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Determinants of the Southern Range Limit of an Infamous North American Forest Defoliator

Andrew M. Liebhold[1,2] | Eugene Luzader[2] | Jacques Régnière[3]

[1]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Suchdol, Czech Republic | [2]US Forest Service Northern Research Station, Morgantown, West Virginia, USA | [3]Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Quebec, Quebec, Canada

Correspondence: Andrew M. Liebhold (aliebhold@gmail.com)

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ABSTRACT

Aim: Predicting climate driven species range shifts requires knowledge of mechanisms limiting species fitness under various climatic conditions. The traditional approach of modelling ranges of herbivorous insects by fitting environmental niche models to occurrence records is generally incapable of differentiating direct effects of climate on insect populations versus indirect effects acting on the range of their host plants. Here, we delimit the southern extent of a major forest defoliator, the spruce budworm, *Choristoneura fumiferana*, in North America, and investigate whether its range is limited directly by climate or indirectly by the range of its host trees.

Location: Eastern North America.

Methods: We use pheromone traps to survey populations; these are sensitive tools for detecting low-density populations. We applied mechanistic models of the effect of temperature on *C. fumiferana* fitness to evaluate whether these patterns of occurrence can be explained by the direct effect of climate.

Results: We found that this insect species is widely present through most of the southern distribution of host spruce and fir species, both in the upper Mississippi River valley and the central and southern Appalachian Mountains. The species was present in ca. 50% of spruce-fir sites surveyed in the Appalachian Mountain region but was absent in the five most southerly sites where spruce and fir occur in eastern North America. Simulation using historical meteorological data indicated that all survey sites are climatically suitable for *C. fumiferana*.

Conclusions: Simulation of climate effects, along with the species' absence from the most southern distribution of hosts, indicate that while the southern range limit of *C. fumiferana* is limited by host availability it is not directly constrained by climate. Furthermore, populations at the species' southern extent may be in a dynamic state of extinction and recolonisation, thus explaining at least the temporary absence of *C. fumiferana* from certain locations.

1 | Introduction

Shifts in species boundaries in response to climate change have been observed in several systems (Thomas 2010) including many insect species (Breed et al. 2013; Pureswaran et al. 2018; da Silva and Diamond 2024). However, most studies of range shifts in insects focus on expansion to higher latitudes or elevations (i.e., at the cold edge) with less attention given to species boundaries at lower latitudes and elevations (i.e., the warm edge). Consequently, there is often little information about factors that limit species at their lower limits.

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The geographical range of herbivorous insects is often determined by the range of plant species upon which they feed (Müller et al. 2011). However, even for insect herbivores that specialise in a single plant genus or family, their ranges may also be directly influenced by climate (Ulrichs and Hopper 2008). One of the challenges faced in fitting environmental niche models to occurrence data for herbivorous insects is the difficulty of differentiating the direct effect of climate on their ranges from indirect effects of climate acting via the distribution of host plants. This is why mechanistic models constitute important tools for forecasting the influence of climate change on species ranges (Cuddington et al. 2013; Van der Meersch et al. 2025). Differentiating the role of biotic versus climatic factors in limiting species ranges is also constrained by the lack of data on species occurrence in portions of their ranges where populations are sparse (Beck et al. 2014).

Here we investigate the determinants of the southern range boundary of the spruce budworm [*Choristoneura fumiferana* (Clem.)]. Through much of the northern portion of this insect's range, it is a very abundant species that periodically reaches outbreak levels causing forest defoliation across large portions of the boreal forest of eastern North America (Nealis and Régnière 2004; Rauchfuss and Ziegler 2011). Throughout its range, *C. fumiferana* larvae mainly feed on spruce (*Picea* spp.) and fir (*Abies* spp.). Though the ranges of these genera in eastern North America are largely limited to latitudes > 43°N, they extend south to ca. 35°N at higher elevations in the Appalachian Mountains (Figure 1). In these regions, *P. rubens* is the only naturally occurring spruce species and is limited to high elevations. Also occurring over smaller areas of the Appalachian Mountains are isolated stands of balsam fir, *A. balsamea*, limited to the highlands of West Virginia and the Pocono Mountains in eastern Pennsylvania. Closely related to *A. balsamea*, Frasier fir, *A. fraseri*, exists in isolated regions of the Smokey Mountains and high elevation sites elsewhere in North Carolina and Virginia. Because these tree species are limited to high elevations, suitable habitat for *C. fumiferana* takes the form of isolated 'sky islands', suggesting that the occupancy of these host patches may be described by a form of metapopulation dynamics (Hanski and Simberloff 1997).

