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Two-dimensional wavelet analysis of spruce budworm host basal area in the Border Lakes landscape

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Abstract. Increases in the extent and severity of spruce budworm (*Choristoneura fumiferana* Clem.) outbreaks over the last century are thought to be the result of changes in forest structure due to forest management. A corollary of this hypothesis is that manipulations of forest structure and composition can be used to reduce future forest vulnerability. However, to what extent historical forest management has influenced current spatial patterns of spruce budworm host species is unknown. To identify landscape-scale spatial legacies of forest management in patterns of spruce budworm host species (i.e., *Abies balsamea* and *Picea* spp.), we analyzed remotely sensed forest data from the Border Lakes landscape of northern Minnesota and northwestern Ontario. Our study area contains three regions with different management histories: (1) fine-scale logging patterns in Minnesota, (2) coarse-scale logging patterns in Ontario, and (3) very limited logging history in the Boundary Waters Canoe Area and adjacent Quetico Provincial Park. We analyzed forest basal-area data using wavelets and null models to identify: (1) at which scales forest basal area is structured, (2) where those scales of pattern are significantly present, and (3) whether regions of local significance correspond to regional boundaries that separate the study area. Results indicate that spatial patterns in host basal area are created by nonstationary processes and that these processes are further constrained by lakes and wetlands. Wavelet analysis combined with significance testing revealed a bimodal distribution of scale-specific wavelet variance and separate zones of host species basal area that partially correspond with regional boundaries, particularly between Minnesota and the Wilderness region. This research represents one of the first comparisons of forest spatial structure in this region across an international border and presents a novel method of two-dimensional wavelet analysis that can be used to identify significant scale-specific structure in spatial data.

Key words: Choristoneura fumiferana; *forest management; forest structure and composition; landscape-scale patterns; logging patterns; MODWT; multi-temporal LANDSAT; remote sensing; spatial legacies; spatial null models; wavelet variance.*

Introduction

The spruce budworm (*Choristoneura fumiferana*; SBW) is an important native defoliator of fir and spruce forests in Canada and the northeastern United States (MacLean 1984, Batzer and Popp 1985). Outbreaks of SBW can affect more area than fire and harvesting combined (Fleming et al. 2002). Associated losses in terms of tree growth and vigor, timber and fiber production, and potential interactions with fire (McCullough et al. 1998, Fleming et al. 2002) make minimizing spruce budworm damage an important goal of forest managers (MacLean et al. 2001).

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SBW outbreaks are driven by natural enemies (Royama 1984), climate (Peltonen et al. 2002), dispersal (Williams and Liebhold 2000), and the availability and spatial pattern of susceptible host trees (Cooke et al. 2007). In particular, the basal area of the SBW's preferred host species, balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*), often accounts for which areas sustain the greatest damage (Batzer and Popp 1985, Bouchard et al. 2006). Of the factors that contribute to outbreaks, the spatial pattern and abundance of host is the one factor over which forest managers have the greatest control, and the silvicultural hypothesis suggests that manipulation of forest structure through management may be an effective means to reduce forest vulnerability to insects (Miller and Rusnock 1993).

Over the last century outbreaks of spruce budworm have become more severe and more extensive, possibly due to changes in forest composition and configuration from forest management and fire suppression (Blais

1983, Cooke et al. 2007). It has been shown that greater stand and neighborhood-level forest diversity can reduce damage sustained during a SBW outbreak (Su et al. 1996, Cappuccino et al. 1998, Campbell et al. 2008). However, the effects of landscape-level forest management legacies and the ability of forest managers to influence SBW outbreak dynamics through manipulations of forest structure remain uncertain (Miller and Rusnock 1993, Muzika and Liebhold 2000).

Forest spatial structure has also been shown to affect the extent and severity of outbreaks in other insect species. Roland and Taylor (1997) demonstrated the influence of forest structure, and in particular forest edges, on forest tent caterpillar (*Malacosoma disstria*) outbreaks in Ontario. Similarly, Johnson et al. (2004) showed that landscape geometry can produce complex spatial outbreak patterns such as travelling waves in the larch budmoth (*Zeiraphera diniana*). Furthermore, the recent outbreak of mountain pine beetle (*Dendroctonus ponderosae*) in western Canada is at least in part attributable to the availability and connectivity of large tracts of mature lodgepole pine (*Pinus contorta*) (Raffa et al. 2008). Examination of the spatial structure of insects' preferred hosts and its relationship to forest management is needed to better understand how human activities affect outbreak risk, to infer landscape-scale forest vulnerability, and to inform sustainable management practices (Sturtevant et al. 2004).

We investigated whether variation in historical management practices has affected the spatial structure of SBW host species in the Border Lakes landscape (BLL; Fig. 1). The BLL straddles northern Minnesota, USA, and northwestern Ontario, Canada, and contains three regions in which forest management and patterns of land ownership have resulted in important differences in landscape structure and composition (Wolter and White 2002, Pastor et al. 2005). In Ontario, forest management is generally carried out as large-scale clearcuts, whereas in Minnesota cutblocks (the blocks of land that are to be cut) are implemented at a finer scale (Wolter and White 2002). In between these two regions lies the wilderness zone of the Boundary Waters Canoe Area and Quetico Provincial Park, which has not been logged since the early 1970s, hereafter referred to as "Wilderness".

In this study we examined whether spatial legacies of forest management can be detected in patterns of SBW host tree species in the BLL using remotely sensed forest data and two-dimensional wavelet analysis. Wavelet analysis is an increasingly common tool for the analysis of spatial and temporal ecological data (Cazelles et al. 2008). However, most ecological applications have been undertaken using one-dimensional transects or time series (Keitt and Urban 2005, Keitt and Fisher 2006, Kembel and Dale 2006, James et al. 2010). There are few examples of wavelet analysis applied to two-dimensional (2D) raster data although the utility of such analyses for remotely sensed data has been described (Falkowski et al. 2006). Relevant recent applications of 2D wavelets to remotely sensed data include the analysis of grassland productivity (Csillag and Kabos 2002) and tree crown feature identification (Falkowski et al. 2006, Strand et al. 2006). Here, we expand the methods presented in James et al. (2010) and demonstrate how wavelets can be used to identify spatial boundaries in 2D data using spatially structured null models.

We first characterized the scale of spatial structure of forest basal area over the entire study area using global summaries of wavelet variance as a function of scale (i.e., scalograms). Here, wavelet variance represents the degree of similarity in shape of the basal-area data and a scalable and translatable wavelet template that is designed to identify peaks in spatial data at multiple scales. Using scalograms we tested whether the different forest basal area types (i.e., total, fir, spruce, deciduous) are similarly structured, and assessed the distribution of spatial variance for each type at different scales relative to a set of stationary null models. We then compared scalograms for each basal area type to the distribution of scalograms produced by a set of null models to determine at which scales the wavelet variance is within the range of expectation. If wavelet variance at a specific scale exceeds the expected range of wavelet variance we conclude that nonstationary processes are responsible for variation in forest basal area at that scale.

