Through space and time: Predicting numbers of an eruptive pine tree pest and its predator under changing climate conditions

Holly L. Munro [*], Cristian R. Montes, Stephen M. Kinane, Kamal J.K. Gandhi

D.B. Warnell School of Forestry and Natural Resources, University of Georgia, 180 E Green Street, Athens, GA 30602, USA

ABSTRACT

Forest biotic populations and communities are undergoing irreversible changes due to climatic perturbations, and these effects may be exacerbated by insect pests. In the southeastern United States (U.S.), *Dendroctonus frontalis* is one of the most important forest pests that can cause substantial tree mortality over large geographic areas. As life-history of *D. frontalis* is dependent on environmental conditions, our objective was to determine the effects of climatic variables on the species occurrence of *D. frontalis* and their main predator, *Thanasimus dubius*. U.S. Department of Agriculture - Forest Service beetle trapping data (proxy for true abundance) for 2014–2018 were assessed with nine climatic variables including: (1) average monthly minimum, maximum, and mean temperatures; (2) mean winter temperature; (3) minimum, maximum and mean annual temperature; and (4) cumulative winter and annual precipitation. Variable selection was performed using least absolute selection and shrinkage operator (LASSO), and selected variables were fit to varying coefficient generalized additive models (GAMs). Minimum temperatures for February and March and maximum temperatures for January and prior year August were found to have a significant effect on *D. frontalis* numbers, and model accuracy was ~89%. Beetle suitability was assessed for 1981–2100 under three different shared socioeconomic pathways (SSP). The model indicated that the suitability of *D. frontalis* has increased from 1981 to 2019 in certain regions of Alabama, Mississippi, and Georgia, while Arkansas, Kentucky, Louisiana, North Carolina, Tennessee, East Texas, and Virginia had low suitability. Future projections indicated comparable *D. frontalis* numbers to current numbers under the lowest SSP of 2.1 °C by year 2100, but *D. frontalis* may decrease under higher warming projections. The same climatic predictors influenced *T. dubius*, except average September maximum temperature replaced August maximum temperatures in the model. Understanding how these abiotic factors influence forest pest populations may better guide prevention and management practices aimed at identifying high risk areas and reducing pest outbreaks.

1. Introduction

Forests comprise approximately 300 million hectares of the terrestrial land surface in the United States of America (U.S.) and provide beneficial services (e.g., carbon storage repositories, soil erosion mitigation, timber products, and wildlife habitat and forage) (Oswalt and Smith, 2014). These forests are subjected to many abiotic and biotic disturbances which inhibit their ability to provide such services and disturbances may be amplified due to climate change (Seidl et al., 2016). Forecasted changes in temperature, precipitation, and the frequency of extreme weather events over the coming decades will irreversibly alter forest structure and productivity (Adams et al., 1990; McNulty et al., 1996; Spittlehouse and Stewart, 2003). Among biotic disturbances,

insect pests are prominent drivers of disturbance and mortality in forests and may exacerbate the effects of climate change (Marini et al., 2017). Large-scale pest-induced tree mortality may convert forests from carbon sinks to sources (Kurz et al., 2008), resulting in a feedback loop whereby the consequences of climate change become partial drivers of future climate change.

The Southeast U.S. contains 40% (~80 million hectares) of the pine (*Pinus* spp.)-dominated timberland in the U.S., thus changing climate may intensify insect damages and is of great ecological and economic concern. *Dendroctonus frontalis* Zimmermann (Coleoptera: Curculionidae) is an aggressive bark beetle that is an important agent of disturbance throughout pine forests in the southeastern U.S (Ungerer et al., 1999). They are obligate tree-killers of pines and they excavate feeding and reproduction galleries in

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the phloem layer causing girdling of the tree and introducing weakly pathogenic fungi (Hain et al., 2011). These beetles can be found in most forests throughout their range at low population levels on stressed or dying trees, and usually co-occur with other less aggressive bark beetles (e.g., *Ips* species) and their main predator, *Thanasimus dubius* Fabricius (Coleoptera: Cleridae) (Thatcher and Pickard, 1966; Nebeker, 2011). *Dendroctonus frontalis* undergo sporadic and eruptive shifts to outbreak population levels, which results in mortality of healthy pine hosts and revenue losses of $43–237 million per year across the Southeast U.S. (Hain et al., 2011; Pye et al., 2011). Better prediction of *D. frontalis* populations will be invaluable for timely and sustainable forest management practices, as this will allow forest managers to focus management efforts on high risk areas.

Insects are poikilothermic with limited thermoregulation, thus weather influences *D. frontalis* gallery construction, development, oviposition rates, emergence and flight, survival, and voltinism (Ayres et al., 2000; Hain et al., 2011; Stephen, 2011). *Dendroctonus frontalis* have one to two generations per year at northern latitudes and up to nine in the warmer southern latitudes, thus resulting in increased population numbers and possibly an increased outbreak risk. *Dendroctonus frontalis* have an upper threshold of approximately 33 °C and lower lethal temperature of −12 °C with complete mortality occurring at −16 °C. *Dendroctonus frontalis* are considered the least tolerant bark beetle species to cold temperatures, thus winter temperatures are an important source of population control and are considered to be the most important factor limiting northern range expansion (Ungerer et al., 1999; Ayres et al., 2000; Stephen, 2011). Consequently, researchers have expressed concern about future warmer temperatures facilitating the species niche expansion into the Northeast U.S. and Canada (Dodds et al., 2018). The historic range of *D. frontalis* was restricted to the southeastern and southwestern U.S., Mexico, and Central America, but range expansion into the northeastern U.S. is now being documented (Thatcher and Barry, 1997; Gan, 2004; Hain et al., 2011). This new distribution may devastate pine species that have not coevolved with *D. frontalis* and therefore, lack adequate defenses (Heuss et al., 2019).

Despite the integral role of weather in *D. frontalis* life history, few studies have been able to quantify the relationship between climatic variables and *D. frontalis* population dynamics. Climatic variables have been used to predict the presence of outbreaks, outbreak growth rate, quantity of infested pines, monetary losses, and range expansion (e.g., Hines et al., 1980; Feldman et al., 1981; Coulson et al., 1989; Turchin et al., 1991; Williams and Liebhold, 2002). Relationships between species capture data and climate records (e.g., temperature and rainfall) are non-linear, multi-dimensional with complex correlation structures, making it very hard to model with traditional techniques. Latest innovations in ecological modeling that incorporate more advanced techniques [e.g., conditional inference framework, generalized additive models (GAM) (Hastie and Tibshirani, 1990), and random forests (Breiman, 2001)] and the availability of georeferenced climatic data over large areas (Thornton et al., 2017, 2018), may allow for better interpretation of insect distributions in relation to climate. Previous work has successfully used these techniques to predict climate-related species distributions for other bark beetle species (DeRose et al., 2013; Hart et al., 2015; Lloret and Kitzberger, 2018) providing a good framework to test these relations with *D. frontalis* and its predator, *T. dubius*.

