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Abstract. A change in climate is known to affect seasonal timing (phenology) of the life stages of poikilothermic organisms whose development depends on temperature. Less understood is the potential for even greater disruption to the life cycle when a phenology shift exposes photoperiod-sensitive life stages to new day lengths. We present a conceptual framework and model to investigate the ways that photoperiod-cued diapause can interact with a change in climate or latitude to influence voltinism in poikilothermic organisms. Our degree-day phenology model combines detailed spatial climate data, latitude- and date-specific photoperiods, and development and photoperiod response parameters. As an example, we model the biological control beetle *Galerucella calmariensis* and map the number of generations expected following its introduction into diverse climates throughout the continental United States. Incorporation of photoperiodism results in a complex geography of voltinism that differs markedly from predictions of traditional phenology models. Facultative multivoltine species will be prone to univoltism when transported to either warmer or southern climates due to exposure of the sensitive stage to shorter day lengths. When moved to more northern locations, they may attempt too many generations for the season duration thereby exposing vulnerable life stages to harsh weather in the fall. We further show that even small changes in temperature can result in large and unexpected shifts in voltinism. Analogous effects may be expected for organisms from wide variety of taxa that use photoperiod as a seasonal cue during some stage of their life cycle. Our approach is useful for understanding the performance and impacts of introduced pests and beneficial organisms as well as for predicting responses of resident species to climate change and climate variability.

Key words: biological control; climate change; diapause; introduced species; invasive pests; model; phenological mismatch; phenology; photoperiod; seasonal adaptation; seasonal asynchrony; voltinism.

Introduction

As a result of both global climate change and human-assisted transport to new regions, plant and animal populations are increasingly being exposed to climates that are different from the ones to which they are adapted. A key characteristic of locally adapted organisms in seasonal environments is that their life cycles are precisely timed to align with favorable environmental conditions and resources (Danilevskii 1965, Tauber et al. 1986, Van Asch and Visser 2007). Organisms use a variety of cues to do this, but a dominant cue in temperate zones is photoperiod (Bradshaw and Holzapfel 2007, Denlinger 2009). Life cycles that are cued by photoperiod occur in wide variety of taxa including insects, mammals, birds, fish, plants, and fungi (Bradshaw and Holzapfel 2007, Nelson et al. 2009). Typically, the photoperiod response takes the form of the initiation or termination of life cycle activities such as development, reproduction, or dispersal when a sensitive life stage is exposed to a photoperiod that is shorter (or longer) than a critical threshold (the critical photoperiod). Although it is an indirect cue, photoperiod is a reliable one for predicting local conditions in the near future because it correlates precisely with the day of year. In contrast, cueing only on the physical conditions themselves (e.g., temperature, moisture) is often unreliable because of the potential for periods of aberrant and unseasonable conditions and because of the need for physiological preparation to occur in advance of those impending conditions.

Since both photoperiod and the expected timing of favorable conditions vary geographically, the critical photoperiod that optimizes phenology for a population is specific to a particular location. This is evidenced by numerous documented geographic clines in the critical photoperiod along climatic and latitudinal gradients for insects and other organisms in their native or long-established ranges (e.g., Danilevskii 1965, Tauber et al. 1986, Gomi 1997, Masaki 1999, Bradshaw and Holzapfel 2007). When a population is moved to a new location with even a slight difference in climate, latitude, or seasonal timing, the genetic-based photoperiod response is likely to be mal-adapted, leading to a life cycle that is asynchronous with resources or that includes too many

or too few generations for the season duration (Danilevskii 1965).

Two recent studies of introduced biological control insects are good examples of these effects. Bean et al. (2007) showed that the tamarisk leaf beetle (*Diorhabda elongata* Brullé *deserticola* Chen, now *D. carinulata* (Desbrochers)), a multivoltine species from central Asia, was unable to establish in the United States south of 38° N latitude because the day length was never long enough to cue a second generation. Instead adult beetles entered diapause early in the summer after just one generation and were unable to survive the extended period of diapause to the following spring. Grevstad et al. (2012*b*) showed that populations of the planthopper *Prokelisia marginata* (van Duzee) originating from four different climate regions (three eastern U.S. states and California) and introduced into common field sites in coastal Washington State emerged from overwintering at different times spanning several weeks. The order of spring emergence of these populations corresponded with the arrival of favorable conditions in their source locations, not their current location, consistent with dependence on a photoperiod cue. Such shifts in phenology relative to resources can be critical for survival. As an example, Van Asch et al. (2007) showed that just five days difference in the egg hatch date of the winter moth (*Operophtera brumata* L.) relative to the budburst of its host reduced larval and pupal survival by approximately 80% and 68% respectively. Bradshaw et al. (2004) showed how decoupling the photoperiod and temperature seasonal cycle using environmental chambers (comparable to a change in latitude) could cause up to 88% reduction in fitness in the pitcher plant mosquito *Wyeomyia smithii* (Coquillett).

Although the adaptive functions and fascinating mechanisms of photoperiodism have received decades of attention, especially in plants and insects (reviewed by Danilevskii 1965, Beck 1980, Tauber et al. 1986, Danks 1987, Thomas and Vince-Prue 1996, Nelson et al. 2009), there is a notable absence of models that predict the consequences of photoperiod adaptations when organisms are moved into a new climate or are exposed to a rapid change in climate in their home location. Such models should be particularly valuable in application to invasive species and biocontrol introductions, and for predicting population responses to climate change and climate variation. Modern computing capabilities, geographic information systems, and detailed continent-wide climate data now make it possible to develop geographically explicit models of phenology and voltinism for applications in these areas.

Here we present a conceptual framework and geographically based model for predicting the phenology and voltinism of photoperiod-sensitive poikilothermic organisms that experience an abrupt change in climate and/or latitude. We model a common multivoltine insect life cycle represented by the introduced loosestrife leaf beetle, *Galerucella calmariensis* L., in which spring emergence is based solely on temperature accumulation and fall diapause is cued by photoperiod. We first apply the model to geographic point locations, demonstrating the interplay of temperature and photoperiod, and then to the entire continental United States, where we show how the inclusion of photoperiodism can lead to geographic predictions of voltinism that are in direct contrast to those made by traditional phenology models (without photoperiodism). Finally, we show how typical year-to-year temperature variation can interact with the photoperiod response and result in amplified variation in voltinism.

