

Spatiotemporal dynamics of forest geometrid outbreaks

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We highlight recent developments and avenues for advancement, which can improve insight into the causes of changes in the spatiotemporal dynamics of forest *Geometridae* moth species (hereafter ‘geometrids’). Some forest geometrids possess fundamental biological traits, which make them particularly liable to outbreak range expansions and host shifts mitigated by climate change. Indeed, recently observed changes in geometrid spatiotemporal dynamics represent both new research opportunities and challenges for empirically testing drivers of intra- and interspecific spatial synchrony, including the role of trophic interactions and biological traits (e.g. dispersal ability). We advocate that the emerging field of near-term ecological forecasting holds promise for studies of the spatiotemporal dynamics of forest geometrids and could be tailored to give both accurate predictions at management-relevant timescales and new insights into the mechanisms that underlie spatiotemporal population dynamics.

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Introduction

The eruptive population dynamics of forest *Geometridae* moth species (geometrids) have been a source of fascination for several centuries. In Fennoscandia, where outbreaks by a guild of forest geometrids are a pronounced feature of the alpine and subarctic birch forest, the earliest mentioning of mass occurrences and their impacts known to us is from 1762. Here, Hermann C. Ruge, a Norwegian priest and a dedicated educator,

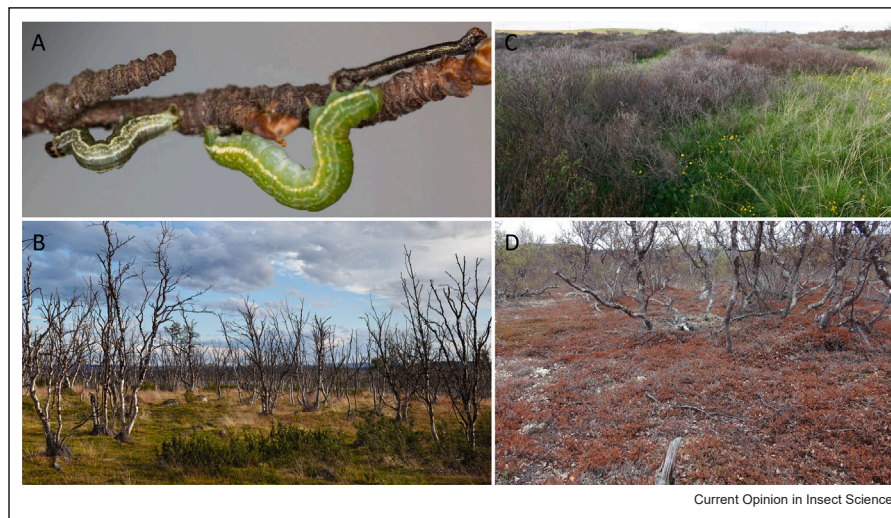
described years where the caterpillars were so numerous that they would “cover the trees and consume all green from them” to the extent where the “birch forests in the mountain slopes can be neither valued nor restored” (our translation of [1]).

Indeed, the Fennoscandian birch forest–geometrid system (Figure 1) has continued to attract attention, and dominates the scientific literature on the spatiotemporal dynamics of forest geometrids (see [Supplementary Material](#), Query 1). This interest is motivated by the urge to understand the drivers of fundamental ecological phenomena such as cyclic dynamics and spatial synchrony for insect populations inhabiting a forest ecosystem that stands out as approaching a natural monoculture [2], as well as a concern for the fundamental services that these forests provide. With recent changes in the geographical distribution of the main defoliators in the system (see *Range expansions and host shifts as a game changer*), the Fennoscandian case has also become an example of how a guild of defoliators can cause expanding and large ecosystem impacts by means of intensified defoliation of woody vegetation in a changing climate.

The birch forest geometrids in Fennoscandia share many ecological traits with outbreaking forest geometrids in other ecosystems (Table 1). Indeed, the term the ‘winter moth syndrome’ [3] has been used to describe the group of forest geometrids with a propensity for eruptive, often cyclic, population dynamics, noticeably in northern environments. They are broadly characterized as capital breeders with nonfeeding adults that fly either very late or very early in the season (‘autumn’ species and ‘spring’ species), frequent occurrence of flightless females, overwintering egg stages, often highly polyphagous spring-feeding larval stages, and the ability for larval dispersal by ballooning.

