Climatic and pathogenic impacts on spongy moth range expansion and contraction

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ABSTRACT

Invasive species cause roughly $137.2 billion in damages annually in the United States, but the factors that govern their spread through new areas are not fully understood. As one of the primary forces that limit species' distributions, climate can influence where and when an invasive species will spread aggressively. In this dissertation I evaluate the potential effects of climate on rates of range expansion (or contraction) in invasive species, using the spongy moth, one of the most destructive forest insects in North America, as my model study system. The climate can alter interactions between pests and their natural enemies, with possible consequences for invasive spread, especially if the natural enemy is a substantial source of mortality in the pest. Motivated by predictions that climate change will lead to rising air temperatures and more frequent summertime drought events, I conducted a manipulative field experiment to test the hypothesis that warmer, drier conditions decrease rates of infection of spongy moth larvae by its host-specific fungal pathogen *Entomophaga maimaiga* (Chapter 2). The number of infected larvae increased under elevated temperature treatments compared to the ambient temperature treatment, but there was no significant effect of supplemental precipitation or an interaction between temperature and precipitation. These results suggest that in colder portions of the spongy moth's range, such as Minnesota where the experiment was conducted, increasing temperatures due to climate change may enhance the ability of *E. maimaiga* to help control populations of the spongy moth. In Chapters 3 and 4 I investigated whether fluctuations in weather and climate at different timescales influence spatiotemporal variability in rates of spread. For example, annual variability in weather may influence year-to-year fluctuations in spread rates, whereas at interannual timescales, regionally synchronized climatic conditions may produce similarly widespread fluctuations in spread. Much past work has focused on how spatial, as opposed to temporal, variability in climate may alter the distributional range limits of invasive species. To help close this knowledge gap, in Chapter 3 I analyzed how rates of spread and population growth of low-density populations responded to annual variability in temperature, precipitation, and snow depth in five ecoregions along the spongy moth's range edge. I found that abiotic conditions strongly influenced spongy moth spread and growth rates, and that the effects varied by ecoregion. Additionally, the rates of population growth and spread usually responded differently to the same abiotic variable. These differences may stem from effects of weather on dispersal (e.g., wind-aided dispersal during storms) and density-dependent effects of abiotic conditions on population growth. In Chapter 4 I investigated whether synchrony in climate at multi-annual timescales would produce synchronized rates of range expansion and contraction at similar timescales. This is the first study to provide evidence of spatial synchrony in rates of range expansion and contraction, and that the drivers of this phenomenon can be similar to the drivers of population synchrony. Specifically, teleconnections led to multi-annual synchronized fluctuations in climate which drove synchrony in spread rates in the northernmost and southernmost ecoregions. Information on the strength and phase of teleconnections could inform managers about when and where spatially synchronized fluctuations in spread may occur. This dissertation broadens our current understanding of drivers of invasive spread and provides novel empirical evidence on the effects of temporal variability in climate on biological invasions. I also demonstrated that climate warming may affect interactions between pest insects and their pathogens, and in some locations these effects may facilitate biological control. The findings presented herein are also relevant for rare species, for which conservation efforts can facilitate range shifts to track a changing climate.

Chapter 1. Introduction

Range expansion in invasive species

Non-native species are present in nearly every region of the planet (Pimentel 2000). They are considered invasive if they cause clear ecological and economic impact or spread aggressively (Elton 1958; Mack et al. 2000; Lockwood et al. 2013). The number of introductions and successful invasions enabled by humans have increased for several regions due to escalating international trade and travel (Liebhold & Bascompte 2003; Hanspach et al. 2008; Hulme et al. 2009; Dyer et al. 2017). With this pattern expected to increase in the future, especially as the climate changes and globalization amplifies (Diagne et al. 2021), it is of heightened urgency to disentangle and isolate the factors that affect arguably the most impactful part of a biological invasion, the process of invasive spread.

If a non-native species becomes established and increases in abundance, spread will occur as individuals disperse beyond their current range limits, reproduce, and establish new populations (Blackburn et al. 2011; Lockwood et al. 2013). The ability of a species to spread and expand its range is a function of population growth and dispersal ability, as formalized by classic invasion theory (Fisher 1937; Skellam 1951). However, there is a suite of abiotic and biotic barriers, that can interfere with both growth and dispersal, and ultimately, range expansion. Some examples of barriers to spread are landforms, unsuitable climate, lack of resources, or limiting interspecific and intraspecific interactions (Gaston 2003).

Factors that govern spread

Climate has long been considered one of the primary forces that limits species' geographical distributions. Temperature is thought to be the strongest climatic factor that restricts most taxa (Merriam 1894; Hutchinson 1918; Jeffree and Jeffree 1994). Moving toward a species' range periphery, temperature regimes may become more novel compared to the original point of

introduction and establishment. If a species cannot adapt to these conditions, population growth rates may decline along the range edge (Cox 2004). In turn, reduced population growth would likely reduce rates of spread.

Biotic factors may also limit range expansion. Interspecific interactions have been shown to slow or stall range expansion as well as shape range boundaries (MacArthur 1972; MacLean & Holt 1997; Roughgarden 1979; Case et al. 2005; Legault et al. 2020). A well-known example of this is Grinnell's (1917) introduction of the niche concept as it applied to the California thrasher, where he observed that the range limits of this species were partially controlled by predation by hawks. Theoretical studies have also provided several predictions on how predator-prey interactions can influence species' range limits, with examples including generalist predators constraining their prey's range limits (Case et al. 2005; Holt & Barfield 2009), and the distributions of specialist natural-enemy species being governed by the distribution of their prey or hosts (Holt 1997; Alexander et al. 2007). In addition, more recent theory suggests that specialist predators can influence the range limits of their prey (Antonovics 2009; Holt & Barfield 2009; Holt et al. 2011). This may occur as predators disperse away from productive prey sites towards areas of lower prey productivity, especially those along the range edge (Holt & Barfield 2009). Specialist predators may stop the range expansion of their prey if predation is intense enough to cause extinction in range edge prey populations (Hochberg & Ives 1999).

The ability of interspecific interactions to impose range limits can change with the abiotic environment (Connell 1961; MacArthur 1972; Davis et al. 1998; Case et al. 2005; Parmesan et al. 2005). For example, in a microcosm experiment, Davis et al. (1998) found that the effect of a thermal gradient on competition and host-parasite interactions determined the realized niches of three *Drosophila* species. More recently, Alexander et al. (2016) emphasized the importance of

an interaction between climate and competition by suggesting that novel competitors encountered along an elevational gradient (representative of a thermal gradient) may alter a spreading species' response to climate. Based on these studies, the potential for interactions between the abiotic environment and biotic factors to limit a species' distributional range is clear, but it remains unknown how these types of relationships may alter rates of range expansion. Future investigations that tie microscale results of experimental studies to broader scale temporal patterns of climate, could enhance our understanding of how biotic and abiotic factors interact to impact the speed of an invasion.

The intrinsic population dynamics of a given species also have a strong impact on patterns of spread (Sexton et al. 2009). Range-edge populations almost always begin at low-densities. These populations are the primary providers of propagule pressure for future dispersal events that may lead to range expansion (Keitt et al. 2001), but they are also more likely to go extinct or decrease in abundance from phenomena such as demographic and environmental stochasticity, and the Allee effect (Terborgh & Winter 1980; Neubert et al. 2000; Robinet et al. 2008; Simberloff 2009).

First observed by ecologist Warder C. Allee (Allee 1931), an Allee effect is exhibited by small populations when there is a positive relationship between fitness components (e.g., survival and/or reproduction) and population size (Stephens, Sutherland & Freckleton 1999). This original definition describes a 'component' Allee effect. A component Allee effect may give rise to a 'demographic' Allee effect, defined as a positive relationship between population growth rate and density, such that a population's per capita growth rate is reduced at low densities (Stephens, Sutherland & Freckleton 1999). When a demographic Allee effect is particularly severe an Allee threshold may arise. The Allee threshold is the population-density below which a

population will exhibit negative per-capita growth rates, leading towards deterministic extinction (Courchamp et al. 1999; Stephens, Sutherland & Freckleton 1999; Wang & Kot 2001; Drake 2004; Taylor & Hastings 2005). A demographic Allee effect severe enough to result in an Allee threshold (at a density > 0) is termed a 'strong Allee effect' (Stephens, Sutherland & Freckleton 1999; Taylor & Hastings 2005). In contrast, populations with a 'weak Allee effect' would exhibit decreased per-capita growth rates at low densities but never negative, and therefore have no Allee threshold (Taylor & Hastings 2005).

As one of the most important demographic processes that can cause negative population growth rates (Courchamp et al. 1999; Drake 2004; Robinet et al. 2008), a demographic Allee effect may also reduce rates of spread and inhibit invasion success (Lewis & Kareiva 1993; Taylor & Hastings 2005; Tobin et al. 2007a; Courchamp et al. 2008; Lockwood et al. 2013). Common factors that can cause a demographic Allee effect are decreased mate-finding ability, failure to satiate predators, inability to cooperatively feed, and decreased cooperative defense at low population densities (Courchamp et al. 1999; Kramer et al. 2009). Lower suitability of climatic conditions along the edge of a species' range compared to the range core may increase the susceptibility of range-edge populations to Allee effects by lowering population growth rates and densities, but this concept is largely unexplored (Walter et al. 2017). Research on this topic could provide important information about how the abiotic environment can create spatiotemporal patterns in population dynamics that ultimately lead to range expansion, contraction, or stasis.

A consideration of time

When predicting the potential range limits and rates of spread for an invasive species, ecologists have often assumed static environmental gradients (Pearson and Dawson 2003;

Parmesan et al. 2005). Not only are abiotic gradients dynamic, but their patterns of variation may also differ substantially at different timescales. Weather and climatological variables, for example, display different patterns of variation at hourly or daily scales than at annual to multi-decadal scales. Effects of fluctuations of an abiotic variable at one timescale may differ from the effects of fluctuations at other timescales (Sheppard et al. 2016; Cazelles et al. 2023). For instance, year to year fluctuations in population growth or spread rates of species with annual life cycles (e.g., univoltine insects) can be impacted by one detrimental frost event (e.g., daily timescale) or annual abiotic fluctuations, whereas population cycling (i.e., where abundances of a population oscillate at regular intervals) may be most strongly affected by shifts in climate at annual to multi-annual timescales.

One phenomenon of population dynamics that can be strongly influenced by the timescale at which climatic conditions fluctuate is spatial population synchrony (Post & Forchhammer 2004). Defined as spatially disjunct fluctuations in population growth or abundance that are correlated through time (Bjørnstad et al. 1999), the main cause of spatial population synchrony is thought to be climate (e.g., the Moran effect; Moran 1953; Ranta et al. 1997; Koenig 2002; Liebhold et al. 2004; Royama 2012; Koenig & Liebhold 2016). The two other main drivers of spatial synchrony are dispersal and trophic interactions (Bjørnstad et al. 1999). Recent statistical advances (Sheppard et al. 2016, 2017, 2019) have allowed for the identification of timescale-specific patterns of synchrony, meaning that the abundances of populations fluctuate in synchrony with each other more strongly at timescales (equivalently, frequencies; timescale is 1/frequency) associated with specific periods of fluctuation and are weakly synchronized or possibly asynchronous at other timescales (Keitt 2008). Population synchrony occurs at the same timescale as its driver and multiple past studies have demonstrated

that climatic synchrony is largely timescale-specific and causes population synchrony at the same timescales (Sheppard et al. 2016, 2019; Haynes et al. 2019; Anderson et al. 2021; Walter et al. 2020a; Castaroni et al. 2022). The results of these studies provide strong evidence that population growth rates are synchronized in a timescale-specific manner. In theory, because population growth rates are closely linked to the spread rate of a species (Skellam 1951), climatic fluctuations that drive spatial population synchrony could produce similar patterns of synchrony in the movement of a species' range edge, but this topic is largely unexplored.

Empirical evidence on spatial synchrony in invasive spread is possibly lacking due to limited spatiotemporal data on low-density range-edge populations (Grayson & Johnson 2018). One exception to this scarcity of low-density population data, is the spongy moth in North America. This species exhibits high annual variability in rates of range expansion and contraction (Tobin et al. 2007b) and one study has shown that annual variability in supraoptimal temperatures during the larval life stage is related to patterns of spread, including range contraction events, in the warmest portions of the spongy moth's range. It is unknown whether multi-annual climatic fluctuations, such as those produced by teleconnections, can lead to specific spatiotemporal patterns of spread, such as timescale-specific synchrony in spread rates. Teleconnection patterns such as the El Niño-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) exhibit quasiperiodicity at multi-annual timescales and can affect temperature and precipitation over large geographic areas (Nigam & Baxter 2015). In light of the importance of climate in defining species' range limits (Gaston 2003) and the broad spatial scales over which teleconnections can affect weather, determining whether these climatic patterns produce spatial synchrony in the spread of invasive species represents an important avenue of research. For example, land managers could forecast synchrony in spread based on seasonal predictions about

teleconnections. This information would allow for advanced planning of when and where management resources should be allocated during a widespread pulse in spread.

Dissertation Objectives

This dissertation uses the spongy moth (*Lymantria dispar* (L.)) as a model study system to examine the independent and interacting effects of climate, range-edge population dynamics, and interspecific interactions on invasive spread. I address three major research questions, each of which represent a separate chapter of the dissertation:

1) What are the effects of temperature, precipitation, and their interactions on *Entomophaga maimaiga*-induced mortality of spongy moth larvae? The fungal pathogen *E. maimaiga* requires adequate moisture both to germinate and infect spongy moth larvae (Hajek 1999), but the interactive effects of temperature and precipitation on rates of infection are unknown. Warmer, drier conditions should decrease rates of infection, especially if *E. maimaiga* moisture requirements are not fulfilled. I tested this hypothesis by evaluating the effects of precipitation and soil and plant canopy temperature on larval mortality caused by *E. maimaiga* with a manipulative field experiment. In the experiment spongy moth larvae were caged and exposed to fungal spores in artificially-warmed and moistened forest soil plots.

2) How does annual variability in the abiotic environment affect rates of spongy moth spread plus two key mechanisms that underly invasive spread—population growth rates and Allee effects in range-edge populations? Much past work has focused on how spatial heterogeneity in climate may alter the distributional range limits of invasive species, but much less is known about how temporal variability in climate influences rates of range expansion. One prior study showed that annual variability in rates of spongy moth spread is affected by annual temperature conditions (Tobin et al. 2014); however, other abiotic variables are also likely important for spread. For example, in the spring, high temperatures can inhibit development of spongy moth larvae and drought may reduce larval mortality caused by the *E. maimaiga*, which requires moisture to infect its host. During the winter, snow cover may provide insulation against lethal temperatures which

can increase survival of spongy moth eggs. I analyze empirical data on spongy moth population growth, Allee effects, and spread rates in low-density populations near the invasion front to determine the role of annual variability of temperature, precipitation, and snow depth on rates of range expansion and contraction.

3) Is there spatial synchrony in spongy moth spread, and do multi-annual fluctuations in climate drive these patterns of spread? Many species exhibit synchronized fluctuations in population abundances that co-occur across space, known as spatial synchrony. One common driver of spatial population synchrony is broad-scale climatic conditions that fluctuate interannually. Because population growth is a component of the process of spread, patterns of spread may also exhibit spatial synchrony at similar timescales to that of their climate driver. I study whether spatial synchrony in spongy moth spread occurs, and if teleconnection patterns are drivers of timescale-specific patterns of synchrony in rates of invasive spread.

In the concluding chapter I argue that this dissertation substantially increases our understanding of how climate alters invasive spread. The implications of this research are broad, as my findings are relevant to both theory and management. For example, from a management perspective, the results from my manipulative field experiment that investigated the effects of temperature and precipitation on larval infections by *E. maimaiga* (Chapter 2) provide insight into the future of *E. maimaiga*'s ability to help control populations of the spongy moth as temperatures increase due to climate change. In Chapters 3 and 4, my analyses on empirical data on population abundances coupled with weather data provide novel evidence about the effects of temporal variability in climate on spatiotemporal patterns of biological invasions. Results from these studies align with a growing recognition that climate can have effects on populations that vary drastically depending on the timescale of study. Research focused on disentangling the effects of local and more broadscale climate drivers (e.g., teleconnections) on population dynamics for species that are of socioeconomic concern, such as invasive species or vectors of

disease, provides insight into whether climate is a dominant driver of changes in a given species' distributional range limits and the processes of such changes (e.g., weather effects on dispersal versus population growth rates). This information will serve in the development of early-warning systems and risk-mitigation procedures to predict and control potential shifts in spread under future climate scenarios.

Natural history of the spongy moth in North America

The spongy moth (*Lymantria dispar* (L.)) is an ideal study organism to investigate the direct and indirect effects of climate on spatiotemporal patterns of invasive spread. It is one of the most destructive forest pests in North America and its invasion across northeastern North America is one of the most thoroughly studied biological invasions in the world (Doane & McManus 1981; Tobin et al. 2012; Grayson & Johnson 2018). In the late 1860s, an amateur entomologist, Étienne Léopold Trouvelot, accidentally released a European strain into Medford, Massachusetts (Wu et al. 2015). Since this accidental release, the spongy moth has spread and is found as far south as the Virginia-North Carolina border, west to Minnesota, and north to the lower eastern Canadian provinces; an invasive range that is over 1,000,000 km^2 (Tobin et al. 2012).

The spongy moth is an extremely polyphagous folivore, feeding on over 300 tree species in North America (Liebhold et al. 1995). During outbreak years, the spongy moth causes widespread defoliation of hardwood forests. The negative ecological and economic implications of defoliation events have prompted scientists to extensively research the spongy moth's natural history and population dynamics (Campbell & Sloan 1977; Doane & McManus 1981; Elkinton & Liebhold 1990; Dwyer & Elkinton 1995; Elkinton et al. 1996; Johnson et al. 2006a; Liebhold

& Tobin 2006; Tobin et al. 2007a; Haynes et al. 2012; Tobin et al. 2014; Haynes et al. 2018; Thompson et al. 2017; Walter et al. 2020b).

Outbreaks of the spongy moth in parts of northeastern North America exhibit periodicity—with a primary period length of 8 -10 years and a secondary period length of 4-6 years (Johnson et al. 2006a, b; Haynes et al. 2009, 2013). Factors thought to contribute to variation in period length are predation pressure (Bjørnstad et al. 2010) and forest type (Johnson et al. 2006a). Predation by generalist small mammals can prevent outbreaks, whereas specialist natural enemies, particularly two host-specific entomopathogens—*Lymantria dispar* multicapsid nuclear polyhedrosis virus (*Ld*MNPV) (Doane & McManus 1981; Elkinton & Liebhold 1990) and the fungus *Entomaphaga maimaiga* (Hajek et al. 1995; Hajek 1999)—can cause collapse of outbreaking populations.

*Ld*MNPV was first reported in North America in 1907 (Glaser 1915) and until 1989, this viral pathogen was the main driver of population crashes of the spongy moth (McManus & Csóka 2007; Alalouni et al. 2013). Since the discovery of the fungal pathogen *E. maimaiga* in North America in 1989, this fungus has replaced the virus as the dominant source of spongy moth larval mortality (Liebhold et al. 2013; Hajek et al. 2015). In addition to collapsing outbreaks, it is possible that *E. maimaiga* could also prevent outbreak occurrence as the fungus can cause high rates of infection in both high and low-density spongy moth populations, which is unique among the spongy moth's natural enemies (Hajek et al. 1990a; Elkinton et al. 1991).

Rates of infection by *E. maimaiga* are strongly influenced by weather conditions (Hajek et al. 1990b; Hajek 1999). Results from laboratory and field observational studies demonstrate a consistent positive effect of moisture (e.g., relative humidity, rainfall, and soil moisture) on germination and infection of spongy moth larvae by both of *E. maimaiga*'s spore types—

azygospores (resting spores) and conidia (Hajek et al. 1990b; Hajek & Soper 1992; Weseloh & Andreadis 1992b; Hajek & Humber 1997; Reilly et al. 2014). In addition, manipulative field experiments have shown that the addition of artificial rain increases rates of infection by both of the spore stages: conidia and resting spores (Hajek & Roberts 1991; Weseloh & Andreadis 1992a; Hajek et al. 1996).

High temperature appears to have a negative effect on *E. maimaiga* germination and infection (Hajek 1999) but results from past research are not consistent. In particular, observational field studies show significant negative effects of soil temperature in some years but not others (Hajek & Humber 1997; Siegert et al. 2008). Reilly et al. (2014) found a significant negative effect of temperature on the mortality of field-collected larvae but no clear relationship for caged larvae. These past studies highlight the important role of weather for this host-pathogen relationship, but the effects of climate change remain unclear, as no studies have investigated the independent and interactive effects of temperature and precipitation under field conditions.

For the spongy moth, there exists extensive literature on the invasive spread and population dynamics of low-density populations along the range edge. This body of research is supported by the monitoring efforts of the Slow the Spread (STS) Program which produces an unparalleled set of spatiotemporal data on spongy moth abundance and spread within the United States (Grayson & Johnson 2018). The program annually deploys 60,000-100,000 pheromone-baited traps across the 'transition zone', an ~170 km wide swath of land along the spongy moth's range edge, including areas that have been recently infested and areas still unoccupied by the pest (Sharov et al. 2002). Across this broad spatial extent, the annual monitoring program provides data on spongy moth densities at a fine spatial resolution (standard trap density of 1 trap per 10.4 km^2 in rural areas and 2.6 km^2 in towns and cities; United States Department of

Agriculture 2009). The dataset has been invaluable for informing spongy moth management decisions and scientific inquiry (Tobin et al. 2012; Grayson & Johnson 2018).

For the spongy moth strain that is established in northeastern North America, short-distance dispersal (< 200 m) occurs by adult males and the larvae of both sexes and adult females are flightless (Doane & McManus 1981; Keena et al. 2008). Because natural dispersal only occurs via adult males or larvae, human-mediated movement of life stages is thought to be a main reason why high rates of spread occur in some years (Liebhold et al. 1992; Johnson et al. 2006b, Tobin et al. 2007 a,b; Tobin & Blackburn 2008). Another source of long-distance dispersal is the wind. A study by Frank et al. (2013) determined that high winds during storm events blew early-instar larvae from established populations in Michigan across Lake Michigan, into Wisconsin. These long-distance dispersal events likely facilitated the initial invasion of the spongy moth into Wisconsin, and contributed to rapid rates of spread through the state (Tobin & Blackburn 2008; Frank et al. 2013). The role of long-distance dispersal via the wind facilitating the spread of the spongy moth in other regions is unknown. In contrast to human-aided dispersal events, the Allee effect is a main cause of reduced spread rates in some years (Johnson et al. 2006b; Tobin et al. 2007a).

Theoretical evidence indicates that stratified diffusion (i.e., multiple modes of dispersal that occur over different distances; Ōkubo 1980; Hengeveld 1989) combined with a strong Allee effects can create periodic pulses in spread (Johnson et al. 2006b). In the spongy moth, peaks in rates of spread occur every 4-6 years (Johnson et al. 2006b; Walter et al. 2015). Walter et al. (2015) found that in Virginia and West Virginia these pulses in spread consistently lag ≈ 1 year behind spongy moth outbreaks that occurred 50-100 km behind the invasion front. This evidence suggests that migrants from outbreaks to the range edge may contribute to the growth and

subsequent spread of low-density populations along the invasion front (Walter et al. 2015). Outbreaks of the spongy moth can display spatial synchrony over distances of up to 1,000 km (Peltonen et al. 2002; Haynes et al. 2009), but patterns of synchrony in spread are unknown.

Within the North American range of the spongy moth, precipitation and temperature exhibit multi-annual periodicity (Allstadt et al. 2015; Haynes et al. 2019) and can display synchrony over distances up to 2,500 km (Koenig 2002; Koenig & Liebhold 2016). Teleconnection patterns such as the El Niño-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) exhibit quasiperiodicity at multi-annual timescales and can affect seasonal temperature and precipitation over large geographic areas (Nigam & Baxter 2015). Sheppard et al. (2016) revealed a strong link between a teleconnection (NAO) and spatial synchrony in the timing of aphid first flights at long (> 4 years) timescales. It is unknown whether timescale-specific synchrony in climate has similar impacts on the spatiotemporal dynamics of the spongy moth's invasive spread.

