How climate extremes—not means—define a species' geographic range boundary via a demographic tipping point

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Abstract. Species' geographic range limits interest biologists and resource managers alike; however, scientists lack strong mechanistic understanding of the factors that set geographic range limits in the field, especially for animals. There exists a clear need for detailed case studies that link mechanisms to spatial dynamics and boundaries because such mechanisms allow us to predict whether climate change is likely to change a species' geographic range and, if so, how abundance in marginal populations compares to the core.

The bagworm *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae) is a major native pest of cedars, arborvitae, junipers, and other landscape trees throughout much of North America. Across dozens of bagworm populations spread over six degrees of latitude in the American Midwest we find latitudinal declines in fecundity and egg and pupal survivorship as one proceeds toward the northern range boundary. A spatial gradient of bagworm reproductive success emerges, which is associated with a progressive decline in local abundance and an increase in the risk of local population extinction near the species' geographic range boundary.

We developed a mathematical model, completely constrained by empirically estimated parameters, to explore the relative roles of reproductive asynchrony and stage-specific survivorship in generating the range limit for this species. We find that overwinter egg mortality is the biggest constraint on bagworm persistence beyond their northern range limit. Overwinter egg mortality is directly related to winter temperatures that fall below the bagworm eggs' physiological limit. This threshold, in conjunction with latitudinal declines in fecundity and pupal survivorship, creates a nonlinear response to climate extremes that sets the geographic boundary and provides a path for predicting northward range expansion under altered climate conditions. Our mechanistic modeling approach demonstrates how species' sensitivity to climate extremes can create population tipping points not reflected in demographic responses to climate means, a distinction that is critical to successful ecological forecasting.

Key words: Allee effect; bagworm, Thyridopteryx ephemeraeformis; *climate change; female mating failure; geographic range boundary; invasion pinning; latitudinal gradient; overwinter survivorship; population-dynamic parameters; Psychidae; reproductive asynchrony; U.S. Midwest.*

INTRODUCTION

One of the biggest unsolved research problems in ecology is understanding what factors determine species' geographic range size and, in particular, what factors limit species' expansion beyond the edges of their ranges (Gaston 2009). An extensive array of "atlas projects" (Araujo and Williams 2000, GBIF 2009) provide increasingly robust information on species' geographic distributions, allowing researchers to generalize about the structure and dynamics of geographic ranges (Brown et al. 1996, Gaston 2003). Furthermore, numerous case

studies document that many species have indeed shifted or expanded their geographic ranges in response to climate change (while others have not) (Parmesan and Yohe 2003). Diverse theoretical range limit models outline alternative mechanisms that can yield geographic range boundaries (Gaylord and Gaines 2000, Keitt et al. 2001, Fagan et al. 2009, Sexton et al. 2009), but with only a few recent exceptions (Battisti et al. 2005, Buckley et al. 2010) there are surprisingly few studies that pinpoint why, at a mechanistic level, species' range boundaries are shifting (or not) or why such boundaries even exist (Gaston 2009).

Interactions among habitat availability, biological processes, and physical factors determine species' geographic range size and the location of their range

boundaries (Caughley et al. 1988, Gaston 2009, Sexton et al. 2009). Empirical data on geographic range sizes make clear that environmental thresholds or gradients (Eckhart et al. 2011), physiological tolerances (Helmuth et al. 2005), and spatially varying physical processes (Gaylord and Gaines 2000) can all determine species' range limits, and that range limits can emerge even in the absence of such gradients (e.g., "invasion pinning," Keitt et al. 2001; sex-biased dispersal, Miller et al. 2011). Holt et al. (2005) proposed a small set of demographic mechanisms related to spatial variation in population-dynamic parameters (e.g., birth, death, and dispersal rates) that may collectively determine a species' range boundaries under many conditions. Critically lacking, however, is an animal model system for which multiple demographic parameters can be concurrently estimated along a spatial gradient that includes both core habitat and the species' range edge. While amphibian models provide some clear opportunities for developing these ideas (e.g., Cunningham et al. 2009), relatively little progress has been made in developing animal models that can be parameterized by empirical data. Crozier and Dwyer's (2006) model addresses many of these issues for a skipper butterfly (e.g., the interaction of multiple life-history elements affected differentially by climate change) but over a restricted portion of the species' range, which makes it difficult to investigate how limiting mechanisms may change near the geographic-range boundary.

Particularly difficult to collect are data on spatial variation in the lifetime reproductive success of female animals, especially in low-density populations (Lester et al. 2007, Gaston 2009). Such data are rarely collected, in part, because of how difficult it is to track female movements over their full reproductive lifetimes (Rhainds et al. 1999). The issue is especially problematic among insects, which are generally small, multiply-mating, and highly mobile, allowing few opportunities to evaluate variation in lifetime female fitness (Cushman et al. 1994, Rosenheim et al. 2008).

Overall, the issue of species' boundaries can be viewed from two complementary perspectives: (1) What processes initially limit a novel species' spatial expansion? (Webb and Gaston 2000, Keitt et al. 2001, Fagan et al. 2009); and (2) What processes govern the long-term size and occupancy of a species' geographic range? (Gaston 2003) In this paper we adopt the second perspective because our focal species, the bagworm *Thyridopteryx ephemeraeformis* (Lepidoptera: Psychidae), is native and its range limit near northern Indiana (USA) has changed little over the last 40 years (Morden and Waldbauer 1971, Rhainds and Fagan 2010). However, the integrative approach we develop also allows us to explore both the problem of non-equilibrial geographic range dynamics (which has been identified as a major challenge in spatial ecology and biogeography [Holt et al. 2005]) and the relative importance of mean vs. extreme conditions (which

may be essential to forecast species' responses to global change [Parmesan et al. 2000, Buckley and Kingsolver 2012]). Sensitivity to extreme climate events can create a dichotomy between predictions made by a model run using fixed (constant) life-history parameters and those made by a stochastic model in which daily temperature patterns, and the life-history parameters that depend on them, change interannually. Predictions of future climate shifts thus require a mechanistic model that explicitly links temperature time series to survivorship and reproductive success and ultimately to population persistence.

To develop a mechanistic understanding of what currently limits bagworm range expansion, we combine detailed observational data (from hundreds of populations across six degrees of latitude) with a synthetic, spatially varying mathematical model to study bagworm dynamics and the maintenance of the northern boundary of the species' geographic range. Our model is completely parameterized by empirical data on stage-specific survivorship and fecundity. Population persistence, and hence the predicted location of the bagworm's northern range limit, emerges from this mechanistic model but is not used in its development; in this sense, it is a "forward" model sensu Dormann et al. (2012). This combination of data and modeling delineates the factors that limit the bagworm's geographic range, and, at the same time, yields a framework that can be extended and adapted to the many species (e.g., some plants, amphibians, insects) that share similar life-history strategies such as limited mobility (e.g., female flightlessness in insects, Barbosa et al. 1989) and asynchronous reproductive timing (Calabrese and Fagan 2004, Calabrese et al. 2008).

Bagworm life history

The bagworm, *Thyridopteryx ephemeraeformis*, is a polyphagous species native to the United States. The species lives throughout the eastern United States (from Florida north to Massachusetts, and west to Texas and Nebraska), but the range features a distinct geographic limit in the Midwest near northern Indiana, which has been stable for decades (Morden and Waldbauer 1971, Rhainds and Fagan 2010). Bagworms afflict urban and agricultural landscapes alike. The larvae develop within a self-constructed, conspicuous bag made of silk and plant material (Fig. 1a) that is easy to monitor. Due to extensive study in many ecological contexts, ecologists have developed a detailed knowledge of this insect's univoltine life cycle (Fig. 1b).

In the fall, the female oviposits in her pupal case within the bag she constructed as a larva. The eggs (Fig. 1c) overwinter inside their maternal bag. In the spring neonates emerge, spin a silken thread, and disperse via ballooning. Many ballooning larvae remain on their natal host (Jones and Parks 1928, Gross and Fritz 1982, Moore and Hanks 2004). Long distance ballooning is rare (Appendix: Fig. A1; see also Cox and Potter [1986])

and consequently contributes more to initiating new infestations than to rescuing local populations near extinction. After landing on a host plant, neonates construct a self-enclosing bag from small pieces of their host. Each larva remains inside its bag throughout development, enlarging the bag as it grows. Upon completion of feeding, larvae tightly attach their bag on the host plant to pupate. Pupal parasitoids can be an important cause of mortality, particularly among the smaller male pupae (Cronin and Gill 1989).

Adults emerge in the fall. Males, which are typical winged moths that actively seek out sexually receptive females, have been reported flying up to 1.5 km from their pupation site (Jones and Parks 1928) and, consequently, are capable of dispersing on a small spatial scale (Rhainds et al. 2008, Rhainds 2013). Males are so short lived that copulation is a considerable time investment relative to their adult life span, and as a result males inseminate relatively few females during their lifetime (Fig. 1d; Rhainds et al. 2009). In contrast, females are neotenous, flightless, and remain in their bag for their entire adult life. Females attract males to their bag during a short-lived "calling stage" in which they disseminate setae impregnated with pheromone. Shortly after mating, the female oviposits a single egg clutch inside her pupal case (Rhainds et al. 2009); this behavior facilitates assessing parameters related to female reproductive output (mating success, fecundity) in the field (Sheppard 1975, Rhainds et al. 1999, 2002).

