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Of clockwork and catastrophes: advances in spatiotemporal dynamics of forest Lepidoptera

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We applied a systematic global literature survey from the last 2.5 years on spatiotemporal population dynamics — broadly defined — of Lepidopteran forest pests. Articles were summarized according to domain-specific (planetary ecology — remote sensing, evolutionary ecology — genetics and genomics, and theoretical ecology — modeling) contributions to contemporary investigation of the above theme. 'Model systems' dominating our literature survey were native *Choristoneura fumiferana* and invasive *Lymantria dispar*. These systems represent opposing ends of a more general equilibrium–disequilibrium gradient, with implications for less-studied taxa. The dynamics of Lepidopteran systems defy simple modeling approaches. Technologies and insights emerging from 'slower' science domains are informing more complex theory, including predictions of spread, impacts, or both posed by more recent invasions and the disrupting effects of climate change.

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Introduction

The complexity of forest-defoliator outbreak dynamics has led to vigorous debate as to how to best characterize, forecast, and respond to them. Periodic, spatially extensive defoliator outbreaks are thought to emerge from one of two possible pathways. In the first, delayed density-dependent predator-prey processes produce harmonic oscillations in time (i.e. 'clockwork' [1]) that are synchronized regionally via spatially autocorrelated, density-independent factors such as weather. Alternatively, the double-equilibrium theory suggests that defoliator populations are held at endemic levels by a combination of mortality and mating failure at low densities [2]. Here, slow ecological processes such as gradually increasing food resources and fast processes such as dispersal and immigration can flip the system into spatially expanding catastrophic outbreaks [3,4]. The management implications of the two theories are profound for native [5] and exotic [6] species alike. While some argue that neither theory is complete, and any given system is likely to contain elements of each [7] — the debate persists [8,9].

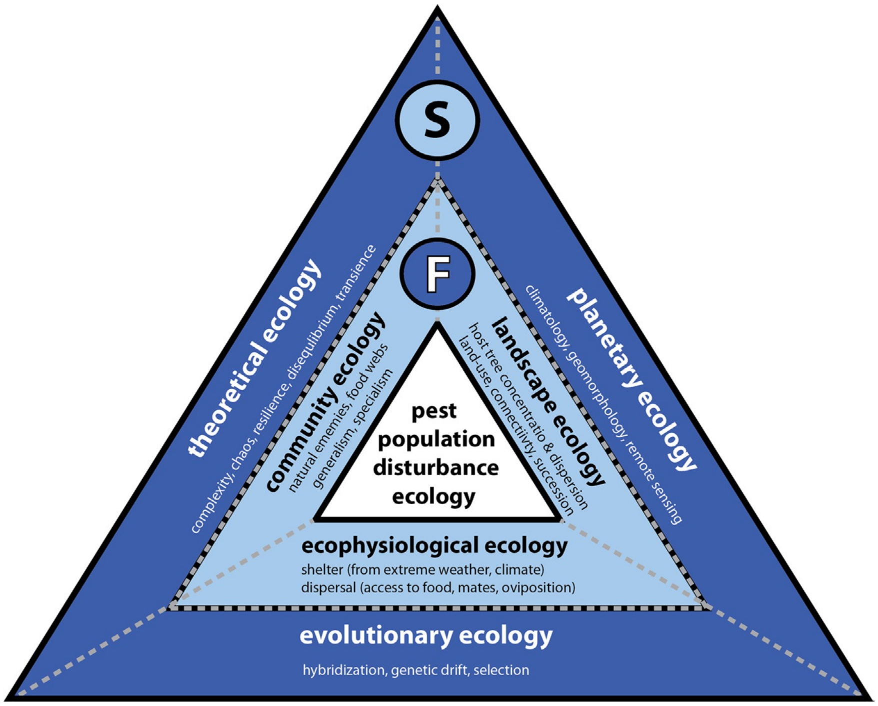
Forest pest population and disturbance ecology examine comparatively fast processes acting on ecological timescales that can be examined effectively with the sciences of ecophysiology, community ecology, and landscape ecology. However, these disciplines are shaped by technologies and insights emerging from 'slow sciences' that are either focused on processes operating at geological timescales (i.e. evolutionary and planetary ecology) or take multiple decades to effectively confront empirically (theoretical ecology). A pest outbreak is thus the emergent consequence of process interactions that cross scales as well as scientific disciplines (Figure 1).

