak duration in this forest type.

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1. Introduction

Forest tent caterpillar (*Malacosoma disstria* Hübner; FTC) is the most important defoliator of hardwood trees in North America (Mattson et al., 1991). The geographical range of this insect is very broad, extending from the Gulf Coast to northern Canada (Fitzgerald, 1995; Parry and Goyer, 2004). Within its range, extensive outbreaks occur in several forest types including aspen parkland and boreal mixed-wood across Canada, oak and maple in the northeastern and midwestern United States, and bottomland hardwood and tupelo ponds in the Southeast and Gulf Coast (Batzer and Morris, 1978; Parry and Goyer, 2004). In the northeastern United States, outbreaks of FTC have been recorded at approximately decadal intervals since the late 1800s in sugar maple (*Acer saccharum* Marsh.) dominated forests (Hodson, 1941; Connola et al., 1957; Wink and Allen, 2007). Although FTC will feed on many hardwoods in the Northeast, outbreaks tend to occur where sugar maple is a dominant component of the cover.

In aspen-dominated forests, spatial patterns in forest cover have been associated with variation in the duration and intensity of outbreaks. Using correlations between forest inventory maps and historical defoliation records, Roland (1993) found that FTC out-

breaks lasted longer in more fragmented forest, with forest edge as the measure of fragmentation. Subsequent research showed a similar pattern at several different scales (Roland and Taylor, 1997; Roland, 2005).

The sensitivity of outbreak duration to changes in forest structure was hypothesized to reflect the efficacy of natural enemies. Parasitoids and diseases are thought to play an important role in the dynamics of FTC (Hodson, 1941; Parry, 1995; Parry et al., 1997), and small-scale experiments and larger scale sampling of natural populations reported that FTC mortality from pathogens (Roland and Kaupp, 1995) and parasitoids (Roland and Taylor, 1997) was reduced in fragmented forests. However, an experimental test of fragmentation on parasitism in areas of continuous forest tracts and isolated forest fragments did not validate this hypothesis (Roth et al., 2006) and the mechanistic basis for the observed correlation between outbreak duration and forest fragmentation remains unknown.

Widespread outbreaks of FTC in the northeastern US afforded us an opportunity to examine the relationship between forest fragmentation and outbreak duration in a forest system where aspen is at most a minor component. During the most recent outbreak of FTC in the northeastern U.S., an estimated 250,000 ha were defoliated in New York, Massachusetts, Vermont, and New Hampshire in 2005, and in 2006 at least 500,000 ha were defoliated in New York State alone; by 2007, populations had collapsed in Vermont and New Hampshire and were declining in New York and Massachusetts. We used detailed aerial defoliation surveys from state agencies in study

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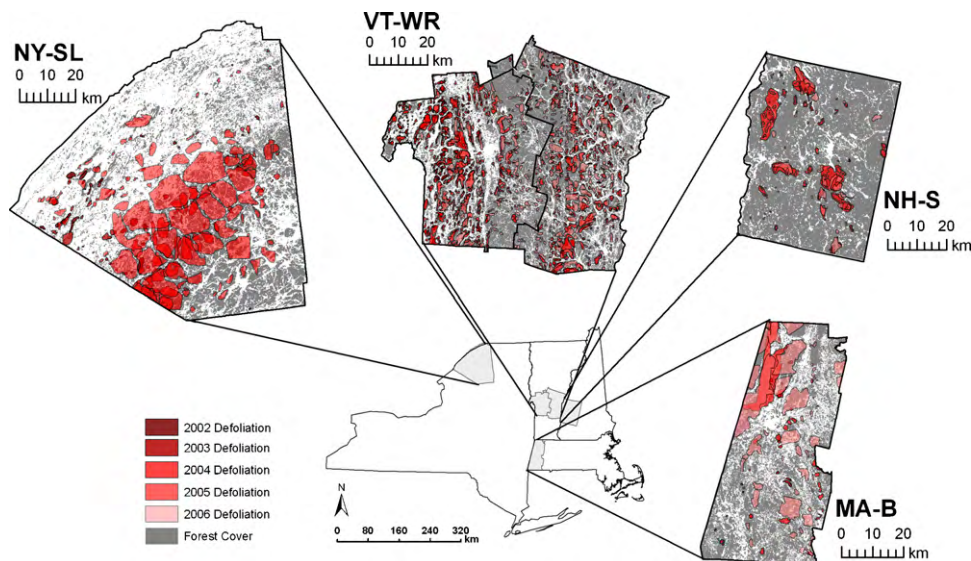


Fig. 1. Study regions showing forest cover and aerially observed defoliation damage. Defoliation by year from 2002 to 2006 is depicted by transparent layers to allow multiple defoliation events to be seen.

regions of these four states to examine whether fragmentation of sugar maple-dominated northern hardwood forests is associated with greater duration of FTC outbreaks.