Limited information exists about the distribution of *C. fumiferana* in these southerly extents of its hosts. Several published descriptions of this species do not mention its presence in this region (Stehr 1967; Harvey 1985; Rauchfuss and Ziegler 2011). Here we use pheromone traps to delimit the geographical extent of populations at the species' southern extent. Identifying the presence of most insect species in low-density populations across large geographic areas is challenging because of the difficulty of detection. However, because this species is a major pest in its northern range, the pheromone compounds that it uses for mate-finding have been identified (Silk and Kuenen 1988) and are commercially available as lures; pheromone-baited traps are powerful tools for detecting low-density populations (Sanders 1988).

Here, we use presence/absence data to characterise the southerly distribution of *C. fumiferana*. We use this information to explore three hypotheses regarding the determination of the species southern boundary: (1) the species lower limit is determined by the distribution of its hosts, (2) the southern extent is determined by the species' climatic requirements and (3) given the distribution of the species in scattered isolated populations, its southern extent is limited by the capacity for recolonisation of distant populations following local extinction. To address hypothesis 1, we compare the distribution of *C. fumiferana* to the distribution of its host trees near its southern extent. To test hypothesis 2, we apply previously developed mechanistic models of climate impacts on components of *C. fumiferana* fitness to evaluate the role of climate in limiting the species range. Finally, we evaluate hypothesis 3 by investigating the capacity of dispersal from northern outbreak areas to southerly host patches as a mechanism for patch recolonisation following stochastic extinctions.

2 | Materials and Methods

2.1 | Occurrence Data

We used range maps (Little and Viereck 1971) of *Picea* spp. *and Abies* spp. to identify areas along the southern extent of these tree genera as candidate regions for *C. fumiferana* surveys. The surveys were concentrated in the southern portions of the range of these genera in the central and southern Appalachian Mountains, and to a lesser extent, in extensions along the Upper Mississippi River valley (Figure 1). Site locations were chosen with an objective of widely sampling forested areas where either *Picea* spp. or *Abies* spp. are present while being within 500 m of a road to facilitate access. A total of 51 sites were surveyed between 2011 and 2022 (Table S1). Surveys at several (but not all) sites were repeated in a second year when *C. fumiferana* was not detected in the first year.

Two traps were placed 200–400 m apart at each site from June through July. Traps were baited with the standard *C. fumiferana* sex pheromone blend, 95:5 E/Z-11 Tetradecenal (Silk et al. 1980). Lures consisted of flex lure dispensers (Synergy Semiochemicals Corporation, Delta, BC Canada). Each lure was inserted in a UniTrap (Agrisense/Biosys, Columbia, MD, USA) and deployed at ca. 2 m height in field locations. A killing strip (active agent: 2, 2-Dichlorovinyl dimethyl phosphate; Hercon Environmental, York, Pennsylvania) was added to each trap to immobilise insects. The identity of *C. fumiferana* in traps was initially visually confirmed, followed by molecular identification of a population subset (Lumley et al. 2020). Records of *C. fumiferana* occurrence from trapping reported here were supplemented by other georeferenced occurrence records (Stehr 1967; Lumley et al. 2020).

2.2 | Effect of Host Density on *C. fumiferana* Presence

To investigate the role of host tree ranges on the geographical distribution of *C. fumiferana*, a statistical model was used to relate the presence or absence of *C. fumiferana* at each site with host tree density. Raster GIS data depicting the cover of red spruce in West Virginia were obtained from the Red Spruce (*Picea rubens*) Cover In West Virginia database (West Virginia Department of Natural Resources 2024). Logistic regression was used to test the combined effect of spruce density and presence/absence of fir on the positive detection of *C. fumiferana* in traps.