Evidence suggests that the bagworm's range limit is not set per se by host plants. The most common bagworm hosts, *Juniperus virginiana* and *Thuja occidentalis*, are widespread in the eastern United States and extend, in abundance, into Michigan and Canada; other important hosts such as *Pinus strobus* or *Picea pungens* actually *increase* in abundance north of the bagworm's range (USDA PLANTS database, *available online*).[7] Likewise, plant quality does not appear to change systematically across the species' range. For example, using the latitudinal database on foliar nutrient content from Kerkhoff et al. (2005), none of the four primary host genera for *Thyridopteryx* exhibit a broadscale latitudinal trend in foliar carbon-to-nitrogen ratio. Such trends are also absent when the latitudinal range is restricted to 35°–45° N. This absence of any latitudinal trend holds whether the data are analyzed for individual genera or as a group of potential hosts.

Overall, the bagworms' life history is unusually tractable (especially among animals) for detailed, replicated investigations of phenology, mating success, and survivorship. Consequently, estimates (and associated uncertainty measures) are obtainable for each key transition in the bagworm life cycle.
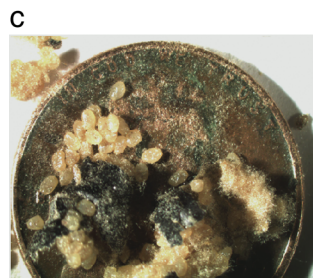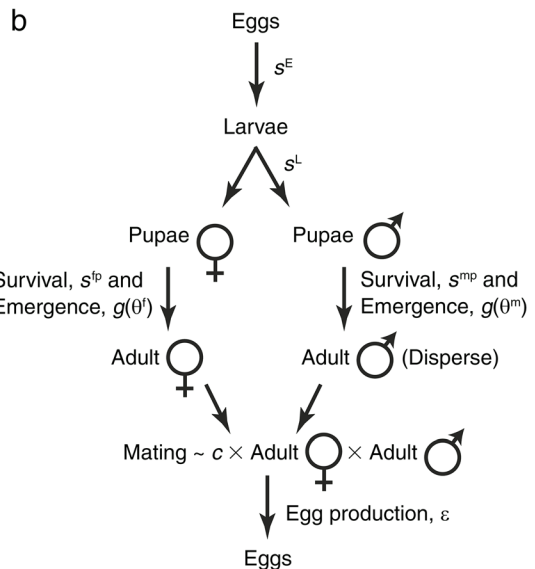

FIG. 1. (a) Overwintering bagworm (*Thyridopteryx ephemeraeformis*) on arborvitae (photo credit: Cliff Sadof). (b) Bagworm lifecycle (s^E, overwinter egg survivorship; s^L, larval survivorship; s^{fp} and s^{mp}, male and female pupal survivorship, respectively; ε, egg production); c is a constant representing the instantaneous mating rate (efficiency). (c) Bagworm eggs on penny (photo credit: Cliff Sadof). (d) Male copulating with female bagworm (photo credit: Patricia Gentili-Poole).

[7] http://plants.usda.gov/

TABLE 1. Extinction probability for populations of the bagworm *Thyridopteryx ephemeraeformis* as a function of latitude and successful female reproduction.

Latitude (°N)	Number of sites (reproductive success)	Probability of extinction
<39	6 (+)	0.00
39–40	13 (+)	0.154
40–41	22 (+)	0.136
>41	4 (−), 13 (+)	0.326

Notes: "Plus" symbols (+) indicate that at least one female successfully reproduced; "minus" symbols (−) indicate that no females successfully reproduced. This table is reproduced from Rhainds and Fagan [2010: Table 4]).

METHODS

Analytical approach

Our modeling goals were fourfold. First, we wanted to know whether a model could predict the latitudinal position of the bagworm's northern range limit. This model, as described in detail below, contains no free parameters and is completely constrained by the extensive life-history data available for *Thyridopteryx ephemeraeformis* (e.g., Balduf 1937, Kaufmann 1968, Barrows 1974, Sheppard 1975, Sheppard and Stairs 1976, Horn and Sheppard 1979, Rhainds et al. 2008, 2009). Second, we wanted to use this model to understand to which components of the bagworm's life history this persistence/extinction threshold was the most sensitive, making a particular distinction between mechanisms resulting in mating failure (see Table 1) and those associated with abundance and subsequent survival of offspring. Third, we wanted to look at the robustness of the model to variation in those parameters for which empirical data were weak. A final goal was to develop a more mechanistic, temperature-based model for those life-history components found to be most important for bagworm persistence that could be used for model validation and prediction of bagworm persistence under future climate scenarios. Here we explicitly compare a non-stochastic model with no interannual variation in life-history parameters to a stochastic model in which life-history parameters vary interannually. Our bagworm model allows us to explore the relative importance of climate extremes vs. climate means as constraints on population expansion at a range edge, and has direct implications for the spatial spread of other potentially invasive species with one or more life stages (e.g., egg mass, seed, and so forth) that are susceptible to extreme temperature conditions.

Model development

As discussed below under *Model parameterization*, existing data provide evidence for latitudinal gradients in four aspects of bagworm life history (reproductive phenology, per-capita egg production, overwinter egg mortality, and pupal survival) and parts of the model corresponding to those four features are all permitted to vary spatially. Larval survivorship is strongly density-dependent (Rhainds and Sadof 2008), and the associated carrying capacity for the larval stage is also allowed to vary spatially. For model parameterization, data from 52 individual sample sites are aggregated into 0.25°-wide latitudinal bands l_i (14 bands starting at 38.25° N, indexed by i) (Fig. 2). Given the bagworm's relatively small dispersal range (see *Introduction: Bagworm life history*, above), we did not include spatial movement in the model. Consequently, bagworm populations in each of the 14 latitudinal bands are allowed to develop independently.

Each iteration of the model begins at the end of the pupal stage (Fig. 1b), immediately prior to the onset of adulthood. The discrete generations are denoted T, $T + 1$, and so on (years), whereas time within the annual lifecycle is denoted by t (days). Where applicable, superscripts are reserved for group membership (gender, stage) and subscripts for latitudinal band. Males and females begin adulthood according to

$$\frac{dM}{dt} = M_0(T)g(t, \theta^m_{l_i}) - \alpha^m(t)M$$

$$\frac{dF}{dt} = F_0(T)g(t, \theta^f_{l_i}) - \alpha^f(t)F \qquad (1)$$

where M_0 and F_0 are total densities of males and females, respectively; $g(t, \theta_{l_i})$ is a probability distribution, with parameter vector θ dictating how maturation events (for males, emergence) are spread over time during the breeding season; and $\alpha(t)$ is a time-dependent per day death rate which will be formulated below to
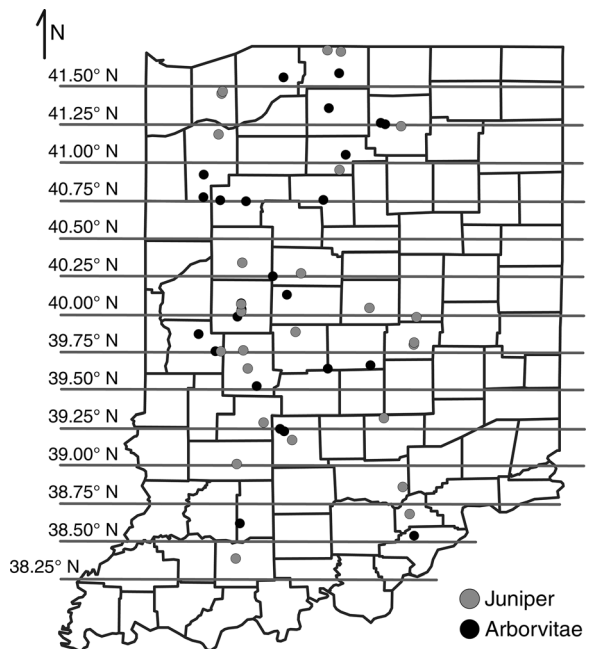

FIG. 2. Location of sampled sites in Indiana, USA, and 0.25° latitudinal bands, 38.25–41.50° N, used to group sites.

accommodate age-specific mortality risk (Calabrese et al. 2008, Calabrese 2012). For clarity in Eq. 1 and in the mathematical development stemming from it, we have suppressed indices associated with latitudinal band for M, M_0, F, and F_0. The superscripts "m" and "f" indicate parameters that are specific to males or females within the population, respectively. A version of this emergence model was originally introduced by Manly (1974) and studied extensively in the context of protandry (e.g., Zonneveld and Metz 1991, Zonneveld 1992). Calabrese et al. (2008) fit a version of this model to mark–recapture data to estimate female matelessness in wild populations of *Parnassius* butterflies, and Fagan et al. (2010) used a reaction–diffusion variant to investigate how the interplay of mating and searching behaviors determines critical patch sizes for asynchronously breeding populations. This so-called "Zonneveld model" is appropriate for the bagworm system because it can accommodate realistic variation in emergence and mortality schedules both among individuals and between the sexes, and can account for how phenology may affect female mating success.

