EFFECTS OF CLIMATE AND FOREST STRUCTURE ON DURATION OF FOREST TENT CATERPILLAR OUTBREAKS ACROSS CENTRAL ONTARIO, CANADA

JENS ROLAND

Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

BRENDAN G. MACKEY

Department of Geography, The Australia National University, Canberra ACT 0200, Australia

and BARRY COOKE

Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9

Abstract

The Canadian Entomologist **130**: 703 – 714 (1998)

We examined the effect of forest structure and climate on large-scale and long-term patterns of outbreaks of forest tent caterpillar, *Malacosoma disstria* Hbn., across central Ontario. This was done using previously published data on outbreak duration and forest heterogeneity, combined with high-resolution climatic data simulated by the recently developed Ontario Climate Model. Our analysis, which eliminates some of the spatially confounding effects of forest structure and climate, suggests that both the predicted long-term temperature minimum for the coldest month and the predicted growing degree-days in the first 6 weeks of the growing season are important determinants of outbreak duration, with colder weather being associated with shorter outbreaks. Forest heterogeneity accounts for more variation in outbreak duration than either of the climatic variables.

Roland, J., B.G. Mackey et B. Cooke. 1998. Effect du climat et de l'hétérogenéité de la forêt sur la durée des épidémies de la livrée de la forêt en Ontario, Canada. *The Canadian Entomologist* **130** : 703–714.

Résumé

Nous examinons l'effet de deux types de facteurs, l'hétérogenéité de la forêt et le climat, sur les patterns à long-terme des épidémies de la livrée de la forêt, *Malacosoma disstria* Hbn., dans la région centrale de la province de l'Ontario, Canada. L'analyse spatiale présentée ici considère simultanément des données forestière et épidémique extraites de la littérature, et de nouvelles données climatiques simulées à fine-échelle avec un nouveau modèle climatique pour l'Ontario. Notre analyse, qui élimine l'effet géographiquement confondant de l'hétérogenéité de la forêt et le climat, démontre que deux indices climatiques, la température minimum quotidienne attendue pendant l'hiver et le nombre attendu de degrés-jours depuis le début du printemps, sont importants en expliquant la variation spatiale dans la durée des épidémies, la froidesse étant associée à de courtes épidémies. Néanmoins, l'hétérogenéité de la forêt explique plus de variation que ces deux indices climatiques.

Introduction

A primary goal of forest insect population studies is to explain patterns of outbreak and decline of fluctuating populations. Many studies of lepidopteran population dynamics have examined factors associated with sudden widespread fluctuations in population density, including the perturbation effects of density-independent factors, such as weather, and regulatory effects of density-dependent factors, such as disease and parasitism. Examples include the effect of drought on fir engraver *Scolytus ventralis* LeC. (Berryman 1973), the impact of parasitoids on populations of forest tent caterpillar *Malacosoma disstria* Hbn. (Hodson 1977) and spruce budworm *Choristoneura fumiferana* (Clem.) (Morris and Miller 1954), and the effect of disease on Douglas-fir tussock moth *Orygia pseudotsugata* (McD.) (Morris 1963). In the case of forest tent caterpillar, studies historically have taken a single-factor approach to testing if a given factor, or kind of factor such as weather, disease, predation, or parasitism, is associated with the release, duration, or collapse of outbreaks.

Outbreak Severity and Perturbation from Weather. Extreme weather has often been cited as a primary factor in initiating releases (Ives 1973) and precipitating collapses (Prentice 1954; Gautreau 1964) of forest tent caterpillar outbreaks. Specifically, cold spring weather has been blamed for the early-season losses of larvae, presumably through freezing and subsequent death of either foliage or young larvae (Blais et al. 1955), and extreme cold winter weather has been blamed for high egg mortality due to freezing (Witter and Kulman 1972). Laboratory experiments have clearly demonstrated that all life-stages are susceptible to cold (Salt 1936; Hanec 1966; Wetzel et al. 1973; Raske 1975). Daniel and Myers (1995) used a correlational approach to test whether, in Ontario, large-scale patterns of annual spring or winter weather corresponded with long-term fluctuations in outbreak severity. They concluded that there was little evidence supporting the spring-weather hypothesis, and only weak evidence supporting the winter-weather hypothesis.

Outbreak Severity and Density-dependent Factors. The fact that correlations between winter cold and fluctuations in tent caterpillar outbreak severity are generally weak (Daniel and Myers 1995) might seem surprising, given the convincing results from cold-treatment experiments. However, such weak correlations between annual fluctuations in a density-independent key factor (e.g., weather) and annual fluctuations in indices of abundance (e.g., defoliation) are expected on theoretical grounds because long-term patterns such as cyclicity, which are caused largely by lagged density-dependent factors, mask the effects of density-independent perturbations (Royama 1981). This is especially relevant for studies of tent caterpillar dynamics because the periodic pattern of outbreaks they exhibit is thought to be driven in part by lagged density-dependent processes such as disease (Stairs 1966) and parasitism (Sippell 1962; Witter et al. 1975; Witter and Kulman 1979).

