THE ROLE OF GROWING DEGREE-DAYS IN EXPLAINING LEPIDOPTERA SPECIES DISTRIBUTIONS AT BROAD SCALES

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Abstract

Understanding how climate determines species' geographic distributions is an important question in ecology with direct implications for predicting climate change-driven range shifts. For Lepidoptera, growing degree-days, a measure of growing season length, has been shown to be an important predictor of species' distributions in some cases. Most studies use a standardized estimate of base development temperature in their calculations of growing degree-days instead of a species-specific threshold so past investigations of the influence of growing degree-days on Lepidoptera distributions may not have been optimal. Species distribution models (SDMs) are a commonly used approach in ecology that typically only implicitly capture the underlying processes that limit a species' distribution. A species-specific estimate of growing degree-days should better characterize these processes than standard thermal thresholds and thus improve the accuracy of species distribution models. In this thesis, I use species distribution modelling to model the geographic distribution of 30 moth species native to North America. I ask whether a) growing degree-days are the best climatic predictor of these moth species distributions at broad scales; b) a lab-estimated biological threshold (i.e., BDT) can scale up and improve the predictive ability of SDMs; and c) the quality of experiments used to estimate species-specific BDT influences the predictive accuracy of SDMs. To do so, I compare the predictive accuracy of a correlative model based on a commonly-used thermal threshold to define growing degree-days to a hybrid model with degree-days defined based on a species-specific thermal threshold. I found that the predictive performance of the hybrid models was indistinguishable from the correlative models likely because growing degree-days was not the best climatic predictor of the geographic distributions of the majority of these moth species. I also found that there was no link between the quality of the lab experiments and the difference in performance of the hybrid and

correlative models. My findings suggest that lab-estimated thermal thresholds may not always scale up to be predictive at a broad scale and that more work is needed to leverage the data from lab experiments into broad scale SDMs. Determining the ultimate factors that limit species' distributions will be critical in accurately predicting species' range shifts response to future climate change.

Résumé

Comprendre comment le climat détermine les distributions géographiques des espèces est une question importante en écologie, avec des implications directes sur la prédiction des changements d'aire de répartition induits par les changements climatiques. Pour les lépidoptères, les degrés-jours de croissance, une mesure de la durée de la saison de croissance, se sont avérés, dans certains cas, être un facteur prédictif important de la répartition des espèces. La plupart des études utilisent une estimation standardisée de la température de base de développement dans leurs calculs des degrés-jours de croissance au lieu d'un seuil spécifique à l'espèce, de sorte que les études passées sur l'influence des degrés-jours de croissance sur les distributions des lépidoptères ne sont peut-être pas optimales. L'utilisation de modèles de distribution des espèces (SDM) est une approche couramment utilisée en écologie. Cependant cette méthode reconnaît généralement que de façon implicite les processus sous-jacents qui limitent la distribution d'une espèce. Une estimation des degrés-jours de croissance spécifique à une espèce devrait mieux caractériser ces processus que les seuils thermiques standards et ainsi améliorer la précision des modèles de distribution des espèces. Dans cette thèse, j'utilise une modélisation de la distribution des espèces pour modéliser la distribution géographique de 30 espèces de papillons de nuit originaires d'Amérique du Nord. Je me demande si a) l'utilisation des degrés-jours de croissance est le meilleur prédicteur climatique de la distribution de ces espèces de papillons de nuit à grande échelle ; b) un seuil biologique estimé en laboratoire (c'est-à-dire un BDT) peut augmenter et améliorer la capacité de prédiction des MDS ; et c) la qualité des expériences utilisées pour estimer les BDT spécifiques aux espèces influence la précision de prédiction des MDS. Pour ce faire, je compare la précision prédictive d'un modèle corrélatif basé sur un seuil thermique communément utilisé pour définir les degrés-jours de croissance à un modèle hybride avec des degrés-jours de croissance définis sur la base d'un seuil thermique spécifique à l'espèce. J'ai constaté que la performance prédictive des modèles hybrides ne se distinguait pas de celle des modèles corrélatifs, probablement parce que l’utilisation des degrés-jours de croissance n’était pas le meilleur prédicteur climatique des distributions géographiques de la majorité de ces espèces de papillons. J'ai également constaté qu'il n'existait aucun lien entre la qualité des expériences en laboratoire et la différence de performance prédictive des modèles hybrides et corrélatifs. Mes résultats suggèrent que les seuils thermiques estimés en laboratoire ne peuvent pas toujours être prédictifs à grande échelle et que des recherches supplémentaires sont nécessaires afin de pouvoir exploiter les données des expériences en laboratoire dans des MDS à grande échelle. La détermination des facteurs qui limitent le plus la répartition des espèces sera essentielle afin de prédire avec précision les changements d'aire de répartition des espèces en réponse aux futurs changements climatiques.

