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Title: Climate change and local host availability drive the northern range boundary in the rapid northward expansion of the eastern giant swallowtail butterfly

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ABSTRACT

Aims

Species distributions result from both biotic and abiotic interactions across large spatial scales. The interplay of these interactions as climate changes quickly has been understudied, particularly in herbivorous insects. Here, we investigate the relative impacts these influences on the putative northern range expansion of the giant swallowtail butterfly in North America.

Location

North America.

Time period

1959-2018.

Major taxa studied

Eastern Giant swallowtail, *Papilio cresphontes* (Lepidoptera: Papilionidae); common hop tree, *Ptelea trifoliata*; common prickly ash, *Zanthoxylum americanum*; southern prickly ash, *Zanthoxylum clava-herculis* (Saphidales: Rutaceae).

Methods

We used data from museum collections and citizen science repositories to generate species distribution models. Distribution models were built for each species over two time periods (T1 = 1959-1999; T2 = 2000-2018).

Results

Models for *P. cresphontes* and associated host plants had high predictive accuracy on spatially-explicit test data (AUC 0.810-0.996). Occurrence data align with model outputs, providing strong evidence for a northward range expansion in the last 19 years (T2) by *P. cresphontes*. Host plants have shifted in more complex ways, and result in a change in suitable habitat for *P. cresphontes* in its historic range. *P. cresphontes* has a northern range which now closely aligns with its most northern host plant - continued expansion northward is unlikely, and historic northern range limits were likely determined by abiotic, not biotic, factors.

Main conclusions

Biotic and abiotic factors have driven the rapid northern range expansion in the giant swallowtail butterfly across North America in the last 20 years. A number of bioclimatic variables are correlated with this expansion, notably an increase in mean annual temperature and minimum winter temperature. We predict a slowing of northward range expansion in the next 20-50 years as butterflies are now limited by the range of host plants, rather than abiotic factors.

INTRODUCTION

Species distributions are known to be greatly influenced by climate (Brown *et al.*, 2016). Climate related range shifts have been and are continuing to be documented globally across taxa and systems: terrestrial (Parmesan & Yohe, 2003), marine (Poloczanska *et al.*, 2013), and aquatic (Rahel & Olden, 2008). With current changes in global climate, species range shifts (Parmesan *et al.*, 1999) and extensions in both altitude and latitude are being observed (Roth *et al.*, 2014; Kerr *et al.*, 2015). While many studies have examined the ongoing changes in climate on biodiversity and species ranges, most consider only abiotic factors in their analyses, missing the potential importance of local interspecific interactions once a species moves into a novel

environment beyond its previous range (Blois *et al.*, 2013; HilleRisLambers *et al.*, 2013; Wisz *et al.*, 2013).

Several interspecific interactions are known to play important roles in shaping range boundaries including competition (Connell, 1961; Huey *et al.*, 2009; Stanton-Geddes *et al.*, 2012), mutualism (Chalcoff *et al.*, 2012; Moeller *et al.*, 2012), facilitation (Bader *et al.*, 2007; Stueve *et al.*, 2011; Ettinger & HilleRisLambers, 2017) and natural enemies (Freeman *et al.*, 2003; Speed *et al.*, 2010). When a species extends into a new local environment, there are a few main scenarios it can encounter (Holt, 2003; Urban *et al.*, 2007; Sexton *et al.*, 2009): 1) ecological conditions that are similar enough to previous conditions that there is little immediate effect on fitness and population growth rate, 2) the new local environment may possess biotic or abiotic conditions that differ from the original local environment and can accelerate (e.g. competitive or predatory release; or 3) decelerate (e.g. nutrient or nesting limitation) range expansion.

For insect herbivores, climate change can influence abundance and distribution through direct mechanisms (physiological impacts on growth, development and reproduction that impact fitness) and indirect mechanisms (impacting biotic factors such as host plant quality or predator abundance) (Bale *et al.*, 2002; Deutsch *et al.*, 2008; Kingsolver *et al.*, 2011; Robinson *et al.*, 2017). How and when climate change will affect herbivorous insect dynamics has received considerable attention generating a diversity of observed responses, especially in the pest management literature (Porter *et al.*, 1991; Cannon, 1998; Harrington *et al.*, 2001; Altieri *et al.*, 2015; Castex *et al.*, 2018). Some species are expanding in ranges and abundance (Battisti *et al.*, 2005; Robinet & Roques, 2010; Robinson *et al.*, 2017) while others are retracting and decreasing in numbers (Robinet & Roques, 2010; Zvereva *et al.*, 2016; Sánchez-Bayo & Wyckhuys, 2019). Host plant abundance and distribution play a key role in generating these

patterns as herbivorous insects are often limited by larval food resources (Dempster & Pollard, 1981; Pearson & Knisley, 1985; Ylioja *et al.*, 1999). Exactly how host-availability translates into patterns of distribution, abundance, and range shifts for insect herbivores is still contentious and particularly complex when combined with direct effects on physiology (Louthan *et al.*, 2015; Lany *et al.*, 2018). Our understanding of the determinants regulating species distributions are becoming more nuanced as we begin to incorporate information on species' dispersal capacity, population abundance trends, and climatic variables into our models (Elith & Leathwick, 2009).

In this study, we investigate the role of host availability and climatic variables on the range expansion of the giant swallowtail butterfly (Papilionidae: *Papillio cresphontes*) in northeast North America over the last 60 years (1959-2018), with an emphasis on accelerated expansion in the last 18 years. We combine evidence from raw occurrence data with a series of species distribution models for *P. cresphontes* and associated host plants to evaluate the rate and direction of range changes in relation to both abiotic and biotic factors. While other studies have incorporated biotic variables as model inputs (Bueno de Mesquita *et al.*, 2016; Palacio & Girini, 2018), our approach was to model the distribution of the insect herbivore and host plants separately and using these independent models to make *post hoc* inferences and comparisons of ranges. Because both this insect and its primary larval host plants (the common prickly ash [Rutaceae: *Zanthoxylum americanum*], southern prickly ash [Rutaceae: *Zanthoxylum clava-herculis*] and common hop tree [Rutaceae: *Ptelea trifoliata*]) are conspicuous, they are often reported in systematic biological surveys and museum collections. In this study, we bring together a combination of museum collection, survey, and citizen science data to understand how host plant availability, climate changes, and butterfly abundance are influencing the rapid expansion of an herbivorous insect. This study is one of few to demonstrate the interplay of both

climate change and biotic interactions in shaping range limits while focusing on the ecologically important role of herbivore and pollinator.

MATERIAL AND METHODS

Study region and time interval

We focused on eastern North America (study area bounded by -94º and -65º longitude and 25º and 55º latitude) where *Papilio cresphontes* has been reported to be expanding rapidly (Finkbeiner *et al.*, 2011; Breed *et al.*, 2012) and data are readily available for both *P. cresphontes* and larval host plants, (*Zanthoxylum americanum, Zanthoxylum clava-herculis* and *Ptelea trifoliata*). Though records of *P. cresphontes* exist further west than -94º, we set this cutoff to minimize complications of misidentification and complex species boundaries with its cogener *P. rumiko*. We categorized and compared two time periods: T1 (1959-1999) representing the period prior to the beginning of the rapid range expansion and T2 (2000-2018) as the period when the rapid range expansion to the north began. This cutoff point was determined from raw occurrence data (Fig. 1).

Data sources

Butterfly and host plant data

Papilio cresphontes (Papilionidae) is a sub-tropical butterfly widely distributed across North America. *P. cresphontes* and host plant occurrence data were obtained from a variety of sources: iNaturalist (www.inaturalist.org), n = 3,007, Global Biodiversity Information Facility (GBIF; www.gbif.org), n = 14,181, the Maine Butterfly Atlas (https://mbs.umf.maine.edu), n = 11, the Maritime Canada Butterfly Atlas (http://accdc.com/mba/index-mba.html), n = 6, Massachusetts Butterfly Club, n = 512, Butterflies and Moths of North America

(www.butterfliesandmoths.org), n = 1,188, and eButterfly (www.e-butterfly.org), n = 3,083. Data

from iNaturalist and GBIF were downloaded using the *spocc* package for R (Chamberlain *et al.*,

2016). We filtered iNaturalist data to include only research grade records before combining with

other data sets. Combined data were filtered for time frame, duplicates, and study area extent

(see below) before further analysis and model building. In total, we used 8,051 occurrence

records for *P. cresphontes* and 2,697 occurrence records (combined) for all three host plant

species.

Environmental data

We used the TerraClimate data set (Abatzoglou *et al.*, 2018), a 4 km x 4 km resolution gridded

set of monthly climatological data from 1958-2017 (at the time of writing this) to generate

environmental features for modeling. We calculated a set of yearly summaries of 19 bioclimatic

variables (Fick & Hijmans, 2017) - frequently used in species distribution modeling) using the

dismo package in R (Hijmans *et al.*, 2017) for each year in each time period (T1 and T2) and

then averaged these summaries across each time period to provide temporally-appropriate

climate summary for each set of models. We included all 19 bioclimatic variables as features

during model selection and evaluation.

Species distribution models

Distributions of *P. cresphontes* and host plants were estimated using Maxent 3.4.0, a machine

learning algorithm based on the principle of maximum entropy (Phillips & Dudík, 2008; Elith *et*

al., 2011; Phillips *et al.*, 2017). Maxent is a presence-background method (Peterson et al. 2011),

which is considered to perform well when modeling climatic niches across a variety of sample

sizes (Wisz *et al.*, 2008). We used the *ENMevaluate* package for model building, testing, and

tuning (Muscarella *et al.*, 2014), ultimately building 8 total models (*P. cresphontes* and three host species for each time period).