METHODS

Model development

Our model aims to predict the phenology and number of generations that would be *attempted* by an insect with a given life cycle and genetically based photoperiod response when it is exposed to a different climate and/or latitude. The model assumes that the photoperiod response has not yet adapted to the new environment. Thus it is appropriate for newly introduced populations (e.g., accidentally introduced pests or intentionally introduced biological control agents) or those exposed to a rapid change in local climate.

The model applies to a life cycle commonly seen in temperate zone insects with the following diapause characteristics (see Koštál 2006). (1) The transition into diapause is triggered when the photoperiod-sensitive life stage is exposed to day lengths shorter than a critical photoperiod. (2) Diapause is maintained for a period of time during which the insect is not developmentally responsive to warm temperatures. (3) At some point during the cold season, but prior to the start of accumulation of degree-days, diapause ends and temperature-dependent development resumes. This development occurs at a rate proportional to the accumulation of heat (measured in degree-days) above a species-specific developmental threshold temperature. (4) During the active season, one or more generations occur until the photoperiod-sensitive life stage is again exposed to day lengths that are shorter than the critical photoperiod. Although our investigation applies to life cycles of this form, the model could easily be modified to accommodate other known variations such as photoperiod-dependent diapause termination or a critical photoperiod that is modified by temperature (Tauber et al. 1986).

We make the assumption that degree-day accumulation begins on 1 January. This is an arbitrary choice suited to locations that have moderate to cold winters, where the temperature is rarely (if at all) above the threshold for development during mid-winter. For conceptual simplicity, we also assume synchronous (nonoverlapping) generations and that all individuals show identical timing of development and reproduction.
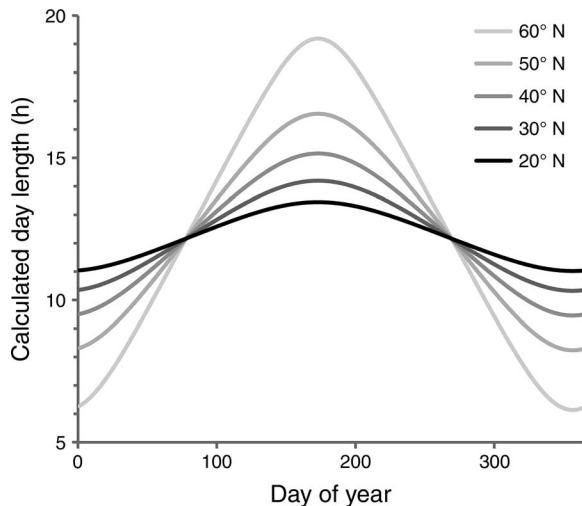
FIG. 1. Calculated photoperiods by latitude and day of year using the method of Forsythe et al. (1995) and including 25% of the civil twilight period.

To be sure that our parameter values fall in a realistic range, our base model uses parameter estimates for the leaf beetle, *Galerucella calmariensis*, which was introduced into North America from Germany in the early 1990s as a biological control agent for purple loosestrife (*Lythrum salicaria* L.) (Blossey 1995, Hight et al. 1995). This insect is known to have one or more generations depending on location and overwinters in the adult stage. Adults emerge and begin to oviposit when approximately 100 Celsius degree-days (DD_{10}) have accumulated and the first eclosion of the F1 adults occurs after 497 DD_{10} with a lower developmental threshold of 10°C (interpreted from McAvoy et al. 1997, McAvoy and Kok 2004). Subsequent generations require approximately 523 DD_{10} including a pre-oviposition period. Newly eclosed adults are the sensitive stage that is responsive to photoperiod; they become reproductive if exposed to day lengths that are longer than the critical photoperiod of 15.25 h and enter diapause without reproducing if exposed to shorter day lengths (Bartelt et al. 2008).

Latitude- and day-of-year-specific photoperiods were calculated using the CBM model described and tested by Forsythe et al. (1995) (Fig. 1). This model has the highest level of accuracy over a wide range of latitudes in comparison to several others and it allows inclusion of different proportions of the twilight period. Most photoperiod response experiments use abrupt light-dark transitions without determining how the organisms would respond to more gradual light transitions in the field. In correspondence with two studies that did measure field responses of insects to photoperiod (Beck and Apple 1961, Bean et al. 2007), we elected to include 25% of the period of civil twilight into the photoperiod calculation, which is equivalent to the period when the sun is up to 1.5° below the horizon.

Voltinism at point locations

For point locations, daily degree-days were calculated using the Oregon State University Integrated Plant Protection Center's Online Degree-Day Calculator using the single sine method (Baskerville and Emin 1969; calculator *available online*).[4] Voltinism was determined by comparing the location-specific photoperiod on the date when the sensitive stage emerges to the critical photoperiod to determine if an additional generation is attempted. For those locations that have sufficient degree-days for the second generation to develop, the photoperiod was again assessed at the time when the F2 sensitive stage emerges to determine if a third generation occurs, etc. A plot of the latitude-specific photoperiod as a function of the site-specific accumulation of degree-days provides a convenient way to visualize the expected voltinism response and also allows for comparison of the seasonal profiles among geographic locations. This "photothermograph" approach was first used by Beck and Apple (1961) in application to the European corn borer *Ostrinia nubilalis* (Hübner) and later applied to a few other insect pests (e.g., Masaki et al. 1968, Riedl and Croft 1978) but it is largely missing from modern applications.

Voltinism maps

To apply the model across the entire continental United States, we used GRASS (Geographic Resources Analysis Support System) geographic information system software. First, we calculated an approximate base layer of degree-days by applying the single sine method (Baskerville and Emin 1969) to available spatially interpolated (800-m grid cell resolution) maximum and minimum 30-year monthly normal temperatures obtained from the PRISM Climate Group at Oregon State University (Daly et al. 2008). As there is inherent error in calculating degree-days directly from time-averaged temperatures, we corrected this base layer by comparing degree-days calculated for 15 000+ weather stations for which daily maximums and minimums were available for the years 2007 through 2013 and then adding the spatially interpolated differences back to the base layer. This approach is generally known as climatologically aided interpolation (Hunter and Meentemeyer 2005) and was automated and placed online at the Integrated Plant Protection Center website (see footnote 4). For *G. calmariensis*, we calculated a series of monthly degree-day maps for the years 2007 through 2013, using 10°C and 37.8°C lower and upper developmental thresholds.

