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Population Ecology

Factors Influencing the Population Fluctuations of *Euproctis chrysorrhoea* (Lepidoptera: Erebidae) in Maine

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Abstract

The browntail moth (*Euproctis chrysorrhoea* (L.)) is a forest pest that was accidentally introduced in the late 1800's and spread throughout New England in the early part of the 20th Century. At its peak range expansion in 1915 it encompassed an area of 150,000 km^2 after which populations declined. By the 1960s, its distribution had receded to relic populations on outer Cape Cod, MA, and islands in Casco Bay, ME. In 1989 browntail moth resurged in Maine, with periodic, moderate outbreaks before a dramatic increase of the population occurred in 2016. We examined the pattern of annual defoliation by browntail moth since its resurgence in the 1990s as well as variation in populations throughout infested areas in Maine during three years of the recent outbreak, 2016–2018, relative to differences in weather, parasitism and habitat characteristics. Levels of defoliation over 24 yr were predicted by the preceding spring precipitation (–, negative effect) and the year's previous late summer and early fall temperatures (+, positive effect) when first to third instar larvae feed and then construct winter hibernacula. Late summer temperatures predicted the abundance of hibernacula across outbreak areas (+). Early spring temperatures (+) and early and late spring precipitation (–) predicted early summer larval and pupal nest abundance. Warmer fall temperatures result in more mature populations coming out of winter hibernacula in the spring, whereas spring precipitation drives epizootic outbreaks of *Entomophaga aulicae* (Reichardt in Bail) Humber (Entomophthorales: Entomophthoraceae). with parasitoids playing a lesser role. Climate trends indicate continued increases in fall temperatures since browntail moth resurgence.

Key words: browntail moth, outbreak, climate effect, defoliation, *Entomophaga aulicae*

Climate change effects have been demonstrated for several forest insect species although generalizations have been difficult to elucidate as individual species respond to a multitude of direct and indirect impacts on their fecundity, dispersal, and survival (Pureswaran et al. 2018). Direct effects of increased temperatures can accelerate development times and allow for range expansion, while climate effects on host plant resistance can lead to more successful colonization and the establishment and subsequent outbreaks (DeLucia et al. 2012, Roitberg and Mangel 2016, Pureswaran et al. 2018). Confounding changes in climate are changes in landscape characteristics and land use that can also have direct and indirect impacts on insect dynamics and outbreaks (Roland 1992, Battipaglia et al. 2014, Ferrenberg 2016). In the northeastern United States, total land in forest, much of it unmanaged and associated with suburban sprawl and reversion of abandoned farmland, has increased over the past 100 yr (Barton et al. 2012).

The browntail moth, *Euproctis chrysorrhoea* (L.), an invasive insect that was first introduced into the northeastern U.S. in the late 1800s, has recently exhibited outbreak populations in Maine on a scale that has not been experienced for 70 yr (Boyd 2020). This species, which is thought to have been initially introduced into Somerville, Massachusetts in 1890 on a shipment of roses from Holland or France (Marlatt 1911), rapidly spread and was found throughout most of New England, north into New Brunswick and Nova Scotia, Canada, and south into eastern Long Island, NY by 1914 (Schaefer 1974). Browntail moth larvae feed on a variety of deciduous tree species, with a preference for oak, apple, and other *Rosaceae* species (Schaefer 1974). However, in addition to its defoliation of these

host plants, outbreaks of this species cause serious health concerns due to the urticating hairs produced by the larvae which cause severe dermatitis in the majority of people who encounter them, and respiratory distress in many (Blair 1979, Bradbury 1999). By 1912, the infestation in the northeastern U.S. was so severe that the federal government put in place Quarantine No. 4. Gypsy Moth and Browntail Moth (The Federal Quarantine Act of 1912). This act established a zone of quarantined area that mirrored the distribution of the moth and prohibited nursery material exports out of quarantined areas (Schaefer 1974).

At the time of the initial outbreak of browntail moth in the early 1900s, a variety of management efforts were deployed by state and federal employees, landowners, and public volunteers throughout New England. These included banding trees; thinning, removing, and burning shrubs and trees that harbored the pest; spraying insecticides; and removing and destroying the overwintering hibernacula of the caterpillars (Burgess 1944). The U.S. Department of Agriculture also initiated a biological control program targeting browntail moth and gypsy moth in 1901, and over the following 20 yr introduced 46 different species of natural enemies, 15 of which were established (Crossman and Webber 1924) with seven considered to be important enemies of browntail moth (Clausen 1956). Additionally, entomologists began rearing browntail moth larvae in outdoor insectaries in 1908 and infecting them with the naturally occurring entomopathogenic fungus, *Entomophaga aulicae* (Speare and Colley 1912). These infected larvae were then transported and released into local populations throughout Massachusetts over four years. The success or failure of any one of these deployed management strategies: habitat manipulations, insecticides, destruction of winter hibernacula, and biological control has not been documented. However, after 1914, browntail moth populations declined and its distribution appeared to contract such that by 1922, problem populations were distributed only through eastern parts of Massachusetts and New Hampshire and the southern third of Maine (Schaefer 1974). Throughout the next several decades, populations continued to contract eastward in New England with some periodic localized outbreaks which elicited coordinated winter hibernacula removal and insecticide treatments (Burgess 1936, Sheals 1945, Corliss 1947, Nutting 1956, and Pratt 1972). By 1974, relic populations appeared to be restricted to an area on outer Cape Cod, Massachusetts, and several islands in the Casco Bay, Maine (Schaefer 1974). In 1986, it was determined that browntail moth no longer presented a threat to US agriculture and the quarantine for this species was lifted.

An outbreak of browntail moth occurred in Maine in 1989 and continued through 1996 over a 12 km^2 area of the coast between Cape Elizabeth and Phippsburg, Maine (Bradbury 1999). The Maine Forest Service indicated the affected region included 22 townships and 31 islands, and several control projects were conducted (Bradbury 1999). Fluctuating but detectable populations continued with some inland spread over the following 20 yr including a four-year outbreak which at its peak in 2003 caused over 4,300 ha of defoliation. However, throughout most of this period, defoliation remained under 2,000 ha until 2016 when browntail moth was responsible for defoliation of more than 10,000 ha in Maine (Fig. 2A).

It has been suggested in previous publications that low winter temperatures may be responsible for declines in overwintering survival of browntail moth and subsequent population reductions (Gilliat 1921, Sheals 1945, Schaefer 1974). Elkinton et al. (2008) investigated this theory and concluded that although climate affects browntail moth, low winter temperatures do not explain the rapid expansion and collapse of their populations in the 1900s following their introduction into North America. They found that browntail moth survival was higher in coastal areas compared to inland habitats in Massachusetts and Maine. This was consistent with their finding of high numbers of the generalist parasitoid, *Compsilura concinnata* (Meigen) (Diptera: Tachinidae), at inland sites, and few parasitoids in coastal habitats (Elkinton et al. 2006). They conclude that parasitism by this species was likely responsible for the multidecade decline of browntail moth in the 1900s (Elkinton et al. 2008).

In its native range of Eurasia, browntail moth is distributed across central and southern Europe, Northern Africa, and east to the Himalayas (Rogers and Burgess 1910). In some parts of its range, most notably England, France, and Germany, its recorded to cause frequent damage to orchards, shade trees, and flowering shrubs and plants (Fernald and Kirkland 1903, Sterling and Speight 1989). Occasional, localized outbreaks of browntail moth have occurred in southern England (Sterling and Speight 1989) and periodic outbreaks have been reported in oak forests in Hungary (Leskó et al. 1995) Bulgaria (Pilarska et al. 2002), and Iran (Arefipour et al. 2005), and on the evergreen shrub, *Arbutus unedo,* in Spain (Frago et al. (2011), as well. As in its introduced range, the cause of browntail moth populations fluctuations in its native range is unclear, though the scale of outbreaks is generally smaller than what was and is being experienced currently in the northeastern U.S.

This study investigates climate related influences on browntail moth population fluctuations in Maine over the past 28 yr and explores what factors may have led to the recent outbreaks. In addition to examining trends in browntail moth defoliation over this time period, we examined: a) fluctuations in relative population densities, b) post-diapause and late-stage larval and pupal survival, and c) relative age distribution of overwintered larvae, in populations during three years of the current outbreak throughout the broadening infestation areas in Maine. These data allow us to consider future trends in browntail moth populations with projected warming and precipitation trends for the state.