Using a systematic, global literature review on the landscape ecology of forest Lepidopteran pests (January 2020–June 2022, Supplementary Information 1 to 2), we examine current trends and approaches to investigate their dynamics, from invasive spread to indigenous outbreak patterns. We place this small slice of literature ($n = 83$ papers) — brief in time but broad in scope — in context via a novel framework depicted in part by Figure 1. Through this framework, we identify new opportunities for synergy and scientific advance in research and applications on the dynamics of forest Lepidoptera.

Planetary ecology — remote sensing

Investigation of pest disturbance ecology in time and space is reliant on spatiotemporal data documenting population density (or proxies thereof); environmental factors affecting growth, survival, and movement; and host abundance and distribution. The planetary sciences provide such information via the disciplines of climatology, geomorphology, and remote sensing. Indeed, in

Figure 1



Current Opinion in Insect Science

Relationship between foundational research domains and approaches to pest ecology that inform operational pest risk assessment and management. ‘Slow’ science domains (S) set the context for the ‘fast’ research approaches (F) that ultimately shape the population ecologies of all pest species, from the well-studied model systems to emerging threats for which we have little data. Complexities underlying pest population disturbance ecology have posed exceptional difficulties for scientific inquiry, suggesting there may be synergies in sharing insights across disciplines (symbolized by permeable dashed boundaries) and across pest problem areas, from indigenous to invasive species.

the last 2.5 years, 15 studies applied remote sensing specifically to the insect taxa covered by this review, indicating that it remains an active area of research. Nonetheless, only 5 of 54 studies investigating the landscape ecology of defoliating pests used remote sensing data as analytical inputs (see Supplementary Information 2).

Trade-offs in remote sensing technology resolution (spatial, temporal, spectral, and thematic) versus extent are well-known [10]. Effective insect host (i.e. tree) mapping often requires genus- to species-level differentiation to quantify conditions for defoliators. For example, multispectral remote sensing of hosts for *C. fumiferana* either aggregated spruce species (*Picea spp.*) [11] or ignored the less-preferred *P. mariana* [12,13], with important consequences for population dynamic inference [14]. Detection of defoliators and the disturbance they cause faces similar challenges. A comparative defoliation detection study demonstrated how the combination of host breadth, tree species and structural diversity, and foliar susceptibility determines the effectiveness of change detection when using Landsat imagery [15]. The combination of analytical methods, public access to archived imagery, and expansion of technologies such as lidar (light detection and ranging) and hyperspectral imagery enables more effective mapping of forest composition and defoliation detection alike — but such improvements are slow to be operationalized [10].

Consequently, investigators continue to rely on traditional source data such as plot- or stand-level forest inventories for hosts, and insect sampling, spot assessments, tree-ring analyses, or aerial surveys of insect detection/disturbance. Each source has its strengths and limitations. For example, three articles focused on the invasion process of *L. dispar* were constrained to county-level (~50 km^2) resolution due in large part to the reliance on plot-based forest inventories for host data [16–18]. Remote sensing can enable the detection of landscape drivers (e.g. terrain, host patterns, etc.) affecting outbreak initiation and spread [19]. Yet, spatial resolution is not the only constraint. Tree-ring analysis of *Malacosoma disstria* defoliation revealed spatio-temporal outbreak dynamics dominated by traveling waves such that correlations between host patterns and outbreaks were inconsistent between outbreaks [20].

Traditional forest inventory and health monitoring sources will remain important to landscape and regional defoliator studies — at least until remote sensing technologies replace them.

Our review indicated progress on this front. Two studies used national-scale forest maps with enough taxonomic detail to be relevant to defoliator outbreak dynamics [21,22]. Semiautomated methods in change detection within imagery time series [23] and a biome-scale effort to map partial disturbances [24] suggests that operational-scale remote sensing for forest health may not be that far off. Application of thermal imagery may enable 'early detection' of tree stress (e.g. [25]), rooted in physiological principles [26], with implications for both novel population control efforts [2] and controlling the spread of invasives [27].

