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ABSTRACT The amber-marked birch leafminer (*Profenusa thomsoni* [Konow]) (Hymenoptera: Tenthredinidae) has caused severe infestations of birch species in Anchorage, AK, since 2002. Its spatial distribution has been monitored since 2006 and summarized using interpolated surfaces based on simple kriging. Results indicate that this insect pest is unevenly distributed, occurring in multi-neighborhood sized patches that migrate from year to year. Patches showing heavy infestation one year are followed by light infestations the following year. In this study, we developed methods of assessing and describing spatial distributions of *P. thomsoni* as they vary from year to year, and speculate on potential causes of these trends in landscape patterns.

KEY WORDS urban landscape, spatial analysis, urban insect pest

The amber-marked birch leafminer (*Profenusa thomsoni* [Konow]) has become one of the most important invasive alien insects in the State of Alaska. Until recently, Alaska had been free of significant invasive alien forest pests. The amber-marked birch leafminer was first found in Anchorage, AK, in 1996, although there is evidence suggesting it was present as early as 1982 near Haines. In recent years, this insect has caused severe defoliation of native birch species (dwarf arctic birch [*B. nana* L.], resin birch [*B. glandulosa* Michaux], paper birch [*B. papyrifera* Marshall], Alaska paper birch [*B. neoalaskana* Sargent], western paper birch [*B. papyrifera* variety *occidentalis* Fernald], and Kenai birch [*B. kenaica* (W. H. Evans)]) as well as horticultural varieties (Digweed et al. 1997, Snyder et al. 2007) in Anchorage, the Fairbanks area, Haines, Skagway, and parts of the Kenai Peninsula (USDA Forest Service 2000–2010). The insect is now rapidly spreading beyond these urban areas into the surrounding wildland forests. The biology and ecology of the amber-marked birch leafminer in Alaska was recently reviewed by Snyder et al. (2007).

Like most leaf-mining sawflies, the amber-marked birch leafminer is univoltine. It overwinters in the forest duff as prepupae, and begins emerging in late May to early July when leaves form on birch trees. Depending on temperature and humidity, adult insects continue to emerge for most of the summer. Adults are 0.2–2.0 cm long, black in color, and almost always females. Oviposition peaks in late June. The larvae that emerge from eggs after 12 d feed on the leaf tissue between the epidermal layers, forming blotch mines that enlarge as sawfly larvae develop, often coalescing when larvae are crowded (Digweed et al. 2009). The larvae pass through six instars, the last of which cuts a hole in the leaf, drops to the litter below, burls into the duff, and pupates (Digweed et al. 2009). Impacts to trees are limited primarily to decreased esthetic values because of browning, distortion, or premature loss of foliage. To avoid these impacts, many landowners apply large volumes of insecticides (M. Rasy, University of Alaska Fairbanks, Cooperative Extension Service, personal communication).

In addition to the amber-marked birch leafminer, the late birch leaf edge miner (*Heterarthrus nemoratus* Fallen) and the birch leafminer (*Fenusa pumila* Leach) are sawflies that also cause considerable impacts to birch trees in Alaska. Leaf-mining sawfly species are commonly identified on the basis of location of injury in the tree crown and the characteristics of the leaf mines. The amber-marked birch leafminer attacks mature leaves in the mid- to lower-half of tree crown, causing brown blotch-like lesions to form mostly in the center of the leaf.

Lesions caused by amber-marked birch leafminer on individual leaves increase in size until the leaves are completely brown; eventually, the entire crown of an infested tree turns brown. Trees growing in different sections of Anchorage vary in severity of infestation. Little is known about how these insects disperse over short distances or the broad-scale spatial patterns that result from this local dispersal. Based on limited field observations, uninfested birch trees within 10 m of an existing amber-marked birch leafminer infestation are likely to become heavily infested within a year; likelihood of infestation and amber-marked birch leafminer abundance both steeply decrease with distance.