For each grid cell in geographic space, we determined the date at which the insect is expected to reach the photo-sensitive stage and stored the results in a map data layer (the phenological event map). Photoperiods were calculated for the event date in each grid cell and these were compared to the critical photoperiod to

4 http://uspest.org/

determine regions where a second generation would be attempted. For the regions where there were sufficient degree-days for the F2 generation to develop, we repeated the assessment of photoperiod on the date when the F2 sensitive stage emerged (at 1020 DD_{10}) to determine regions where a third generation is attempted, and again (where appropriate) for the date when the F3 sensitive stage emerged (1542 DD_{10}). Further detail on the programming approach for the phenological event mapping and model is presented in the Appendix.

In order to evaluate the importance of photoperiodism in determining voltinism, we ran the model both with and without the photoperiod response. *Without* the photoperiod response, the model is similar to most phenology models, and provides an estimate of the *potential* generations that could be completed during the growing season based only on temperature accumulation. It assumes that the photoperiod response is already adapted to allow the optimal number of generations for the season duration. *With* the photoperiod response, the model provides an estimate of the number of generations that would be *attempted* by the newly introduced insect, even though it may not be optimal. The maps of attempted generations (for each of three tested values of critical photoperiod) were compared to the map of potential generations, and the difference was quantified in a third map that provides an estimate of the degree to which the introduced organism will be mismatched to its new climate/seasonal regime with regard to voltinism.

To investigate the influence of the critical photoperiod for diapause on patterns of voltinism, we ran the model using three critical photoperiods: 15.25 h, 14.75 h, and 14.25 h. These values could be expected from populations coming from northern, central, and southern Europe based on photoperiod response experiments of other European insects (Danilevskii 1965). To keep things simple, we did not simultaneously vary development rate in the model, but acknowledge that it could vary among geographic populations.

Year to year variation in climate

To examine the effects of year-to-year variation in climate on a photosensitive insect, we used a location in Auburn, California, USA as an example and compared model outcomes using the temperature accumulation data from each of the past 7 years (2007–2013) in place of the 7-year averages that were used in the original model. This site was chosen as representing a region where three levels of voltinism converge in the map, thus suggesting populations in that area would be particularly sensitive to climate variation. This span of 7 years includes unusually warm years (2008, 2013) and unusually cool years (2010, 2012). Daily degree-days for these years were obtained from the Integrated Plant Protection Center's online degree-day calculator (see footnote 4).

Outcomes for point locations

We present photothermographs for six locations representing different climatic zones to illustrate how voltinism is affected by the interplay of temperature and photoperiod responses (Fig. 2) for a case in which the critical photoperiod is 14.75 h. Three situations can lead to just one attempted generation. In the first situation, represented by Little Rock, Arkansas, USA (Fig. 2A), the day length is never longer than the critical photoperiod even on the longest day of the year. Only one generation will be attempted even if there are sufficient degree-days for more. In the second case (e.g., Sacramento, California, USA; Fig. 2B), day lengths are longer than the critical photoperiod around the summer solstice, but warm spring temperatures lead to emergence of the sensitive stage well before the summer solstice when the days are still too short to cue a second generation. The third case of univoltism occurs in cool areas, such as Astoria, Oregon, USA (Fig. 2C), where development is slow and the sensitive stage emerges late in the season after days have shortened below the critical threshold.

Examples of point locations where two generations are attempted include Corvallis, Oregon (Fig. 2D) and International Falls, Minnesota, USA (Fig. 2E). In the case of Corvallis, there are sufficient degree-days to allow the second generation to fully develop (Fig. 2D). In International Falls, there are not sufficient degree-days for the second generation and developing stages are vulnerable to freezing fall temperatures. One final case is represented by Moses Lake, central Washington State, USA (Fig. 2F). Here, both the F1 and F2 sensitive stages eclose to long days resulting in three generations and there are just enough degree-days to complete all three.

Maps of voltinism

The number of potential generations based on available degree-days (no photoperiodism) throughout the contiguous 48 United States ranges from 0 to 4 or more (Fig. 3). We combined regions with 4 or more generations in the map because these warmer areas would probably see more continuous reproduction (overlapping generations) for which our model is not appropriate. Fig. 3 shows a trend toward fewer generations in higher altitudes and more northern latitudes. The geographic pattern of heat accumulation is relatively simple in the eastern United States where temperatures tend to correlate directly with latitude. It is more complex in the west, where coastal influences and mountain ranges have large effects.