Our study aims to build on previous work by investigating the effects of climatic variables on pest populations using a novel modeling approach that has both explanatory and predictive power. This study addresses issues of variable selection, multi-dimensional and correlated data, spatial and temporal resolution, model uncertainty, and cross-validation to generate a framework that can be used by ecologists and foresters interested in expanding our results. Specifically, our objectives were to: (1) determine which variables (precipitation and temperature) are significant predictors of *D. frontalis* and *T. dubius* numbers and how these variables influence species occurrence; and (2) predict the spatial–temporal effects of these variables under climatic changes over

time. First, we hypothesized that beetle numbers would increase as precipitation decreases due to reduced host trees defense (e.g., alterations in physiological properties and secondary metabolites). Under the growth-differentiation balance hypothesis, secondary defensive compounds may initially increase under low water stress due to a reduction in resources for growth but would subsequently be reduced under more severe water stress (Herms and Mattson, 1992). Second, we hypothesized that as temperature increases beetle numbers would increase due to increased survival and faster development (Vose et al., 1993; Ayres et al., 2000; Hain et al., 2011; Stephen, 2011). Understanding how climate has influenced *D. frontalis* populations over the last few decades may elucidate future population dynamics in their native range, possible future range shifts and/or expansion, and can be integrated in outbreak prediction models. These applications may allow for more effective and timely management [i.e., prevention methods that increase forest health (thinning) or loss reduction (removal of infested trees)] of one of the most economically important herbivorous beetles on pine trees in the eastern U.S.

2. Materials and methods

2.1. Data

Data for *D. frontalis* and *T. dubius* were obtained from the annual springtime trapping survey conducted by the United States Department of Agriculture Forest Service (USDA-FS), the methodology for which is described in Billings and Upton (2010) and Billings (2011). Lindgren funnel traps (Lindgren, 1983) baited with beetle attractants are placed on federal and state-owned land in spring every year to monitor *D. frontalis* populations. Trap establishment coincides with the blooming of eastern redbud (*Cercis canadensis* L.) and the growth/differentiation period of pine trees (Billings and Upton, 2010; Billings, 2017), which is also the time for *D. frontalis* emergence and peak spring flight (Sullivan et al., 2016). Traps were baited with frontalin and terpenes prior to 2017, however the *D. frontalis* pheromone component *endo*-brevicomin was added to the bait in 2017. These lure components are produced by *D. frontalis* (frontalin and *endo*-brevicomin) and host trees (terpenes). Frontalin and terpenes are attractive to both *D. frontalis* and *T. dubius,* while *endo*-brevicomin is only attractive to *D. frontalis*. Trap collections are sorted, identified, and counted by USDA-FS personnel. We obtained five years of data (2014–2018) for 13 states (782 total observations) (Fig. 1). The number of observations per year for 2014–2018 were 141, 141, 153, 158, and 189 observations, respectively. Due to variability in the collection period (i.e., traps were emptied once every 7–8 days for four weeks), all beetle counts were standardized to the number of beetles captured per trap per day during spring emergence. Due to the cryptic nature of *D. frontalis* and use of lures and traps*,* abundance is difficult to obtain and thus, trap catch data are described as occurrence, catches or numbers.

We used climatic variables as independent predictors to make inference about insect occurrence, as well as for backcasting and forecasting. Predictors were summarized from past weather values obtained from Daymet Daily Surface Weather and Climatological Summaries (DAYMET) (Thornton et al., 2017, 2018). Three temporal scales were considered for this study for the period prior to the annual trapping survey (April $_{t-1}$ through March): (1) average monthly minimum, maximum, and mean temperatures; (2) mean winter temperature (November$_{t-1}$ – February); and (3) minimum, maximum and mean annual temperature. The effects of precipitation likely occur over a longer temporal scale, therefore we included cumulative winter (November$_{t-1}$ – February) and annual precipitation only. All data were at a 1 km^2 spatial resolution.

2.2. Variable selection

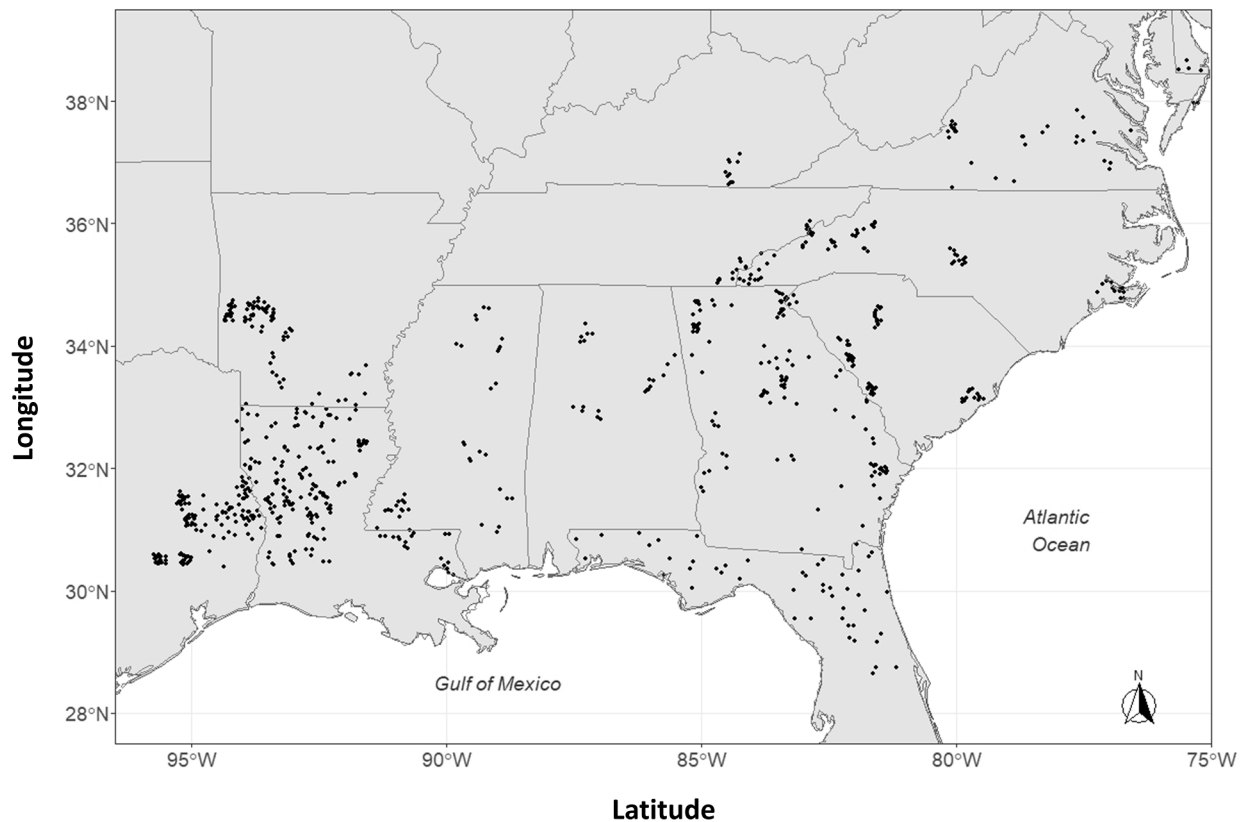Given the number of independent predictors as well as their corre-