In the following, we highlight recent developments and avenues for advancement, which we believe will improve insight into the causes of changes in the spatiotemporal dynamics of forest geometrids. We focus on three broad topics: first, how range expansions and sudden hosts shifts mitigated by climate change can act as a game changer in ecosystems subject to defoliator outbreaks. Second, how drivers of spatial synchrony may be empirically tested through spatial study designs and by adopting a guild approach. Third, why the emerging field of near-term ecological forecasting holds promise

Figure 1



In northern and alpine Fennoscandia, cyclic outbreaks by the geometrids *Operophtera brumata* ((a), left), *Epirrita autumnata* ((a), middle), and more locally also *Agriopis aurantiaria* ((a), right) have profound implications for the birch- (*Betula pubescens* var. *pumila*) dominated forest ecosystem, as a driver of regional- and local-scale tree ((b); [47]) and tundra shrub ((c) *Salix* sp.; [11]) mortality, vegetation-state transitions in the field layer ((d); *Empetrum nigrum* die-off), changes in nutrient cycling and soil community composition, as well as a provider of resource pulses for insectivores and dead wood-associated organisms. Photo: Jon Aars (a), Jakob Iglhaut (b), Jane Uhd Jepsen (c,d).

for studies of the spatiotemporal dynamics of forest geometrids. We draw on studies of other taxa and general conceptual or methodological advances when they hold relevance and promise for studies of forest geometrid spatiotemporal dynamics in the future.

Range expansions and host shifts as a game changer

Many outbreaking forest geometrids display dietary generalism and high mobility through wind-dispersed larval stages (Table 1), both of which are traits that promote a consumer's ability for range expansions. Even in the absence of female flight (Table 1), this may render forest geometrids to effectively colonize new habitats when abiotic (e.g. climatic) or biotic (e.g. trophic) constraints are relaxed. Indeed, that plasticity in dietary niche width is a key to understanding rapid range expansions in Lepidoptera, is highlighted by several recent studies [4–6]. A global review of Lepidoptera [5] showed that the well-documented [7,8] latitudinal cline in niche width emerges as a consequence of range dynamics, and that the position of a population within the species' range is a better predictor of dietary width than latitude per se. Recent studies of nongeometrids, *Euphydryas editha* [6] and *Pieris mannii* [4], support the notion that younger populations (i.e. more recently established) tend to have a broader niche, and that niche width decreases over time after establishment. These studies, albeit mostly based on nonpest species, have implications for both the nature and the rate of ecosystem-level changes we may anticipate in the wake of range

expansions of forest defoliators in general, because they suggest that diet diversification at range margins may be better viewed as a consequence of range expansions, rather than a cause.

We argue that similar patterns can likely be found in range-expanding forest geometrids, known to be dietary opportunists, the winter moth being a prime candidate. This species has undergone relatively rapid range expansions at its northernmost distributional border in Europe [9], as well as several invasions, followed by establishment, in North America [10]. The literature holds a vast number of studies of winter moth dietary range within single populations, but to our knowledge, no attention has been given to latitudinal or other broad-scale patterns in dietary width, in light of historical and recent range expansions. At the northernmost range margin of the species, the Low Arctic tree line at $\sim 70^\circ\text{N}$ in NE Norway, range expansions have occurred beyond forest habitats into coastal tall shrub tundra where outbreaks cause mortality in *Salix* shrubs [11]. While not an entirely unexpected host, given the dietary records for the species, this cross-biome expansion of a boreal forest pest into shrub tundra, is nevertheless an unanticipated event, which, depending on whether it is only a transient phenomenon, can have wide implications for the tall shrub tundra ecosystem. Such host shifts may also give important clues to whether population dynamics patterns (e.g. cyclicity and synchrony) are related to plant host traits (e.g. chemistry and phenology).

Table 1

Geometrids known to display pronounced population outbreaks in natural forest ecosystems.