2. Methods

2.1. Study region selection

We focused on four study areas in the northeastern U.S.: St. Lawrence County, New York (NY-SL), 7306 km²; Windsor and Rutland Counties, Vermont (VT-WR), 4975 km²; Berkshire County, Massachusetts (MA-B), 2451 km²; and Sullivan County, New Hampshire (NH-S), 1430 km² (Fig. 1). These areas were selected because northern hardwoods were the dominant forest cover type, they experienced significant defoliation during the recent outbreak, and defoliation was aerially mapped and subsequently ground-truthed to determine the defoliating insect species. The NY-SL study region experienced approximately 175,000 ha of FTC defoliation in 2005, with lesser amounts in 2004 and 2006. The VT-WR study region also suffered defoliation from 2004 to 2006 although the area affected was smaller than in NY. The MA-B and NH-S study regions had their most severe defoliations in 2006.

2.2. GIS layers

Defoliation was aerially sketch-mapped each summer after the cessation of larval feeding by experienced technicians from state environmental or forestry agencies in NY, VT, MA, and NH. During the flights, defoliation polygons were drawn on digital aerial photos using real-time GPS on a touch-screen tablet PC. The polygons were then converted into ArcGIS shapefiles (ESRI, 2006). Reflecting the history of the outbreak, we used FTC defoliation layers from 2002 to 2006 in NY-SL, 2003 to 2006 in VT-WR, 2004 to 2006 in MA-B, and 2005 to 2006 in NH-S. Across all years, defoliation was greatest in NY-SL, covering 26% of the study region land area, followed by VT-WR (24%), MA-B (23%) and NH-S (11%). Forest tent caterpillar populations collapsed following the 2006 season in VT and NH; no defoliation was observed in aerial surveys in 2007. We did not include defoliation data after 2006 in MA or NY, either, although minor areas were still affected in our study regions (USDA Forest Health Monitoring reports, 2006, 2007, 2008) (<http://fhm.fs.fed.us/fhh/neregion.shtml>). Point sam-

ples from all study regions were coded by the number of years of defoliation within the current outbreak (zero, one, and two or more years).

Forest cover was extracted from the 2001 National Land Cover Database (Vogelmann et al., 2001), which has a resolution of 30 m. We defined forest cover as a composite of deciduous, coniferous, forested wetlands, and mixed forest. Species-level forest cover data were not available. Sugar maple, birch (*Betula* spp.), white ash (*Fraxinus americana* L.), black cherry (*Prunus serotina* Ehrh.), aspens (*Populus* spp), and occasionally American beech (*Fagus grandifolia* Ehrh.) are defoliated by FTC during outbreaks. Oaks (*Quercus* spp.) are minor species in this forest type but are also defoliated by FTC (Connola et al., 1957; Batzer and Morris, 1978). Wandering late-stage larvae will feed on red maple (*Acer rubrum* L.) in these forests, but it is rarely defoliated (Wink and Allen, 2007).

Within each study region, we sampled points using a square grid. The grid size was selected so that polygons of defoliation would be independently sampled. A 5 km² grid was used for the VT-WR, MA-B, and NH-S study regions. A larger grid was used in NY-SL (7.5 km²) because defoliation occurred in larger patches there (Fig. 1). Point samples were used only if they fell on or within 50 m of forest cover (Fig. 2). We did not use plots if they contained large areas of agriculture, water, or urban development. Outbreak duration was assessed at the center of the plot.

At each point, we created plots with radii of 100 m (0.03 km²), 500 m (0.79 km²), and 1000 m (3.14 km²) in ArcGIS 9 (ESRI, 2006). For all three plot sizes, percent forest cover was derived by dividing the total forested area by the plot area. We expressed forest edge as km of edge per ha of forest area, where higher values of forest edge indicate greater forest fragmentation.