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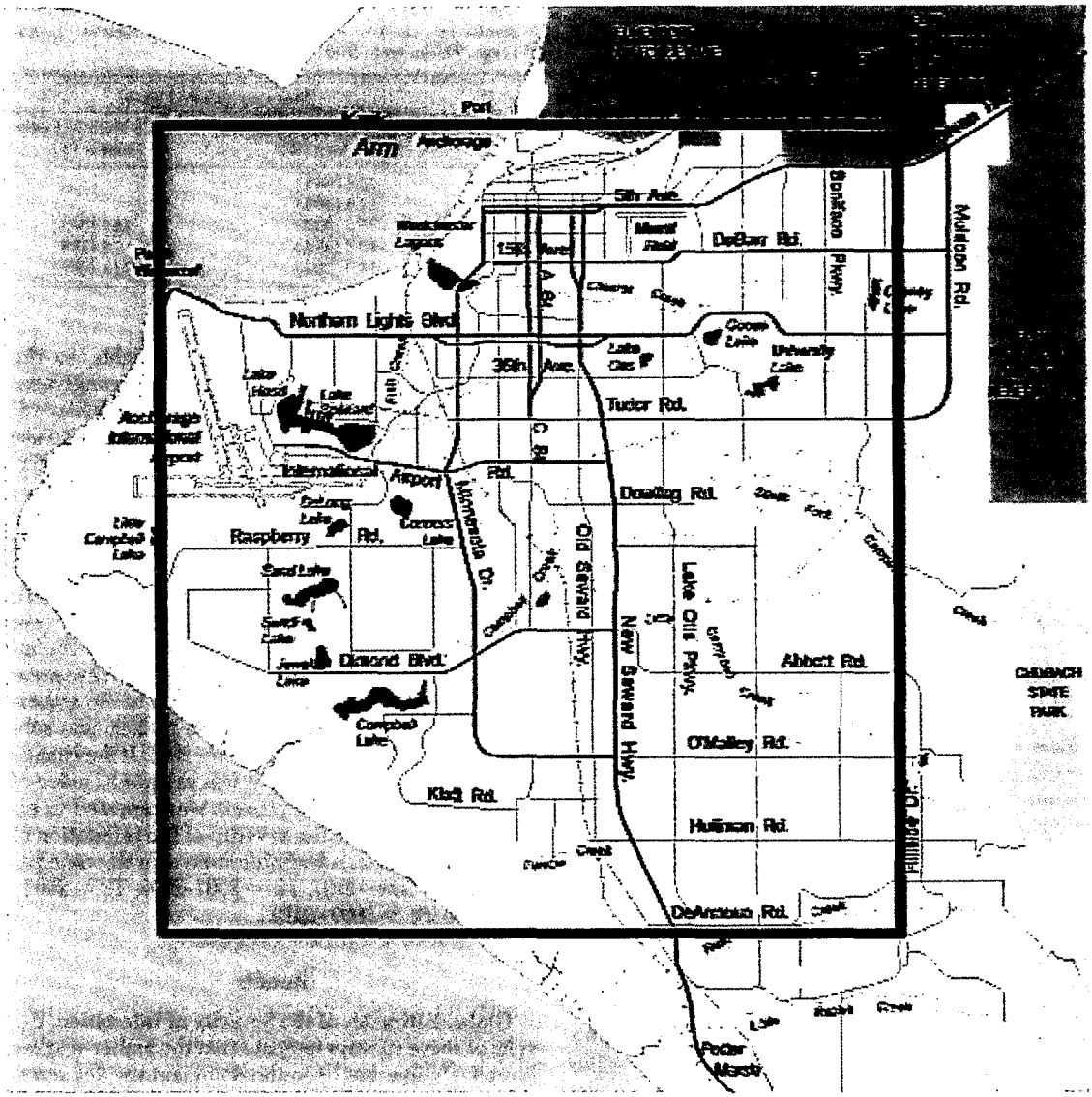

Fig. 1. Outline of study area within the Anchorage urban area. This covers 5,079 km^2 of land base area.

The objectives of this study were as follows: 1) examine trends in amber-marked birch leafminer infestation severity in the Anchorage area using various methods to characterize the global averages; 2) generate spatial models of the distribution of the amber-marked birch leafminer; and 3) compare and contrast spatial distributions across years.

