Advances in Research on Spatial Patterns of Forest Pest Occurrence: Postprint

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Abstract

Forest insect populations exhibit diverse spatiotemporal patterns, with spatial synchrony being among the most common. This review summarizes advances in the characteristics, formation mechanisms, and research methodologies of spatial synchrony in forest insects. Synchrony in forest pest outbreaks is widespread, but its magnitude varies among different insect species. Spatial synchrony typically declines with increasing distance and is also dependent on temporal scale. The Moran effect and dispersal represent the two primary mechanisms explaining spatial synchrony, with the Moran effect generally exerting a greater influence than dispersal. Advances in research methodologies for spatial synchrony are discussed from three perspectives: acquisition of outbreak data, measurement of synchrony, and investigation of its underlying causes. The approach of reconstructing forest pest outbreak histories using dendroecological principles can obtain reliable data retrospectively and merits adoption and application by domestic researchers. For measuring spatial autocorrelation, both spatial statistical and geostatistical methods are powerful tools, but their application in synchrony research is constrained by their inability to handle multi-temporal data. In studies investigating the causes of synchrony, employing variation partitioning with distance-based Moran eigenvector maps (dbMEM) as spatial variables to examine drivers of pest outbreaks represents a relatively novel research methodology.

Full Text

Spatial Patterns of Forest Insect Outbreaks: A Review

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Abstract

Forest insect populations exhibit diverse spatio-temporal patterns, among which spatial synchrony is the most common. This paper reviews advances in understanding the characteristics, underlying mechanisms, and research methodologies of spatial synchrony in forest insects. Spatial synchrony of forest insects is ubiquitous but varies among species. Synchrony typically decreases with distance and is related to temporal scale. The Moran effect and dispersal represent the two primary mechanisms explaining spatial synchrony, with the Moran effect generally exerting a greater influence than dispersal. We also review research methods related to pest occurrence data acquisition, synchrony measurement, and causal analysis. Dendroecological reconstruction of forest insect outbreak histories can provide reliable data many years post-occurrence, representing a valuable approach worthy of adoption by Chinese researchers. Both spatial statistics and geostatistical methods are powerful tools for measuring spatial autocorrelation; however, their application in synchrony studies is limited by their inability to handle multi-temporal data. Variation partitioning using distance-based Moran' s eigenvector maps (dbMEMs) as spatial variables represents a relatively novel method for investigating the drivers of forest insect outbreaks.

Keywords: outbreak mechanism; spatial synchrony; spatial autocorrelation; dendroecological analysis; Moran' s eigenvector maps

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Introduction

Spatio-temporal processes refer to the spatial patterns of objects that evolve over time. Two independent processes may produce identical patterns, also known as spatial structure. The coupling between processes and patterns is often imperfect. Since direct process investigation is typically very difficult, researchers commonly approach the problem through pattern analysis. As an ecological process, forest pest outbreaks inevitably exhibit certain spatio-temporal patterns. Analyzing these patterns across different scales can provide clues for understanding pest population outbreak mechanisms. Population spatio-temporal patterns can be highly complex, including chaos and lattice structures. For instance, the western tussock moth (*Orgyia vetusta*) population displays a chaotic pattern, while periodic waves emerge during outbreaks of the larch budmoth (*Zeiraphera diniana*). However, in natural systems, such complex patterns are rare. A more common pattern is synchronized population oscillations across broad geographic regions, also termed spatial autocorrelation. Studying broad-scale synchrony has long been central to population ecology because as regional correlation increases, global population persistence declines, and population resilience is closely related to the degree of correlation in population dynamics. This paper primarily reviews advances in spatial synchrony of forest insects, its causes, and research methodologies.

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1. Spatial Synchrony and Its Detection

Population synchrony typically refers to synchronized oscillations in population density across different locations. Population density may involve either conspecific or heterospecific populations. The simplest method for detecting spatial synchrony involves calculating pairwise correlations between time series of spatially nonadjacent subpopulations, then using the overall average correlation across the study region as regional-level synchrony. Correlation coefficients are commonly used to study linear correlations between two series, with Spearman rank correlation also employed to measure synchrony. Such approaches are called "correlation-based detection of synchrony" and were widely applied in the 1990s. However, correlation-based measures lack ecological meaning and cannot account for heterogeneous synchrony.

Hanski and Woiwod proposed that synchrony should refer to covariation in rates of change, which can be represented by the correlation of ratios between successive years' abundances (R = log N - log N). This approach, termed "change correlation," directly measures how often two series move in the same direction and thus best represents the definition of synchrony. Kendall' s tau, a variant of this method, detects the number of times series i and j move in the same direction: A = (n - n)/n, where n and n represent concordant and discordant movements, respectively.