Following our summary of the global scale-specific attributes of forest basal area, we used local wavelet summaries to identify nonstationary subregions (i.e., hotspots) in wavelet variance at the significant scales identified above. These hotspots represent areas of high forest basal area at particular scales. Hotspots in SBW host species represent areas of greater potential outbreak risk. We identified hotspots in each forest type using local summaries of wavelet variance that exceed the expected distribution of spatially structured null models (Gardner et al. 1987, Goovaerts and Jacquez 2005, James et al. 2010). Emergent boundaries that demarcate these hotspots were interpreted in terms of how much they corresponded to the regional administrative boundaries that separate the study area. Emergent boundaries are those not imposed a priori (e.g., existing regional administrative boundaries) and are instead objects identified though comparison to our simulated null model (Jacquez et al. 2000).

Finally, emergent scale-specific patches of high wavelet variance in SBW host species were used to identify forest areas of greatest potential vulnerability. Patches of high basal area in SBW host species indicate regions that would likely facilitate an outbreak. In particular, hotspots at coarse scales represent large regions of connected host and are most likely to support or sustain an outbreak. We expected that the managed regions, and in particular, managed regions in Ontario, would have more large patches of connected SBW host than the wilderness region.

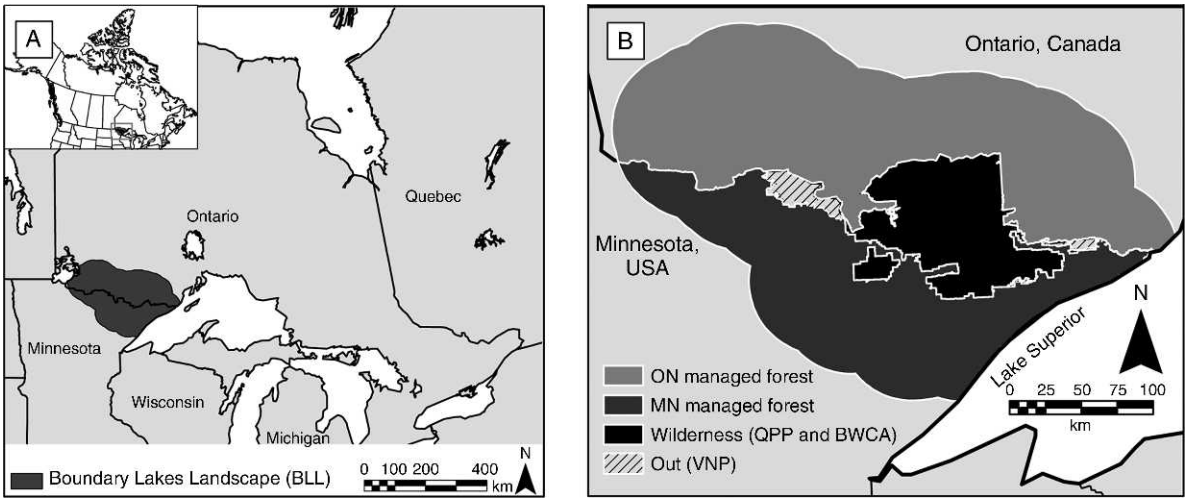

FIG. 1. (A) Location of the Border Lakes Landscape (BLL) study area between Minnesota (MN; USA) and Ontario (ON; Canada), with inset indicting continental context, and (B) the detailed study area, with management zones outlined (white lines). Wilderness is composed of Quetico Provincial Park (QPP) and the Boundary Waters Canoe Area (BWCA). VNP refers to the Voyageurs National Park and was omitted from analysis. The total study area is 6.9×10^6 ha.

METHODS

Study area

The Border Lakes landscape (BLL; Fig. 1) is a transitional forest region between the Great Lakes–Saint Lawrence and boreal forest regions that contains a mix of coniferous and deciduous tree species and is typified by a high density of lakes and wetlands. Included in the BLL are private lands and managed forests in Minnesota (MN; USA), including Superior National Forest and Kabetogama State Forest, as well as managed forest in Ontario (ON; Canada). Between these managed regions lies an approximately 1-million hectare wilderness and recreation area that includes Quetico Provincial Park in Ontario and the Boundary Waters Canoe Area. The wilderness is not managed for timber and represents a region free from the recent influence of logging. For the purpose of this analysis, the three principal regions within the ecoregion (MN, ON, and Wilderness; Fig. 1B) are surrounded by a 50-km buffer that comprises the total BLL study area of ~6.4-million hectares.

Spatial data: forest basal area

Continuous forest basal area, expressed as square meters per hectare, was used to assess the effects of management practices on the scale of spatial structure of budworm host species basal area, to identify emergent spatial boundaries, and to identify local scale-specific hotspots in relative forest vulnerability. Species-specific basal area data were derived from partial least squares (PLS) regression models using forest plots and multi-temporal LANDSAT data collected between 2000 and 2005 (Fig. 2; Wolter et al. 2008). PLS regression has been previously used to model relationships between remotely sensed data and physical forest conditions (Ourcival et al. 1999, Smith et al. 2002, Townsend et al. 2003). Wavelet analysis was performed on maps representing PLS models of total basal area ($R^2 = 0.62$), relative basal area of budworm host species (i.e., balsam fir with $R^2 = 0.88$, and spruce species (white and black spruce) with $R^2 = 0.64$), and relative deciduous forest cover ($R^2 = 0.86$). Commission errors with non-host conifers (e.g., *Pinus* spp.) were corrected by constructing a non-host conifer mask, defined as locations where non-host conifers were present and host-species basal area was <15 % of the total basal area (P. Wolter and P. Townsend, *unpublished data*). Masked pixels were assumed to contain no host species.

Original basal area data were represented at a resolution of 30 m. The large extent and fine grain of these data presented formidable challenges to manipulation and analysis and were therefore aggregated through summation of all basal area for all pixels within a 6×6 pixel moving window. This resulted in a data set with a pixel size of 180 m^2 and total extent of approximately 2000×2100 pixels. Following aggregation, a 5×5 "majority filter" was run to smooth patch edges using ArcInfo 9.2 (ESRI 2008).