Methods and Materials

Survey Data. Beginning in 2006, the U.S. Forest Service (USFS) Forest Health Protection (FHP) identified 140 trees for incorporation into a long-term monitoring network to follow the distribution, spread, and severity of the amber-marked birch leafminer infestation in a large section of the city of Anchorage (Fig. 1). Sites were selected throughout the study area based on ease of access (e.g., parks, parking lots, etc.). A small branch was removed with pole pruners from mid-crown as possible and on the outside edge of the crown. Fifty leaves were randomly selected from each clipped branch and the number of leaves with at least one amber-marked birch leafminer blotch was tallied. The same trees were sampled each year. Beginning in 2008, the number of leaves with evidence of late birch leaf edge miner were also identified and counted. For 2006 and 2007, only *P. thomsoni* was tallied. Beginning 2008, *H. nematorus* was counted when the incidence of this insect became increasingly notable. As its name implies, the late birch leaf edge miner causes lesions at the edge, but these lesions are a distinct reddish orange color, free of frass, and with surfaces that crack easily.

Global Estimates of the Severity of Infestation. *Arithmetic Mean.* The mean average intensity, or global mean, across the study area is a commonly

metric used to characterize intensity of insect infestation. The simplest method of estimating the global mean is to calculate the average severity of the infestation at the 140 sample sites. Because of restrictions in identifying sample sites and the need to spread the sample uniformly throughout the city, there was a tendency to select more sites in the heavily infested areas of the city. While it is likely that these samples give good information of the mean in these areas, they may not be representative of the remaining area. Consequently, the arithmetic mean may provide a poor estimate of the population mean.

Thiessen Polygons. The second method used to estimate the global mean was based on a polygon method that assigns each data point a zone of influence. Thiessen polygons that are the simplest to construct were defined such that the boundaries of a given polygon are closest to the polygon's spatial data point than to any other spatial point in the study region. Once the polygons have been constructed, the global estimate was obtained by weighting the sample data (z_i) proportional to the size of the polygon:

$$\hat{z}_G = \frac{\sum_{i=1}^{n} A_i z_i}{A} \quad [1]$$

where A_i is the size of the ith polygon and A is the total area of the study region. Thus, clustered samples will get small weights, while samples associated with large polygons will be more heavily weighted.

Inverse Distance Weighting (IDW). IDW was used to interpolate the sample data to a 1,700 × 1,617 grid with a 9.1 × 9.1 m (30 × 30 feet) spacing. IDW is a deterministic estimation method where values at the grid intersections were determined by a linear combination of values at known sampled locations. IDW makes the assumption that values closer to nonsampled locations are more representative of the value to be estimated than samples further away. Weights change according to the linear distance of the samples from the nonsampled location. The spatial arrangement of the sample data does not affect the weights. A remove-one cross validation was used to determine the number of sample points to use in the interpolation that would minimize the mean squared prediction error. The estimate of the global mean was obtained by averaging the interpolated values across the grid

$$\hat{z}_G = \frac{1}{rc} \sum_{i=1}^{r} \sum_{j=1}^{r} \hat{z}_{ij} \quad [2]$$

where r and c are the dimensions of the grid and $\hat{z}_{ij}$ are the interpolated values.

Kriging. Kriging was used to interpolate the sample data to a 1,700 × 1,617 grid. Kriging is a stochastic method similar to IDW in that it uses a linear combination of weights at known locations to estimate the value at an unknown location. Kriging uses a semivariogram, which measures the average degree dissimilarity between unsampled locations and nearby (known) points in computing the weights, so the weights change according to the spatial arrangement of the sample data. A remove-one cross validation was used to determine the number of sample points to use in the interpolation as well as selecting the semivariogram model (Gaussian, exponential, and spherical) that would minimize the mean squared error of prediction. The global mean was obtained by averaging the interpolated values across the grid (equation 2).

Table 1. Changes in the severity of the amber-marked birch leafminer and the late birch leaf edge miner infestations in Anchorage, Alaska from 2006 to 2010

Year	Mean no. infested leaves	
	Amber-marked birch leafminer (%)	Late birch leaf edge miner (%)
2006	26.9 (54%)	
2007	22.8 (46%)	
2008	16.7 (33%)	18.2 (36%)
2009	12.4 (25%)	7.7 (15%)
2010	14.0 (28%)	15.1 (30%)

Spatial-Temporal Dynamics of the Infestation. To study the dynamics of the insect infestation, we were interested in observing where the severity of the infestations increased each year. To identify these areas the interpolated surface of the severity of the amber-marked birch leafminer infestation in 2006 was subtracted from the one developed for 2007. If the change in the severity was positive it was assigned a value of 1, and 0 otherwise. This process was repeated to estimate the change in the severity of the infestation of amber-marked birch leafminer between the time periods: T1 = 2006–2007, T2 = 2007–2008, T3 = 2008–2009, and T4 = 2009–2010.