We use the standard and widely applicable kinetic approach to describe mate encounter, assuming that the number of matings per unit time is proportional to the product of male and unmated female density (Wiklund and Fagerström 1977, Wells et al. 1990, Zonneveld and Metz 1991, Zonneveld 1992, Hutchinson and Waser 2007). We assume that females are monandrous and that males can mate repeatedly. The rate of change in the density of *unmated* females, denoted U, is then

$$\frac{dU}{dt} = F_0(T)g(t, \theta_{l_i}^f) - cMU - \alpha^f(t)U \qquad (2)$$

where c is a constant representing the instantaneous mating rate (efficiency) (see *Model parameterization*, below). The cumulative density of mated females at any time $R(t)$, is given by the solution to

$$\frac{dR}{dt} = cMU. \qquad (3)$$

Female bagworms commence laying their eggs immediately after copulation (Jones 1927), allowing us to neglect post-mating mortality of female bagworms. All reproductive activity takes place within a season of length τ, and the total density of mated females at the end of the season is

$$R(\tau) = \int_0^\tau cMU\,dt. \qquad (4)$$

By extension,

$$q^* = 1 - \frac{R(\tau)}{F_0} \qquad (5)$$

is the total, season-long proportion of females that die mateless (see Plate 1). To begin the next generation,

bagworm mating yields eggs according to:

$$E(l_i, T + 1) = \varepsilon_{l_i}R(\tau) \qquad (6)$$

where ε (per capita egg production by females) depends on the latitude l_i. Eggs survive the winter with probability $s_{l_i}^E$, which also depends on latitude l_i, and the surviving eggs hatch into larvae according to:

$$L(l_i, T + 1) = s_{l_i}^E E(l_i, T + 1). \qquad (7)$$

Available data suggest that total larval survivorship, denoted s^L, is negatively density-dependent when density is measured at the scale of individual host-plant shoots. Next, we use $s_{l_i}^{fp}$ and $s_{l_i}^{mp}$ as the survivorship of female and male pupae, respectively, to accommodate sex-specific pupal parasitism (Cronin and Gill 1989), which we allow to vary with latitude l_i. With these considerations, the density of male and female bagworms at the onset of adulthood in generation $T + 1$ can be written as follows:

$$M_0(T + 1) = s^L s_{l_i}^{mp} L(T + 1)/2$$

$$F_0(T + 1) = s^L s_{l_i}^{fp} L(T + 1)/2. \qquad (8)$$

Note that this formulation assumes that at the end of the larval phase (i.e., after egg laying, egg hatch, larval redistribution, and larval survivorship have all concluded) the local sex ratio remains 1:1 (hence the division by two in Eq. 8), but, after this point, sex-dependent pupal survivorship may occur. To extend the process of population growth into the next year, the total male and female densities calculated by Eq. 8 are used in the next iteration of Eq. 1.

Model parameterization

Season length.—We estimate season length, τ, as 101 days, running from the first to the last dates that any adult was observed to have emerged at any site (23 August to 18 November [87 days]) plus the maximum observed bagworm longevity (337 h [14 days]). This simply constrains the upper bound of integration; as no bagworms are alive at the end of this period, the exact value for τ has no effect on the final results.

Adult maturation functions.—We estimated the maturation functions for each latitudinal band, $g(t, \theta_{l_i}^f)$ and $g(t, \theta_{l_i}^m)$, using a detailed procedure that differed slightly for male and female bagworms. For males, the monitoring protocol involved repeated (typically 4–10) visits to a site. During each visit, one of us (M. Rhainds) collected a sample of bags (up to 33 bags per visit per site) to determine the proportion of male bags that harbored un-eclosed pupae (denoted p^{mp}) vs. the proportion of male bags from which adults had already emerged (denoted p^{me}). For each latitudinal band, monitoring data of the proportion of males emerged were grouped together to form a cumulative distribution function (CDF) of the empirical pattern of the "onset of adulthood" for that site as $p^{me}/(p^{mp}+p^{me})$.
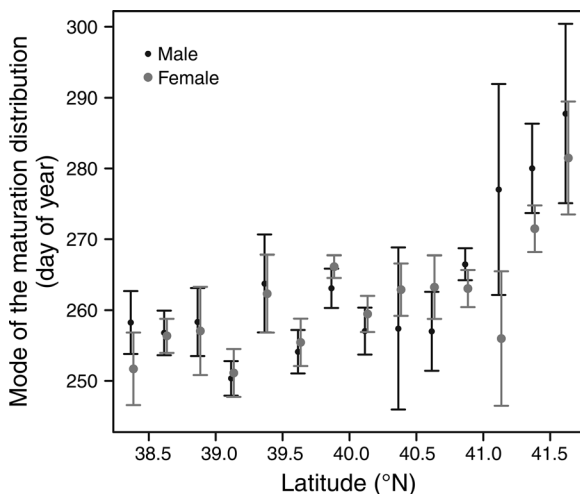
Fig. 3. Mode (± 2 SE) of the maturation distribution for male and female bagworms in each latitudinal band. Male and female modes have been offset slightly for clarity.

For females, the procedure was similar except that the number of live pheromonally "calling" females (denoted p^{fc}) was also recorded and, for the purposes of assessing the fraction of all mature adults, grouped with the proportion of bags containing dead adult females (both unmated p^{fu} and mated p^{fm}). The proportion of female bags that harbored un-eclosed pupae (denoted p^{fp}) was calculated as for males. The proportion $(p^{fc} + p^{fu} + p^{fm}) / (p^{fc} + p^{fp} + p^{fu} + p^{fm})$ provides an estimate of the onset-of-adulthood CDF for female bagworms at a site.

We next fit a gamma distribution to each of the male and female site-specific onset of adulthood CDFs using maximum likelihood with a binomial error structure to account for the binary nature of a bag containing a pupa or not. This approach provides standard errors for the parameters of the gamma distribution while accounting for unequal sample sizes across monitoring dates. Because monitoring dates differed among sites within a given latitudinal band, we used the fitted CDFs for each site to interpolate the relevant proportions for the union set of dates sampled across all sites within each band. Aggregating actual and interpolated proportions for the union set of dates across sites within bands, we then fit band-wide male and female gamma distributions for the onset of adulthood which we used as $g(t, \theta_{l_i}^f)$ and $g(t, \theta_{l_i}^m)$. (Appendix: Fig. A2; Fig. 3).

Adult death rates.—We estimated the adult death rates, $\alpha^m(t)$ and $\alpha^f(t)$, via a two-step process. First, we fit a Weibull distribution to longevity data for adult male ($n = 84$) and female ($n = 144$) bagworms. Constant death rates, corresponding to exponentially distributed longevity, were used extensively in earlier studies of protandry and asynchrony (Zonneveld and Metz 1991, Zonneveld 1992, Calabrese et al. 2008, Fagan et al. 2010). However, bagworm longevity data have an unambiguous interior mode (i.e., the peak occurs at neither limit), which makes

the Weibull distribution a more reasonable functional form. The best-fit male and female Weibull distributions were converted to time-specific death rates (Appendix: Fig. A3) by first noting that the survivorship function of the Weibull distribution is

$$S(a; \delta, \gamma) = e^{-(a\gamma)^\delta} \qquad (9)$$

where δ and γ are the shape and scale parameters, respectively. The survivorship function gives the probability that an individual survives to be a days old. The probability that an individual emerges on day t and lives a days is given by $g(t, \theta_{l_i}) S(a; \phi)$, where $\phi = (\delta, \gamma)$. The time-dependent age distribution is then obtained by normalizing this quantity, yielding the following (Calabrese 2012):

$$A(a, t; \theta, \phi) = \frac{g(t - a; \theta_{l_i}) S(a; \phi)}{\int_{-\infty}^{t} g(z; \theta_{l_i}) S(t - z; \phi) dz}. \qquad (10)$$

The Weibull hazard function is written as follows:

$$H(a; \phi) = \delta \gamma^\delta a^{\delta - 1} \qquad (11)$$

and describes how an individual's death rate changes with its age. The average death rate in the population at time t can then be obtained by averaging the hazard function over the age distribution (Calabrese 2012):

$$\alpha(t; \theta_{l_i}, \phi) = \int_{-\infty}^{t} H(t - a; \phi) A(t - a, t; \theta_{l_i}, \phi) da. \qquad (12)$$

Egg production per female.—We used the linear relationships between fecundity and total egg mass (Appendix: Fig. A4a) and fecundity as a function of latitude to derive a simple linear relationship between the number of eggs laid per female and latitude (Appendix: Fig. A4b):

$$\varepsilon = 4015.18 - 88.15 \times \text{latitude}. \qquad (13)$$

Egg production for a latitudinal band l_i is calculated at its midpoint.