We used a combination of geographically-structured and regular k-fold cross validation for model testing and tuning. We generated 10,000 random background points per model and used the *blockCV* package (Valavi *et al.*, 2019a) to divide our study area into 4 km x 4 km blocks. Blocks were randomly assigned to folds 1-5 over 250 iterations to determine a block design that maximized evenness of occurence and background points spread across all folds. This procedure was repeated for every model (8 times in total). The data from folds 1-4 were used as training data for Maxent cross-validation and tuning, while fold 5 was reserved as a set of out-of-sample test data for final model evaluation. Throughout the manuscript, we refer to these data as test data. We used another set of random 5-fold cross validation within the training data while to tune model parameters. Throughout the manuscript, we refer to these data as validation data. We tested the full suite of Maxent feature combinations (linear, quadratic, product, threshold, hinge and combinations) and a combination of regularization multipliers (0.5-4 in 0.5-step increments). We examined models using a range of evaluation metrics (Supplementary Figures 1-8), but eventually chose the model with the highest area under the receiver operating characteristic curve (AUC) on validation data. All evaluation metrics were reported for the separate set of spatially-explicit test data generated by *blockCV* (Table 1). Following the classification of (Swets, 1988), AUC values range between 0.5 for models with no predictive ability and 1.0 for models giving perfect predictions; hereby, values > 0.9 describe a 'very good', > 0.8 a 'good' and > 0.7 a 'useable' discrimination ability of the model and allow to assess the ability of the model to distinguish between species records and background data (Phillips *et al.*, 2006). Once the optimal parameters for a given species and time-frame were determined, we built full models using all available occurrence data to generate predictions for

subsequent visualizations and analyses. We mapped the 'cloglog' Maxent output, which can be interpreted as probability of occurrence under the assumption that the species presence or absence at nearby sites are independent ((Phillips & Dudík, 2008; Elith *et al.*, 2011; Phillips *et al.*, 2017). Importance of predictors was assessed using the percent importance metrics generated when building full models. These metrics are built as Maxent steps through modifications of coefficients for single features - Maxent tracks which environmental variables those features depends on, and calculates the total percentage of contribution of each environmental variable at the end of training (Phillips *et al.*, 2006). Thresholds for binary presence-absence maps and presence distributions were generated using the maximum test specificity plus sensitivity (Liu *et al.*, 2005).

Maxent has become a popular modeling resource because of its predictive power, ease of use, and a well-detailed literature to get researchers started (Phillips & Dudík, 2008; Elith *et al.*, 2011; Phillips *et al.*, 2017). However, this framework has also received criticism, with researchers advocating for more explicit examinations of tuning parameters, evaluation metrics, and the incorporation of tools to deal with sampling bias (Radosavljevic & Anderson, 2014). Recent software additions have addressed some of these challenges, and opened up the 'black-box' of Maxent (Phillips *et al.*, 2017), though issues remain, particularly in the transparency of researchers' hyperparameter tuning and evaluation (Morales *et al.*, 2017). To this end, we have implemented recently developed tools (*ENMevaluate* and *blockCV* packages in R; (Muscarella *et al.*, 2014; Valavi *et al.*, 2019b)) to explicitly outline tuning (Supplementary Figures 1-8), and to incorporate a spatially-independent evaluation design to minimize overfitting (along with the built-in regularization in Maxent).

Northern Range Limits

We calculated the distance between the northern limit modeled for *P. cresphontes* for T1 and T2 using a longitude class approach (Leroux *et al.*, 2013). For each 4-km longitude class (i.e. the horizontal resolution of the grid used to predict species range), we determined the latitude of the northernmost grid cell where the species was predicted to be present during T1 and T2. We selected the latitude-pairs (pairs of data for a single latitude at T1 and T2) for which we had grid cells with occurrence for *P. cresphontes* in both time periods for each longitude class and tested whether the average northern limit distribution of *P. cresphontes* differed between T1 and T2, using a non-parametric paired t-test. We used similar methods to determine differences between northern range limits of *P. cresphontes* and *Z. americanum* for both time periods. All analyses were performed using the R statistical software version 3.6.0 (R Core Team 2019).

RESULTS

Evidence of northward range shift of *P. cresphontes* from raw occurrence data

Patterns of occurrence (as opposed to the predictive outputs from species distribution models) indicate a strong trend of a rapid and recent northward range expansion in *P. cresphontes* since the earliest recorded records of the species in our dataset (1959). The butterfly's highest recorded latitude in a given year has increased dramatically since 2000 (Figure 1a), and the likelihood of occurrence has shifted from rare to frequent in many cities close to the current northern edge of the range (Figure 1b).

Predictive accuracy of species distribution models

Hyperparameter tuning was performed using a variety of evaluation metrics (Supplementary Fig. 1-8), but ultimately, the feature classes and regularization multiplier of the final model used for each species-time period pair were chosen because they produced the highest AUC score on

validation data (within Maxent, opposed to the spatially-explicit test data we used for final evaluation). Once the final feature set was chosen, models were evaluated on spatially-explicit out-of-sample test data created by *blockCV*. Overall, models had high predictive accuracy on test data, with AUC scores ranging from 0.810 to 0.996 (Table 1). Final models were generated using the parameter set (feature classes and regularization multiplier) described above, but built with the full set of data (training + test) to generate predictive maps (Fig. 2-3) and distributions (Fig. 4-5).

Papilio cresphontes has expanded northward due to recent climate warming

Predictive maps generated from MaxEnt models clearly show a change in the distribution of *P. cresphontes* between T1 and T2, with a northward expansion since 2000 (Fig. 2a-b). Kernel density estimate plots generated from threshold occurence predictions mirror this result (Fig. 4), and highlight that different parts of *P. cresphontes*' range match host plant use. *Z. americanum* closely matches *P. cresphontes* in the north, while the middle and southern part of the range is defined by the presence of *Z. clava-herculis* and *P. trifoliata*.

Host plant range shifts

Overall, host plants (*Z. americanum, Z. clava-herculis* and *P. trifoliata*) demonstrated more complex changes in distribution between T1 and T2 compared to *P. cresphontes* (Fig. 3a-b). Historically, the species were split latitudinally (with significant overlap) with *Z. americanum* occupying the northern part of the study area, *P. trifoliata* the middle, and *Z. clava-herculis* in the far south (Fig 3b). However, this pattern changes in T2, with a range expansion of *Z. americanum* northward, but also westward to the boundary of our study area. There are also significant distribution changes for the other two host species, with *Z. clava-herculis* expanding

northward out of Florida and across the southeast coastal areas and *P. trifoliata* expanding

southward throughout the southeastern United States.

Northern range limits for *P. cresphontes* have shifted northward and closely match *Z.*

americanum

The northern range limit of *P. cresphontes* was significantly higher in T2 compared to T1 (t =

-35.08, df = 563, p < 0.001; Fig. 5a) where the average northern-most occurence for T2 (median

= 46.3125 ± 0.937º) was 2.83º (~ 311 km) higher in latitude than T1 (median = 43.47917 ±

1.699º). *Z. americanum* also demonstrated a significant northern range shift between T1 and T2

(t = -19.302, df = 559, p < 0.001; Fig. 5b) where the average northern-most occurence for T2

(median = 45.604 ± 1.261º) was 1.75º (~ 192 km) higher in latitude than T1 (median =

43.85417. ± 1.217º). We also tested whether the northern range limits of *P. cresphontes* and *Z.*

americanum differed from each other during each time period. In each time period, there was a

significant difference between the northern range limits of *P. cresphontes* and *Z. americanum*

(T1: t = -8.3712, df = 506, p < 0.001; T2: t = 13.014, df = 635, p < 0.001). The difference

between butterfly and host plant northern range limits shrank from 0.75º (~ 82 km) in T1 (with *Z.*

americanum having a higher northern range limit) to 0.71º (~ 78 km) in T2 (with *P. cresphontes*

having a slightly higher northern range limit; Fig 5b-c).

Climatic variation in the study area between T1 and T2

Overall, T2 had a higher mean annual temperature (9.45 ± 6.20º C) than T1 (8.67 ± 6.27 º C)(t =

-45.274, df = 534850, p < 0.001). Bioclim variables 6 (minimum temperature of the coldest

month), 8 (mean temperature of the wettest quarter), and 10 (mean temperature of the warmest

quarter) had the largest importance in predicting the occurrence of *P. cresphontes* and host

plants (Figure 6). These variables showed significant differences between T1 and T2 on average across our study area, with an overall trend of warmer patterns from 2000-2015 (T2) compared to 1959-1999 (T1) (Table 2).

DISCUSSION

The determinants of species distributions have long been debated not just because they are essential in ecology and evolutionary biology, but also because where organisms are and where they will be is central to successful conservation and restoration practices in light of rapid climate change (Buckley *et al.*, 2013; Gallagher *et al.*, 2013; Robillard *et al.*, 2015). Our study details a recent and rapid northward range expansion by *P. cresphontes* between 2000 and 2018 (Fig. 1). We also model the distributions of the butterfly's naturally occurring larval host plants, which, when combined with analysis of *P. cresphontes* range, result in different predictions for the future distribution of this butterfly than if we had relied on abiotic variables alone (Fig. 2-3). Recent climatic shifts have allowed *P. cresphontes* to rapidly expand northward to now match or even surpass the slower moving northward range expansion of the northernmost host plant, *Z. americanum*, with further northward expansion of *P. cresphontes* now limited by host plant range (Fig. 4). Our results highlight the importance of including biotic interactions (and interactions between herbivorous insects and host plants in particular) in examinations of range shifts, an idea often highlighted, (Urban *et al.*, 2016) but infrequently implemented (Lemoine, 2015; Dilts *et al.*, 2019; Svancara *et al.*, 2019).

Poleward range shifts in herbivorous insects, particularly butterflies, have been documented for a number of species (Parmesan *et al.*, 1999; Warren *et al.*, 2001; Pöyry *et al.*, 2009; Breed *et al.*, 2012). Additionally, northward expansions of other butterfly species have been shown to

have dramatic impacts on community composition through linked biotic interactions (Audusseau *et al.*, 2017), which could be happening in this system as well, but would require further examination to determine. While studies demonstrating range shifts in multiple taxa provide valuable insights into the magnitude and direction of shifts for different taxa, gaps in knowledge remain (Pöyry *et al.*, 2009). Namely, 1) how has warming acceleration affected recent range shifts during the last 10-15 years in poleward latitudes, and 2) how do abiotic and biotic factors interact to shape range shifts? Our study addresses both of these questions. We show a rapid northward range shift in *P. cresphontes* over the last 18 years (predicted most northward occurrences differ by 2.83º of latitude (~ 311 km) between T1 and T2, or a northward expansion of 165 km/decade) that is more than 27 times faster than the average of northward movement of global meta-analyses for plants, lichens, birds, mammals, insects, reptiles and amphibians, fish and marine organisms (Parmesan & Yohe, 2003) and over 9 times faster than butterfly species in Britain (Hickling *et al.*, 2006). Our findings largely follow Pöyry *et al.* (2009) who postulate that mobile species utilizing woody host plants should exhibit large range shifts northward, and that habitat availability and dispersal capacity largely determine success.