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1. Introduction

Understanding the factors that determine species' distributions is a fundamental challenge in ecology and evolution and is critical for accurately predicting how species will shift their ranges in response to climate change (Parmesan et al., 1999; Sexton et al., 2009; Chen et al., 2011; Chapman et al., 2014). At broad spatial scales (e.g., continental), climate (e.g., precipitation, temperature) has long been considered the most important factor in determining species' poleward distribution limits (Merriam, 1894; Good, 1931; Gaston, 2003; Chuine, 2010). For example, winter temperature is most important for some species (Kukal et al., 1991; Crozier, 2003) whereas for other species it is summer temperature (Crozier, 2004; Härkönen et al., 2010). However, the way(s) in which climate limits species' distributions are still uncertain as the importance of other seasons (e.g., autumn) and temperature mechanisms (e.g., direct vs indirect) are poorly studied and understood (Chuine, 2010; Tremblay et al., 2021). It remains difficult to explain the substantial variation in the degree and direction of range shifts documented over recent decades in response to climate change given this lack of understanding (Chen et al., 2011; Devictor et al., 2012; Lenoir & Svenning, 2015).

Some have postulated that climatic constraints may limit species' distributions through their impact on phenological processes. For example, degree-days, the total amount of heat required between the lower and upper development temperature thresholds for an organism to develop from one point to another in its life cycle, is a commonly used metric to describe insect phenology. At an ecological scale, the accumulated number of degree-days over a specified period of time, typically the growing season (i.e., growing degree-days) is used as an estimation of an organism's growing season length. It can provide a mechanistic link between thermal conditions and rates of insect development and survival, and ultimately influence annual population size (Saunders et al., 2018; Edwards & Crone, 2021). For Lepidopterans, growing degree-days is thought to be an important constraint on polar range edges by limiting the amount of time available for development and/or the completion of a full life cycle (Buckley et al., 2011; Luoto et al., 2006). It is often included as one of the climatic factors in butterfly species distribution models (e.g., Eskildsen et al., 2013; Hill et al., 1999 & 2002) and is a focus of phenological models for pest species (e.g., Crimmins et al., 2020). Some studies have identified growing degree-days as an important climatic factor for predicting Lepidopteran ranges at broad scales (Eskildsen et al., 2013; Luoto et al., 2006; Tremblay et al., 2021; but see Bryant et al., 1997).

Yet, one understudied, but potentially important, simplification underlying this work is that studies include the same lower developmental threshold or base development temperature (BDT; Trudgill et al., 2005) for all species (e.g., Hill et al., 1999, 2002, Luoto et al., 2006, Eskildsen et al., 2013). This is problematic since insects are known to have species-specific thermal requirements (Buckley & Kingsolver, 2012; Crimmins et al., 2020). At an ecological scale, BDT affects the length of the growing season: a species with a lower BDT has a longer growing season, and vice versa. Therefore, past work might not have accurately assessed the role of growing degree-days in influencing Lepidoptera species' distributions.

A growing body of evidence shows that spring and fall temperatures are increasing with climatic warming, which is lengthening growing seasons, and therefore the thermal development window for insects in many regions (Deutsch et al. 2008; IPCC, 2021). This means that conditions at higher latitudes could become more suitable for species and lead to poleward range expansion. Thus, growing degree-days could play an even greater role at species' poleward range limits with climatic warming.

Species distribution models (SDMs) are a commonly used approach in ecology and conservation biology to identify the most important abiotic factors that determine the geographic distribution of species, evaluate recent range shifts due to climate change and forecast future shifts due to climate change (Elith & Leathwick, 2009; Pearson & Dawson, 2003; Sillero, 2011; Evans et al., 2016). SDMs use correlations between georeferenced occurrence records and environmental variables with geospatial data to predict a species' suitable habitat in geographical space. Data required to fit these models are widely available, and thus this approach has been extensively used. While this correlative approach is useful for many applications, these models typically only implicitly capture the underlying processes that limit a species' distribution (Buckley & Kingsolver, 2012; Evans et al., 2016), thus potentially limiting its predictive ability when extrapolating into novel climate conditions.