Outbreak Duration and Climate. Province-wide defoliation maps of Ontario (Sippell 1962) and Alberta (Ives 1971) show that severe outbreaks become less prevalent as one moves northward from the warmer deciduous forests of southern Canada to the colder coniferous forests of northern Canada. Due to latitudinal confounding, however, it is unclear whether climate, forest structure, or both help to shape the northern limit of tent caterpillar outbreaks. Indeed, when considering such a large latitudinal range, almost any arbitrarily chosen bioclimatic gradient would correlate spuriously with outbreak duration. One simple way to assess the roles of climate and forest structure in determining spatial variation in outbreak duration would be to consider climatic and habitat factors simultaneously, being sure to choose a study area that minimizes latitudinal confounding between those factors.

Outbreak Duration and Density-dependent Factors. Teasing apart the effects of density-independent and density-dependent factors has been a major challenge for studies of population dynamics (Royama 1996). Although there is an increasing interest in doing so at larger and multiple scales, data availability is a universal constraint. For example, in Canada, historical weather data sample a wide geographic range but with relatively poor resolution; spatial data for density-dependent factors, such as disease and parasitism, are by and large nonexistent for the forest tent caterpillar.

In the absence of well-resolved, large-scale data on density-dependent factors, one solution is to consider an alternative exogenous factor that has a strong impact on the key density-dependent factors, that varies significantly over the study area, and for which well-resolved, large-scale data are available. Forest structure is one such factor. It has been shown, for instance, that the presence of agricultural clearings, either through edge effects or stand-isolation effects, reduces the efficacy of forest tent caterpillar viruses (Roland and Kaupp 1995) and parasitoids (Roland and Taylor 1995, 1997; Roland et al. 1997). Also, forest heterogeneity, measured as the ratio of forest edge to forest area, is positively correlated with mean duration of forest tent caterpillar outbreaks in Ontario (Roland 1993). Thus forest structure might be considered a filter through which density-dependent mortality operates: large-scale variation in forest heterogeneity may lead to spatial variation in outbreak dynamics through its differential effects on these regulatory processes.

By examining the relationship between forest heterogeneity and mean outbreak duration over a restricted latitudinal range, namely the southern edge of Ontario's mixed boreal forest, Roland (1993) attempted to limit latitudinal confounding of forest and climate effects. Consequently, the relationship between forest heterogeneity and outbreak duration could be extracted. However, as climate was not explicitly included in that analysis, elimination of latitudinal confounding between forest and climate could not be guaranteed. More importantly, 62% of the township-level (fine-scale) variation in outbreak duration could not be accounted for by forest heterogeneity. Here we seek to determine the roles of both climate, as simulated by a new climate model for Ontario (Mackey et al. 1996), and forest heterogeneity in determining patterns of forest tent caterpillar outbreaks across central Ontario.

Materials and Methods

Outbreak duration was estimated by counting the total number of years of outbreak by forest tent caterpillar during 1950–1984 for each of 297 townships (each approximately 100 km^2) located across nine forest districts in Ontario (see Roland 1993). Outbreak duration was related to three independent variables estimated for the same townships: degree of forest heterogeneity (HETEROG), predicted long-term temperature minimum for the coldest month (MINCOLD), and predicted growing degree-days in the first 6 weeks of the growing season (DEGDAYS).

Forest Tent Caterpillar Outbreak Data. Historical data on duration of outbreaks of forest tent caterpillar were obtained from long-term defoliation maps produced by the Forest Insect and Disease Survey (FIDS) of the Canadian Forest Service, Great Lakes Region (Roland 1993). Sketch maps of defoliation are produced by a combination of aerial and ground surveys across each forest district each year, and a township was considered to have an outbreak year if, in that year, more than one-third of it was indicated as being defoliated. This 35-year interval included three periods of general outbreak and collapse.

Forest Structure Data. To assess forest structure, we used 1 : 50 000 scale National Topographic System of Canada (NTS) topographic maps, which indicated forested and nonforested land for various years between the late 1970s and early 1980s. Forest heterogeneity (HETEROG) was estimated for each township as the number of kilometres of