When the photoperiod response is added to the model, very different maps of voltinism are produced (Fig. 4A–C). The most striking difference is that the southern regions that had sufficient degree-days for three to four (or more) generations, now have either two
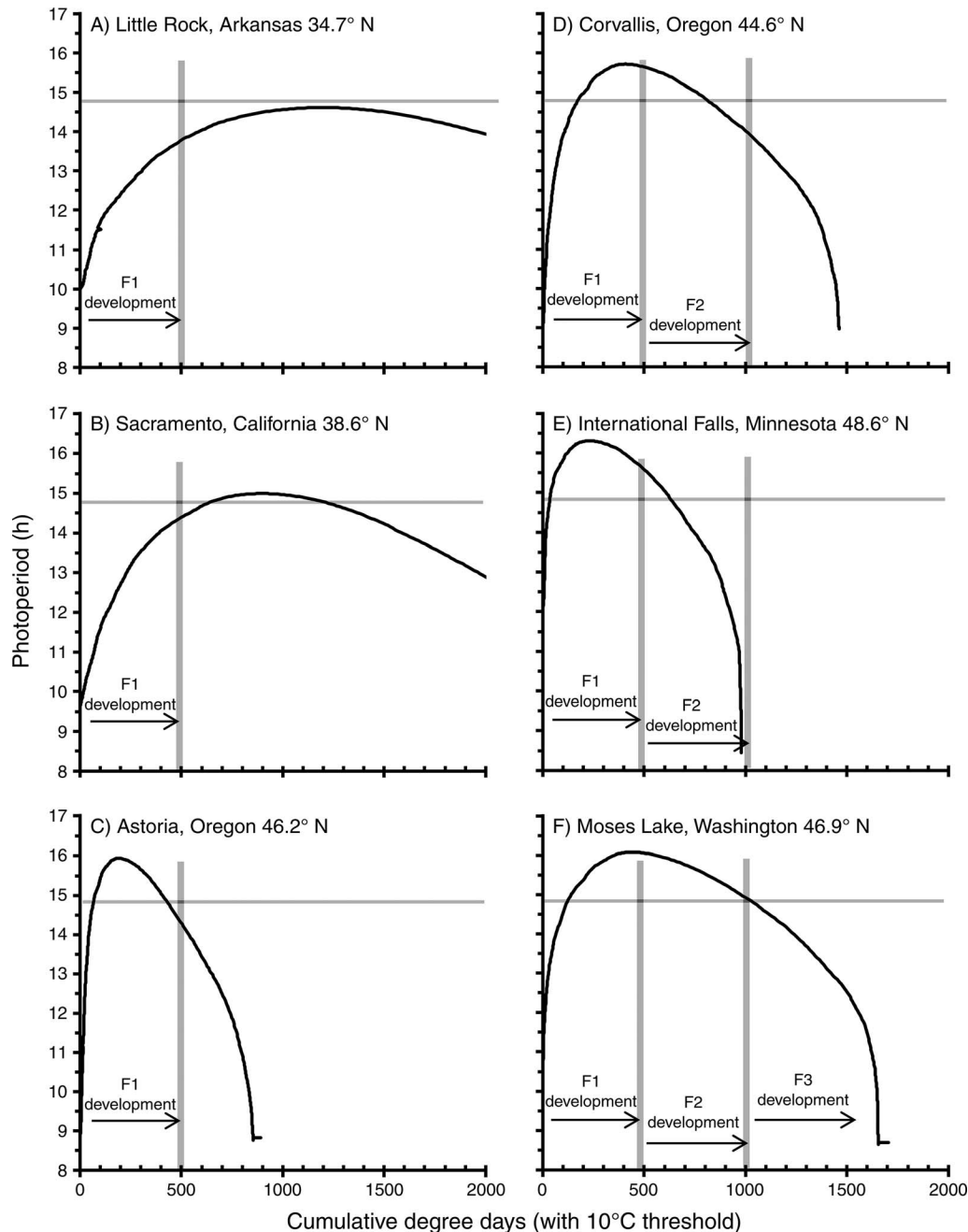
FIG. 2.   Plots of site-specific day length vs. site-specific degree-day accumulation can be used to determine voltinism. If day length (solid curve) at the time of emergence of the sensitive stage (vertical gray line) is longer than the critical photoperiod (horizontal gray line), the population goes on to reproduce; otherwise it enters diapause. All locations are in the United States. Black arrows span development times for generations F1, F2, and F3.

(at middle latitudes) or only one (in southernmost latitudes) generation. The populations are prevented from having more generations in this southern region because day lengths at the time of emergence of the sensitive stage are shorter than the critical photoperiod that allows reproduction. The boundary between regions of one vs. two or more generations is fairly distinct in the Midwestern and Eastern states where it approximately

corresponds with the latitude where day lengths never exceed the critical photoperiod. The actual boundary tends to vary to the north of this latitude because adult eclosion date usually does not align with the longest day of the year. A decrease in the critical photoperiod leads to a shift of the boundary of the one generation zone to the south (compare Fig. 4A, B, C). In the case of a 15.25-h critical photoperiod, the critical latitude is 40.6°
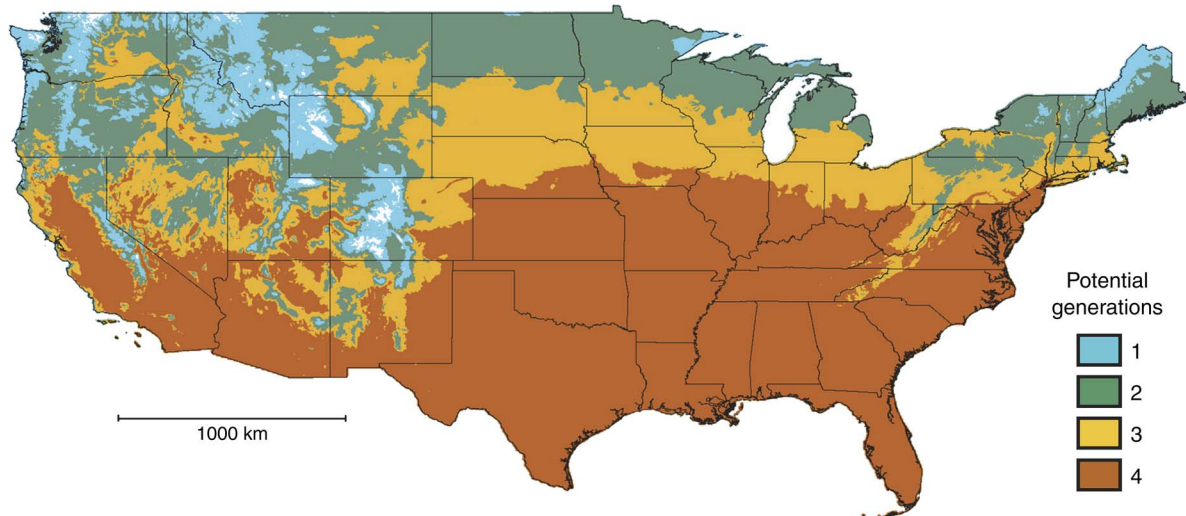
FIG. 3. Map of predicted voltinism based on total degree-days alone (no photoperiod response). Map data are unprojected (latitude and longitude).