Materials and Methods

Study Organism

The browntail moth life cycle is initiated in the later part of July in Maine when females lay their eggs in masses on the undersides of leaves at the terminal ends of the branches in the upper canopy of host trees (Fig. 4). Eggs hatch after two to three weeks, and larvae feed gregariously on the undersides of leaves, skeletonizing and causing bronzing of the foliage. While feeding, larvae construct and move in and out of a communal "winter web" or hibernaculum where their egg mass was laid. This consists of whole or skeletonized leaves tightly wound together and coated with tightly woven sheets of silk, providing the insulating structure for diapause. Pre-diapause larvae typically go through 1–3 molts before they cease feeding and enter diapause as second, third, or fourth instars. Larvae remain in the hibernaculum for approximately seven months from mid- to late-September through mid- to late-April depending on temperature and food availability. Post diapausing larvae frequently emerge from their hibernacula before bud break and can be observed congregated on the outer surface of the hibernaculum. They begin feeding on host leaf buds as they expand, laying silk trails between the hibernacula and their feeding sites. Larvae abandon their hibernacula after one to two weeks and continue to feed individually for another seven to eight weeks, completing three to four larval stadia post diapause. Mature larvae then aggregate on remaining foliage or search for

new foliage in the understory where they construct individual or communal pupation nests by loosely wrapping leaves together with silk in early July. Pupae require approximately two weeks to complete development, and adult moths emerge and mate and disperse in the latter half of July.

Climate Influences Over Time

Climate influences on browntail moth populations over time were explored with predictive statistical models using 23 yr of annual defoliation estimates for Maine and climate data from the National Oceanic and Atmospheric Administration National Centers for Environmental Information's (NOAA-NCDC'S) for Portland, ME, the most complete data set available for the region (NOAA 2019). Aerial assessment of browntail moth defoliation was conducted by the Maine Forest Service, Department of Agriculture Conservation and Forestry entomologists every June between 1994 and 2017. The area flown was based on the previous summer's defoliation and winter hibernacula surveys with an expanded perimeter to ensure the entire infestation was mapped. Much of the browntail moth infestation has been along the coast, down the peninsulas, and on the offshore islands of Maine. Flight routes were based on terrain and infestation as using predetermined flight lines along the coast was not efficient. Infested areas would generally be flown on five-mile-wide flight lines traversing the area until it was fully mapped. Surveys were conducted using the Maine Forest Service Cessna 185, Cessna L-19, or Bell Jet Ranger at an altitude of 1,200–2,000 feet.

From 1994 to 2006 maps were hand-drawn on Maine Delorme Atlas & Gazetteer maps in flight. The maps were then resolved and digitized by Greg T. Miller, Maine Forest Service GIS Programmer Analyst. In 2007 sketch mapping migrated to a digital sketch pad provided by the United States Department of Agriculture, Forest Service. Areas of defoliation were delineated by polygons outlining the affected areas. Mapping parameters changed over the years and included both the pattern and severity of defoliation. The pattern described whether it was isolated trees, patchy damage, or contiguous damage to trees. Defoliation was defined at three levels: severe >75% defoliation of most affected trees, moderate 50–75%, or light <50% defoliation. Polygons were drawn broadly as defoliation under 25% is difficult to observe from the air, especially in mixed wood stands. The USDA-FS database records combine those two parameters into one. Mapped areas were ground-truthed either before or after the aerial survey.

Climate data for the Portland, ME JetPort weather station (USW00014764) was downloaded from NOAA-NCDC'S Climate Data Online (CDO). This station has a complete data set for the period of interest and is within the outbreak area. It is also the closest weather station to Peaks Island (5.6 km) in Portland, ME, where a population of browntail moth has been known to persist since the early part of its invasion in Maine and was studied by Schaefer (1974) when populations had seemingly disappeared in other areas. Monthly summaries of the temperature and precipitation variables included in the analysis were grouped by relevance to browntail moth life stages and phenology (Table 1) with each year's June defoliation estimate ($DEF_{(year=t)}$) examined relative to climate variables from the previous July (year = t – 1) through June of each year (year = t). Extreme maximum and minimum temperatures (ETMAX, ETMIN) were identified, temperatures were also averaged daily and then by month (TAVG), and precipitation was totaled (PRCP) over the months of the life stage periods. Climate variables for each life stage period were selected based on their hypothesized significance to the survival of the life stage (Table 1).

Table 1. Browntail moth lifestages and the relevant corresponding periods over which climate variables were summarized for analysis of defoliation at year (t)

Life Stage	Corresponding Period of climate variables	Variables Included for Life Stage
Adults & Eggs	July (t – 1)	TAVG (July), PRECIP (July)
Small Larvae pre-diapuase feeding, development, & winter hibernacula construction	August –September (year t – 1)	TAVG (Aug–Sept), PRECIP (Aug–Sept)
Small larvae in winter hibernacula, early diapause	October–November (year t – 1)	TAVG (Oct–Nov), PRECIP (Oct–Nov)
Small larvae winter diapause in hibernacula	December (year t – 1) – February (year t)	ETMIN (Dec–Feb), TAVG (Dec–Feb), PRECIP (Dec–Feb)
Small larvae in and emerging from winter hibernacula post diapause early spring	March–April (year t)	ETMIN (Mar), ETMAX (Mar), ETMAX (Apr), TAVG (Mar–Apr), PRECIP (Mar–Apr)
Emerged post diapause larvae feeding and development & pupae	May–June (year t)	TAVG (May–June), PRECIP (May–June)

We selected only climate variables that were pertinent to each specific life stage. This life-cycle-based selection was performed *apriori,* before model construction. For example, the extreme lowest temperature (ETMIN) would likely have its most significant impact during the winter months when unusual cold events might cause high mortality, whereas the extreme warmest temperature over a period (ETMAX) may be most significant in the early spring months as larvae are breaking diapause. Every life stage period included the average temperature and total precipitation variables. Also included in the model were cooling degree days (CDSD, base = 18.3°C) for the previous summer and fall (year = t – 1) and for spring (year = t), heating degree days (HDSD, base = 18.3°C) for July–December (year = t – 1) and January–June (year = t), and annual degree-days base 12°C (Frago et al. 2009) (DD_{12}) to capture any relationships between browntail moth populations and cumulative temperature trends over the year. No *apriori* selection was performed for the other modeling parameters represented by landscape habitat variables and spatial distance variables. All 19 of these variables plus the previous year's defoliation were used for the analysis of annual defoliation over time.

Statistical Modeling

The generalized linear model approach was used to develop a predictive model for summer defoliation by the browntail moth from 1995–2016 (22-yr time series utilizing the 23 yr of data to include $DEF_{(year=t-1)}$). The Poisson error term was selected and Adaptive Lasso maximum likelihood estimation, a penalized regression technique (Zou 2006, SAS 2017), was used to select a significant set of predictors from the full set that we considered (previously described sets of climate, landscape habitat, spatial distance, and population variables). After variable selection by the Lasso method, validation of the best predictive model was based upon the corrected Akaike Information Criterion, AICc

(SAS 2017). Overall model fit was based upon the likelihood ratio test (SAS 2017). In addition, deviance plots were used to assess model fit.

Variation Between Localized Populations

Browntail moth populations were sampled across the mid-coast Maine (Cumberland, Sagadahoc, Lincoln) region and parts of central Maine (Penobscot, Kennebec, Waldo) over three years, from 2016 through 2018 to explore climate, habitat, and parasitoid-driven variations in population abundance and survival throughout the region during the current outbreak. Initial sample sites were selected to encompass the geographic extent of the infestation in 2016 based on winter hibernacula density estimates provided by the Maine Forest Service. Twenty-one sites across 14 Maine townships were monitored throughout the entire study (Fig. 1), and as browntail moth spread throughout the state, 25 additional sites were added in 2017 and 2018. Sites were selected to be evenly distributed across the geographic range of the outbreak, and that included low to moderate height (2 m–10 m) trees that could be successfully observed from the ground and sampled with 6 m pole pruners.