Our largest plots, 1 km in radius, were separated by a minimum of 3 km at their outer edges (5.5 km in NY-SL), in cases where adjacent point samples were used. To test whether these points functioned as independent samples, we assessed spatial autocorrelation in our measures of forest fragmentation (Baskent, 1999), using GeoDA software (Anselin, 2003) and our ArcGIS shapefiles. For the largest plots, we found that spatial autocorrelations were weak (values closer to 0 than to 1 for Moran's I), averaging 0.24 for cover and 0.23 for edge across the four study regions. The highest values were 0.46 for cover in NY-SL and 0.46 for edge in NH-S. The smaller plots (500 m and 100 m radii), not surprisingly, showed even weaker autocorrelations: 0.02–0.03 in NY-SL, MA-B, and NH-

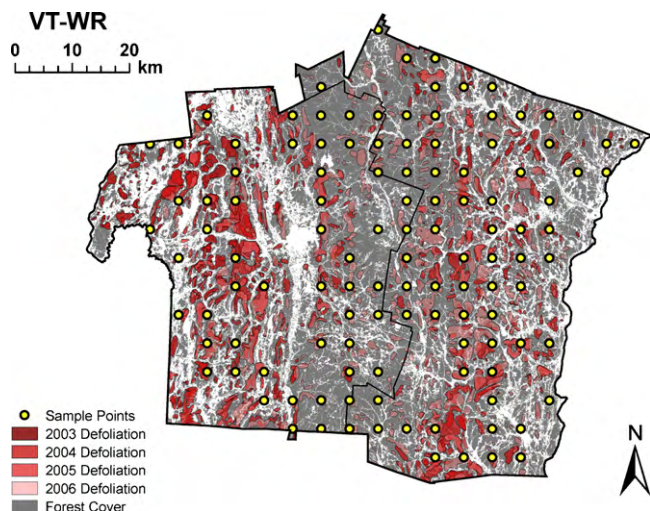


Fig. 2. The VT-WR study region showing the sample locations. Sampling points were used only if they fell on or within 50 m of forest cover.

S, and 0.10 in VT-WR, indicating that the grid size and plot size we used provided independent observations of forest fragmentation.

2.3. Statistical analysis

Differences in forest cover and forest edge were tested using a general linear model with Waller-Duncan grouping. Outbreak duration was modeled as a function of forest cover and forest edge using general linear models. Because some study regions had higher overall fragmentation than others, we included the interaction with study region in the model in addition to the main effects to determine if the relationship differed by study region. All statistical analyses were performed using SAS statistical software (SAS Institute, Cary, NC, USA).

3. Results

Forest cover was consistently greater in the plots in New Hampshire and Vermont than in Massachusetts or New York ($P < 0.001$; Fig. 1). The NH-S study region had the highest percentage of forest cover in the 500-m and 1000-m radius plots (84% in both), and VT-SL had 77–81% forest cover at these plot sizes (Fig. 3). The NY-SL (58–64%) and MA-B study regions (69–73%) were generally less forested, due to a greater amount of agriculture in NY-SL and urban and residential development in MA-B (Fig. 3). Forest edge relative to forest area, the other measure we used of forest fragmentation, was high where forest cover was low (Pearson correlation $r = -0.75$), as expected (Fig. 3).

Forest cover tended to be greater and forest edge lower in smaller-sized plots (Fig. 3), because plots were not included if the plot center was not forested. In VT-WR, the smallest plots (100-m radius) averaged 99.9% forest cover with very little edge. In NY-SL, the plots without defoliation had the opposite pattern, with greater fragmentation encountered in the largest plots.

Defoliation was greatest in NY-SL, covering 26% of the study area, followed by VT-WR (24%), MA-B (23%) and NH-S (11%) (Fig. 1). In total, there were 98 point samples with defoliation: 71 with one year of defoliation and 27 with two or more years. Points with zero defoliation represented 254 of the 352 samples in the study.

Contrary to our expectations, outbreak duration increased with forest cover in all study regions (Fig. 3, Table 1). The relationship was strong ($P < 0.0001$) at all three plot sizes: 100-m, 500-m, and 1000-m radius. The effect of regions was significant for the 100-m