Interestingly, the northward incursion of *P. cresphontes* in northeastern North America is not a new phenomenon. Accounts detail movement into the region 145 years ago that lasted several decades (Scudder 1889). In 1875, *P. cresphontes* were found in southern New England and by 1882 there are documented records just south of Montreal, Quebec. By the 1930s, the species had apparently retracted southward and were considered 'extremely rare' in Massachusetts (Farquhar 1934) and didn't push northward into the region again until recently. Multiple long-term climate reconstructions (paired with historic instrument data) for the 145-year incursion period indicate a strong warming trend compared to the previous century (Marlon *et*

al., 2016). However, this warming trend continues through the 1930s, so it is unclear which factors may have resulted in a retraction, though hydroclimatic reconstructions indicate an increase in drought in the northeastern United States over this time period, which likely had strong impacts on vegetation and host-plant distributions and quality through the range of *P. cresphontes (Marlon et al., 2016)*.

Our work also highlights the importance of including biotic interactions when predicting range shifts. *P. cresphontes*' current northern range now closely matches the northernmost host plant (*Z. americanum*) (Fig. 3, 5d) and is now limited by the ability of *Z. americanum* to expand its range northward. Because of the differences in life-history strategies, dispersal capabilities, reproductive outputs and environmental tolerances between *P. cresphontes* and *Z. americanum*, the northern expansion of *P. cresphontes* appears to now be largely curbed. Though sightings of the mobile adult stage of *P. cresphontes* will likely continue to be seen further north than the naturally occurring host plant range (Fig. 5d), without a suitable host plant, further northward expansion seems unlikely in nature outside of recently documented *P. cresphontes* occurrences in horticultural settings. Horticultural settings may allow it to expand beyond the northern limits or range gaps of native host plants. *Papilio cresphontes* lay eggs and larvae feed successfully on two non-native garden plants, Garden Rue (*Ruta graveolens*) and Gas Plant or Dittany (*Dictamnus albus).* It also uses Wafer Ash or Common Hop Tree (*Ptelea trifoliata*), which is planted as an ornamental in the Northeast but is a native species from central and southeastern North America. We even documented the successful use of a potted, cultivated non-native *Citrus* tree kept outdoors during the growing season north of the butterfly's range. Although these exotic plant species are not distributed uniformly across the region, dispersing *P. cresphontes* has an uncanny ability to find these host plants, perhaps further

enabling it to expand its range as abiotic conditions allow. Data from citizen science sources continue to grow as platforms become more popular, and can provide tremendous boons to researchers across disciplines (Bonney *et al.*, 2009, 2014; Dickinson *et al.*, 2010), including those interested in creating species distribution models (Kéry *et al.*, 2010; Yu *et al.*, 2010). There has been debate about the quality and veracity of citizen science data, but recent work has demonstrated that citizen science initiatives can reliably produce research quality data though it often has similar biases to professionally-gathered data (Kosmala *et al.*, 2016). Here, we use citizen science data sources supplemented by data from museum collections to generate species distribution models using the well-established Maxent modeling framework (Phillips & Dudík, 2008; Elith *et al.*, 2011; Phillips *et al.*, 2017), and advocate for continued development and use of citizen science data and its pairing with museum collection data in developing species distribution models in ecology and conservation.

Though we focused mostly on the distributional changes of *P. cresphontes*, there were also surprisingly large range shifts in host plant species (Fig 3). In contrast to the straightforward northward expansion of *P. cresphontes*, the distributional changes in host plants was more complex and nuanced. *Z. americanum* and *P. trifoliata* have both shifted northward since 2000 in slightly different patterns (Fig. 3-4). While *Z. americanum* appears to have shifted mostly northward, *Ptelea trifoliata* has undergone a northward and westward shift, and occupies areas that overlap with the range of *Z. americanum* (Figure 3). The potential effects of this overlap on *P. cresphontes* (i.e., population dynamics, apparent competition, selection for oviposition behavior) are to our knowledge currently unknown, but would be interesting to examine in light of *P. cresphontes* westward expansion and previous work demonstrating significant within-population variation in oviposition behavior in *Papilio* (Thompson 1988). Interestingly,

precipitation in the wettest month and in the wettest quarter (Bioclim variables 13 and 16) had the strongest impact in predicting the distribution of *Z. americanum* in T2, highlighting the impact that rainfall may have in shaping and limiting current distribution. In contrast, the range of *Z. clava-herculis* appears to have expanded in the southern United States - a large expansion from a relatively small range along the coast of the southeastern United States. Compared to pre-2000 distributions, available host plants to *P. cresphontes* are more widely distributed with greater overlap, but with notable gaps throughout Kentucky, Ohio, and Indiana. These complex distributional changes are likely driving part of the overall range shift northward for *P. cresphontes* (Fig. 1b) and could also be potential drivers of speciation, and the evolution of specialization or host plant switching (Descombes *et al.*, 2016).

CONCLUSION

Multiple biotic interactions have evolved between insects and other species to create a wide variety of ecosystem services important to human health and wealth (Losey & Vaughan, 2006). Anthropogenic climate change and habitat loss are creating a growing urgency for quantifying range size, understanding range boundaries, and assessing range shifts across insect species in order to preserve the integrity of future ecosystem function. Our work outlines the power of using increasingly abundant citizen science data, as well as the importance of including biotic interactions alongside environmental factors when developing predictions for range shifts due to climate change. We advocate for expanded incorporation of these factors, particularly when examining insect herbivores.

ACKNOWLEDGEMENTS

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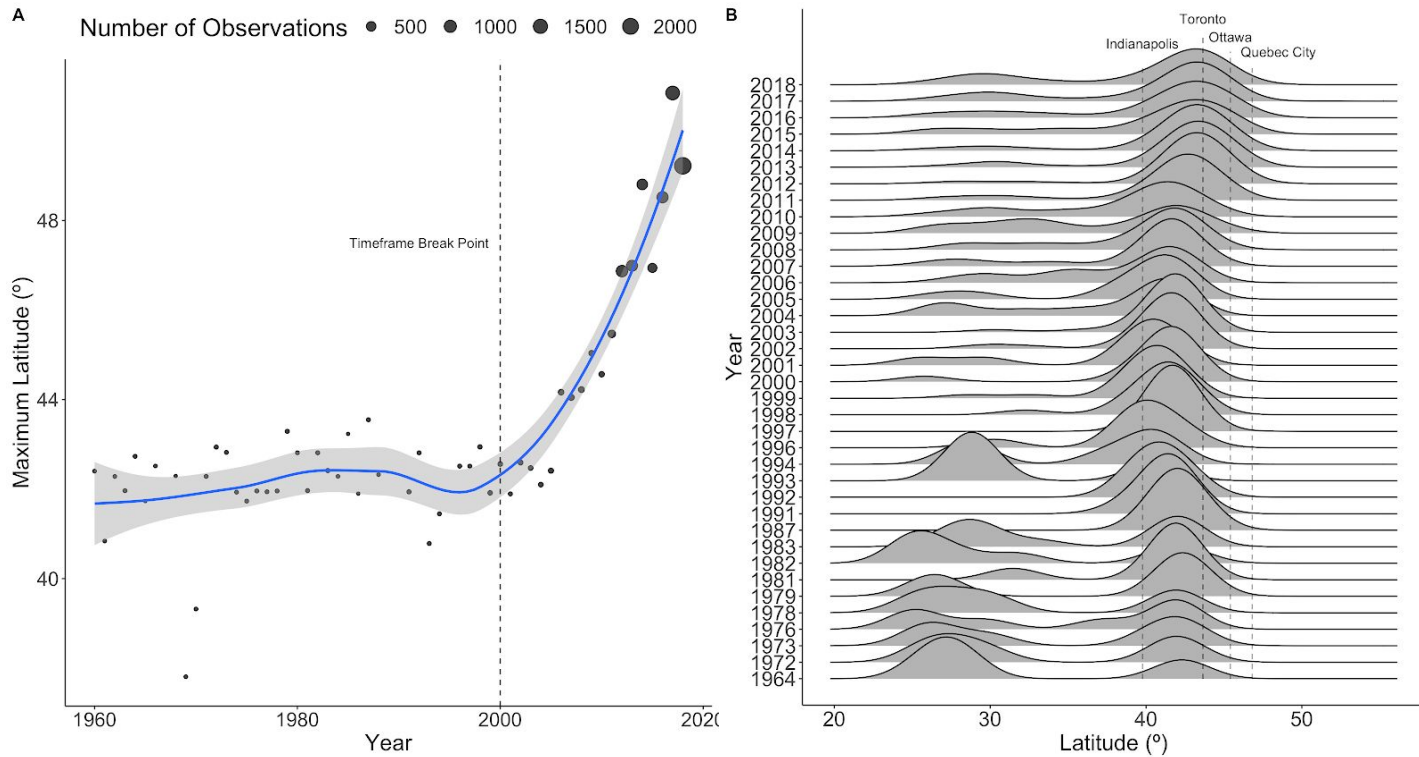
FIGURES