Browntail moth abundances were sampled at three different life stages. Diapausing larvae (in winter hibernacula) and pupae were sampled each year, and late-stage larvae were sampled in a subset of sites in 2017 and 2018. For diapausing larvae in winter hibernacula, surveys were conducted in collaboration with the Maine Forest Service (Jan–Mar). Technicians from the Maine Forest Service conducted road surveys throughout the infested areas and estimated the range of density of winter hibernacula in the surrounding trees via visual inspection. Hibernacula are visible from the ground due to light reflectance by the silk. Hibernacula densities were recorded as: 0 nests, 1–9 nests, 10–99 nests, 100–499 nests, 500–999 nests, 1,000–4,999, and >5,000 nests for groups of 10 or fewer trees at a given site. Sampling of late-stage larvae and pupal nests were conducted during June and July, respectively, via timed observations. One or more observers walked around and under host trees at each site for a 10-min interval recording all live, feeding caterpillars and pupal nests readily visible in the canopies. In areas with high densities of browntail moth larvae or nests, multiple observers sampled separate areas within the site. These repeated counts were averaged across all observers.

Estimates of overwintered larval survival were obtained by collecting these life stages at field sites and rearing them in the laboratory. Winter hibernacula were collected from late March through early April presumably after the majority of the winter mortality had occurred. One to five accessible hibernacula were collected per site with hand or pole pruners (maximum of 6 m). Samples were then held in cold storage at 4°C until all collections were complete (2–3 wk). Over two weeks, three randomly selected hibernacula from each site were removed from cold storage and placed in a Fabri-Kal deli cup container (473 ml plastic cup) or plastic freezer bag. These containers were then held at an ambient laboratory temperature ~21°C and monitored daily for the emergence of larvae. Emergent larvae were counted and after at least 7 days with no additional emergence, hibernacula were dissected and the number of dead larvae determined.

Additionally, late-stage larvae and pupal nests were collected from sites and reared in the laboratory to assess sources of mortality for these life stages. Late-stage larvae were collected in early

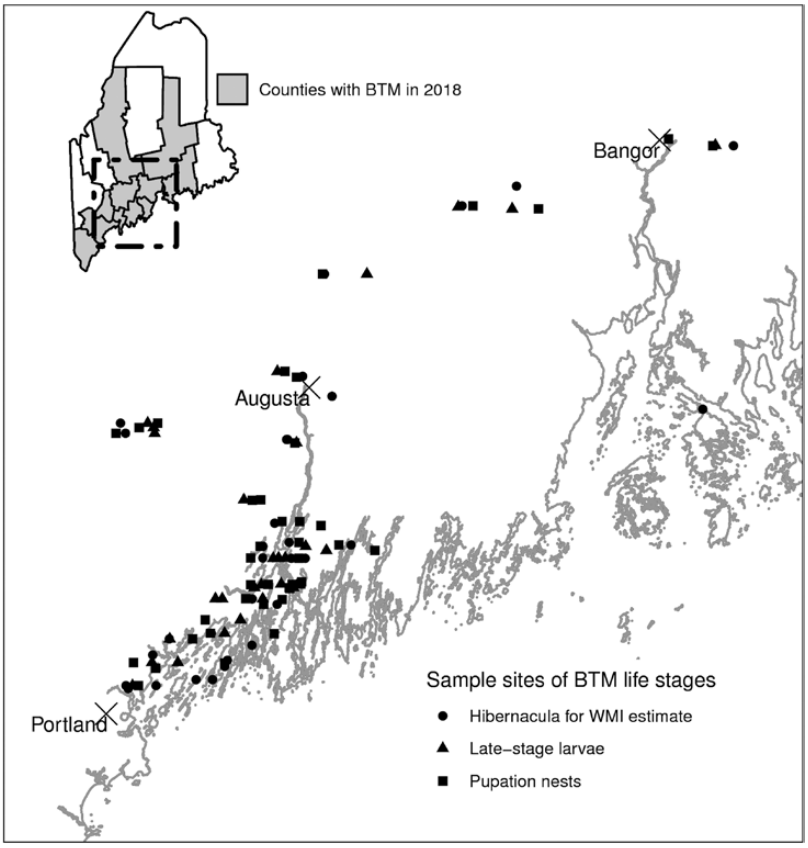

Fig. 1. Browntail moth distribution and sample sites during the current study.

to mid-June before larvae began pupating using pole pruners as described above. Up to 50 individuals were collected from each site, with one-third of those individuals reared out as described above, and the others stored at −80°C in 70% ethanol for later studies. Larvae were stored at 10°C until processed, typically within 24–48 h. Larvae were placed in groups of 10–12 in petri dishes lined with moist filter paper and fed fresh foliage. Either red oak (*Quercus rubus*) or apple (*Malus* spp.) was used to feed the larvae. Dishes were sealed with parafilm and kept in an environmental chamber with a 12-h daylight cycle at 20°C. Larvae were monitored daily for mortality and natural enemy emergence, with dead larvae removed daily and inspected for signs of fungal infection or parasitism.

Pupal nest collections were also made at each site after timed density counts were conducted in late-June to mid-July. Pupal nest collection and storage methods were the same as for diapausing and late-stage larvae. Once collected, pupal nests were immediately set up in 473 ml Fabri-Kal clear plastic drink cups with dome lids with the center hole for a straw that covered with cloth or loose mesh to allow oxygen and humidity exchange. In 2016, individual pupae were removed from nests and reared in individual 60 ml Fabri-Kal® clear plastic condiment containers with lids. In 2017 and 2018, entire nests were reared after the number of pupae was recorded. This method was adopted to reduce the handling time of nests which had very high quantities of hazardous setae. Nests were kept on the laboratory bench in a room with open windows to experience ambient temperature (~17.3°C). All containers were checked daily for the emergence of moths and parasitoids. After emergence was complete, nests were dissected to confirm moth sex ratios, survival of pupae, and proportion parasitized (Boyd 2020). Parasitoids were identified to species and detailed data are being reported in a separate manuscript.

To explore differences between populations in the maturity of larvae coming out of diapause, the head capsule width of larvae emerging from winter hibernacula were measured and the weighted mean instar (Fulton 1975) was calculated for hibernacula collected in March and April at 10, 18, and 6 sites in 2017, 2018, and 2019, respectively. A randomly selected sample of 10–50 larvae emerging from a single hibernaculum was measured for one to seven hibernacula available per site. The frequency distribution of the head capsule widths was plotted in 0.01 mm intervals, and the lowest points between peaks were identified as boundaries for each of four instars. Larvae with head capsule widths <0.49 mm were considered first instars, 0.491 – 0.588 mm were considered seconds, 0.589–0.799 mm were considered thirds, 0.8 – 1.01 mm were considered fourths, and >1.01 mm were fifths. All larvae measured per site in each year were pooled for a collective estimate of weighted mean instar per site-year. The weighted mean instar was calculated as: $WMI = \Sigma_{(i=1)}^{s}(p_i * s_i)$, where s is the total number of instars during larval development, s_i is the stadium, and p_i is the proportion of emerging larvae in stadium i.

Climate data were obtained from the NOAA-NCDC'S Climate Data Online (CDO) for sites sampled from 2016 to 2019 (NOAA 2019). Sites were assigned to the weather stations nearest to them (no greater than 30 km). Because of site proximities, multiple sites were frequently linked to the same climate station (see Boyd 2020 for complete list). Climate variables used in the analyses for each life stage included the temperature (TAVG) and total precipitation (PRECIP) experienced for each cohort starting from the egg stage. For example, analysis of the abundance of winter hibernacula included climate data between 1 August and 30 September, which encompasses the period over which eggs are laid and hatch, and early instars feed and construct and enter winter hibernacula. Survival of overwintered larvae included climate data from August (year = t – 1) through April (year = t), whereas late-stage larval abundance and pupal nest count analysis included climate data from August (year = t – 1) through June (year = t). As with the defoliation analysis, climate variables were grouped by browntail moth phenology periods. For analysis of weighted mean instar, in addition to average temperatures and precipitation variables, we calculated and included in the model accumulated degree-days base 0°C (DD_0), degree-days base 12°C (DD_{12}), and average maximum temperatures (TMAX) which are common predictors for development. These variables were calculated for each life stage period between August (year = t – 1) and April (year = t).

Habitat vegetation, distance from the closest marine coast, and distance from the hypothesized origin of the current outbreak (Peaks Island, Portland, ME) were also included in models exploring variation in browntail moth between sites. Habitat vegetation data was obtained through the National Land Cover Dataset (Dewitz 2019). The amount of potential habitat present at each site was determined by identifying a 1.5 km radius around the center of the site using ArcGIS version 10.1 (ESRI, Redlands, CA). The total area (m^2) of deciduous, evergreen, and mixed forest habitat within this 7 km^2 area was then determined for each site. Distance to nearest marine coastline and distance to Peaks Island were determined using Google Maps measurement tool (Google 2020).