Fig. 1. *Dendroctonus frontalis* trap locations obtained from the United States Department of Agriculture - Forest Service annual trapping survey for 2014–2018 for 13 states (782 total observations) across the southeastern United States of America.

lated structure, we used least absolute shrinkage and selection operator (LASSO) to determine the weather variables that significantly affected *D. frontalis* and *T. dubius* numbers. LASSO was fit using a generalized linear model with a Poisson distribution (Eq. (1)):

$$g(E(Y_i)) = \alpha + X_{i1} + \cdots + X_{i42} \tag{1}$$

where $E(Y_i)$ is the expected number of *D. frontalis* per day during spring emergence, $g(Y_i)$ is the log link function for the Poisson distribution, and X_i indicates the 42 weather explanatory variables. LASSO regression extends the common Ordinary Least Squares loss function by including a weighting penalty (λ) (L1 regularization) on the absolute value of the coefficient sums for standardized predictors (Eq. (2)):

$$L_{lasso}(\widehat{\beta}) = \sum_{i=0}^{n}(y_i - x_i^{'}\widehat{\beta})^2 + \lambda \sum_{j=0}^{m}\left|\widehat{\beta}_j\right| \tag{2}$$

LASSO shrinks coefficients to zero if they are poor predictors or are highly correlated (i.e., the variable with the lowest coefficient is reduced to zero), dropping unnecessary variables while reducing model over-fitting. In our case, λ parameter was found through a ten-fold cross-validation against a training set comprised of 80% of the data. The model for each insect species was then fit using the calibration data and λ, which was subsequently used to make predictions on the test data. The variables with non-zero coefficients were selected for each of the final models.

2.3. Model description

To determine the effects of weather and predict *D. frontalis* and *T. dubius* numbers, we used varying coefficient generalized additive models (GAMs) with a negative binomial error distribution. Given the

zero inflated nature from our data a negative binomial distribution for the expected response was selected as it has been shown to perform better than traditional transformations (O'Hara and Kotze, 2010). GAMs extend linear regressions (Eq. (1)) to obtain:

$$g(E(Y)) = \alpha + s_1(X_1) + \cdots + s_p(X_p) \tag{3}$$

where $E(Y)$ is the expected number of *D. frontalis* per trap per day during spring emergence, $g(Y)$ is the log link function for a negative binomial distribution, and $s(X)$ indicates the smoothing function of each of the explanatory variables. GAMs are an extension of the linear model framework that allow for nonparametric forms through the inclusion of smoothing splines (i.e., basis functions). To avoid overfitting, GAMs penalize the smoothing parameter based on the magnitude of smoothing in a similar way as the LASSO regression. This modeling framework allowed the accommodation of non-linear relations between the predicted variable and weather predictors without the need of a beforehand parametric form, while maintaining the ease of interpretability of a linear model. In this work, we used one kind of smooth, the thin plate splines (TPS), which does not require an *a priori* error covariance matrix further simplifying model formulation (Hutchinson and Gessler, 1994). We implemented the GAMs as varying coefficient models to account for the two different insect baits (i.e., inclusion of *endo*-brevicomin in baits where year ≥ 2017). *endo*-Brevicomin has been shown to enhance trap catches (Sullivan et al., 2007) and the presence of this pheromone component may have influenced the results, so the varying coefficient model allowed us to look at how the coefficients change depending on the presence or absence of *endo*-brevicomin. Our final model was implemented using maximum likelihood estimation. The log-likelihood function for each coefficient can be expressed as:

$$lnL(\theta,\beta) = \sum_{i=0}^{n}\left(y_i ln\theta + y_i(f(x_i)\beta) - \left(y_i + \frac{1}{\theta}\right)ln\left(1 + \theta e^{f(x_i)-\beta}\right) + ln\Gamma\left(y_i + \frac{1}{\theta}\right) - ln\Gamma(y_i + 1) - ln\Gamma\left(\frac{1}{\theta}\right)\right) \tag{4}$$

This function seeks to maximize the dispersion parameter (θ) and coefficient estimate (β) given the number of either *D. frontalis* or *T. dubius* captured per trap per day during spring emergence (y: response variable) as a function (i.e., TPS) of the weather predictor variables [f(x): explanatory variable] grouped by the presence or absence of *endo*-brevicomin and interaction between latitude and longitude (Eq. (4)). A separate GAM was run for *D. frontalis* and *T. dubius* that included all variables with non-zero coefficient from the LASSO regression. Predicted number of *D. frontalis* per day during spring emergence was included in the model for *T. dubius*, as the number of predator beetles is likely highly dependent on the presence of prey. To prevent violating the assumption of independent observations, year was placed in the model as an autoregressive model (AR1) to test and account for temporal autocorrelation and an interaction between latitude and longitude was included in the systemic portion of the model to account for the spatial autocorrelation between trap locations.

Coefficients from the final GAMs for *D. frontalis* and *T. dubius* were extracted and used to create interpolated prediction maps in 20-year intervals during 1981–2100, allowing for the visualization of changes in species occurrence and range over time. This temporal interval was selected based on the availability and format of climate data available for forecasting. Historical temperatures (1981–2019) used for back-casting were obtained from DAYMET. DAYMET provides historical weather data for every year, so predictions were made for each year (1981–2019) based on the temperatures that year and then a moving average of those predictions were calculated for each interval (1981–2000 and 2001–2019). Future scenarios used for forecasting were obtained from the WORLDCLIM climate dataset. WORLDCLIM provides future gridded climatic variables obtained via the Coupled Model Intercomparison Project Phase 6 (CMIP6) multi-model on a 2.5-minute resolution ($\sim$21 km^2), which has a coarser resolution than DAYMET (1 km^2). Climatic data is provided for four different shared socioeconomic pathways (SSP) developed under CMIP6 (Eyring et al., 2016). These SSPs are described further in Meinshausen et al. (2019).