N (Fig. 4A); for a 14.75-h critical photoperiod, the critical latitude is approximately 36.5° N; and, for a 14.25-h critical photoperiod, the critical latitude varies around 34° N.

Decreasing the critical photoperiod also tends to increase the number of generations. For example, with the longest critical photoperiod of 15.25 h (Fig. 4A), there is only one small region of central Washington State where there is both sufficient degree-days to complete the second generation to the sensitive stage and where the photoperiod at that time is long enough to cue a third generation. In the 14.75-h critical photoperiod case (Fig. 4B), the region with three attempted generations expands to include isolated locations in Northern California, the intermountain west, central midwest, and the mid-Atlantic. In the 14.25-h case (Fig. 4C), the region with three generations greatly expands to cover a large area of the central and eastern United States as well as scattered regions in the west.

One surprising outcome is that the one-generation zone is sometimes immediately adjacent to regions where three generations are predicted. This is most prominent in the 14.25-h critical photoperiod case, where such a transition stretches across the southeastern states. The transition from one to three generations occurs in locations where the sensitive stage emerges before the solstice at a time when the photoperiod is close to the critical photoperiod. In locations warmer than at this boundary (mostly to the south), the day length is shorter than the critical photoperiod at this time. Where slightly cooler (to the north), the sensitive stage is reached when days are long enough to avoid diapause. These populations remain reproductive until days again become short in the late summer, two generations later.

Regions of mismatch

Fig. 5 quantifies the difference in potential (Fig. 3) and attempted voltinism (Fig. 4) to show regions where our modeled populations will have an inappropriate number of generations for the duration of the season. Assuming that it is optimal to have as many generations as degree-days allow (which may or may not be true), our modeled insects (with critical photoperiod from 14.25–15.25) will have an appropriate number of generations throughout much of the northern part of the country (green zones in Fig. 5A–C). The area of the matched zone was greatest in the case of a 14.25-h critical photoperiod, suggesting that such a population might be better suited for introduction into the United States, especially for establishment in middle to southern states. In cold northern areas such as northern North Dakota and Minnesota (and presumably parts of Canada), the photoperiod cue will lead populations to have one too many generations for the available degree-days (blue zones) and in more southern and warmer locations, it will lead to too few generations (yellow, orange, and red zones). Either of these outcomes could be potentially catastrophic for the population depending on the organism's ability to survive an extended period of time in diapause and resist harsh conditions in the fall.
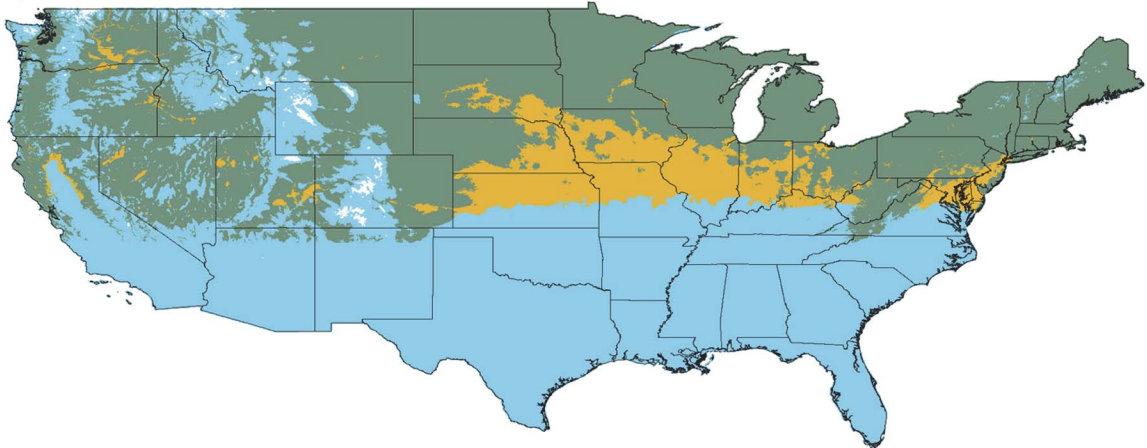
Year to year variation

Typical year-to-year variation in degree-day accumulation profiles greatly affected voltinism in our example location of Auburn, California. Here, a population with a 14.75-h critical photoperiod and sensitive stage emergence scheduled at approximately 500 DD_{10} (for the F1) and 1000 DD_{10} (for the F2) can have either one, two, or three generations (Fig. 6), depending on the year. For 2011 (a normal year), there would have been