Relationships between the previously described climate, habitat, and distance variables and five different browntail moth life stage variables were explored using statistical models described below (Table 2). The life stage variables included: 1) mean density rank for winter hibernacula, 2) larval overwintering survival, estimated by proportion emergence from hibernacula, 3) late-stage larval abundance, estimated from timed counts, 4) pupal nest abundance, estimated from timed counts, and 5) maturity of emerging post-diapause larvae, estimated by head capsule width of larvae emerging from hibernacula. Additionally, differences between years and sites and mean mortality of laboratory-reared larvae and pupae were examined in RStudio (RStudio 2019, version 1.1.414) using two-way analysis of variance on an untransformed dependent variable (mean mortality) as the errors were homogeneous and normally distributed. The estimate of pupal parasitism from field-collected, laboratory-reared pupae was included as an additional independent variable in the pupal nest abundance model. An estimate of fungal infection was not included in either the larval or pupal nest abundance models because the limited sample numbers reduced the data points available to the model.

Statistical Modeling

Preliminary modeling of the localized populations involved using mixed models with year as a random effect and latitude and longitude as repeated measures. This approach was used to account for the random effects of year and spatial distance between populations at different sites (Littell et al. 2006). Both isotropic and anisotropic covariance matrices either with or without a nugget (to account for abrupt changes over short distances in a locale) were used to fit a spatial regression model (SAS 2017). Year and spatial distance were not significant for any of the dependent variables (winter hibernacula relative abundance, pupal nest relative abundance, overwintering larval survival, late-stage larval relative abundance, and overwintered larval developmental maturity). Therefore, to better fit the error distribution in the predictive models we decided to use generalized linear models for estimating predictors of the dependent variables. Error terms that were used for the dependent variables were the Normal and negative binomial distribution and model

development and testing procedures were as described previously for modeling summer defoliation. Although we did not detect autocorrelation with distance between sites, we did still test for distance from the coast and distance from Peaks Island in our models.

The direct effect of parasitism was investigated by determining if late-stage larval relative abundance, hibernacula relative abundance, and pupal nest relative abundance, all in year (t + 1), were determined by either primary or total parasitism (due to primary parasitoids and hyperparasitoids) in year (*t*). Generalized linear models were constructed and evaluated as described previously. The hypothesis was that an increasing proportion of parasitism would be followed by a decreasing life stage relative abundance.

Trends in Climate Variables

To explore whether changes in climate correlate with the recent resurgence of browntail moth, trends in climate variables were examined over time for the periods before the recent reemergence of browntail moth (outbreak of 1989), and since its reemergence. The first period included data from 1941–1987, and the second included data from 1988 (1 yr before the first outbreak) through 2018. Linear least squares regression was used to examine relations between time (year) and the climate variables identified in the above models as significantly influencing browntail moth life stage variables, using NOAA-NCDC's data for Portland, ME, from 1941 through 2018 (NOAA 2019).

Results

Climate Influences Over Time

Aerial surveys of browntail moth tree defoliation during the summers from 1994 to 2015 showed fluctuations in the area impacted from 36.4 to 4,342.4 ha before a dramatic increase and the initiation of the current outbreak starting in 2016 (Fig. 2A). Analysis of this 23-yr period identified two climate variables explaining 34% of the variation in summer defoliation (Table 2). The average air temperature during the previous August – September and cumulative precipitation in May and June were the significant predictors in the model. Temperatures during the preceding late summer/early fall larval feeding period positively influenced defoliation, whereas precipitation during the late spring/early summer post diapause larval feeding period negatively influenced summer defoliation (Fig. 2B).

Variation Between Localized Populations

Variation between browntail moth populations across the state during the current outbreak, were best explained by climate variables with only one life stage estimate significantly related to habitat and distance. Relative abundance of winter hibernacula was best predicted by average temperatures for August and September and distance from Peaks Island (presumptive origin of outbreak). Hibernacula relative abundance increased with increasing temperatures and decreased with increasing distance from Peaks Island (Table 2). The proportion of larvae surviving winter and emerging in the spring for all sites and years was 0.61 ± 0.04 (mean ± SE). Survival of browntail moth larvae through the winter in the hibernacula was best predicted by precipitation and habitat (Table 2), with total winter precipitation (December through February) positively determining survival and early spring precipitation (March through April) negatively determining survival. The amount of evergreen forest was also significantly negatively related to overwinter survival. The overall amount of variance in survival explained by the predictive model was 47.4%, the greatest variation explained by any of the models (Table 2).

Variation in relative abundance of late-stage larvae was significantly determined by total precipitation in the early spring (March - April) and late spring/ early summer (May–June) periods with high levels of precipitation resulting in the lower relative abundance of larvae (Table 2). The causal effect of early spring precipitation was marginally significant at $P = 0.07$. Eliminating this variable from the model increased the significance of May–June precipitation ($P = 0.014$), but reduced the overall predictability of the model ($r^2 = 0.146$ with single independent variable versus $r^2 = 0.224$ with both). Survival from subsamples of larvae collected in 2017 and 2018 indicated no significant differences between

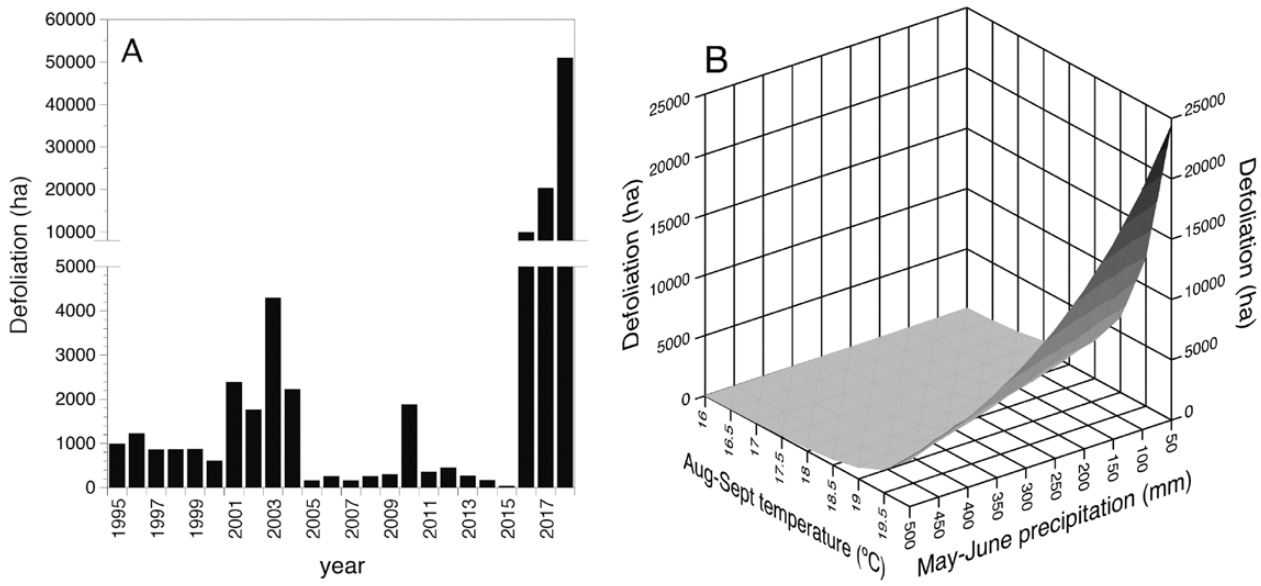

Fig. 2. Summer defoliation by browntail moth in Maine, 1994 through 2018, from aerial surveys conducted by the Maine Forest Service (**A**). Browntail moth summer defoliation as a function of average temperatures in the previous August and September and total precipitation in May and June (**B**).