Evolutionary ecology — genetics and genomics

Genetic data are increasingly used to improve understanding of the spatial and temporal dynamics of outbreaking forest insect pests. Several studies have detected meaningful population genetic structure and connectivity at regional to continental scales across a variety of Lepidoptera taxa (Supplementary Information 2). For invasive species, detection of population structure within their native ranges can refine anticipated invasion dynamics or the possible climatic envelopes of the invading populations (e.g. [28]). Importantly, however, observed or genetically inferred connectivity and spread rates do not necessarily translate into outbreak dynamics [29].

For native or naturalized species, population genetic variation may be exploited to investigate the relative importance of different spatial processes in driving outbreaks. For example, Larroque et al. [30] used population differentiation at the leading edge of a *C. fumiferana* outbreak to document a genetic traveling wave, indicating dispersal as an important factor underlying outbreak spread, while Larroque et al. [21] applied landscape genetics to understand the role of spatial heterogeneity in *C. fumiferana* population connectivity. Nonetheless, genetic differentiation in space can be sensitive to the timing of sampling relative to the outbreak phase [4] and challenging to detect within cyclic-irruptive systems [31]. Meaningful contributions of population genetics to managing forest pest outbreaks will require a new framework that accounts for the influence of population cycling (bottlenecks, synchrony, phase-dependent dispersal, etc.) and is an active area of research across multiple taxa [32].

Genomics and genetics are also making contributions to the characterization of trophic interactions in outbreaking systems. Recent examples include studies of within-species genomic differentiation among populations sampled on different host tree species [33], characterization of predator diets [34], and parasitoid identification [35]. Such tools have potential to improve monitoring of trophic interactions thought to affect the outbreaks of forest Lepidoptera. More specific to spatial ecology, genetic approaches are further contributing to our understanding of the population connectivity of parasitoid natural enemies relative to their insect hosts [36].

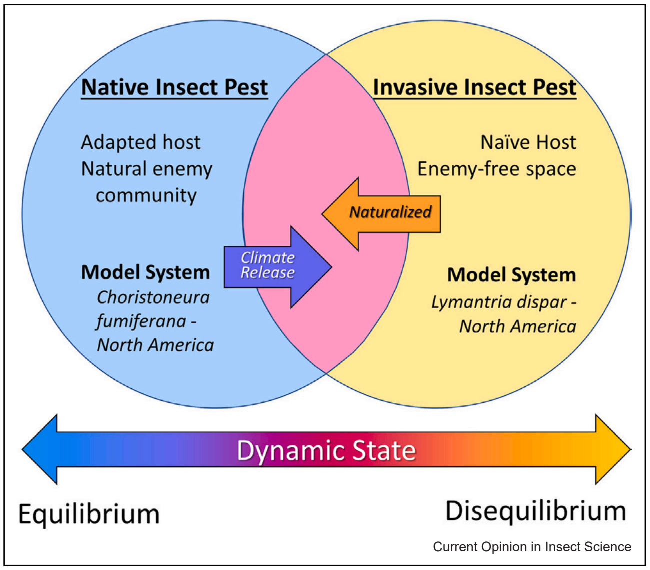
Finally, the development of reference genomes may advance our understanding of pest outbreak dynamics and suggest novel methods for pest mitigation or control. Reference genomes have recently been developed for multiple outbreaking species (Supplementary Information 2) and hold potential to further clarify the role of eco-evolutionary adaptation in outbreaking population dynamics (e.g. [37]). As with remote sensing technology, these recent advances are only beginning to have an impact on the field of insect pest disturbance ecology. Continued emphasis on interdisciplinary collaboration is needed however to fully leverage the benefits of these novel genomic resources and to make meaningful contributions to understanding and managing outbreaks.

Theoretical ecology — modeling

Modern computing technologies are giving rise to new methods in statistical analysis, applied mathematics, and risk analysis. As with the above technological advances, we found heavy research investment in so-called 'model systems' — *C. fumiferana* in Canada and *L. dispar* in the United States — supplemented with a more diverse global research effort devoted primarily to 'emerging threats' (Supplementary Information 1 to 2). These two model systems span the full array of dynamical state space — from equilibrium to disequilibrium — and thus potentially serve as useful templates for understanding emerging threats resulting from new species introductions or rapid changing native pest dynamics in response to climate change (Figures 2, 3).