Results

Global Estimates of the Severity of Infestation. Results of these surveys indicate that the amber-marked birch leafminer has been the dominant species across the Anchorage bowl, but that its overall severity has been steadily decreasing. From 2006–2009, leaf mining severity caused by amber-marked birch leafminer decreased by half; after which, it showed a slight increase (Table 1). In contrast, the late edge birch leafminer showed a notable drop in severity from 2008 to 2009, followed by an increase in 2010, where it was slightly more severe than amber-marked birch leafminer. All four methods provided similar estimates of the global mean for both sawflies (Fig. 2). The arithmetic mean consistently overestimated the level of amber-marked birch leafminer infestation compared with the other three methods, but by very little. This could be because of the restrictions imposed on selecting the sample sites and any inherent biases associated with selecting infested trees over noninfested trees for sampling.

Spatial Distribution of Amber-Marked Birch Leafminer. Figure 3 compares the interpolated surfaces of the intensity of the amber-marked birch leafminer infestation in 2007. All three interpolation

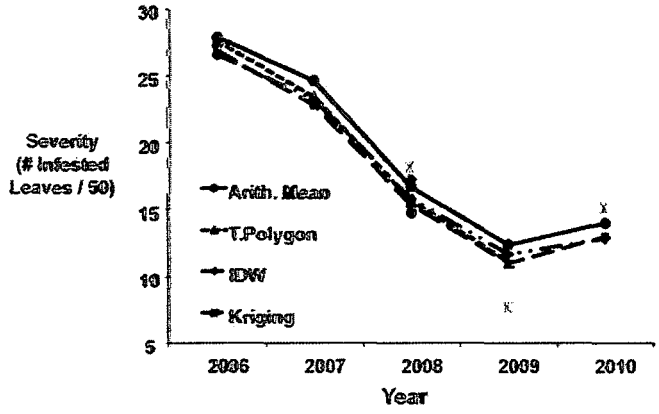

Fig. 2. Changes in the severity (number of infested leaves out of 50 total) of the amber-marked birch leafminer infestations in Anchorage, AK, from 2006 to 2010. Four methods were used to estimate the level of infestation; (1) arithmetic mean, 2) Thiessen polygons, (3) inverse distance weighting, and (4) kriging.

methods produced similar surfaces. The Thiessen polygons provided a simplistic view of the infestation in that relatively large areas received a single value. The surfaces generated using IDW and kriging better reflect the infestation in that both interpolation methods provided details in areas that were not sampled. The surfaces generated using kriging were closer to the Thiessen polygon maps than the IDW surfaces, suggesting a better approximation to the original data and so the surfaces generated using kriging were selected for use in the latter analysis.

Spatial Dynamics of the Severity of Amber-Marked Birch Leafminer Infestation. Figure 4 displays the locations where the severity of infestation increased from the previous year. Notably, the areas showing an increase in severity form somewhat disjoint groups. Areas that experienced an increase in infestation tended to not experience another increase in at least the next two time periods.

In 2006, the entire study area is infested with amber-marked birch leafminer with an average severity of 26.9. Between 2006 and 2007 (T1) 28% of the area experienced an increase in the intensity of the infestation (24.4–30.6), while 72% of the area showed a decrease (27.9–19.8) (Fig. 5). Because most of the area experienced a decrease, the overall severity decreased to 22.8 (Table 1).