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Chapter 2. Rising temperatures may increase fungal epizootics in northern populations of the invasive spongy moth in North America

Abstract

Insect pest species are generally expected to become more destructive with climate change, but responses will vary by species due to a variety of factors, including altered interactions with their natural enemies. Entomopathogens are a substantial source of mortality in insects and are important agents of biological control, but the likelihood of epizootics caused by these pathogens can depend strongly on climatic conditions. Previous research indicates that rates of infection of the spongy moth (*Lymantria dispar*) by its host-specific fungal pathogen, *Entomophaga maimaiga*, increase with environmental moisture and decrease as temperatures rise, but interactive effects are unclear. Here, I test the hypothesis that warmer, drier conditions will decrease rates of infection of spongy moth larvae by *E. maimaiga*. I evaluated the effects of precipitation and soil and plant canopy temperature on larval mortality caused by *E. maimaiga* with a manipulative field experiment. To do this, I caged laboratory-reared spongy moth larvae in experimentally warmed forest plots, exposing the larvae to soil inoculated with *E. maimaiga* resting spores. Across 36 plots, caged larvae (2 cages per plot) were exposed to three temperature treatments—ambient, +1.7°C above ambient, and +3.4°C above ambient. To test the effects of precipitation, I added supplemental precipitation to 1 of 2 randomly selected cages per plot. There was a significant positive effect of increasing temperature on number of infected larvae, with the number of infected larvae increasing by 45%, on average, under the elevated temperature treatments compared to ambient temperature. However, there was no significant effect of supplemental precipitation and no significant interaction between temperature and precipitation. Experimental warming may have increased infections because ambient temperatures at the field site, which was located in one of the coldest portions of the spongy moth's range, were suboptimal for fungal germination. The lack of a precipitation effect may have been due to high rainfall that occurred before the experiment began, potentially fulfilling fungal moisture requirements. The results from this experiment suggest that in colder portions of the spongy moth's range, increasing temperatures due to climate change may enhance the ability of *E. maimaiga* to help control populations of the spongy moth.

Introduction

Climate change is generally expected to amplify the overall impacts of insect pest species worldwide, although responses will vary among species (Pureswaran et al. 2018; Lehmann et al. 2020; Halsch et al. 2021). This variability stems from differences in how climate affects the pest species' physiology (Huey & Kingsolver 2019), phenology (Jakoby et al. 2019), and life history and their interactions with host plants (Haynes et al. 2022) and natural enemies (Frank 2021). Regarding interactions with natural enemies, entomopathogens (e.g., bacteria, fungi, viruses, and nematodes of insects) are extremely susceptible to changes in the environment, particularly temperature and environmental moisture (e.g., precipitation, soil moisture, relative humidity) (Dara et al. 2019). These pathogens are major mortality agents of insects (Roy et al. 2009) and climate conditions that inhibit the transmission of disease may increase the probability that insect pest populations grow to outbreak levels (Skendžić et al. 2021). In a multi-year study, Feng et al. (1992) found that aphids could cause damage to cereal crops even during epizootics caused by entomopathogenic fungi; however, crop damage was reduced in one year due to an earlier and higher-level epizootic triggered by frequent and heavy rainfall in June. Most studies on the potential effects of climate change on host-pathogen systems have focused on the impacts of rising temperatures (Altizer et al. 2013; MacDonald et al. 2023). There are few manipulative field studies that test the independent and interactive effects of multiple abiotic variables on host-pathogen relationships (but see van Doan et al. 2021). In light of climate change predictions that indicate drought events will increase in frequency and severity (IPCC 2022), we need to understand effects of other aspects of climate change such as drought on insect pests and their pathogens (St. Leger 2021).

Increasing drought could have important implications for host-pathogen interactions that regulate populations of one of the most damaging forest pests in North America, the spongy

moth (*Lymantria dispar* (L.)). Springtime drought may create favorable conditions for outbreaks of the spongy moth by inhibiting infections by the host-specific fungal pathogen *Entomophaga maimaiga* (Pasquarella et al. 2018). Results from laboratory and field observational studies have consistently demonstrated a positive effect of moisture (e.g., relative humidity, rainfall, and soil moisture) on germination of *E. maimaiga* resting spores, sporulation, and infection of spongy moth larvae by both spore types—azygospores (resting spores) and conidia (Hajek et al. 1990b; Hajek & Soper 1992; Weseloh & Andreadis 1992b; Hajek & Humber 1997; Reilly et al. 2014). In addition, manipulative field experiments have shown that the addition of artificial rain increases rates of infection by both conidia and resting spores (Hajek & Roberts 1991; Weseloh & Andreadis 1992a; Smitley et al. 1995; Hajek et al. 1996). High temperatures appear to have a negative effect on *E. maimaiga* germination, sporulation, and infection (Hajek 1999) but results from past research are not consistent. For example, observational field studies show significant negative effects of soil temperature in some years but not others (Hajek & Humber 1997; Siegert et al. 2008). In an observational field study, Reilly et al. (2014) found a significant negative effect of temperature on the mortality of field-collected larvae but no clear relationship for laboratory-reared larvae exposed to field conditions. These past studies highlight the important role of weather for this host-pathogen relationship, but the effects of climate change remain unclear as no studies have investigated the independent and interactive effects of temperature and precipitation under field conditions. Additionally, most past field studies occurred in regions with more moderate climates compared to the coldest portions of the spongy moth's range (e.g., upper midwestern states, eastern Canada, Maine), making it difficult to extrapolate effects of weather across the range.

Here, I experimentally tested the effects of temperature and precipitation on the host-pathogen relationship between the spongy moth and *E. maimaiga*. The spongy moth is a non-native defoliator of hardwood forests in northeastern North America and causes approximately $3.2 billion of damage annually (Bradshaw et al. 2016). *Entomophaga maimaga* is the dominant source of spongy moth larval mortality (Liebhold et al. 2013; Hajek et al. 2015) and can cause high rates of mortality in both high and low-density spongy moth populations (Hajek et al. 1990a; Elkinton et al. 1991). The ability of *E. maimaiga* to cause epizootics over a wide range of spongy moth population densities is unique in that the moth's other main pathogen, the *Lymantria dispar* nucleopolyhedrovirus, only causes high levels of mortality in host populations that are at high densities (e.g., outbreaking) (McManus & Csóka 2007; Alalouni et al. 2013). Because *E. maimaiga* epizootics can occur in low-density populations, it is possible that the fungus could slow or stop the spread of spongy moth by causing mortality in newly established populations along the insect pest's expanding range front.

The motivation for this study was to understand how predicted climate changes, rising air temperatures and increasing summertime drought (IPCC 2022), may affect spongy moth mortality caused by *E. maimaiga* infection. The effects of soil and plant canopy temperature and precipitation were evaluated in a manipulative field experiment. Although warmer and drier conditions are generally predicted to cause infections to decrease because *E. maimaiga* resting spores require adequate moisture to germinate and infect larvae (Hajek 1999), my experiment occurred in the Arrowhead Region of Minnesota (Fig. 1), where typical springtime and early summer conditions may be too cold to support germination (Siegert et al. 2009). Therefore, I predicted that infection levels would increase under experimentally elevated temperatures. Additionally, because of *E. maimaiga* moisture requirements, I predicted that adding

supplemental precipitation would increase infection rates. Understanding the effects of these abiotic conditions in the northwesternmost portion of the U.S. range is important because spongy moth spread is occurring more rapidly in this region than anywhere else. Furthermore, a climatic suitability study estimated that the Arrowhead Region would increase in suitability for the spongy moth under a 1.5°C increase in mean daily temperature compared to historical averages (Gray 2004).

Materials and methods

Entomophaga maimaiga life history

The infection cycle of *E. maimaiga* begins in the spring, when overwintering resting spores in the forest soil begin to germinate approximately 1-2 weeks before spongy moth larvae emerge (Hajek & Humber 1997). *E. maimaiga* resting spores are always responsible for the primary infection cycle of the season, which occurs when infectious germ conidia are released from germinating resting spores. These germ conidia can become airborne and when they land on spongy moth larvae they germinate, infect, and then kill a larva in approximately five days (Hajek et al. 1995). Prior to larval death, *E. mamaiga* grows inside of the insect and after host death it grows outward through the cuticle and ejects thousands to millions of new conidia (Shimazu & Soper 1986; Hajek et al. 1993). Infections initiated by germ conidia released from resting spores (e.g., the primary infection cycle) only produce conidia, never resting spores (Hajek 1997). Conidia released from a dead spongy moth larva (e.g., cadaver), are responsible for all subsequent infection cycles. When spongy moth larvae reach later instars (5^{th}-6^{th}), infected larva begin to produce resting spores as opposed to more conidia (Hajek & Shimazu 1996). The exact environmental cues that cause spore production to switch from conidia to resting spores are unknown, but temperature and larval instar are both contributing factors (Hajek & Humber 1997; Hajek 1999). Resting spores produced in later instar spongy moth cadavers go dormant and

overwinter, adding to the reservoir of resting spores in the soil. Resting spores are typically dormant for 1-2 years prior to germination and can survive for at least 6 years in the field (Weseloh & Andreadis 1997; Hajek et al. 2004; Hajek et al. 2018).

Manipulative field experiment

In the summer of 2022, I conducted a field experiment to test the effects of temperature and precipitation on spongy moth larval infection by *E. maimaiga*. The experiment was conducted at the University of Minnesota's Hubachek Wilderness Research Center (HWRC) near Ely, Minnesota. The HWRC is located in the northwesternmost portion of the spongy moth's expanding range front (Fig. 1). I used experimentally warmed forest (closed canopy) plots that were part of a long-term climate change experiment, the Boreal Forest Warming at an Ecotone in Danger (B4WarmED) project (Rich et al. 2015). Within each of three spatial blocks, there were two replicate 7.1 m^2 circular plots for each of three temperature treatments (ambient temperature, +1.7°C above ambient, and +3.4°C above ambient; Fig. 2a). Plots within a block were separated by 4-13 m and were 8 m apart on average. Blocks were spaced approximately 15-23 m from each other, with an average separation of 19 m. Temperature is manipulated in the plot treatments annually from May to November.

Caged larvae were exposed to temperature and precipitation treatments in three separate trials, conducted June 30-July 5, July 6-10, and July 12-17, respectively. I introduced simulated rainfall to one of the two cages per plot (randomly selected), creating two precipitation treatments: ambient and supplemental (Fig. 2a). The total volume of water added to a cage receiving supplemental precipitation was 518 ml. I applied one-third of the total volume of water during each four-day trial, with half of the water added at dusk on the first and third days of each

trial. To reduce confounding effects from water contaminants (e.g., minerals, pollutants, etc.), I used deionized water. I sprinkled water on each cage with a watering can.

To determine the amount of simulated precipitation to add, I obtained long-term precipitation records from two nearby NOAA weather stations in Ely, Minnesota, which together, provided coverage from 2000 to 2021 (USC00212561 47.9056°, -91.8283°; USC00212543 47.9239°, -91.8586°). From these data, I calculated the mean and standard deviation in precipitation from 2000 to 2021 for the duration of the experiment (June 30-July 16). The total volume of water added was equal to 1 SD of the long-term mean, with this volume calculated as:

$$water\ volume\ (ml) = catchment\ area\ (cm^2) \times rainfall\ depth\ (mm) \quad (1)$$

where catchment area was the area of a single cage (31 x 23 cm^2) and rainfall depth was 1 SD of the long-term mean of 7 mm.

I tested the effects of temperature and precipitation on fungal infection by deploying two cages, each containing 19 4^{th}-instar larvae, in each plot (Fig. 2a, b). The cages were made by folding aluminum window screening to a dimension of 31 × 23 cm^2, with a 2-cm high interior cavity (Hajek & Humber 1997; Reilly et al. 2014; Fig. 2b). To ensure contact with the soil, I brushed aside the leaf litter and installed the cages flush with the soil. Each cage was protected from vertebrate predators and weather-related hazards (e.g., fallen limbs) by 12-mm^2 hardware mesh and both the cage and cover were anchored to the soil with landscape staples (Reilly et al. 2014; Fig. 2b). Two cubes of artificial wheat germ diet were provided in every cage.

Prior to the field experiment, I reared eggs of a disease-free spongy moth colony from the PPQ S&T Otis Laboratory (USDA-APHIS, Buzzards Bay, MA) to the 4^{th} instar in an environmental chamber. The environmental settings of the chamber were 25 °C, 70% relative humidity, and 15 hours of light. Larval infection by resting spores begins to increase rapidly

during the 4th instar (Hajek & Shimazu 1996), which makes this instar the ideal developmental stage for studying fungal infection. To align the timing of my experiment with when wild spongy moths at the field site would be in the 4th instar, I estimated when wild larvae would reach this stage using a model of temperature-dependent spongy moth phenology (Régnière & Sharov 1997, 1998, 1999; Gray et al. 2001). I conducted a trial when 5% (6/30-7/5), 50% (7/6-7/10), and 95% (7/12-7/17), respectively, of larvae at HWRC were predicted to have reached the 4th instar. Matching the trials with larval phenology also helped ensure the experiment aligned with *E. maimaiga*'s resting-spore germination period, which begins approximately 2 weeks before larval emergence and ends when spongy moth larvae reach later instars (e.g., 5-6th instars) (Hajek & Humber 1997).

To ensure the presence of *E. maimaiga*, in the summers of 2019 and 2021, I inoculated the study plots with cadavers of spongy moth larvae that contained resting spores. These inoculation events were necessary because spongy moth densities were likely very low at the field station, as determined from data from the Slow the Spread (STS) Foundation. STS is a national monitoring program that tracks spongy moth populations with pheromone-baited traps. Because of low spongy moth densities, it was uncertain whether *E. maimaiga* was already present at HWRC. For the inoculation events, I obtained cadavers from Massachusetts and Virginia where there were ongoing *E. maimaiga* epizootics. Additionally, the cadavers were found hanging upside down on the trunks of trees with prolegs extended at 90°, a visual cue that suggests death from infection by the fungus (Blackburn & Hajek 2018). The inoculations were carried out using procedures that have been shown to be effective (A. Diss-Torrance personal correspondence; Hajek et al. 2021). First, I ground the field-collected spongy moth cadavers in a food processor and divided the ground material into 36 equal portions (0.54 grams), one for each

experimental plot. I then mixed each portion with 30 g of sterile potting soil. For each inoculation, I spread the mixture in the same two randomly selected locations in each plot. I placed caged spongy moth larvae over each inoculation location. Additional details about the inoculation procedures are provided in Appendix A1.

Baseline climatic and abiotic conditions at the field site

To understand how the weather conditions prior to, and during, my experiment compared to average climatic conditions, I obtained long-term climate data for 2000 to 2022 from the same two NOAA weather stations used to calculate the amount of supplemental precipitation (USC00212561 47.9056°, -91.8283°; USC00212543 47.9239°, -91.8586°). Plot-level daily data on soil moisture for June 20-July 17, 2022 was measured by B4WarmED project personnel with a water reflectometer (Model CS616 from Campbell Scientific).

Post-field experiment larval monitoring

Following each field trial, I transferred the larvae to the lab and secured individual larva in lidded 1 oz. plastic cups containing a small piece of artificial wheat germ diet (Blackburn & Hajek 2018). I maintained larvae at 18-22 °C and monitored them for 10 days or until death, whichever occurred first (Blackburn & Hajek 2018). Larvae that died within the 10-day monitoring period were placed on 1.5 % water agar plates and checked daily for 3 days for conidial production (Hajek et al. 1990b). Although conidia are often visible without magnification, I noticed during the first trial's observation period that conidia were sometimes only apparent under a dissecting microscope. I did not include trial one data for statistical analyses because of the possibility that I missed conidia on cadavers that I inspected without a dissecting microscope. I examined trial two and three cadavers under both a dissecting microscope and a phase contrast microscope. For phase contrast microscopy, I macerated and

smeared a larva onto a microscope slide and observed the specimen at 200-400× magnification (Blackburn & Hajek 2018). I counted a larva as infected by *E. maimaiga* if I saw conidia either externally or via phase contrast. It is also possible for larvae to have resting spores present instead of, or in addition to, conidia (Hajek 1999), but I did not expect this because previous research indicates that infections initiated by germ conidia from resting spores only produce conidia, not resting spores (Hajek 1997).

Statistical analyses

I tested the hypotheses that temperature, precipitation, and their interaction would affect the number of spongy moth larvae infected by *E. maimaiga.* I built a model with these variables and also included a fixed effect of block and random effect of plot. Including plot as a random effect allows for the model to account for variance among plots e.g., potential non-independence of values within a given plot (Crawley 2013). Block was modelled as a fixed effect, not a random effect, because there were only three levels in block and the estimates of variance of random effects with such few levels are inaccurate (Arnqvist 2020). A linear mixed effects model with all of these variables was overparameterized. Therefore, I assessed that block or plot could be dropped without adversely affecting model parsimony (fit balanced by a penalty for the number of parameters), with parsimony quantified using AIC values. Models with $\Delta AIC < 2$ were considered to have substantial support (Burnham & Anderson 2002), where ΔAIC of model i equal to AIC_i – min(AIC) and min(AIC) is the AIC of the highest-ranking model. For both trials, I selected the model that was not overparameterized, had substantial support ($\Delta AIC < 2$), and the fewest number of variables dropped (Table A1). For both trials, a model that included block but not plot was selected (Table A1). I assessed the effects of temperature, precipitation, the temperature × precipitation interaction, and block on the number of infected larvae using

generalized linear models (GLM). For each model, I specified a Poisson distribution and a log link. I performed all statistical analyses in R (R Development Core Team 2022). The models were fit using the 'glmer' function of the 'lme4' package (Bates et al. 2015). To conduct pairwise comparisons, I performed Tukey's tests using the package 'emmeans' (Lenth et al. 2022).

Results

Baseline climatic and abiotic conditions at the field site

Compared to the long-term mean from 2000 to 2021, mean daily minimum and maximum temperatures during this experiment were near-average and slightly below-average, respectively (Table 1). Air temperature gradually increased during the experiment. The average minimum and maximum daily temperatures during the first, second, and third trials were 10.4 °C and 21.9 °C; 11.4 °C and 23.5 °C; 12.4 °C and 24.5 °C, respectively.

Mean daily precipitation during the experiment was 72% lower than the long-term mean (Table 1). However, during the month of May, prior to the experiment, mean daily precipitation was 38% higher than the long-term average over the same time period (Table 1). Soil moisture decreased during the experiment and on the last day soil moisture was 0.18 Θ ($cm^3H_2O\ cm^{-3}soil$), compared to 0.25 Θ at the start of the experiment. On average, plots under the high temperature treatment (3.4 °C above ambient) had the driest soil (Θ = 0.19) and plots under the low (1.7 °C above ambient) and ambient temperature treatments had similar soil moisture, Θ = 0.24 and Θ = 0.23, respectively.

Effects of temperature and simulated precipitation on number of infected larvae

There was no significant effect of block in either trial two (χ_2^2 = 2.60, P = 0.272) or three (χ_2^2 = 3.67, P = 0.160). For trials two (χ_1^2 = 0.22, P = 0.637) and three (χ_1^2 = 0.25, P = 0.617), there was no significant effect of supplemental precipitation on number of infected larvae. Temperature had a significant, positive effect on the number of infected larvae in the second (χ_2^2

= 11.23, $P = 0.004$) and third ($\chi_2^2 = 13.23$, $P = 0.001$) trials (Fig. 3). I did not find a significant interactive effect of temperature and precipitation for trials two ($\chi_2^2 = 4.45$, $P = 0.108$ or three ($\chi_2^2 = 0.91$, $P = 0.634$). On average, across trials 2 and 3, the number of infected larvae was 45% higher in the elevated temperature treatments compared to ambient temperature, where very few infections occurred.

Discussion

Multiple studies have reported positive effects of environmental moisture on spongy moth larval infections by *E. maimaiga* (Hajek 1999; Reilly et al. 2014), but using a manipulative field experiment, I found that only the temperature treatments, not supplemental precipitation, affected larval infections by this pathogen. Consistent with my prediction, which was based on a climate similarity study that concluded that the northwesternmost portion of the spongy moth's invasive range may be too cold to support *E. maimaiga* (Siegert et al. 2009), I found that larval infections increased under the elevated temperature treatments. These results suggest that rising temperatures associated with climate change may increase larval mortality by *E. maimaiga* in cold portions of the spongy moth's range (e.g., Minnesota, northern Wisconsin, eastern Canada).

Contrary to my predictions, supplemental precipitation and its interaction with temperature, did not affect the number of larvae that became infected by the fungus. This finding was surprising, given that multiple past studies have found positive associations between rainfall and larval infections by resting spores (Weseloh & Andreadis 1992 a,b; Hajek et al. 1996; Reilly et al. 2014). One potential explanation for the lack of a precipitation effect in this study is that moisture requirements for resting spore germination were fulfilled before the experiment began given that precipitation before the experiment, in the month of May, was above average (Table 1). Supporting this possibility, a past study modeled the relationships between rainfall,

temperature, and the phenology of infection, and found that the timing of rainfall, not just amount of rainfall, is a critical factor influencing infection rates (Weseloh et al. 1993). Additionally, using empirical data on *E. maimaiga* epizootics, Hajek et al. 2015 found that only May rainfall had a positive relationship with infection level, whereas precipitation in June had a negative relationship with infection levels and April precipitation was not significantly associated with amount of infection. Future field experiments that incorporate a reduced-moisture treatment along with an increased-moisture treatment would help resolve how infection levels will change with increasing drought severity.

Results from this study highlight the importance of considering geographic location when assessing the impacts of temperature and moisture conditions on larval infection. The general consensus of past research on the role of weather for this host-pathogen relationship is that warmer and drier conditions inhibit infections by *E. maimaiga* (Hajek 1999); however, epizootics have occurred in years that were warmer and drier than average (Hajek et al. 1996). Prior field studies on the effect of temperature on the spongy moth-*E. maimaiga* interaction were conducted in areas with warmer climates compared to the present study (Hajek et al. 1996; Hajek & Humber 1997; Reilly et al. 2014), which may explain why the positive effect of increasing temperature found in this experiment was in the opposite direction to that found in warmer regions.

It is unclear whether similar effects of temperature and precipitation on larval infection to what were found in this experiment would occur in years with different ambient climatic conditions, such as during a drought. Conducting multi-year studies that assess the effects of annual variability in weather on this host-pathogen relationship could help quantify the range of temperature and precipitation conditions under which larval infections can occur at a given

location and infection prevalence. If rising temperatures lead to increased infections of *E. maimaiga* in the colder regions of the spongy moth's range in North America, as is suggested by the results of this experiment, it is possible that rates of spongy moth range expansion in these regions could decrease in the future. However, temperatures in the northwesternmost portion of the spongy moth's range are expected to become more suitable for the pest under a 1.5°C warming scenario (Gray 2004). Therefore, the overall effects of climate warming on spongy moth populations in these colder ecoregions is unclear. To inform management decisions on slowing the spread of spongy moth, particularly in the northwesternmost region of the nonnative range where rates of range expansion are fastest, it is imperative that we untangle the independent and interactive responses of this host-pathogen relationship to climate. Doing this will help land managers identify when and where climatic conditions are expected to inhibit or enhance larval mortality due to *E. maimaiga*, which in turn, would inform decisions on employing methods to slow the spread of the spongy moth.

Tables & Figures:

Table 1: Long-term climate data for 2000 to 2022, sourced from NOAA weather stations USC00212561 and USC00212543 in Ely, Minnesota. Values reported are mean daily averages ± standard deviation, during the dates of the experiment (June 30-July 17) for the long-term (2000 to 2021) and in 2022. Also reported is precipitation during May because above-average rainfall in 2022 may have influenced *E. maimaiga* germination.