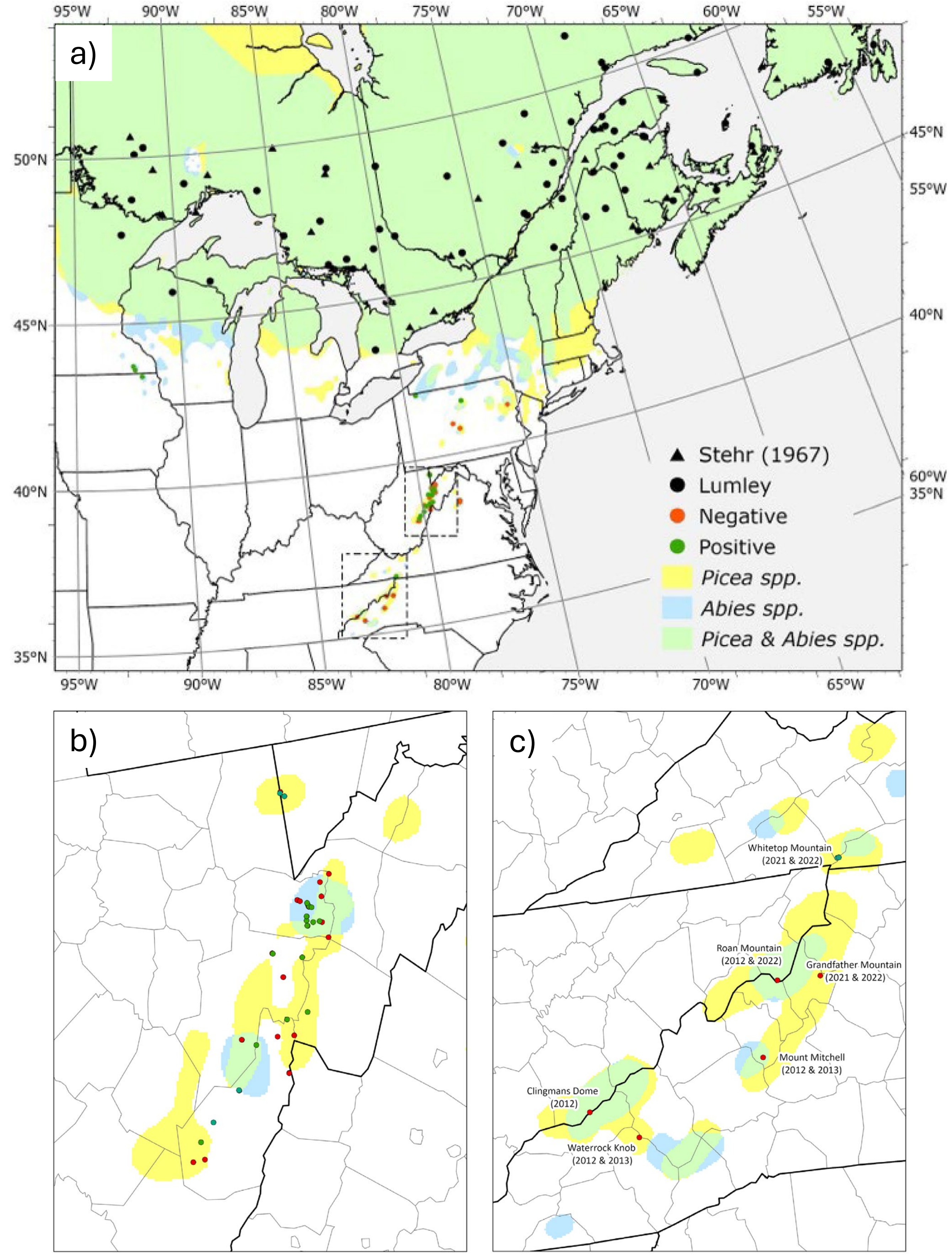

FIGURE 1 | Legend on next page.