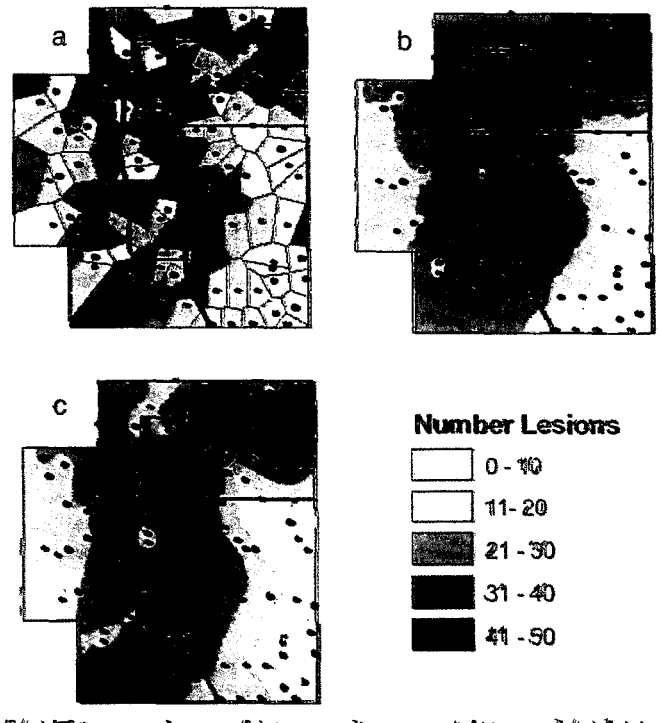

Fig. 3. Comparison of (a) Thiessen polygons, (b) inverse distance weighting, and (c) kriging in describing the spatial distribution of the severity of the amber-marked birch leafminer infestation in Anchorage, AK, in 2007.

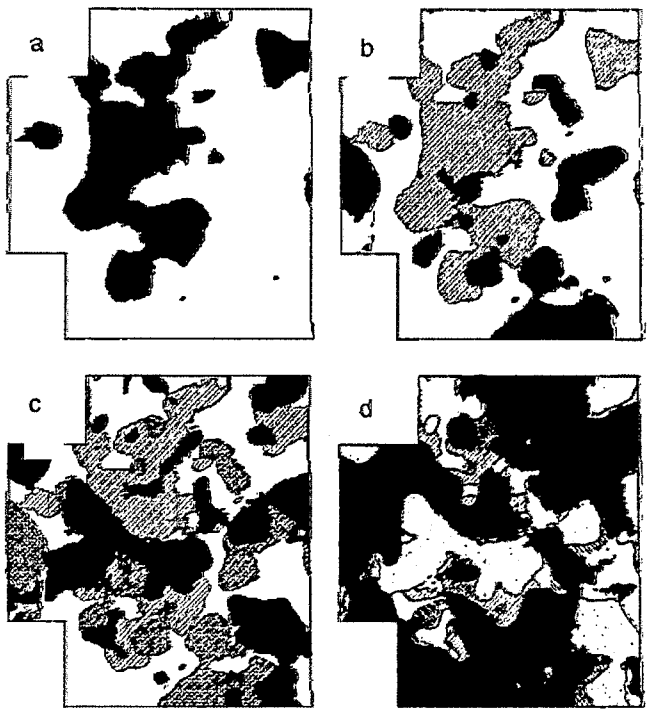

Fig. 4. Comparison of the areas (black polygons) that showed an increase in the severity of amber-marked birch leafminer infestation between (a) 2006–2007, (b) 2007–2008, (c) 2008–2009, and (d) 2009–2010. The shaded areas represent areas that experienced an increase in the severity of infestation in previous time periods.

In the second time period (T2) the severity of the infestation increased in new areas, with some overlap from previous time period (Fig. 4). The area of increase (19%) was less than that observed in the first time period. Eighty-eight percent of this increase was in new areas, while only 11% was in areas that experienced an increase in T1 (Table 2). This latter increase occurred in areas that had severities on the lower end and having more potential to increase than areas having higher levels of severity. In the areas showing an increase, the severity increased from 16.8 to 22.3, while areas showing a decrease the severity decreased from 24.2 to 13.8 (Fig. 5). Because most of the area experienced a decrease, the overall severity decreased to 16.7 (Table 1).

In the third time period (T3), the severity of the infestation increased to cover 31% of the area representing the largest increase (Fig. 4). Sixty-four percent of this increase was in new areas, 24% in areas showing an increase in T1, and 10% in areas showing an increase in T2 (Table 2), which suggests that overtime areas become more susceptible to higher levels of infestation. In the areas showing an increase, the severity increased from 10.1 to 15.8, while areas showing a decrease in severity decreased from 17.8 to 8.8 (Fig. 5). Because most of the area experienced a decrease, the overall severity decreased to 12.4 (Table 1).