	June 30-July 17			*May*
Year	**Minimum temperature (°C)**	**Maximum temperature (°C)**	**Precipitation (mm)**	**Precipitation (mm)**
Long-term mean (2000 to 2021)	12.7 ± 3.1	26.7 ± 4.2	0.9 ± 1.5	2.5 ± 5.4
2022	12.3 ± 3.1	24.3 ± 2.4	3.3 ± 7.1	4.0 ± 8.2

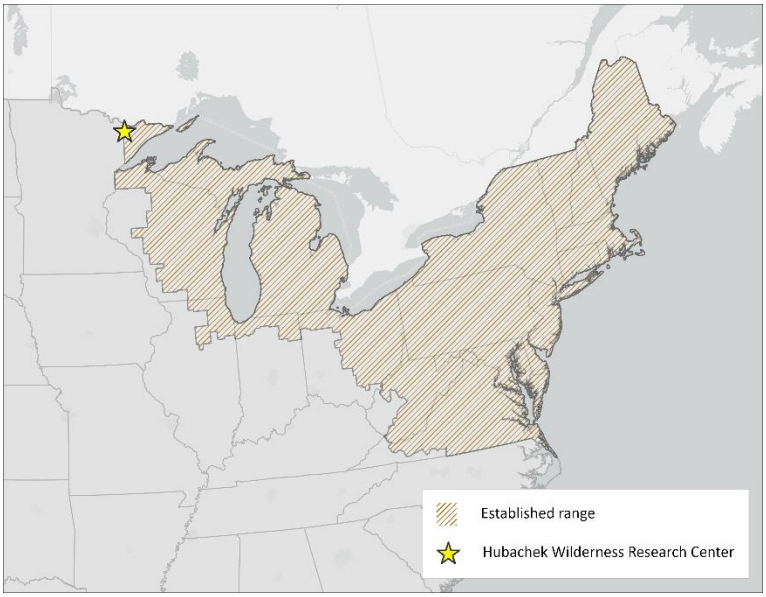

Figure 1: The star represents the Hubachek Wilderness Research Center in Ely, Minnesota. Hatched area represents the nonnative, established range of the spongy moth in eastern North America. Data for the spongy moth range were sourced from the USDA APHIS PPQ spongy moth quarantine records.

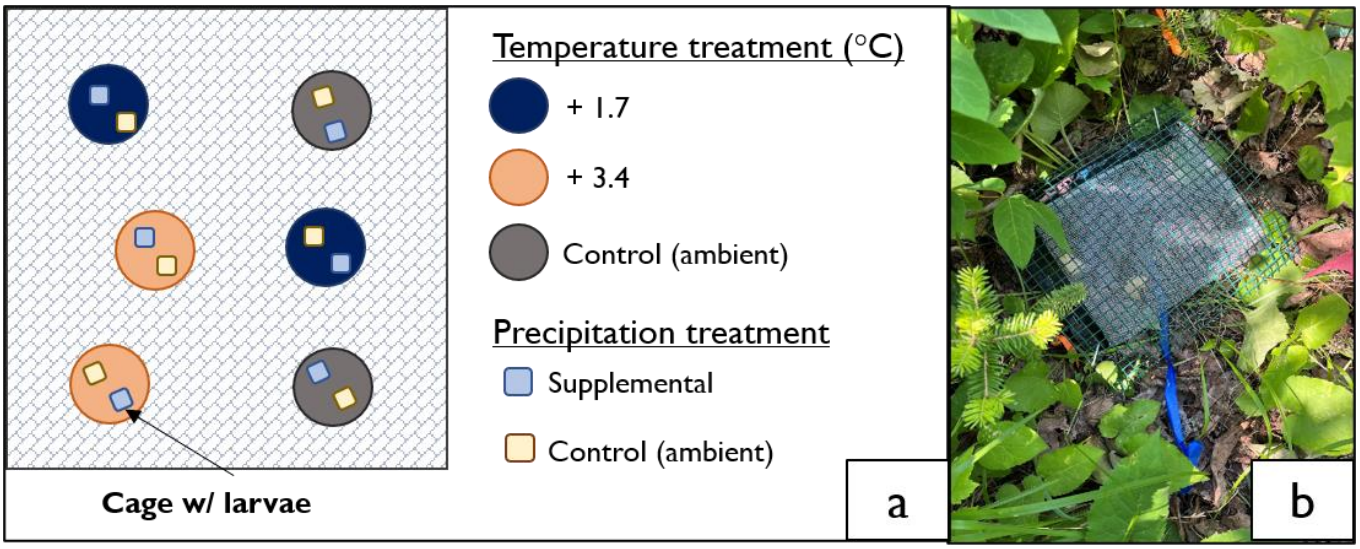

Figure 2: a) Diagram of one experimental block. I installed two cages of spongy moth larvae per plot (figure adapted from Rich et al. 2015), b) The cage design I used to expose larvae to *E. maimaiga* resting spores in the soil (Reilly et al. 2014).

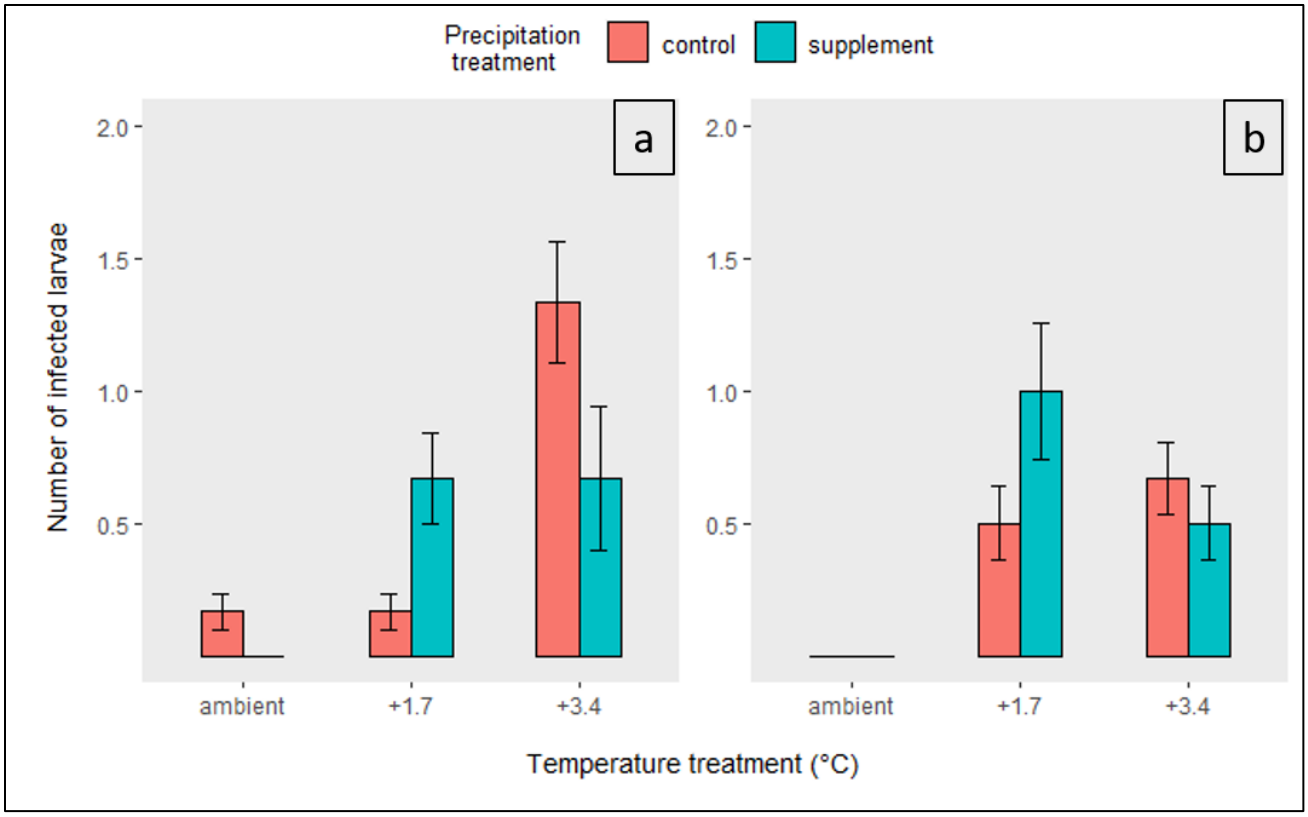

Figure 3: Effect of temperature and precipitation treatments on number of spongy moth larvae infected by *Entomophaga maimaiga* (mean ± SE) in (a) trial two and (b) trial three.

Appendices:

Appendix A1: Details on soil inoculation procedure with *Entomophaga maimaiga*

On August 20 of 2019 and 2021 I inoculated the soil at the HWRC field site for my experiment in 2022. Cadavers for the 2019 inoculation event were collected and provided by Dr. J. S. Elkinton, Univ.Massachusetts, Amherst. In 2021, I collected spongy moth cadavers filled with *E. maimaiga* resting spores from forested areas outside of Shenandoah National Park, in Madison County, Virginia.

In 2019, I first ground the cadavers in a food processor and divided the ground material into 36 equal portions (the number of cages within the study plots; 0.54 grams). I then mixed the ground cadavers for each plot with 30 g of sterile potting soil. To inoculate the soil, first I brushed aside the top layer of leaf litter and then I spread the pre-weighed soil-cadaver mixture at two randomly selected locations within each plot. Each location was marked with a flag to ensure cages with spongy moth larvae were placed at inoculation sites during the experiment.

In 2021, I sought to release a similar number of resting spores as I had in 2019. While the exact number of resting spores within a cadaver varies, especially with instar stage, but on average, there are an estimated 1×10^6 resting spores in a single late-instar spongy moth cadaver (personal correspondence, A.E.H.). To estimate the number of resting spores I released at each cage site in 2019 based on the resting spores per cadaver estimate, I first estimated the number of cadavers I had released at each plot in 2019. To do this, I used my 2021 cadaver samples, to determine the average mass of one cadaver, whereby I weighed 3 random samples of 10 spongy moth cadavers each.

With the average mass of 10 cadavers, I then estimated the mass of 1 cadaver to be 0.15 g. I then retroactively estimated the number of 2019 cadavers at each cage site as:

$$number\ of\ cadavers\ per\ cage\ site\ = \frac{mass\ of\ ground\ cadavers\ per\ cage\ site\ in\ 2019\ (g)}{average\ mass\ of\ one\ cadaver\ (g)} \quad (1)$$

where the mass of ground cadavers released per cage site was equal to 0.54 g and the average mass of one cadaver to 0.15 g. I rounded up the estimate of 3.6 cadavers released per cage site in 2019 (Eq. 1), and released 4 cadavers per cage site in 2021. With these quantities of cadavers released, I estimated the number of resting spores per cage site for each inoculation event as:

$$resting\ spore\ count = (1 \times 10^6\ resting\ spores\ ) \times number\ of\ cadavers\ per\ cage\ site \quad (2)$$

Based on this, I released approximately 3.6×10^6 and 4×10^6 resting spores at each cage site in 2019 and 2021, respectively. To complete the 2021 inoculation event, I ground 144 cadavers (4 cadavers × 36 cage sites) in a food processor, and divided the ground samples into 36 equal samples. I chose to combine the total cadavers and divide them equally, as opposed to distributing 4 cadavers per cage site because the latter approach may have biased my resting spore count if I had selected different sized cadavers for each cage site. I combined each batch of ground cadavers with 30 g sterile potting soil each and then spread the cadaver mixture at the cage sites. Therefore, the total possible number of resting spores added to soil at each cage site by the year 2022 was 7.6×10^6.

Appendix A2: Model selection using AIC scores

Table A2: AIC and Delata AIC scores for models with all variables retained, block removed, plot removed, and block x plot removed. Each model always included main effects of temperature (temp) and precipitation (precip), and a temperature × precipitation effect. For both the second and third trials, a model with main effects of block, temperature, precipitation and an interactive effect of temperature × precipitation, but without a random effect of plot, met the three model selection criteria of—(1) the fewest variables were dropped, (2) the model was not overparametrized, and (3) the delta AIC score < 2.

Trial 2

Model	**AIC**	**delta AIC**	**overparameterized**
temp, precip, temp × precip, block, plot	76.7	3.353	yes
temp, precip, temp × precip, block	75.3	1.953	no
temp, precip, temp × precip, plot	74.745	1.398	yes
temp, precip, temp × precip	73.347	0	no

Trial 3

Model	**AIC**	**delta AIC**	**overparameterized**
temp, precip, temp × precip, block, plot	67.6	2	yes
temp, precip, temp × precip, block	66.412	0.812	no
temp, precip, temp × precip, plot	65.6	0	yes
temp, precip, temp × precip	66.076	0.476	no

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Chapter 3. Spatiotemporal variability in weather and snow depth affects the invasive spread of a nonnative forest pest

Abstract

Few studies have examined the effects of yearly variation in weather conditions on rates of invasive spread or how these effects vary geographically. Along the southern range edge of the spongy moth (*Lymantria dispar* L.), a nonnative forest pest in northeastern North America, range contractions have occurred in locations with higher frequencies of supraoptimal temperatures during the larval stage. However, the potential for weather to contribute to spatiotemporal variation in rates of invasion by the spongy moth is largely unknown. In this study, I examined the effects of annual variation in temperature and precipitation during the springtime larval period, and minimum temperature and snow depth during the overwintering egg stage, on rates of spread (km yr^{-1}) of the spongy moth in five ecoregions. I also assessed the responses of two key mechanisms that underlie invasive spread—population growth and Allee effects in range-edge populations. I used extensive spatiotemporal data on spongy moth abundances and spread rates, coupled with weather data, for the period of 1990-2020. The effects of weather and snow depth on spongy moth spread and population growth rates in each ecoregion were examined using generalized additive models. I found that the responses of population growth and spread rate to the same abiotic variable were usually different and varied by ecoregion. For example, I found negative relationships between precipitation and population growth rates, which is consistent with the hypothesis that increasing precipitation would reduce growth rates due to increased larval infections by the fungal-pathogen *E. maimaiga*, whereas spread rates generally increased with increasing precipitation results for spread suggest effects of weather on dispersal. Using localized polynomial regression to determine how abiotic conditions altered Allee effects I found that abiotic conditions seemed to influence Allee effects and other forms of density dependence. For example, in the coldest and northernmost ecoregion, Allee effects were present during years when snow depth was above-average, and there were other density dependent responses of population growth for below- and near-average snow depth. The results suggest that fluctuations in density-dependent processes in response to annual changes in weather may be an important factor contributing to spatiotemporal variability in rates of invasive spread. Annual variability in weather may have previously unrealized effects on the temporal dynamics of invasive spread, such as the potential for increased rates of spread when an Allee effect is present.

Introduction

Anthropogenic global change is altering species' distributions worldwide (Parmesan & Yohe 2003). This redistribution often occurs through human-mediated movement of nonnative species. The ability of a nonnative species to spread and expand its range, i.e., to become invasive, is a function of population growth and dispersal ability (Fisher 1937; Skellam 1951). However, abiotic and biotic barriers such as unsuitable climate or interspecific interactions can interfere with both growth and dispersal, and ultimately, range expansion (Gaston 2003). Of these factors, climate has long been considered one of the primary forces that limit species' geographical distributions (Merriam 1894; Hutchinson 1918; Jeffree & Jeffree 1994). When predicting the potential range limits and rates of spread for an invasive species, ecologists have often assumed static environmental gradients (Parmesan et al. 2005). Recent theory, however, suggests that temporal variability in the environment may affect species' range expansion through effects on population growth rates of range-edge populations (Holt et al. 2022), but there remains little empirical evidence.

Range-edge populations are the primary providers of propagule pressure for future dispersal events that may lead to range expansion (Keitt et al. 2001). However, these populations almost always begin at low densities, which makes them more susceptible to extinction or decrease in abundance from phenomena such as demographic and environmental stochasticity (Lande 1988) and the Allee effect (Allee et al. 1949). A demographic Allee effect is defined as a positive relationship between population growth rate and density, such that a population's per-capita growth rate is reduced at low densities (Stephens, Sutherland & Freckleton 1999). As one of the most important demographic processes that can cause negative population growth rates (Courchamp et al. 1999; Drake 2004), a demographic Allee effect may also reduce rates of spread and inhibit invasion success (Lewis & Kareiva 1993, Keitt et al. 2001). A severe

demographic Allee effect can lead to an Allee threshold, a population density below which a population will exhibit negative per-capita growth rates, leading towards deterministic extinction (Odum & Allee 1954, Taylor & Hastings 2005). Recent theory demonstrated that a diverse family of Allee effects are possible beyond the well-known weak and strong Allee effects (Fadai et al. 2020; Fadai & Simpson 2020). Fadai & Simpson (2020) state that these previously unreported Allee effects can display multiple equilibria and stabilities, depending on whether a threshold density is present at which a population displays altered patterns of growth (Frankham 1995; Rossingnol et al. 1999; Metzger & Décamps 1997). Temporal variability in climatic conditions along the invasion front may affect the susceptibility of range-edge populations to Allee effects, with susceptibility increasing during periods of unsuitable climate because lowered population growth rates could cause weak Allee effects to become strong if populations drop below their Allee threshold, but this concept is largely unexplored.

For this study I used the spongy moth (*Lymantria dispar* (L.)), a nonnative forest pest, as a model study system to investigate how temporal variation in abiotic conditions affect invasive spread. The spongy moth is an ideal system for this research because there exists an unparalleled dataset from the "Slow the Spread" (STS) program (Tobin & Blackburn 2008) on annual fluctuations in spongy moth range-edge population abundances. Empirical evidence such as this is scarce, mainly because data on low-density range-edge populations are difficult to collect (Grayson & Johnson 2018). To track spongy moth abundances, the STS program annually deploys 60,000-100,000 pheromone-baited traps to attract male moths along the spongy moth's range edge (Sharov et al. 2002).

The spongy moth was first introduced into North America in the late 1860s near Boston, Massachusetts (Wu et al. 2015). Since this accidental release, spongy moth has spread and

established an invasive range that is over 1,000,000 km^2. The range spans as far south as the Virginia-North Carolina border, west to Minnesota, and north into southeastern Canada. Rates of spongy moth spread often vary year to year (Tobin et al. 2007b) and the presence of an Allee effect is thought to be a main cause of reduced spread rates in some years (Johnson et al. 2006b, Tobin et al. 2007a). Reduced spread rates due to an Allee effect may be influenced by environmental factors such as topography (Walter et al. 2015a) but it is unknown whether Allee effects interact with spatial or temporal variation in weather.

Spongy moth population growth and spread rates vary across space, partly due to variability in weather conditions. Larvae hatch during spring and require temperatures that are consistently between 20-25 °C for successful development (Gray et al. 2001). Along the southernmost range edge (e.g., the Virginia Coastal Plain and Piedmont regions), supraoptimal springtime temperatures occur (> 28 °C temperature; Logan et al. 1991) and have been linked to reduced rates of spread in this region (Tobin et al. 2014). Along the spongy moth's entire invasion front, Metz & Tobin (2022) found that supraoptimal temperatures in July are also linked to reduced population growth rates. Effects of temperature on the spongy moth are evident during the egg life stage as well. Overwintering eggs need low temperatures to break diapause (Gray et al. 2001), but egg mortality occurs below the supercooling point of ≈ −28 °C (Summers 1922; Doane & McManus 1981). Reduced population growth (Metz & Tobin 2022) and spread (Liebhold et al. 1992) have occurred in years when wintertime temperatures were < −18 °C and < 7 °C, respectively; however, snow cover may insulate eggs against lethal winter temperatures (e.g., Leonard 1972; Nealis et al. 1999; Streifel et al. 2019). It is unknown whether snow cover increases rates of population growth or spread.

Precipitation and moisture (e.g., humidity, soil moisture) may indirectly affect spongy moth range expansion by altering biotic interactions. Infections of spongy moth larvae by two host-specific entomopathogens—*Lymantria dispar* multicapsid nuclear polyhedrosis virus (*Ld*MNPV) and the fungus *Entomophaga maimaiga* Humber, Shimazu, and Soper—both increase with increasing precipitation (*Ld*MNPV—D'Amico & Elkinton 1995; *E. maimaiga*—Smitley et al. 1995; Siegert et al. 2008). Both *Ld*MNPV and *E. maimaiga* can collapse high-density populations, but only *E. maimaiga* can also cause high rates of mortality in low-density spongy moth populations (Hajek et al. 1990; Elkinton et al. 1991). The population dynamics of range edge populations influence whether a species' range will expand, stabilize, or contract (Sexton et al. 2009; Grayson & Johnson 2018). Thus, *E. maimaiga* may slow the invasive spread of the spongy moth if it causes epizootics in these low-density populations.

In this study I sought to understand the effects of temporal variability in abiotic conditions on annual variation in rates of invasive spread by the spongy moth. I also studied how temporal variability in the abiotic environment alters two key mechanisms that underlie invasive spread—population growth and the Allee effect in range-edge populations. I was also interested in determining if the effects of the abiotic environment differed between different climatic regions. To achieve these objectives, I investigated the effects of temperature, precipitation, and snow depth across five ecoregions on annual rates of population growth and spread by using a spatially joined dataset on moth densities and daily weather from 1990-2019. In the colder northern ecoregions of the spongy moth's range in North America, temperatures experienced by overwintering eggs are regularly below the lower critical limit for survival; therefore, I predicted that population growth and spread would increase when wintertime temperatures were above-average. Because of the potential insulating effect of snow against these cold temperatures

(Streifel et al. 2019), I expected increasing snow depth to have a positive effect on population growth and spread in the colder ecoregions. Because average spring temperatures in northern regions can be suboptimal for larval development, I expected increased population growth and spread during warmer springs. In contrast, in the warmest, southernmost ecoregion, I predicted that above-average temperatures during the larval period would negatively affect population growth and spread rates since supraoptimal temperatures are known to reduce larval survival (Thompson et al. 2017) and spread rates (Tobin et al. 2014). I anticipated that increasing precipitation would reduce population growth and spread rates due to increased *E. maimaiga* germination and infection (Smitley et al. 1995; Siegert et al. 2008) except in the northernmost ecoregions because typical temperatures may be too cold for the pathogen to readily germinate and infect (Siegert et al. 2009). Regarding Allee effects, I expected that lowered population growth rates, independent of variation in spongy moth density, could cause weak Allee effects to become strong Allee effects if population abundances dropped below the Allee threshold. Additionally, because the Allee effect tends to reduce rates of spread as its strength increases (Tobin et al. 2007a), I expected that invasion speed should be fastest for the abiotic conditions that promote high enough rates of population growth such that the Allee effect is weak or not present.

Methods

Study area

The study area was the spongy moth's invasion front, as determined by the annual STS data (i.e., the transition zone). To determine if there were regional differences in the effects of abiotic conditions, I used the Environmental Protection Agency's (EPA) Level II Ecoregions to divide the invasion front into five ecoregions—Mixed Wood Shield (MWS), Mixed Wood Plains

(MWP), Central United States Plains (CUP), Appalachian Forest (AF), and Southern United States Plains (SUP) (Fig. 1). This classification system delineates areas based on similar climate, geography, and other factors (e.g., geology, topology, vegetation) (Omernik 1987; Omernik & Griffith 2014).

Population growth and spread rates

I used the STS trap catch data from 1990-2019 to examine spatial variation in annual rates of population growth and spread. First, I converted the data on moth densities (male moths/trap) into a smooth surface of male moth densities at a 1×1-km resolution using a median indicator kriging interpolation method (Isaaks & Srivastava 1989). I excluded areas within 1.5 km of spongy moth population suppression treatments; this exclusion amounted to a small portion of the dataset being removed as STS treats <2% of the monitoring area each year (Tobin et al. 2012).

I estimated annual population growth rates from the interpolated surface of population densities. To do this, I paired each 1×1-km cell's estimate of male moth density in successive years (i.e., density in year $t - 1$ with density in year t). I then omitted any pair with density in year t or $t - 1 > 700$ male moths because pheromone-baited traps become less effective above ≈ 700 moths (Elkinton 1987). To exclude areas where populations were well established and potentially affected by negative density dependence (e.g., viral epizootics from *Lymantria dispar* multicapsid nuclear polyhedrosis virus [*Ld*MNPV]; Alalouni et al. 2013), I excluded a pair if the estimated density for a cell in year $t - 1$ was ≥ 30 male moths/trap. Lastly, I also disregarded a pair if the density in year $t - 1$ was 0. I calculated the population growth rates from year $t - 1$ to year t as:

$$growth\ rate = log_e(\frac{N_t}{N_{t-1}})$$

(1)

where N represents the interpolated density of male moths per trap.