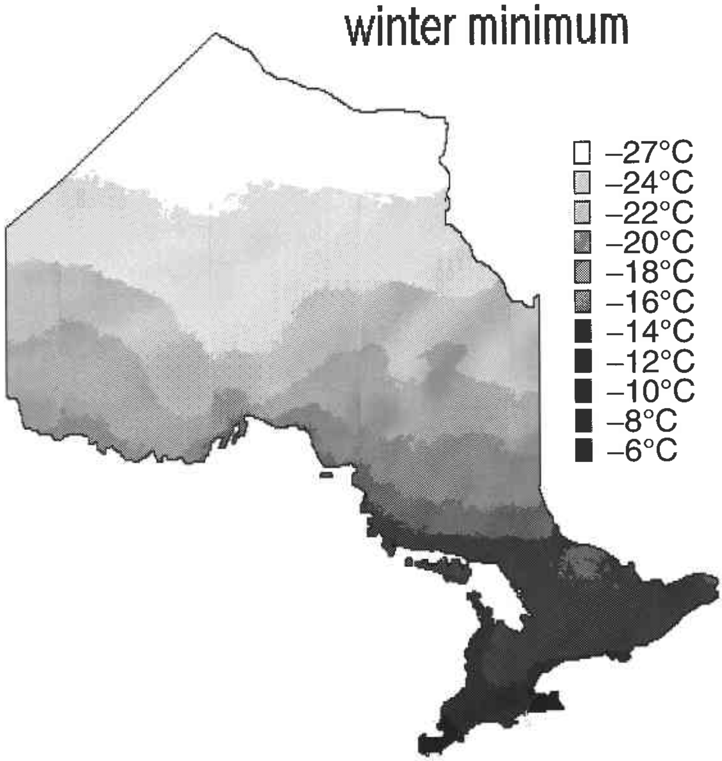

FIG. 1. Predicted long-term mean monthly minimum temperature for the coldest month (MINCOLD) across Ontario.

forest edge per square kilometre (Roland 1993). All townships had between 50 and 100% forest cover, so low forest heterogeneity was indicative of fairly continuous forest, while high forest heterogeneity was indicative of moderate forest cover with large amounts of forest edge, due mostly to agricultural clearing.

Climate Data. Two climatic variables were used in analyses of weather effects on tent caterpillar population dynamics. We used the predicted long-term temperature minimum for the coldest month (MINCOLD, Fig. 1) as an index of the risk of tent caterpillar eggs freezing in winter, and we used the predicted growing degree-days (above a threshold of 5°C) in the first 6 weeks of the growing season (DEGDAYS, Fig. 2) as an index of post-hatch larval development and vulnerability of caterpillars and foliage to spring frost, with warmer weather leading to favourable survival in both cases.

Estimates of the two climatic parameters were generated for each township using the Ontario Climate Model (OCM) (Mackey et al. 1996). Thin-plate smoothing splines were used to fit interpolation surfaces (Mackey et al. 1996) to long-term mean monthly temperature and precipitation data for 471 meteorological stations across Ontario. These surfaces were fitted as a function of latitude, longitude, and elevation, thereby capturing many of the fine-scale topographic dependencies of climate such as temperature lapse rates. The model can be used to describe climate at any location in the province for which latitude, longitude, and elevation are known.

A sequence of predicted minimum and maximum daily temperatures was calculated from the long-term monthly means. These were used to calculate predicted growing degree-days. Here the start of the growing season was defined as the first day past

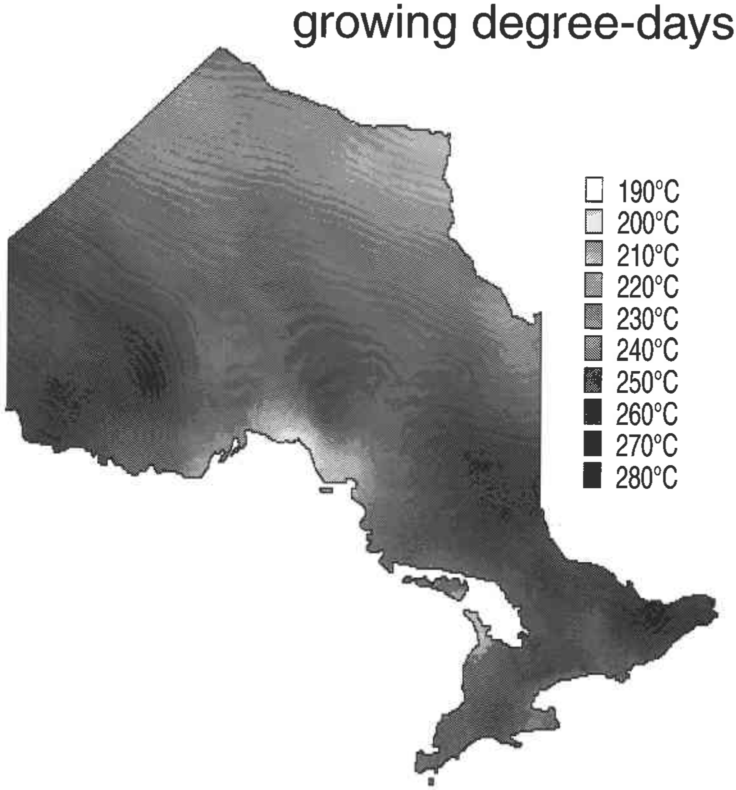

FIG. 2. Predicted degree-days in the first 6 weeks of the growing season (DEGDAYS) for Ontario. Wave patterns result from the combination of two estimated climate variables, namely date of the start of the growing season and degree-days since the start of the growing season.

March 1 when the simulated mean daily temperature had exceeded or equaled 5.0°C for five consecutive days, and the end was 6 weeks later.

Analysis. Correlation analysis was conducted on the forest and climate data, at two spatial resolutions, to assess the degree to which restricting the latitudinal extent of the study area prevented the confounding of these variables. Isotropic spatial autocorrelograms (GS+, Gamma Design Software, Plainwell, Michigan) were used to determine the extent to which township-level and district-level observations were spatially independent. Stepwise multiple linear regression (SYSTAT, Wilkinson et al. 1992) was then used to relate the two climate variables and forest heterogeneity to the duration of tent caterpillar outbreak. This was also done at two spatial resolutions: among all 297 townships and among the nine forest districts. Standardized correlation coefficients from the regression were used to assess the relative importance of each independent variable to outbreak duration.