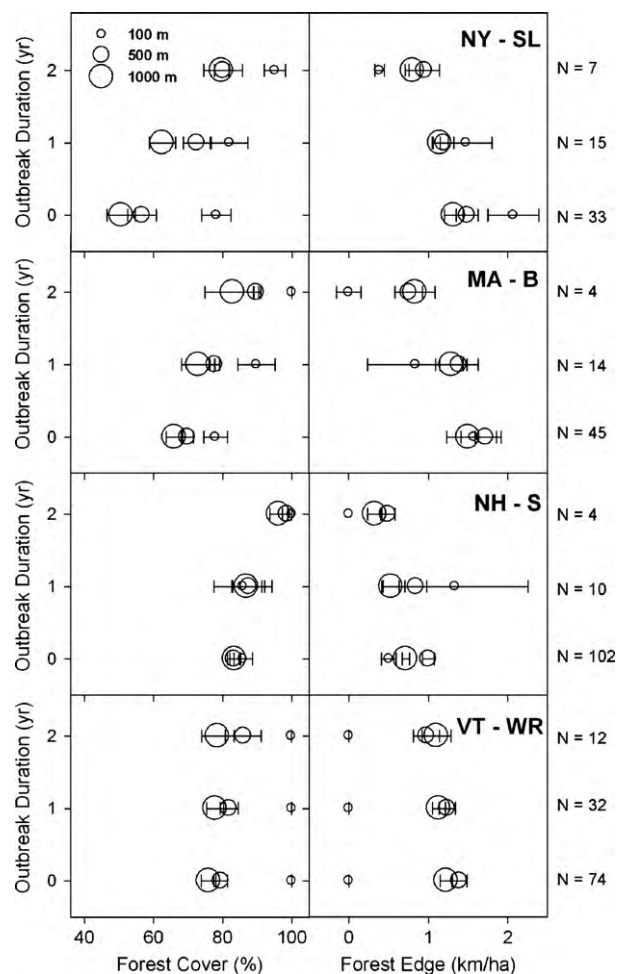


Fig. 3. Outbreak duration (0, 1, ≥ 2 y) as a function of average forest cover and average forest edge for each of the four regions. The sizes of the symbols indicate the three plot sizes used in the study. Error bars represent the standard error of the mean.

plots ($P < 0.0001$), but not the 500-m ($P = 0.69$) or 1000-m ($P = 0.30$) plots. The average outbreak duration on our plots was longest in NY-SL (0.53 y) and VT-WR (0.45 y) and shortest in NH-S (0.16 y); MA-B was intermediate (0.34 y). The interaction of forest cover and region was significant at the 100-m scale ($P < 0.0001$); in VT-WR, there was no effect of forest cover on outbreak duration on these plots because they were almost all completely forested.

Outbreak duration was longer in plots with less forest edge (Fig. 3), consistent with our results for forest cover. This pattern was significant in the 500-m ($P < 0.0001$) and 1000-m ($P = 0.0002$) plots, but not for the 100-m plots ($P = 0.18$). Again, the regions differed significantly in outbreak duration. There were no significant interactions of forest edge and region (Table 1).

In contrast to our observations at the 100-m to 1000-m scale (0.03–3 km²), at the scale of the four study regions (1430–7306 km²), the most fragmented area, NY-SL, had the most defoliation. However, there was no relationship of outbreak duration and forest fragmentation when comparing the other three regions.

4. Discussion

In our study of northern hardwood forests in four northeastern states, FTC outbreaks were shorter in more fragmented forest, in contrast to conclusions drawn from studies of this insect in Canadian aspen forests (Roland, 1993, 2005). As in previous research

Table 1
Analysis of variance of outbreak duration as a function of fragmentation (forest cover or forest edge).

Variable	Sampling radius					
	100 m		500 m		1000 m	
	F	Pr > f	F	Pr > f	F	Pr > f
Forest cover	26.88	<0.0001	20.93	<0.0001	18.11	<0.0001
Study region	9.46	<0.0001	0.50	0.69	1.23	0.30
Forest cover × study region	10.54	<0.0001	1.65	0.18	2.27	0.08
Edge	1.78	0.18	15.94	<0.0001	14.07	0.0002
Study region	6.97	0.0001	5.57	0.0001	3.49	0.08
Edge × study region	1.57	0.20	0.69	0.56	0.98	0.40

with aspen forests, we used the amount of forest edge and forest cover as indicators of fragmentation. We found a stronger relationship between defoliation and forest fragmentation with forest cover as the independent variable than with forest edge, as was the case in some (Rothman and Roland, 1998; Roland, 2005) but not all of the Canadian studies (Roland, 1993; Roland and Kaupp, 1995; Roland et al., 1998; Cooke and Roland, 2000).

The explanation proposed for the longer duration of outbreaks in fragmented forests in the Canadian studies was that fragmentation disrupts the effectiveness of natural enemies, especially pathogens and parasitoids (Roland, 1993), thus reducing FTC mortality and lengthening the duration of outbreaks. Initial correlational and experimental studies provided some support for this hypothesis (Roland and Kaupp, 1995; Roland and Taylor, 1997). However, an experimental test of this relationship in aspen forests found that two parasitoids were unaffected by fragmentation and a third was more prevalent in more fragmented forests (Roth et al., 2006).