To estimate annual spread rates of the spongy moth, I spatially delineated population isoclines from the interpolated surfaces of annual moth densities. I used an isocline of 10 moths per trap at a 1×1-km resolution to represent the range edge of the spongy moth. This so called "10-moth line" is the most stable in space and time compared with other boundary estimates (e.g., 1, 3, 30, 100, and 300) (Sharov et al. 1995, 1997). Next, I measured the annual boundary displacement between population isoclines for successive years within each ecoregion along evenly spaced (0.5°) transects (Sharov et al. 1995; Tobin et al. 2007b). The transects radiated to the 10-moth line from fixed locations that were chosen to ensure that the maximum number of transects that intersected the 10-moth line were at angles as close to 90° as possible (Tobin et al. 2007b). The coordinates of the fixed points used in the analyses are as follows: 43.6°N, −84.2°W for MWS, MWP, and CUP (Tobin et al. 2007b); 39.4°N, −76.6°W for the AF and SUP (Tobin et al. 2014) (Fig. 2). I carried out all processes for estimating spread rates using ArcGIS Pro 3.1 software.

Based on my hypotheses of factors affecting population growth and spread rates, I focused on the effects of annual abiotic conditions during the larval (spring) and egg (winter) life stages. I defined winter as December-February. For the winter period, I extracted daily values for minimum temperature and snow depth from the Parameter-elevation Regressions on Independent Slopes Model (PRISM; Daly et al. 1994) and National Snow and Ice Data Center (Broxton et al. 2019), respectively, each at a 4-km resolution.

There is considerable year-to-year variability in the timing of larval emergence due to variability in degree-day accumulation. In addition, the seasonal timing of *Entomophaga maimaiga* germination and infections is closely linked to spongy moth larval phenology (Hajek

et al. 1995; Hajek & Humber 1997). Therefore, I estimated the date range of the larval life stage (i.e., date from when 5% of eggs hatched to when 95% of a population pupated) for a given year and cell based on outputs of a temperature-driven phenology model for spongy moth (Régnière & Sharov 1997, 1998, 1999; Gray et al. 2001) using BioSIM software (Régnière 1996). For our examination of the effects of annual abiotic conditions on spread rates, I estimated the date range for the location of 10-moth isocline each year. To increase computational efficiency, for population growth rates I estimated the dates of the larval period each year based on 25% of the cells (randomly selected) within each ecoregion. Based on the estimated larval period dates for each year, I extracted the corresponding daily values for mean temperature and total precipitation from PRISM (Daly et al. 1994).

I spatially joined each estimate of population growth rate in year *t* with the nearest annual values for the larval period abiotic variables, mean temperature and total precipitation, in the same year. Because the calendar year turns over during the middle of winter and population growth and spread rates are estimated from pheromone trap catches of adult males during the summer, I spatially joined growth rate estimates in year *t* to the wintertime abiotic variables, minimum temperature and snow depth, from the winter that preceded summertime trap catch efforts.

To understand how the abiotic environment affects spread rates, I calculated mean values of each abiotic variable within a circular buffer centered at the point of intersection between each transect and the 10-moth line (Fig. 3). Abiotic conditions were estimated within buffers rather than at the points of intersection between the transects and each year's 10-moth line because individuals in spreading (or contracting) populations may experience the abiotic environment at a

variety of locations over the course of a year. I set the diameter of a buffer as an ecoregion's average annual displacement distance (km) of the 10-moth line from 1990-2019.

Data analyses

Effects of weather and snow depth on spongy moth spread and population growth rates

I examined the effects of annual fluctuations in abiotic conditions on rates of population growth and spread in each ecoregion. Prior to analyzing these relationships, I used a detrending procedure to detect and account for multi-annual trends in spread and growth rates. First, I selected data cells for which there were at least 10 consecutive years of observations (Table 1). Then I detrended the time series of each variable with a 15-year cubic spline using the "dplR" package (Bunn 2008, 2010; Bunn et al. 2023). Detrending removes long-term trends (e.g., changes in climate, long-term increases in population abundances) while isolating short-term annual fluctuations (e.g., weather patterns). The procedure also decreases the potential of finding spurious relationships between predictor and explanatory variables (Yaffee & McGee 2000). This and all subsequent statistical analyses were carried out in the R language, version 3.6.3 (R Core Team 2021).

Prior to assessing the influence of the abiotic environment on annual population growth and spread rates, I prewhitened the growth rate and spread rate time series for each location to remove temporal autocorrelation. To prewhiten, I fit an autoregressive moving average (ARMA) model to each response time series using the 'arima' function. Following Ives et al. (2010), I used ARMA models with $p = q$, where p is the order of the autoregressive component of the model and q is the order of the moving average component, to control for measurement error. To choose p and q, I selected values that minimized Akaike's Information Criterion (AIC). I then confirmed that the residuals from the ARMA model were not temporally autocorrelated. I

considered models with p and q values that ranged from 0-4 for analyses of spread rates. For the population growth rate analyses, I considered models with p and q values between 0-8 because temporal autocorrelation often persisted with lower-order models (i.e., 0-4). I extracted the residual time series from the ARMA models to use in our subsequent analyses.

I examined the relationships between the abiotic variables and detrended and prewhitened rates of population growth and spread using generalized additive models (GAMs; Hastie & Tibshirani 1990; Wood 2017). GAMs allow for consideration of nonlinear relationships, which often exist between environmental variables and population growth rates (Haynes et al. 2018). I examined how population growth and spread in year t were affected by abiotic conditions in year t. Specifically, I assessed how the response variables were affected by 1) annual minimum temperature and snow depth during winter (December-February) and 2) annual mean temperature and precipitation during the larval life stage (dates differed among years based on BioSIM phenological model estimates). I evaluated these effects for all available years for each of the five ecoregions (AF, SUP, CUP, MWS, and MWP; Table 1). In addition to temperature, precipitation, and snow depth, I included the total area of defoliation (km^2) that occurred 50-100 km from the range edge in year t as a covariate. Defoliated area is a useful proxy for spongy moth population densities (Johnson et al. 2006a; Bjørnstad et al. 2010; Haynes et al. 2012). Inclusion of defoliation allowed us to account for potential effects of spongy moth outbreaks within already infested areas, as individuals dispersing from outbreak events may enhance spongy moth population growth and spread at the range edge (Walter et al. 2015b). For each model, I assessed the degree of concurvity (i.e., a generalized version of collinearity for nonlinear relationships) and removed predictor variables if concurvity exceeded 0.6 (Schimek 2009). To reduce the likelihood of overfitting, I followed the approach of Walter et al. (2016) and

increased the penalty on spline degrees of freedom recommended by Kim & Gu (2004) to 2.8. Following combined approaches from Wood & Augustin (2002) and Wood (2017), I removed variables from the full model if 1) the 95% confidence region of a spline overlapped zero across all values of the predictor variable and 2) taking out a predictor variable lowered the overall generalized cross validation (GCV) score of the model. The GAMs were implemented using the "mgcv" package (Wood 2017).

Spatial autocorrelation is known to be present in spongy moth population growth and spread rates (Walter et al. 2016; Metz & Tobin 2022). To account for spatial autocorrelation, I integrated an approach typically applied to centered conditional autoregressive (CAR) models (Besag 1972; Caragea & Kaiser 2009; Crase et al. 2012) into our GAMs. For this approach, I first fit a GAM and calculated autocovariate (*ac*) values from the model residuals. The *ac* value represents how similar the value of the response variable is at a given location with its values at nearby locations. I then reran the GAM with *ac* included as an additional predictor variable (Crase et al. 2012). Traditionally, the response variable values were used for the calculation of *ac*, but this approach usually leads to biased model outputs due to underestimated effects of explanatory variables (Dormann 2007; Dormann et al. 2007). By calculating the *ac* value from the model residuals, this bias is eliminated (Crase et al. 2012). I calculated the *ac* for each ecoregion using the 'autocov_dist' function from the 'spdep' package (Bivand et al. 2022).

Allee effect

I examined the effects of abiotic conditions on the Allee effect in range-edge populations using a protocol developed by Tobin et al. (2007a) and Walter et al. (2020). First, I grouped cell pairs into sequential density categories (bins) based on density estimates (male moths/trap) in year $t - 1$. Bins were in intervals of one moth (i.e., $0 < N_{t-1} \leq 1$, $1 < N_{t-1} \leq 2$, etc.) (Walter et al.

2020). Within each bin I calculated the population replacement rate as the proportion of cells where $N_t \geq N_{t-1}$ and defined the Allee threshold as the density at which the population replacement rate = 0.5 (Tobin et al. 2007a).

To investigate whether the strength of the Allee effect may be altered by annual variability in abiotic conditions in year *t*, I categorized each annual value of an abiotic variable as near-, above-, or below-average. A value was deemed above- or below-average if it deviated 0.5 standard deviations (SDs) above or below the variable's long-term mean over 1990-2019, respectively. A value was considered near-average if it was within 0.5 SDs of the long-term mean. For each ecoregion, I then determined the relationship between the population replacement rate from year $t - 1$ to year *t* and moth density (for densities ranging from 1-700) using locally weighted polynomial regression (Fan & Gijbels 1996). I estimated the relationship for years with below-, near-, or above-average values of each abiotic variable. I assessed the presence/absence of Allee effects (i.e., positive relationships between the population replacement rate and density in year $t - 1$ at low densities) and whether Allee effects were weak or strong.

Results

Population growth rates

GAM analyses revealed relationships between population growth rates in year *t* and detrended weather and snow depth anomalies during year *t* that varied by ecoregion. Based on model selection criteria, I did not retain defoliation in year *t* in final GAMs for any of the ecoregions. Based on spline correlograms from the model residuals, I saw that inclusion of the autocovariate (*ac*) value substantially reduced spatial autocorrelation compared to models without the term (Appendix A1).

In the southernmost and warmest ecoregion of our study area, the Southeastern USA Plains (SUP), I found a positive linear relationship between mean temperature during the larval period and population growth rate (Fig. 4a). Precipitation during the larval period also had a positive effect on population growth rates, but the trend was slightly weaker (Fig. 4b). The relationship between wintertime minimum temperature and population growth rate was hump-shaped, with the highest growth present when temperature anomalies were near-average (Fig. 4c). Growth rate decreased with increasing wintertime snow depth between anomalies of −2000-3000 mm, but remained roughly constant for snow depth anomalies > 3000 m (Fig. 4d).

In the Appalachian Forest (AF), the relationship between mean temperature during the larval period and population growth rate was roughly hump-shaped, peaking near −1 °C (Fig. 4e). Population growth rates were depressed when larval period temperature anomalies were < −1.5 °C or > 1.5 °C. I found a highly nonlinear relationship between wintertime minimum temperature and population growth rate (Fig. 4f). I found a positive effect of snow depth on population growth rate; the trend was strongest when anomalies were > 5,000 mm (Fig. 4g).

In the Central USA Plains (CUP) ecoregion, larval period mean temperature had a hump-shaped relationship with population growth rate, with the highest rates of growth present when temperature anomalies were 0-1 °C (Fig. 4h). I found a nonlinear but generally negative relationship between population growth rate and precipitation during the larval period (Fig. 4i). Population growth rates decreased as wintertime minimum temperature anomalies warmed from −4 °C to 0 °C but were stable in years when anomalies were > 0 °C (Fig. 4j).

In the Mixed Wood Plains (MWP) ecoregion there was a hump-shaped relationship between mean temperature during the larval period and population growth rate. The highest rates of growth occurred when temperature anomalies were slightly above-average (~ 1 °C) (Fig. 4k).

Precipitation during the larval period had a weak negative effect on population growth rate (Fig. 4l). Increasing wintertime minimum temperature had a slight, positive effect on population growth (Fig. 4m). Snow depth had a negative effect on population growth rate (Fig. 4n).

For the coldest and most northern ecoregion, the MWS, I found that larval period mean temperature had a highly nonlinear effect on rates of population growth (Fig. 4o). However, the effect of increasing temperature was largely positive as there was a clear increase in population growth rate when temperature anomalies exceeded 1 °C and a sharp decline in growth when anomalies were < −1 °C. Population growth rates increased when precipitation anomalies were < −100 mm but was largely unaffected for other amounts of precipitation (Fig. 4p). Population growth rates increased with increasing wintertime minimum temperature anomalies but were slightly depressed during years when anomalies were > 1 °C (Fig. 4q). Increasing snow depth generally had a negative effect on population growth rates (Fig. 4r).

Allee effect

In the Southeastern USA Plains (SUP), replacement rates were generally below the Allee threshold (i.e., population replacement proportion below 0.5), the most prominent exception occurring at abundances near 200 moths under below-average snow depth, where it appears that the Allee threshold was crossed (Fig. 5d). There was likely a strong Allee effect when wintertime minimum temperatures were above-average based on the presence of an Allee threshold (Fig. 5c). For this abiotic condition, the Allee threshold occurred at ~80 moths. Similarly, it is possible, that an Allee effect occurred when precipitation during the larval period was below-average given the apparently positive slope in the relationship between moth density and the population replacement rate for moth densities between 50 and 100 moths/trap (Fig. 5b). Under near-average values for each of the four abiotic variables considered, I found negative density

dependence at the lowest densities, positive density dependence at intermediate densities, and replacement rates consistently below the Allee threshold, a pattern consistent with a type of Allee effect that Fadai & Simpson (2020) refer to as the 'extinction regime'.

In the Appalachian Forest (AF), an Allee effect was evident when wintertime minimum temperatures were below-average (Fig. 5g). Below-average snow depth (Fig. 5h), below-average precipitation during the larval period (Fig. 5f), and above-average mean temperature during the larval period (Fig. 5e) may also have generated Allee effects, though the presence of positive density dependence at low densities is uncertain based on the confidence intervals. In all cases, because the confidence intervals for the estimated population replacement rates overlapped the Allee threshold at a density of zero moths, it is not clear whether the Allee effects were weak or strong.

Similar to the SUP ecoregion, in the Central USA Plains (CUP) I found that the population replacement rates were generally below the Allee threshold (0.5) (Figs. 6a-d). I did not find clear indications of Allee effects in this ecoregion. For the Mixed Wood Plains (MWP) negative density dependence was present under nearly all abiotic conditions (Fig. 6e-h). In the Mixed Wood Shield (MWS), there was a weak Allee effect when mean temperatures during the larval period were above-average (Fig. 6i). There may have been a weak Allee effect when snow depth was below-average (Fig. 6l), however, the presence of positive density dependence at low densities cannot be confirmed given the width of the confidence intervals.

Spread rates

Results from our GAM analyses on the effects of detrended weather and snow depth anomalies on spread rate in year *t* varied by ecoregion. In contrast to the population growth rate analyses, defoliation in year *t* was retained as a predictor variable in every ecoregion model

except for the SUP. Inclusion of the *ac* value as an additional model term substantially reduced spatial autocorrelation in all ecoregions (Appendix A1).

In the SUP ecoregion larval period mean temperature (Fig. 7a) and precipitation (Fig. 7b) both had nonlinear but generally positive relationships with spread rate (Fig. 7a). I found a nonlinear relationship between wintertime minimum temperature and spread rate (Fig. 7c). For this variable, the highest rates of spread occurred when temperature anomalies were either 1-1.5°C or < −2 °C; spread rate decreased when temperature anomalies were slightly below-average or exceeded 1.5 °C. The effect of snow depth on spread rate was highly nonlinear (Fig. 7d). Spread rates were highest when snow depth was near-average or well above-average (~ 5,000 mm).

In the AF ecoregion, where rates of range expansion are known to be among the highest, the relationship between mean temperature during the larval period and spread rate was hump-shaped, with the peak centered around near-average anomalies (Fig. 7e). Minimum temperature during the winter had bimodal hump-shaped relationship with spread rate. The largest peak in spread rates was centered near 1.5-2 °C and the smaller near −2 °C (Fig. 7f). I found a negative relationship between snow depth and spread rate and the effect was strongest for above-average snow depth anomalies (Fig. 7g). There was a hump-shaped relationship between defoliation and spread rate peaked at ~ 500 km^2 area defoliated (Fig. 7h).

In the CUP ecoregion, rates of spread barely changed when anomalies of larval period mean temperature were near- and slightly-above average, but when anomalies were high (> 1.5 °C) or low (< −0.5 °C), spread rates rapidly increased or were slightly depressed, respectively (Fig. 7i). Precipitation during the larval period (Fig. 7j) and increasing wintertime snow depth

(Fig. 7k) both had positive effects on spread rates. For defoliation, spread rates increased when area defoliated was 0-60 km^2, beyond this range, there was no relationship (Fig. 7l).

For the second most northerly ecoregion, the MWP, I found positive effects of larval period mean temperature (Fig. 7m) and total precipitation (Fig. 7n) on spread rates. Spread rates were elevated during years when wintertime minimum temperature anomalies were > 2 °C (Fig. 7o). Snow depth had an overall hump-shaped relationship with spread rate with fastest spread occurring when snow depth anomalies were slightly below-average (Fig. 7p). The was a sharp decrease in spread rate when snow depth anomalies were well below-average (< −5,000 mm) and slightly depressed spread when anomalies were around 5,000 mm. Spread rate decreased between 0-100 km^2 of defoliated area and dramatically increased with increasing defoliation (Fig. 7q).

In the coldest and most northerly ecoregion of the MWS, I found a shallow U-shaped relationship between larval period mean temperature and spread rate (Fig. 7r). The lowest rates of spread occurred when temperature anomalies were near-average and spread was elevated when anomalies were < −1 °C or > 1.5 °C. The relationship between wintertime minimum temperature and spread rate was strongly negative from the lowest recorded temperature anomalies to ~ 2 °C (Fig. 7s). But there was a positive effect of mean temperature on spread rate when anomalies were > 2 °C (Fig. 7s). There was a negative relationship between snow depth and spread rate (Fig. 7t). There was a U-shaped relationship between defoliated area and spread rate; spread was lowest during years when defoliated area was ~ 200 km^2 and highest when defoliated area was at its maximum (Fig. 7u).

Discussion

By leveraging unparalleled spatiotemporal data on range-edge populations, I revealed that rates of range-edge population growth and invasive spread are affected by annual variability in the abiotic environment. This is one of the first studies to demonstrate that annual variability in abiotic conditions can modify spatiotemporal patterns of invasive spread (but see Tobin et al. 2014). I also found that the presence and type of Allee effects (e.g., weak or strong Allee effects) in these populations were influenced by annual variability in abiotic conditions. To my knowledge, no prior studies have demonstrated that the presence or absence of an Allee effect may depend upon temporal fluctuations in abiotic conditions. Together, these findings highlight previously unknown relationships between temporal variability in the abiotic environment, low-density range-edge population dynamics, and spatiotemporal patterns of invasive spread.

Results show that every abiotic variable, except wintertime snow depth, had effects on population growth rate that generally aligned with my predictions (Fig. 4). I found hump-shaped relationships between larval period mean temperature and rates of growth that are consistent with intermediate temperatures being optimal in the three most central ecoregions of the spongy moth's range, the AF (Fig. 4e), CUP (Fig. 4h), and MWP (Fig. 4k). In the northernmost and coldest ecoregion, the MWS, the finding of a generally positive effect of larval period mean temperature on population growth rate (Fig. 4o) was consistent with the hypothesis that typical springtime temperatures in the colder portions of the spongy moth's range may be suboptimal for larval development and ultimately reduce population growth here. In agreement with prior knowledge that moist conditions increase larval infections by *E. maimaga* (Hajek 1999), I found negative effects of precipitation during the larval period on population growth rates in multiple

ecoregions (Figs. 4i, l, p), including the northernmost ones where I anticipated temperatures to be too cold for the fungus to persist (Siegert et al. 2009).

The positive relationship between mean temperature during the larval period on population growth that occurred in the SUP ecoregion does not align with past research that demonstrated that supraoptimal temperatures can slow larval development (Thompson et al. 2017) and that larval exposure to these temperatures have likely led to range retraction in this ecoregion (Tobin et al. 2014). This apparent discrepancy may be explained by differences in the variables and life stages examined in each study; I examined the effects of mean temperature during the larval period, whereas Tobin et al. (2014) examined the effects of hours per year during the larval and pupal stages with extreme temperatures (> 28 °C). Another possibility is that between 2010-2020, the time period that my analyses extend beyond the Tobin et al.'s (2014) study period of 1989-2010, the spongy moth has begun to adapt to warm temperatures in this ecoregion (Walter & Liebhold 2023). Multiple studies indicate that genetic traits associated with tolerance to high temperatures are more common in spongy moth populations that originate from areas with hot spring and summer temperatures, suggesting that these populations are adapting to supraoptimal temperatures (Banahene et al. 2018; Faske et al. 2019; Thompson et al. 2017, 2021).

Contrary to the expectation of a positive effect of snow depth on population growth, especially in the northern ecoregions where snow cover may insulate eggs against extreme wintertime temperatures (Madrid & Stewart 1981; Streifel et al. 2019), the relationship between snow depth and population growth was negative in all ecoregions (Fig. 4d, n, r) except the AF (Fig. 4g). A potential explanation for this result involves how the effects of snow cover were measured in prior studies compared to this study. Past studies that concluded a positive effect of

snow cover on overwintering eggs did not use *in-situ* snow depth records. Instead, the effect was inferred from the height at which eggs were oviposited, either below or above the snow line (Summers 1922; Leonard 1972; Sullivan & Wallace 1972; Nealis et al. 1999; Streifel et al. 2019; but see Andresen et al. 2001). These past studies found that eggs oviposited below the snow line had higher survival compared to those above the snow line, but overall, egg mortality remained high due to extreme wintertime temperatures. Given that minimum wintertime temperature is the likely strongest abiotic control over egg survival (Gray 2001), extreme wintertime temperatures in the MWP and MWS may reduce egg survival regardless of snow cover. In contrast, in ecoregions with milder winters such as the AF, where I found a positive relationship between snow depth and population growth, the insulating effects of snow may sufficiently insulate egg masses against extreme wintertime temperatures. To evaluate this possibility, there is a need for research examining potential interacting effects of wintertime temperatures and snow depth.

Spread rates (Fig. 5) and population growth rates (Fig. 7) often exhibited opposing responses to the same abiotic variable. This is surprising because population growth is a critical factor contributing to invasive spread (Skellam 1951). The causes of these differences are unknown, but a plausible explanation is that dispersal was influenced by abiotic conditions (Lockwood et al. 2013). For example, the consistently positive relationship between precipitation during the larval period and spread rate (Figs. 7b, j, n) might be explained by storms that not only increased precipitation but also brought strong winds that transported individuals from higher-density, more established populations to nascent colonies near and ahead of the invasion front. Supporting this possibility, Frank et al. (2013) concluded that early instar larvae from high-density populations in Michigan were likely blown across Lake Michigan to Wisconsin during storm events. Similarly, wind-aided dispersal may have contributed to the invasive spread of two

Drosophilia species, *D. suzukii* (Asplen et al. 2015) and *D. melanogaster* (Leitch et al. 2021). Additional research is needed to confirm whether the positive relationship between precipitation and spread rate is due to wind-aided dispersal during storm events, or whether the relationship is due to a different effect of precipitation.

I assumed that certain abiotic conditions would alter the strength of Allee effects by lowering population growth rates in a density-independent fashion. However, I found that annual variability in abiotic conditions seemed to alter density dependence in all ecoregions, in some cases affecting the presence or absence of Allee effects. For example, in the MWS, an Allee effect occurred during years with above-average mean temperature during the larval period (Fig. 6i). Under near- or below-average temperatures, the shapes of the population-replacement curves showed density dependence, but there was no Allee effect (Fig. 6i). Similarly, in the AF (Fig. 5g) there was an Allee effect during years with below-average snow depth and other density dependent structures when snow depth was near- or above-average.