We selected three SSP scenarios (SSP1-2.6, SSP2-4.5, and SSP5-8.5) for our analyses based on The Canadian Earth System Model version 5 (CanESM5) (Swart et al., 2019), which represent an average warming of 2.1 °C (SSP1-2.6), 3.3 °C (SSP2-4.5), and 5.5 °C (SSP5-8.5) from years 1990 to 2100.

Statistical analyses used an alpha level of 0.05. All analyses and visualizations were completed using R statistical software version 3.6.2 (R Core Team, 2019) and RStudio (RStudio Team, 2016) using the packages glmnet (Friedman et al., 2010), ggplot2 (Wickham, 2016), lattice (Sarkar, 2008), mgcv (Wood, 2003, 2011, 2017), raster (Hijmans, 2019), rgdal (Bivand et al., 2019), and tidyverse (Wickham et al., 2019).

2.4. Model validation

A leave-one-out cross-validation was used to assess model performance:

$$CV_{(k)} = \frac{1}{k}\sum_{k=1}^{k}(y_i - \hat{y}_i)^2 \tag{5}$$

This is a k-fold validation technique where the number of folds (k) is equal to the number of observations (n = 782 traps). For every $i = 1, \ldots, n$, the model was calibrated on every observation except for one for which the test error was computed, finally, an average test error was calculated based on all iterations (Eq. (5)). The model and cross-validation sum of squared estimate of errors (SSE) (i.e., test error) were then compared to estimate model performance.

3. Results

3.1. Dendroctonus frontalis

Across the five-year study, *D. frontalis* spring trap catches ranged from 0 to 380 beetles per day, however the mean beetles captured per day was 0.208 when *endo*-brevicomin was absent and 20.9 when present. Raw *D. frontalis* and temperature data indicated that the number of beetles captured per day increased for areas with higher temperatures

Table 1

Varying coefficient generalized additive model (GAM) with thin plate spline smoothing functions for *Dendroctonus frontalis* and *Thanasimus dubius*. A large estimated degrees of freedom (EDF) indicates more wiggliness, while an EDF close to one indicates a more linear form.

Variable	*endo*-brevicomin	EDF	Reference degrees of freedom	Chi-square	p-value
Dendroctonus frontalis					
January maximum temperature	–	2.05	2.58	1.98	0.38
	+	1.74	2.15	12.7	<0.01**
February minimum temperature	–	2.41	2.96	10.4	0.02**
	+	5.06	5.85	15.8	<0.01**
March minimum temperature	–	2.82	3.50	6.98	0.13
	+	7.84	8.51	41.8	<0.01**
August maximum temperature	–	1.00	1.00	0.567	0.45
	+	3.30	4.11	32.9	<0.01**
Latitude × longitude	n/a	22.1	24.2	192	<0.01**
Thanasimus dubius					
February minimum temperature	–	1.09	1.16	4.61	0.04**
	+	4.09	4.88	6.25	0.20
March minimum temperature	–	4.02	4.96	26.3	<0.01**
	+	4.72	5.84	42.3	<0.01**
August minimum temperature	–	5.21	6.28	34.0	<0.01**
	+	5.76	6.82	22.1	<0.01**
September minimum temperature	–	4.55	5.62	15.8	<0.01**
	+	4.78	5.93	14.6	0.02**
Latitude × longitude	n/a	24.5	27.4	221	<0.01**

** Indicates a significant result at an alpha-level of 0.05.

and were nominal in locations if temperatures were <10 °C. Trap catches were highest for locations where temperatures were between ~ 18–22 °C. LASSO identified prior year August ($\beta = 0.93$) and current year January ($\beta = 0.30$) maximum temperatures, and February ($\beta = 0.98$) and March ($\beta = 0.31$) minimum temperatures as important predictors of *D. frontalis* numbers. All other temperature variables were shrunk to zero. Neither annual nor winter precipitation were found to influence *D. frontalis* numbers ($\beta = 0$). Coefficients were obtained using the LASSO with a cross-validated $\lambda = 0.81$. The four temperature variables identified by LASSO and an interaction between longitude and latitude were included in the final GAM.

The addition of the latitude and longitude interaction reduced autocorrelation to acceptable levels (Supplemental File 1). Conversely, temporal autocorrelation was low (0.29) and would have increased the complexity of forecasting, so AR1 was removed from the final model (Supplementary figure 1). All variables included in the final model were significant predictors of *D. frontalis*. Interestingly, all variables were significant for observations only when traps were baited with the *D. frontalis* pheromone component *endo*-brevicomin except for February minimum temperature (Table 1). The number of beetles per day during spring decreased for areas where prior year August temperatures were above 28 °C and reached zero when temperatures were above 34 °C. For January through March temperatures, there was a decrease in numbers at either temperature extreme. The model had an adjusted r-squared of 0.57 and explained ~ 88.5% of the deviance. The SSE for both the model (SSE = 0.598) and leave-one-out cross-validation (SSE = 0.672) were comparable, indicating a good model fit.

Predicted number of beetles per day during spring emergence increased over the last four decades (1980–2019) in Alabama, Georgia, southwestern Mississippi, and northern Florida, and these states were also found to have the highest number of trapped beetles per day as compared to other southeastern states. Conversely, Arkansas, Kentucky, Louisiana, North Carolina, Tennessee, East Texas, and Virginia had low numbers (<2 beetles per trap per day in spring). Future projections indicate that the temperature variables (i.e., January and prior year August maximum temperatures, and February and March minimum temperatures) used in the model are comparable to present day predictions (Fig. 2; Supplemental File 2), and beetle numbers nominally fluctuate under the lowest warming scenario (SSP1-2.6) (Figs. 3 and 4; Supplemental File 3). There is a more pronounced increase in monthly temperatures and decline in predicted beetle numbers as the rate of warming temperatures increases (Figs. 3 and 4; Supplemental File 3). These predictions indicate that *D. frontalis* may be primarily constrained to Alabama and Georgia between years 2041–2060 under SSP5-8.5 and

years 2061–2080 under SSP2-4.5. Additionally, it predicts the climate may not be advantageous for *D. frontalis* across most of the southeastern U.S. under a 5.5 °C increase in temperatures by year 2100. Uncertainty around these projections increased with time and from the lowest SSP to the highest SSP (Supplemental File 3).

3.2. *Thanasimus dubius*

The number of *T. dubius* captured per day during spring ranged from 0 to 411 beetles. Similar to *D. frontalis,* traps baited with the *D. frontalis* pheromone component *endo*-brevicomin captured more *T. dubius* (9.6 beetles), while traps where this pheromone component was absent captured less (3.95 beetles). There was an increase in *T. dubius* numbers as temperature increased until ~18 °C, at which point numbers decreased. LASSO identified previous year's August ($\beta = 3.45$), and current year February ($\beta = 1.32$) and March ($\beta = 0.96$) minimum temperatures as important predictors of *T. dubius* numbers, while all other temperature variables were shrunk to zero. Neither annual nor winter cumulative precipitation had an effect on *T. dubius* numbers ($\beta = 0$). LASSO coefficients were obtained using a cross-validated $\lambda = 0.42$. The three temperature variables identified by LASSO and an interaction between longitude and latitude were included in the GAM.