Results

Correlation of Forest and Climate Variables. The forest and climate variables were uncorrelated with each other over the study region, although there were some statistically significant correlations among townships within individual districts (Table 1). For

TABLE 1. Pearson correlation coefficients (r^2) for the independent variables analyzed in Tables 2 and 3, for townships within each Ontario district

District	No. of townships	HETEROG and DEGDAYS	HETEROG and MINCOLD	MINCOLD and DEGDAYS
Thunder Bay	33	–0.468**	0.729**	–0.849**
Sudbury	32	0.035	0.316	–0.018
North Bay	34	0.036	0.433*	0.162
Sault Ste. Marie	31	0.026	0.733**	–0.476**
Blind River	31	0.175	0.459**	–0.241
Espanola	28	–0.847**	0.862**	–0.944**
Wawa	35	0.452**	–0.551**	–0.783**
Kirkland Lake	32	0.07	0.318	–0.351*
Fort Frances	41	0.041	0.358*	0.043
All districts	297	0.082	0.016	–0.149

* Significant at $\alpha = 0.05$.
** Significant at $\alpha = 0.01$.

example, Espanola, Thunder Bay, Sault Ste. Marie, and Wawa districts exhibited particularly strong within-forest district correlations, whereas the other districts showed weak correlations or no correlation.

Spatial Correlogram Analysis. Almost all variables in almost all districts showed significant positive spatial autocorrelation in distance classes ≤ 12 km, which diminished in significance for distances >12 km (correlograms not shown for all districts). Thunder Bay district showed the greatest amount of spatial dependence and is presented as a worst-case scenario vis à vis violation of the independence assumption of regression analysis (Fig. 3). In Thunder Bay district, correlograms of all four variables had the classic shape of a spatial gradient: positive autocorrelation in the short distance classes and negative autocorrelation in the long distance classes (Legendre and Troussellier 1988).

When all 297 townships were considered together, the climatic variables were positively spatially autocorrelated for distance classes ≤100 km, whereas forest and outbreak variables were positively spatially autocorrelated for distance classes ≤ 20 km and ≤ 30 km, respectively (Fig. 4). Because these patterns imply some pseudoreplication, especially of climatic variables, subsequent regression analyses were performed at two spatial resolutions, namely among townships and among district means.

Climate, Forest Structure, and Outbreak Duration. Residual plots of a multiple linear regression of outbreak duration on forest heterogeneity, spring degree-days, and minimum temperature, for all 297 townships, indicated that the error variance was not homogeneous (Fig. 5). Consequently, outbreak duration was $\log_{10}$ transformed for subsequent regression analyses.

With spatial resolution set to the township level (fine scale), both MINCOLD and DEGDAYS were significantly related to the duration of tent caterpillar outbreaks: townships with the coldest mean minimum temperature in winter had shorter tent caterpillar outbreaks, and townships with few degree-days in the first 6 weeks of the growing season had shorter outbreaks (Table 2). Forest heterogeneity (HETEROG) explained more of the variation in outbreak duration than did climatic variables, either singly or combined (Table 2). The fit of the township-level model is illustrated in Figure 6. Regressions involving district means provided similar results, despite the small sample size (Table 3; Fig. 7) and are not subject to the problem of lack of independence.

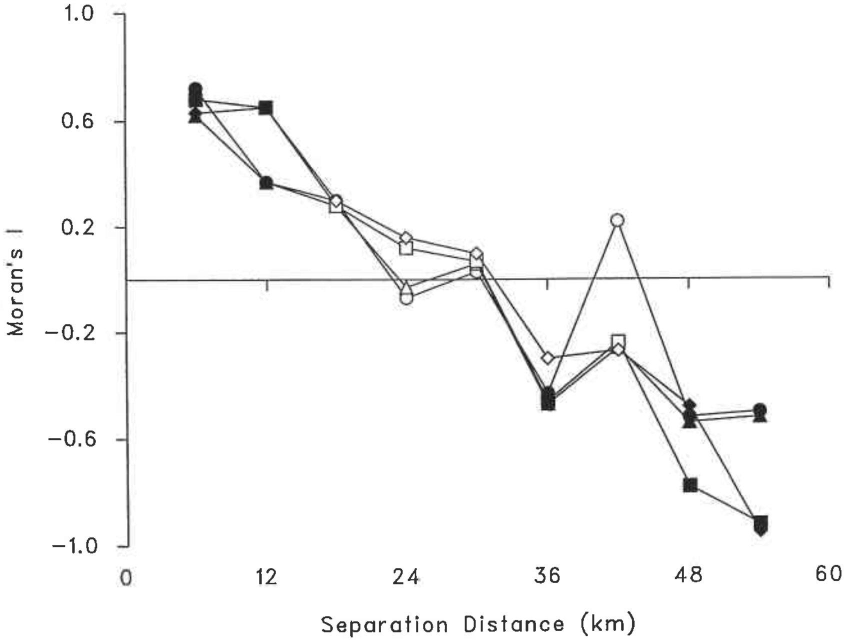

FIG. 3. Isotropic spatial autocorrelograms within Thunder Bay district (as an example). ○, outbreak duration; △, forest heterogeneity; □, minimum temperature; ◇, spring degree-days. Solid symbols indicate significant correlations at $\alpha = 0.05$.