Table 2. Model results for prediction of variation in browntail moth life stages sampled across Maine with relevant corresponding periods over which climate variables were summarized for analyses

Life Stage Modeled	Time period for climate variables	Error distribution* generalized r^2	Coefficients	Estimates**	Significance***
Summer defoliation	1995–2017 monthly temperature/precipitation data year (t – 1) and year (t) (Table 1)	Poisson $x^2_{(2)}$ = 63673.121 P < 0.001 r^2 = 0.348	Intercept Aug–Sept Avg Temp May–June Precip	–41.556 ± 10.628 0.762 ± 0.159 –0.105 ± 0.045	$x^2_{(1)}$ = 15.297, P < 0.001 $x^2_{(1)}$ = 22.824, P < 0.001 $x^2_{(1)}$ = 5.540, P = 0.019
Abundance of winter hibernacula	August (year = t – 1) through September (year = t – 1)	Negative binomial $x^2_{(2)}$ = 20.464 P < 0.001 r^2 = 0.259	Intercept Aug–Sept Avg Temp Km from Peaks Island	–12.166 ± 4.309 1.045 ± 0.233 –0.038 ± 0.011	$x^2_{(1)}$ = 7.969, P = 0.005 $x^2_{(1)}$ = 20.034, P < 0.001 $x^2_{(1)}$ = 11.669, P < 0.001
Survival of overwinter larvae	August (year = t – 1) through April (year = t)	Normal $x^2_{(3)}$ = 13.487 P = 0.004 r^2 = 0.474	Intercept Amount conifer forest Dec–Feb Precip March–April Precip	–0.006 ± 0.380 –1.599 ± 0.477 0.0002 ± 6.561e-5 –0.0002 ± 7.440e-5	$x^2_{(1)}$ = 0.0003, P = 0.987 $x^2_{(1)}$ = 9.016, P = 0.003 $x^2_{(1)}$ = 9.501, P = 0.002 $x^2_{(1)}$ = 7.022, P = 0.008
Abundance of late stage larvae	August (year = t – 1) through June (year = t) Use survival of overwintered larvae	Negative binomial $x^2_{(2)}$ = 7.621 P = 0.022 r^2 = 0.224	Intercept March–April Precip May–June Precip	7.386 ± 1.398 –0.0005 ± 0.0003 –0.0004 ± 0.0002	$x^2_{(1)}$ = 27.894, P < 0.001 $x^2_{(1)}$ = 3.264, P = 0.071 $x^2_{(1)}$ = 4.351, P = 0.037
Abundance of Pupal nests	August (year = t – 1) through June (year = t) Use survival of overwintered larvae	Negative binomial $x^2_{(2)}$ = 15.281 P < 0.001 r^2 = 0.182	Intercept March–April Avg Temp March–April Precip	4.113 ± 0.929 0.461 ± 0.201 –0.0004 ± 0.0001	$x^2_{(1)}$ = 19.573, P < 0.001 $x^2_{(1)}$ = 5.283, P = 0.022 $x^2_{(1)}$ = 11.172, P < 0.001
Maturity of emerging overwintered larvae (weighted mean instar)	August (year = t – 1) through April (year = t)	Normal $x^2_{(2)}$ = 25.469 P < 0.001 r^2 = 0.553	Intercept Aug–Sept Avg Max Temp March–April Avg Max Temp	–2.658 ± 1.597 0.151 ± 0.073 0.248 ± 0.065	$x^2_{(1)}$ = 2.769, P = 0.096 $x^2_{(1)}$ = 4.282, P = 0.039 $x^2_{(1)}$ = 14.632, P < 0.001

*Likelihood ratio test, Chi-square test for difference between whole (all independent variables) and reduced (intercept only) model.
**To predict life-stage relative abundance models fit with Poisson or negative binomial exponentiate the linear additive equation of model coefficients.
***Wald Chi-square test.

Table 3. Fate of browntail moth larvae and pupae collected and reared from infested sites in Maine, 2016–2018

Year	Stage	N	% Survival to Pupae or Adult	% Parasitized	% Fungi	% Unidentified mortality
2016	Larvae	–	–	–	–	–
	Pupae (nests)	2,028 (592)	52.3 ± 6.1	49.4 ± 7.8	–	–
2017	Larvae	264	–	–	79.0 ± 2.5	20.8 ± 2.5
	Pupae (nests)	1,364 (440)	27.4 ± 5.0	17.7 ± 5.4	1.2 ± 0.6	52.0 ± 7.2
2018	Larvae	225	38.9 ± 7.0	13.3 ± 3.84	0	33.4 ± 5.8
	Pupae (nests)	1,418 (494)	36.7 ± 5.6	26.2 ± 3.6	9.6 ± 4.8	26.9 ± 4.8

– Indicates data was not collected.

site and year (Table 3). The majority of larvae that died over both years exhibited signs of *E. aulicae* infection, which had a higher prevalence in 2017. Evidence of parasitism of late-stage larvae was minimal with only a few individuals having Tachinidae puparia in browntail larvae.

Pupal nest relative abundance was best predicted by early spring precipitation and temperature (Table 2). Average temperatures in March and April positively determined pupal nest abundance, while total precipitation during these months had a negative impact on pupal nest relative abundance. The proportion of collected browntail moth pupae from which healthy adult moths emerged differed between years but not between sites ($F_{(2,39)}$ = 5.42, P = 0.01; Table 3). The sex ratio was fairly even with M:F being 1.2:1.0 in 2017, and 1:1 in 2018. Survival of pupal nests was 52 ± 6.1%, 27 ± 5.0%, and 36 ± 5.5% in 2016, 2017, and 2018, respectively. Looking at pupal nests across all years, parasitism accounted for 30 ± 3.42% mortality of pupae, fungi accounted for 5 ± 1.3% mortality, and there was 37 ± 4.3% for which the cause of mortality was unidentified.

Proportion parasitism was not a significant factor in any of the models that explained local population variation by climate variables. In addition, assessment of the effect of proportion parasitism in year (t) on life stage relative abundance in year (t + 1) did not provide any evidence that either parasitism from primary parasitoids or total parasitoids (primary parasitoid and hyperparasitoids) determined relative abundances.

Head capsule measurements of emerging overwintered larvae ranged from 0.40 to 1.22 mm, with a mean (±SE) of 0.682 ± 0.012 mm. Corresponding stadia determination indicated that overall, 75 % of larvae emerge in the spring as third instars. The maturity (weighted mean instar) of the larval populations was best

predicted by the average maximum temperatures experienced during their development pre-diapause in August and September and post-diapause in March and April (Table 2). The model explained 43.6% of the variance in weighted mean instar.

Trends in Climate Variables

Climate trends before and after browntail moth resurgence were examined for significant predictors. The parameters examined were average daily temperatures and average maximum temperatures over August and September, and March and April, and total precipitation over December through February, March through April, and May through June (Fig. 3). No significant linear trends were detected for any variable for the period before resurgence, nor for March and April temperatures (TAVG, TMAX), and total precipitation in March through April and May through June since the resurgence. There were significant trends in both average daily and average maximum temperatures for August and September, as well as precipitation in December through February, all of which increased between 1988 and 2018.