Overwinter egg survivorship.—Because eggs overwinter within their maternal bag, egg survivorship, $s_{l_i}^E$, can be assessed by recording whether neonates emerged from their bag or died as eggs (Sheppard 1975). We estimated egg survivorship, which generally occurred uniformly as a bag-specific all-or-none event, for each of 104 populations between Tennessee and north Indiana ($n = 1$ to 32 bags per population). Overwinter survivorship data were modeled using logistic regression to yield estimates of egg survivorship s^E as a function of latitude (in °N):

$$\text{logit}(s^E) = 89.302 - 2.155 \times \text{latitude} \qquad (14)$$

where, as above, egg survivorship for a latitudinal band l_i is calculated at midpoint. Overwinter egg survivorship was very high in the south, but decreased steadily

above 40° N as a consequence of colder winters (Rivers et al. 2002; see also *Discussion*) (Appendix: Fig. A5).

Larval survivorship.—Larval survivorship was estimated based on data in Table 1 of Rhainds and Sadof (2008), and averaged 0.4 but was strongly dependent on bagworm density when measured on the scale of individual host plants (Appendix: Fig. A6). We modeled larval survivorship as a logistic function of larval density,

$$\text{logit}(s^L) = 1.041 - 0.007 \times \left(\frac{L}{K_L(l_i)}\right) \qquad (15)$$

where the larval carrying capacity $K_L(l_i)$ was modeled as an exponential function of latitude:

$$K_L(l_i) = \text{ceiling}[a_0 e^{-b_0 l_i}]. \qquad (16)$$

The coefficients a_0 and b_0 were estimated to be 41.9 and 0.50, respectively, using maximum likelihood for the resulting model-estimated matelessness q^* and assuming binomial error (Appendix: Fig. A7). The ceiling function in Eq. 16 enforces $K_L(l_i) \geq 1$ so that the latitudinal gradient in larval carrying capacity does not, in and of itself, reduce the maximum population to the point of creating an artificial extinction barrier.

Pupal survivorship.—Enemies, particularly pupal parasitoids (Balduf 1937, Kulman 1965, Sheppard 1975, Cronin 1989), can cause significant bagworm mortality. Pupal mortality affects males more than females (Cronin and Gill 1989), in some cases causing a shift from male-biased sex-ratio among pupae to female-biased sex ratio among adults (Rhainds and Sadof 2009). The parameters s^{fp} and s^{mp} were calculated for each site as 1 minus the fraction of female and male pupae, respectively, that showed evidence of predation or parasitism (e.g., perforated bags). Site-specific estimates of pupal survivorship declined with latitude (Appendix: Fig. A8a). We fit a logistic function to these data to estimate pupal survivorship in each latitudinal band, with estimates ranging from 0.68–0.97 for female pupal survivorship to 0.40–0.94 for male pupal survivorship. These estimates are in good agreement with literature estimates (Rhainds and Sadof 2009, Rhainds et al. 2009).

Mating-efficiency function.—The mating efficiency constant c governs the rate at which local densities of males and unmated females yield mated females. Because there is no evidence to suggest that mating efficiency in bagworms is related to male age or male density (see Calabrese et al. 2008), we adopted here the simplest functional form,

$$c = c_M \qquad (17)$$

where c_M is a constant that controls the rate of mating between males and unmated females. Because the sample size for actively calling females was too low to allow for direct estimation, the mating efficiency parameter, c_M, was estimated using data on mating success q^* (Eq. 5) and the carrying capacity of larvae measured in a study near Lafayette, Indiana (40°25′ N; Rhainds and Sadof 2008). In other words, c_M was fixed so that at the latitude of 40°25′ N (Latitude band 9), the model yielded female matelessness that agreed with empirical data. This value of c_M (0.98) was held constant for all latitude bands.

Creating a temperature-based model.—To link life-history variation in latitude to a mechanistic model based on air temperature time series, we extracted daily maximum temperature time-series data from all Indiana weather stations for the 50-year period 1960–2010 as supplied by the Global Historical Climatology Network (GHCN)-Daily database (Menne et al. 2012). We used these temperature time series to construct statistical models linking observed overwinter egg survivorship, fecundity, and female pupal survivorship to air temperatures in winter (October–March) and spring (February–May and April–May), respectively. For overwinter egg survivorship, we used the functional form developed in Rhainds et al. (2013) for the probability of surviving a single 24-hour period as a function of maximum air temperature and egg mass, and overall overwinter egg survivorship as the product of this function over the 182-day period between 1 October and 31 March:

$$s^E(T_{\max}, m) =$$

$$\prod_{i=1}^{182} \frac{1}{1 + \exp(-[p_1 * T_{\max} + p_2 * m + p_3 * T_{\max} * m])} \qquad (18)$$

where the parameters p_1, p_2, and p_3 were estimated by fitting this function to survivorship in those latitudinal bands that had climate data over the winter period, and egg mass (in grams, not to be confused with egg number as described in Eq. 13) was modeled as a function of latitude as

$$m = 2.315 - 0.0508 \times \text{latitude}. \qquad (19)$$

The six-month time period used to calculate overwinter egg survivorship is wider than required but survivorship is ~1 for days at the margins of this period and the exact span used does not affect the final survivorship estimates.

The number of eggs produced per female is a function of female size, which itself is a function of the number of degree days accumulated during larval development in early spring. We modeled egg production as a function of the mean (1960–2010) cumulative number of degrees over 14.4°C (Neal et al. 1987) between 1 February and 31 May as

$$\varepsilon = 80.5795 - 0.904 \times \text{DD} \qquad (20)$$

where the number of degree days DD is measured using the maximum daily temperature as opposed to the more traditional mean daily temperature. Unlike Eq. 13, which is a phenomenological model linking egg production to latitude, Eq. 20 allows us to predict egg production under future climate scenarios.

The final component required to create a temperature-based dynamical model for the bagworm is female pupal survivorship (fps). We used a logistic regression to model female pupal survivorship as a function of mean spring air temperature (Appendix: Fig. A8b) and found the following relationship:

$$\text{logit(fps)} = -19.41 + 1.08 \times T_{\text{spr}} \qquad (21)$$

where T_{spr} is the mean value of daily maximum air temperatures for the spring months of April and May.

Model validation across the northeast corridor.—Our temperature-based bagworm model allows us to validate the model using a different portion of the bagworm's northern range boundary; here we apply our model to temperature time series extracted from long-term weather stations along the northeast corridor stretching from Kentucky to Maine.

As before, we used maximum daily temperature data for the 50-yr period 1960–2010 as supplied by the GHCN-Daily database (Menne et al. 2012). We selected weather stations with complete or nearly complete temperature records over this period, restricting our analysis to those stations below 200 m in elevation. Years with missing temperature data over the periods of interest for the model were excised from the time series. As a result, some time series are shorter than 50 years in length, but all time series are long enough to establish the persistence/extinction dynamics implied by the model. We compared our model predictions to the most recent range map of bagworm occupancy available (Wollerman 1971).

Predicted range changes with future climate change.—To generate future temperature time series under various climate warming scenarios over the original spatial extent of the data (for which we have the best current occupancy data), we fit second-order polynomial curves to the historical (1960–2010) daily maximum temperature data to capture the underlying pattern of temperature change over the period of interest (October–March for overwinter survivorship; February–May for fecundity). We fit a different polynomial curve for each latitudinal band but averaged all the complete temperature time series available for all weather stations within a band across the years (so the maximum number of time series averaged was the number of stations × 50). The difference between each time series and that polynomial curve "average" was saved as a time series of residual variation capturing not only the variance of daily air temperature but also its temporal autocorrelation. New time series were generated as

$$T_{\text{max}} = \text{baseline} + \text{offset} + \text{variance scaling factor}$$
$$\times \left(\frac{\text{residual time series}}{\text{SD(residual time series)}} \right) \qquad (22)$$

where "baseline" is the latitude-specific polynomial curve capturing the average temperature profile over the period of interest, "offset" is the increase in mean temperature due to climate change, and "residual time series" is sampled from the distribution of residual time series for that latitudinal band. By dividing this residual time series by its standard deviation and multiplying by a variance scaling factor, we simulate time series with known standard deviation to study the impact of changing day-to-day variability under potential climate-change scenarios.

We simulated time series over a combination of mean and standard deviation scenarios, where mean temperatures were increased in the range 0–5°C (consistent with the general scale of temperature warming predicted to occur by 2051 by the Canadian Regional Climate Model version 4.2 [Music and Caya 2007]). We considered standard deviations for the residuals in the range of 2–7°C, which reflects both increasing and decreasing variance relative to the historical average (historical winter residual standard deviation ~6.0°; historical spring residual standard deviation ~5.8°). For each latitudinal band we generated 500 replicate potential future time series under each of the different future climate scenarios. Using Eqs. 18–21 we estimated female pupal survivorship, overwinter egg survivorship, and fecundity under each of these 500 replicate time series. To examine bagworm persistence under mean conditions, we ran our model (Eqs. 1–12, 15–17) using these mean life-history values. To examine situations where temperature, and hence life-history parameters, varied stochastically from year to year, we sampled with replacement from the distribution of life-history values predicted under each future climate scenario. Average bagworm persistence in a stochastically varying environment was calculated as the fraction of trials ($n = 100$) in which the bagworm population survived 20 years from the initial conditions, a period extending beyond the timing of population collapse under non-stochastic conditions.