A) Critical photoperiod = 15.25 h

Attempted generations

1

2

3

4

1000 km
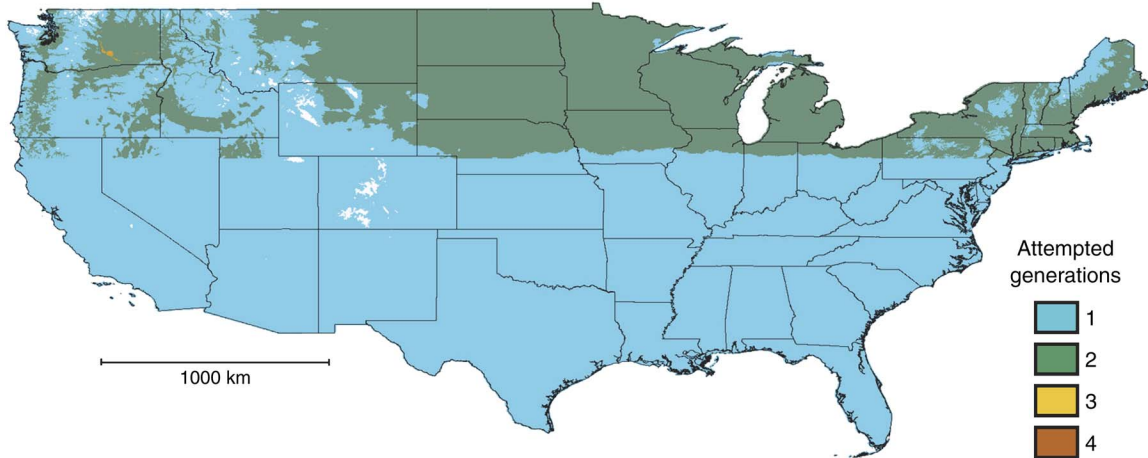
B) Critical photoperiod = 14.75 h
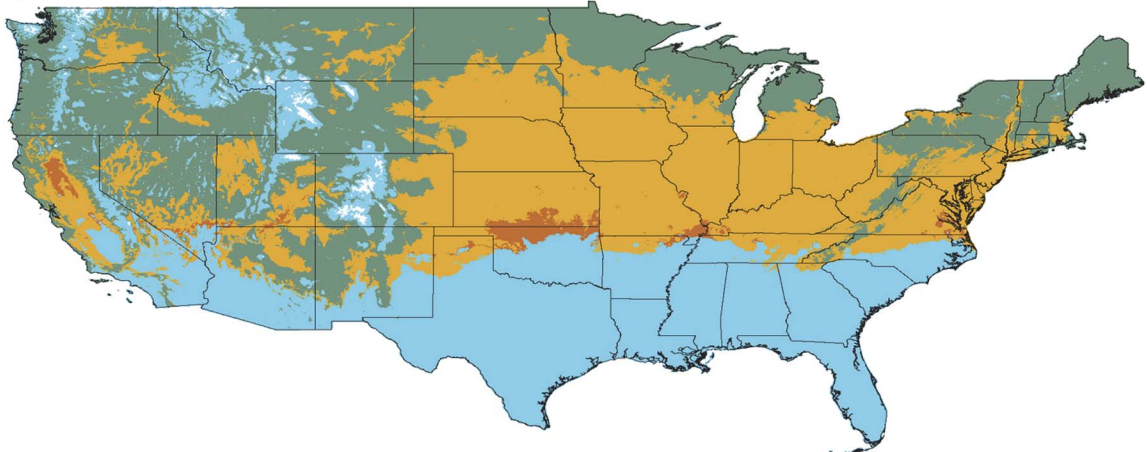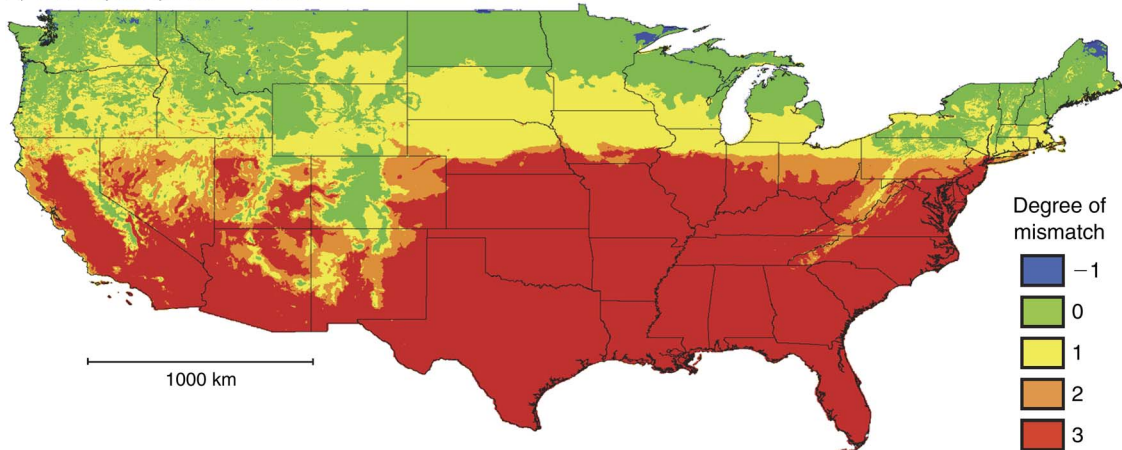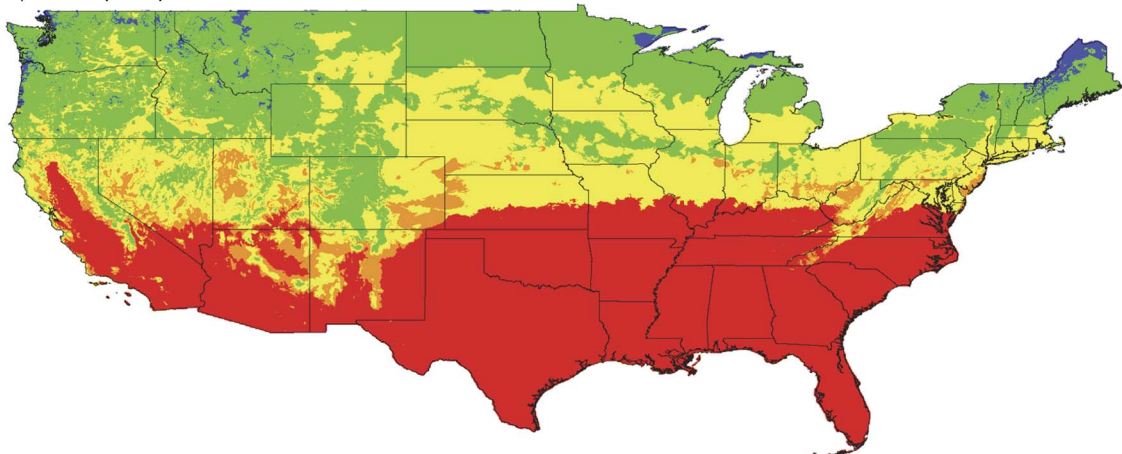
C) Critical photoperiod = 14.25 h

Fig. 4. Maps of predicted voltinism when the photoperiod response is included in the model for three levels of critical photoperiod: (A) 15.25 h; (B) 14.75 h; (C) 14.25 h.