FIGURE 1 | Distribution of spruce budworm occurrence records and major hosts in Eastern North America. "Positive" refers to trapping location with a positive detection and "Negative" refers to a trapping point with no detection. (a) Distribution in the Maritime provinces of Canada and eastern USA. (b) Distribution in West Virginia Highlands. (c) Distribution in southern Appalachian Mtn. region of Virginia, North Carolina, and Tennessee.

Spruce density was averaged across all raster cells within 5 km and within 10 km of trap locations using ArcGIS Pro (version 3.3). The presence of fir was based on visual inspection of stands where traps were located. Logistic regression analysis was limited to the 35 trap locations in West Virginia because geospatial data on spruce cover were not available elsewhere.

2.3 | Effect of Climatic Suitability on *C. fumiferana* Presence

We evaluated climatic suitability for *C. fumiferana* with a previously developed process-based model of its seasonal biology (development, reproduction and survival) in response to temperature (Régnière, St-Amant, et al. 2012). This model predicts the insect's potential annual rate of change in density (Royama 1992), that we call potential growth rate here for simplicity. This rate is affected by two main processes that take place during the spruce budworm's life cycle. The first process, reproduction rate, describes the effect of summer temperatures on the development and survival of all immature stages and the reproduction of adults. It determines the ability of spruce budworm eggs to hatch and 1st instar larvae to establish overwintering sites in late summer, prior to the first frost. It can be expected to be most limiting at northern latitudes and higher elevations. The second process, overwinter survival, describes the effect of exposure of second instar larvae to warm temperatures in early diapause (Han and Bauce 1997) and determines their survival from late summer to spring emergence. This second process affects survival under warm conditions and therefore can be expected to be limited by climates at southern latitudes and lower elevations. Potential growth rate, $R = N_{t+1}/N_t$, (a unitless measure) is identical to the product of reproduction rate (obtained through the first process from overwintered second instar in spring of year t to larvae entering diapause in late summer), and overwinter survival of those larvae to emergence in the following spring (from the second process).

Another process through which climate can limit population viability in *C. fumiferana* is developmental synchrony between larvae and the shoots of host plants (Fuentealba et al. 2017; Portalier et al. 2022). Second instar larvae often emerge prior to budbreak and are capable of mining and feeding on host needles until vegetative buds swell sufficiently to be mined (Trier and Mattson 1997). However, to grow to later instars, larvae require growing needles and must therefore feed on flushing buds. As growing foliage matures, it hardens and becomes less suitable as larval food (Fuentealba et al. 2018). Thus, there is an optimal phenological window in the development of *C. fumiferana* hosts that is ideal for budworm growth and reproduction (Lawrence et al. 1997), and therefore an optimum moment for them to start and end larval development relative to shoot elongation (Nealis and Régnière 2018). We used the previously developed spruce budworm seasonal biology model (Régnière, St-Amant, et al. 2012) to predict the date of peak emergence of overwintered larvae in the spring. From experimental data, it is known that spruce budworm larvae can mine buds once these have reached development stage 1.5, halfway between stages 1 and 2 on Auger's 5-stage shoot development scale (Desbiens 2006; Podadera et al. 2024). Using a recent physiologically based model of conifer shoot development (Cartenì et al. 2023), we calculated the average number of days between peak larval emergence and the passage of host shoots (balsam fir, white and black spruce) as an index of asynchrony with host development.

Both models (Régnière, St-Amant, et al. 2012; Cartenì et al. 2023) were run under BioSIM 11 (Régnière et al. 2017), a system that provides simulation models with georeferenced daily weather data spatially interpolated from a network of weather stations (compiled from NOAA and other publicly available sources), adjusted for elevation with local thermal gradients (Régnière and St-Amant 2007). Because our two models are stochastic in nature, 30 iterative simulations were made using the weather data for each trapping location and year (simulations were run using data from 2 years at sites with 2 years of trapping data), and the results were averaged over replicated model runs.