RESULTS

Predicting the bagworm's northern range limit

The current northern range limit of *Thyridopteryx ephemeraeformis* in Indiana (USA) is predicted by the model to lie at 41° N (Figs. 4 and 5). Despite containing no free parameters, this is remarkably close to the empirical range limit, which lies between 41° and 41.5° N (bagworms are found north of 41.5° N in Indiana but in very low numbers). Although a latitudinal gradient in larval carrying capacity $K_L(l_i)$ (Eq. 16) was necessary for the model to reproduce the empirical increase in lifetime female matelessness $q*$ observed near the geographic range boundary, the prediction of the northern range limit at 41° N is unchanged if a constant carrying capacity is used instead. Consequently, our calculated location of the range boundary is not simply an artifact of decreasing larval carrying capacity with increasing latitude.
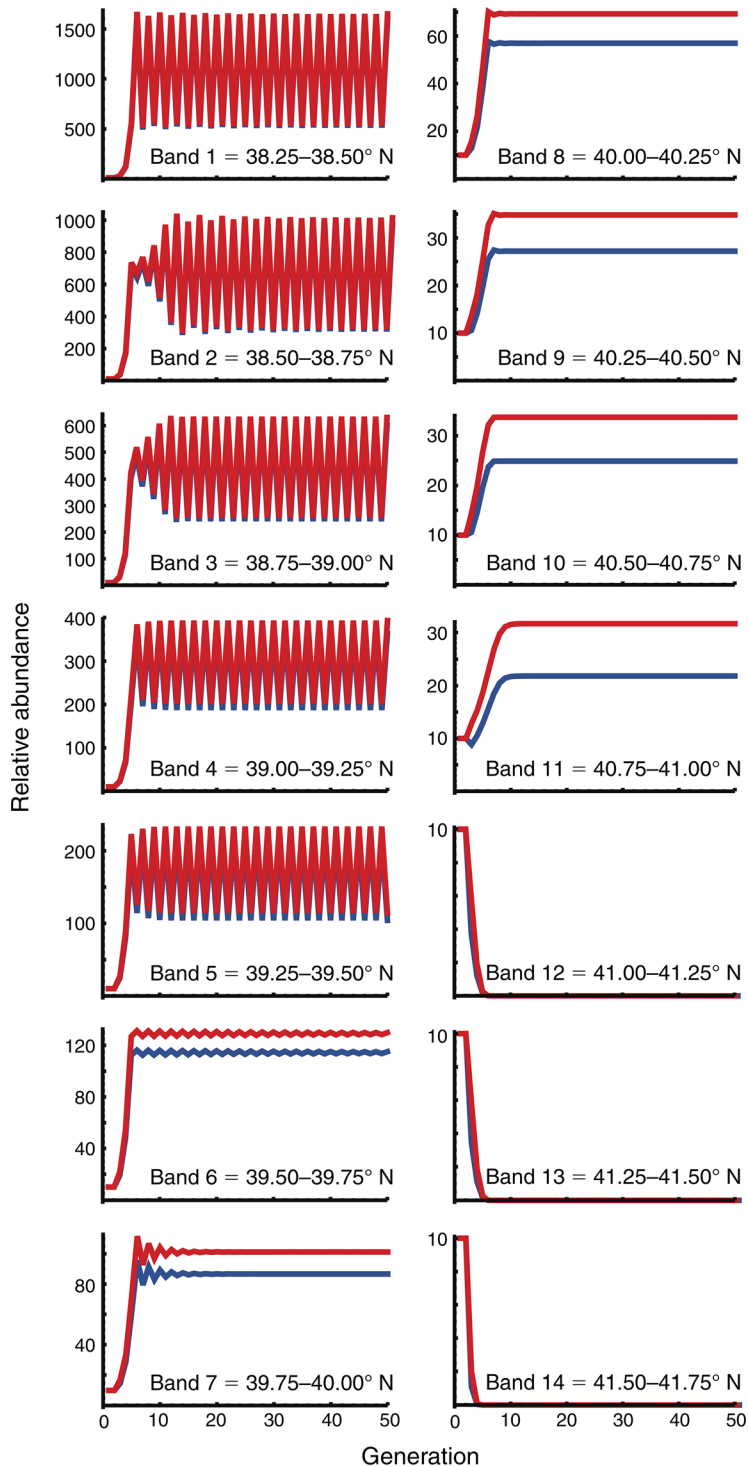
FIG. 4. Model-predicted time series (males in blue, females in red) for each of the 14 latitudinal bands examined using the empirically estimated parameter values. Populations uniformly go extinct in the three northern bands (41–41.25° N, 41.25–41.5° N, and 41.5–41.75° N).

PLATE 1. Female bagworm that died prior to successfully mating. Photo credit: Cliff Sadof.

Sensitivity of the northern range limit to components of life history

To assess the relative importance of egg production, egg overwinter survivorship, and male and female pupal survivorship for the geographic range boundary, we took all life-history values for an intermediate latitude band (39.50–39.75° N, where the model predicts persistence) and decreased each of these four factors in turn until the model yielded extinction. Persistence was least sensitive to male pupal survivorship, which required an 89% reduction from its initial value. Female pupal survivorship required a 63% reduction for extinction to occur. Egg production and overwinter egg survivorship are both directly related to the number of larvae produced each year, and each required a 54% reduction for extinction to occur. While the latter two factors (egg production and egg survivorship) are the most important for bagworm persistence, overwinter egg survivorship declines more sharply with latitude than egg production and, in Indiana, is ultimately limiting for bagworm populations at its northern range limit (Fig. 5).

Our model uses empirically derived adult maturation phenology (and hence, reproductive asynchrony) and uses the constraints imposed by data on lifetime female matelessness q^* to estimate the mating-efficiency coefficient c_M. There are, however, tradeoffs between these two facets of reproductive biology and other model parameters (e.g., overwinter egg survivorship), which can shift the persistence/extinction threshold spatially (Fig. 6).