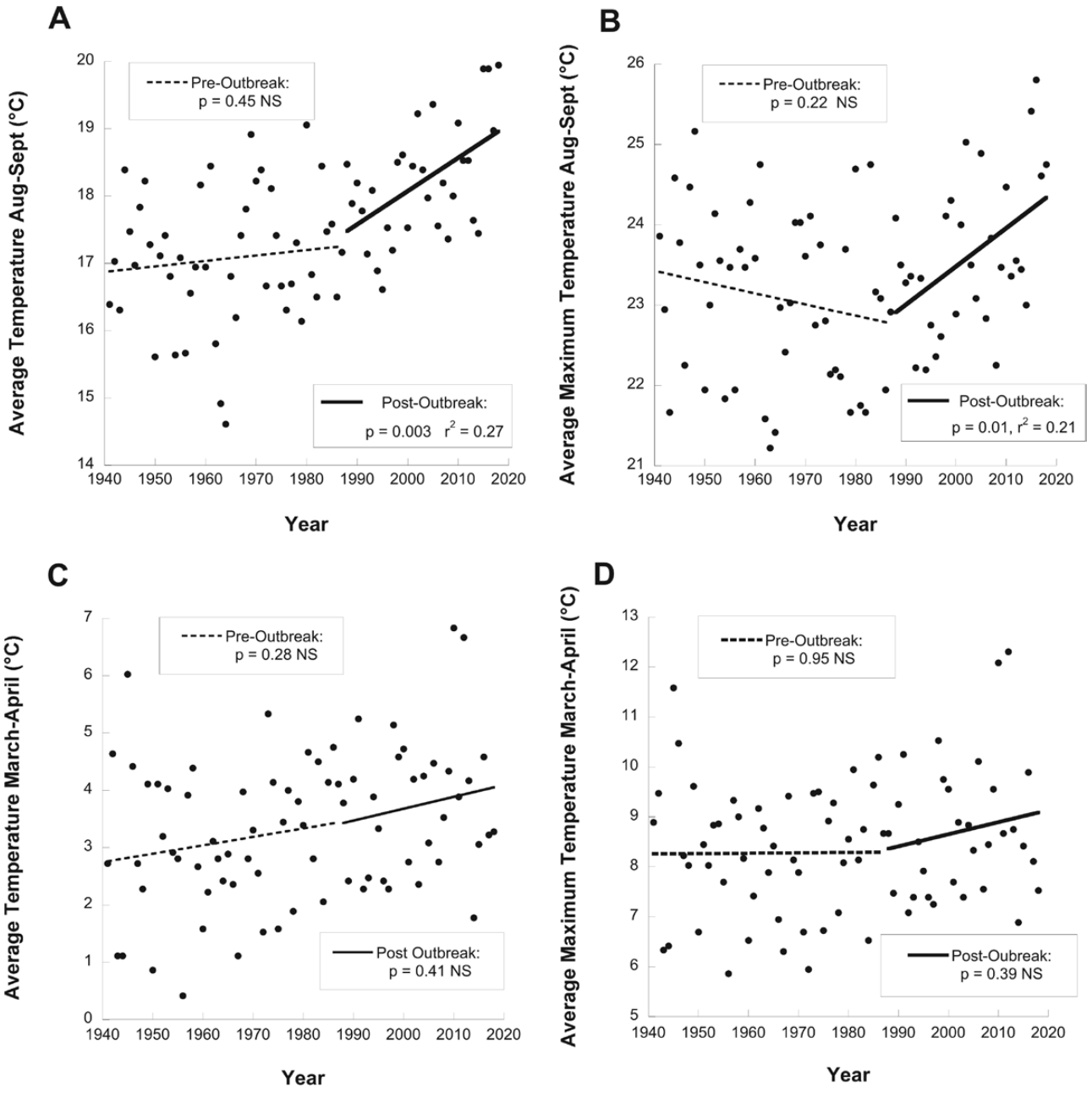

Fig. 3. Trends in climate variables identified as significant predictors of browntail moth populations, Portland ME, 1941–2018: mean daily and mean maximum temperature during the pre-diapause larval feeding period (August–September) (**A & B**), mean daily, and mean maximum temperature during the post-diapause period in and emerging from winter hibernacula (March–April) (**C & D**), total precipitation during winter diapause (December–February) (**E**), total precipitation during the post-diapause period in and emerging from winter hibernacula (**F**), and total precipitation during the spring and early summer post-diapause larval feeding period (May–June) (**G**). Lines depict linear trends analyzed for the periods up to and after one year before the 1989 outbreak, which marked the recent resurgence of browntail moth in Maine; Pre-outbreak: 1941–1987, and Post-outbreak: 1988–2018.

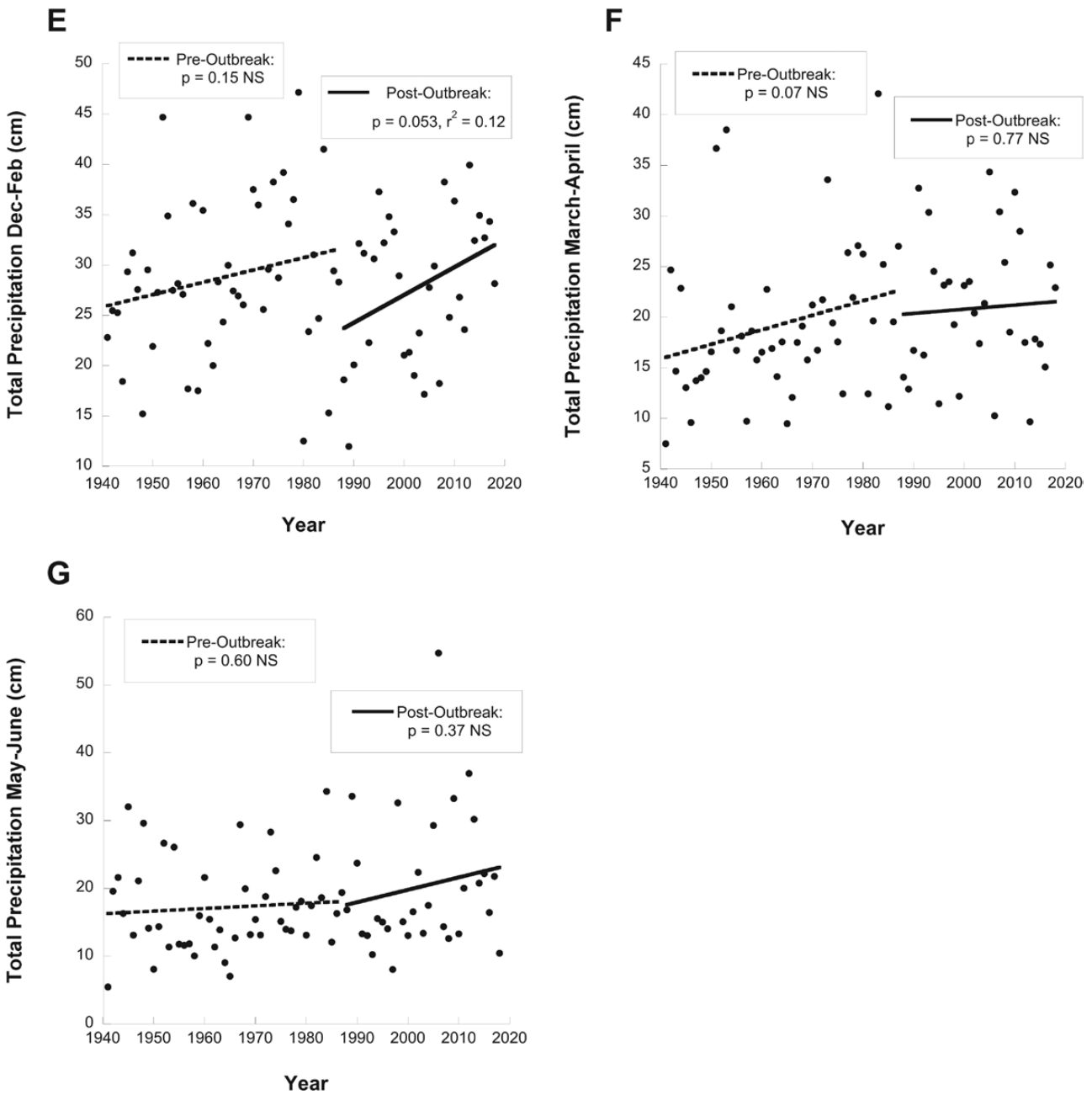

Fig. 3. Continued.

Discussion

The browntail moth resurgence since 1989 in areas along the mid-coast of Maine defoliated 12.5–43.4 km^2 every 4–5 yr until 2016 when the current outbreak was initiated resulting in defoliation of over 100 km^2. This area doubled by the following year and reached greater than 500 km^2 by 2018, a resurgence of this pest that has not been seen in over 70 yr. Our study of variation in populations across infested areas in Maine and over this latest resurgence period suggests that climatic factors, particularly spring and summer temperatures, and spring precipitation are significant predictors of population outbreaks (Fig. 4).