All temperature variables included in the final model were significant predictors of *T. dubius,* except February minimum temperature when *endo*-brevicomin was included in the bait (Table 1). Like *D. frontalis,* predicted *T. dubius* numbers have increased slightly since the 1980s (Fig. 5; Supplemental File 4). Numbers were predicted to stay approximately the same under SSP1-2.6 and decrease under SSP2-4.5 and SSP5-8.5 (Fig. 6; Supplemental File 5). Unlike *D. frontalis,* the model indicated that *T. dubius* may not be as constrained by temperature (Figs. 5 and 6; Supplemental File 5). The model had an adjusted r^2 of 0.34 and explained approximately 63.6% of the deviance, and the model (SSE = 0.482) and cross-validation (SSE = 0.562) test errors were comparable. Like *D. frontalis,* uncertainty around these projections increased with time and from the lowest SSP to the highest SSP (Supplemental File 5).

4. Discussion

Our study provides the first in-depth assessment of how monthly, seasonal, and annual temperatures and precipitation prior to peak spring flight influences the species occurrence (i.e., trap catches as a proxy for abundance) for *D. frontalis* across the entire sampled geographic range in southeastern U.S. We found that temperature plays an important role in
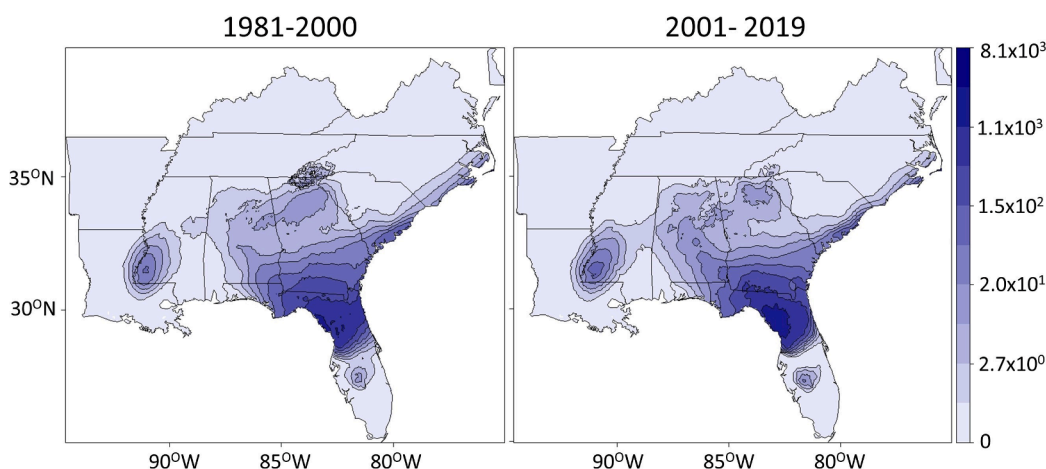

Fig. 2. The spatial suitability of *Dendroctonus frontalis* for 1981–2000 (Left) and 2001–2019 (Right) for the southeastern United States of America (U.S.). Suitability is expressed as the average number of beetles per day during spring emergence as a function of temperature (maximum January and August and minimum February and March monthly temperatures). Interpolated predictions were created through a varying coefficient generalized additive model with thin plate spline smoothing functions. Due to the significance of the addition of the *D. frontalis* pheromone component *endo*-brevicomin in the baits, all predictions were made as if *endo*-brevicomin was included in the baits. Historic temperature data were obtained from DAYMET. Uncertainty for predictions are in Supplemental File 2.
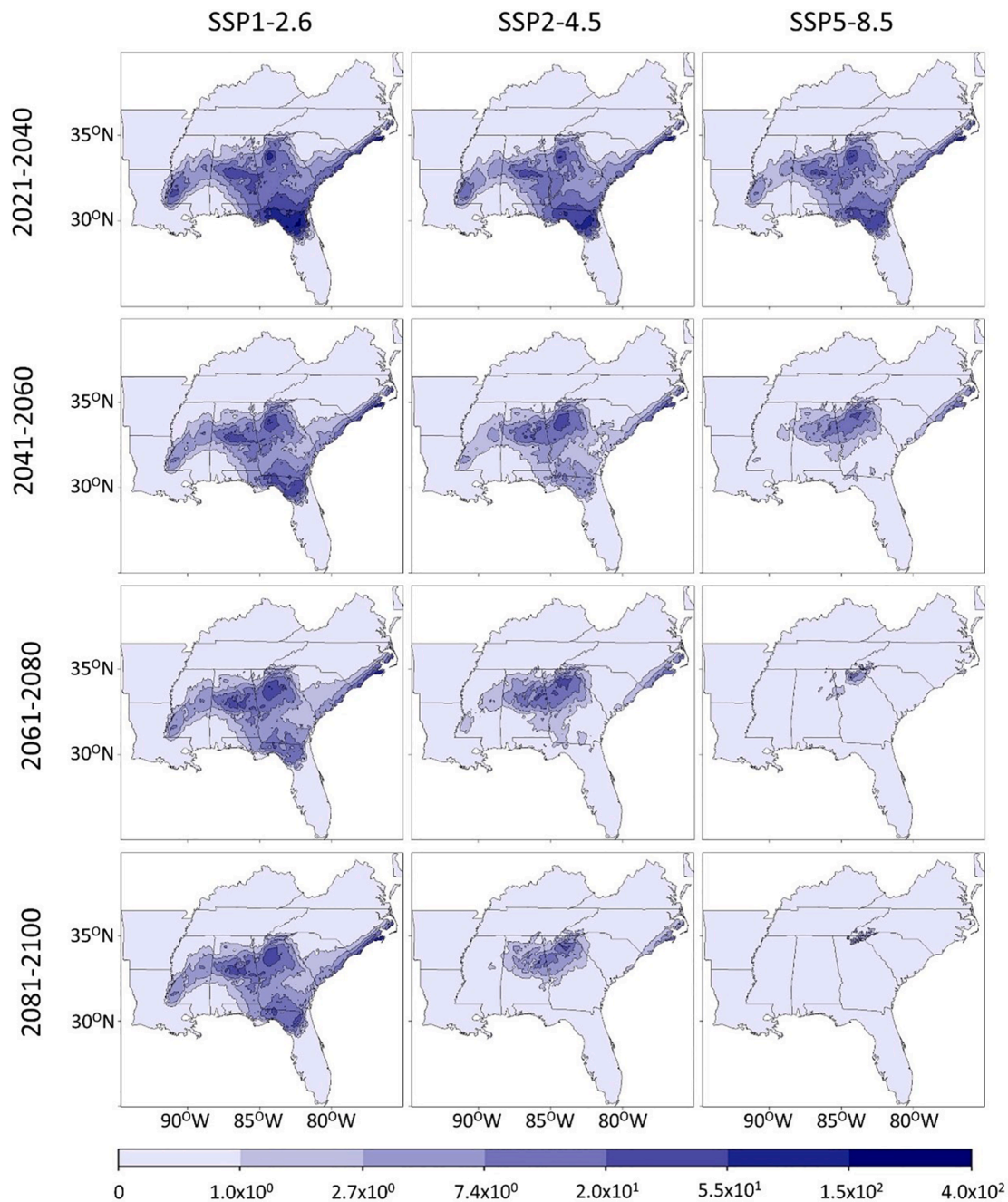
Fig. 3. The spatial suitability of *Dendroctonus frontalis* for 2021–2100 in 20-year intervals for the southeastern United States of America (U.S.). Suitability is expressed as the average number of beetles per day during spring emergence as a function of temperature (maximum January and August and minimum February and March monthly temperatures). Interpolated predictions were created through a varying coefficient generalized additive model with thin plate spline smoothing functions. Due to the significance of the addition of the *D. frontalis* pheromone component *endo*-brevicomin in the baits, all predictions were made as if *endo*-brevicomin was included in the baits. Future temperature data were obtained from WORLDCLIM based on The Canadian Earth System Model version 5 (CanESM5), which represents a multi-model average warming of 2.1 °C (SSP1-2.6), 3.3 °C (SSP2-4.5), and 5.5 °C (SSP5-8.5). Uncertainty for predictions are in Supplemental File 3.