Methods for detecting matching of peaks or other extreme behaviors are often used to study whether pest outbreaks are regular in the region of interest. Chi-square tests have been applied in such studies, with newer developments including phase analysis, which can measure more complex spatial patterns beyond simple spatial synchrony. Simulation studies show that these metrics sometimes align with synchrony assessments but sometimes do not.

Another important aspect of spatial synchrony research is the relationship between synchrony and distance. Methodologies for this can be divided into parametric and nonparametric approaches. Parametric tests assume a specific functional relationship between synchrony and distance, while nonparametric methods, which can handle more complex spatial patterns, are more widely used. The Mantel test has served as a standard method for such research since its proposal in 1967. The Mantel test examines the overall relationship between plot distances and similarities, with 衍生 methods including distance-based partial correlation statistics, multiple regression on distance matrices (MRM), and tests of concordance among multiple distance matrices. Mantel correlograms divide distances into classes and test whether autocorrelation within each class, calculated from pairwise values, exceeds or falls below the overall inter-plot average, then plot standardized z-values against distance classes.

Another widely used nonparametric method employs smoothing splines to produce direct, continuous estimates of spatial covariance as a function of distance lag, with bootstrap methods generating confidence intervals for these estimates. Gouveia et al. extended this approach by incorporating secondary covariances.

Direct descriptors of spatial autocorrelation include correlograms such as Moran' s I and Geary' s c. Beyond correlograms, variograms—originating from geostatistics—are commonly used structural functions for detecting, modeling, and estimating spatial patterns. The variogram is essentially the unstandardized form of Geary's c. Variograms can reflect the degree and distance range of spatial heterogeneity caused by spatial autocorrelation. For example, geostatistical analysis of the pine sawyer beetle (*Monochamus alternatus*) revealed spatial autocorrelation extending 93 m, with intensity decreasing with distance and explaining over 99.9% of total spatial variation.

The above methods address global spatial correlation across entire study regions, with results that cannot reveal regional details. Anselin (1995) proposed decomposing global spatial correlation coefficients into local statistics for each sampling unit, termed LISA (Local Indicators of Spatial Association). Ecologists and spatial statisticians have debated whether simple autocorrelation refers to static patterns while spatial synchrony involves temporal variation—a special form of spatial autocorrelation that varies over time. For multi-temporal spatial data, variograms can only be analyzed separately for each time point.

2. Characteristics of Forest Insect Population Synchrony

Spatial synchrony is widespread among insects. Thirty-one years of monitoring data show that butterfly populations in the UK exhibit spatially synchronized dynamics. Studies of 15 insect species across different orders (Lepidoptera, Hymenoptera, and Diptera) confirm this pattern. Data from 1938-2002 indicate that forest tent caterpillar (*Malacosoma disstria*) populations in northwestern Ontario, eastern Ontario, western Quebec, and eastern Quebec show synchronized dynamics. The pine processionary moth (*Thaumetopoea pityocampa*) exhibits synchronized outbreaks in neighboring regions with similar climates. Spatial synchrony has also been documented in the Douglas-fir tussock moth (*Orgyia pseudotsugata*), beech caterpillar (*Quadricalcarifera punctatella*), spruce budworm (*Choristoneura fumiferana*), larch budmoth (*Zeiraphera diniana*), mountain pine beetle (*Dendroctonus ponderosae*), and gypsy moth (*Lymantria dispar*).

Different insect species exhibit varying degrees of spatial synchrony. Aphids show higher spatial synchrony than moths. Spatial synchrony is distance-dependent, typically decreasing with distance. On islands in northern Troms County, Norway, the winter moth (*Operophtera brumata*) shows synchronized dynamics within mature birch forests on individual islands but maximum asynchrony between islands. Although synchrony generally declines with distance, its range can extend up to 1,000 km. In eastern North America, spruce budworm outbreaks show spatial synchrony reaching 2,000 km, with synchrony declining as distance increases but approaching zero only at 800 km. Some cases show synchrony initially decreasing then increasing with distance, depending on the scale employed.

Spatial synchrony also relates to temporal scale. In the UK, aphid synchrony increases at longer time scales but decreases at shorter time scales.