Figure 1. Evidence of northward range shift of *P. cresphontes* from raw occurrence data. (a) The maximum latitude of a recorded occurrence of *P. cresphontes* by year. Larger circles indicate years with higher numbers of occurrence records (high numbers in more recent years are due to increased citizen-science activity). The dashed lines represents the breakpoint between T1 and T2. Three years with extremely low maximum latitudes (< 35º) were omitted for clarity. The blue line and gray bar represent the loess smoothing curve and 95% confidence interval. (b) A ridge-plot of kernel density estimates of occurrences for *P. cresphontes*. Vertical dashed lines represent latitudes of major cities within the range. Years with < 5 occurrence records were removed from plotting.
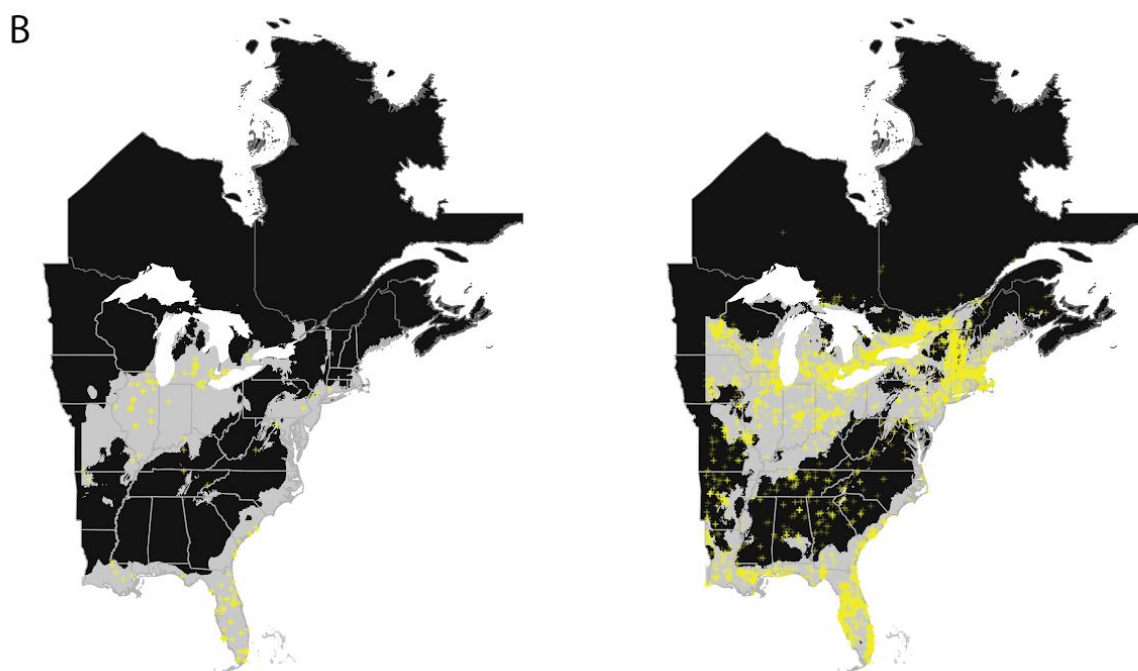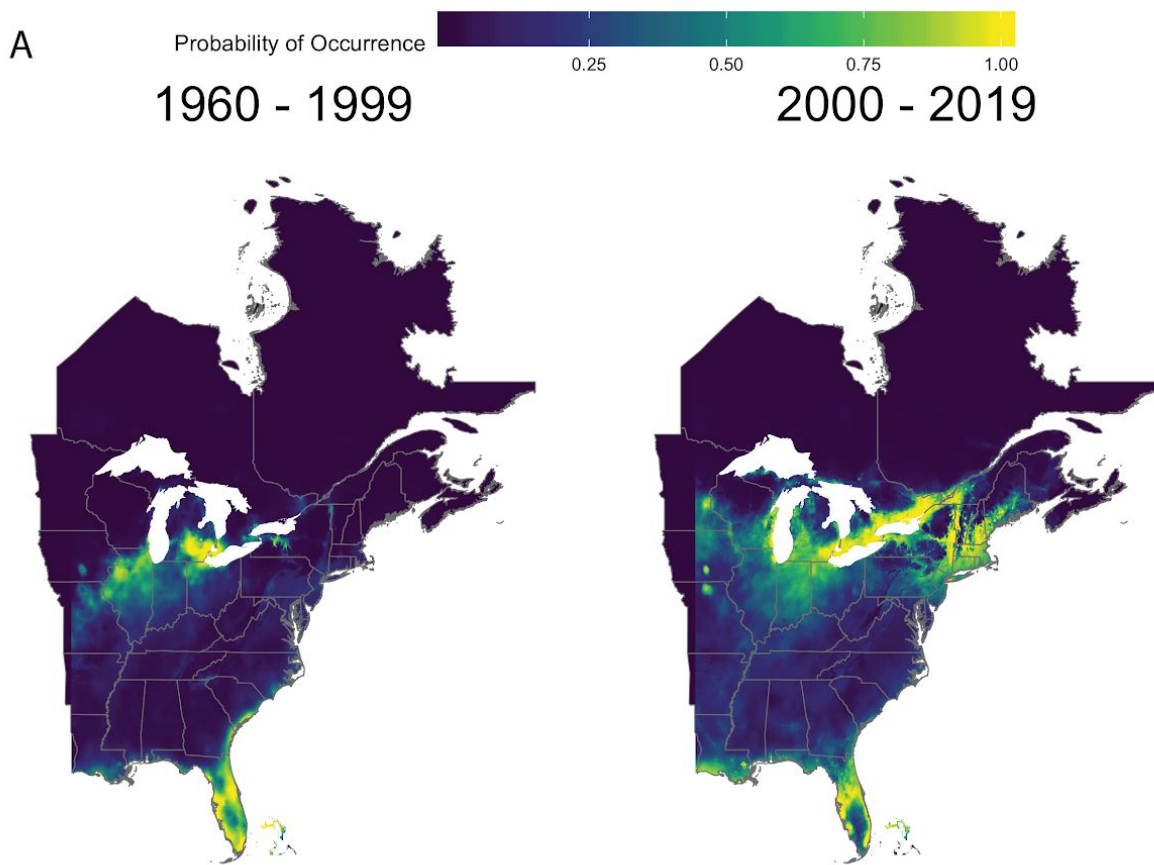
Figure 2. Maxent model predictions for *P. cresphontes* for t_1 (1959-1999) and t_2 (2000-2018). (a) cloglog transformed output from full MaxEnt models for two time periods. Lighter yellow areas denote higher probabilities of occurrence. (b) Threshold maps of presence absence for the two time periods. Gray areas represent predicted occurrence and black represents predicted absence. Yellow crosses represent actual occurrence data for each time period.
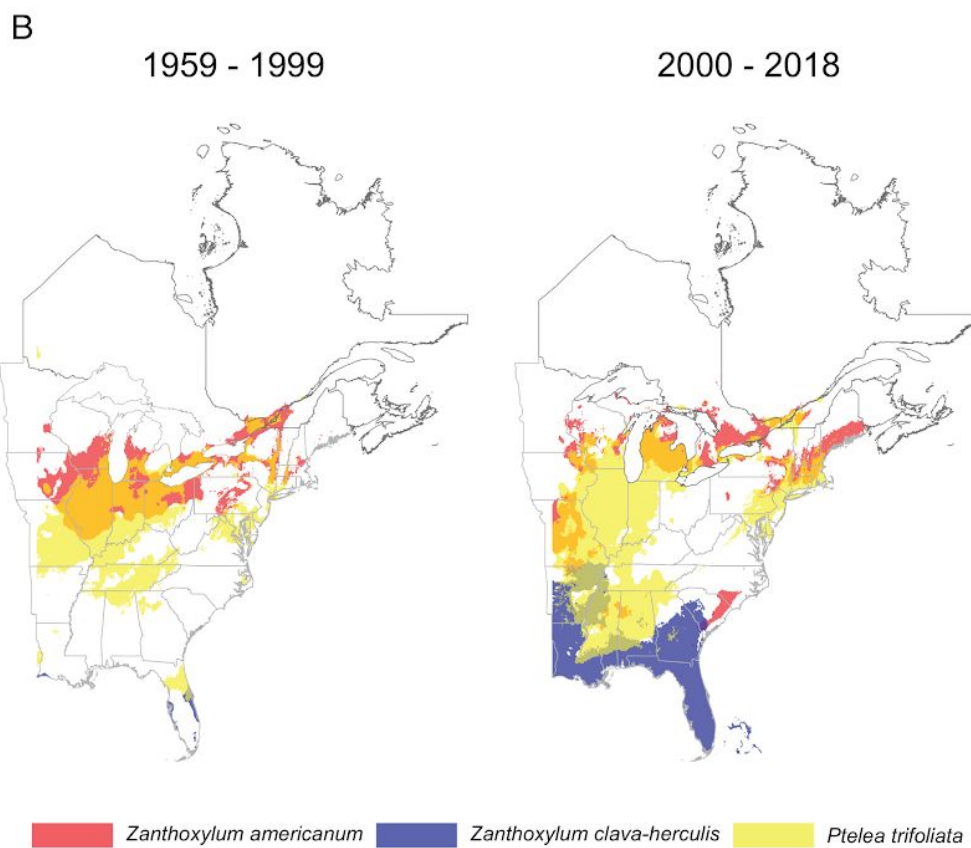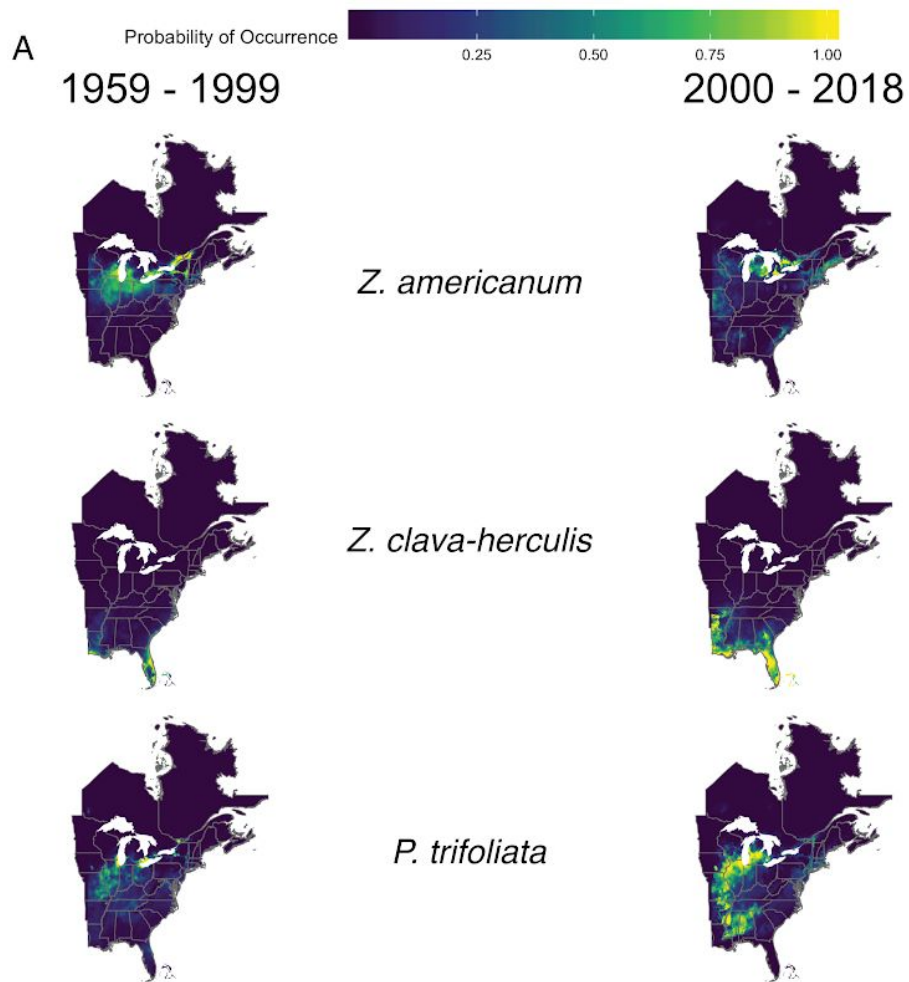