beetle occurrence, which aligns with prior work that has supported the importance of optimal thermal ranges, extreme temperatures, and warmer winter temperatures on bark beetle ecology (Beal, 1933; Tran et al., 2007; Friedenberg et al., 2014; Goodsman et al., 2018). In our study, trap catches were highest when temperatures were between ~ 18–22 °C, with nominal trap catches below 10 °C. The monthly temperatures found to be the best predictors of *D. frontalis* numbers correspond with the time period leading to *D. frontalis* peak flight, which occur around the end of March through April with a second smaller flight period around August (Hedden and Billings, 1977; Billings, 1979). Further, host tree physiology is changing during spring, including the

formation of new tissue and resin defenses, which likely influences insect development and thus species abundance (Lorio, 1986). The fall and winter temperatures seem to significantly influence adult emergence after their overwintering period, but temperatures may be influencing beetle dispersal. Fall dispersal has not been fully investigated in prior research and these data are not present in our study; however, the inclusion of these data may allow for increased model accuracy when investigating the relationship between weather and population dynamics.

While outbreak prediction was not the scope of this study determining how weather and climate are influencing *D. frontalis* numbers
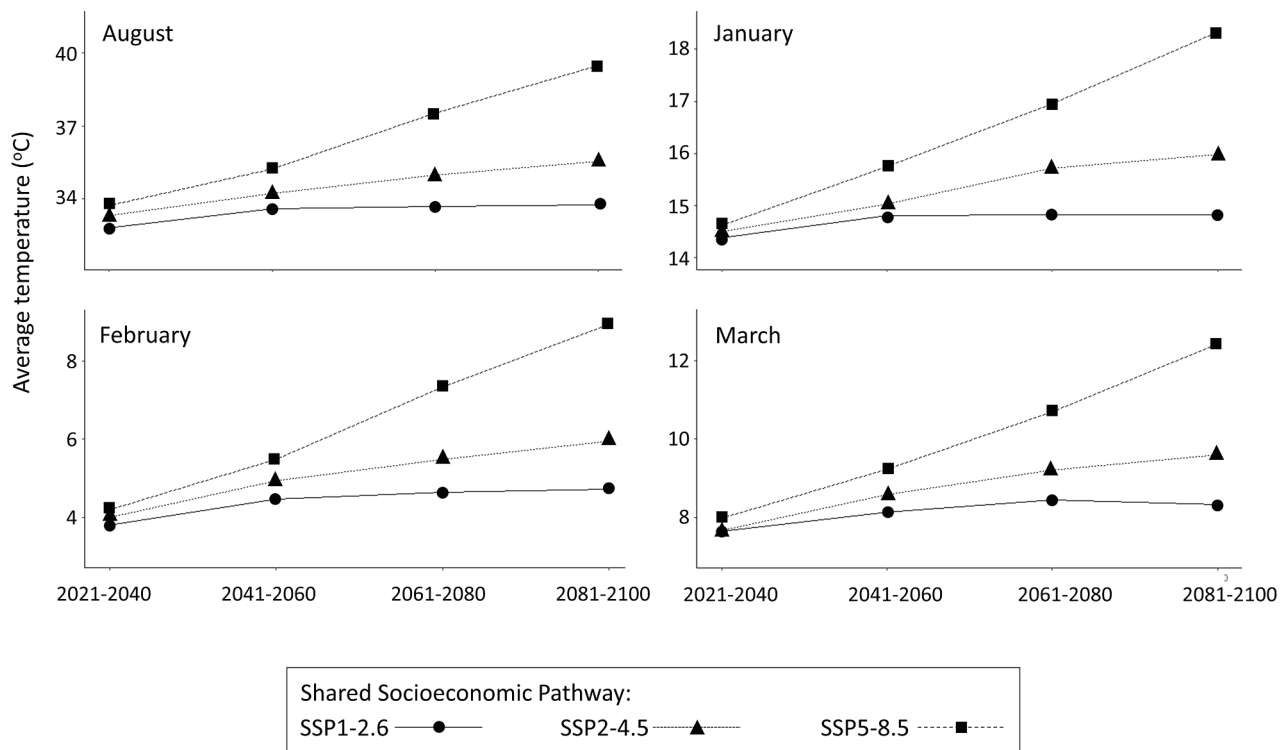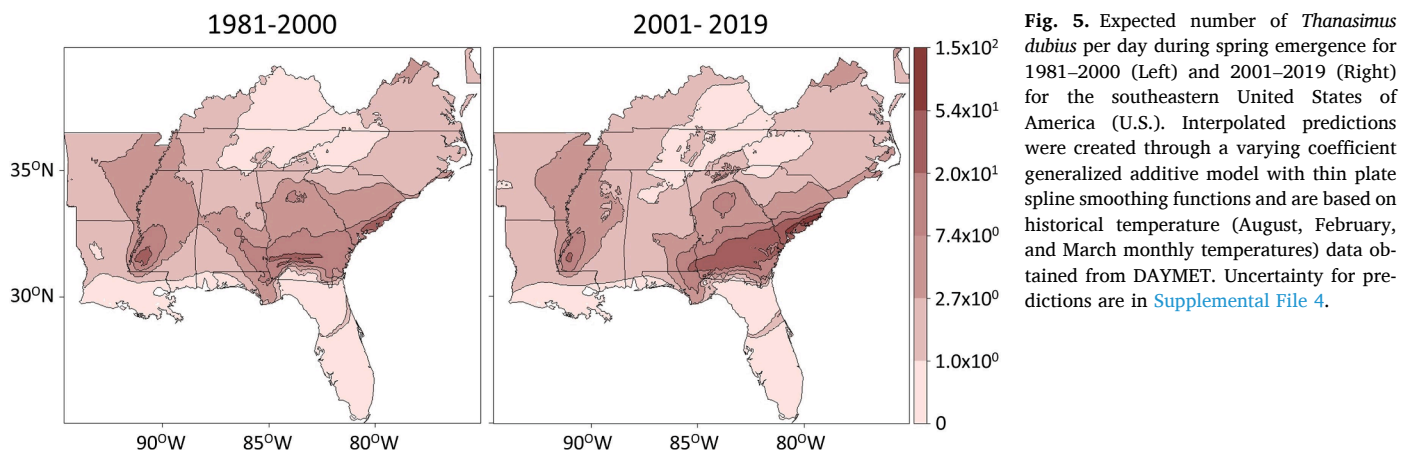
Fig. 4. Projected average temperatures for the climatic variables found to be correlated with *Dendroctonus frontalis* numbers. Averages were calculated from 13 states (Alabama, Arkansas, Delaware, Florida, Georgia, Kentucky, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, East Texas, and Virginia) under three shared socioeconomic pathways (SSP): SSP1-2.6, SSP2-4.5, and SSP5-8.5. Future temperature data were obtained from WORLDCLIM based on the Canadian Earth System Model version 5 (CanESM5), which represents an average warming of 2.1 °C (SSP1-2.6), 3.3 °C (SSP2-4.5), and 5.5 °C (SSP5-8.5).