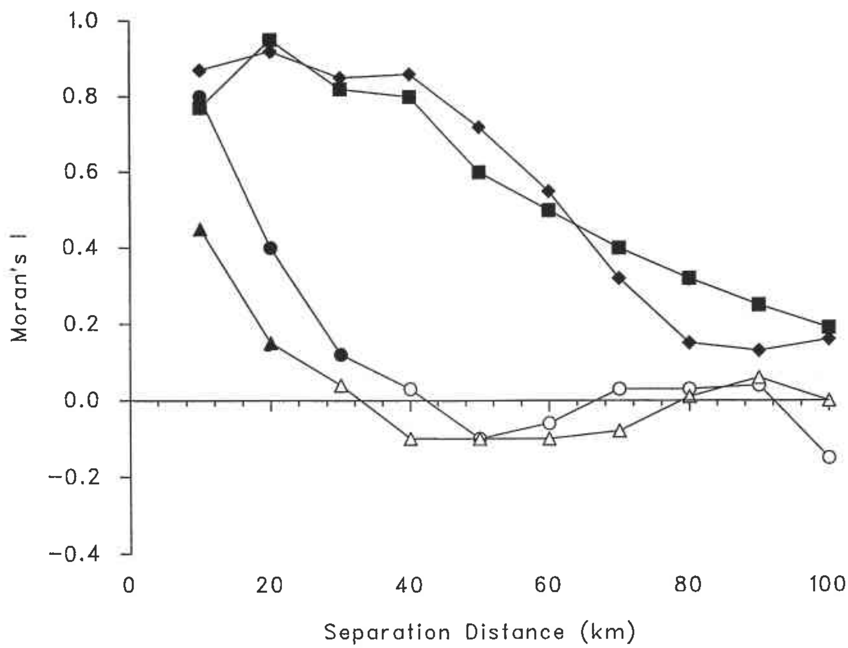

FIG. 4. Isotropic spatial autocorrelograms for all 296 districts. ○, outbreak duration; △, forest heterogeneity; □, minimum temperature; ◇, spring degree-days. Solid symbols indicate significant correlations at $\alpha = 0.05$.

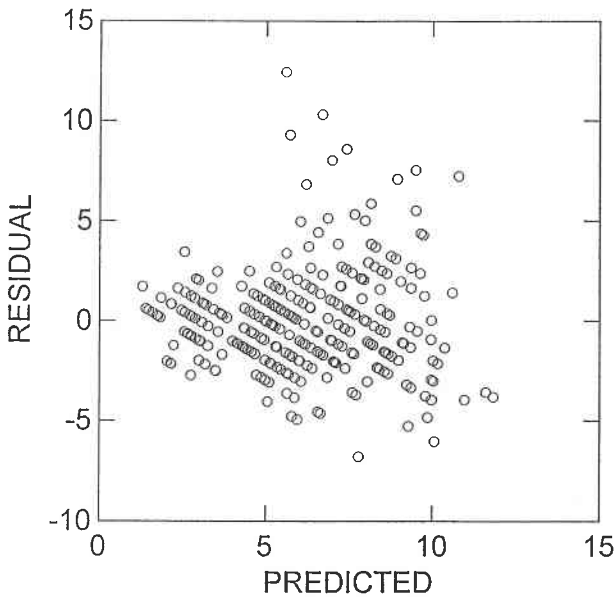

FIG. 5. Residual plot of township-level regression of outbreak duration on forest and climate variables.

TABLE 2. Among-township regression statistics from multiple linear regression of the effect of forest structure and climate variables on number of years of tent caterpillar outbreak ($\log_{10}$ transformed) in Ontario

Variable	Coefficient (SE)	Standardized coefficient	t	Significance P
HETEROG	0.170 (0.016)	0.458	10.57	<0.0001
DEGDAYS	0.005 (0.001)	0.358	8.33	<0.0001
MINCOLD	0.020 (0.004)	0.249	5.83	<0.0001

NOTE: R^2 for the full model is 0.48; N = 296.