3. Mechanisms of Spatial Synchrony in Forest Pest Outbreaks

Theoretical studies indicate that regional stochasticity and dispersal are the two primary mechanisms reasonably explaining spatial synchrony. The most obvious factor causing regional stochasticity is meteorological. If two spatially isolated populations with identical density-dependent dynamics experience similar regional density-dependent factors (typically weather), they become synchronized. Dispersal influences spatial synchrony through phase-locking of cyclic populations, depending on dispersal patterns. When both environmental correlation and dispersal rates are small, these mechanisms can operate independently; however, they typically function jointly through non-additive patterns. Because the interaction effect' s sign opposes that of environmental correlation, population synchrony calculated by simple addition is usually smaller than actual synchrony when inter-plot environmental correlations are positive. As management intensity increases, population synchrony decreases, necessitating joint consideration of dispersal and environmental correlation when interpreting synchrony patterns.

A third widely recognized mechanism involves interactions with other species (predators, pathogens). However, these trophic-level interactions rarely significantly influence large-scale synchrony in some insects because the mobility of natural enemies and pathogens is generally equivalent to or less than that of the insects themselves.

Most studies demonstrate that meteorological factors exert greater influence on spatial synchrony than dispersal. This pattern holds for noctuid moths and aphids. Gypsy moth outbreak synchrony is also Moran effect-driven. Analysis of 70 outbreak records from 11 forest Lepidoptera species across the Northern Hemisphere (North America and Europe) shows that outbreak periods and cool weather correlate with sunspot minima. Peltone et al. studied landscape-scale occurrence data for 15 forest insects, finding that spatial correlation of meteorological factors explained synchrony levels, suggesting the Moran effect may be the decisive process influencing spatial dynamics for these insects. In central Appalachian deciduous forests, spatial synchrony of 11 butterfly species is driven by meteorological factors. Dendrochronological analysis of larch tree-ring width series from the Alps indicates that larch budmoth (*Zeiraphera diniana*) outbreaks align with two centuries of temperature variation. In south-central and southwestern Alaska, climate variability drives outbreaks of the spruce beetle (*Dendroctonus rufipennis*). The North Atlantic Oscillation (NAO) index correlates with spatial synchrony of the green spruce aphid (*Elatobium abietinum*) in the UK. A three-century reconstruction of western spruce budworm

(*Choristoneura occidentalis*) outbreaks in the Pacific Northwest shows correspondence with drought history. Research across the UK demonstrates that long-term aphid synchrony is driven by winter climate. The beet webworm (*Loxostege sticticalis*), a migratory insect, shows highly synchronized outbreaks across Asian Russia and Mongolia, likely driven by upper-air currents.

Except for migratory insects, dispersal-induced synchrony is typically short-range, though not negligible. In eastern North America, spruce budworm outbreak synchrony results from combined Moran effects and high dispersal rates.

However, some pest outbreaks cannot be explained by dispersal and Moran effects alone. Even minimal individual exchange between isolated populations can generate synchrony. Local environmental condition synchrony may mask meteorological drivers, as gypsy moth synchrony declines faster than meteorological synchrony. Analysis of 31 years of data shows meteorological spatial autocorrelation barely affects spruce budworm (*C. fumiferana*) distribution and occurrence in Ontario, Canada. Forest insect outbreak synchrony is influenced by forest management practices; spruce budworm dynamics under varying silvicultural intensities cannot be explained by climate differences among sampling sites. After removing habitat characteristic effects (phenological asynchrony, pesticide use, non-host plant abundance), the remaining defoliation variation shows spatial autocorrelation ranging 788–4,461 m, while gypsy moth larval dispersal ranges only 100 m, indicating greater influence than intensive management.

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4. Research Methods for Spatial Synchrony Causation

Spatial pattern causation stems from two sources: intrinsic spatial structure (true spatial autocorrelation) and external factors with spatial autocorrelation (e.g., environmental factors), termed induced spatial dependence. Distinguishing these is difficult. For pest outbreaks, true spatial autocorrelation mainly arises from dispersal, while induced dependence primarily reflects Moran effects. Forest protection managers can do little about true autocorrelation but must understand induced dependence to develop management measures based on environmental variation.

Because spatial correlation violates the independence assumption required by classical statistical methods, alternative approaches are necessary. Haynes et al. used multiple regression on resemblance matrices (MRM) to study relationships between dependent distance/similarity matrices and explanatory variable matrices, partitioning variance into environmental and spatial sources. Foster et al. employed linear models and hierarchical partitioning to examine host abundance, topography, and insecticide use effects on gypsy moth density, then used variograms to study residual spatial autocorrelation.