Figure 3. Maxent model predictions for host plants (*Z. americanum, Z. clava-herculis* and *P. trifoliata*) for t_1 (1959-1999) and t_2 (2000-2018). (a) cloglog transformed output from full maxent models for each host plant across two time periods. Lighter yellow areas denote higher probabilities of occurrence. (b) Threshold maps of presence absence for the two time periods. Different colors (red, blue, yellow) represent areas of predicted occurrence for each host plant and black represents predicted absence. Mixed colors (orange, purple, brown) indicate areas of overlap.
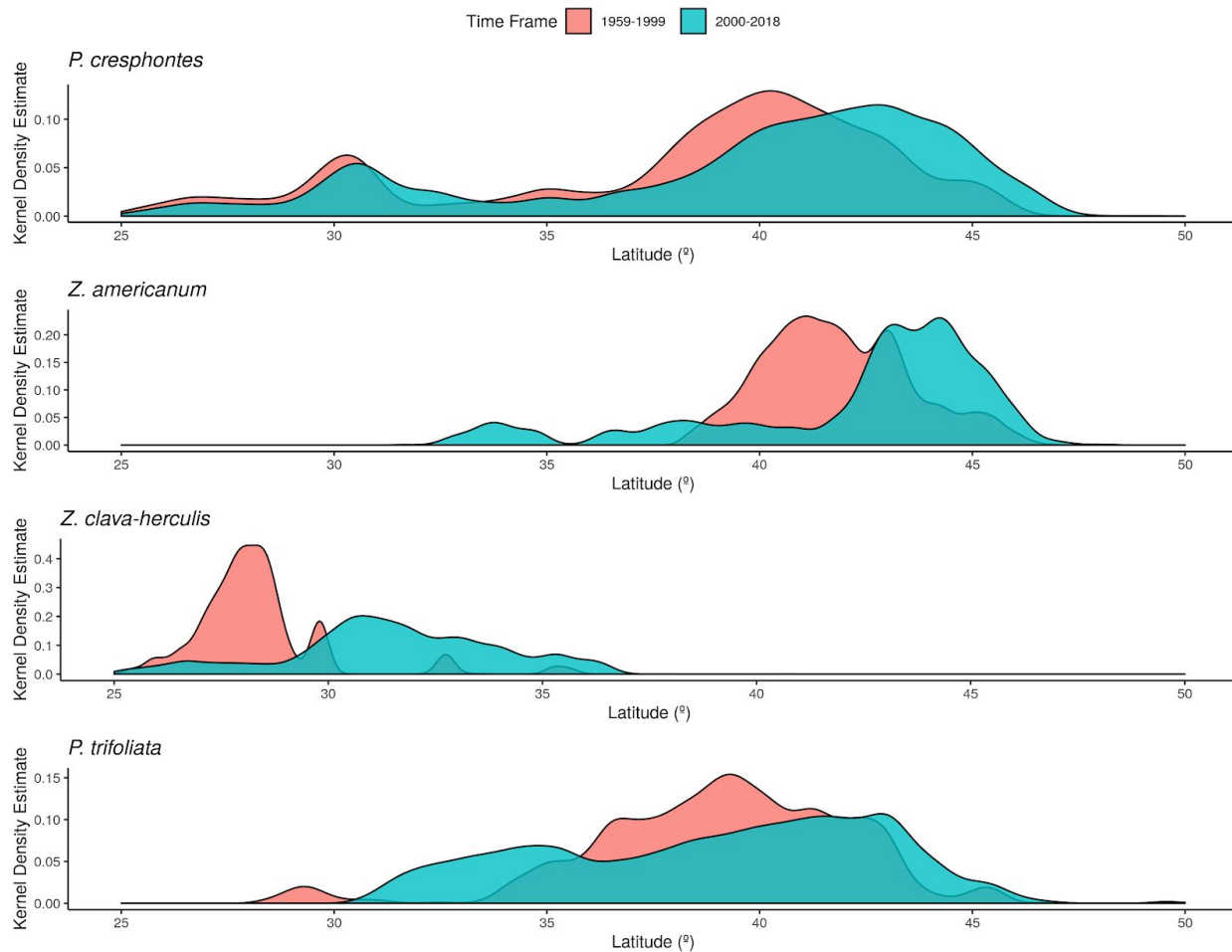
Figure 4. Kernel density estimates for modeled predicted presence of *P. cresphontes* and host plants (*Z. americanum, Z. clava-herculis* and *P. trifoliata*) for T1 (1959-1999) and T2 (2000-2018). Red plots are from T1 (1959-1999) and blue plots are from T2 (2000-2018).
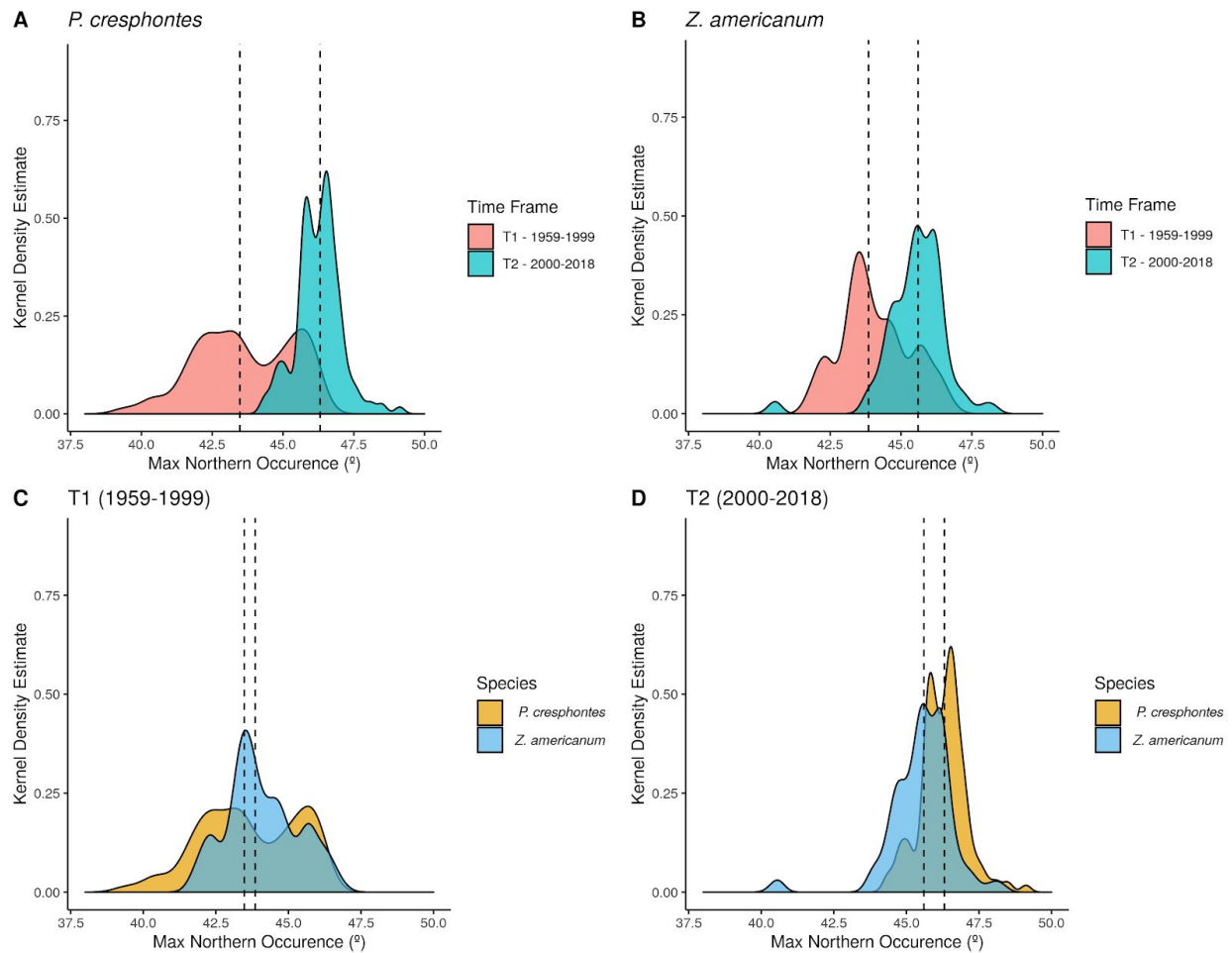
Figure 5. Predicted maximum northern occurence for *P. cresphontes* and host plants for T1 (1959-1999) and T2 (2000-2018). Dashed vertical lines represent the median value for each group. (a) *P. cresphontes* northern range limit between the two time periods. (b) *Z. americanum* northern range limit between the two time periods. (c) Northern range limit comparison for T1 (1959-1999) for *P. cresphontes* and *Z. americanum*. (d) Northern range limit comparison for T2 (2000-2018) for *P. cresphontes* and *Z. americanum*.
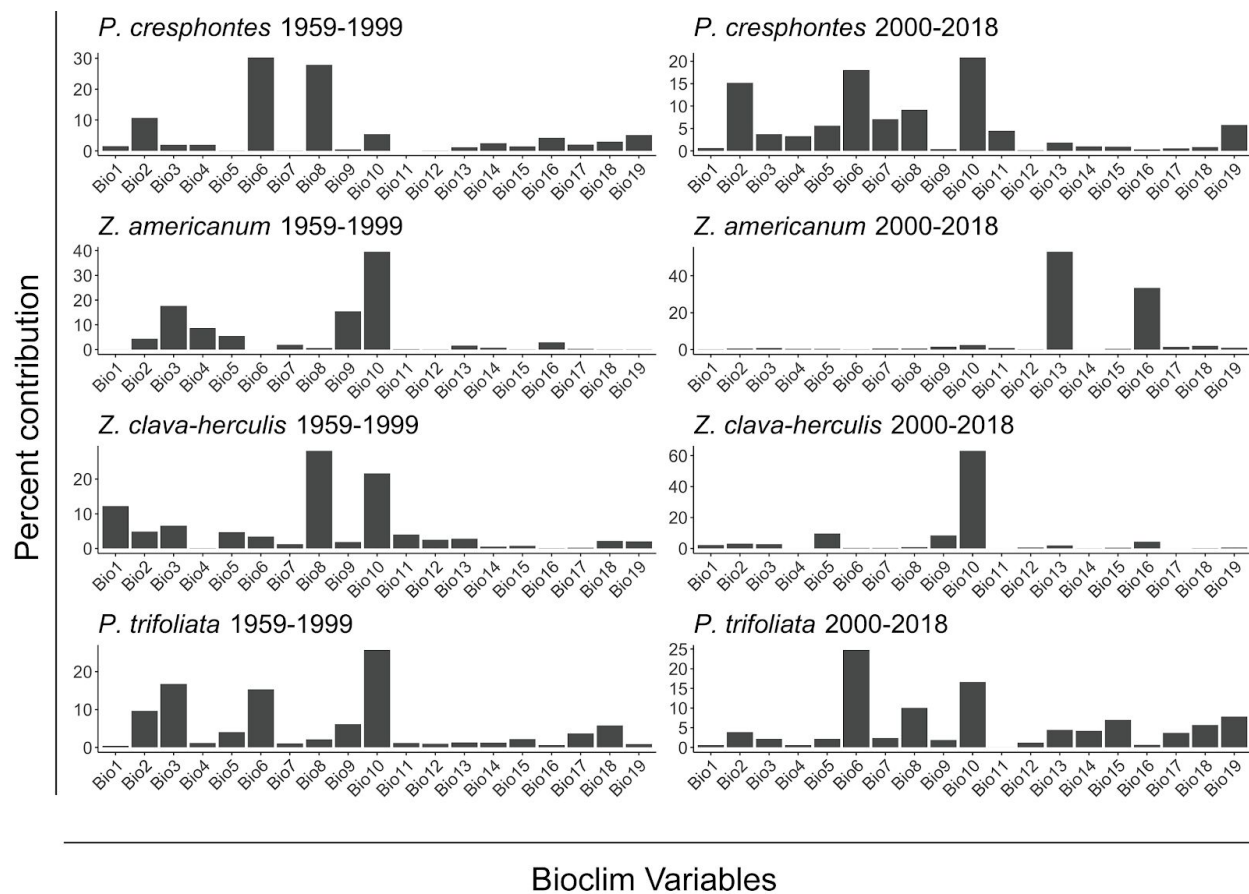
Figure 6. Percent contribution of each of the 19 bioclim variables to final models for each species and time period. Percentages are computed from Maxent model training - as predictive gains increase, environmental factors contributing to feature generation are calculated and summarized in the final model. Common major contributors across many models include BIO6