Temporal dynamics

For fixed life-history parameter combinations leading to persistence, the temporal development of bagworm populations involves a monotonic rise to a steady-state condition of equilibrium, or two-phase oscillation, preceded by transient dynamics that disappear after the first 1–20 generations (Fig. 4 and Appendix: Fig. A9). At lower latitudes, closer to the bagworm's core range, we predict a two-phase steady state that declines with increasing latitude until only a single unvarying steady state is achieved. At further increasing latitudes, the population abundance at this fixed-point solution declines until no nonzero population can be sustained.
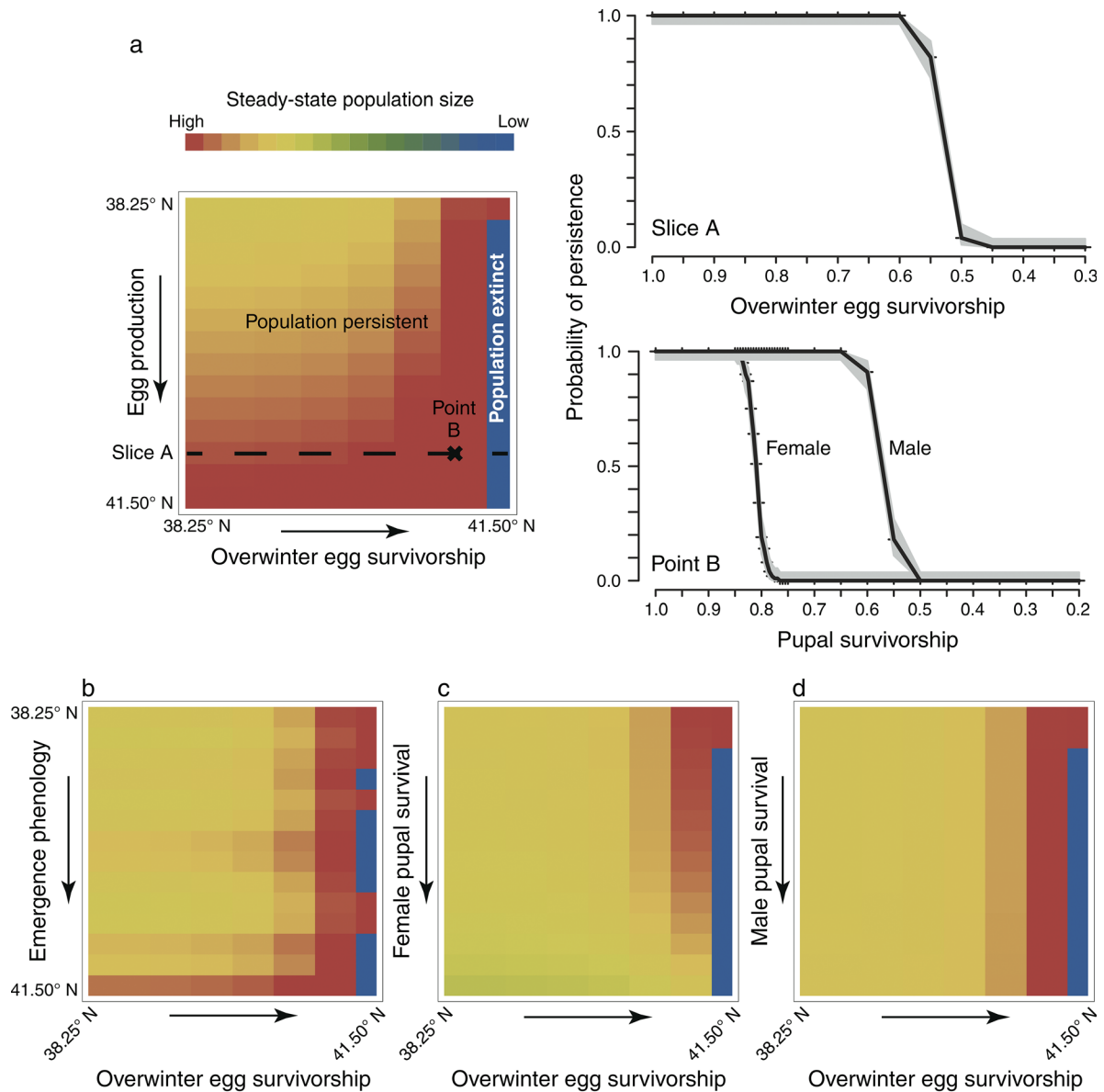
FIG. 5. Female bagworm dynamics under varying combinations of life-history parameters. All parameters not varied are held at their values for the southernmost latitudinal band (38.25–38.50° N). Note that increasing mean abundance as overwinter survivorship declines is an artifact of holding all other parameters fixed and is a consequence of the strong density dependence associated with larval survival. Decreasing overwinter survivorship (in the absence of changes to the other model parameters expected with increasing latitude) leads to a decrease in the amplitude of abundance oscillations with no corresponding change in the abundance at steady state; as a result the mean abundance actually increases as the range boundary is approached. (a) The figure at the left shows the average steady-state population of female bagworms for varying values of egg production and overwinter egg survivorship. The line graph to the upper right shows the probability of bagworm persistence as a function of mean overwinter egg survivorship, representing the cross-section "Slice A" indicated at left by the horizontal dashed line. The number of eggs surviving winter in each model time step is drawn from a binomial distribution, so the probability on the x-axis represents the mean probability of survivorship. The confidence interval (95th percentile) calculated using Clopper-Pearson exact confidence interval is indicated by gray shading. The line graph to the lower right shows the probability of bagworm persistence as a function of mean female or male pupal survivorship, respectively (with male pupal survivorship held at 1.0 for the curve labeled "Female" and female pupal survivorship held at 1.0 for the curve labeled "Male"), representing a profile at "Point B" indicated at left by the black "x." The number of surviving pupae in each model time step is drawn from a binomial distribution, so the probability on the x-axis represents the mean probability of female or male pupal survivorship. (b) Average steady-state population of female bagworms for varying values of adult emergence phenology (i.e., set to the empirical value for each latitudinal band), (c) female pupal survivorship, and (d) male pupal survivorship; all vs. overwinter egg survivorship.
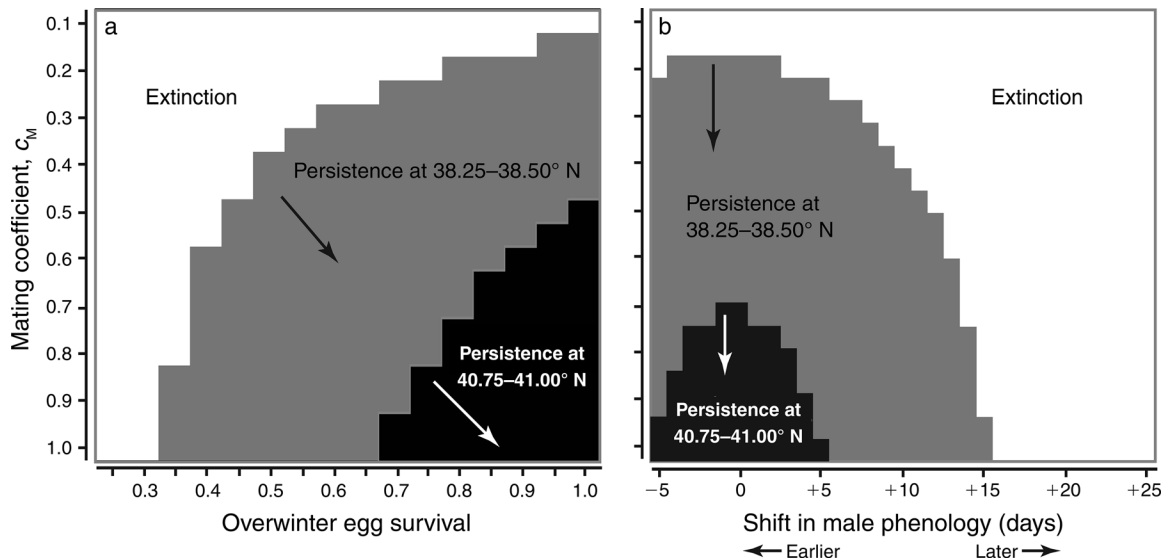
FIG. 6.   Population persistence as a function of the mating coefficient c_M and (a) overwinter egg survivorship or (b) male phenology shift, with all remaining parameters taken from the latitudinal bands 38.25–38.50° N and 40.75–41.00° N. Male phenology was shifted by changing the shape parameter of the emergence distribution so that the mean emergence was increased or decreased by an integer number of days relative to the empirical data. As noted in the text, we found $c_M = 0.98$ for the bagworm (*Thyridopteryx ephemeraeformis*).

The dynamics under empirical interannually varying temperature profiles are more complex and represent a convolution of the two-phase oscillation generated under fixed life-history parameters and stochasticity associated with climate variability (Fig. 7). The dynamics of persistent populations near the range edge suggest a slowing down and reduction in amplitude of the oscillations consistent with what was found under fixed life-history parameters.

Model validation along the northeast corridor

Using temperature time series for weather stations along the northeast corridor, we find broad agreement between our model predictions and the available occupancy data, although fine-scale comparison along the range boundary is difficult because the occupancy map is of relatively low spatial resolution, and metadata to distinguish stable populations from transient populations or collections of vagrant individuals are not available. Our model predicts population persistence south of (and including) Pennsylvania, and extinction north of (and including) New York with populations that persist briefly but ultimately go extinct in New Jersey and northern Ohio (Fig. 7).

While, as discussed above, we found overwinter egg survivorship to be the limiting factor for bagworm persistence in Indiana, our application of the temperature-based model to the northeast corridor indicates that the limiting factor for bagworms actually changes along the range edge (Appendix: Fig. A10). Bagworm populations in inland areas (such as Indiana) appear limited by overwinter survival of eggs (extreme overwinter temperatures) whereas in coastal areas (Long Island, New York; southern New Jersey), bagworm populations appear more strongly limited by female pupal survivorship (colder spring temperatures). In some cases, multiple factors appear responsible for population extinction. For example, the temperature profiles for Dobbs Ferry, New York, and Holtwood, Pennsylvania, are very similar and both populations experience a sharp population decline following low egg production and low female pupal survivorship in year 7. The Dobbs Ferry population, however, declines to extinction following low egg survivorship in year 8 while the Holtwood, population recovers and ultimately persists for the full time series considered (Appendix: Fig. A11). In other words, low egg survivorship was the proximate cause for the predicted extinction at Dobbs Ferry, New York, even though it was low egg production and low female pupal survivorship that made the population vulnerable to extinction.