Mixed-effects models effectively address data non-independence. Adding spatial correlation structures represented by variograms to GLM, GLS, LME, GLMM, and GAMM models resolves non-independence issues. The book *Mixed Effects Models and Extensions in Ecology with R* provides detailed applications. Dormann et al. (2007) reviewed and simulated these methods, finding good performance for normal and Poisson data but poorer fit for binomial data. Model selection should consider response variable error distribution types. For normally distributed data, GLS and SAR (simultaneous autoregressive) methods are appropriate, though SAR requires high storage capacity for large samples and is thus limited in practice. CAR (conditional autoregressive) models are suitable for missing values and non-grid data. A practical strategy involves fitting different models and comparing them using criteria like AIC.

Increasingly, studies use spatial proximity as an explanatory variable for unmeasurable processes like dispersal. These studies often employ Moran's eigenvector maps (MEM) as spatial variables—orthogonal eigenvectors derived from spatial coordinate networks at certain distance thresholds. MEM characteristics include: orthogonality among vectors, linear independence among submodels, ability to model spatial variation at all scales, and applicability to both linear modeling and time series analysis (including variation partitioning). For time series, MEMs derive from temporal distance networks at certain lags.

Variation partitioning decomposes total pest outbreak variation into independent components: a pure environmental component, a pure spatial component from proximity effects, a shared component, and unexplained variation. A linear model can partition total variation, visually revealing primary outbreak drivers. Results are typically presented in Venn diagram form.

5. Data Acquisition for Forest Pest Outbreaks

Forest pest outbreak data can be obtained through: (1) observational or historical records, (2) remote sensing or aerial surveys, and (3) dendrochronological reconstruction. In China, field forest protection workers' professional levels need improvement, and practitioners often lack stable positions, making the first data source frequently criticized. Remote sensing data are limited by duration and cloud interference, making long historical series difficult to obtain.

The third approach, based on the principle that pest outbreaks affect tree radial growth, offers high reliability ("trees don' t lie") and can provide long historical series limited only by tree age. Widely used in archaeology, meteorology, and ecology, this mature method is rarely reported in Chinese literature. Since China manages harmful organisms as disasters based on impacts to tree growth, this approach can avoid long-standing debates about pest "economic thresholds." While some researchers worry about damage from increment borers, physical damage is negligible; the main consequence is potential fungal infection causing discoloration around wounds, which is minimal overall and not significantly reduced by sterilization or plugging bore holes.

The theoretical basis is that biological disasters affect radial growth. Dendrochronological methods identify years when growth was disturbed, then exclude other influencing factors (inherent growth trends, climate). The ring-width index (RWI) method determines outbreak years: RWI = R /G , where R is actual ring width in year t and G is detrended ring width. Two variants exist: host-nonhost comparisons and regional chronology methods, both aiming to remove climatic effects. The host-nonhost method assumes differential pest impacts on host versus non-host species, requiring similar climate responses. The regional method assumes outbreaks occur in some sub-regions within larger areas, making proper area delineation critical. Fire, another major radial growth factor, cannot be excluded by the host-nonhost method but theoretically can by the regional method; fire history can be determined through fire scar surveys or manager interviews. Most Chinese forests are natural secondary or plantation forests with relatively young ages and documented fire histories.

Swetnam's method calculates a corrected index: I_c = (I_h - Ī_n)/SD, where h indicates host, c indicates correction, t indicates year, n indicates non-host, and SD is standard deviation. Outbreak years are then identified by standardized I_c values. Ryerson et al. used criteria where outbreak intervals contain at least 30% of cores with RWI < -1.28 SD. Point Years method identifies years where rings are significantly narrower than adjacent years. Paritsis et al. used multiple criteria: (1) Pointer Years method indicating disturbance, (2) RWI method indicating pest occurrence, and (3) at least 30% of cores with RWI < -1.28 SD. For individual cores, years meeting all three criteria are high-confidence outbreaks; two criteria indicate medium confidence; one criterion indicates low confidence. For plots and regions, years meeting both criteria 1 and 2 are high-confidence outbreaks.

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6. Summary

China experiences frequent forest biological disasters, and studying spatial patterns of forest pests is key to revealing outbreak mechanisms. Spatial synchrony is a common pattern, though distinguishing true spatial autocorrelation from induced spatial dependence remains challenging. This review synthesizes research progress on forest pest synchrony and methodologies, particularly dendrochronological reconstruction of outbreak histories and emerging methods using dbMEM as spatial variables to explain variation in dependent variables, aiming to advance research on forest pest outbreak mechanisms in China.

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