In the fourth time period (T4) the severity of the infestation increased to cover 58% of the area that is almost double that observed in T3 (Fig. 4). Forty-five percent of this increase was in new areas, 22% in areas showing an increase in T1, 19% in areas showing an increase in T2 and 10% in areas showing an increase in T3 (Table 2). This is similar to the trends observed in T3. In areas showing an increase, the severity increased from 8.6 to 16.2, while areas showing a decrease the severity decreased from 14.3 to 8.9 (Fig. 5). Because the area associated with this increase exceeded half, the overall intensity increased to 14.0 (Table 1). Looking at the average trend over time (Fig. 5), one can see that the intensity of the infestation decreased at an increasing rate irrespective of whether the area experienced an increase or decrease in the intensity of the infestation.

At the end of the fourth time period the infestation had very little room to increase and it is predicted that the overall severity of infestation will decrease. Only 10% of the area has never experienced an increase in the severity of infestation (Fig. 4). In addition, only 19% of the area that was associated with an increase in severity in T1 is available (or 5% of the area), 14% of T2 (or 3% of the area) and 75% of T3 (23% of the area). The area associated with an increase in infestation will be on the lower side resulting in an overall decrease in the level of infestation.

Discussion

This survey shows that the amber-marked birch leafminer is irregularly distributed across the Avadvorage landscape, and that the distribution varies from year to year. The changing distribution of this insect

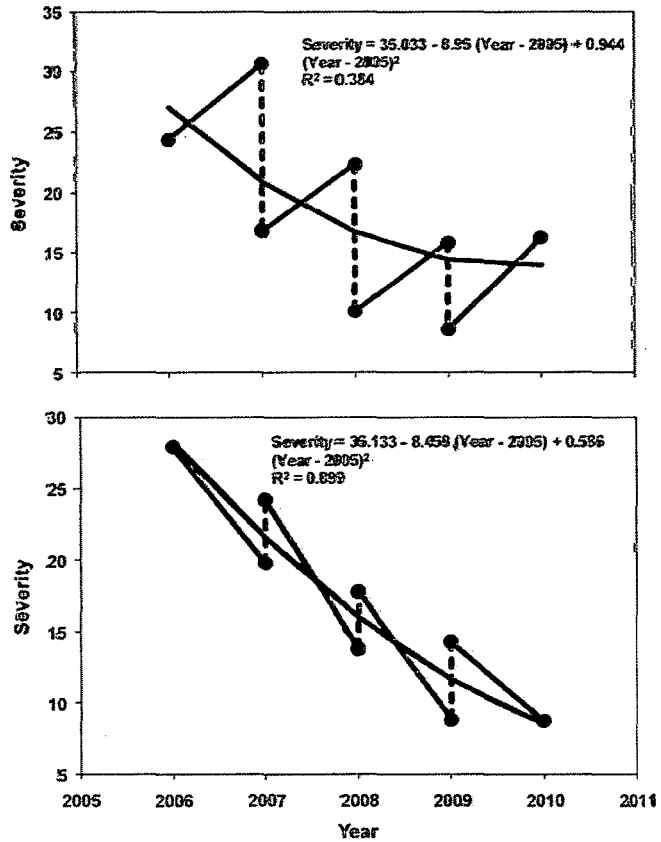

Fig. 5. The change in the severity of amber-marked birch leafminer infestation in the areas associated with an increase (**A**) or decrease (**B**) in the severity of the infestation over time. The smooth lines represent the average change in the severity of the infestation over time. Severity is equal to number of infested leaves out of 50 total leaves examined.

creates distinct, patchy landscape-scale patterns involving multiple trees synchronized across multiple urban neighborhoods. Furthermore, annual trends suggest that locations of relatively high severity one year experience relatively low intensity the following year. These trends and patterns would likely be hidden at spatial scales smaller than the landscape. However, synchronization among patches at lesser spatial scales create a distinct pattern of infestation at the landscape scale. How different insect species respond to different environmental variables or conditions varies with spatial scale of observation.