(minimum temperature of the coldest month), BIO8 (mean temperature of the wettest quarter)

and BIO10 (mean temperature of the warmest quarter).

Tables

Table 1. Model features and evaluation metrics on geographically-structured test data

Species	Timeframe	Occurrences*	Feature Classes**	Regularization Multiplier	AUC (test data)	Threshold
P. cresphontes	T1	219	LQH	1	0.924	0.095
	T2	7832	LQH	1	0.869	0.188
Z. americanum	T1	153	LQHP	0.5	0.971	0.293
	T2	1170	H	2	0.979	0.266
Z. clava-herculis	T1	9	LQHP	0.5	0.996	0.956
	T2	364	LQHP	1	0.892	0.189
P. trifoliata	T1	139	LQHP	0.5	0.960	0.154
	T2	862	LQHP	0.5	0.810	0.187

* Full number of occurrences, not the number of occurrences within the test set.
**Feature classes tuned in MaxEnt (L = linear, Q = quadratic, H = hinge, P =product, T = threshold)

Table 2. Bioclimatic shifts between T1 (1959-1999) and T2 (2000-2015)

| Bioclim Variable	T1 Average	T2 Average	t	df	p
1 (Mean annual temp)	8.67 ± 6.27 ° C	9.45 ± 6.20 ° C	-3508.4	267460	< 0.001
6 (Min temp of coldest month	-12.22 ± 9.44 ° C	-11.04 ± 9.25 ° C	-1499.2	267460	< 0.001
8 (mean temp of wettest quarter)	14.01 ± 4.63 ° C	15.03 ± 4.87 ° C	-354.69	267460	< 0.001
10 (mean temp warmest quarter)	20.31 ± 4.25 ° C	20.87 ± 4.23 ° C	-2383.5	267460	< 0.001