Wavelet analysis

Wavelet analysis can be used to identify pattern at different scales in time series, spatial transects, or two-dimensional images through the decomposition of signal variance into separate scale-specific components (Daubechies 1992, Dale and Mah 1998, Cazelles et al. 2008). Wavelets are similar to localized Fourier analysis and involve successive passes of a wavelet template of increasing size over a set of data and assessing the degree of similarity between the pattern of the data and the wavelet template at each location (Torrence and Compo

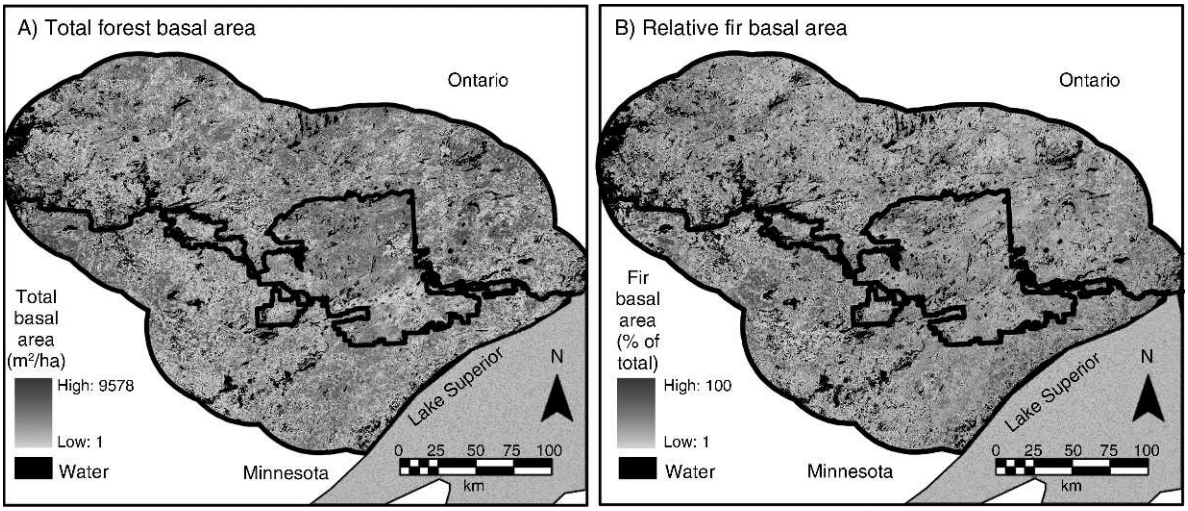

FIG. 2. Forest basal area in the BLL derived from multi-temporal LANDSAT data (2000–2005; Wolter et al. 2008). (A) Total basal area in m^2/ha. (B) Relative basal area of fir as a percentage of the total basal area. The relative basal area of spruce and deciduous species is not shown. Black lines represent regional divisions of the BLL (Fig. 1B: white lines). Basal area data for the different forest classes were originally represented in raster format at a resolution of 30 m.

1998). This is similar to a moving-window analysis in which the moving window is applied repeatedly as it is increased in size. The values that describe this degree of fit are referred to as "wavelet coefficients." The size of the wavelet template determines the scale of structure captured and, in the discrete context, increases as powers of two (i.e., 2^2, 2^3, 2^4) in terms of pixels. At a given location and template size, the value of the wavelet coefficient is high when the pattern of the data matches the template and close to 0 when it does not (Bradshaw and Spies 1992, Dale and Mah 1998). This comparison between template and data is repeated at all locations for multiple template sizes to decompose the data into a set of new coefficients for each scale. Reducing a data set into its scale-specific components is called "multi-resolution analysis" (Mallat 1999). For the purposes of this analysis, the term *scale* refers to the different sizes of wavelet template, and the term *level* refers to the separate sets of coefficients produced through variance decomposition. A given decomposition level represents the information extracted from a particular scale.

To identify scale-specific structure in the BLL we used a two-dimensional (2D) maximal-overlap wavelet transform (MODWT; Percival and Walden 2000). The MODWT, also known as the "stationary wavelet transform," or "translation-invariant wavelet transform," is distinct from the standard discrete wavelet transform (DWT) in that that resulting levels of the multi-resolution analysis are not orthogonal, and contain a high degree of redundant information (Percival and Walden 2000). The DWT decomposes 2D data such that each level of the decomposition has $(2^{\log2(N)-j})^2$ coefficients, where N is the number of data points in the original data, and j is the level of the decomposition that proceeds from fine ($j = 1$) to coarse ($j = \log_2(N)-1$), assuming originally dyadic dimensions (Fig. 3). In contrast, the number of coefficients in each level of the MODWT decomposition is equal to the original dimensions (N). The benefit of this redundant information (the "overlap") among levels and the conservation of the original resolution is that the MODWT can be used to produce meaningful images of the separate levels of the decomposition (Fig. 3). Furthermore, the MODWT is generally preferable to the DWT because its assessments of global and local wavelet variance are more robust (Percival and Walden 2000) and although the individual levels of the multi-resolution analysis are not independent, they are less affected by differences in wavelet template than the DWT (Percival and Walden 2000). Two-dimensional MODWT analysis was performed using the Daubechies 4 (D4) wavelet template and the "*waveslim*" package in R (Whitcher [2010] R package version 1.6.4, *available online*).[6] The D4 wavelet is a frequently used wavelet template that can be used to identify peaks in data in either one or two dimensions. More details on wavelet analysis and the calculation of wavelet variance using the MODWT can be found in Liang and Parks (1994), Bruce and Gao (1997), Mallat (1999), and Percival and Walden (2000).

A plot of wavelet coefficients by scale and location is referred to as a *wavelet power spectrum*. In the case of two-dimensional spatial data, the wavelet power spectrum can be represented as a three-dimensional cube of wavelet coefficients with dimensions x, y (i.e., the dimensions of the original data), and scale. To determine scale-specific information independent of location, we examined each level of the decomposition using the