Discussion

The significant effect of both weather variables on outbreak duration supports the hypothesis that poor weather, at certain times of year, can shorten outbreaks and favourable weather may prolong outbreaks. This is different from saying that certain types of weather directly cause increased or decreased outbreak severity. Daniel and Myers (1995) found a poor correlation between climate and change in defoliation (i.e., outbreak initiation or collapse) among all years. A poor correlation is not surprising because their hypothesis was that weather in any given year is the sole cause of change in defoliation index. Change in defoliation should correlate poorly with weather because most years with no defoliation (which are numerous) show no change in defoliation, yet weather in those years varies greatly. A strong relationship between change in defoliation and weather is possible only when the analysis is limited to that part of the outbreak cycle where changes in defoliation are in fact detectable. Even then, however, the strength of the relationship is limited by the fact that periodicity in tent caterpillar outbreaks arises partly from lagged density-dependent processes such as viral replication and parasitism which would be expected to obscure a relationship between weather and population change (Royama 1981). In contrast, our analysis relates outbreak duration to climatic means through space only. By using climatic means we avoid the problem of

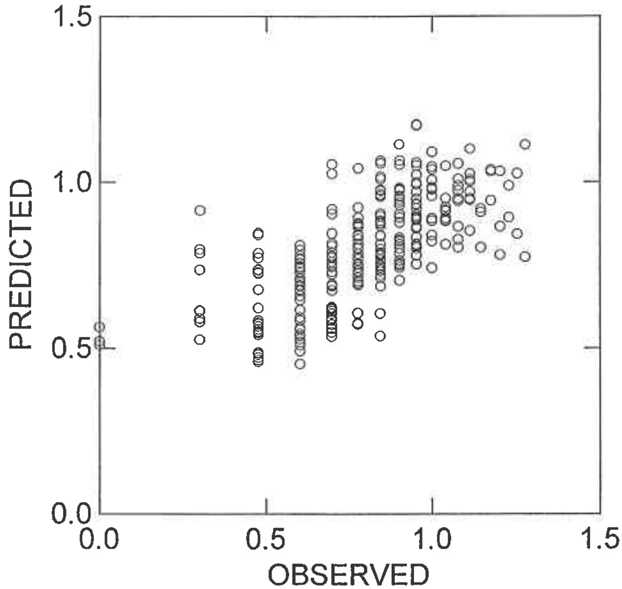

FIG. 6. Observed and predicted (from the fitted model, Table 2) township-level outbreak duration ($\log_{10}$ transformed).

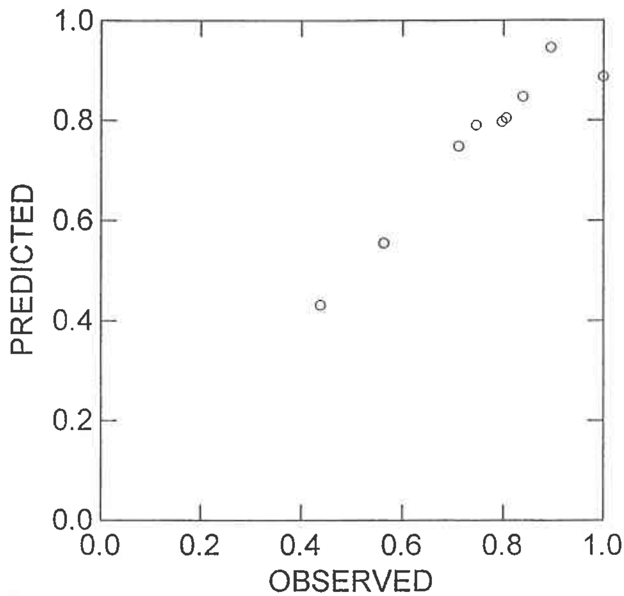

FIG. 7. Observed and predicted (from the fitted model, Table 3) district-level outbreak duration ($\log_{10}$ transformed).

searching for temporal correlations with density-independent factors which would be obscured in the presence of such lagged effects. What was sacrificed with our approach was the possibility of obtaining direct evidence of climatic perturbation effects via temporal coincidence between perturbations and population response.

TABLE 3. Among-district regression statistics from multiple linear regression of the effect of forest structure and climate variables on number of years of tent caterpillar outbreak ($\log_{10}$ transformed) in Ontario (1948–1989)

Variable	Coefficient (SE)	Standardized coefficient	t	Significance P
HETEROG	0.347 (0.083)	0.621	4.18	0.009
DEGDAYS	0.004 (0.001)	0.381	2.57	0.05
MINCOLD	0.020 (0.007)	0.377	3.01	0.03

NOTE: R^2 for the full model is 0.92; N = 9.

The lack of large-scale correlations between climate and forest data suggests that restricting the latitudinal extent of our study area was largely successful in limiting, but not eliminating, the confounding of these variables; finer scale correlations were not eliminated. Thus conclusions made at the large scale (e.g., between districts) may be less evident over smaller spatial extent such as among townships within districts.

In our study area, townships within a district were chosen to be at least 10 km apart from each other and more often a minimum of 20 km apart. Most variables in most districts showed significant positive spatial autocorrelation at distances less than 12 km. This slight dependence among some samples suggests that analysis of township-level data within a district may detect more significant differences than are warranted (Legendre 1993); the damping of the autocorrelations beyond 12 km suggests it is minimally so. We did not conduct regression analyses at that scale, however, because our goal was to explain variation in outbreak duration across the whole study area. Spatially explicit analytical techniques such as those described by Legendre (1993) may be useful in explaining finer scale variation in outbreak duration, and this possibility is under investigation.