A) Critical photoperiod = 15.25 h

B) Critical photoperiod = 14.75 h

C) Critical photoperiod = 14.25 h

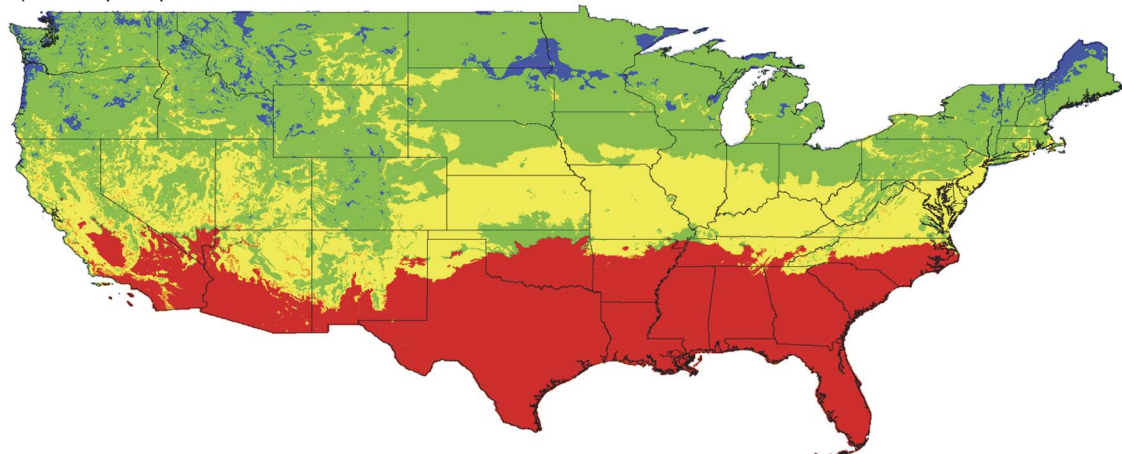Degree of mismatch

−1
0
1
2
3

1000 km

Fig. 5. Degree of phenological mismatch measured as the difference between attempted voltinism resulting from the photoperiod response (Fig. 4) and potential voltinism based on total degree-days (Fig. 3). A value of 0 means that the population will attempt the same number of generations as the available degrees-days allow. A value of +1 means that a population will attempt one too many generations for the available degree-days, a value of −1 means that it attempts one too few generations.
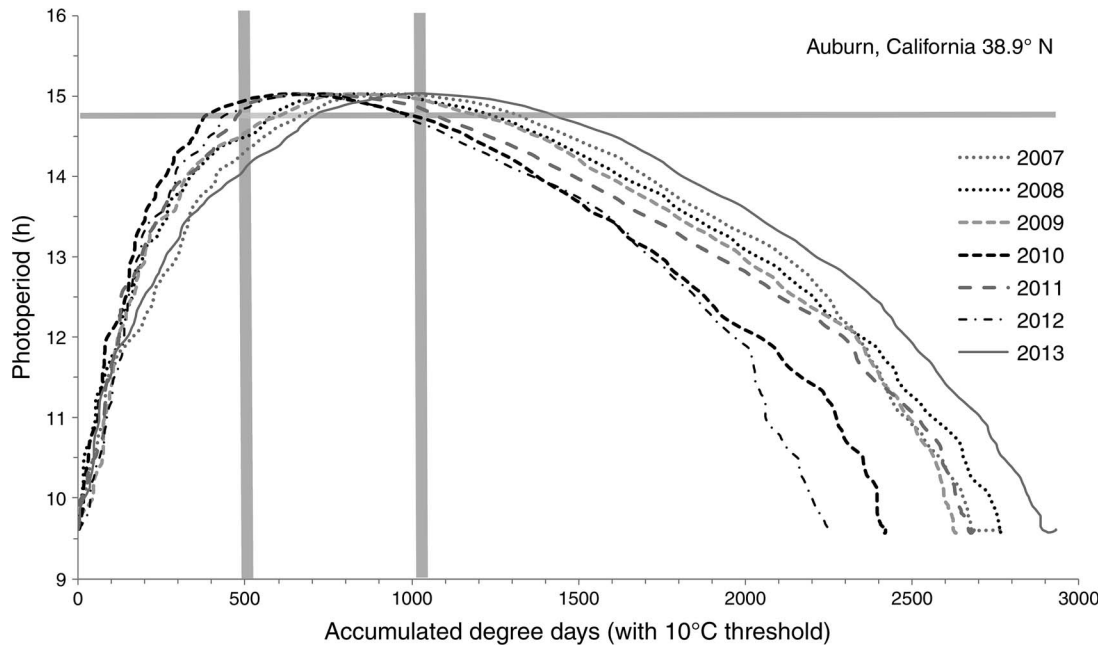
FIG. 6. Example of the potential effect of year-to-year temperature variation. In Auburn, California, USA, an insect that diapauses in response to day lengths shorter than 15.25 hours would have three generations in 2011 (cold year), two generations in 2012 (normal year), and only one generation in 2013 (warm year).

two generations. In 2012 (a cool year) there would be three generations, and in 2013 (a warm year), there would be only one generation. Thus the outcome runs contrary to our intuition (and most phenology models) that warmer temperatures lead to more generations. Instead, a warmer-than-average spring leads to emergence of the sensitive stage at a time when the days are still too short to cue a second generation.

DISCUSSION

Using a simple degree-day phenology model that incorporates a photoperiod diapause response, we predicted patterns voltinism for insect populations newly exposed to a wide range of climate and latitude. The expected number of generations is determined by a complex interaction between temperature and photoperiod: the rate of accumulation of thermal degree-days affects the date of emergence of the photo-sensitive stage, which, along with latitude, determines the day length to which that stage is exposed, which determines whether or not an additional generation occurs. As a result of this interaction, photoperiodism can have consequences for voltinism when there is a change in temperature, even if there has not been a change in latitude. The expected geographic pattern of voltinism is strikingly different from predictions of standard degree-day phenology models that do not incorporate photoperiod.

The approach of combining thermal requirements and photoperiod response in models of phenology and voltinism is not new, though its use has been limited.