In addition to testing predictor variables mean R and mean asynchrony, we also tested distance to outbreaks as predictors of *C. fumiferana* occurrence. This distance variable was quantified as the distance of each trapping site to the nearest location where defoliation has historically occurred. Historical defoliation consisted of cumulative defoliation from 1945 to 1988 recorded from aerial surveys and described in Williams and Liebhold (2000) (Figure 2c). Distances were calculated using the buffer tool in ArcGIS Pro. During outbreaks, *C. fumiferana* are known to disperse in large numbers (Greenbank et al. 1980; Anderson and Sturtevant 2011) and it is possible that such emigration events could be responsible for recolonising areas where hosts are present, but populations have previously gone extinct.

The variables mean R, mean asynchrony, and distance to outbreaks were tested for their ability to predict the presence/absence of *C. fumiferana* across the 51 trapping locations. We explored several alternative logistic regression models that included all possible combinations of these three variables for their ability to explain presence/absence. Each variable was tested in a univariate logistic regression model of presence as well as in models combining pairs of explanatory variables and all three variables. The best model was selected based on AIC levels and the significance of predictor variables.

3 | Results

Based on trapping, *C. fumiferana* was confirmed as present at 26 sites and absent at 25 sites (Table S1, Figure 1). The largest number of moths captured (403 in two traps) was from the Whitetop Mtn. site in southwestern Virginia in 2021. Among all