[6] ⟨http://CRAN.R-project.org/package=waveslim⟩

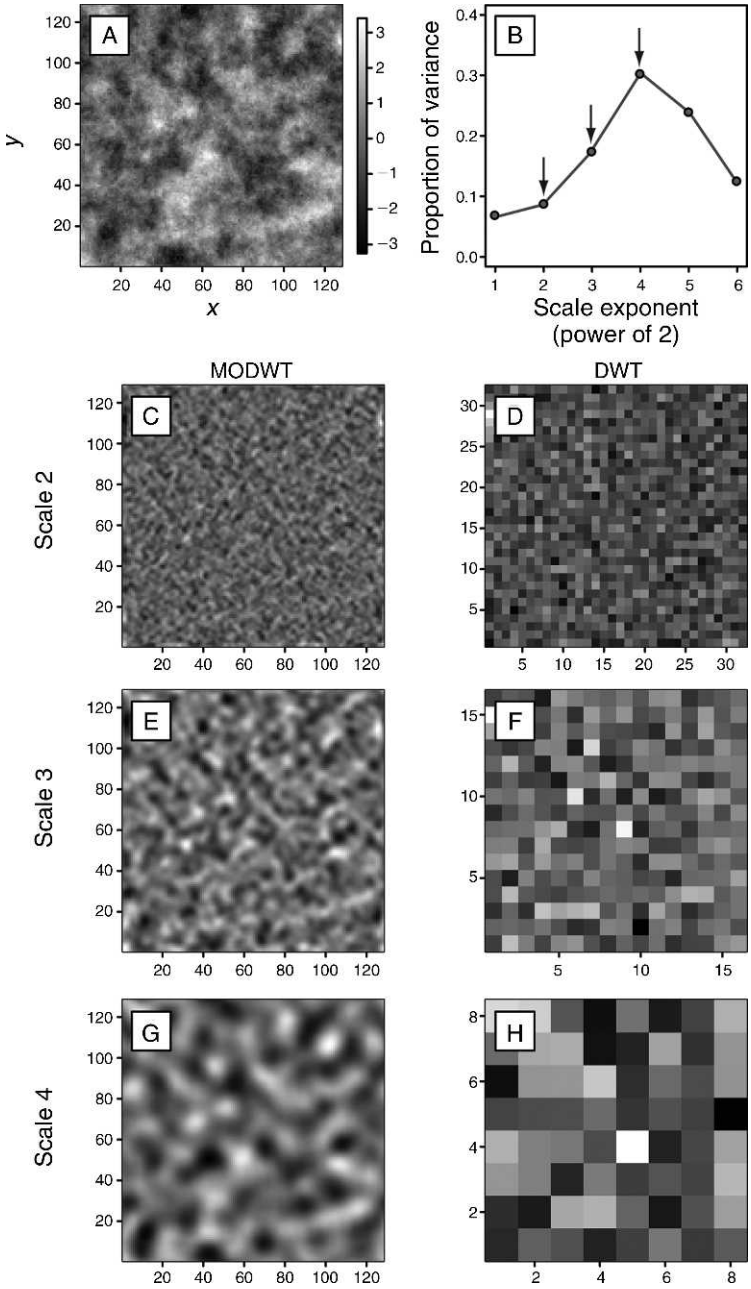

FIG. 3. (A) Simulated autocorrelated spatial data; the x- and y-axes are simply spatial indices of the coefficients. Data were simulated using a Gaussian random field model (Appendix A). Variogram model parameters are: range = 16, sill = 1, mean = 0, and nugget = 0. (B) Scalogram that describes the distribution of scale-specific variance in the simulated data. The peak is at a wavelet template size of 2^4 (16) and corresponds to the input simulated range. (C–H) These panels show the different levels of the decomposition created by (C, E, G) the MODWT (2-D maximal-overlap wavelet transform) and (D, F, H) the DWT (discrete wavelet transform) for scales 2, 3, and 4 (arrows in panel B). Note the decreased resolution (fewer coefficients) of each level of the DWT decomposition, while those produced using the MODWT retain the same resolution as the original simulated data in panel A. The spatial extent of each panel (A and C–H) is the same.

wavelet variance (Percival 1995). *Wavelet variance* is the sum of the squared wavelet coefficients at a particular level over all locations weighted by the number of coefficients (Bradshaw and Spies 1992, Percival 1995). Levels that exhibit high wavelet variance can be considered scales of interest (Bradshaw and Spies 1992). A plot of wavelet variance vs. scale is called a *scalogram* (Fig. 3B) or global wavelet spectrum (GWS; Percival 1995, Torrence and Compo 1998). Wavelet coefficients can also be locally summarized to produce

maps of average wavelet variance at an individual or at multiple levels (i.e., averaging in scale; Torrence and Compo 1998). In combination with a significance testing procedure, scale-averaged maps that represent different levels of the basal area data were used to identify hotspots and emergent spatial boundaries. Here, "boundaries" refers to linear features that delineate regions that exceed the expected null distribution of wavelet variance at specific scales.

A null model

A Gaussian random field (GRF) model that simulates a Gaussian stochastic process using an exponential variogram model was used as a spatial null model for each forest type (Diggle and Ribeiro 2006). Multiple GRF realizations ($n = 100$) were simulated for each forest type using estimated parameters to generate a null reference distribution to determine which scales of pattern in the basal area were significant, and to identify scale-specific boundaries. Details of the GRF model and variogram parameter estimation are described in the Appendix.

Prior to wavelet analysis, all maps, including null model simulations, were normalized to a mean of 0 and unit variance and each dimension was padded with zeroes to the next highest power of 2 (i.e., dyadic dimension). Wavelet analysis was performed on each null realization to generate a distribution of wavelet power spectra (scalograms) to which the equivalent spectra of the corresponding basal area maps were compared (James et al. 2010). Previous work has demonstrated the importance and utility of using autocorrelated null models relative to random noise (Fortin and Jacquez 2000, Goovaerts and Jacquez 2005, James et al. 2010). Indeed, non-autocorrelated null models tend to present too "weak" a contrast and result in false positives (Goovaerts and Jacquez 2005).

Significant scales of pattern

Global scale-specific structure for each forest type was characterized using scalograms. Significant scales of pattern were determined through comparison of the scalogram of each forest type and the 95th percentile of the associated null scalogram distribution. Scales at which the empirical scalogram contained higher wavelet variance than the 95th percentile from the null distribution were considered significant (Torrence and Compo 1998, James et al. 2010).

Boundary detection

To identify boundaries and local hotspots in host and non-host forest basal area we assessed the local significance of the scale-averaged wavelet variance for the three coarsest scales (8, 9, and 10). These scales correspond to wavelet template sizes of 256, 512, and 1024 pixels, respectively, or 46 km, 92 km, and 184 km, respectively. These scales were chosen because they are comparable to the spatial scale at which the region is subdivided by the regional boundaries. Locally significant boundaries at finer scales identify locations of small hotspots that could be useful to local prediction of probability of outbreak, but are not informative regarding regional differences in forest structure.

Boundaries were identified at the three coarsest levels of the wavelet decomposition using the 95th percentile of the local wavelet variance for each null realization. The mean value calculated from the set of 95th percentiles ($n = 100$) from each simulated realization at each scale represents the local significance threshold. Regions where local basal area wavelet variance exceeds these values represent local, scale-specific regions of significantly high basal area. These hotspots indicate patches of high basal area at different spatial scales. Continuous patches of SBW host-species basal area at coarse spatial scales may indicate areas of greater relative vulnerability. Visualization of these regions was achieved by placing contours onto maps of wavelet variance such that the contours represent emergent statistically significant boundaries in forest basal area.

Results

Global wavelet spectra

The scalograms (global wavelet spectra, GWS; Fig. 4) for all four forest cover types show similar scale-specific structure. Basal area scalograms show high levels of wavelet variance at very fine and fine scales, followed by a reduction in variance at intermediate scales, followed by an increase in wavelet variance from scales 6 to 10 (Fig. 4). In general, spatial structure is most strongly present at very fine (scale 2), fine (scale 3), and coarse scales (scales 8, 9, and 10) for all forest types.

Significant scales of pattern are those that exceed the null scalogram distribution. In comparing the basal area scalograms to the null distributions for each forest type it became obvious that the global and stationary Gaussian random field models did not fully capture the scale-specific properties of the basal area data. Each null distribution contained two scales of pattern: a fine and a coarse scale pattern indicated by the peak at the far left of the GWS (scale 2), and the second peak centered further to the right (Fig. 4A–D, roughly scales 7–9). However, these two dominant scales of pattern do not correspond well to the GWS calculated from the four basal area types, indicating that the processes that influence basal area are not stationary. Additionally, there was little variability in the distribution of the null GWS, particularly at fine scales where the mean and 95th percentile were nearly identical, and which indicates very consistent simulation of those particular scales of pattern and that the MODWT (maximal-overlap wavelet transform) is a reliable tool to characterize spatial scale.