We found the first photothermograph in Beck and Apple (1961), who were able to explain variation in voltinism in the European corn borer in different regions of the midwestern United States. A few similar assessments followed (e.g., Masaki et al. 1968, Riedl and Croft 1978). In one case, it was used to predict, in advance of its invasion, regions where a new pest to Japan was likely to establish or fail (Masaki et al. 1968) similar to what we have done here. These early models were limited in scope to a few geographic point locations and used less precise climate data and photoperiod calculations than are available today. In modern applications, including biological control introductions, invasive species risk assessment, and population response to climate change, predictions of voltinism usually rely solely on thermal responses to degree-days (e.g., McClay and Hughes 1995, Pilkington and Hoddle 2006, Coetzee et al. 2007, Jönsson et al. 2009, Hartley et al. 2010, Buergi et al. 2011, Myint et al. 2012, Ziter et al. 2012). By ignoring the effect of a genetically based photoperiod response, the traditional phenology model is effectively making the assumption that the critical photoperiod adapts instantaneously to the local climate and latitude. This is inappropriate for newly introduced species or those experiencing a rapid change in climate locally. An exception is Tobin et al. (2008) who predicted the effects of climate change on voltinism in the grape berry moth *Paralobesia viteana* (Clemens) in the midwestern United States. This model incorporates individual variation in development timing and made predictions that were measured in partial generations. In

congruence with the current study, they found that incremental increases in temperature could lead to rather abrupt (non-linear) increases in voltinism due to earlier emergence of the sensitive stage and corresponding exposure to longer day lengths. Like the earlier mentioned models, this model was limited to a few geographic point locations and unable to reveal larger spatial patterns.

The current paper is the first presentation of a model used to predict and map photoperiod-cued voltinism across continuous space at the scale of a continent. Three patterns are revealed for introduced populations with long-day reproduction. The first is that populations originating from northern locations (higher latitude) introduced to more southern locations (lower latitude) are likely to be limited to just one generation due to short day lengths, even if there are plenty of degree-days to complete more generations. The case of the tamarisk leaf beetle *D. carinulata* (mentioned in the introduction) is a real example of this phenomenon that resulted in failed establishment in southern locations (Bean et al. 2007). In *G. calmariensis*, phenology studies carried out shortly after introduction report only one generation in a southern latitude (McAvoy et al. 1997), but two generations in several northern locations (Dech and Nosko 2002, Landis et al. 2003). Related to this geographic pattern is the counter-intuitive result that a warmer climate could lead to a *decrease* in the number of annual generations. This could occur when warmer temperatures lead to earlier emergence of the sensitive stage to shorter, diapause-inducing day lengths before the summer solstice. To our knowledge, this possibility has not previously been recognized among the predicted effects of a warming climate.

The second geographic pattern revealed by this study is that populations moved from lower to higher latitudes may be prone to diapausing too late in the season (too many generations) and thus exposing vulnerable developing life stages to harsh conditions at the onset of the cold season. In biological control introductions, a non-suited climate is the most frequently implicated reason for establishment failure (Crawley et al. 1986, Stiling 1993). However, failure might be mistakenly attributed to the direct effects of cold temperatures when it is really the *timing* of exposure of vulnerable stages that is the problem. A call to pay more attention to seasonal timing, ahead of the direct effects of climate, has been made recently in the context of global climate change (Bradshaw and Holzapfel 2010). It could be even more important for species introduced to new regions.

The third pattern revealed by this model is that the number of attempted generations can vary greatly with relatively small changes in temperature. In some regions, incremental changes such as those arising over relatively short geographic distance or as variation between years can cause a jump from one to three (possibly more) generations without first passing through two generations. This represents a possible source of insect

outbreaks and sporadic range expansion. It may help explain why intentional introductions (or accidental ones) often require multiple attempts over many years and many site locations before establishment is finally successful (Grevstad et al. 2012a).

Our model represents a population in which all individuals take on the mean values for development timing and photoperiod response. This simplification made it possible to clearly delineate geographic patterns in voltinism and estimate what the bulk of the population will do. Inclusion of variation among individuals would certainly result in some blurring of the boundaries on the maps and allow for partial generations, where some individuals of a generation reproduce and others enter diapause. If such variation were included, we would still expect some degree of punctuated, non-linear transitions in voltinism similar to what Tobin et al. (2008) found for the grape berry moth. Future versions of this model could benefit by including individual variation.

Given the existence of heritable variation in photoperiod response and development rate (Danilevskii 1965, Bradshaw and Holzapfel 2007), it is reasonable to assume that introduced insects will eventually adapt to their new climate. In correspondence with our model, evolutionary adaptation toward appropriate voltinism could occur either through a change in development rate or a change in the critical photoperiod (thus moving the position of the crossing point of horizontal and vertical lines in the photothermographs; Fig. 2). The photoperiod response appears to be particularly evolutionarily labile, more so than the speed of development (Bradshaw and Holzapfel 2007). Artificial selection experiments have demonstrated a change in the critical photoperiod in a range of 3–15 generations (Danks 1987). In the tamarisk leaf beetle, Bean et al. (2012) detected evolutionary change in the critical photoperiod within 7 years of introduction, which allowed this beetle to extend its range further to the south. The speed of development can also evolve, as it did for two biological control agents introduced against tansy ragwort (*Jacobaea vulgaris* Gaertn.), allowing them to occupy colder, high-elevation habitats (McEvoy et al. 2012, Szűcs et al. 2012). An open question is whether adaptation occurs rapidly enough that the consequences of an inappropriate photoperiod response can be effectively ignored, as they generally have been. Failures of introduced species are most likely to occur in the very first year of introduction (Crawley et al. 1986), which would not give them the chance to adapt. On the other hand, resident species exposed to more gradual global climate change may well have the time to adapt as has been seen in the pitcher plant mosquito (Bradshaw and Holzapfel 2001) and the fall webworm (Gomi et al. 2007). For species with longer generation times than insects, evolution of the photoperiod response may lag behind the rate of climate change, as in the case of photoperiod-

cued seasonal coat color in the snowshoe hare (Mills et al. 2013).

The conceptual framework and modeling approach presented in this paper serve as an example that could be expanded to a wide variety of different organisms and applied problems in fields such as biological control, invasive species ecology, species range limits, and climate change ecology. Given that photoperiod is a common seasonal cue used by a wide variety of organisms, ecological studies that involve the exposure of organisms to new climates should always consider the potential interaction of a photoperiod response.

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SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/14-2071.1.sm

Data Availability

Data associated with this paper have been archived online: http://dx.doi.org/10.7267/N9X63JT3