*Range shifts due to climate change—climate means vs. climate extremes*Using mean life-history parameter estimates, bagworm persistence is a strong function of climate means; assuming no change in variability, increases of 1–2°C would be required to permit persistent bagworm populations in the three northern-most latitudinal bands considered (41.0–41.75° N) (Fig. 8). However, a more realistic scenario is captured by the stochastic model in which survivorship and fecundity are allowed to vary annually. In this latter case, increasing mean temperatures are no longer sufficient to allow bagworm persistence, and the model predicts persistent populations only for much larger increases in mean temperatures or under a combination of increasing mean and decreasing variance (Fig. 8).
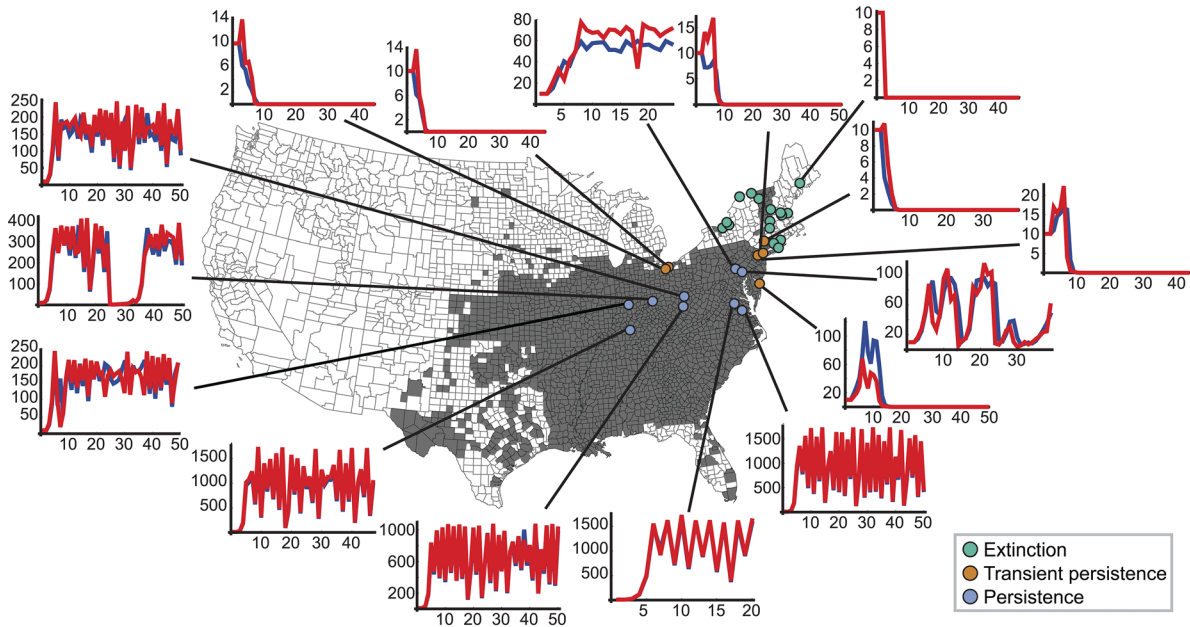
Fig. 7. Map of bagworm occupancy (gray counties; adapted from Wollerman [1971: Fig. 1]) and abundance time series (red, females; blue, males) predicted by the temperature-dependent model for temperature time series extracted from long-term weather stations throughout the northeast United States. All insets represent relative abundance (*y*-axis) vs. year (starting in 1960). We discarded any years for which the required temperature data were missing; as a result, some of the time series are <50 years in length. Only stations <200 m in elevation were selected. Only one representative time series is shown for the sites at which bagworm populations went immediately extinct.

DISCUSSION

Understanding which factors determine the size of a species' geographic range, and, in particular, which factors operate at the edge of the geographic range to prevent the species from spreading further can provide crucial insight into many issues. These issues include the relative dominance of narrowly endemic species (vs. widespread species), latitudinal gradients in diversity and food-web complexity, the differential success of potentially invasive species, and the roles that density dependence plays in ecological systems (Liebhold and Tobin 2008, Gaston 2009). Understanding the mechanisms behind species' geographic range boundaries is all the more urgent because ongoing climate change has tremendous potential to reshape species distributions globally (IPCC 2007). Such changes in distribution will likely affect species differentially, making them especially problematic because they may disrupt species interactions and food webs locally (Post et al. 2009).

Climate envelope models, the traditional models for projecting the biogeographic consequences of climate change, focus on apparent physiological tolerance as a driver of current (and hence future) distributions. These approaches ignore the potential contributions of ecological and behavioral mechanisms to distributions (Pearson and Dawson 2003, Guisan and Thuiller 2005, Chown and Gaston 2008), cannot distinguish between mechanisms sensitive to climate means or climate extremes, and cannot easily capture a change in the range-limiting factor along a range boundary. Our stochastic simulations of potential future temperature time series highlight the importance of temperature extremes, not only within a single year but over multiple years, as constraints on population expansion, even when mean climate conditions would suggest population persistence and subsequent range expansion should occur. Because even rare cold snaps can drive an otherwise persistent population extinct, the long-term population and range dynamics governed by climatic extremes are fundamentally different than would be suggested by considering just an "average" year. This distinction would be difficult to capture using a climatic envelope model parameterized using average climatic conditions.

Density-independent factors dominant drivers of the northern bagworm range limit

One of the oldest debates in ecology surrounds the relative importance of fecundity and mortality factors (both density independent and density dependent) as population controls (e.g., Stiling 1988). In the bagworm system, at least three kinds of density-dependent processes operate intensely (i.e., density-dependent larval mortality, inversely density-dependent parasitism [Cronin 1989], and inversely density dependent asynchrony-driven mating failure), but even so, we found strong evidence that two density-independent factors (extreme midwinter temperatures and average spring

temperatures) were primarily responsible for determining the bagworm's northern range limit.

While Cronin (1989) attributes the bagworm's high rate of local extinction (Table 1) to unspecified density-independent mortality factors, the only previous study to cite overwinter egg mortality, specifically, as a key bagworm population constraint was an early study by Balduf (1937) in Illinois, USA. Previous studies in milder U.S. climates focused on parasitism as a key factor in controlling population growth (Kulman 1965 [West Virginia], Barrows 1974 [Kansas]), or found multiple factors (including parasitism, predation, and biased sex ratio) variably important across space and time (Horn and Sheppard 1979 [Ohio]). Emerging from these studies, and our own synthetic life-history model, is a consensus that the relative importance of demographic constraints on population growth varies considerably across the species' range. We found that, as measured by percentage change, bagworm persistence in Indiana is most sensitive to a decline in overwinter egg survivorship, but our application of the temperature-dependent bagworm model to the U.S. northeast illustrates that, in some coastal areas, female pupal survivorship is expected to decrease more sharply than overwinter egg survivorship due to a moderation of extreme temperatures and relatively colder spring temperatures. As a result, female pupal survivorship appears to be the dominant constraint in coastally influenced microclimates even as overwinter survivorship is more important at larger scales. While our analysis of temperature time series for the U.S. Northeast predicts a range boundary that is slightly further south than suggested by the U.S. Forest Service occupancy map (Fig. 7), we hypothesize that this discrepancy stems from a bias in the locations of the weather stations themselves, transient populations that lead to county records, and unusual circumstances such as the repeated, human-aided transport of infested plants to Christmas tree nurseries in New England (Wollerman 1971).

In sum, factors limiting local populations throughout the bulk of the bagworm's range may not set the geographic range boundary, and factors determining the range limit in one area may not be responsible for the range limit in other areas. Even along a single range boundary, the dominant constraint on expansion may depend on site-specific microclimatic conditions that may be overlooked using a less mechanistic climate-envelope approach. This spatial heterogeneity permits spatial occupancy to respond to climate change via multiple modes, including range translations, expansions, and contractions (Doak and Morris 2010), particularly if changes in climate variability outpace expected increases in mean temperatures. This spatio-temporal complexity highlights the importance of comparative population studies across range core and range margin habitats.

Temporal dynamics

Our model predicts that bagworm populations at the "metapopulation" scale of 0.25° latitudinal bands will exhibit oscillatory behavior toward the core of their range, which dampens and disappears toward the species' northern range limit. Strong density dependence in larval survivorship drives this periodicity; as larval density (relative to carrying capacity) declines with increasing latitude, these oscillations decrease in magnitude and eventually disappear. Foliage-feeding forest insects frequently demonstrate such oscillatory behavior (Liebhold and Kamata 2000). However, the only time-series data available for *T. ephemeraeformis* populations exhibit a single peak in abundance followed by a dramatic population crash to local extinction (Horn and Sheppard 1979). That early study included only six years of data for one local population. As such, the results are unlikely to map cleanly onto larger spatial scales (i.e., high defoliation rates may have decreased local food availability [Rhainds et al. 2009]). At larger spatial scales, male bagworm dispersal among local populations would be expected to stabilize the meta-population dynamics, yet our model predicts two-phase cycles dampening with increasing latitude. Unfortunately, the data are not currently available to describe the dynamics at these larger spatial scales.

Range shifts with climate change

Our findings of a clear latitudinal threshold in egg survivorship confirm laboratory studies (Rivers et al. 2002) demonstrating that bagworm eggs have a finite tolerance for extended cold temperatures. As minimum winter temperatures are expected to increase in the U.S. Midwest over the next few decades, a non-stochastic model capturing only the mean life-history response to warming temperatures would predict a significant northward expansion of the bagworm range through northern Indiana and Illinois, Wisconsin, and Michigan's Upper Peninsula. However, our results illustrate the importance of climate extremes in setting geographic range limits. Interannual variability in survivorship and fecundity significantly decreases the climatic parameter space under which bagworm populations can be maintained and demonstrate the importance of day-to-day temperature variability (which is generally expected to decrease in the U.S. Midwest under climate change [Vinnikov et al. 2002, Medvigy and Beaulieu 2012]) that can produce extreme conditions with sufficient frequency that populations are driven to extinction even where mean conditions are suitable for persistence.