At the individual patch scale, survival, and spatial extent of individual insect populations depend on various intrinsic and extrinsic factors that influence birth (B), death (D), immigration (I), and emigration (E) rates. In this regard, the size of an insect population at any location can be represented by the following equation (Berryman 1986):

$$\Delta N = B - D + I - E \qquad [3]$$

where ΔN = change in population number within a given area, B = birth rate, D = death rate, I = immigration rate, and E = emigration rate. Equation 3

Table 2. Areal distribution of the increase in severity of amber-marked birch leafminer in Anchorage, Alaska from 2006 to 2010

Time period	% area showing an increase in severity of infestation (1)	% area showing an increase in severity of infestation (1) in areas that never exhibited an increase in severity in previous time periods (2)	Percent area showing an increase in severity of infestation in areas that exhibited an increase in severity in a previous time period				Total (%) Sum (2)–(6)
			Lag one time period, e.g., T2–T1 (3)	Lag two time periods, e.g., T3–T1 (4)	Lag three time periods, e.g., T4–T1 (5)	Other time lag combinations (6)	
T1 (2006–2007)	26	100				0	100
T2 (2007–2008)	19	88	12			0	100
T3 (2008–2009)	31	64	10	24		2	100
T4 (2009–2010)	58	45	30	19	32	4	100
Average (%)			11	22	32	3	

Severity is defined as the no. of infested leaves in a cluster of 50 leaves.

suggests many reasons for the increasing or diminishing abundance in individual patches, and thus the diversity among patches. Following is a discussion of the factors and the roles they may play in influencing the spatial distribution and abundance of amber-marked birch leafminer across municipal landscapes.

Density Dependent Forces. Endogenous density dependent forces could cause areas with high density larval populations to be crowded, such that larvae may compete with each other or become cannibalistic, increasing D while decreasing B. In support of this idea, it is common, especially late in the season, to find two or more larvae sharing a lesion formed when two or more individual blotches coalesced.

Natural Enemies. Anderson and May (1980, 1981) suggested that cyclic fluctuations of insect populations could be driven by natural enemies. Impacts of fluctuating native parasitoid and predator populations could affect the spatial distribution of *P. thomsoni*. The roles of natural enemies of urban and forest insects are thought by many to be significant factors controlling fluctuations and stability of host insect populations (Elton 1927, Andrewartha and Birch 1954). Reeve (1988) coins the term "equilibrium theory" as "the regulation of insect populations about an equilibrium point by the density-dependent coupling between the insect and its natural enemies . . ." A massive body of literature has focused on this subject (Dwyer et al. 2000, 2004). Work on developing biological controls of the amber-marked birch leafminer in Anchorage has received much attention in recent years.

In this regard, the city of Edmonton, Alberta, Canada, had a similar problem with the amber-marked birch leafminer during the 1970s and 1980s. This nearly 20-yr infestation ended with the emergence of a native parasitoid, *Lathrolestes luteolator* Gravenhorst, which switched hosts, becoming parasitic to *P. thomsoni*. This parasitoid is credited with eliminating the amber-marked birch leafminer from Edmonton. In 2003, a cooperative biological control program featuring *L. luteolator* began in Anchorage. This work has generated a much better understanding of the biology, ecology and impacts of the amber-marked birch leafminer, and ultimately the application of *Lathrolestes* sp. will probably have a very significant impact on the population of amber-marked birch leafminer. Nevertheless, operational use of *Lathrolestes* sp. is probably still some years away.

Induced Resistance. Changes in tree physiology that influence susceptibility could result in delayed induced resistance. Plants defend themselves against herbivores like *P. thomsoni* in many ways. These defense mechanisms can be classified as constitutive or induced. Constitutive mechanisms are preexisting chemical or structural barriers that prevent, reduce, or otherwise minimize the impact of a plant feeding insect. Induced mechanisms are stimulated by nonlethal ingress of an herbivore or other source of damage or injury (Karban and Baldwin 1997, Tollrian and Harvell 1998, Agrawal et al. 1999). The induced resistance hypothesis states that plants attacked by insect herbivores are stimulated to produce chemicals that negatively impact the development and growth of the insects. This phenomenon has been examined in several host-insect herbivore systems (Ohgushi 2005), especially birch species (Neuvonen and Niemelä 1991). According to Bryant et al. (1993), delayed induced resistance is expressed in Alaska paper birch as a prolonged condition of decreased leaf food quality for early instar insect defoliators, smaller leaf size, declining nitrogen levels in leaves, and increasing concentrations of phenolics and other secondary compounds.