In addition to affecting the presence or absence of Allee effects, abiotic conditions also appeared to affect the type of Allee effect. Recent theory suggests that a diverse family of Allee effects are possible (Fadai & Simpson 2020). These new types of Allee effects are thought to occur when a population exhibits a threshold effect (Frankhamm 1995; Rossingnol et al. 1999; Metzger & Décamps 1997), an abrupt switch in population growth rate at a critical density (Fadai & Simpson 2020). There are numerous mechanisms that can cause a threshold effect, such as phenotypic plasticity (Friedl & Alexander 2011; Böttger et al. 2015) and resource depletion (Hopf & Hopf 1985). Forms of density dependence found in this study mirror some of the newly proposed types of Allee effects (Fadai & Simpson 2020), suggesting that threshold effects may be present. For example, the population replacement curve for below-average snow depth in the

MWS (Fig. 6j) is similar to the 'positive tangential manifold' Allee effect described by Fadai & Simpson (2020), whereby growth rates peak at two densities below the Allee threshold. In the SUP, the population replacement curves for near-average abiotic conditions for each abiotic variable (Figs. 5a-d) are similar to those of the 'extinction regime' or 'junction point' Allee effects. Further research is needed to explore potential mechanisms that lead to different forms of the Allee effect under certain abiotic conditions.

The response of spread rate to an abiotic variable was nonlinear in almost all cases (Fig. 7). Nonlinear rates of spread always occurred in response to abiotic variables that also had density-dependent effects on population replacement rates (Figs. 5 and 6). Therefore, one possibility is that the spread dynamics of the spongy moth were altered by effects of abiotic conditions on density dependence in population growth rates. Though I did not examine effects of abiotic variables on density dependence in population growth, the effects on replacement rates may be informative. In cases where the relationship between spread rate and an abiotic variable was linear, the abiotic variable typically did not affect the density dependence of population replacement rates (e.g., precipitation in the CUP and MWP ecoregions). Alternatively, relationships between dispersal rates and some abiotic conditions may be nonlinear. Although research on this topic is limited, weather can have strong impacts on dispersal rates. For example, Kuussaari et al. (2016) found that annual variability in weather conditions explained 79-91% of between-year variation in the dispersal of the Clouded Apollo (*Parnassius Mnemosyne*) butterfly.

Theory (Lewis & Kareiva 1993; Taylor & Hastings 2005; Courchamp et al. 2008; Walter et al. 2017) and empirical studies (Johnson et al. 2006b, Tobin et al. 2007a) have shown that Allee effects in low-density populations can reduce rates of range expansion. However, I found

that spread rates were usually elevated under abiotic conditions for which an Allee effect was also present. Rates of spread in the MWS, for example, were highest when snow depth was below-average (Fig. 7t). There was an Allee effect in the MWS under below-average snow depth, but not under other snow depths (Fig. 6l). Also, in the AF ecoregion, spread rate was highest when snow depth was below-average (Fig. 7g), despite an Allee effect occurring under this abiotic condition (Fig. 5g). There was only one exception to this finding, which occurred in the SUP ecoregion, where an Allee effect was present and spread rates declined when precipitation was below-average (Fig. 5b). An Allee effect only reduced spread rates when the underlying abiotic conditions yielded generally low rates of population growth.

As demonstrated by this study, annual variability in abiotic conditions was a major factor influencing rates of range-edge population growth and rates of invasive spread. Abiotic conditions usually affected population growth and spread rates differently. These differences may have occurred due to effects of weather on dispersal (e.g., wind-aided dispersal during storms, Frank et al. 2013) and density-dependent effects of the abiotic environment on population growth. I frequently found different forms of density dependence in population replacement rates under different levels of a given abiotic variable, and that this was commonly associated with nonlinear relationships between the abiotic variable and rates of invasive spread. Alteration of density-dependent processes by annual variability in abiotic conditions may have unanticipated consequences for range expansion, such as increased spread rates even when an Allee effect is present.

Tables & Figures:

Table 1: Total number of observations and length of time series for each ecoregion.

ECOREGION	MODEL	# OBSERVATIONS	YEARS
Southeastern USA Plains	spread	1685	1990-2019
	population growth rate	9830	
Appalachian Forest	spread	2737	1990-2019
	population growth rate	13324	
Central USA Plains	spread	889	1997-2019
	population growth rate	6401	1994-2019
Mixed Wood Plains	spread	877	1997-2019
	population growth rate	10142	1994-2019
Mixed Wood Shield	spread	285	1998-2019
	population growth rate	10185	1990-2019

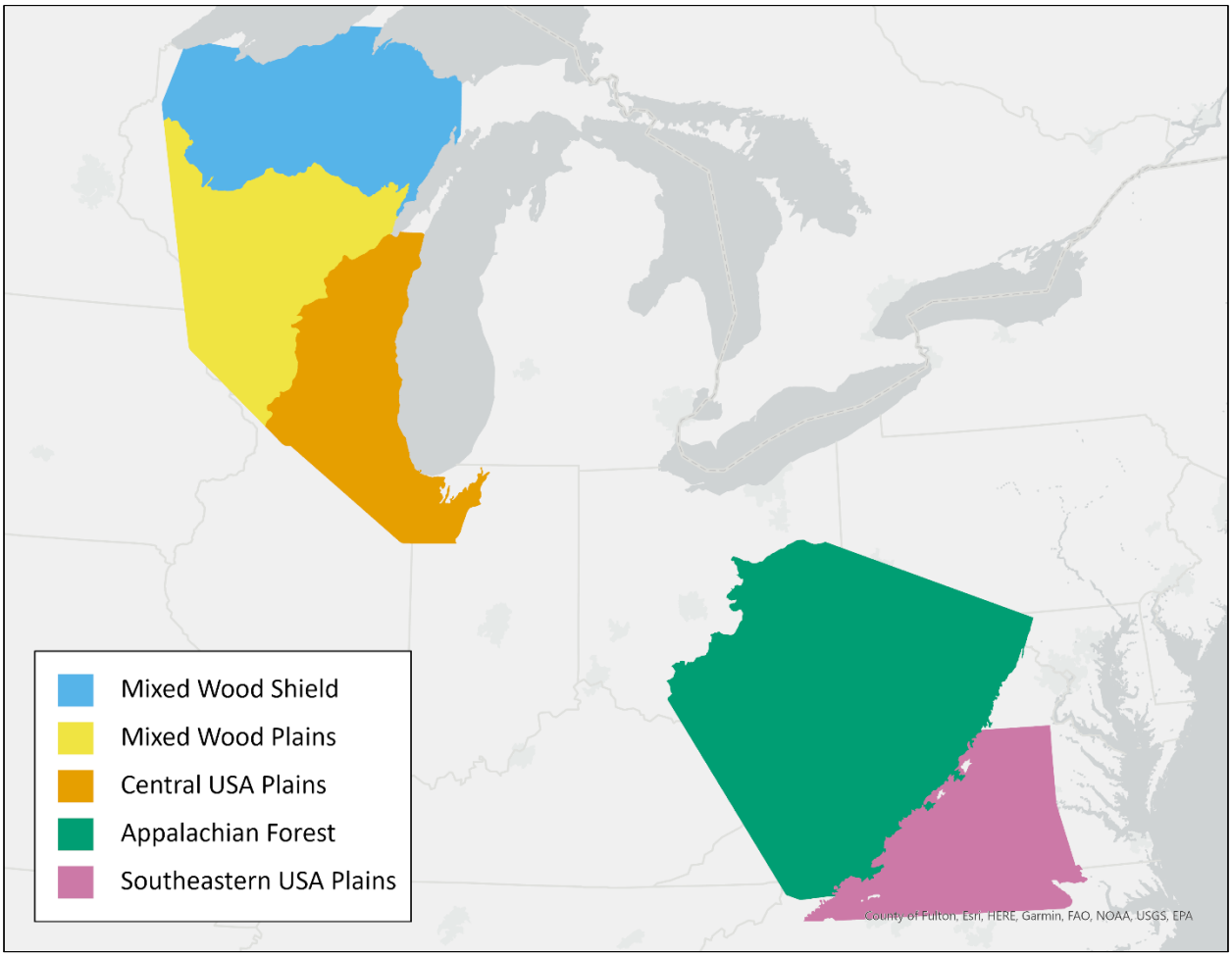

Figure 1: Map of the study area delineated with EPA Level II Ecoregions (Omernik 1987; Omernik and Griffith 2014).

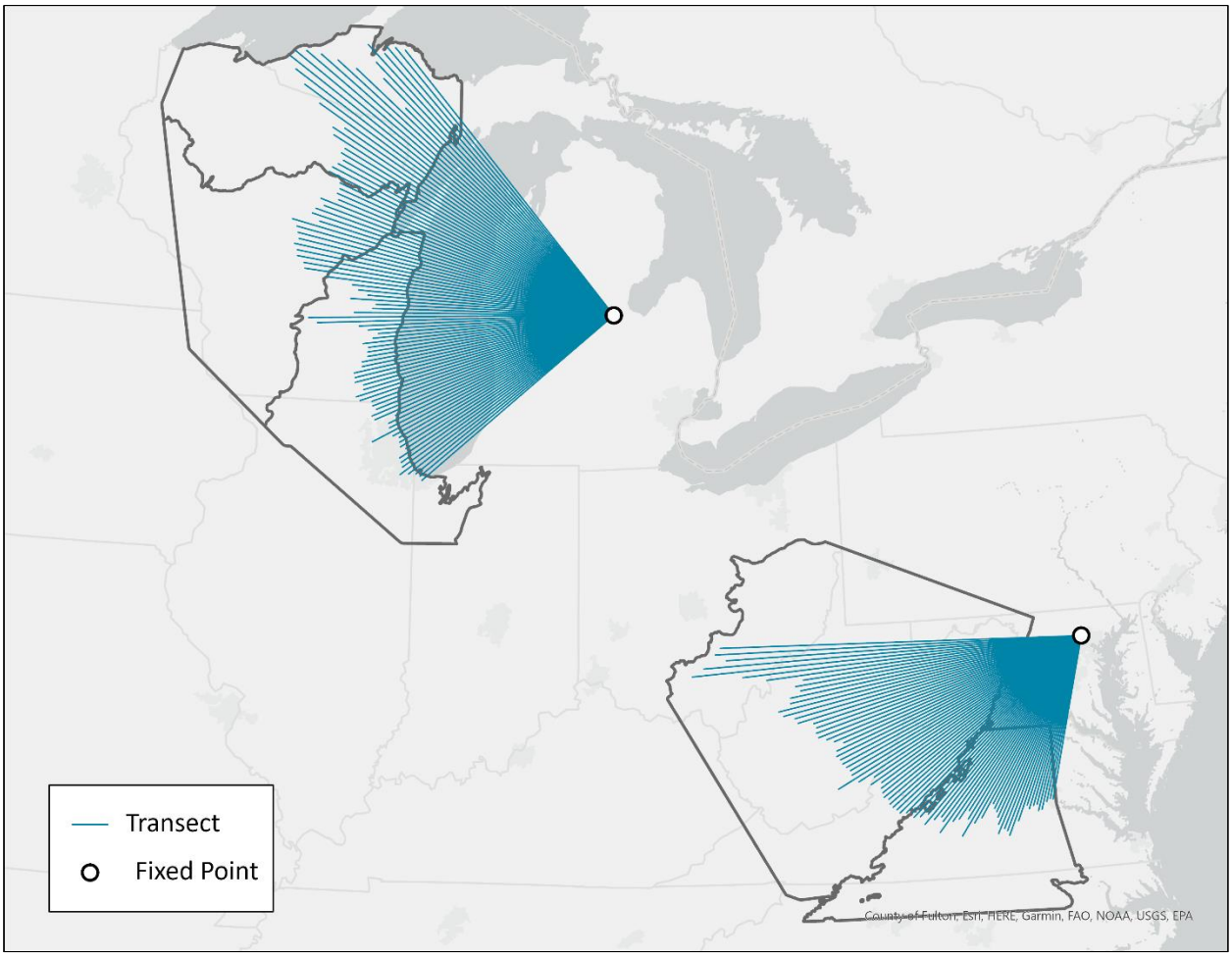

Figure 2: Evenly spaced (0.5°) transects radiating from the two fixed points used to create 10-moth isoclines for the estimation of annual spread rates. Northern point is located at: 43.6°N, −84.2°W (Tobin et al. 2007b) and southern point at: 39.4°N, −76.6°W (Tobin et al. 2014).

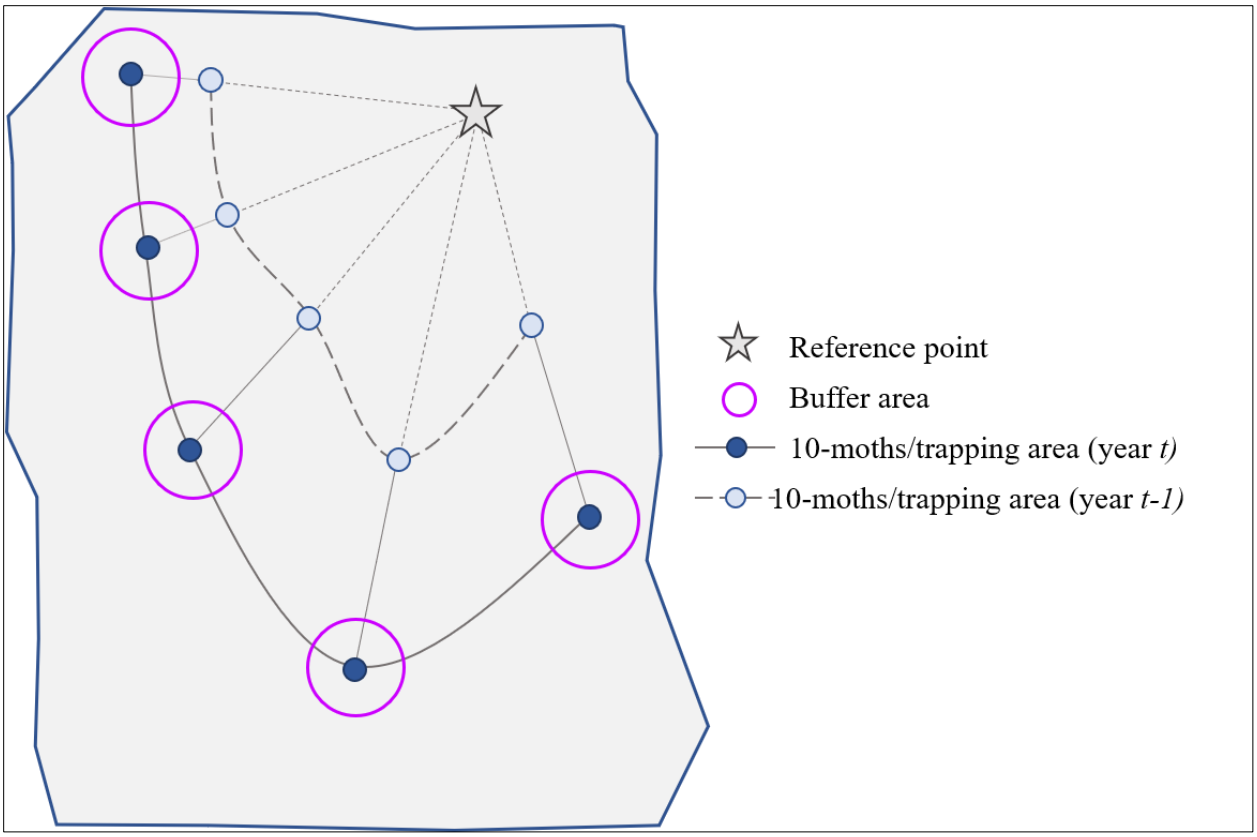

Figure 3: Diagram illustrating the areas from which data on the explanatory abiotic variables (temperature, precipitation, snow depth) was extracted. The rate of spread was estimated based on the displacement between 10-moth lines in year $t - 1$ and year t, for each transect radiating from the reference point. The mean annual value of each explanatory variable within a buffer centered at the intersection of each transect and the 10-moth line was calculated to examine the effects of weather and snow depth on rates of spread to. The buffer size was equal to the average rate of spread that occurred in an ecoregion from 1990-2019.

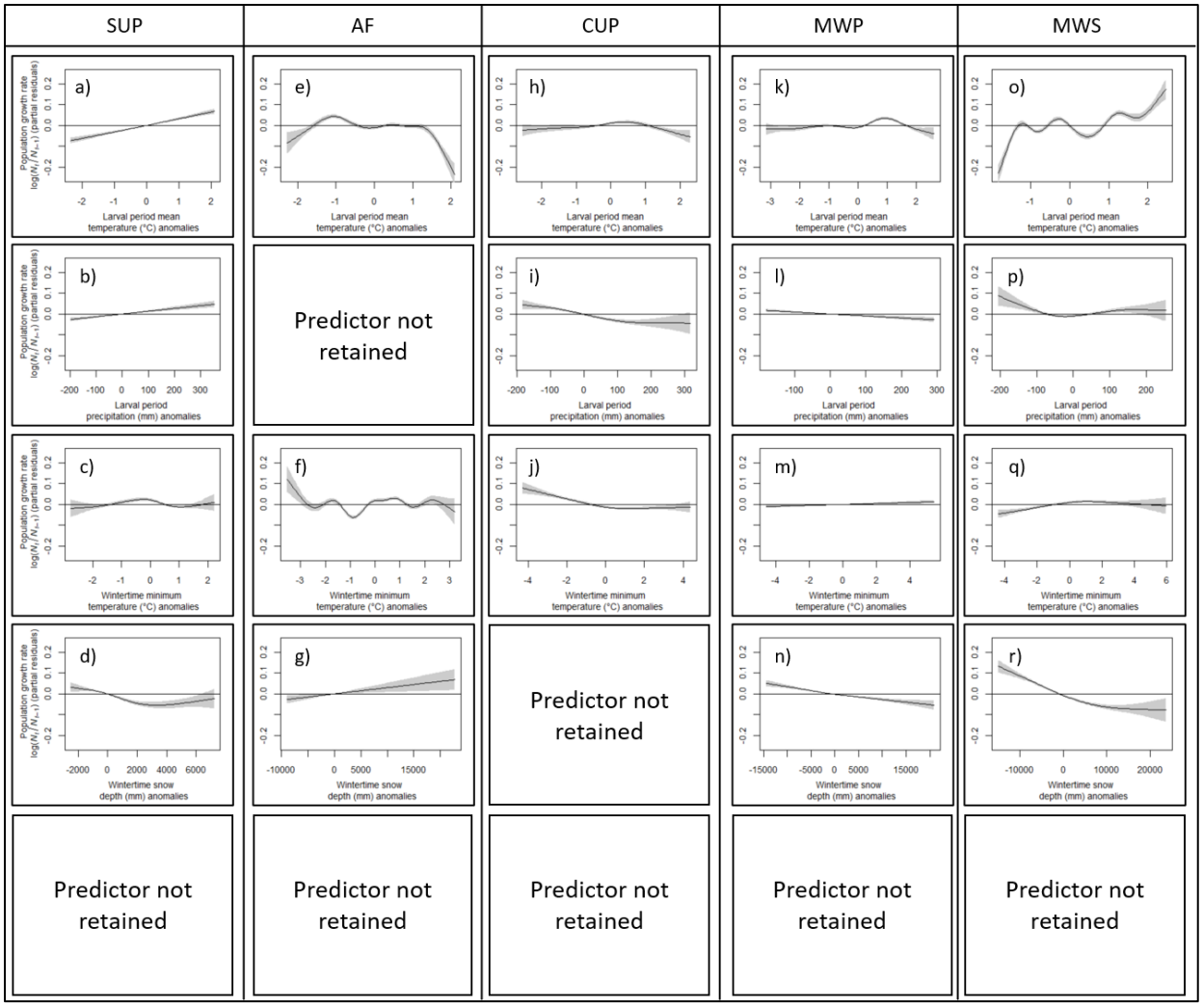

Figure 4: Fitted relationships from the Generalized Additive Models (GAMs) representing the responses of population growth rate to the abiotic variables in each of the five ecoregions. Each column represents the fitted relationship for an ecoregion—Southern USA Plains (SUP); Appalachian Forest (AF); Central USA Plains (CUP); Mixed Wood Plains (MWP); Mixed Wood Shield (MWS). The abiotic variables are represented across each row—larval period mean temperature (a, e, h, k, o) and total precipitation (b, i, l, p); wintertime minimum temperature (c, f, j, m, q) and snow depth (d, g, n, r); defoliation in year *t* (none retained).

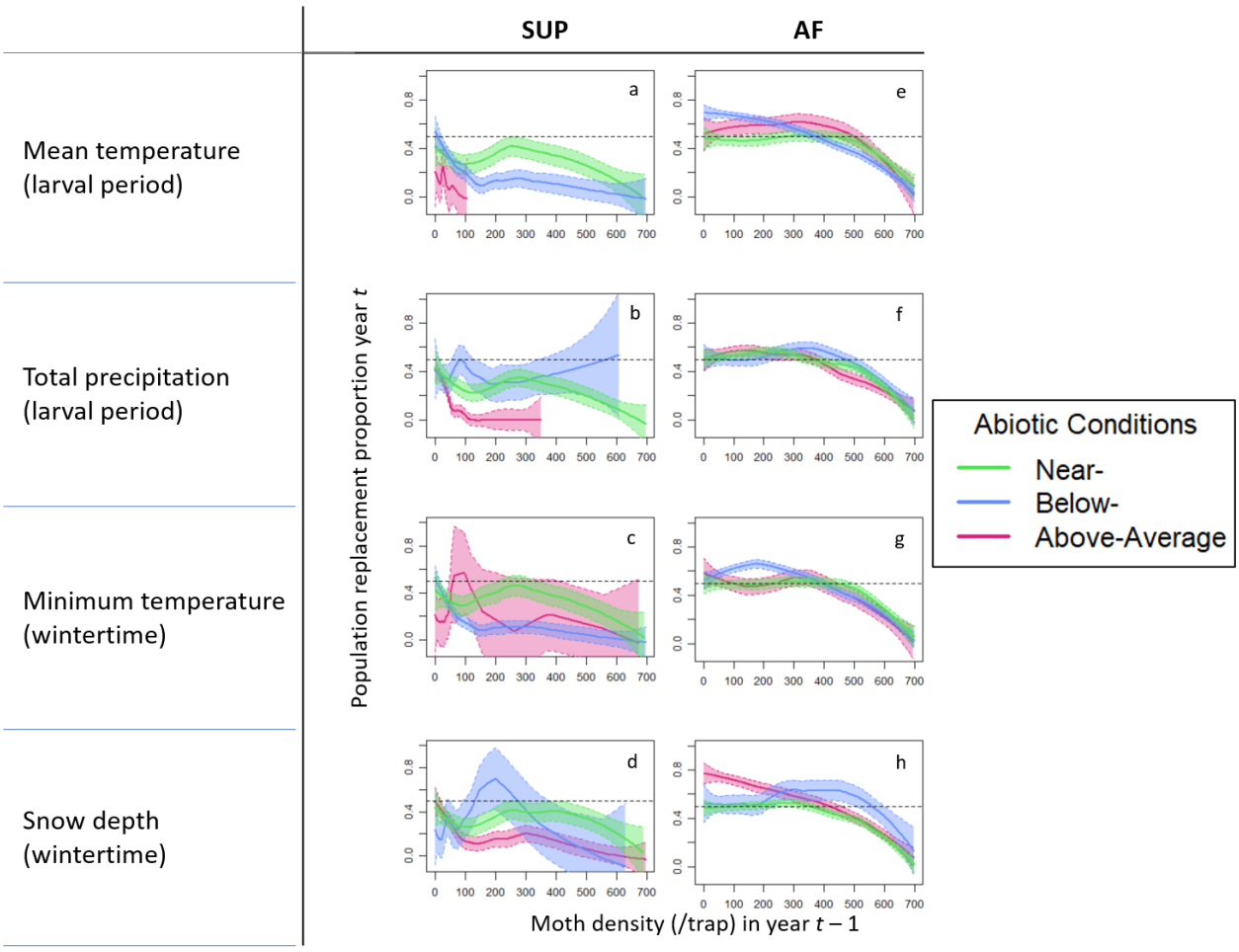

Figure 5: Relationships between population replacement rate and differences in mean temperature (a,e), total precipitation (b,f), minimum temperature (c,g), and snow depth (d,h) in the Southeastern USA Plains (SUP) and Appalachian Forest (AF). The abiotic variables were categorized as near-average (A), above-average (H), or below-average (L). A value was considered above- or below-average if it deviated 0.5 standard deviations (SDs) above or below the variable's long-term mean over 1990-2019. A value was deemed average if it was within 0.5 SDs of the long-term mean. The Allee threshold is the density at which the population growth curve intersects with a population growth rate = 0.5 (dashed horizontal line).