There are many differences between the forest types that might explain the opposite relationship of outbreak duration to forest fragmentation in our study and those conducted in Canada. Outbreak duration in temperate hardwoods tends to be short; severe defoliation occurred in only a single year in most of our plots. In contrast, aspen forests often sustain several consecutive years of heavy defoliation at a given site (Sippell, 1961; Ives, 1971; Witter et al., 1975; Hodson, 1977; Cooke et al., 2009). Longer outbreaks may indicate that natural enemies in aspen-dominated forests are less effective, perhaps taking longer to respond to population growth of FTC. The same species of parasitoids dominate in both forest types, namely *Arachnidomyia aldrichi* Parker, *Patelloa pachygyga* Aldrich & Webber, *Leschenaultia exul* Townsend, and *Carcelia malacosomae* Sellers (Sippell, 1961; Parry, 1995; Eggen, 1987). However, the relative importance of different natural enemies may vary, as has been shown along a latitudinal gradient for autumnal moth (*Epirrita autumnata*), a major defoliator in northern Europe (Klemola et al., 2002). Collapsing populations in our study area were associated with larval mortality from the fungus *Furia gazpachae* and pupal parasitism by *A. aldrichi* and not with anomalous weather conditions.

Other factors that differ between these forest types include physiography, climate, and species composition. Several of the Canadian studies took place in aspen parklands, which are mostly situated on lacustrine plains with gentle topography (Ricketts et al., 1999). The region is fairly dry; mean annual precipitation ranges from 38 cm to 70 cm. In contrast, the northern hardwood forests we studied occur on hilly to mountainous topography, at elevations of up to 1000 m (Eyre, 1980). The climate is cool and moist, with annual precipitation commonly in excess of 100 cm. These differences in the physical environment undoubtedly affect the population dynamics of the insect and potentially its interactions with its natural enemies.

The climate and topography in the northern hardwood region sustain a mixture of micro-sites that support diverse forest communities across the landscape (Ricketts et al., 1999). These forests

include a significant proportion of less-favored hosts such as American beech (*F. grandifolia* Ehrh.) and yellow birch (*Betula alleghaniensis* Britton) (Fitzgerald, 1995) and non-hosts such as red maple and conifers. This matrix of preferred and non-preferred hosts may contribute to the spatial patterns of outbreaks. In contrast, aspen in sub-boreal forest types commonly occurs in pure stands (Eyre, 1980), often of the same clone (Brinkman and Roe, 1975). In aspen forests, outbreaks affect large contiguous areas at fairly regular intervals (Cooke and Roland, 2007; Hartmann and Messier, 2008), while outbreak patterns in northern hardwood forests are more patchy in space and time (Fig. 1), which may contribute to the differences in factors controlling outbreak duration.

Clearly, more research is needed to ascertain a mechanistic basis for the different relationship with forest fragmentation between the regions. We had hoped that our analysis of effects at different spatial scales would identify likely mechanisms, but we found similar effects at all the scales we tested, from 3 ha to 300 ha. In Ontario, Roland's (1993) observational units were township sized plots (~10,000 ha), which were considered defoliated if a third or more of the township was defoliated in any given year. Thus, the spatial scale was both larger and coarser than in our study. The temporal scale of Roland's study spanned 34 years, a much longer period than ours. Although long time spans may provide better resolution about spatial dynamics of insect outbreaks, the relationship between defoliation and fragmentation in our study is so clearly different from that shown in Ontario that it seems unlikely that a longer time series in the northern hardwood forest type would reveal a different pattern.

Multiple years of defoliation predisposes sugar maple to decline, especially on marginal sites (Allen, 1987; Houston et al., 1990; Horsley et al., 2002). Sugar maple is important economically for wood products, syrup production, and tourism for fall foliage displays (NERAG, 2002; NYSDEC, 2007). Understanding the factors controlling outbreak duration could have implications for forest management. Better information on the conditions that make some stands susceptible to defoliation and subsequent damage especially following multiple defoliation events (Wood et al., 2009) can help direct mitigation efforts such as harvesting or operational spraying with *Bacillus thuringiensis* (*Bt*).

5. Conclusion

Forest tent caterpillar outbreaks occur in many forest types, which vary dramatically in climate, species composition, and natural enemy complexes (Parry and Goyer, 2004). The idea that forest fragmentation increases the duration of FTC outbreaks has been widely accepted, but the evidence has been mostly correlational and derived from one forest type. Our study, while also correlational, suggests that the relationship between the duration of insect outbreak and forest fragmentation may not be universal, even within the range of a single defoliator species.

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