Late Summer and Fall

Temperature has a direct effect on insect development rates and direct and indirect effects on survival (Ponsonby and Copland 1996, Bale et al. 2002, Delatte et al. 2009, Cui et al. 2018). During early to mid-August in Maine, browntail moth eggs complete their development and hatch, and early-stage larvae feed gregariously on foliage while constructing their winter hibernacula. Both the density of hibernacula and the maturity (WMI) of larvae emerging in the spring are determined in part by temperatures experienced by larvae in the previous August and September (Fig. 4). The analysis of summer defoliation trends supports that these late summer/ early fall temperatures are key determinants of population levels the following year, suggesting that the conditions experienced by early-stage (pre-diapause) larvae are a major factor governing the subsequent population trajectory. Faster development in several insect species can have positive indirect effects on larval survival reducing the time susceptible stages are exposed to attack by predators, parasitoids, and pathogens (Culler

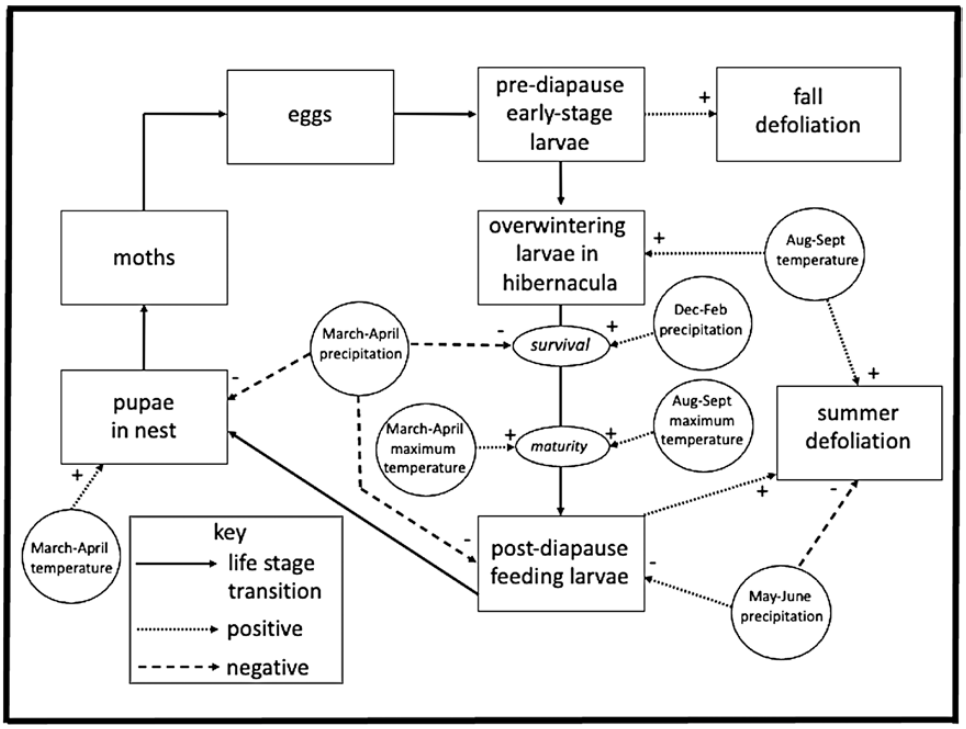

Fig. 4. A systems diagram of the climate factors that affect the dynamics of browntail populations in Maine based on the results of our statistical models. Browntail moth's univoltine life cycle is initiated with oviposition in late July to early August followed by larval feeding both pre- and post-diapause, resulting in two periods of defoliation separated by a 7 mo overwintering period in a communal hibernaculum. Mature larvae pupate either individually or communally in leaf nests in early July before emerging as moths two – three weeks later. For each life stage modeled, climate variables experienced during all previous stages from oviposition to the life stage modeled were assessed, and factors that significantly influenced the predictability of the modeled stage are depicted.

et al. 2015, Laws 2017). In gypsy moth (*Lymantria dispar* L.), higher temperatures influence survival by increasing the developmental rate, allowing larvae and pupae to escape natural enemies (Leonard 1974, Alalouni 2013). Predator and parasitoid interactions can also be altered due to changes in abiotic conditions which influence the chemical signaling of prey from host plants (Laws 2017). Early-instar larvae that experience higher temperatures in the fall and develop faster may escape parasitism by their specialist tachinid parasitoid, *T. nidicola*, which must overwinter in hibernating larvae to complete development (Clausen 1956). Entomophagous fungal pathogens are also sensitive to temperature and relative humidity, as these abiotic conditions affect the viability of conidia, virulence, spore production, and successful infection (Bugme et al. 2008, Mishra et al. 2015).

Winter

Neither average nor minimum winter temperatures experienced by browntail moth larvae when they are in diapause in the late fall (October and November) and winter (December through February) determine overwintering larval survival nor abundance of larvae or pupae the following spring and summer (Fig. 4). Browntail moth can survive extreme low temperatures, between –17°C and –29°C, with some larvae able to withstand longer periods of exposure at –24°C (Gilliatt 1921, Schaefer 1974). Elkinton et al. (2008) found that extreme winter temperatures during the 1920's did not explain the decline in browntail moth at either inland or coastal sites. The expansion phase (1897–1914) actually had a greater number of days below –25°C than the contraction phase (1915–1932) of the infestation. Winter hibernacula lend substantial insulation depending on the host material used, height off the ground, amount of silk used, and the number of larvae within the structure (Schaefer 1974). Temperature within hibernacula may also influence survival. Hibernacula with higher densities of larvae have higher temperatures than that of the external environment (Skoptsov 1968), with internal hibernacula temperatures averaging 7°C above ambient temperatures during the day and 0.1°C higher at night (Schaefer 1974).

In contrast to temperature, winter precipitation did affect the survival of overwintering larvae, with survival increasing with increased total precipitation over the winter (Fig. 4). Total winter precipitation in Maine is highly correlated with snow depth. Hibernacula that are closest to the ground and covered by snow have the highest survival, while those higher in the canopy have varied survival based on the amount of solar radiation and exposure to wind/extreme ambient temperatures (Schaefer 1974). Cold air holds less moisture hence temperatures during winter put diapausing insects simultaneously at risk of desiccation as well as freezing (Dank 2000). Physiological preparation for these adverse conditions in insects includes the seasonal accumulation of cryoprotectant glycerols, which have been shown to lower the supercooling point and provide resistance to water loss (Dank 2007). This response is more marked for insects like browntail moth that overwinter in supranivean hibernacula (Williams et al. 2002). Based on our results we hypothesize that sensitivity to limitations in moisture may be more important for overwintering browntail moth larvae than winter temperature fluctuations. With more precipitation larvae in hibernacula in the upper canopy may be less likely to desiccate during these months.

Early Spring Through Mid-Summer

Browntail moth larvae emerge from their hibernacula in late April in Maine and are frequently seen clustered over the outside of these

structures before bud break and the subsequent availability of host plant foliage. In the laboratory we have observed that emerging larvae are capable of surviving for up to two weeks at ambient temperatures without food. Larval instar and size, determined by both late summer/early fall and early spring (March–April) average maximum temperatures directly influence their survival at this critical point in their life cycle (Fig. 4). Ward et al. (2019) found that fall temperatures impacted the number of larch casebearers *(Coleophora laricella* Hübner) reaching the third instar stage of development for overwintering before needle drop in their host tree. Although these warmer autumnal temperatures also resulted in delayed and reduced spring activation of casebearer larval post diapause, their data suggests that increases in annual degree-day accumulation have helped facilitate recent outbreaks of this invasive species.

Average maximum temperatures in August and September and in April and March were better predictors of browntail moth development than accumulated degree-days calculated from average temperatures over these periods (Fig. 4). Temperatures fluctuate at these times of the year in Maine, frequently dropping below freezing and likely below the developmental threshold of larvae at night, while warming considerably during the day. These warmer daytime temperatures allow larvae hours of time for feeding and development that are not evident when temperatures are averaged with the cool nighttime conditions.

We did not find that late spring nor early and mid-summer temperatures experienced during post diapause larval feeding and development, pupation, and adult dispersal were predictive of abundance of these stages, nor defoliation trends (Fig. 4). Klapwijk et al. (2013) reported an overall trend of increasing browntail moth severity over the past several decades with outbreaks positively linked to temperatures in July (year = t) and the previous June (year = $t - 1$), hence during adult emergence and dispersal, and late-stage larval feeding and development the previous year. Their analysis was based on the sum of defoliation evaluated four times over the year, so may include the damage from two consecutive generations that occurs in a single season, overwintered late-stage larvae in June, and pre-diapausing early-stage larvae in August and September. This is difficult to compare with our estimates of defoliation which were timed to coincide with the end of the late-stage larval feeding each summer, but before the feeding by the early-stage larvae of the subsequent generation in August.