Species subfamily common name	Main host genera	Native range	Flightless females	Evidence of caterpillar ballooning	Evidence of cyclicality	Evidence of large- scale spatial synchrony	Selected references
<i>Epirrita autumnata</i> Larentiinae autumnal moth	<i>Betula</i>	Eurasia	No	Yes	Yes	Yes	[16,34]
<i>Operophtera brumata</i> Larentiinae winter moth	<i>Betula, Quercus, Salix</i>	Eurasia	Yes	Yes	Yes	Yes	[16]
<i>Operophtera fagata</i> Larentiinae northern winter moth	<i>Fagus, Betula</i>	Eurasia	Yes	Yes	No?	No?	[35]
<i>Bupalus piniaria</i> Ennominae pine looper	<i>Pinus, Picea, Pseudotsuga, Larix</i>	Eurasia	No	No?	Yes	Yes	[36,37]
<i>Agriopsis aurantiaria</i> Ennominae scarce umber moth	<i>Betula, Quercus, Salix</i>	Eurasia	Yes	Yes	Yes	Yes	[38]
<i>Agriopsis leucophaearia</i> Ennominae Spring Usher	<i>Quercus Fagus</i>	Eurasia	Yes	?	No?	No?	[39]
<i>Erannis defoliaria</i> Ennominae mottled umber moth	<i>Crataegus, Prunus, Salix, Tilia, Quercus</i>	Eurasia	Yes	Yes	Yes	Yes	[40]
<i>Operophtera bruceata</i> Larentiinae Bruce spanworm	<i>Acer, Fagus, Populus</i>	North America	Yes	Yes	Yes	No?	[41,42]
<i>Lambdina fiscellaria</i> Ennominae Hemlock looper	<i>Tsuga, Pinus, Picea, Abies</i>	North America	No	Yes?	Yes	Yes	[43]
<i>Alsophila pomataria</i> Ennominae Fall cankerworm	<i>Ulmus, Fraxinus, Acer</i>	North America	Yes	Yes	Yes	Yes	[44]
<i>Ennomos subsignarius</i> Ennominae Elm spanworm	<i>Ulmus, Betula, Acer, Quercus</i>	North America	No	Yes	Yes	Yes	[45]
<i>Apocheima cinerarius</i> Ennominae Poplar looper	<i>Populus, Salix</i>	Asia	Yes	?	No?	No?	[46]

Species for which outbreaks are known only from plantations (e.g. [32]) are excluded. Similarly, species with a very localized distribution for instance due to island endemism (e.g. [33]) are not considered. Evidence of cyclicality is considered affirmative if regular population cycles have been documented in at least part of the species' distributional range. By large-scale spatial synchrony, we refer to synchronized dynamics on a landscape-regional scale (e.g. thousands of km²). Entrances for which uncertain or contrasting evidence was found are marked by a question mark.

Mechanisms behind population synchrony

Population synchrony denotes the tendency for local populations to exhibit simultaneous fluctuations either within the same species regionally (spatial synchrony) or between different species locally (interspecific synchrony). The study of population synchrony is a vibrant field within forest insect ecology because it helps to elucidate mechanisms driving population dynamics, and because ecosystem impact of outbreaks becomes enhanced with the degree of scale and strength of

synchrony [12]. Indeed, outbreak cyclicality is a characteristic that is expected to be linked to profound spatial synchrony [13], and this conjecture appears to be reflected in the presence of synchrony among different geometrid species (Table 1). Trophic interactions, dispersal, and synchronized weather phenomena are potential drivers of synchrony, but their relative importance may be difficult to disentangle, especially when they interact [14]. The potential for interaction effects between weather phenomena (e.g. winds) and

Box 1 Near-term iterative forecasting

NTIF is an emerging paradigm in ecology, where the goal is to make quantitative forecasts with specified uncertainty about the state of ecological variables in the near future [28]. Because the accuracy of near-term forecasts can be assessed in the near future, NTIF can give rise to an efficient iterative loop of scientific learning, where researchers make forecasts, evaluate them against new data, update models, and forecast again. Near-term forecasts can also make ecological science more relevant to adaptive management, where planning and actions are typically concerned with future timescales of a day to years, rather than decades (Figure 2).

dispersal may be particularly high in geometrids as ballooning larvae appear to be prevalent in most species (Table 1). Finally, climate change is presently changing the synchrony patterns in many species [15]. The expansion of the outbreak range of *O. brumata* [11] implies that this also regards some geometrids.

Long-term, spatially distributed population time series are required for empirical analyses of population synchrony. However, most insight can be obtained from specifically targeted survey designs that tactically include spatial features acting more or less as barriers to dispersal [16,17]. This is because dispersal likely is the only synchronizing mechanism that it may be possible to rule out by the design of large-scale population surveys. Combining such surveys of population density dynamics with sampling that allows analyses of population genetic structure may be rewarding in highlighting the role of dispersal in shaping spatial synchrony patterns [17,18]. However, genetic studies may not always be informative, especially when there is little spatial genetic structure (i.e. [18]), since less dispersal may be needed to homogenize genetic structure than to synchronize population dynamics.

Patterns of spatial and interspecific synchrony within guilds of folivorous insects can be instructive for elucidating the role of different dispersal abilities, for instance, between geometrids with winged versus wingless females [16]. A high degree of interspecific spatial synchrony among species with different life history [19] suggests drivers other than dispersal, such as synchronizing effects of trophic interactions (with host plants or enemies) and weather phenomena, are more important. In case of synchrony between populations exploiting different host plants, plant-herbivore interactions are likely not a synchronizing mechanism. When trophic interactions are involved, lagged synchrony between species within the same guild may occur [19].