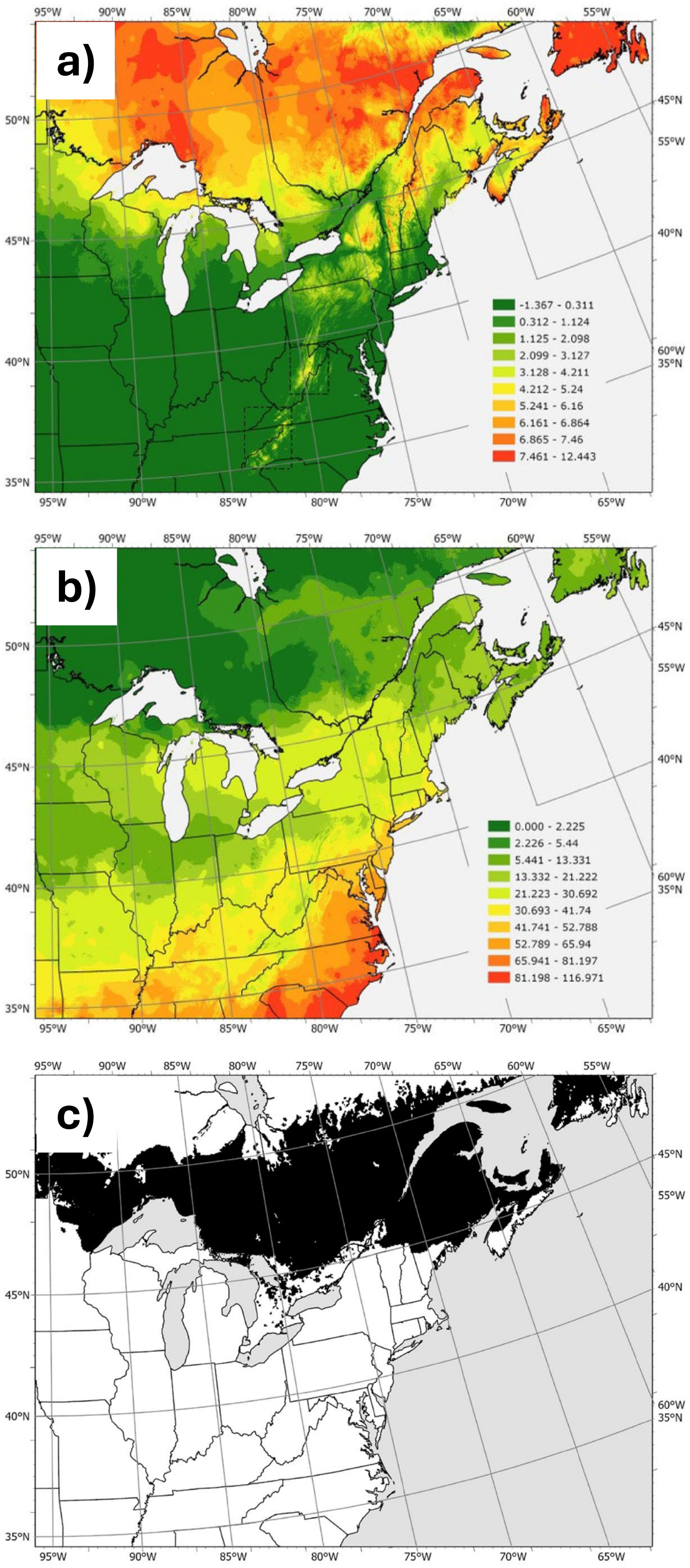

FIGURE 2 | Maps of data used in model estimation. (a) Modelled population growth rates. (b) Modelled budworm-host asynchrony (days). (c) cumulative area of defoliation, 1945 to 1988.

other locations, trap counts were much lower; the next highest trap capture was 44 from two traps placed in 2011 at the Black Mountain site in Pocahontas Co., West Virginia. The Whitetop Mountain site was visited again on 5 June 2022, and a moderate population of late instar *C. fumiferana* larvae was observed feeding on *P. rubens* foliage.

The distribution of sites with positive and negative detections was relatively uniform throughout the central Appalachian region except that there were no detections in any of the five most southerly sites when they were surveyed in 2012 and 2013 (Figure 1). These sites were located in North Carolina and Tennessee. Both *Picea rubens* and *A. fraseri* were present at all of these sites.

Spruce density in West Virginia within 5 km of each trapping location varied from 0 to 56.56 km^2 and spruce density within 10 km varied from 0 to 185.25 km^2. Analysis of trapping data from West Virginia did not indicate a significant effect of either local spruce density within 5 km ($z = 0.091$, $p = 0.927$), spruce density within 10 km ($z = 0.313$ $p = 0.754$), or the presence of *A. balsamea* ($z = 1.368$, $p = 0.171$) on the positive detection of *C. fumiferana*.

Models indicated variation in mean R and mean asynchrony among sites of latitude ranging from 36° to 53°N (Figures 2a and 3a). The lowest values of mean R were from sites with latitudes of 39° to 45°N, all at relatively low elevation (< 800 m; Figure 3a). Above and below this range of latitudes, mean R was higher, with the highest values in locations of < 37°N and > 47°N. Areas with the lowest mean R did not coincide with the five most southerly locations (< 37°N). Most of the variation in mean R was caused by overwintering survival ($r = 0.96$), which is itself the result of exposure to heat early in diapause (Han and Bauce 1997). Failure to hatch prior to the first frost in late summer occurs at high latitude and elevation.

Similarly, mean asynchrony was not exceptionally high in the 5 most southerly locations where *C. fumiferana* was absent (Figure 2b). Though there was considerable variation in asynchrony among sites, it fell through a similar range of values among sites with latitudes ranging from 36° to 45°N.

Across all sites, distance to outbreak varied from 114 to 886 km, mean R varied from 0.20 to 7.33 (1/years) and mean asynchrony varied from 14.8 to 19.9 days. Logistic regression analysis indicated that distance to outbreak area alone was the best predictor of *C. fumiferana* presence versus absence (Table 1). The univariate model with distance had the lowest AIC and was the only model with a significant slope.

4 | Discussion

Trapping results indicate that the southern range of *C. fumiferana* extends south in the central Appalachian Mountains to a latitude of 36.64°N in Virginia and south in the upper Mississippi River Valley to a latitude of 43.40°N in Iowa (Figure 1; Table S1, Figure S1). These locations represent a previously unknown southern extent of the species. However, it should be noted that