Unlike winter precipitation, early spring (March and April) precipitation when larvae emerge from hibernacula and in the late spring/ early summer (May and June) during post diapause larval feeding and development, have negative effects on overwintering survival, and abundance of late-stage larvae and pupal nests (Fig. 4). Precipitation coinciding with freezing-thawing temperatures in the late winter and early spring may have a direct effect on larvae in overwintering hibernacula and as they are emerging from hibernacula. As mentioned previously, larvae can spend a week or more exposed to harsh spring conditions before bud break and the foliage provides food and some level of protection. Rainfall can directly impact insect survival by displacing establishing larvae (Hagley 1972). We have observed what appears to be a high level of water repellency provided by the setae of larvae clustered together on the outside surface of their hibernaculum following diapause. Our larval survival data and observations in the field indicate that spring and early summer precipitation, particularly that which occurs in May and June, likely affects browntail larval survival by facilitating infection with the entomopathogen, *E. aulicae*. Larvae infected and sporulating with a fungus were observed in the field each year of the study and the fungus was confirmed as *E. aulicae* both via microscopic examination of the spores (Boyd 2020) and examination of extracted DNA and sequence data (unpublished data, methods followed Kereselidze et al. 2011). A localized epizootic was observed in 2017 with the fungus causing 79% mortality of larvae collected across the study sites, and noticeably few pupal nests at many sites around the Merrymeeting Bay area (see Fig. 1). Details of our *E. aulicae* studies are being addressed in another manuscript, but the significant causal effect of May and June precipitation on browntail moth populations since their resurgence in 1989 indicate that this fungus may be a critical factor in browntail moth year to year population fluctuations.

Causes of Population Outbreaks

Parasitism impacts on browntail moth populations between 2016 and 2018 were comparable to those reported by Burgess and Crossman (1929) during the earlier outbreak in 1915, and were primarily due to three species of Tachinidae with the host specific species, *Townsendiellomyia nidicola* Townsend, accounting for 48 % of parasitism, and the two generalists, *C. concinnata* and *Carcelia laxifrons* Ville., accounting for 2% and 35%, respectively (Boyd 2020). The proportion parasitized did not add to the predictability of browntail moth pupal abundance nor the abundance of hibernacula in the subsequent generation. This and the relatively low levels of parasitism by *C. coccinnata* and other generalists suggest that the current outbreaks in Maine are not strongly impacted by generalist parasitoids as suggested by Elkinton et al. (2006). Hymenopteran hyperparasitoids increased over the current outbreak from 2016 to 2018, which might have had a suppressive effect on primary parasitism (Boyd 2020).

Population outbreaks of browntail moth in its native range in Europe have been found to occur synchronously over large regions with no regular periodicity (Sterling and Speight 1989, Leskó et al. 1995, Klapwijk et al. 2013), which Klapwijk at al. (2013) suggests indicates the importance of exogenous weather fluctuations rather than natural enemies or other bottom-up controls. Sterling and Speight (1989) describe populations in England as being primarily limited to the southeast coast in periods between outbreaks, but spreading inland during periods of population increases. Populations that primarily persist or are more severe in coastal habitats have also been reported in the Netherlands (Moraal and Jagers op Akkerhuis 2011) and Spain (Frago et al. 2011), though there are many areas in continental Europe where browntail moth distribution is not predominantly coastal (Sterling and Speight 1989). We did not see a relationship between distance from the coast and abundance of browntail moth life stages during its current outbreak in Maine, although distance from Peaks Island which has supported persistent populations since at least the 1970s, was a significant predictor of the rank density of overwintering hibernacula. However, the trend of browntail moth in North America since its initial collapse in the 1930s and 1940s, has been similar to that described by Sterling and Speight (1989) in England, with populations primarily persisting at coastal locations in Casco Bay, ME, and Cape Cod, MA (Schaefer 1974, Elkinton et al. 2006), with increased densities and expansion inland during the current outbreak. Indeed, a study by Marques et al. (2014) of genetic diversity and differentiation in 13 browntail moth populations across Europe and one from Casco Bay, Maine, suggests that the UK is the likely source of the invasive populations in the US. Outbreaks in Hungary (Csóka 1997) and Iran (Arefipour et al. 2005) have been reported to follow several years of drought, however analyses of long-term trends in defoliation and population surveys over 48 and 61 yr in Hungry (Klapwijk et al.

2013) and the Netherlands (Moraal and Jagers op Akkerhuis 2011), respectively; showed no relationship with precipitation. This contrasts with our analyses which showed significant negative effects of spring precipitation (Fig. 4). Sterling and Speight (1989) and Frago et al. (2011, 2012) conducted surveys and evaluated the impacts of natural enemies of browntail in Europe. They both reported a number of different parasitoid species, and Sterling and Speight (1989) identified microsporidia and virus infections in England, attributing microsporidia as a key factor responsible for most of the variation in mortality between sites. We examined many larvae microscopically and saw no indication of microsporidia presence in live or dead caterpillars in Maine. Although Frago et al. (2011) recognized that some unexplained mortality was likely due to pathogen infections, pathogens were not identified and quantified in their study. *Entomophaga aulicae* is globally distributed and has been reported attacking lepidopteran hosts in the United Kingdom, France, the Netherlands, Germany, and Russia (Gama 2018). Pilarska et al. (2002) identified *E. aulicae* in multiple high density browntail moth populations in Bulgaria and described it as one of the key factors causing reduction in populations with *E. aulicae* induced mortality ranging from 8–100%. Tabakovic-Tosic et al. (2018) published the first report of the fungus in browntail moth populations in Serbia and attributed reduced populations in 2016 to the frequency of rainy days and favorable temperatures in the later part of May in two previous years, which were favorable for the germination of *E. aulicae* resting spores and infection of larvae.

Although our findings demonstrate that spring precipitation patterns are partial determinants of browntail populations and defoliation, analysis of climate trends both pre- and post-resurgence of browntail moth in Maine show that spring precipitation patterns have not changed markedly between these two periods. In contrast, average daily and average maximum temperatures during the late summer/early fall when early-stage larvae are feeding and constructing their hibernacula, have increased significantly, as has precipitation in the winter months. We hypothesize that this warming period that promotes development during critical stages of the pre-diapause browntail moth larval development, accounts for what appears to be an increased frequency of population cycles (outbreaks ca. every 4–5 yr) that we have seen since the resurgence in 1989, where warmer temperatures promote population increases, and when variable spring rains favor *E. aulicae*, browntail moth populations will be reduced the subsequent year. However, a perplexing issue is why we have not seen a similar resurgence of browntail moth in Massachusetts. An analysis of climate trends from Hyannis, MA, shows that the same climate trends of increasing late summer, early fall, and early spring temperatures have been experienced over the past 30 yr on Cape Cod as they have in Maine. Barbosa and Schaefer (1997) propose that the observed patterns of abundance and spread of four significant forest insects, including the invasive gypsy moth and browntail moth are driven by host plant availability and quality. Specifically, for browntail moth, they suggest that declines in host plant quantity and quality were brought on by gypsy moth defoliation as this species expanded its distribution and overlapped with browntail moth in the early 1900s. The extensive and repeated spring defoliation of their common host plants on which browntail moth, with their narrower host range, were dependent, led to limited suitable trees for female oviposition and subsequent larval development in the mid and late summer. Schaefer (1974) noted a rejection of small re-foliated leaves by ovipositing females, and that the size and number of overwintering larvae as well as larval survival vary with host plant species. Elkinton et al. (2006) proposed that browntail moth's limitation to coastal habitats is related to host plant diversity and availability through the indirect mediation of parasitoid natural enemies, particularly the generalist, *C. coccinnata*. Therefore, browntail moth can thrive in these habitats in the relative absence of parasitoids which suppress its populations in more diverse inland forest habitats with more lepidopteran hosts, including gypsy moth. We have found some gypsy moth larvae coinciding with browntail moth larvae feeding on oak in the Midcoast area of Maine during our study, but always at very low densities, even during the recent gypsy moth outbreaks that occurred from southern Maine through southern New England in 2015–2018. Midcoast and central Maine forests and their lepidopteran herbivore community, particularly gypsy moth, do not impose the same limitations on browntail moth populations that occur in Massachusetts and as such have been able to respond to favorable warming conditions.

With climate warming, the spread of other invasive species, such as the emerald ash borer and southern pine beetle, and changing patterns of human development and suburban spread, Maine's forests are changing, although specific patterns are hard to discern given the long-lived nature of trees and the complexity of forest communities (Fernandez et al. 2015, Fernandez et al. 2020). As such, it is difficult to predict long-term trends in browntail moth populations. Current climate trends, particularly warming, favors their development, but over time, these same factors may affect the range expansion of other lepidopterans which could introduce more competitors, altering host plant quality and the dynamics of natural enemies.

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