Weather phenomena are likely the key driver of those cases with most large-scale synchrony, such as those of cyclically outbreaking birch forest geometrids in northern Fennoscandia. Identifying which of the weather variables acting on the different life stages (see Graphical abstract) that have synchronizing effects requires spatiotemporally matching meteorological and population data as well as adequate statistical models applied to those data. In particular, it appears essential to apply models that appropriately account for biotic

processes (e.g. density dependence) to obtain accurate estimates of the synchronizing effects of weather variables [20]. A geography of synchrony approach [21] appears to be particularly rewarding when applied to geometrid populations in geographic regions subjected to spatially heterogeneous climate change [15].

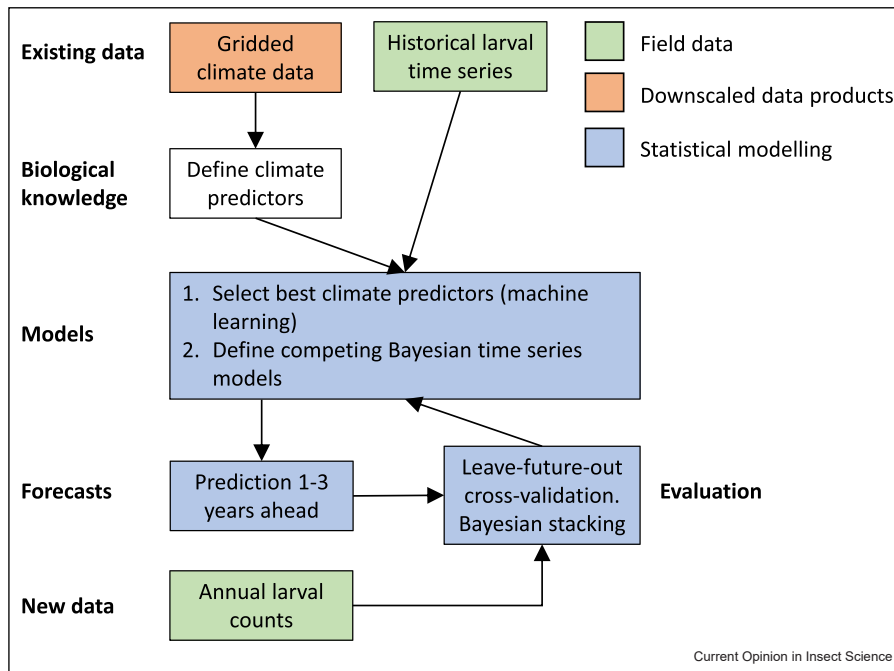
Near-term forecasting of outbreak dynamics

Studies of forest pest insects — including geometrids — commonly make forecasts about long-term (i.e. decades ahead) developments in the spatiotemporal population dynamics and ecological impacts of their focal species. For instance, [22] predicted the outbreak ranges of *O. brumata* and *A. aurantiaria* in Fennoscandia 30 years into the future based on cold tolerance in the egg stage. Such forecasts can highlight possible long-term system trajectories but are also fraught with caveats. The data required to evaluate the accuracy of decadal-scale forecasts only become available in the far future, so that opportunities for model validation are limited. Further, the changes that climate warming may induce in ecological dynamics over decadal timescales are potentially so complex, transient, and unforeseeable that long-term forecasts run the risk of being widely inaccurate.

Owing to these issues, ecologists have lately been encouraged to put more focus on near-term (i.e. a few years ahead at most) iterative forecasting (NTIF, Box 1) [23]. However, our literature query (Supplementary Material, Query 2) suggests that the potential of NTIF remains largely untapped for forest insects. We found only four papers from the last two years that had attempted to forecast insect abundance or infestation risk on short timescales (< 10 years), two for mountain pine beetle [24,25], one for emerald ash borer [26], and one for spruce budworm [27], but none for geometrids. Notably, three of these studies used machine learning algorithms, which are becoming increasingly popular for complex prediction tasks in ecology.