The large amount of spatial autocorrelation that resulted from increasing the spatial extent of the study area to include all nine districts led to a pseudoreplicated design (Hurlbert 1984). The stronger autocorrelation in climatic variables relative to forest heterogeneity suggests that the climatic variables were accounting for large-scale variation in outbreak duration (e.g., variation among districts) while forest heterogeneity was explaining more finely scaled variation in outbreak duration (e.g., variation among townships). Interestingly, the district-level regression, which remedied the pseudoreplication problem by drastically reducing the degrees of freedom, yielded the same conclusion as the township-level regression: forest heterogeneity and both climatic variables are significantly and positively related to outbreak duration, forest heterogeneity exhibiting a stronger relationship than either spring degree-days or minimum temperature. It seems that forest heterogeneity may be functional over both scales.

The exact mechanism by which forest heterogeneity affects tent caterpillar population dynamics is as yet not known, but there are several plausible explanations. The impact of several natural enemies is lower in fragmented forests than in continuous forests, because of either reduced dispersal (Roland and Kaupp 1995; Roland and Taylor 1995; Roland et al. 1997) or reduced efficacy (Roland and Taylor 1997). Several species of parasitoids attacking forest tent caterpillar (Batzer 1955; Parry 1995; Roland et al. 1997) cause lower rates of parasitism along forest edges, a pattern seen for other forest insects such as gypsy moth *Lymantria dispar* (L.) (Weseloh 1972, 1976) and the tortricid *Epinotia tedella* (Cl.) (Münster-Swendsen 1980). Isolation effects of habitat fragmentation do limit dispersal of other insect parasitoids (Kruess and Tscharntke 1994), and may do the same for parasitoids of the tent caterpillar (Roland and Taylor 1995, 1997; Roland et al. 1997). Density-dependent response of parasitoids to tent caterpillars abundance is significant in continuous forests and absent in fragmented forests

(Roland and Taylor 1997). Finally, although we have shown that some effect of forest heterogeneity is independent of climate, climate may still interact with forest structure. For example, cold spring weather may be ameliorated in open, sunny, fragmented forests, possibly resulting in more rapid development of caterpillars and pupae (Fitzgerald 1995).

Our main point is that inclusion of climatic data in our analysis in no way overturned the conclusions drawn by Roland (1993): continuous forests may permit density-dependent regulatory processes to function "normally," whereas fragmented forests may reduce this capability. Indeed, our results support the view that weather, as a perturbation on early stage survival, and forest heterogeneity, as a filter for density-dependent processes, both affect the duration of tent caterpillar outbreaks, and may serve as a general explanation for large-scale variation in forest tent caterpillar dynamics. We emphasize that our conclusions are scale dependent, and that other factors may be governing other processes relevant to tent caterpillar dynamics, particularly at scales much larger and much smaller than those employed in this study.

Acknowledgments

Gordon Howse (Canadian Forest Service) provided access to defoliation map data, and Darcy Ortiz (Canadian Forest Service) assisted with collation of data. Access to Ontario Climate Model data was kindly provided by Dan McKenney (Canadian Forest Service) as part of on-going collaborations with the NatGRID Project. Research was supported by the Canadian Forest Service and a Natural Sciences and Engineering Research Council of Canada Operating Grant to JR.

References

Batzer, H.O. 1955. Some effects of defoliation of aspen, *Populus tremuloides* Michx., stands in northern Minnesota by the forest tent caterpillar, *Malacosoma disstria* Hbn., with notes on parasitism of cocoons by *Sarcophaga aldrichi* Park., and cocooning habits of the host. M.Sc. thesis, University of Minnesota, St. Paul, MN.

Berryman, A.A. 1973. Population dynamics of the fir engraver, *Scolytus ventralis* (Coleoptera: Scolytidae). I. Analysis of population behavior and survival from 1964 to 1971. *The Canadian Entomologist* **105**: 1465–1488.

Blais, J.R., R.M. Prentice, W.L. Sippell, and D.R. Wallace. 1955. Effects of weather on the forest tent caterpillar, *Malacosoma disstria* Hbn., in central Canada in the spring of 1953. *The Canadian Entomologist* **87**: 1–8.

Daniel, C.J., and J.H. Myers. 1995. Climate and outbreaks of the forest tent caterpillar. *Ecography* **18**: 353–362.

Fitzgerald, T.D. 1995. The tent caterpillars. Cornell University Press, Ithaca, NY.

Gautreau, E.J. 1964. Unhatched forest tent caterpillar egg bands in northern Alberta associated with late spring frost. *Canadian Department of Forestry Forest Entomology and Pathology Branch Bi-monthly Progress Report* **20**: 3.

Hanec, A.C. 1966. Cold-hardiness in the forest tent caterpillar, *Malacosoma disstria* Hübner (Lasiocampidae; Lepidoptera). *Journal of Insect Physiology* **12**: 1443–1449.

Hodson, A.C. 1977. Some aspects of forest tent caterpillar population dynamics. pp. 4–16 *in* Kulman, H.M., and H.C. Chaing (Eds.), Insect ecology: papers presented in the H.C. Hodson ecology lectures. *University of Minnesota Agriculture Experiment Station Technical Bulletin* 310.

Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**: 187–211.

Ives, W.G.H. 1971. The forest tent caterpillar in Alberta. *Environment Canada Forest Service Internal Report* **NOR-4**.