Relative to the simulated null distribution, all scales of pattern in total basal area were significant except scales 2, 6, 7, and 8 (Fig. 4A). For relative deciduous basal area, the only nonsignificant scale was the finest, but

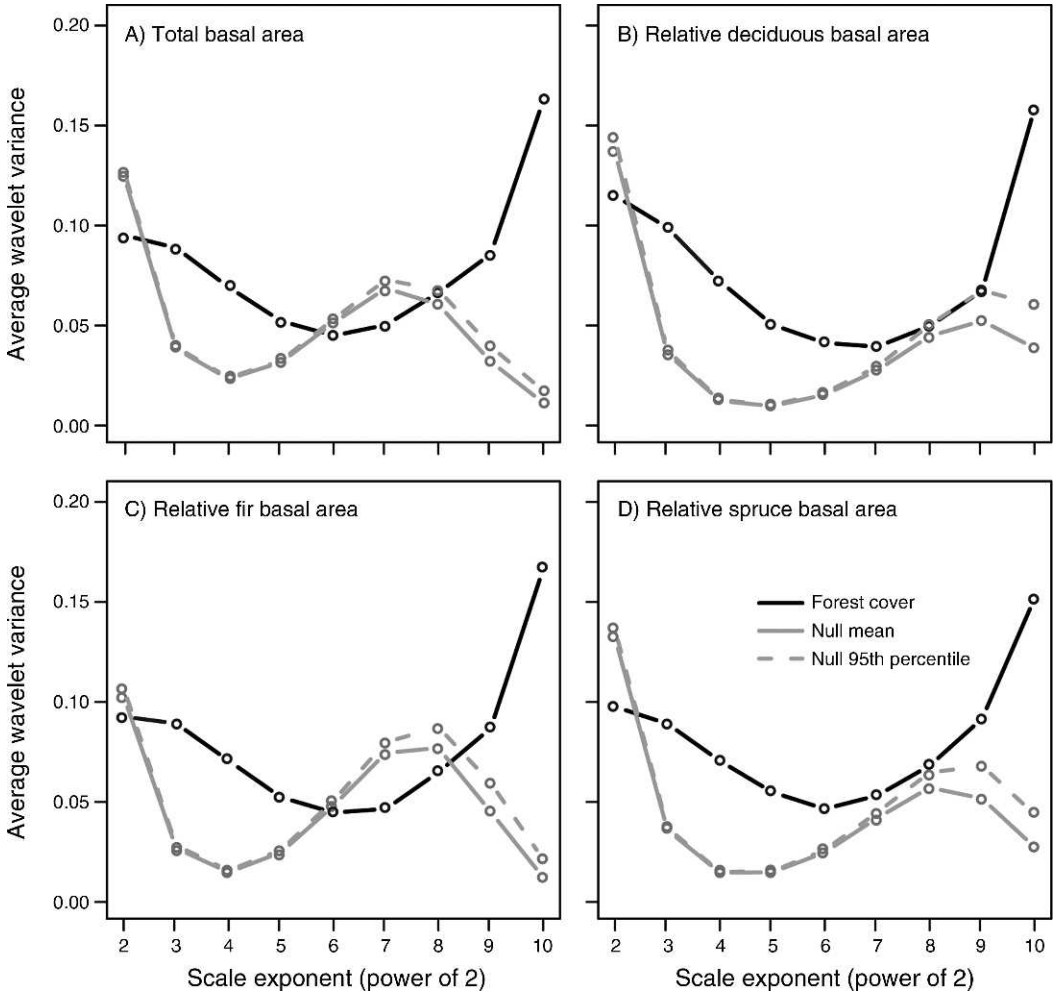

FIG. 4. Global wavelet spectra (scalograms) of remotely sensed forest basal area (solid black lines) and the corresponding global wavelet spectra for the mean and 95th percentile (solid gray lines and dashed gray lines, respectively) of the simulated null models ($n = 100$) for (A) total basal area, (B) relative deciduous basal area, (C) relative fir basal area, and (D) relative spruce basal area. Average wavelet variance represents the average squared wavelet coefficients over all locations. Scale exponents describe the dimensions of the wavelet template as a power of 2 (e.g., 2^2, 2^4, 2^8).

marginal significance is shown at scales 8 and 9 (Fig. 4B). Relative fir basal area showed patterns very similar to total basal area and only scales 2, 6, 7, and 8 were not significantly greater than expected (Fig. 4C). Finally, relative spruce basal area showed patterns similar to relative deciduous basal area and only the finest scale of spatial structure (scale 2) was nonsignificant (Fig. 4D).

Boundary identification

Contours plotted on maps of wavelet variance at three scales (8, 9, and 10) for the four basal area classes (Figs. 5–8) identify regions that exceed the 95th percentile of the null distribution of local wavelet variance. The area within the contours represents significant regions relative to the null model at a particular scale. We hypothesized that the boundaries that delineate these areas would correspond with the regional boundaries in the Border Lakes landscape (BLL; Fig. 1B).

The pattern of significant basal area in the different forest types tends to follow that of total basal area, particularly at coarse scales. At scale 10 (template size ~184 km), large portions of the BLL are significantly different from the null model to the extent that the 95th percentile contours appear to enclose regions that are within the range of expectation rather than those that exceed it. This is particularly obvious in total basal area (Fig. 5A) where only a small band in Ontario is not significantly different from the null model's 95th percentile; practically all regions are significant. Relative fir basal area closely follows the patterns in total basal area (Fig. 7A), whereas relative deciduous basal area (Fig. 8A) and relative spruce basal area (Fig. 6A) show unique patterns. Deciduous forest basal area shows a significant region mainly in Minnesota with a contour that follows the United States–Canada border and one that identifies a strong region in the east of the