Fig. 5. Expected number of *Thanasimus dubius* per day during spring emergence for 1981–2000 (Left) and 2001–2019 (Right) for the southeastern United States of America (U.S.). Interpolated predictions were created through a varying coefficient generalized additive model with thin plate spline smoothing functions and are based on historical temperature (August, February, and March monthly temperatures) data obtained from DAYMET. Uncertainty for predictions are in Supplemental File 4.

will provide a foundation for these models. *Dendroctonus frontalis* outbreaks have become less common over the last few decades in areas that are intensively managed but are still common in overstocked or unmanaged forest land (Asaro et al., 2017), thus extensive efforts are ongoing to predict outbreaks. Studies linking temperature to outbreak risk reported: (1) February temperatures were an important predictor of *D. frontalis* outbreaks (Kroll and Reeves, 1978); (2) higher winter and spring temperatures increased the risk of outbreaks and higher fall temperatures reduced outbreak risk (Gan, 2004); and (3) average climatic conditions increased outbreak likelihood with the exception of extended periods of low temperatures and high precipitation (Duehl et al., 2011). Conversely, no relationship between weather and outbreaks has also been reported (Turchin et al., 1991). Since our study was

looking at species trapping data which differs from the outbreak data, comparison between studies should be done with caution. For example, it is possible that climate may only initiate or sustain outbreaks but not both and there may be different climatic drivers of species occurrence compared to outbreaks. Nevertheless, building on this novel model on species count data may allow for the prediction of frequency and magnitude of future outbreaks and merging these two models may greatly improve the accuracy of outbreak predictions on a temporal and spatial scale.

There has been concern about possible future temperatures facilitating an increase in beetle numbers and range expansion and has already been noted in *D. frontalis* and other bark beetles (Ungerer et al., 1999; Williams and Liebhold, 2002; Safranyik et al., 2010). We found
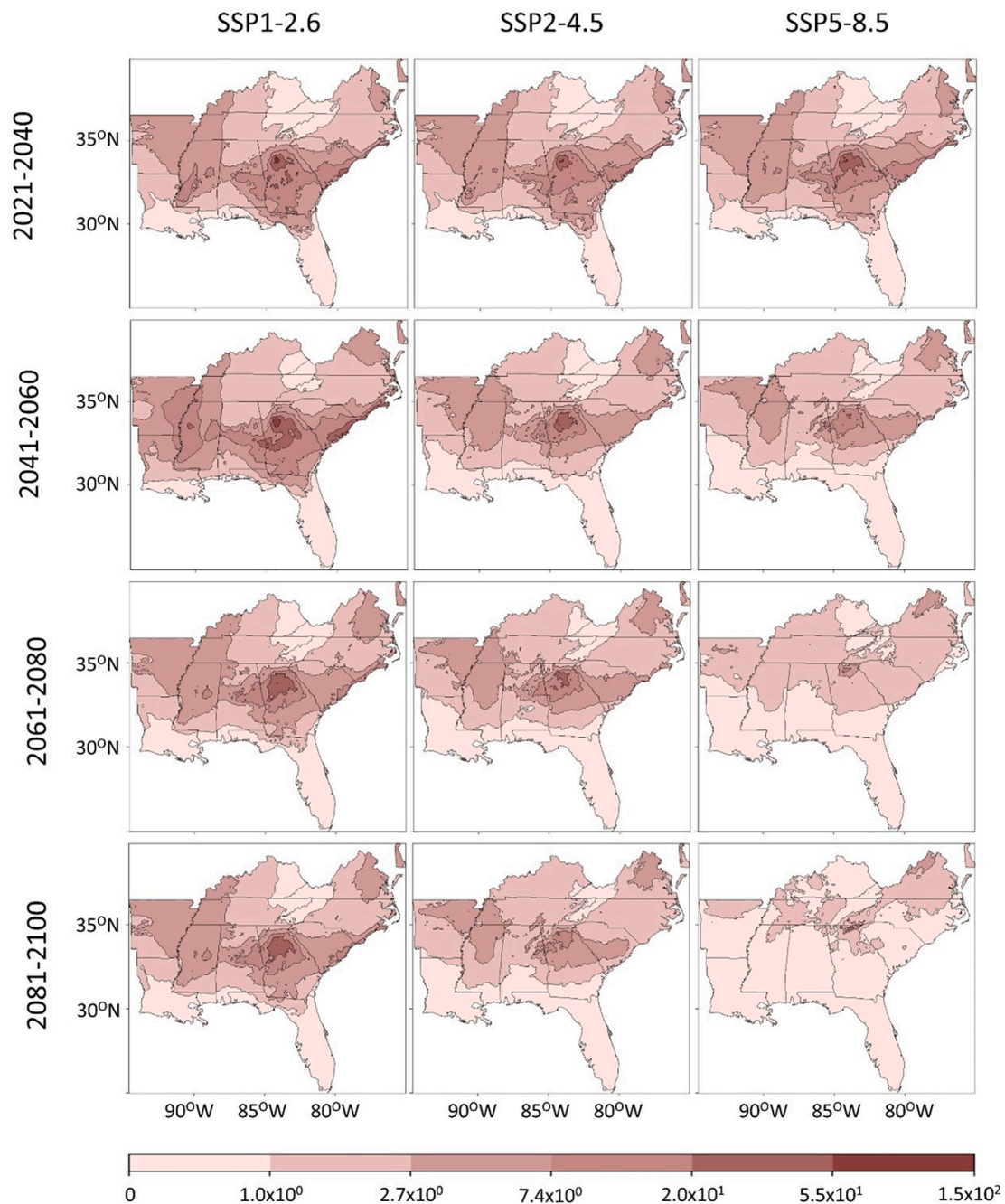
Fig. 6. Expected number of *Thanasimus dubius* per day during spring emergence for 2021–2100 in 20-year intervals for the southeastern United States of America (U. S.). Interpolated predictions were created through a varying coefficient generalized additive model with thin plate spline smoothing functions. Predictions are based on future temperature (August, February, and March monthly temperatures) data obtained from WORLDCLIM based on the Canadian Earth System Model version 5 (CanESM5), which represents an average warming of 2.1 °C (SSP1-2.6), 3.3 °C (SSP2-4.5), and 5.5 °C (SSP5-8.5). Uncertainty for predictions are in Supplemental File 5.