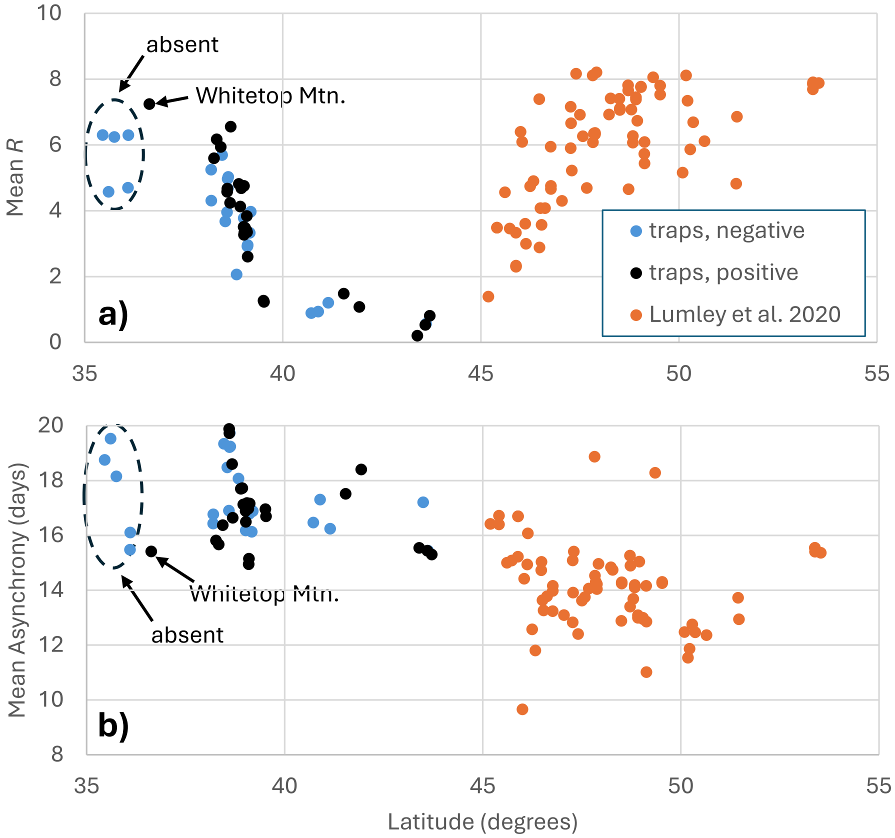

FIGURE 3 | Components of *C. fumiferana* fitness modelled at each trapping location (including locations where *C. fumiferana* is absent and present) and occurrence locations recorded by Lumley et al. 2020. (a) Modelled population growth rates. (b) Modelled budworm-host asynchrony.

TABLE 1 | Coparison of univariate, bivariate and full logistic regression models predicting the probability that *C. fumiferana* is detected in each of 51 sites.

	Estimate	*p*	AIC
Univariate models			
Distance to outbreak range	−0.0052	0.050	67.7
Mean *R*	−0.1613	0.309	71.9
Mean asynchrony	−0.2360	0.280	71.8
Bivariate models			
Distance to outbreak range	−0.0084	0.066	68.7
Mean R	0.2565	0.354	
Distance to outbreak range	−0.0050	0.601	69.1
Mean asynchrony	−0.1727	0.460	
MeanR	−0.1285	0.429	73.2
Mean asynchrony	−0.1972	0.382	
Full model			
Distance to outbreak range	−0.0089	0.058	69.6
MeanR	0.3240	0.232	
Mean asynchrony	−0.2454	0.319	

when Clemens (1865) initially described *C. fumiferana*, the locality of the type specimen was recorded as 'Virginia' though no additional collection information for that specimen is available, and the veracity of this location record has been questioned (Powell 1980). Clemens (1865) indicated that the type specimen originated from the collection of the Entomological Society of Philadelphia. Though no collection date is available, it is likely that at the time of collection, the territory of West Virginia was considered part of Virginia, so it is possible that the specimen originated from what is now West Virginia.

The Whitetop Mountain site (Virginia) was the most southerly point of positive detection (Figure 1) and, surprisingly, had the highest *C. fumiferana* population level (Table S1). Such a phenomenon in which population levels are highest at the edge of a species' geographical range is the opposite of what is typical for most species (Lawton 1993). The exceptionally high *C. fumiferana* abundance at the Whitetop Mountain site is thus exceptional. Just south of Whitetop Mountain, but also at high elevations in the Appalachian Mountains, *C. fumiferana* was absent from the five most southerly sites even though host trees were present; these sites spanned a substantial area in North Carolina and Tennessee (Figure 1).