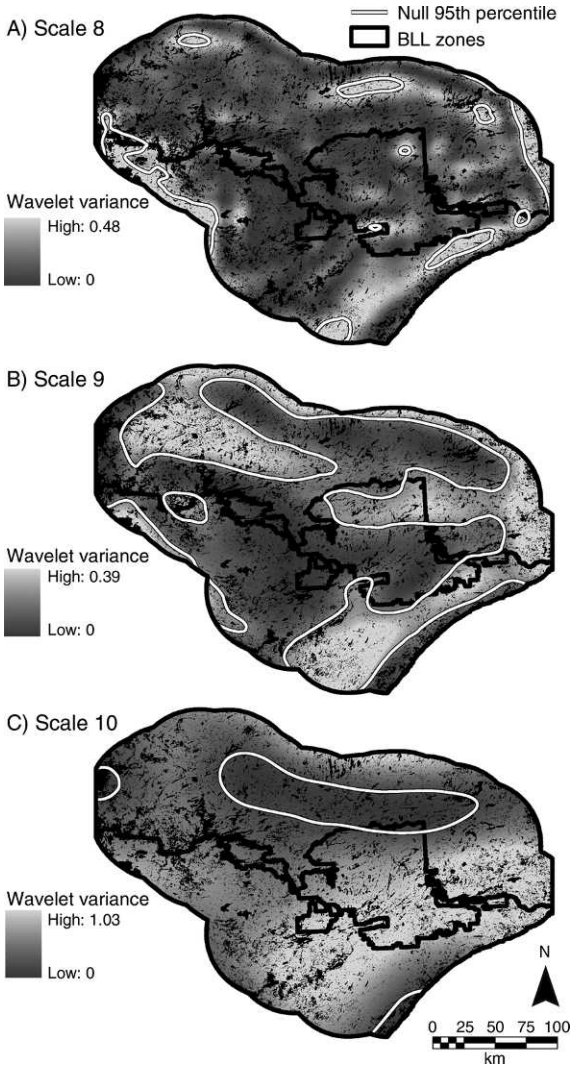

FIG. 5. Total forest basal area. Local wavelet variance for total forest basal area at (A) scale 8, (B) scale 9, and (C) scale 10, where light shading indicates high wavelet variance, and dark shading indicates low wavelet variance. Scales refer to the size of the wavelet template and correspond to template sizes of 46, 92, and 184 km, respectively. Black lines indicate regional boundaries in the BLL between Ontario managed forest, Wilderness, and Minnesota managed forest. (A, B) White lines represent 95th-percentile contours that outline significant patches of wavelet variance and correspond to scale-specific patches of high forest basal area for scales 8 and 9. (C) White-line contours that enclose areas in scale 10 identify nonsignificant regions, as the majority of the study area is significantly different from the null model at this coarse scale. Significance was assessed through comparison of wavelet variance to the 95th percentile of 100 simulated replicates of the GRF (Gaussian random field) using parameters estimated from original basal area data (Appendix A).

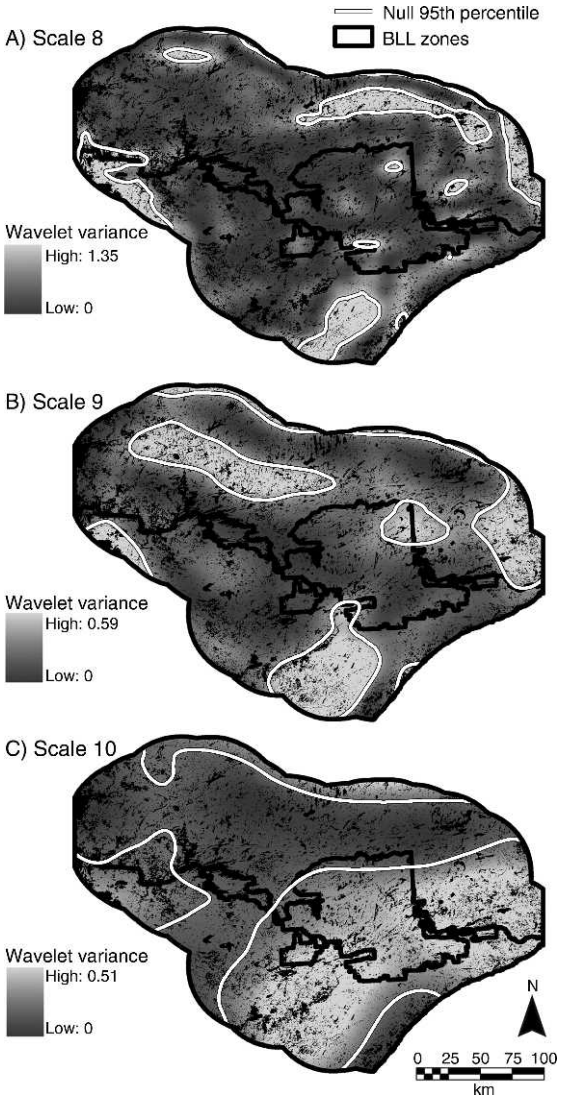

FIG. 6. Relative spruce basal area. Local wavelet variance for relative spruce forest basal area at (A) scale 8, (B) scale 9, and (C) scale 10, where light colors shading indicates high wavelet variance, and dark shading indicates low wavelet variance. Scales refer to the size of the wavelet template and correspond to template sizes of 46, 92, and 184 km, respectively. Other elements are the same as in Fig. 5.

study area (Fig. 8A). Relative spruce basal area shows most of the south and east of the BLL as significant (Fig. 6A).

Significant regions are also similar among basal area types at scale 9 (template size ~92 km; Figs. 5B, 6B, 7B, and 8B). This scale provides the best and most meaningful comparison to regional boundaries in the BLL. Total basal area and relative spruce basal area both show significant hotspots covering much of northwestern Ontario (Figs. 5B, 6B). Deciduous and fir cover identify similar, but smaller and more westerly patches. Another region that is consistent among all forest types is a central region in the middle of the Minnesota managed zone. In maps of wavelet variance for total, relative fir, and relative deciduous basal areas, this patch extends along the north shore of Lake Superior. Relative spruce basal area contains only a

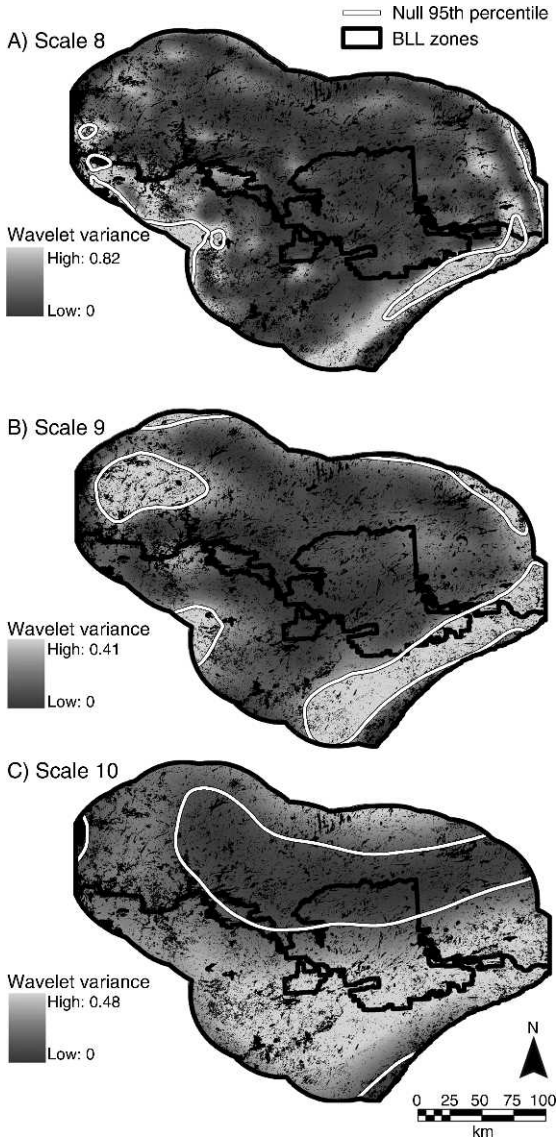

FIG. 7. Relative fir basal area. Local wavelet variance for relative fir forest basal area at (A) scale 8, (B) scale 9, and (C) scale 10, where light shading indicates high wavelet variance, and dark shading indicates low wavelet variance. Scales refer to the size of the wavelet template and correspond to template sizes of 46, 92, and 184 km, respectively. Other elements are the same as in Fig. 5.