Supplemental Figures
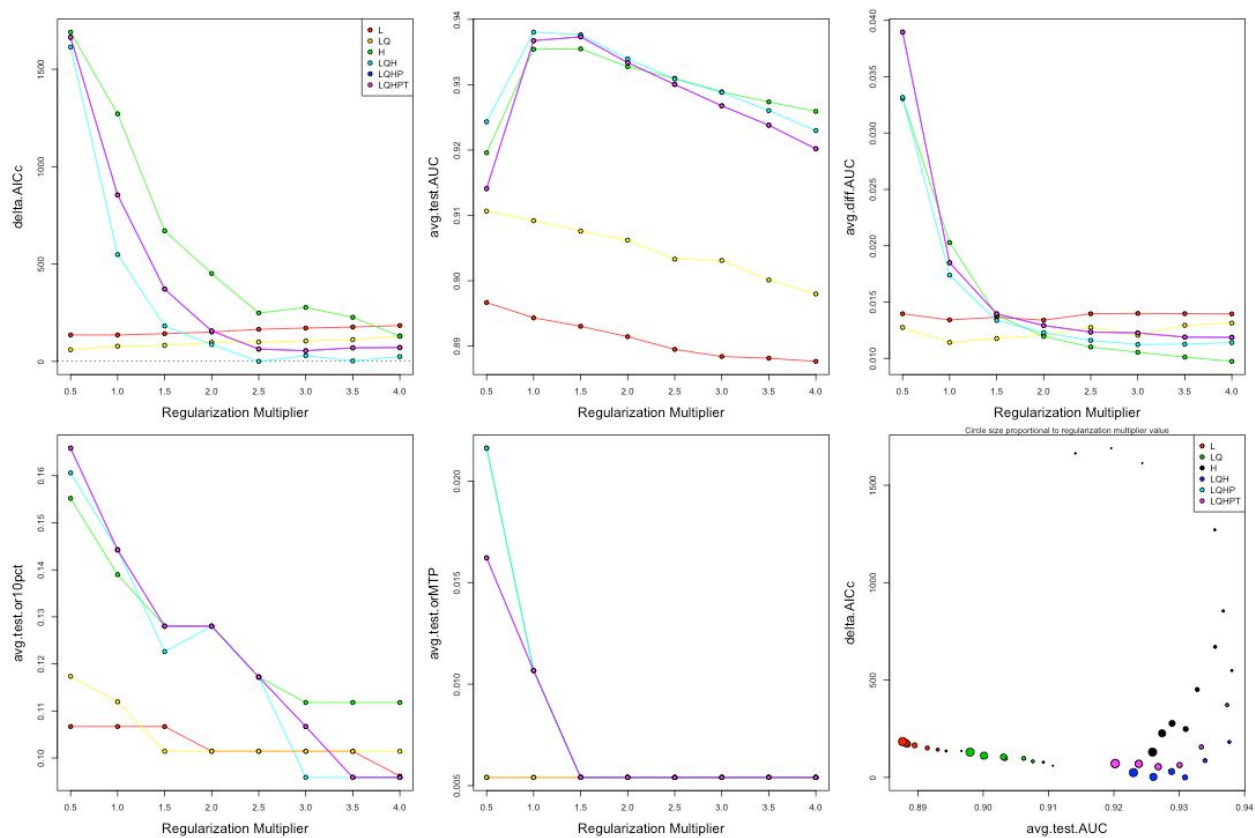
Sup. Fig. 1: Hyperparameter tuning and model evaluation of *P. cresphontes* distribution during the T1 period.
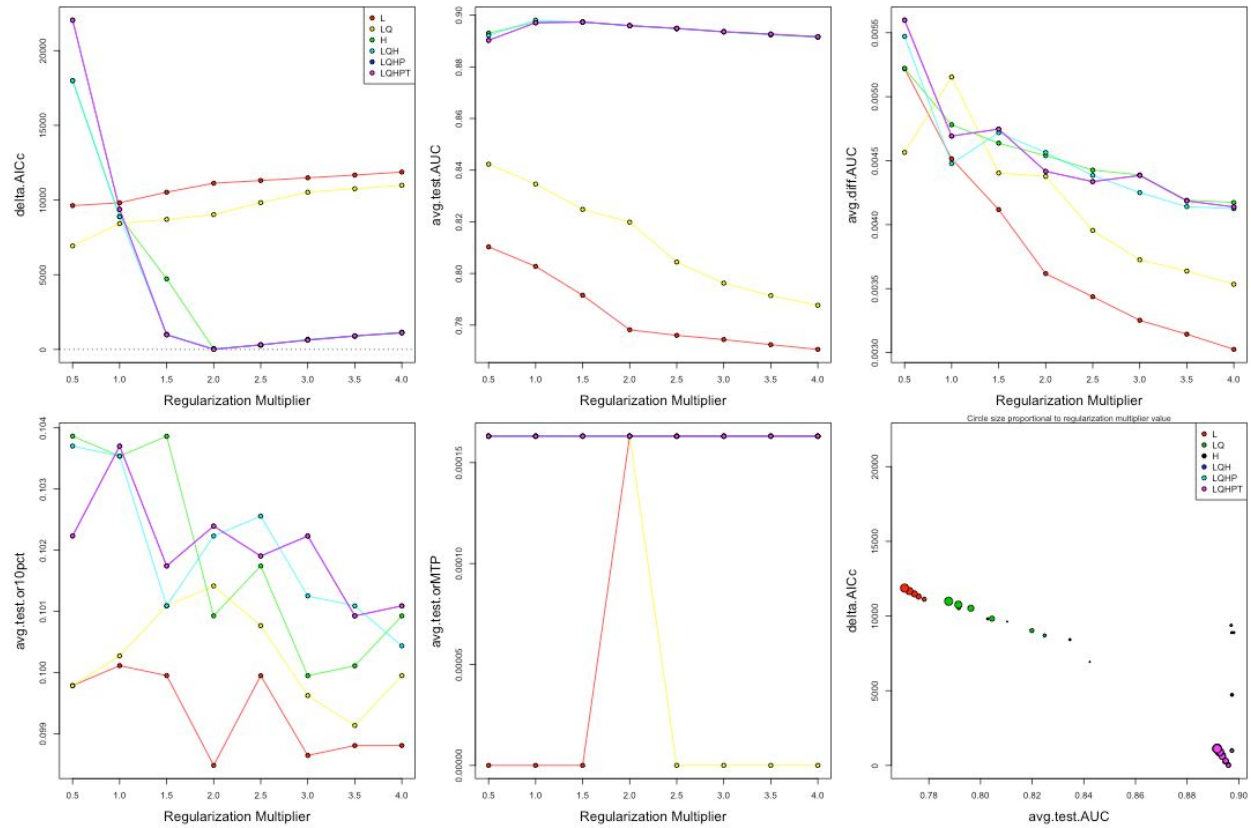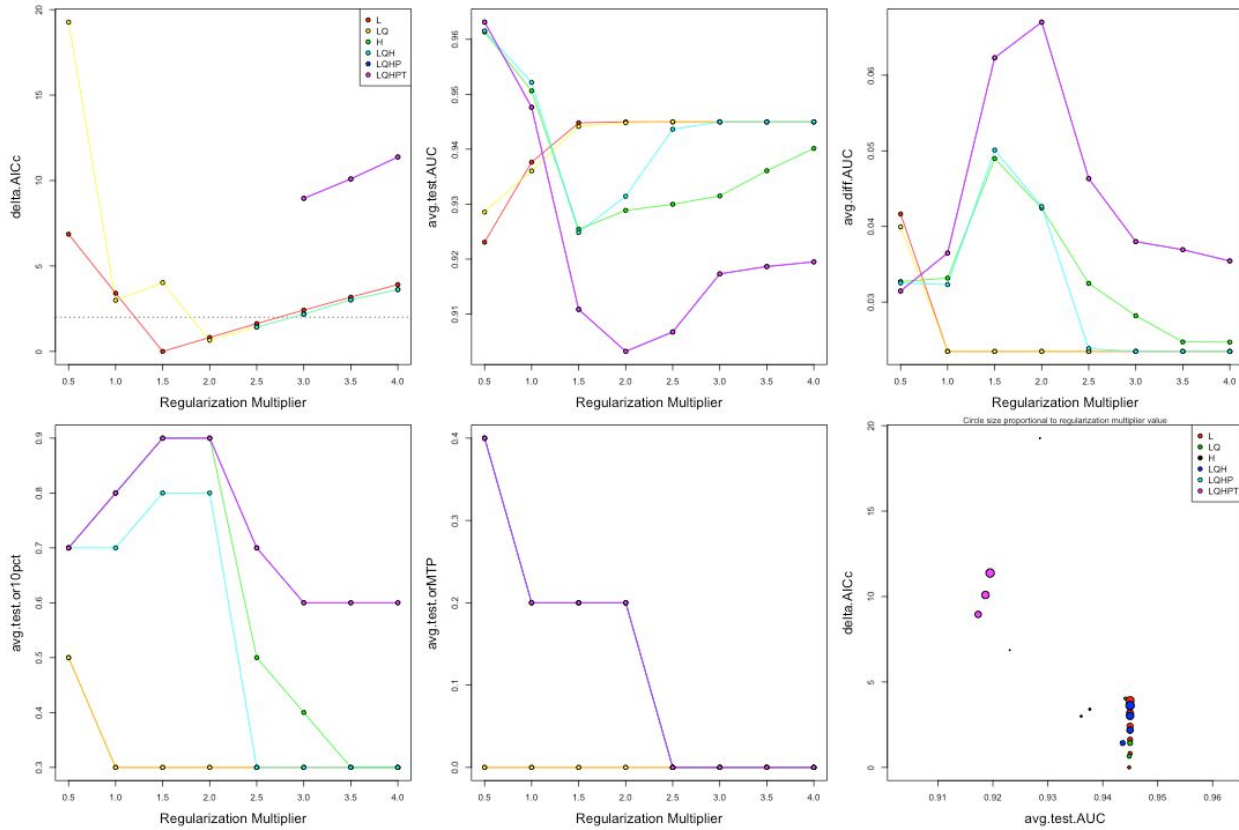
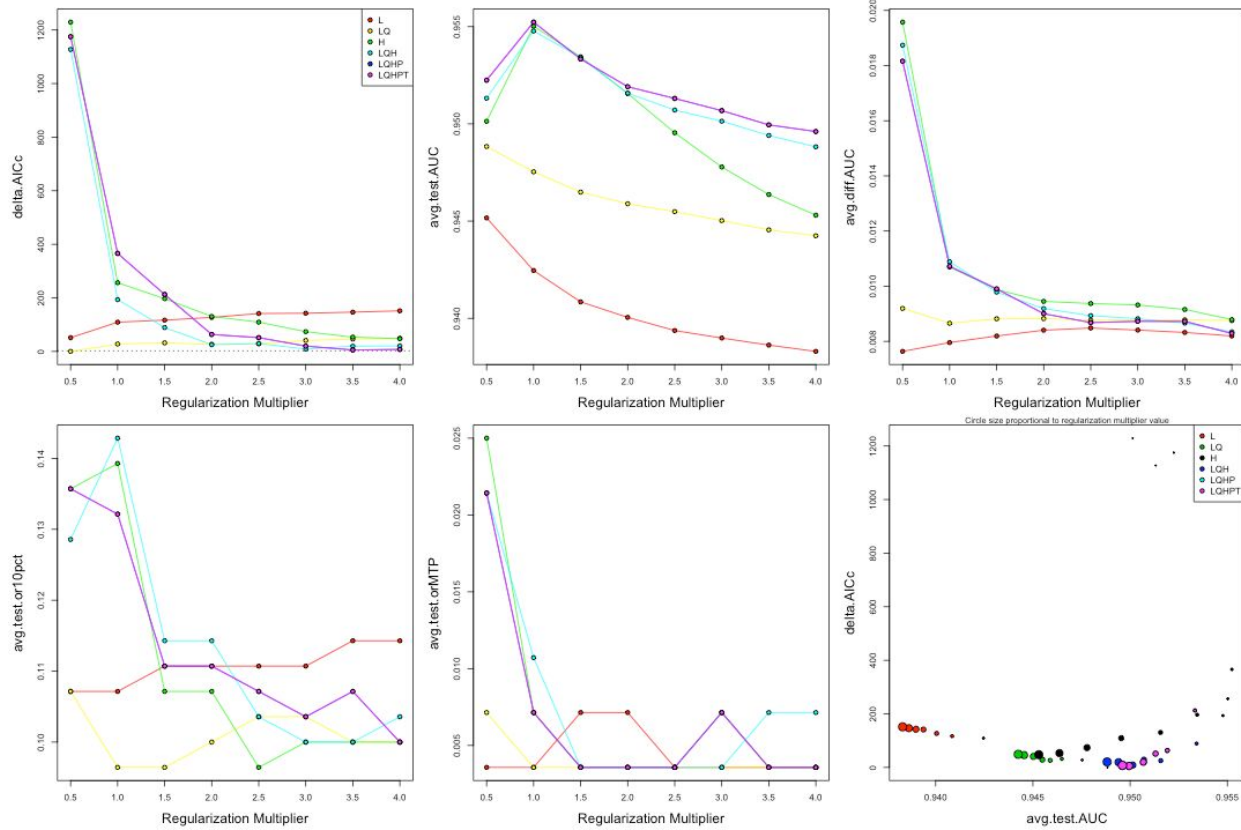**Sup. Fig. 2:** Hyperparameter tuning and model evaluation of *P. cresphontes* distribution during the T2 period.
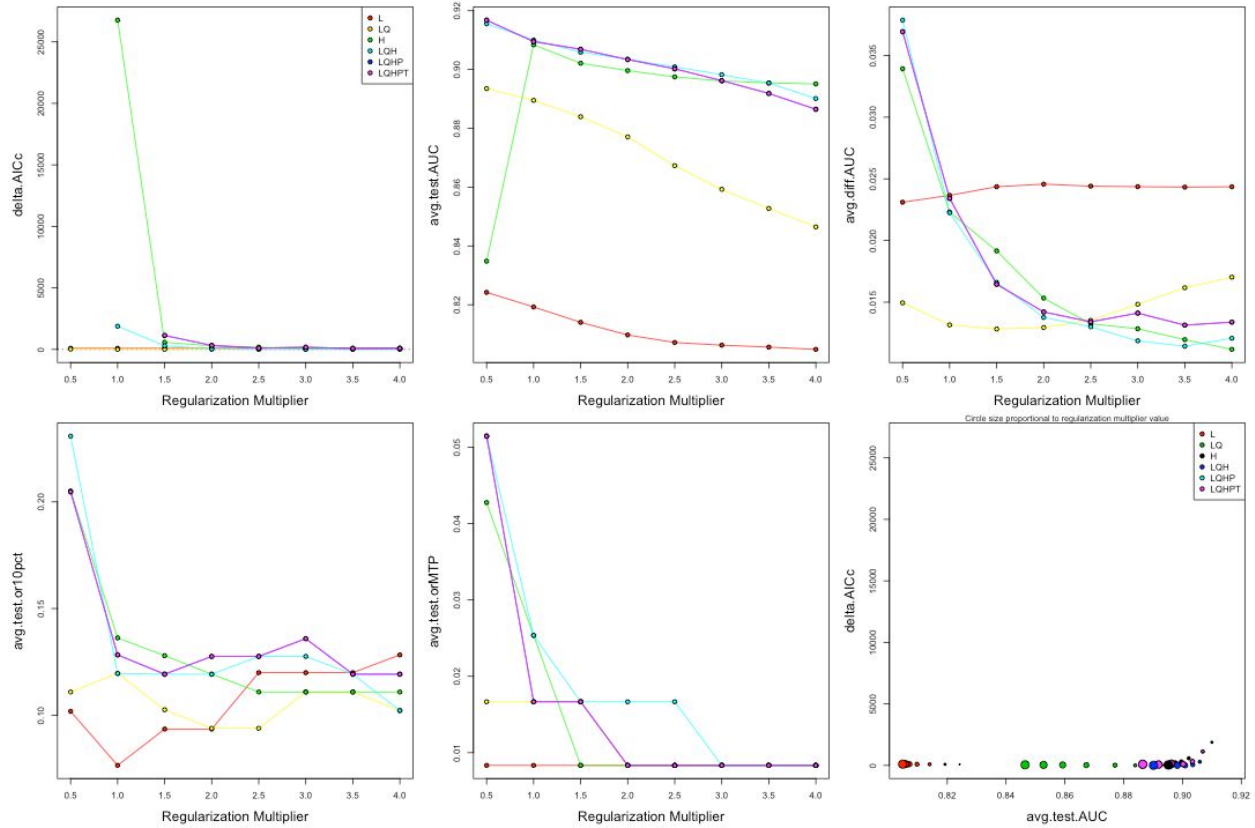
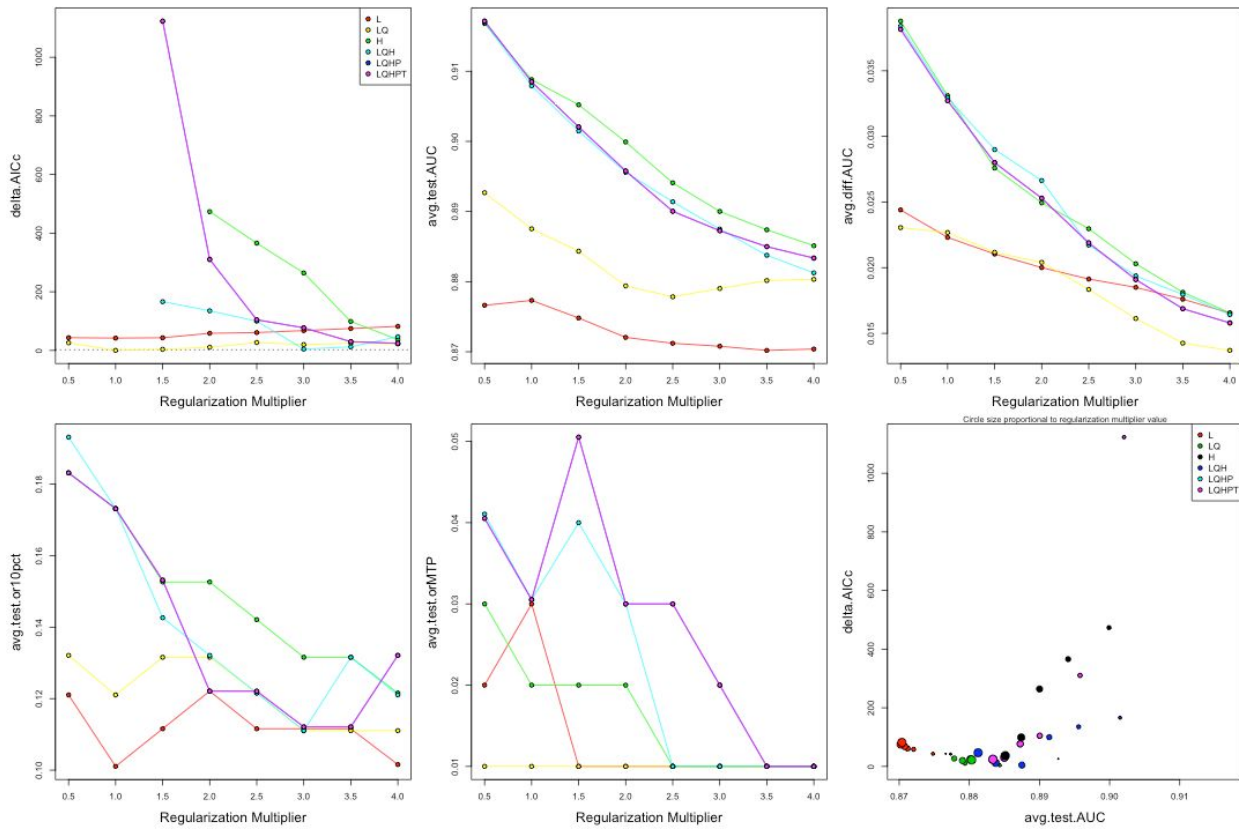**Sup. Fig. 3:** Hyperparameter tuning and model evaluation of *Z. americanum* distribution during the T1 period.
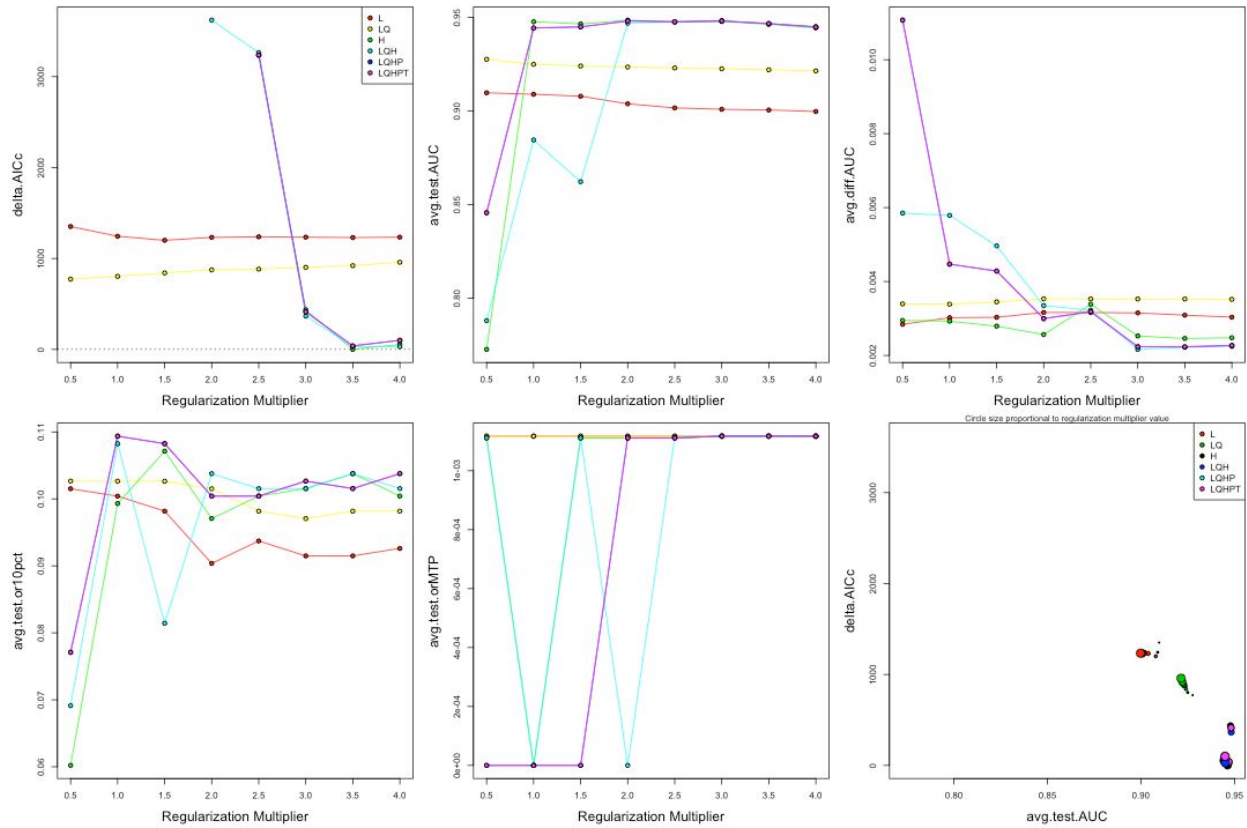
Sup. Fig. 4: Hyperparameter tuning and model evaluation of *Z. americanum* distribution during the T2 period.
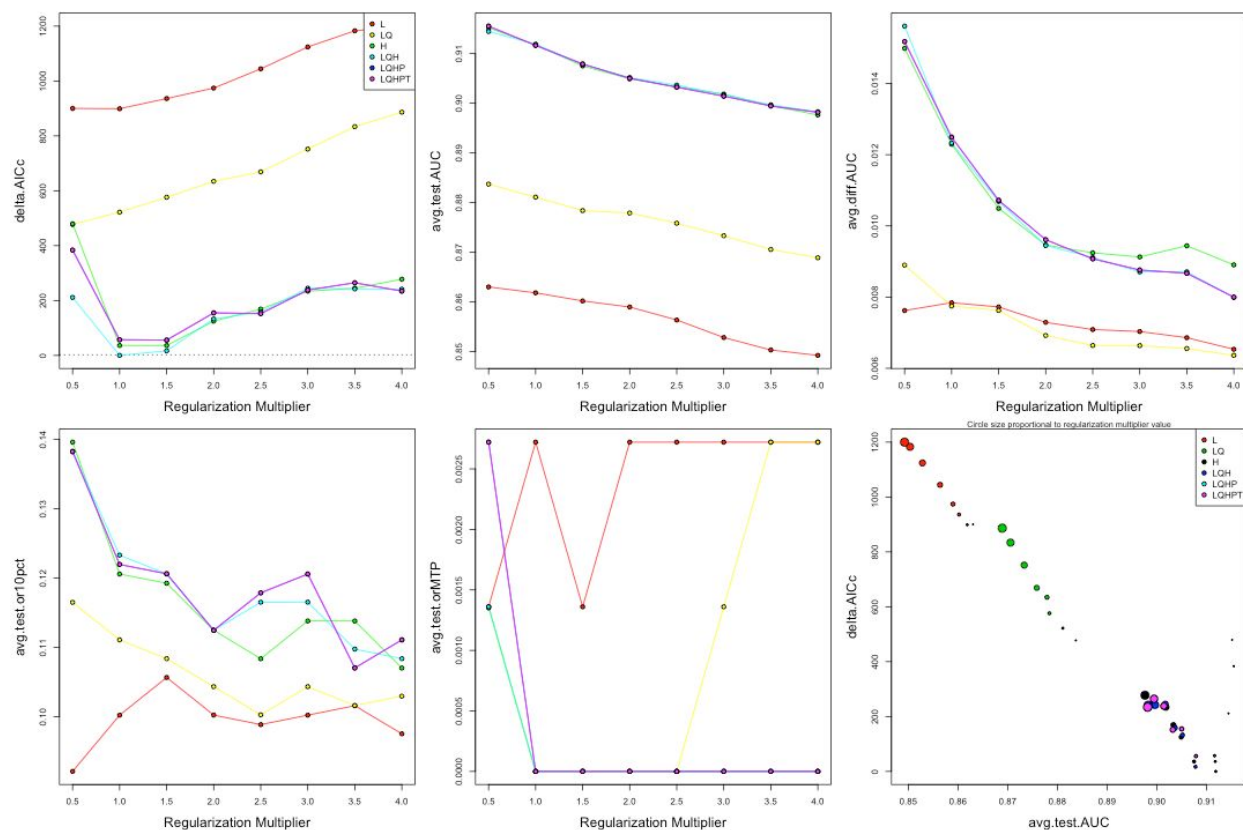
Sup. Fig. 5: Hyperparameter tuning and model evaluation of *Z. clava-herculis* distribution during the T1 period.

Sup. Fig. 6: Hyperparameter tuning and model evaluation of *Z. clava-herculis* distribution during the T2 period.

Sup. Fig. 7: Hyperparameter tuning and model evaluation of *P. trifoliata* distribution during the T1 period.

Sup. Fig. 8: Hyperparameter tuning and model evaluation of *P. trifoliata* distribution during the T2 period.

Supplementary Table 1. Bioclim variable definitions

Bioclim Number	Definition
BIO1	Annual mean temperature
BIO2	Mean diurnal range
BIO3	Isothermality
BIO4	Temperature seasonality
BIO5	Max temperature of warmest month
BIO6	Min temperature of warmest month
BIO7	Temperature annual range
BIO8	Mean temperature wettest quarter
BIO9	Mean temperature driest quarter
BIO10	Mean temperature of warmest quarter
BIO11	Mean temperature of coldest quarter
BIO12	Annual precipitation
BIO13	Precipitation of wettest month
BIO14	Precipitation of driest month
BIO15	Precipitation seasonality
BIO16	Precipitation of wettest quarter
BIO17	Precipitation of driest quarter
BIO18	Precipitation of warmest quarter
BIO19	Precipitation of coldest quarter