Choristoneura fumiferana has specific host requirements and therefore populations cannot persist in areas where spruce, fir or larch are absent. Thus, much of the geographical range of this species is determined by the geographical range of its hosts. However, the species was absent from about half of the locations sampled despite the presence of hosts. Furthermore, logistic regression analyses of survey data from West Virginia indicated that the presence of the species was not associated with local host density. The absence of *C. fumiferana* from a large number of sites where hosts are present (Figure 1) indicates that the range of this species is not entirely defined by the distribution of hosts. It also suggests some level of stochasticity in occupancy patterns (Hanski 1994). Thus, the southern range limit in this insect species is not determined by the limit of its host.

Climatic modelling indicated geographic variation in both mean *R* and mean asynchrony among sampling locations (Figure 3). Interestingly, sites located south of 40°N had predicted values of mean *R* and mean asynchrony that were comparable to those much farther north (i.e., >45°N) where outbreaks are common. The Whitetop Mtn. site had the highest mean *R* (Figure 3a) and one of the lowest levels of asynchrony (Figure 3b) among the southernmost trap locations (<37° N). The five most southerly locations where *C. fumiferana* was absent also appear to be climatically suitable for the species (Figure 3a,b). Furthermore, logistic regression analysis did not indicate that either mean *R* or mean asynchrony significantly explained presence or absence across sites (Table 1). Taken together, these results indicate that the southern range limit of *C. fumiferana* is not constrained by climate.

Given that host species are generally limited to isolated mountaintops in the central and southern Appalachians, populations in these host islands may be particularly subject to adverse weather conditions in certain years, or to the mating failure Allee effect (Régnière, Delisle, et al. 2012) which may cause *C. fumiferana* populations to occasionally decline to local extinction. Given the well-known phenomenon of long-distance dispersal by large numbers of *C. fumiferana* gravid females emanating from outbreaks (Greenbank et al. 1980; Anderson and Sturtevant 2011; Garcia et al. 2022), it is possible that such localities may be recolonized by immigration from outbreak populations to the North. For example, populations occasionally reach defoliating levels in the Adirondack Mountains of New York (Westveld 1946) and may serve as a source of propagules dispersing into the central Appalachian region. This hypothesis is supported by our finding that the presence/absence of populations was significantly explained by distance to historical outbreak populations.

The hypothesis that central Appalachian *C. fumiferana* populations are derived from frequent recolonization by individuals immigrating from the North is not supported by the findings of Lumley et al. (2020) who found that central Appalachian *C. fumiferana* populations (sourced from our trap captures) are genetically distinct from more northerly populations. However, it is possible that extinctions and recolonizations occur infrequently such that these isolated populations have sufficient time to differentiate.

In summary, analyses presented here provide insight into the question of whether the southern limit of *C. fumiferana* is limited by host availability or climate. While it is clear that this insect can only establish in localities where host trees are present, our failure to detect populations in the five most southerly locations as well as other isolated locations where hosts are present (Figure 1) indicates that host availability is not the only factor limiting the range of this species. However, there is little support for the hypothesis that climate is responsible for this species' absence from this most southerly extent of host forest; mechanistic population models based on climatic data indicate that climate in these five southern Appalachian locations is suitable for *C. fumiferana* population growth and reproduction (Figure 3). We hypothesize that the species' absence from the most southerly distribution of spruce/fir forests is a result of this region being too distant from source populations that periodically restore extinct populations. As suggested above, it is possible that adult females dispersing from northerly outbreak populations rescue extinct populations in the central Appalachians but are unable to reach the most southerly spruce-fir forests, thus explaining this species southern extent.

Author Contributions

Andrew M. Liebhold: conceptualisation; data curation; formal analysis; investigation; methodology; data curation; formal analysis; visualisation; writing – original draft; writing – review and editing; visualisation. **Eugene Luzader:** investigation; data curation; visualisation; writing – review and editing. **Jacques Régnière:** investigation; methodology; formal analysis; writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the main text of this article.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.