——— 1973. Heat units and outbreaks of the forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae). *The Canadian Entomologist* **105**: 529–543.

Kruess, A., and T. Tscharntke. 1994. Habitat fragmentation, species loss, and biological control. *Science (Washington, D.C.)* **264**: 1581–1584.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm. *Ecology* **74**: 1659–1673.

Legendre, P., and M. Trousellier. 1988. Aquatic heterotrophic bacteria: modeling in the presence of spatial autocorrelation. *Limnological Oceanography* **33**: 1055–1067.

Mackey, B., D.W. McKenney, Y.-Q. Yang, J.P. McMahon, and M.F. Hutchinson. 1996. Site regions revisited: a climatic analysis of Hills' site regions for the province of Ontario using a parametric method. *Canadian Journal of Forest Science* **26**: 333–354.

Morris, O.N. 1963. The natural and artificial control of the Douglas-fir tussock moth, *Orygia pseudotsugata* McDunnough, by a nuclear polyhedrosis virus. *Journal of Insect Pathology* **5**: 401–414.

Morris, R.F., and C.A. Miller. 1954. The development of life tables for the spruce budworm. *Canadian Journal of Zoology* **32**: 283–301.

Münster-Swendsen, M. 1980. The distribution in time and space of parasitism in *Epinotia tedella* (Cl.) (Lepidoptera: Tortricidae). *Ecological Entomology* **5**: 373–383.

Parry, D. 1995. Larval and pupal parasitism of the forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), in Alberta. *The Canadian Entomologist* **127**: 877–893.

Prentice, R.M. 1954. Decline of populations of the forest tent caterpillar in central Saskatchewan. *Canadian Forest Service Bi-Monthly Progress Reports* **10**(5): 2.

Raske, A.G. 1975. Cold-hardiness of first instar larvae of the forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae). *The Canadian Entomologist* **107**: 75–80.

Roland, J. 1993. Large-scale forest fragmentation increases the duration of tent caterpillar outbreak. *Oecologia* **93**: 25–30.

Roland, J., and W.J. Kaupp. 1995. Reduced transmission of forest tent caterpillar NPV at the forest edge. *Environmental Entomology* **24**: 1175–1178.

Roland, J., and P.D. Taylor. 1995. Herbivore – natural enemy interactions in fragmented and continuous forests. pp. 195–208 *in* Cappuccino, N., and P.W. Price (Eds.), Population dynamics: new approaches and synthesis. Academic Press, San Diego, CA.

——— 1997. Insect parasitoid species respond to forest structure at different spatial scales. *Nature (London)* **386**: 710–713.

Roland, J., P.D. Taylor, and B. Cooke. 1997. Forest structure and the spatial pattern of parasitoid attack. pp. 97–106 *in* Watt, A.D, N.E. Stork, and M.D. Hunter (Eds.), Forests and insects. Chapman and Hall, New York.

Royama, T. 1981. Fundamental concepts and methodology for the analysis of animal population dynamics, with particular reference to univoltine species. *Ecological Monographs* **51**: 473–493.

——— 1996. Analytical population dynamics. 2nd ed. Chapman & Hall, New York.

Salt, R.W. 1936. Studies on the freezing process in insects. *University of Minnesota Agricultural Experiment Station Technical Bulletin* **16**.

Sippell, W.L. 1962. Outbreaks of the forest tent caterpillar *Malacosoma disstria* Hbn., a periodic defoliator of broad leafed trees in Ontario. *The Canadian Entomologist* **94**: 408–416.

Stairs, G.R. 1966. Transmission of virus in tent caterpillar populations. *The Canadian Entomologist* **98**: 1100–1104.

Weseloh, R.M. 1972. Spatial distribution of gypsy moth (Lepidoptera: Lymantriidae) and some of its parasitoids within a forest environment. *Entomophaga* **17**: 339–351.

——— 1976. Behavior of forest insect parasitoids. pp. 99–110 *in* Anderson, J.F., and H.K. Kaya (Eds.), Perspectives in forest entomology. Academic Press, New York.

Wetzel, B.W., H.M. Kulman, and J.A. Witter 1973. Effects of cold temperatures on hatching of the forest tent caterpillar, *Malacosoma disstria* (Lepidoptera: Lasiocampidae). *The Canadian Entomologist* **105**: 1145–1149.

Wilkinson, L., M. Hill, S. Miceli, G. Birkenbeuel, and E. Vang. 1992. SYSTAT for Windows: version 5. Systat Inc., Evanston, IL.

Witter, J.A., and H.M. Kulman. 1972. A review of the parasites and predators of tent caterpillars (*Malacosoma* spp.) in North America. *University of Minnesota Agricultural Experiment Station Technical Bulletin* **289**.

——— 1979. The parasite complex of the forest tent caterpillar in northern Minnesota. *Environmental Entomology* **8**: 723–731.

Witter, J.A., W.J. Mattson, and H.M. Kulman. 1975. Numerical analysis of a forest tent caterpillar (Lepidoptera: Lasiocampidae) outbreak in northern Minnesota. *The Canadian Entomologist* **107**: 837–854.

(Date received: 2 July 1997; date accepted: 24 April 1998)