that while *D. frontalis* have been present in Alabama, Georgia, and Mississippi, our model predicted an increase in beetle numbers in these areas over the last few decades. However, our model also indicated that future beetle numbers will be highly dependent on the rate of warming but may drastically decrease as the rate of warming increases. Thus, future low climate suitability in the South may result in a range shift North, rather than an expansion North. Interestingly, our model shows low suitability of *D. frontalis* in East Texas and western Louisiana despite these areas being part of their historical native range, which supports field observations of undetectable *D. frontalis* populations in these areas (Asaro et al., 2017). Our model performed well when predicting

D. frontalis numbers in the southeastern U.S., but uncertainty increased as the distance from the trap locations increased. Hence, greater *D. frontalis* monitoring data for the northeastern U.S. and eastern Canadian provinces would help reduce the uncertainty and should be included prior to looking at range expansion in this northern extent.

To our knowledge, we provide the first empirical analysis looking at the effects of climate on *T. dubius* numbers. In our study, we did not see a decline in *T. dubius* numbers until January through March temperatures were above 18 °C or when August temperatures were above 25 °C. Like *D. frontalis*, *T. dubius* has displayed two peak emergence periods in spring and fall, which may be why temperatures in these months were

important predictors of the number of beetles per day (Reeve, 2000). These effects are important to consider, as *T. dubius* is considered a major natural source of population control for *D. frontalis* (Vité and Williamson, 1970; Frazier et al., 1981) and there will likely be an interactive effect between climate change and this predator–prey relationship (e.g., directly through predation rate or indirectly through the presence/absence of other prey species). Predicted *T. dubius* numbers have increased over the last four decades, but the model indicated that temperatures in most of the Southeast have been suitable for *T. dubius*. Since *T. dubius* is a generalist predator whose presence is highly dependent on available prey, including the presence of all prey species may improve model fit.

The *D. frontalis* pheromone component *endo*-brevicomin was added into the monitoring bait in 2017 and dramatically increased trap catches (Sullivan et al., 2016). Most predictors in our model for *D. frontalis* were not significant in the absence of *endo*-brevicomin, which indicates that the addition of *endo*-brevicomin may allow for increased precision in predicting *D. frontalis* numbers. A more attractive lure should produce a higher dynamic range of trap catches and thus potentially provide greater information content. Consequently, this may help elucidate why some prior models have been unable to ascertain the relationship between and/or the effects of weather and/or climate on *D. frontalis* populations or outbreaks, but this is unclear due to differences in the dependent variables between studies. For *T. dubius,* most predictors were significant regardless of the presence or absence of *endo*-brevicomin. While the effects of *endo*-brevicomin on *T. dubius* has not been fully explored, thus far they have not shown increased attraction to traps baited with *endo*-brevicomin (Mizell et al., 1984; Sullivan et al., 2016).

Few studies have investigated the role of precipitation in *D. frontalis* numbers or outbreaks. Kroll and Reeves (1978) found that seasonal (i.e., previous year spring, summer, and fall) cumulative rainfall influenced the likelihood of *D. frontalis* infestations and Kalkstein (1976) found that evapotranspiration was an important predictor of *D. frontalis* activity. To our knowledge, no prior work has looked at the relationship between the presence of *T. dubius* and precipitation. Interestingly, precipitation levels did not seem to affect the numbers of either *D. frontalis* or *T. dubius*. Due to the effects of severe drought on tree physiology and the possible subsequent susceptibility to pests, it is possible that extreme precipitation events (i.e., sudden onset and/or prolonged severe drought), rather than cumulative precipitation, over longer temporal scales need to be further investigated.

The scope of the present study was to look at trends in *D. frontalis* and *T. dubius* occurrence over space and time, and while the models performed well, there is a level of uncertainty. We addressed the model uncertainty but there may be other sources of uncertainty for the climatic predictor variables as largescale climatic data obtained from weather stations and/or satellites are often associated with large uncertainty. These data are projected over space and time via interpolation and other modeling techniques, to provide predicted values for unknown locations (Thornton et al., 2017, 2018). Use of these data may introduce uncertainty into the model, thus biasing the model output. Few studies on ecological species abundance have incorporated the uncertainty surrounding climatic predictor variables; however, modelling advances, such as SIMEX (Delaigle and Hall, 2008), may provide solutions for addressing error within predictor variables in the future.

Overall, we evaluated the effects of current weather and past climatic conditions on an eruptive forest pest and their main predator using LASSO regression and generalized additive models. These techniques allowed us to account for nonlinearity, spatial autocorrelation, and the inclusion of climatic variables without the effects of multicollinearity. Our findings show that temperature plays an important role in *D. frontalis* occurrence and range limits, and to a lesser extent that of *T. dubius* occurrence. *Dendroctonus frontalis* model predictions performed well with ~89% accuracy and may be extrapolated on to build predictive models to be used by foresters for pest population levels in upcoming summer, through simple tools with Apps and/or online

resources. Additionally, given the flexibility and success of these modeling procedures (LASSO and GAM) in this study, we propose these as alternative techniques for modeling other forest pests. Recent research has emphasized the importance of prevention management strategies that increase tree health (Nowak et al., 2008), but early detection and prediction is critical for mitigating outbreaks, particularly since research supports spatial and temporal changes in pest risk due to climate change.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118770.

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