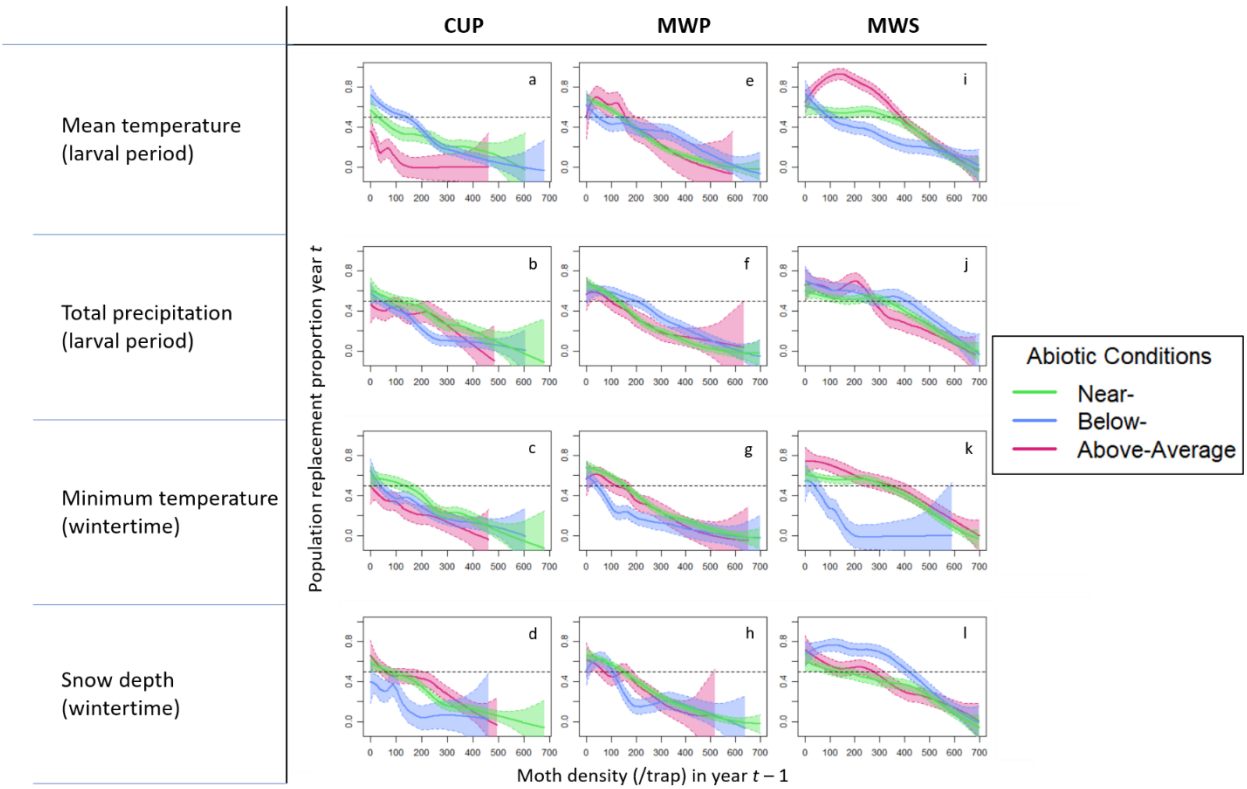

Figure 6: Relationships between population replacement rate and differences between population replacement rate and mean temperature (a,e,i), total precipitation (b,f,j), minimum temperature (c,g,k), and snow depth (d,h,l) in Central USA Plains (CUP), Mixed Wood Plains (MWP), and Mixed Wood Shield (MWS). The abiotic variables were categorized as near-average (A), above-average (H), or below-average (L). A value was considered above- or below-average if it deviated 0.5 standard deviations (SDs) above or below the variable's long-term mean over 1990-2019. A value was deemed average if it was within 0.5 SDs of the long-term mean. The Allee threshold is the density at which the population growth curve intersects with a population growth rate = 0.5 (dashed horizontal line).

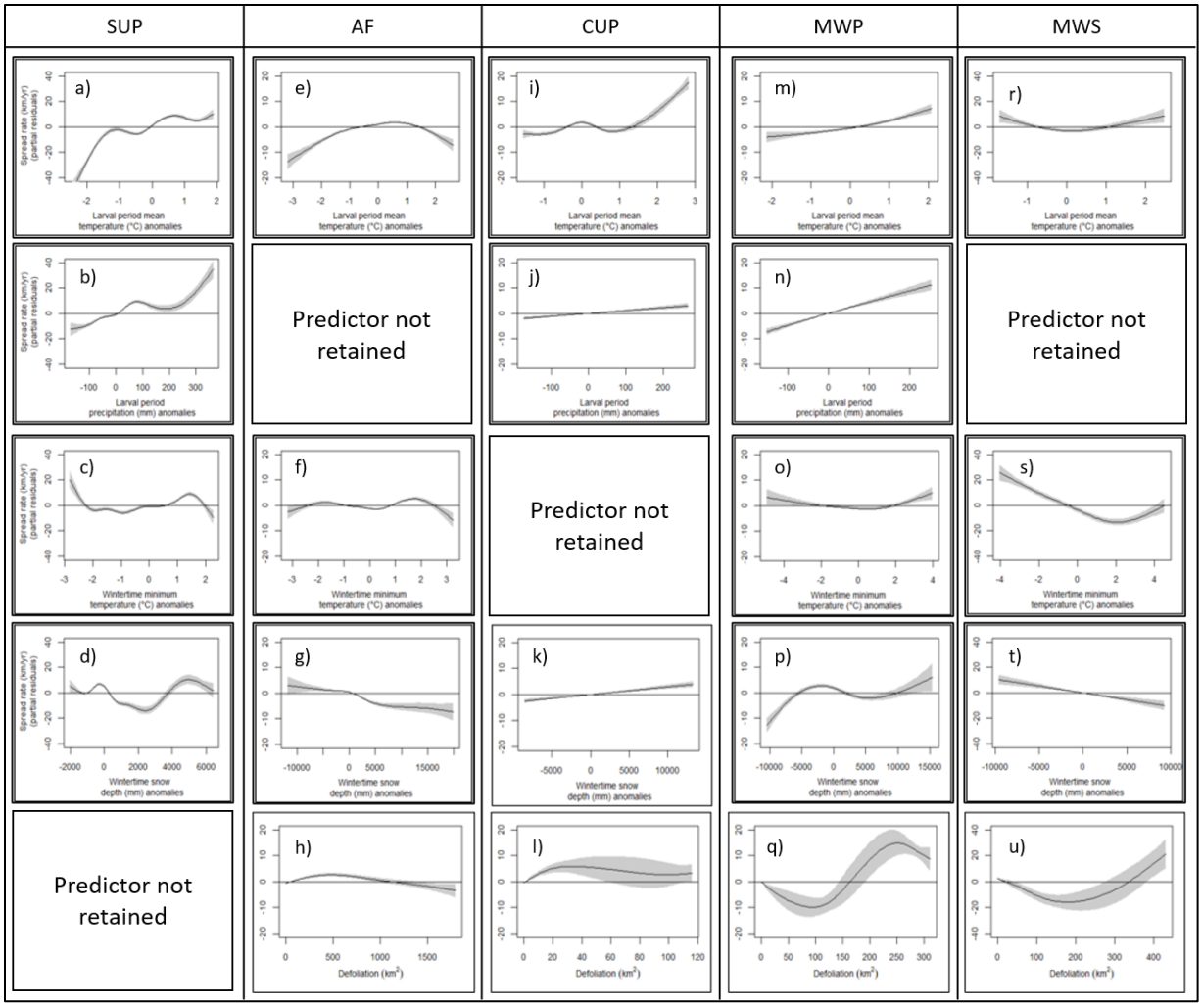

Figure 7: Fitted relationships from the Generalized Additive Models (GAMs) representing the responses of spread rate to the abiotic variables in each of the five ecoregions. Each column represents the fitted relationship for an ecoregion—Southern USA Plains (SUP); Appalachian Forest (AF); Central USA Plains (CUP); Mixed Wood Plains (MWP); Mixed Wood Shield (MWS). The abiotic variables are represented across each row—larval period mean temperature (a, e, i, m, r) and total precipitation (b, j, n); wintertime minimum temperature (c, f, o, s) and snow depth (d, g, k, p, t); defoliation in year *t* (h, l, q, u).

Appendix A1: Spatial autocorrelation in population growth and spread rates

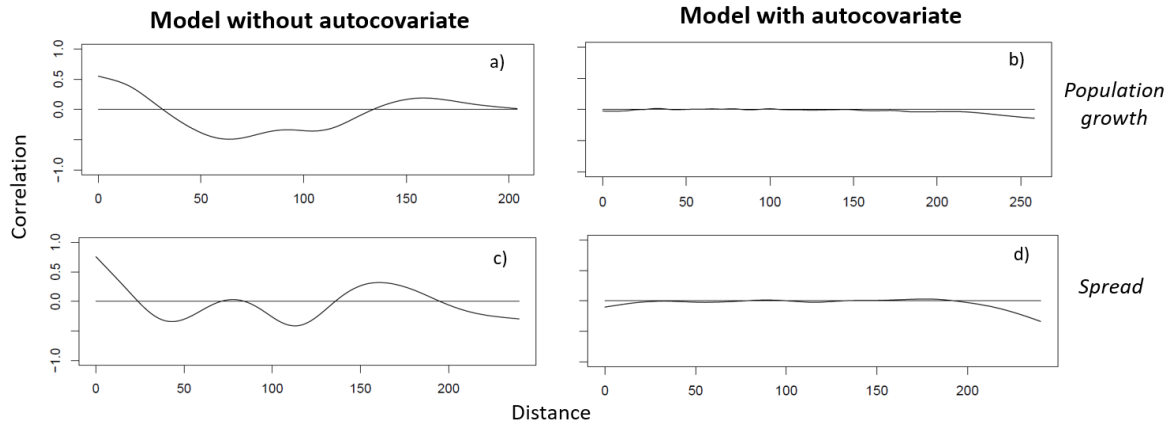

Figure A1: Spatial autocorrelation in the residuals of a generalized additive model (GAM) for spongy moth population growth (a) and spread rates (c) in the Southeastern USA Plains (SUP), assessed using a spline correlogram. Inclusion of an autocovariate value (*ac*) in each GAM effectively reduced spatial autocorrelation in the model residuals for population growth (b) and spread rate (d). These plots represent one year of data but similar results were obtained for nearly all years. Including *ac* in the GAMs for other ecoregions also reduced spatial autocorrelation.

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Chapter 4. Spatial synchrony in climate produces synchronized pulses in the invasive spread of a forest pest

Abstract

Isolating climate drivers of invasive spread is essential for understanding biological invasions, as well as anticipating periods of high rates of spread. A possible driver of variability in rates of spread that is understudied is multi-annual fluctuations in climate that arise from teleconnections. In this study, I investigate whether rates of spread by the spongy moth, an invasive species in northeastern North America, are synchronized by climatic conditions at multi-annual timescales within five ecoregions spanning its invasion front. To study this, I used extensions of wavelet analysis on a robust spatiotemporal dataset of abundances of low-density populations along the range edge spatially joined to temperature, precipitation, and snow depth data for the period 1989-2019. Notably, synchrony in spread was present throughout the entire study area, but only in the northernmost and southernmost locations was synchrony explained by climate variables. Springtime precipitation drove synchrony in spread in the southernmost and warmest ecoregion, and wintertime snow depth in the northernmost and coldest ecoregion. I also found that teleconnections were responsible for synchrony in the climate variables that drove synchrony in spread in these ecoregions. Invasive spread that is synchronized at regional scales may be difficult to manage because resources to combat spread must be distributed to many locations at one time. Possibly alleviating some of these difficulties, land managers could use meteorological forecasts of the phases and strength of teleconnections to anticipate where and when synchronized spread may occur. This is likely the first study to investigate effects of climate on synchrony of spread, therefore it is necessary for future investigations to assess whether this relationship is common throughout nature.

Introduction

Broad-scale climate patterns can create widespread, synchronous fluctuations in the abundances of animals (Elton 1924). P.A.P Moran developed a theory about the cause of this phenomenon, when he postulated that synchronized fluctuations in densities of locally regulated populations can reflect the synchrony of a widespread environmental disturbance (e.g., climate) (Moran 1953). This phenomenon, termed the Moran effect, has become fundamental to the study of population spatial synchrony, defined as spatially disjunct fluctuations in population growth or abundances that are correlated through time (Bjørnstad et al. 1999). There are two other main causes of spatial synchrony, dispersal and trophic interactions (Bjørnstad et al. 1999), but the Moran effect is thought to be the primary mechanism (Moran 1953; Ranta et al. 1997; Koenig 2002; Liebhold et al. 2004; Royama 2012; Koenig & Liebhold 2016). Population spatial synchrony can have important ecological implications. For example, spatially synchronous abundances of pest species may cause more destructive and widespread outbreaks, with the potential to have ecosystem-wide impacts (de Valpine et al. 2010; Liebhold et al. 2012). Much less is known, however, about the pervasiveness or drivers of spatial synchrony in rates of range expansion or contraction. Just as regionalized outbreaks of pests are more concerning from a management perspective than localized ones (Liebhold et al. 2012), high spatial synchrony in invasive spread over large areas would be more difficult to manage because resources would be strained during a widespread pulse in spread.

The strength of population synchrony can be timescale-specific, meaning that the abundances of populations fluctuate in synchrony with each other more strongly at timescales (equivalently, frequencies; timescale is 1/frequency) associated with specific periods of fluctuation and are asynchronous at other timescales (Keitt 2008). Climatic synchrony is generally timescale-specific and causes population synchrony at the same timescales. This

phenomenon has been observed in many organisms, such as deer (Anderson et al. 2021), phytoplankton (Sheppard et al. 2019), kelp (Castaroni et al. 2022), and agricultural (Sheppard et al. 2016; Walter et al. 2020) and forest pest species (Haynes et al. 2019). These results imply that population growth rates are synchronized in a timescale-specific manner. Rates of population growth are an important determinant of the rates of range expansion and contraction (Skellam 1951). Despite this well-established relationship, it is unknown whether rates of range expansion (e.g., invasive spread) are synchronized in a similar fashion.

The fact that extensive spatiotemporal data on population abundances, especially for low-density populations, are notoriously difficult to gather (Grayson & Johnson 2018) may explain why the spatial synchrony of range expansion and contraction is understudied. The low-density populations that are present along the outer range limits of a species provide a large fraction of the propagules for range expansion events (Lockwood et al. 2013). Therefore, population dynamics along the range edge strongly influence whether the species' range will expand, stabilize, or contract (Sexton et al. 2009).

The invasive spongy moth (*Lymantria dispar* L.) in North America is an ideal organism for studying spatial synchrony in spread. This damaging forest pest has been extensively monitored since its original introduction from Europe to North America in the late 1860s (Tobin et al. 2012; Wu et al. 2015). Since 2000, the Slow the Spread (STS) Program has tracked spongy moth abundances along the invasion front by deploying 60,000-100,000 pheromone-baited traps annually (Sharov et al. 2002; Tobin et al. 2012). Specifically, managers deploy the traps across the 'transition zone', a ~170 km wide swath of land along the spongy moth's range edge, including areas that have been recently infested and areas still unoccupied the pest (Sharov et al.

2002). The traps are deployed in a grid, with a standard trap density of 1 trap per 10.4 km^2 in rural areas and 2.6 km^2 in towns and cities (United States Department of Agriculture 2009).

The spongy moth exhibits periodicity in rates of spread, with pulses in spread occurring roughly every 4 years (Johnson et al. 2006b). Theory indicates that stratified diffusion combined with a strong Allee effect can create these patterns of spread (Johnson et al. 2006b). A slightly different temporal pattern of spread was observed by Walter et al. (2015) who found that pulses in spread occur every 6 years in Virginia and West Virginia, and that pulses consistently lag ≈ 1 year behind outbreaks that occurred 50-100 km behind the invasion front. This finding suggests that migrants from outbreaks may contribute to the growth of range edge populations (Walter et al. 2015). Outbreaks of the spongy moth display spatial synchrony over distances up to 1,000 km (Peltonen et al. 2002; Haynes et al. 2009), but patterns of synchrony in spread are unknown.

Rates of spongy moth spread are influenced by seasonal and annual weather conditions (Tobin et al. 2014; Chapter 3), but the effects of fluctuations in climate at longer timescales have not been investigated. Within the North American range of the spongy moth, precipitation and temperature exhibit multi-annual periodicity (Allstadt et al. 2015; Haynes et al. 2019) and can display synchrony over distances up to 2,500 km (Koenig 2002; Koenig & Liebhold 2016). Teleconnection patterns such as the El Niño-Southern Oscillation (ENSO) and the North Atlantic Oscillation (NAO) exhibit quasiperiodicity at multi-annual timescales and can affect seasonal temperature and precipitation over large geographic areas (Nigam & Baxter 2015). Sheppard et al. (2016) revealed a strong link between a teleconnection (NAO) and spatial synchrony in the timing of aphid first flights at long (> 4 years) timescales. It is unknown whether timescale-specific synchrony in climate has similar impacts on the spatiotemporal dynamics of the spongy moth's invasive spread.

Here, I investigated spatial synchrony in rates of invasive spread by the spongy moth and its drivers. I evaluated the hypothesis that synchrony in the fluctuations of climate variables at multi-annual timescales leads to spatial synchrony in rates of spread at similar timescales. To achieve this objective, I examined the spatial synchrony of climatic conditions and rates of spread across five ecoregions from 1990-2019 using extensive spatiotemporal abundance and weather data. Because climate oscillations (i.e., teleconnections) create multi-annual, periodic fluctuations in weather across broad scales (Nigam & Baxter 2015), I expected that teleconnections would explain synchrony in the climate variables used for this study. I chose to focus on climate variables that prior work suggests have impacts on spongy moth survival or reproduction. In the spongy moth's North American range, temperatures in the coldest most northern ecoregions are often below critical limits for egg survival (winter) and larval development (spring). Therefore, I expected above-average temperatures during the spring or winter in these ecoregions to lead to increased rates of spread. Because snow may insulate eggs against lethal winter temperatures (Summers 1922; Streifel 2019), I predicted that spread would increase with increasing snow depth in the colder ecoregions. A past laboratory study revealed that supraoptimal temperatures can reduce larval survival (Thompson et al. 2017). In the warmest, southernmost ecoregion, temperatures that are supraoptimal for larval and pupal development (> 28 °C; Logan et al. 1991) have been linked to range retraction (Tobin et al. 2014; but see Chapter 3). Based on these findings, I predicted a negative effect of high temperatures during the larval period (springtime) on rates of spread in the warmest ecoregion of the spongy moth's range. I also examined effects of springtime precipitation because infection of larvae by the host-specific pathogen, *Entomophaga maimaiga*, increases with environmental moisture (Smitley et al. 1995; Siegert et al. 2008). In all but the northernmost ecoregions where

average temperatures may be too cold for persistence of the pathogen (Siegert et al. 2009), I anticipated that increasing precipitation would reduce spread rates due to increased *E. maiamaiga* infections. To investigate these hypotheses, I focused on four climate variables—mean temperature and precipitation during the larval period, and wintertime minimum temperature and snow depth—as potential drivers of synchrony in the spread of the spongy moth.

Methods

The study area was the STS program's transition zone. Each year the STS program moves the zone boundaries in response to expansion of contraction of the spongy moth's range edge, which lies roughly at the center of the zone. To assess how patterns of spatial synchrony in spread and climate varied across climatic regions, I used the Environmental Protection Agency's Level II Ecoregions (Omernik 1987; Omernik and Griffith 2014) to divide the invasion front into five ecoregions—Mixed Wood Shield (MWS), Mixed Wood Plains (MWP), Central United States Plains (CUP), Appalachian Forest (AF), and Southern United States Plains (SUP) (Fig. 1 in Chapter 3).

To estimate annual rates of spread, I used STS trap catch data from 1990-2020. First, I converted the data on moth densities (male moths/trap) into a smooth surface of densities at a 1 × 1-km resolution using a median indicator kriging interpolation method (Isaaks & Srivastava 1989). I excluded areas within 1.5 km of spongy moth population suppression treatments. Only a small portion of the dataset was removed because STS treats <2% of the monitoring area each year (Tobin et al. 2012). The location of the spongy moth's range edge each year was represented using a population isocline where densities were equal to 10 moths per trap. This so called "10-moth line" is the most stable in space and time compared with isoclines of other densities used

by the STS program (i.e., 1, 3, 30, 100, and 300 moths) (Sharov et al. 1995, 1997). To estimate annual rates of range expansion or contraction, I measured the boundary displacement between population isoclines for successive years within each ecoregion along evenly spaced (0.5°) transects (Sharov et al. 1995; Tobin et al. 2007). The transects radiated to the 10-moth line from fixed locations, chosen to ensure that the majority of transects intersected the 10-moth line at as close to 90° as possible (Tobin et al. 2007). The coordinates of the fixed points were: 43.6°N, −84.2°W for the MWS, MWP, and CUP (Tobin et al. 2007); 39.4°N, −76.6°W for the AF and SUP (Tobin et al. 2014) (Fig. 2 in Chapter 3). I carried out all processes for estimating spread rates using ArcGIS Pro 3.1 software.

Based on my hypotheses of abiotic environmental conditions that may affect rates of spread, I focused on spatial synchrony in climatic conditions during the larval (spring) and egg (winter) life stages. I defined winter as December-February and estimated the date range of the larval life stage for a given year and cell based on outputs of a temperature-driven phenology model for spongy moth (Régnière and Sharov 1997, 1998, 1999; Gray et al. 2001) using BioSIM software (Régnière 1996). I estimated this larval date range for the locations where the transects intersected with the 10-moth isocline each year. Based on these estimated date ranges for each year, I extracted mean temperature and total precipitation for the days within the larval period (Daly et al. 1994). These data were sourced from the Parameter-elevation Regressions on Independent Slopes Model (PRISM; Daly et al. 1994). I then calculated mean values of the larval and wintertime climatic variables within a circular buffer centered at the point of intersection between each transect and the 10-moth line (Fig. 3 in Chapter 3). The diameter of a buffer equaled each ecoregion's mean annual displacement distance (km) of the 10-moth line from 1990-2020. For the winter period, I extracted daily values for minimum temperature and snow

depth from PRISM (Daly et al. 1994) and National Snow and Ice Data Center (Broxton et al. 2019), respectively, each at a 4-km resolution. Because the calendar year turns over during the middle of winter and spread rates are estimated from pheromone trap catches of adult males during the summer, I used the values of the wintertime abiotic variables, (minimum temperature and snow depth) from the winter that preceded summertime trap catch efforts.

To understand whether synchronous multi-annual fluctuations in the climate variables can be attributed to teleconnections, I calculated mean monthly values for the North Atlantic Oscillation (NAO), the multivariate El Niño Southern Oscillation Index (MEI), and Pacific Decadal Oscillation (PDO) for the months that corresponded to the larval period and wintertime (December-February) for each ecoregion. These teleconnections were chosen because they are known to influence temperature, precipitation, and snow depth within the study area. Although the dates of the larval period fluctuate slightly from year to year, I used fixed months for each ecoregion that corresponded to the range of estimated larval periods. I ensured that the entire range of dates (across all years) of the estimated the larval periods in a given ecoregion fell within the selected months.

Statistical analyses

I used wavelet-based approaches including wavelet mean fields and spatial wavelet coherence (Sheppard et al. 2016, 2017) to examine whether multi-annual fluctuations in the climate variables—mean temperature and precipitation during the larval period, and wintertime minimum temperature and snow depth—are drivers of spatial synchrony in spread rates. To account for the possibility that periodic spongy moth outbreaks behind the invasion front contribute to synchronized fluctuations in the spread of range-edge populations, I also examined the relationship between synchrony in total area of defoliation (km^2) that occurred 50-100 km

from the range edge in year *t* (Walter et al. 2015) and the synchrony of spread. Defoliated area is a useful proxy for spongy moth population densities (Johnson et al. 2006a, Bjørnstad et al. 2010, Haynes et al. 2012). Prior to analyzing these relationships, I normalized each time series using a Box-Cox transformation (Sheppard et al. 2016). I then linearly detrended, demeaned, and standardized the variances of each time series to 1. I excluded time series <20 years in length (Table 1) because the wavelet-based approaches require relatively long time series.