Multiple Causes for the Patchy Patterns of Infestation. The top-down hypothesis argues that natural enemies keep the herbivore population in check. The bottom-up hypothesis argues that plant quality controls herbivore populations. According to Ylioja et al. (1999), "many factors that affect population abundance. can act in either a density-dependent or density-independent fashion, but the relative contribution of exogenous and endogenous effects remains an open question . . ." According to Hunter and Price (1992), "The real issue is whether or not we can accept the fact that many ecological factors simultaneously determine the patterns we observe in natural communities (Southwood 1975, 1977b, Quinn and Dunham 1983, Courtney 1988, Leibold 1989), that the dominant forces will vary within and among systems (Karr et al. 1992), and that incorporating and measuring that variability will increase our understanding of population and community ecology."

Dispersal. One way that insects respond to defense mechanisms is to modify feeding behavior (Stamp and Casey 1993) by dispersing to different locations, which could be reflected in the changing spatial distribution of *P. thomsoni*. Equation 3 suggests various explanations for the changing abundance of the amber-marked birch leafminer in individual patches across Anchorage, but not what causes populations to immigrate or emigrate en masse among locations. Dispersal is important for all insect populations at all spatial scales (Sharov 1996). Generally, insect herbivores occupy hosts growing in habitats in which insects and plants are adapted for growth and reproduction. Often, however, the factors that drive dispersal and the resulting patterns of distribution are difficult to determine. Habitat selection theories (Rosenzweig 1991) and the dynamics of insect populations have been the focus of countless studies (Sharov 1996), and many population dynamics models have been developed specifically for forest and tree insects (Berryman 1986, Liebhold 1994). Most of these latter models apply to a single population in a discrete homogeneous environment (Garvie and Golinski 2010). Many studies have found spatial variation and environmental heterogeneity to be significant factors in determining pest distributions. The application of metapopulation principles to forest entomology is relatively new, but there seems to be increasing interest in this approach from modelers (e.g., Garvie and Golinski 2010, Mistro et al. 2009, Han et al. 2009, Soubeyrand et al. 2009, Cronin 2009, Sun et al. 2008, Burton and Travis 2008, Goodnight et al. 2008). Ac-

cording to Cronin (2009), "movement, and particularly the colonization of new habitat patches, remains one of the least known aspects of the life history and ecology of vast majority of species."

Spatial Heterogeneity and the Distribution of Amber-Marked Birch Leafminer in Anchorage. The spatial heterogeneity expressed by this insect pest emphasizes the need for spatially explicit studies (Sun et al. 2008). According to Sobyrand et al. (2009), ".we are usually limited in our ability to investigate the numerical dynamics of natural populations across large spatial scales and over long periods of time." Equation 3, for instance, applies to a population of individuals interacting over limited contiguous area, which would be equivalent to one of the infested patch areas found in Anchorage. The dynamics that result from interactions between the amber-marked birch leafminer and its host birch (Strong et al. 1984), or natural enemies and the amber-marked birch leafminer (Reeve 1988, 1990) are greatly influenced by this patchy landscape pattern (Comins et al. 1992). Many studies have shown and discussed the importance of patchy environments in promoting sustainable host populations (Hassell et al. 1991). Reeve (1988) described one possible mechanism for stability in patchy environments, "insect populations persists because they are divided into a large number of subpopulations, weakly linked by migration; because the subpopulations experience different environments, they are to some extent asynchronous, making the simultaneous extinction of all subpopulations unlikely."

In conclusion, this study looked at the spatial dynamics of amber-marked birch leafminer at a spatial scale associated with an urban landscape. At larger scales, there is evidence that the spread of amber-marked birch leafminer may be primarily because of human activities and not by natural dispersal. Data from this study indicates that the natural dispersal rates are low, especially in an urban landscape and very little is known about how amber-marked birch leafminer would expand throughout the wildland forests of Alaska. The spatial dynamics of amber-marked birch leafminer at larger scales may be quite different than what was observed at smaller scales. Caution should be taken when concluding that particular processes are unimportant, given that the scale of study can influence whether or not effects are observed. Given the slow natural spread of amber-marked birch leafminer, it may take a long time for the spatial processes observed in an urban landscape to influence the large-scale distribution of amber-marked birch leafminer throughout Alaska.

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