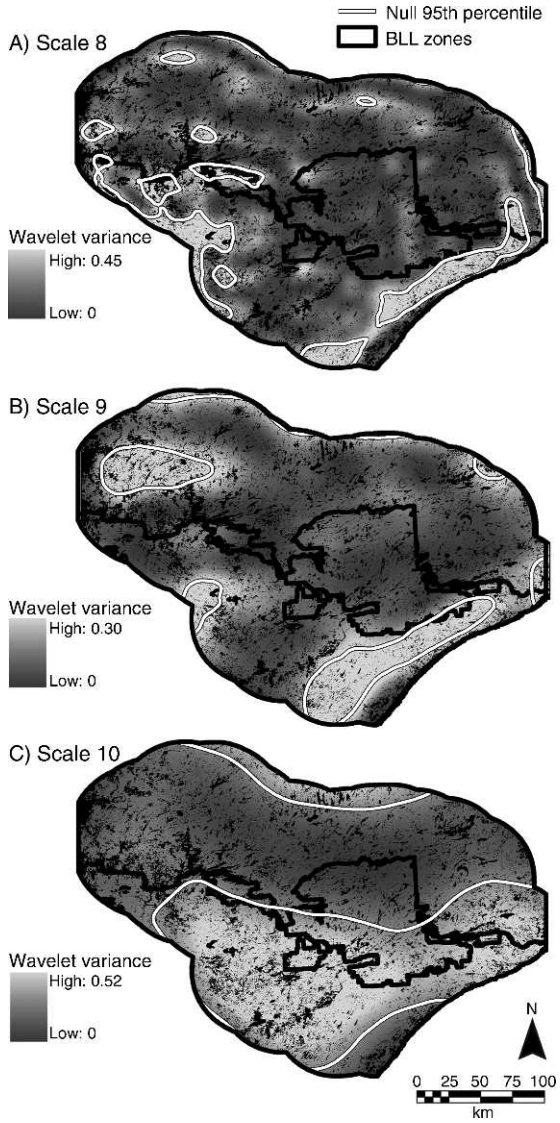

FIG. 8. Relative deciduous basal area. Local wavelet variance for relative deciduous forest basal area at (A) scale 8, (B) scale 9, and (C) scale 10, where light shading indicates high wavelet variance, and dark shading indicates low wavelet variance. Scales refer to the size of the wavelet template and correspond to template sizes of 46, 92, and 184 km, respectively. Other elements are the same as in Fig. 5.

large central patch (Fig. 6B) whose boundaries follow the southern boundary of the wilderness zone.

Local significant regions at scale 8 (template size ~46 km) include multiple patches that generally represent smaller versions of the patches identified at coarser scales (Figs. 5C, 6C, 7C, and 8C). Here, spruce is distinct and exhibits a significant region in the central portion of Ontario (Fig. 6C), and does not share the significant band along the north shore of Lake Superior that is found in total, fir, and deciduous basal area (Figs. 5C, 7C, 8C). Although we also identified additional small patches, we do not report on them here as our objective was to identify large areas of highly connected host basal area (coarse-scale patterns) that may indicate greater vulnerability, as well as significant boundaries that can be meaningfully compared to the regional administrative boundaries that divide the region into the three subregions: MN (Minnesota), ON (Ontario), and Wilderness.

DISCUSSION

Spatial legacies of forest management can affect forest ecosystems through feedbacks with selective disturbanc-

es such as the spruce budworm (Blais 1983, Cooke et al. 2007). Here, we analyzed forest basal area in the Border Lakes Landscape to assess whether management legacies can be detected in forest structure. Using continuous forest basal area data, we tested for stationarity at multiple scales and identified emergent boundaries in host and non-host forest basal area using wavelet analysis and spatially structured null models.

Wavelet analysis

Global wavelet spectra (GWS) were used to compare the scale of structure among forest basal area classes. Unlike wavelet analyses that use normalized wavelets (e.g., Torrence and Compo 1998), the approach taken in our study permits one to make direct comparisons among the wavelet variances summarized at different scales (Maraun and Kurths 2004), and among the different basal area classes. Characterization of the different scales of spatial structure in basal area is a necessary first step to identifying scale-specific hotspots of spruce budworm host species.

The global wavelet spectra indicated similar spatial structure for all forest classes and that basal area is structured at both very fine and very coarse scales (Fig. 4). Comparison against the null models indicated that basal area is significantly structured at intermediate and coarse scales. The differences between the null-model scalograms and those of basal area (Fig. 4) suggest that the underlying processes that generate spatial pattern in basal area are nonstationary (Fortin and Dale 2005). Because our null model assumed stationarity (i.e., a single set of parameters was used to summarize the entire study area), scales at which basal area differs from the null model indicates the scales at which the nonstationary processes are operating. If the processes responsible for patterns in basal area were stationary at all scales we would expect to see no difference from the null wavelet spectra of the null models. If that were the case, and the entire study area had the same scale of spatial structure (i.e., patchiness) we would conclude that there were no differences among regions and that the differences in forest management in the three zones in the BLL do not contribute to the spatial structure of basal area. Because we did find differences between empirical scalograms and the null distributions, we can conclude that there are likely differences among regions, and that these differences are at specific spatial scales. Through our local significance-testing procedure, we then identified where in the BLL these patterns at specific scales are most strongly represented.

Although some subtle differences exist, the consistent shape of the basal area scalograms among forest types suggests that a feature common to all types dominates forest structure. Lakes and wetlands are an important feature in this landscape that could account for the similarities among forest types by constraining the extent of the spatial patterns of natural and human disturbances (logging). The endogenous scale-specific forcing of the water features may act to obscure the different processes of forest management. As a result, it may not be possible to identify specific legacies of different management processes in the separate regions of the BLL because of these constraining water features.

Emergent boundaries

Wavelet based significance testing has been previously described for one-dimensional data (e.g., time series) using the wavelet power spectrum (WPS; Cazelles et al. 2008, Rouyer et al. 2008). For linear data, the WPS is two dimensional and significance in frequency and locations can be assessed simultaneously relative to an expected spectral WPS or a distribution derived from a parametric bootstrap procedure. For analysis of two-dimensional spatial data, the WPS is three-dimensional and the consequent WPS is not amenable to statistical significance testing and visualization in the same way that it is for one-dimensional data. Methods that examine global scale-specific properties separately from local properties are useful in this context (James et al. 2010). We analyzed the significance of scales and locations independently through comparison of the global wavelet power spectrum to that generated using a simulated null model, and then similarly identified locally significant regions relative to the distribution of scale-averaged wavelet variance at significant spatial scales. The strength of this approach is that wavelets can be used as a filter to remove "noise," defined as nonsignificant or nonrelevant scales, to identify globally dominant scales of pattern, and then to identify significant local variation in wavelet power. Local significant regions represent relative hotspots of forest basal area at unique spatial scales.