Although these model systems have been investigated for decades (Supplementary Information 1), they are revealing important new complexity when scrutinized using novel techniques and datasets. For *C. fumiferana*, high-resolution tree-ring data going back to the start of the 20th century indicate that although populations cycle somewhat synchronously across the province of Quebec, there are significant differences in outbreak timing and duration among intervals in time and space important in forecasting future outbreak impacts, but whose cause is not yet understood [38]. For *L. dispar*, defoliation monitoring in the eastern United States

Figure 2

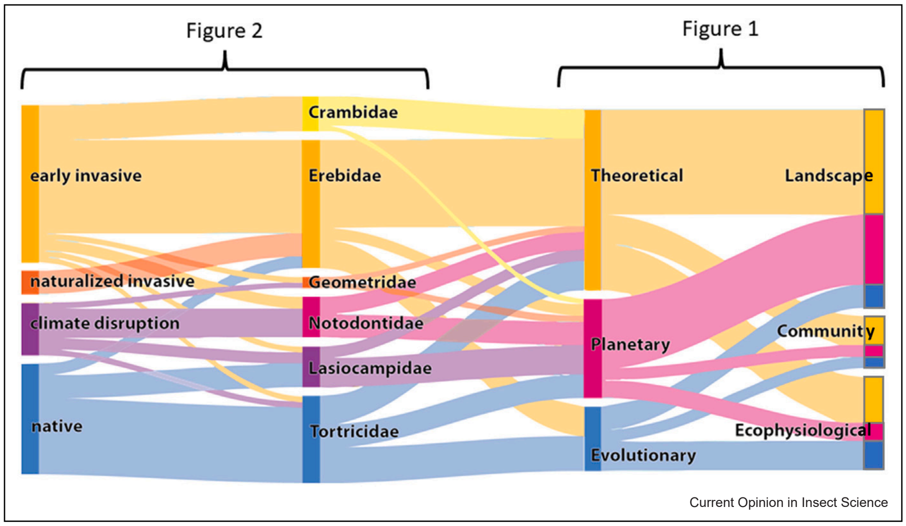


Dynamical behavior across taxa. Native insect pest systems (blue) are more likely to exhibit equilibrium (i.e. dynamic stability) relative to invasive pests (gold). However, climate change could cause equilibrium systems to move toward disequilibrium (right arrow, purple) and naturalization could cause invasive pest outbreaks to attenuate (left arrow, orange).

exhibited roughly periodic outbreaks through most of the 20th century, with occasional minor outbreaks between the major decadal cycles [39]. Yet, before that, they exhibited a sustained pattern of eruption. This fundamental shift in dynamics was attributed to the introduction of a viral biocontrol agent vectored by an introduced parasitic fly. The sudden transition in 1906 from sustained catastrophe to clockwork, and another abrupt decline in outbreak intensity in 1989 coinciding with a new fungal agent, represents a significant development in our understanding of dynamic stability. Not only is stability not guaranteed, but the dynamics may emerge out of community ecology, involving factors we have yet to study, let alone understand.

Consistency is starting to emerge from dynamics in the native *C. fumiferana* [40] and *M. disstria* [20] systems, and even the invasive *L. dispar* [41]: outbreak behavior is mediated by host forest landscape structure, but it takes high-quality forest and pest data, combined with modern analytical methods to tease out the drivers underlying the dynamics. Indeed, similar dynamics have been detected with emerging pests such as *Cydalima perspectalis* by using sophisticated nonlinear growth models borrowed from the ecology of model systems [42]. Landscape-driven departures from expected clockwork-like

Figure 3



Sankey plot of information flows across the thematic nodes identified in Figure 1 (linkages between research domains and approaches) and Figure 2 (dynamical behavior across taxa) (Methods in Supplementary Information 1 to 2). The recent literature reviewed covered six taxonomic families (second column) and spanned the full range of scientific approaches identified in Figure 1 (third and fourth columns). The systems studied ranged from equilibrium cycling ecology to disequilibrium invasion ecology, and everything nonstationary in-between (first column, following a color ramp consistent with Figure 2). The two ‘model systems’ proposed in Figure 2 stand out as thick information flows, in gold (dominated by *L. dispar*, family Erebidae) and blue (dominated by *C. fumiferana*, family Tortricidae), suggesting that insights from model systems might assist with understanding the dynamics of the less well-studied systems. Taxonomic information flows transition to scientific domains (i.e. Figure 1) by column 3, ultimately informing ecological disciplines (column 4).

outbreak behavior are often responsible for the most significant forest impacts (e.g. [43]).