We propose that the spatiotemporal population dynamics of forest geometrids represents a highly suitable case for the employment of NTIF. Geometrid outbreaks are frequently a subject of concern for both the public and management authorities, meaning that forecasts about imminent outbreak dynamics are in high demand. Owing to the long tradition for collecting geometrid abundance data in several forest systems, the time series that are required to build forecasting models are already available. Moreover, new

Figure 2



Conceptual overview of NTIF, as applied to Fennoscandian geometrid larval time series. The input data consists of historical time series of annual larval counts and downsampled gridded climate data (temperature and precipitation). Knowledge about physiological effects of climate throughout the moth life cycle is used to formulate climatic predictors that are hypothesized to influence moth population dynamics (see Graphical abstract). In the modeling phase, multiple statistical approaches might be employed. In the Fennoscandian case, machine learning is employed to identify the predictors that are best able to explain residual variation in the larval time series after accounting for density dependence. The best climate predictors are then employed in Bayesian time series models, which are used to forecast larval density 1–3 years into the future. Forecasts are evaluated against new annual larval counts as they become available, based on Bayesian techniques that allow competing models (different sets of climate predictors) to be compared based on forecasting ability. By iterating the forecast-evaluation loop over time, increasing evidence will accumulate for the models that produce the best forecasts. New model structures may also be introduced if the evaluation reveals that the forecasts from existing models are not acceptably accurate.

developments in statistical downscaling mean that gridded climate data are increasingly available at a spatial resolution (tens to a few hundred meters) that is sufficient to capture local climatic gradients expected to influence geometrid population dynamics. This can compensate for a lack of in situ climate data for some of the older geometrid time series. The extensive literature on the physiological effects of temperature throughout the geometrid life cycle means that a priori expectations about population dynamical effects can be formulated for many climate variables (see Graphical abstract). If this leads to a set of candidate climate variables that is too large to be practical, machine learning algorithms such as boosted regression trees [29] can be used to rank the ability of these variables to predict geometrid abundance and thereby facilitate the selection of the most important climate predictors from the candidate set [27]. Depending on prior knowledge about the population dynamics of the focal species, forecasting models may initially be formulated in an entirely phenomenological manner, or incorporate more mechanistic formulations of key population dynamical processes. In both cases, the identification of climate variables and biotic interactions that improve

forecast accuracy can pave the way for additional mechanistic studies of the spatiotemporal population dynamics, thereby hopefully leading to improvements in both ecological understanding and forecasting performance. Thus, NTIF has the potential to accelerate learning in research on the spatiotemporal dynamics of geometrids, while at the same time enhancing the societal value of that research by providing management-relevant forecasts.

We advocate that forecasting models are built in a Bayesian framework, as this will allow the modeling to benefit from recently developed methods that can be used to evaluate and rank forecasting models [30]. Finally, it is worth noting that forecasts can readily be derived from successful population dynamical modeling frameworks that were not explicitly developed for forecasting purposes, for example, eco-evolutionary models, which have recently been shown to be capable of explaining insect population cycles in field data [31]. Thus, the analytical tools to implement NTIF for forest geometrids are already available, and the main challenge for researchers is arguably to change the focus of their

modeling, so that successful prediction of future data-points receives more attention.

Conclusions and perspectives

While geometrids with more or less regular and synchronized population outbreaks have provided important insights to forest insect population dynamics, recent shifts associated with climate change — especially in northern Fennoscandia — represent both new research opportunities and challenges. Fundamental biological traits termed ‘the winter moth syndrome’ such as polyphagia and larval ballooning — combined with a propensity for population outbreak cyclicity and synchrony — likely make some geometrids particularly liable to rapid outbreak range expansions. Recent studies demonstrate that such range expansions may involve host plant switches. Host plant switches give opportunities for investigating how herbivore-plant interactions influence spatiotemporal population dynamics. Geometrid range expansions also alter folivore insect guild structure, which opens opportunities to study how guild structure affects food web interactions, including folivore insect impacts on shared host plants.

As geometrid outbreak range expansions can have profound impacts on the services provided by the affected ecosystems, stakeholders may benefit from near-term forecasting to guide management. While there are alternative modeling approaches to near-term iterative forecasting, we advocate that geometrid population models should be tailored to give both accurate predictions and new insights about the mechanisms that underlie the spatiotemporal population dynamics. Finally, as empirically based models will be no better than the data on which they are based, we emphasize the importance of obtaining high-quality monitoring data for the dual purpose of prediction and understanding. In the context of geometrid population dynamics subjected to the impact of climate change, long-term monitoring designs that include geographic features forming spatial climate gradients and barriers to dispersal will be particularly rewarding.

Conflict of interest statement

Nothing declared.

Data Availability

No data were used for the research described in the article.

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Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.cois.2022.100990](https://doi.org/10.1016/j.cois.2022.100990).

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