Recent dendrochronology work has found that the spruce budworm (SBW) outbreak dynamics are different among the three regions of the BLL (L.-E. Robert, D. Kneeshaw, and B. R. Sturtevant, *unpublished manuscript*). Because of this we expected to identify distinct regions of basal area wavelet variance that corresponded to the regional boundaries. We found that the scale-specific emergent boundaries did not follow regional boundaries exactly, but are somewhat suggestive of differences among regions. Emergent boundaries at scale 10 (template size of 184 km) separated the northern portion of the BLL from its southern portion. Maps of local wavelet variance at scales 8 and 9 indicate that there are more significant hotspots of spruce basal area in Ontario than in Minnesota, with the exception of a single large patch in central Minnesota (Fig. 6B and C). Conversely, Minnesota has more significant regions in fir and deciduous basal area at these scales (Figs. 7A, B, and 8A, B). Agreement between the basal area data and the spatial null model in the wilderness zone for fir and deciduous basal area suggests that the greatest proportion of mixed-wood forest is found there and indicates reduced vulnerability to the SBW. In contrast, large significant host patches at coarse scales in

Minnesota and Ontario indicate greater relative vulnerability to spruce budworm, particularly in the central and eastern portion of Minnesota and the northwestern portion of Ontario, where fir basal area is particularly high. It is in these regions that one might expect the greatest budworm vulnerability in the near future. However, it is important to note that these hotspots are relative indicators of basal area. That is, significant hotspots are regions that have the greatest amount of host basal area at a given scale relative to the distribution of host basal area across the landscape. In the case of balsam fir, hotspots are not "hot" in an absolute sense because of the highly dispersed distribution of fir throughout the BLL. It is also interesting to note that the significant local regions of fir strongly overlap with those of deciduous forest cover at scale 8 (Figs. 7B and 8B). This indicates that although regions may appear as suitable host for SBW with respect to a high density of fir, these sites may be mixed forests that actually have a very low vulnerability.

Few contours cross existing regional borders and this further suggests that legacies of previous management have persisted in forest basal area. The two important exceptions to this are the boundaries that define a large hotspot in total basal area (Fig. 5B) and a small zone of relative spruce basal area across the Ontario–wilderness border (Fig. 6B) at scale 8. All boundaries identified in Minnesota stop abruptly at the edge of the wilderness and indicate that the forest spatial pattern, at least in terms of total and relative spruce basal area, is more similar between Ontario and the wilderness than between Minnesota and the wilderness, and this further suggests that the patterns created by forest management practices in Ontario may be better at creating "natural" patterns than those in Minnesota. These patterns could be the result of either the scale of cutblocks (i.e., those more similar to natural openings created by fire), or due to silviculture and forest successional responses to management. It remains to be examined whether such "natural" conditions are to be preferred with regards to influencing forest vulnerability to SBW. One might also expect there to be greater similarity in forest vulnerability and patterns of budworm defoliation between Ontario and the wilderness than between the wilderness and northern Minnesota.

SBW vulnerability

We are limited in our ability to fully infer the relevance of management legacies to landscape-level forest vulnerability to future SBW defoliation based on these findings. Given that these analyses pertain to the type and scale of spatial pattern of forest basal area in the BLL, and do not relate empirical SBW damage per se to these different regions, we cannot say for certain which type of pattern is the most vulnerable and results in the greatest defoliation damage. However, because forest vulnerability is inversely related to the proportion of hardwood content in a region (Su et al. 1996, Cappuccino et al. 1998, Campbell et al. 2008), large, significant hotspots of SBW host-species basal area (i.e., fir and spruce) likely represent regions of greatest relative vulnerability. For example, the large spruce hotspots in the managed zone central-western Ontario and central Minnesota (Fig. 6B) as well as the fir hotspots in western Ontario and eastern Minnesota represent areas of highest potential vulnerability (Fig. 7B). In support of this, a recent and ongoing budworm outbreak in Minnesota has recently spread eastward into the central Minnesota patch we identified (Mike Albers [Minnesota Department of Natural Resources], *personal communication*).

The regions of local significance that we identified did not conform strongly with our expectations and other work that has demonstrated important differences in forest structure and outbreak dynamics among regions (e.g., L.-E. Robert, D. Kneeshaw, and B. R. Sturtevant, *unpublished manuscript*). Furthermore, the ambiguous patterns make it difficult to infer budworm vulnerability within and among regions. One of the possible explanations for this mismatch between expectations and what the wavelet analysis revealed is that other processes have structured forest basal area in the BLL. Additional processes such as fire, other insect outbreaks, and forest succession can obscure the legacies of management and make it difficult to identify clear cause-and-effect relationships (Veblen et al. 1994, James et al. 2011). As a result, legacies may be temporary (James et al. 2007) and identifying the correct time frame to investigate them represents a significant challenge to understanding the role that forest management can play in mitigating future insect outbreaks. Further work in this area will include investigating forest spatial structure in the BLL at different time periods using the scale-specific methods presented here.

Conclusions

Descriptions of the dynamic interactions among spatial legacies and forest disturbances are important for forest management and further development of ecological theory (Levin 1992, Cooke et al. 2007). We examined spatial patterns in forest composition and boundaries in forest basal area at multiple scales using a novel wavelet-based significance-testing method. Using this method, we identified nonstationarity in forest basal area in the BLL and observed that the local regions that most strongly exhibit this nonstationarity have boundaries that are somewhat similar to regional boundaries. These results suggest that different histories of forest management have the potential to influence the spatial distribution of spruce budworm host species and hence relative forest vulnerability to SBW defoliation. Local significance testing revealed large continuous patches of SBW host-species basal area at coarse scales in northwestern Ontario and central northern Minnesota that are more likely to support an outbreak.

The differences between what we know about historical management in the BLL and the patterns we detected on the landscape are likely due a combination of the constraining influence of lakes and wetlands, forest succession, and the forest-changing consequences of other disturbances (e.g., fire, wind, insects). The legacy-eroding effects of such successional stochasticity and compounded disturbances (Veblen et al. 1994, James et al. 2007), in combination with the relatively long return intervals for successive spruce budworm outbreaks (Candau and Fleming 1998), suggest that patterns in forest basal area created through forest management may not affect forest vulnerability as strongly or directly as the silvicultural hypothesis might suggest. Furthermore, legacies in species composition and basal area are not the only relevant measures of forest vulnerability. Forest age is also important (MacLean 1980) and age-specific legacies have been shown to have long-lasting influence on forest structure (James et al. 2007). As a result, the boundaries identified and vulnerability inferred are only a partial assessment of spruce budworm defoliation potential in the BLL. Additional research into the relationships among management legacies, forest composition, basal area, forest age, and vulnerability is still required to better understand the complex interactions among human management activities and insect outbreak dynamics.

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APPENDIX

Gaussian random field (GRF) simulation and variogram parameter estimates (*Ecological Archives* A021-099-A1).