A similar exchange of insights has occurred regarding 'Allee effects' and 'fat-tailed' dispersal kernels. Once in the domain of invasion ecology, these insights were foundational to the 'Slow the Spread' program for *L. dispar* in the United States [27] but they are now central to the 'Early Intervention Strategy' for *C. fumiferana* in eastern Canada [2,5]. Disentangling the independent roles of dispersal and population growth in driving pest spread is a central theme in pest population modeling, and advances are being made in both native dynamics and invasion ecology.

There is increasing model-based evidence that long-range dispersal in some Lepidoptera is common, is adaptive [44], and is driven by weather, population density, and forest condition [45], resulting in a broader range of spatial dynamics beyond weather-driven cycle synchronization — with genetic analyses providing fresh insights [4,21,30]. For invasive species, a common trend, even where females are flightless, is to formulate models that treat dispersal implicitly, to demonstrate the movement effects wrought by host forest landscape structure [17] or human vectoring [16]. The implicit approach has also been used successfully in spread analysis of emerging threats to quantify the effects of landscape geometry, host distribution, and human infrastructure on dispersal and spread [42,46,47].

A major source of population disequilibrium that is being investigated for both indigenous and invasive species is climate change. To firmly link climate change to the growth, dispersal, and spread of populations, sophisticated mechanistic models of causation are required [48]. Species distribution models are premised on the idea of adaptation to a range of environmental parameters, and there are several examples where these models are clarifying the conditions under which invasive spread may occur [49]. It is increasingly clear that climate warming can result in a wide range of changes in dynamical behavior, from damping [50–52] to excitation [22,53,54], depending on how climate affects the underlying trophic interactions.

Conclusions

Reviewing the full breadth of literature of the past few years, we note that studies of invasive pests are dominated by studies of *L. dispar* (*Erebidae*), and studies of native pests are dominated by studies of *C. fumiferana* (*Tortricidae*) (Figure 3). These two model systems are still being studied from every angle possible — from the slow sciences of evolutionary, planetary, and theoretical ecology — to the faster sciences of ecophysiology, landscape ecology, and community ecology — and using every new technology that the 21st century has to offer — from remote sensing, to high-throughput genetics, to advanced computational mathematics, and statistics. These systems continue to defy simplistic modeling approaches (e.g. [55]), suggesting that these models are only a starting point for a necessary deep dive into real-world spatiotemporal complexity in outbreak dynamics. Even the most sophisticated models of *C. fumiferana* eruption dynamics 'explain' only 50% of the target variance, and these 'explanations' are heuristic, not mechanistic [56]. Population ecology continues to adopt perspectives and approaches from community ecology. As this happens, simplified analytical mathematics of theoretical ecology [9,57] start to lose relevance. The question is not whether a clockwork approximation [1] of Lepidopteran outbreak behavior is superior to Holling's catastrophe theory [3], but rather which processes are dominant where and when (i.e. system's context).

The emerging threats that receive less or only recent attention are well-positioned to benefit from insights derived from the model systems we have discussed. Our review suggests deep insights are emerging from interdisciplinary research of model systems that has been adequately framed such that it may be generalized and therefore more readily adaptable for use in different operational contexts [58]. Our Figures 1–3 are our attempt to highlight the strong basis for exactly this kind of generalization, from model systems to emerging threats, from indigenous species to invasive species, and from North America to forested systems worldwide.

CRediT authorship contribution statement

Brian R. Sturtevant – Conceptualization, Data curation, Investigation, Methodology, Roles/Writing – original draft, Writing – review & editing. **Barry J. Cooke** - Conceptualization, Formal Analysis, Methodology, Roles/Writing – original draft, Writing – review & editing. **Patrick M.A. James** - Roles/Writing – original draft, Writing – review & editing.

Conflict of interest statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

The data used in this article consist of citations exported from Web of Science, and are included as Supplementary Information.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.cois.2023.101005.

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- • of special interest
- •• of outstanding interest

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Leaning on a previous article outlining a more general approach, the study illustrates the value of generalizable template models that can accommodate the specificity of individual systems — in this case dispersal kernel models applied to project invasive spread. This article is a good example of leveraging the deep science from model systems (here, *L. dispar*) to inform less-studied emerging threats.