Many studies have considered how range boundaries will respond to 21st century climate change (Williams and Leibhold 1995, Parmesan et al. 1999, Musolin 2007, Deutsch et al. 2008, Hill et al. 2011). Minimum winter temperatures are often bottlenecks for overwinter survival of eggs and diapausing adults (Bale 1991, Carroll et al. 2004, Bale and Hayward 2010) and, as a consequence, are thought to constrain range expansion
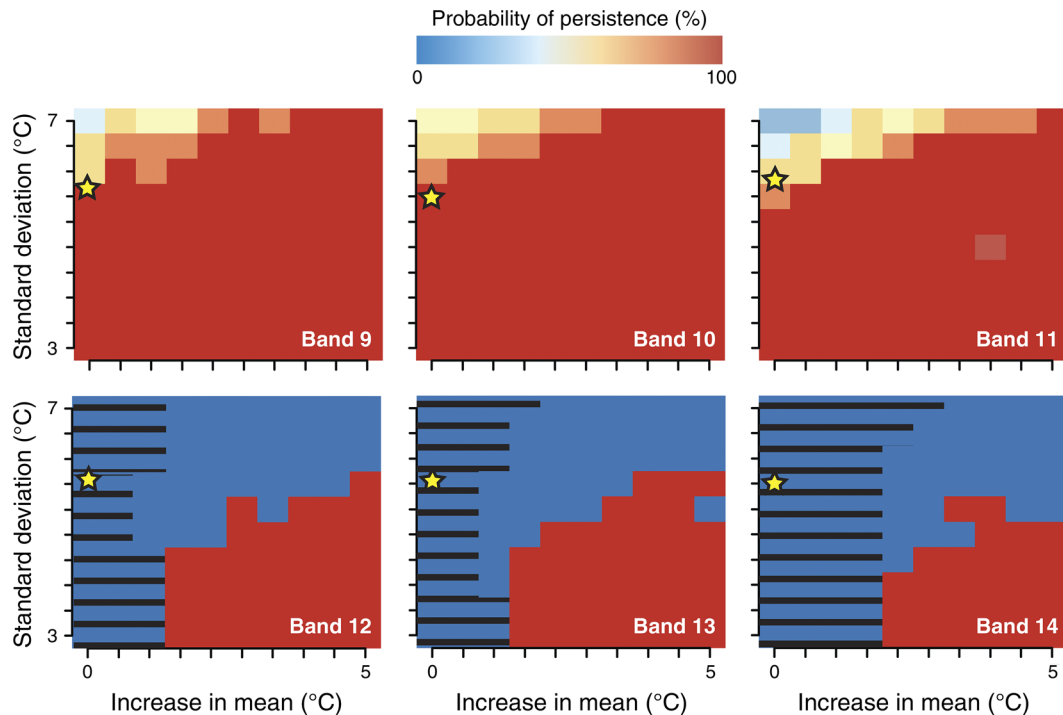
FIG. 8. Bagworm population persistence under a stochastic population model and varying scenarios of future climate in latitudinal bands 9–14, which are the three bands just south (9–11) and north (12–14) of the current bagworm northern range limit. All parameters except those explicitly modeled as a function of temperature were held fixed at the value estimated for that latitudinal band (e.g., emergence phenology, male pupal survivorship). The color scale represents the probability of persistence (out of 100 trials) to year 20 of the simulation. The areas with black horizontal striping represent climate conditions under which bagworm populations go extinct even under a non-stochastic model. Note that conditions for persistence are always more strict under a stochastic model compared to the non-stochastic model. The yellow star represents current climate conditions for each latitudinal band (these are similar but not exactly the same for each band).

for many insect species (Baskauf and McCauley 2001, Crozier 2003, 2004, Crozier and Dwyer 2006, Robinet and Roques 2010). Ungerer et al. (1999) found the northern range limit for the southern pine beetle *Dendroctonus frontalis* was set by lethal overwinter temperatures and predicted a northern expansion with climate change. Tran et al. (2007) found that previously unexpected southern pine beetle outbreaks as far north as Ohio were directly related to shifting mid-winter temperatures. A similar mechanism was invoked to explain widespread mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in British Columbia (Kurz et al. 2008), and northern range expansion of the pine processionary moth *Thaumetopoea pityocampa* (Battisti et al. 2005) and the winter moth *Operophtera brumata* (Jepsen et al. 2008). Pupal parasites, which represent an important source of mortality for bagworms, may also be affected by climate extremes (Hance et al. 2012), but the effect of climatic extremes on the parasitoid–host dynamic of bagworms remains an open question.

Applications

Our synthetic modeling approach, while clearly applicable to many insect species, is also broadly applicable to other seasonally reproducing animal and

plant systems. For example, amphibian populations possess many of the characteristics input into our model. Amphibians, being ectothermic, are also sensitive to extreme overwinter climatic conditions (Tattersall and Ultsch 2008). For example, populations of the Columbia spotted frog are expected to enjoy increased viability due to improved survivorship and reproduction associated with milder winters brought by climate change (McCaffery and Maxell 2010), and yet occupancy predictions from species distribution models are unreliable at spatial scales relevant for amphibian conservation (Trumbo et al. 2011). Development of detailed, mechanistic models like that developed here to help understand constraints on amphibian range expansion may help predict distribution changes for these species, which are some of the most vulnerable to climate change (Lawler et al. 2009). Likewise, similar approaches could benefit our understanding of plant species' responses to global climate change, where the interplay between phenology and demography can significantly impact population growth (Cleland et al. 2007, Doak and Morris 2010).

Key research needs

To extend our efforts to other taxa and/or explore bagworm dynamics in other contexts, a better under-

standing of the mating coefficient c_M and, more broadly, the mating function $c(\cdot)$ is essential. This metric, which quantifies how contacts between males and females translate into successful fertilization, is likely to vary widely across species. Often, $c(\cdot)$ will also vary as a function of such factors as female reproductive histories, male density, male age (or other measures of male quality or experience), and behavioral strategies (Caswell 2001). Interest in the consequences of, and empirical evidence for, various mating functions has blossomed recently (Calabrese et al. 2008, Bessa-Gomes et al. 2010, Miller and Inouye 2011). Ecologists now recognize that subtle variations in mating functions can have substantial impacts on core population metrics, with different functional forms for mating efficiency leading to widely divergent population fates (e.g., collapse to extinction vs. persistence) even when all other factors are held constant (Fagan et al. 2010).

For bagworms, we assumed that c_M was fixed as a function of latitude, but larger sample sizes of pheromonally "calling" females as a function of time would permit direct estimation of the mating rate in local populations. The mating coefficient might be expected to decline with decreasing male and female abundance if low densities made it difficult for male bagworms to find calling female bagworms during their short life spans. Our model demonstrates how a decrease in c_M would drive the northern range limit further south than would be predicted by overwinter mortality alone (Fig. 6). Such an Allee effect would also constrain northward expansion of bagworm populations even if environmental conditions were to ameliorate and allow colonization and persistence in more northerly locales. Researchers studying gypsy moths, another lepidopteran pest species with flightless females, have demonstrated the critical roles that Allee effects play in the establishment and persistence of nascent populations (Vercken et al. 2011) and in determining the species' overall rate of spatial spread (Johnson et al. 2006, Contarini et al. 2009). Additional data on populations at the bagworm's range boundary and, if possible, populations experimentally introduced north of the boundary, are needed to identify what density and spatial distribution of peripheral populations are sufficient for successful mating and population persistence.

Insect populations' adaptations to climate change may include changing physiological tolerances (Chown et al. 2011), and shifts in voltinism (Hansen et al. 2001, Jönsson et al. 2009), host species (Braschler and Hill 2007), phenology (Yurk and Powell 2009, Hodgson et al. 2011), or morphology (Hill et al. 2011). Our predictions for bagworm range expansion addressed only the physiological-tolerances mechanism, but a thorough consideration of insect adaptation, particularly for species spreading into formerly unsuitable habitat, may permit more biologically realistic predictions for future biogeographic patterns. Studies of butterflies find larger thorax size and changes in wing aspect ratio in recently colonized sites, consistent with adaptation for greater dispersal (Hill et al. 1999). Similarly, a study of damselflies found higher wing aspect ratios (i.e., narrower wings, which influence flight capability) in populations at the range margin (Hassall et al. 2009). Morphological measurements on species taken across a broad latitudinal range may illuminate some of the same evolutionary mechanisms and, by reflecting variation deemed adaptive at the range margin, may identify constraints on population persistence in founding populations (Bridle and Vines 2007; see also Cwynar and MacDonald 1987 and Phillips et al. 2006). Were it to be found, the evolution of greater dispersal capacity in range-margin bagworm populations would have profound effects on the time scale of redistribution and would likely facilitate metapopulation persistence in marginal areas through greater exchange among isolated populations.

Our synthetic modeling approach, which allows researchers to explore the interplay among multiple demographic mechanisms, some of which change spatially, offers clear advantages for exploring how the balance between births and deaths sets species range boundaries. Expanding this approach to consider adaptive evolutionary change may allow even more accurate predictions of species' future distributions (Travis and Dytham 2002). Identification of other animal model systems for exploring range-margin dynamics will allow us to unravel the feedbacks between ecology and evolution in species' response to climate change.

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SUPPLEMENTAL MATERIAL

Appendix

Eleven additional figures showing the fit of each element of the model to the empirical data available (e.g., bagworm dispersal, male and female emergence phenology, life span, and fecundity) (*Ecological Archives* M084-007-A1).

Data Availability

Data associated with this paper have been deposited in Dryad: http://dx.doi.org/10.5061/dryad.1v02q