I used wavelet mean fields (WMFs) to quantify patterns of spatial synchrony in spongy moth spread rates (Fig. 1 a-d; Sheppard et al. 2016). WMFs quantify the strength of synchrony as a function of time and timescale, with values near 0 representing weak synchrony and values near 1, strong synchrony. WMFs measure whether the oscillations in a set of time series tend to have aligned phases and correlated magnitudes (strengths) through time, as a function of timescale (Sheppard et al. 2016). If the phases of population oscillations are aligned, this indicates phase synchrony (phase locking in other contexts) (Rosenblum et al. 1996; Blasius et al. 1999). Perfect synchrony occurs when both the phases and abundances of the population oscillations are synchronized. To test the statistical significance of phase synchrony in spread rates, I compared magnitudes of wavelet phasor mean fields to the null hypothesis of random (i.e., unsynchronized) phases or no synchrony (Sheppard et al. 2013, 2016, 2017; Fig. 1 e-h) using the significance threshold of $P < 0.001$ (Sheppard et al. 2019).

To evaluate whether climate variables are drivers of synchronized fluctuations of spread, I examined spatial wavelet coherence between each climate variable and spread rates (Table A1; Sheppard et al. 2016, 2017). This technique reveals whether pairs of variables have phase differences and magnitudes of oscillations that are consistent through time and across space, as a function of timescale. Coherence between two variables, such as weather and population growth,

is a strong indication that the environmental variable drives synchrony in the biological variable, providing evidence of transmission of synchrony from the environment to the population (Sheppard et al. 2016). Phase differences provide information on the temporal lag between oscillations of two variables. No lag is present when variables are in-phase or synchronous with each other, and anti-phase or asynchronous dynamics occur when there is a lagged relationship. Mean phase differences ($\bar{\theta}$) are reported in fractions of π, and range from 0 (in-phase) to ±1 (anti-phase), with intermediate values representing fractional (i.e., ¼ cycle) lagged relationships. Significance testing of coherence was based on surrogate datasets that are generated by resampling the observed data such that the phase relationships are randomized away. This randomization allows for the surrogate datasets to represent a null hypothesis of no coherence, while retaining the spatial and temporal autocorrelation present within the raw data (Sheppard et al., 2016, 2017). I compared spatial coherences from 2,000 surrogate time series to spatial coherence values for the observed data for two separate timescale bands—short timescales as 2-4 year period lengths, and long timescales as > 4 year periods. These timescales were chosen because the 4-year cutoff separates cycles that are negatively lag-1 autocorrelated (short timescale) from those that are positively lag-1 autocorrelated (long timescale) (Sheppard et al. 2016). Following Walter et al. (2020), significance was tested at the $P < 0.1$ threshold due to the conservative nature of the test.

After identifying the climate variables that were coherent with rates of or spread, I built wavelet linear models to determine how much synchrony in the fluctuations of spread can be explained by synchronous, multi-annual climatic fluctuations (Table 2). Wavelet linear models can test the effects of multiple predictor variables on a response variable (Sheppard et al. 2019). I applied the wavelet Moran theorem (Sheppard et al. 2016) to quantify the percentage of

synchrony in a response variable that could be attributed to synchrony in the predictor variables. In addition, I calculated model 'cross-terms', which indicate whether the model meets the assumptions of the wavelet Moran theorem. Cross-terms must be small (<10%) for the model to meet these assumptions; large cross-terms indicate that the model erroneously captures synchrony between drivers at a given location and model residuals at other locations (Sheppard et al. 2016). Lastly, I tested for significant coherence between timescale-specific synchrony in the climate variables selected for modeling (Table 2) and climate indices representative of the teleconnections NAO, PDO, and MEI (Table S2). Climate indices are not spatially resolved, and therefore, could not be included in a wavelet linear model. To employ these wavelet methods, I used the 'wysn' package (Reuman et al. 2022) in the R language, version 3.6.3 (R Core Team 2021).

Results

Results from the WMFs showed that patterns of synchrony in spread varied considerably among ecoregions (Fig. 1a-e). See Figure 1 in Chapter 3 for a map of the ecoregions. In the SUP, strong synchrony in spread (red areas of the WMF; Fig. 1a) was present at the *c.* 2-3 year timescale band until around 2010 when synchrony became weaker at these timescales and strong at the *c. 3-4* year timescale band. At long timescales, synchrony in spread was moderate to weak (Fig. 1a). In the AF, asynchrony persisted at short timescales until about 2002, when low strength synchrony appeared at the *c.* 4-year timescale (Fig. 1b, g). Around 2005, synchrony became stronger towards shorter timescale bands, with a marked period of strong synchrony in spread from 2010-2015 at a *c.* 2-3 year timescale band (Fig. 1b). At long timescales, spread displayed strong synchrony across nearly the entire time series (Fig. 1g), most consistently so at the *c.* 7-year timescale (Fig. 1b). In the CUP, timescale-specific patterns of synchrony in spread at short

timescales somewhat resembled those in the SUP (Fig. 1a), however, synchrony was weaker (Fig. 1c) and not as consistently present across time in the CUP (Fig. 1h). At long timescales, synchrony in spread was moderately strong (green-yellow portions of the WMF; Fig 1c), and the strength of synchrony gradually increased through time. In the MWP, at both short and long timescales, there was a moderate degree of synchrony in spread that gradually became weaker over time (Fig. 1d, i). Additionally, at short timescales, synchrony decreased in frequency toward a 5-year timescale (Fig. 1d); this timescale-specific pattern of synchrony was also found in the MWS at short timescales (Fig. 1e). In the MWS, synchrony in spread was strong and persisted through time at long timescales (*c.* 5 years; Fig. 1e, j). Wavelet phasor mean fields confirmed the statistical significance of these patterns of synchrony in spread rates for most times and timescales ($P < 0.001$; Fig. 1f-j).

Patterns of synchrony for a given climate variable tended to be different in the northern (i.e., CUP, MWP, MWS) versus southern ecoregions (i.e., AF, SUP) (Fig. 2). There were some notable similarities between patterns of synchrony for the climate variables (Fig. 2) and those found for synchrony in spread rate (Fig. 1a-e). In the SUP, patterns synchrony in spread (Fig. 1a) and precipitation were similar at short timescales (Fig. 2b). In the MWS and MWP, patterns of synchrony in spread (Fig. 1d, e) were similar to synchrony in snow depth (Fig. 2p, t) at both short and long timescales. In other ecoregions and for other climate variables, spread and climate generally displayed dissimilar patterns of synchrony.

WMFs for total area defoliated (km^2) in year *t* showed strong synchrony at long timescales in all ecoregions except the CUP, and in general, the strength of synchrony was more variable at shorter timescales (Fig. A2). In the AF, patterns of synchrony in defoliation at long

timescales (Fig. A2b) resembled synchrony in spread at long timescales (Fig. 1b). In other ecoregions, patterns of synchrony in defoliation were largely dissimilar to those of spread.

Spatial wavelet coherence analysis revealed that only at short timescales (2-4 years), and in two ecoregions, the MWS and SUP, was synchrony in spread rate significantly coherent with any of the climate variables (Table 2, A1). In the warmest and most southern ecoregion, the SUP, synchrony in spread rate was nearly in-phase (as indicated by the phase difference, given in units of π radians) with precipitation during the larval period at short timescales ($P = 0.025$, $\bar{\theta} = 0.242$). Synchronous interannual fluctuations in precipitation explained 52% of synchrony in spread (Table 2). The WMF of synchrony in spread in the SUP predicted by the wavelet linear model (Fig. 3a) was most similar to the WMF of observed synchrony (Fig. 3b) at the *c*. 2-3 year timescale band from about 1995-2005. The plot of observed and predicted timescale specific synchrony across all years (i.e., mean squared synchrony; Fig. 3c) also indicated that the wavelet linear model most closely predicted synchrony in spread at *c.* 2-3 year timescales. The multi-annual synchronous fluctuations in precipitation that drove synchrony in spread were significantly coherent and in-phase with the PDO ($P = 0.027$, $\bar{\theta} = 0.0125$; Table 3).

In the MWS, the northernmost and coldest ecoregion, synchrony in spread rate was coherent with wintertime snow depth at the $P < 0.1$ significance threshold ($P = 0.057$). The mean phase difference between spread rate and snow depth across short timescales indicated an approximate quarter-cycle phase shift ($\bar{\theta} = 0.543$), which means that spread rate declined a quarter-cycle (~ 1 year) after years with increasing snow depth. Synchrony in snow depth during the wintertime explained 71% of synchrony in spread rate at short timescales (Table 2). Further, the WMF based on predictions from the wavelet linear model, showed that the model best predicted synchrony in spread at *c.* 3-4 year timescales (Fig. 3d-e). This is further confirmed by

the plot of observed and predicted mean squared synchrony (Fig. 3f). Multi-annual synchronous fluctuations in snow depth were in an anti-phase (negative) relationship with the MEI climate index ($P = 0.077$, $\bar{\theta} = -0.9315$; Table 3).

Spread rate was not coherent with climate variables in the other ecoregions (Table A1). Total area of defoliation (km^2) that occurred 50-100 km from the range edge was also not significantly related to synchrony in spread rate (Table A1).

Discussion

By leveraging an unparalleled spatiotemporal dataset on low-density populations along the outer edge of a species' range, I provide evidence of spatial synchrony in rates of invasive spread by the spongy moth, a major forest pest in North America. Although synchrony in population growth rates and abundance is ubiquitous across many taxa (Hanski & Woiwod 19993; Ranta et al. 1995; Bjørnstad et al. 1999; Hudson & Cattadori 1999; Liebhold et al. 2004), and population growth is an important component of spread (Skellam 1951), to my knowledge this is the first study to demonstrate the phenomenon of spatial synchrony for rates of spread. I also revealed that multi-annual synchronized fluctuations in climate, explained considerable portions of spatial synchrony in the rates of range expansion and contraction in two of five ecoregions (Table 2; Fig. 3), the northernmost (MWS) and southernmost ecoregions (SUP). The climate variables that explained synchrony in spread in these ecoregions were significantly coherent with teleconnection patterns (Table 3). These findings align with past studies showing that broadscale teleconnection patterns produce multi-annual, synchronized fluctuations in local climate conditions that drive population synchrony at similar timescales (Sheppard et al. 2016; Anderson et al. 2021; Castaroni et al. 2022) and, for the first time, provide evidence that climate teleconnections can influence spatiotemporal patterns of invasive spread.

Spatial synchrony in the spread of the spongy moth was present in all five ecoregions, but the timescale-specific patterns of synchrony varied among ecoregions (Fig. 1). For example, across the time periods of analyses (Table 1), there was most often strong synchrony in spread, albeit on different timescale bands, in the SUP, AF, and MWS ecoregions (Figs. 1a, b, e). Of these three ecoregions however, synchrony in spread was only significantly related to climate variables in the MWS and the SUP (Table 2; Fig. 3). In the MWS, there was a phase-lagged negative relationship between snow depth and spread, with peaks in spread that occurred ~ 1 year after periods of low snow depth (Table 2). This result is inconsistent with my prediction that spread rate would increase with increasing snow depth, based on past studies that suggested that snow cover may insulate overwintering eggs against lethal temperatures during the winter, thereby increasing their survival (Madrid & Stewart 1981; Streifel et al. 2019). It is possible that higher snow depth occurred during years when winters had more extreme cold temperatures, which possibly outweighed positive effects of snow depth on egg survival or caused snow cover to persist into the spring during larval emergence. Supporting this explanation is my finding that increased snow depth in the MWS was significantly related to lower MEI (climate index for El Niño Southern Oscillation) index values (Table 3). Smaller MEI values correspond to La Niña years and in the northern portions of the United States, La Niña years are associated with cooler than normal winter temperatures. In the MWP ecoregion, just south of the MWS, timescale-specific patterns of synchrony in spread (Fig. 1d) and snow depth (Fig. 2p) were very similar to patterns of synchrony in the MWS (Figs. 1e, 2t), but the relationship in the MWP was not statistically significant (Table A1). In Chapter 3, I found that annual variability in snow depth had a negative relationship with spread rate in the MWP and MWS. The consistently negative relationship between snow depth and spread rate across annual to multi-annual timescales

suggests that snow depth is an important determinant of spread close to the northernmost range limits of the spongy moth.

In the SUP, I found that synchronous peaks in spread were in-phase with synchronous peaks in precipitation (Table 2), which contradicts my prediction of a negative effect of precipitation on spread rate due to higher larval mortality from the fungal-pathogen *E. maimaiga* when moisture levels are high (Hajek 1999). This finding, however, aligns with my results from Chapter 3. The positive relationship between precipitation and spread rate may be due to an effect of weather on dispersal. For example, periods of increased precipitation may be associated with storm events that cause strong winds to transport individuals from higher-density, more established populations towards the invasion front (Tobin & Blackburn 2008). Frank et al. (2013) concluded that historically high rates of spongy moth spread in Wisconsin occurred because strong winds during storms blew early instar larvae across Lake Michigan from high-density populations that originated in Michigan. Similarly, there it is believed that wind-aided, long-distance dispersal has facilitated invasive spread by two *Drosophilia* species, *D. suzukii* (Asplen et al. 2015) and *D. melanogaster* (Leitch et al. 2021). 'Warm' phases of the PDO (positive climate index values) are associated with increased precipitation in the southeastern United States (Wei et al. 2021). Consistent with this, in the SUP I found a highly significant positive relationship between multi-annual synchronized fluctuations in precipitation and the PDO (Table 3). The PDO has typically exhibited decadal to multi-decadal variability but recent research suggests a shift in these long timescale cycles towards shorter ones beginning in 1999 (Zhang & Delworth 2015, 2016; Li et al. 2020). The PDO has been in a strong warm phase since 2014, but between 1999-2014, PDO phases were roughly 2-4 years long, well within the range of timescales examined in this study.

There was strong synchrony in spread in the AF at long timescales (> 4 years), especially at the *c.* 6-year timescale (Fig. 1b), and patterns of synchrony in temperature (Fig. 2e) and precipitation (Fig. 2f) had somewhat similar patterns at long timescales; however, none of the climate variables tested in this study were significant drivers of synchronized spread in the AF (Table A1). Walter et al. (2015) found that 6-year pulses in spongy moth spread in Virginia and West Virginia, which overlap with the AF, lagged one year after defoliation events that occurred 50-100 km behind the invasion front, which they attributed to immigrants arriving from established populations to nascent colonies near the invasion front. Although I did not find a significant relationship between synchrony in defoliation during year *t* and synchrony in rates of spread (Table A1), synchrony in spread (Fig. 1b) and defoliation (Fig. A2b) were consistently strong at the *c.* 6-7 year timescale band. Therefore, I cannot rule out the possibility that increased influx of individuals from established populations of the spongy moth to the invasion front during periodic outbreaks contributes to the synchrony of rates of spread.

Based on results from wavelet linear models (Table 2), predicted synchrony in spread most closely reflected observed synchrony in spread in the SUP (Fig. 3a-c) and MWS (Fig. 3d-f) ecoregions at approximately 2-year and 3-year timescales, respectively. These timescale-specific patterns of synchrony in spread (driven by synchrony in springtime precipitation in the SUP and wintertime snow depth in the MWS; Table 2; Fig. 3), occurred at slightly shorter timescales than the approximate 4-year pulses in invasion found by Johnson et al. (2006b). These differences in the timing of fluctuations in spread may relate to the time period and spatial resolution of data used in each study. Johnson et al. (2006b) used spongy moth county quarantine records from 1960-2002. Here, I estimated spongy moth spread based on Slow the Spread (STS) pheromone-baited trap records from 1989-2020. Additionally, Johnson et al. (2006b) did not consider

regional variability in rates of spread, and here, I investigated patterns of spread across five different ecoregions. These temporal and spatial differences in data representation may be responsible for differences in results between this study and that of Johnson et al. (2006b). Another possibility is that the results of my study point to a shift in the frequency of multi-annual fluctuations in spread towards shorter timescales in more recent years.

The fact that synchrony in spread was only significantly related to climate variables in the MWS and SUP (Table 2), the northernmost and southernmost ecoregions, may be explained by the greater annual variability in spread rates (km yr^{-1}) that occurred in the MWS (SD = 37.2 km yr^{-1}) and SUP (SD = 39.1 km yr^{-1}) ecoregions compared to the AF (SD = 20.3 km yr^{-1}), CUP (SD = 18.7 km yr^{-1}), and MWP (SD = 22.8 km yr^{-1}). Greater variability in rates of spread in the MWS and SUP may be due to higher variability in population growth rates due to more frequent exposure to adverse effects of extreme weather conditions at the northern and southern extremes of the range. In aphid and moth species, Hanski (1990) found and Hanski & Woiwod (1993) later confirmed, a positive relationship between annual variability in population abundances and spatial population synchrony due to regional stochasticity (e.g., Moran effects). Spatial synchrony in spread may also then increase with increasing annual variability in population growth rates given that population growth is an important component of invasive spread. More research on this topic is needed. An initial step could be modeling studies that investigate whether greater variability in population growth rates in response extreme weather conditions tends to increase synchrony in rates of spread.

This study provides new insights about the potential for multi-annual fluctuations in climate to synchronize rates of invasive spread. Annual and seasonal variability in weather has been shown to affect the spread of the spongy moth (Tobin et al. 2014; Chapter 3), but prior to

this study there was little understanding of the relationship between multi-annual fluctuations in climate and spatiotemporal patterns of spread. There is some predictability in the phase and strength of teleconnections, but predictions are generally limited to seasonal timescales (Williams et al. 2023). A recent review by Wan et al. (2022) highlighted the importance of using this information to anticipate changes in spatial population synchrony driven by multi-annual climatic patterns. Managers focused on slowing the spread of the spongy moth could use projections of climate indices to anticipate when synchronized fluctuations in spread will occur, especially near the latitudinal extremes of the range front. It is unknown whether similar relationships between teleconnections and synchrony in spread exist for other species. Knowledge of whether this is a widespread phenomenon could prove critical to management efforts aimed at either controlling the spread of pests and disease vectors, or facilitating the movement of rare species as the climate changes.

Tables & Figures:

Table 1: Total number of transects for which there were consistent data through study period for each ecoregion.

Ecoregion	Transects	Years
Southeastern USA Plains (SUP)	47	1993-2020
Appalachian Forest (AF)	85	1994-2020
Central USA Plains (CUP)	25	1999-2020
Mixed Wood Plains (MWP)	10	1999-2020
Mixed Wood Shield (MWS)	10	2000-2020

Table 2: Summarized results of significant spatial wavelet coherence tests for the variables used in wavelet linear models. Significance was tested at the $P < 0.1$ threshold (Walter et al. 2020). This table does not include non-significant coherence results; see Table A1 for a full summary of results on the spatial coherence between spread rates and the climate variables in each ecoregion. The *P-value* and *mean phase* columns come from spatial wavelet coherence tests. The columns *synchrony explained* and *cross term* are produced by the wavelet linear models. The *Predictor* variables are snow depth (mm; Snow) during the winter and total precipitation (mm; Prcp) during the larval period. *Mean phases* ($\bar{\theta}$), in units of π radians, provide information on the phase relationship between the response and predictor variables. The positive sign of the mean phases indicates that synchrony in the response variable preceded that of the predictor variable.

Model	Ecoregion	Timescale	Response	Predictor	*P*-value	Mean phase ($\bar{\theta}$)	% synchrony explained	Cross term
1	SUP	2-4	Spread	Prcp	0.0245	0.2419	51.9157	-1.5015
2	MWS	2-4	Spread	Snow	0.0565	0.5433	71.0530	-2.0953

Table 3: Spatial wavelet coherence tests between climate variables and climate indices. These tests revealed whether synchrony in the climate variables included in wavelet linear models (Table 2) was produced by synchrony in multi-annual climatic fluctuations that occur from teleconnections. The *time series* column indicates which dataset the climate variables correspond to. The *response* column contains the wintertime climate variables minimum temperature (°C; Tmin) and snow depth (mm; Snow) and the larval period variables mean temperature (°C; Tmean) and total precipitation (mm; Prcp). The *predictor* variables are the North Atlantic Oscillation (NAO), Pacific Decadal Oscillation (PDO), and the multivariate El Niño Southern Oscillation (MEI) climate indices. Significance was tested at the $P < 0.1$ in accordance with Walter et al. 2020. Mean phases ($\bar{\theta}$) in units of π radians were only provided if meaningful, i.e., when coherence relationships were significant. A positive mean phase value indicates that synchrony in the response variable preceded that of the predictor variable and a negative mean phase, that synchrony in the predictor variable preceded that of the response. All values have been rounded to four digits.

Time series	Ecoregion	Timescale	Predictor	Response	*P*-value	Mean phase ($\bar{\theta}$)
Spread	MWS	2-4	NAO	Snow	0.5225	
Spread	MWS	2-4	PDO	Snow	0.6783	
Spread	MWS	2-4	MEI	Snow	0.0769	−0.9315
Spread	SUP	2-4	NAO	Prcp	0.7952	
Spread	SUP	2-4	PDO	Prcp	0.0270	0.0125
Spread	SUP	2-4	MEI	Prcp	0.9271	

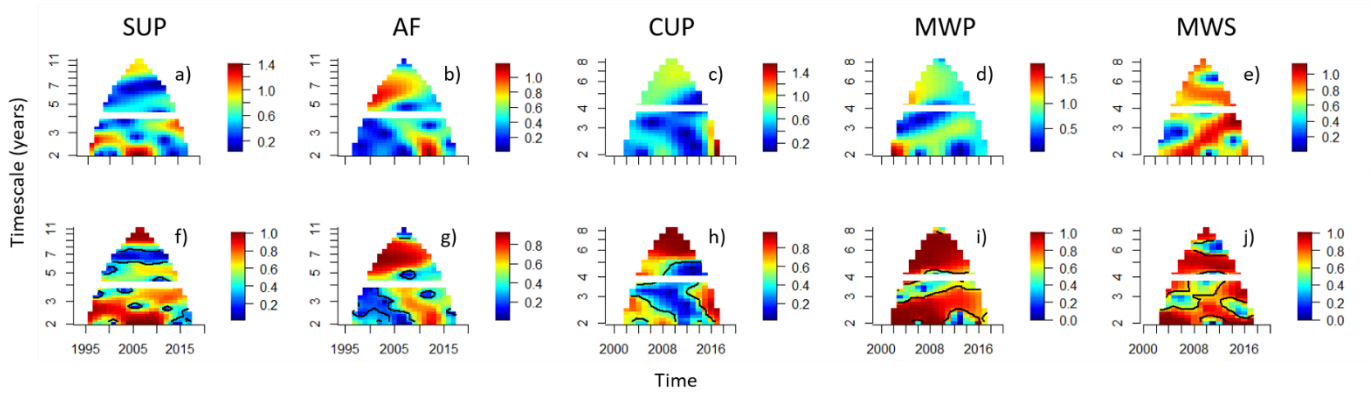

Figure 1: Wavelet mean field (WMF) magnitude (a-e) and wavelet phasor mean field (WPMF) (f-j) plots of the synchrony and phase synchrony (respectively) in rates of spread rate across time and timescale in each ecoregion —the Southeastern USA Plains (SUP), Appalachian Forest (AF), Central USA Plains (CUP), Mixed Wood Plains (MWP), and Mixed Wood Shield (MWS) ecoregions. The black contours (f-j) delineate significant phase synchrony at the $P < 0.001$ threshold (Sheppard et al. 2019). The values of the plots that are near 0 represent weak synchrony and values near 1, strong synchrony, at the indicated times and timescales. Mathematically, the time-averaged wavelet mean field magnitude is constrained to the interval (0,1), but it can exceed 1 for some times if it is balanced by times where it is < 1 (Sheppard et al. 2016). The horizontal white line in each plot displays the cutoff between the timescales of interest—short (2-4 years) and long (> 4 years).

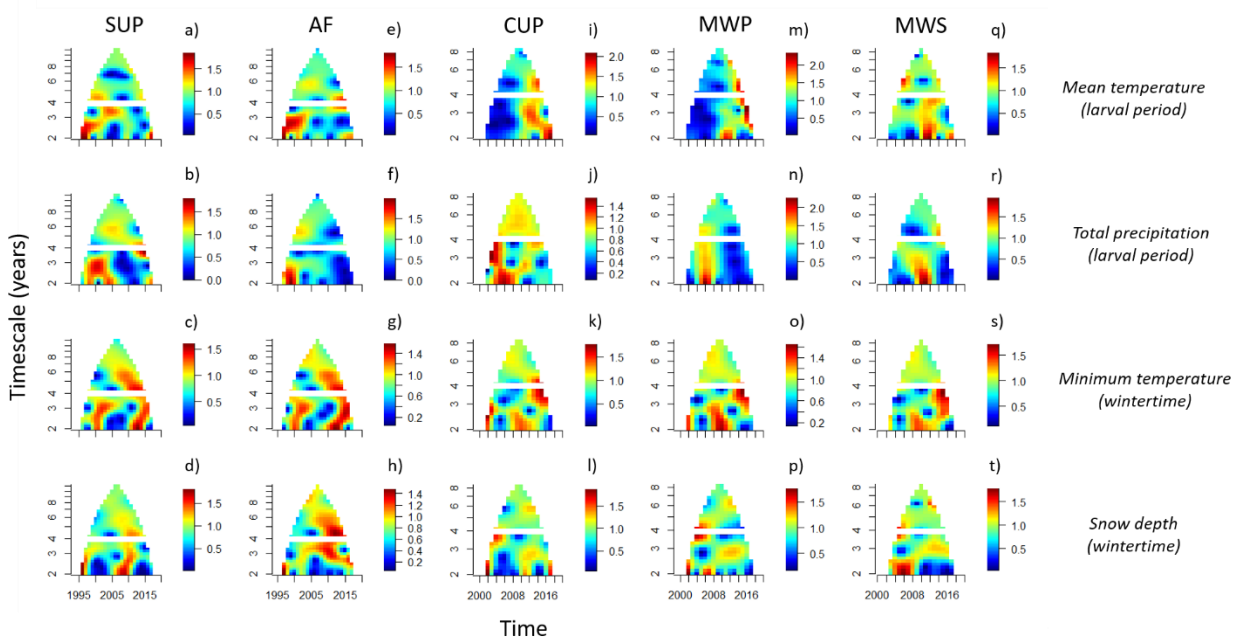

Figure 2: Wavelet mean field magnitude plots of time- and timescale-specific spatial synchrony in mean temperature during the larval period (row 1), total precipitation during the larval period (row 2), wintertime minimum temperature (row 3), and wintertime snow depth (row 4). The columns represent the climate variables by ecoregion—the Southeastern USA Plains (SUP), Appalachian Forest (AF), Central USA Plains (CUP), Mixed Wood Plains (MWP), and Mixed Wood Shield (MWS) ecoregions. The values of the plots that are near 0 represent weak synchrony and values near 1, strong synchrony, at the indicated times and timescales. Mathematically, the time-averaged wavelet mean field magnitude is constrained to the interval (0,1), but it can exceed 1 for some times if it is balanced by times where it is < 1 (Sheppard et al. 2016). The horizontal white line displays the cutoff between the timescales of interest—short (2-4 years) and long (> 4 years).

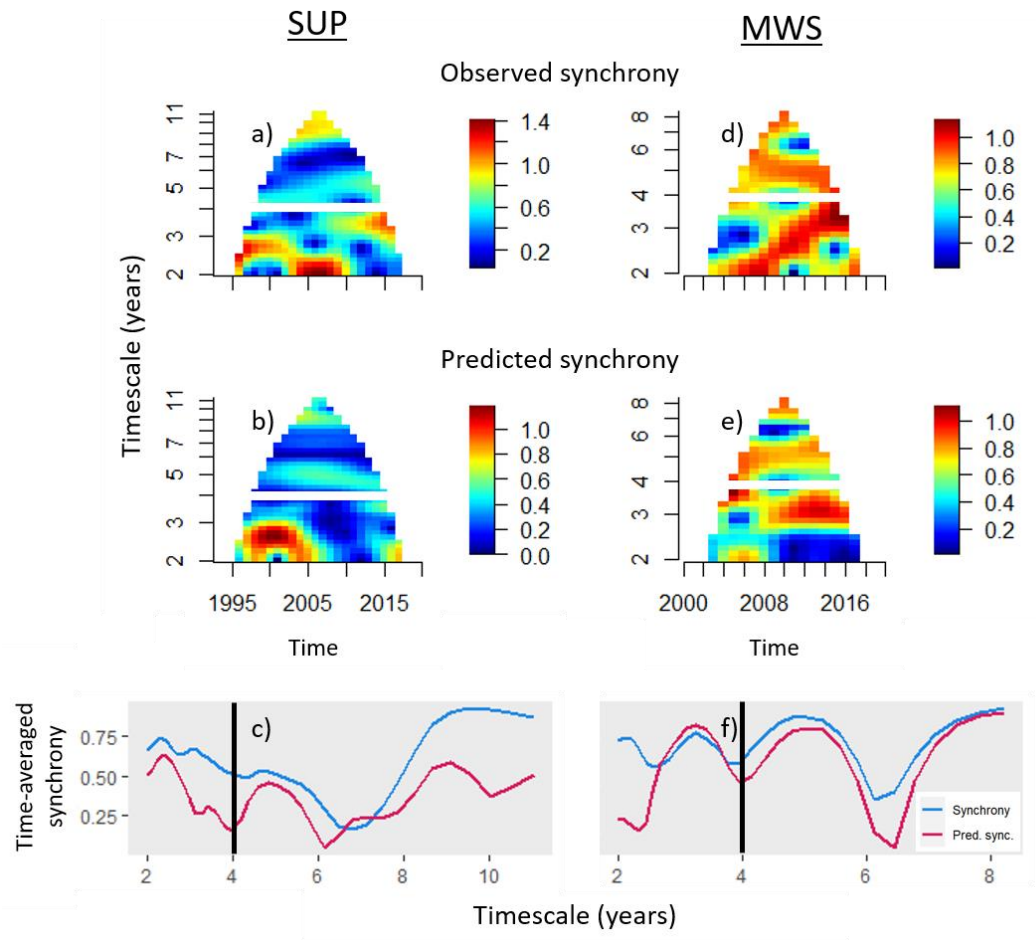

Figure 3: Spatial synchrony in spread is explained by springtime precipitation in the Southeastern USA Plains (SUP) (a-c) and wintertime snow depth in the Mixed Wood Shield (MWS) (d-f). Observed time- and timescale-specific synchrony in spread depicted by wavelet mean fields (WMFs) for the SUP (a) and MWS (c). In the SUP ecoregion, predicted synchrony in spread rate (b) was modeled with precipitation during the larval period as the predictor variable (Model 1, Table 2). In the MWS ecoregion, predicted synchrony in spread rate (e) was modeled with snow depth as the predictor variable (Model 2, Table 2). The bottom panels (c, f) provide the same information as the WMFs for observed (a, d) and predicted (b, e) synchrony in spread rate except the timescale-specific synchrony has been averaged across all years, representing the *mean squared synchrony*. Model 1 (c) explains 52% of the time-average spatial

synchrony in spread rate at short timescales (Table 2). Model 2 (f) explains 71% of the time-averaged spatial synchrony in spread rate at short timescales (Table 2). The values of the plots that are near 0 represent weak synchrony and values near 1, strong synchrony, at the indicated times and timescales. Mathematically, the time-averaged wavelet mean field magnitude is constrained to the interval (0,1), but it can exceed 1 for some times if it is balanced by times where it is < 1 (Sheppard et al. 2016). Horizontal white lines (a, b, d, e) and black vertical lines (c, f) delineate the timescales of interest—short (2-4 years) and long (> 4 years).

Appendices:

Appendix A1: Summarized results of spatial wavelet coherence tests.

Table A1: Results from spatial wavelet coherence tests on all pairwise combinations of spread rate and each abiotic variable and defoliation. The *P-value* and *mean phase* columns are test statistics from the coherence tests. To identify potential drivers of synchrony in spread rates, coherences tests were performed on the relationship between synchrony in spread rate (response variable) and synchrony in each climate variable (predictor variables). The *Predictor* variables are the wintertime climate variables minimum temperature (°C; Tmin) and snow depth (mm; Snow) and the larval period variables mean temperature (°C; Tmean) and total precipitation (mm; Prcp). Total area of defoliation (km^2; Defol) that occurred 50-100 km from the range edge was also tested as a predictor variable. Significance was tested at the $P < 0.1$ in accordance with Walter et al. 2020. Mean phases ($\bar{\theta}$) in units of π radians were only provided if meaningful, i.e., when coherence relationships were significant. The positive sign of the mean phases indicates that synchrony in the response variable preceded that of the predictor variable. All values have been rounded to four digits.

Ecoregion	Response	Predictor	Timescale	*P*-value	Mean phase ($\bar{\theta}$)
MWS	Spread	Tmin	2-4	0.3872	
MWS	Spread	Tmin	4-8	0.3559	
MWS	Spread	Tmean	2-4	0.3752	
MWS	Spread	Tmean	4-8	0.9334	
MWS	Spread	Prcp	2-4	0.3079	
MWS	Spread	Prcp	4-8	0.7459	
MWS	Spread	Snow	2-4	0.0565	0.5433
MWS	Spread	Snow	4-8	0.4528	
MWS	Spread	Defol	2-4	0.7772	
MWS	Spread	Defol	4-8	0.3686	
MWP	Spread	Tmin	2-4	0.8298	
MWP	Spread	Tmin	4-8	0.1962	
MWP	Spread	Tmean	2-4	0.6259	

MWP	Spread	Tmean	4-8	0.9459	
MWP	Spread	Prcp	2-4	0.6970	
MWP	Spread	Prcp	4-8	0.1589	
MWP	Spread	Snow	2-4	0.1134	
MWP	Spread	Snow	4-8	0.2084	
MWP	Spread	Defol	2-4	0.4396	
MWP	Spread	Defol	4-8	0.4406	
CUP	Spread	Tmin	2-4	0.7379	
CUP	Spread	Tmin	4-8	0.2909	
CUP	Spread	Tmean	2-4	0.9619	
CUP	Spread	Tmean	4-8	0.5552	
CUP	Spread	Prcp	2-4	0.9105	
CUP	Spread	Prcp	4-8	0.2659	
CUP	Spread	Snow	2-4	0.9916	
CUP	Spread	Snow	4-8	0.3103	
CUP	Spread	Defol	2-4	0.8132	
CUP	Spread	Defol	4-8	0.7413	
AF	Spread	Tmin	2-4	0.2048	
AF	Spread	Tmin	4-11	0.4386	
AF	Spread	Tmean	2-4	0.8172	
AF	Spread	Tmean	4-11	0.3976	
AF	Spread	Prcp	2-4	0.9760	
AF	Spread	Prcp	4-11	0.2448	
AF	Spread	Snow	2-4	0.3606	
AF	Spread	Snow	4-11	0.2707	
AF	Spread	Defol	2-4	0.5614	
AF	Spread	Defol	4-11	0.3566	
SUP	Spread	Tmin	2-4	0.9350	
SUP	Spread	Tmin	4-11	0.8456	
SUP	Spread	Tmean	2-4	0.3028	
SUP	Spread	Tmean	4-11	0.9165	
SUP	Spread	Prcp	2-4	0.0245	0.2419
SUP	Spread	Prcp	4-11	0.9465	
SUP	Spread	Snow	2-4	0.7676	
SUP	Spread	Snow	4-11	0.7031	
SUP	Spread	Defol	2-4	0.6284	
SUP	Spread	Defol	4-11	0.9241	

Appendix A2: Wavelet mean field plots displaying synchrony in total area of defoliation (km^2) in year *t*.

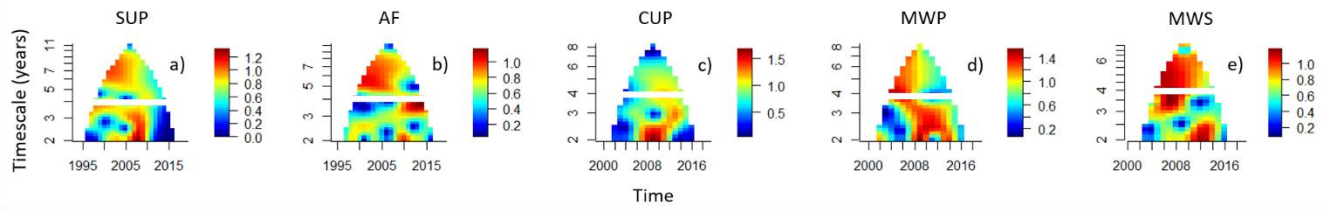

Figure A2: Wavelet mean field (WMF) magnitude plots of synchrony in total area of defoliation (km^2) that occurred 50-100 km from the range edge in year *t* across time and timescale in each ecoregion—the Southeastern USA Plains (SUP), Appalachian Forest (AF), Central USA Plains (CUP), Mixed Wood Plains (MWP), and Mixed Wood Shield (MWS) ecoregions. The values of the plots that are near 0 represent weak synchrony and values near 1, strong synchrony, at the indicated times and timescales. Mathematically, the time-averaged wavelet mean field magnitude is constrained to the interval (0,1), but it can exceed 1 for some times if it is balanced by times where it is < 1 (Sheppard et al. 2016). The horizontal white line displays the cutoff between the timescales of interest—short (2-4 years) and long (> 4 years).

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Chapter 5. Conclusions

The spread of invasive species can cause widespread environmental, ecological, and economic impacts (Pimentel et al. 2005). To successfully predict and manage spread, we ultimately must understand the various processes that lead to different rates of spread both among and within species (Goldstein et al. 2019). Studying how novel climatic conditions experienced by a species expanding their range is an important component of this effort, especially because climate is considered to be one of the primary factors that limit species' range limits (Gaston 2003). The studies that comprise this dissertation use an extremely damaging and well-studied invasive species, the spongy moth, as a model system to identify possible indirect effects of climate on spread through alterations to a host-pathogen relationship (Chapter 2), as well as novel effects of weather and climate on temporal variability in spread (Chapters 3 and 4). Together, this work broadens our understanding of the role of climate for shaping spatiotemporal patterns of range expansion and contraction.

Research on how climate change may affect relationships between forest pests and their diseases is integral to management efforts aimed at reducing pest prevalence and their capacity for future spread. Motivated by climate change predictions of rising air temperatures and increasing summertime drought (IPCC 2022), in Chapter 2 I conducted a manipulative field experiment to test the effects of precipitation and temperature on larval mortality caused by *Entomophaga maimaiga*. Based on past studies that found that the number of larval infections by this fungus tend to increase with increasing precipitation (Hajek 1999), I expected that warmer and drier conditions would decrease infections. I found, however, that only elevated temperatures, not supplemental precipitation, affected larval infections by this pathogen. Specifically, the number of infected larvae increased by 45% on average, under elevated compared to ambient temperatures. Experimental warming may have increased infections

because ambient temperatures at the field site, which was located in one of the coldest portions of the spongy moth's range, were suboptimal for fungal germination (Siegert et al. 2009). A possible explanation for the lack of a precipitation effect is that above average rainfall prior to the experiment fulfilled the moisture requirements of *E. maimaiga.* The results of Chapter 2 suggest that rising temperatures due to climate change may increase the potential for epizootics to occur in the cold portions of the spongy moth's range, such as Minnesota where I conducted this experiment. If epizootics increase with climate change in northern portions of the range, rates of spongy moth range expansion in these regions may slow. However, these portions of the range are also expected to become more suitable to the spongy moth as temperatures rise due to climate change (Gray 2004). These potentially conflicting effects of climate change on this host-pathogen relationship indicate a need for further research on how climatic conditions affect this system, such as whether drought decreases mortality of spongy moth by *E. maimaiga*, and whether similar effects of drought occur in different areas occupied by the spongy moth. Other forest pest insects have similar fungal pathogens to *E. maimaiga* (Skrzecz et al. 2023); therefore, knowledge of how predicted climate changes will affect interactions between the spongy moth and *E. maimaiga* has broad implications for future risks to hardwood forests.

Most past work on the relationship between climate and distributional range limits of invasive species have focused on the effects of spatial heterogeneity, as opposed to temporal variability, in climate. Chapter 3 is one of the first studies to demonstrate the influence of annual variability in abiotic conditions on spatiotemporal variability in spongy moth spread (but see Tobin et al. 2014). Chapter 3 also fills a long-standing need for a comprehensive assessment of the role of weather on spongy moth spread, as it considers the effects of multiple abiotic variables (temperature, precipitation, and snow depth) across five ecoregions along the entire

invasion front. I hypothesized that temporal variability in weather conditions that cause changes in vital rates, such as reduced survival during periods of extreme weather or mortality caused by natural enemies, would subsequently alter population growth rates along a species' range edge, and lead to temporal variability in rates of spread. Using empirical data on spongy moth population abundances spatially joined to weather data, I found that annual variability in weather strongly influenced population growth and spread rates and that the effects generally varied by ecoregion. No prior studies had investigated the effects of annual variability in abiotic conditions on population growth (Metz & Tobin 2022) and spread rates (Tobin et al. 2014) in parallel. Because spread rates are at least in part determined by population growth rates, knowledge of the effects of temporal variability in weather on both population growth and spread rates is vital to understanding whether effects of weather on spread stem from effects on population growth or dispersal. By studying both population growth and spread, I was able to discover that the responses of population growth and spread rate to the same abiotic variable were usually different. For example, I found negative relationships between precipitation and population growth rates, which is consistent with the hypothesis that increasing precipitation would reduce growth rates due to increased larval infections by the fungal-pathogen *E. maimaiga*, whereas spread rates generally increased with increasing precipitation. The positive relationship between precipitation and spread rate might be explained by storms that not only increased precipitation but also brought strong winds that transported early-instar larvae ahead of the invasion front.

In Chapter 3 I also investigated whether temporal variability in abiotic conditions altered Allee effects. Multiple studies have found spatiotemporal variation in Allee effects, suggesting the dynamic nature of this phenomenon that occurs in small populations (Tobin et al. 2007; Robinet et al. 2008; Walter et al. 2015, 2020), but no prior studies investigated whether temporal

variation in weather was a source of variability in Allee effects (Walter et al. 2017). I found that abiotic conditions seemed to influence Allee effects and other forms of density dependence. For example, in the coldest and northernmost ecoregion, Allee effects were present during years when snow depth was above-average. This finding contrasts the commonly held view that effects of the abiotic environment are largely density-independent (but see Hansen et al. 2019).

Even a weak Allee effect in low-density populations can reduce rates of range expansion because of its negative effect on population growth at low densities (Taylor & Hastings 2005). As the strength of the Allee effect increases, "invasion pinning" becomes more likely, whereby a population is constrained or "pinned" to its current range limit because it cannot overcome Allee effects (Keitt et al. 2001). Contrary to theoretical (Lewis & Kareiva 1993; Taylor & Hastings 2005; Courchamp et al. 2008; Walter et al. 2017) and empirical (Johnson et al. 2006, Tobin et al. 2007) evidence supporting this negative relationship between an Allee effect and spread rate, I found that spread rates were usually elevated under abiotic conditions for which an Allee effect was also present. Mirroring this finding, population replacement rates at low densities were usually similar under differing abiotic conditions, but replacement rates at high densities were generally higher under abiotic conditions that led to Allee effects than under conditions that did not. The mechanisms whereby abiotic conditions affected the presence of Allee effects in range edge populations are not clear. A review on the topic of spatiotemporal variability in Allee effects by Walter et al. (2017) highlighted the importance of identifying mechanisms that cause variation in Allee effects. Such information would help clarify the role of low-density population dynamics for invasive spread, as well as extinction events. Further research is needed to explore potential mechanisms through which different forms of density dependence may arise under

differing abiotic conditions, as well as how spread rates respond to population growth rates that have been altered by the environment in a density-dependent manner.

With the knowledge that annual variability in temperature, precipitation, and snow depth strongly influence year-to-year variation in rates of spongy moth spread, in Chapter 4 I investigated the extent to which these relationships are consistent across space and over multi-annual timescales. Using extensions of wavelet analysis, I demonstrated for the first time, that invasive spread can be spatially synchronized. This finding has important management implications, because, just as regionalized outbreaks of pests are more concerning from a management perspective than localized ones (Liebhold et al. 2012), high spatial synchrony in invasive spread over large areas would be difficult to manage because resources dedicated to controlling the invasion would be strained during a widespread pulse in spread. Given that population spatial synchrony is ubiquitous across many taxa (Liebhold et al. 2004) and that population growth is an important component of spread (Skellam 1951), spatial synchrony in rates of spread may be common across invasive species.

To make use of the information that the spread of spongy moth exhibits spatial synchrony, such as for management guidance on controlling spread, we must understand the drivers of the synchrony. I investigated whether multi-annual fluctuations in certain climate variables were responsible for the spatial synchrony in spread observed along the spongy moth's invasion front. Within the spongy moth's nonnative range in North America, temperature and precipitation exhibit multi-annual periodicity (Allstadt et al. 2015; Haynes et al. 2019) and can be regionally synchronized over distances up to 2,500 km (Koenig 2002; Koenig & Liebhold 2016). Such broad-scale and quasiperiodic spatiotemporal patterns in climate are often driven by teleconnections (Nigam & Baxter 2015). Aligning with past studies that investigated climate

drivers that lead to synchronous fluctuations in the abundances of spatially disjunct populations through time (i.e., population synchrony; Bjørnstad et al. 1999), I found that synchrony in spread could be explained by synchrony in climate, but only in two of the five ecoregions, the northernmost and southernmost ones. Snow depth explained synchrony in spread in the northernmost ecoregion, and springtime precipitation explained synchrony in spread in the southernmost. Synchrony in springtime precipitation and snow depth were driven by the Pacific Decadal Oscillation and the El Niño-Southern Oscillation. Based on this finding, efforts to slow the spread of the spongy moth near the latitudinal extremes of the range front could be informed by projections of the phases and strengths of teleconnections to better anticipate when synchronized fluctuations in spread will occur. It is unknown whether similar relationships between teleconnections and synchrony in spread exist for other species. Knowledge of whether this is a widespread phenomenon could prove critical to management efforts aimed at either controlling the spread of invasive species and vectors of disease, or facilitating range shifts for rare species as the climate changes.

The research presented here highlights the enormous complexities surrounding the role of climate in governing invasive spread. By teasing apart the spatial and temporal 'layers' of climate, I showed that our interpretation and understanding of how the spread of the spongy moth may respond to abiotic conditions is limited in part by our knowledge about the effect of climate on interspecific interactions and low-density population dynamics. Although our understanding of invasive spread has advanced rapidly since Skellam's (1951) classic work that modeled the geographic range of a species as increasing linearly over time, here I provide novel evidence on the potential for climate-driven population dynamics to contribute to variability in rates of spread at both annual and multi-annual timescales (Cazelles et al. 2023). In particular,

my findings of density-dependent effects of abiotic conditions on population replacement rates and elevated rates of spread despite the presence of an Allee effect provide a foundation for future research in the field of invasion ecology. There is a need to develop a better understanding of mechanisms that give rise to density-dependent effects of abiotic conditions (Walter et al. 2017), followed by studies focused on understanding the implications of different forms of density dependence for variability in spread rates. One possible mechanism that deserves attention is a possible threshold host density that causes *E. maimaiga* epizootics to occur. If identified, future research should attempt to confirm past modeling results which suggest that abiotic environmental conditions can change this density (Kyle et al. 2020). If an epizootic threshold density and possible weather variables that may cause the threshold to fluctuate are identified, the STS dataset on spongy moth population abundances would be invaluable for further exploration of this topic. By incorporating data on spongy moth spread rates into this effort, it may be possible to determine whether effects of climate on the spongy moth-*E. maimaiga* interaction are linked to spatiotemporal variability in rates of spongy moth spread.

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