A potential improvement to correlative SDMs—hybrid SDMs—has been the focus of recent work. In addition to including general environmental variables, such as mean annual temperature, hybrid SDMs also include species-specific traits (e.g., dispersal in Brotons et al., 2012; critical thermal minimum in Tremblay et al., 2021), and thus have the potential to improve the accuracy of SDM predictions by explicitly incorporating prospective range-limiting processes (Elith et al., 2010). However, there has been mixed evidence about if, and when, hybrid models outperform correlative models (Tourinho & Vale, 2021). In a few cases, the predictions and accuracy of hybrid models typically only diverge and/or outperform correlative SDMs when projecting species distributions into future time periods (using lower developmental thresholds for six UK butterfly species in Buckley et al., 2011; pond temperature extremes and juvenile and adult activity levels for a European amphibian in Enriquez-Urzelai et al., 2019; and dispersal of a Mediterranean bird species in Brotons et al., 2021). It could be that the trait incorporated into the hybrid model is not predictive or ecologically functional in the species' environment at the scale of the model (Evans et al., 2016). While including trait data in SDMs has the potential to better characterize the underlying climatic constraints on species' distributions, and thus improve the predictive accuracy of SDMs, this approach requires the input of data that is time-consuming to generate (i.e., physiological, morphological or behavioural).

In this thesis, I use species distribution modelling to model the current geographic distribution of 30 moth species native to North America and test two hypotheses. First, that growing degree-days are an important climatic factor for predicting moth species' distributions at this scale. To test this hypothesis, I use lab-estimated species-specific BDT to calculate growing degree-days and compare its contribution to that of other climatic variables to modelled suitability across geographic space. Second, given that a lab-estimated species-specific BDT is likely to be more accurate than a standard, non-species-specific estimate of BDT (e.g., 5°C), I test that hybrid models outperform correlative models. To test this hypothesis, I compare the performance of a correlative model to a hybrid model based on the same climatic variables with the sole exception of the estimation of growing degree-days. In the correlative model, I use the same commonly-used BDT across all species to calculate growing degree-days whereas I use a lab-estimated species-specific BDT to calculate growing degree-days in the hybrid model. Finally, I further evaluate whether the quality of the experiments used to estimate the species-specific BDT influences the performance of hybrid SDMs. The findings of this study can be used to inform the use of thermal thresholds in SDMs to predict changes in species' distributions under a changing climate.

2. Methods

2.1 Overall approach

I used SDMs to predict the current geographic distribution of 30 moth species native to North America (Canada and the United States; Table 1). Species were first selected based on the availability of species-specific estimates of BDT and then the number of occurrence records available based on specific thresholds for the SDMs (explained below in Section 2.4.1). Using these models, I compared the contribution of growing degree-days to the other climatic predictors to climatic suitability.

I then compared the predictive performance of a correlative- and a hybrid- SDM. With the exception of the growing degree-days calculation, both models were built using the same climatic variables, model settings etc. I estimated growing degree-days for the correlative model based on the same BDT for all species: 5°C, a commonly used BDT for butterflies and other insects (hereafter the DD5 model; e.g., Hill et al., 1999, 2002; Luoto et al., 2006; Buckley et al., 2011; Eskildsen et al., 2013). I evaluated the sensitivity of results to the choice of this threshold using another commonly used BDT: 10°C (hereafter the DD10 model; e.g., Nufio et al., 2010; Cayton et al., 2015; Tremblay et al., 2021). Growing degree-days for the hybrid model was estimated based on a species-specific BDT compiled by Jarošík et al., 2011, as explained below. All analyses were conducted in R v4.1.2.

2.2. Base development temperature

Degree-days is a measure of the thermal energy accumulated above an organism's BDT (also known as the lower development threshold) (Trudgill et al., 2005) and below an organism's upper development threshold. Below the BDT, an organisms' development ceases (Jarošík et al., 2011). Since it is difficult to observe BDT directly because no development occurs, BDT is typically estimated based on the relationship between development rate and temperature that is generated from rearing a species at different temperatures in controlled environmental conditions (Arnold et al., 1956).

In a relationship known as a species' thermal response curve (Figure 1), as temperatures rise, developmental rate increases until an optimal developmental temperature (t_{opt}) is reached, after which developmental rate decreases and eventually comes to a halt at an upper lethal temperature (also called critical thermal maximum, or CT_{max}) (Trudgill et al., 2005). Likewise, as temperatures decrease from the optimum, developmental rate decreases until it ceases – the temperature at which this occurs is a species' BDT (Trudgill et al., 2006; Jarošík et al., 2011). Further below the BDT lies the critical thermal minimum (CT_{min}), where organisms lose the ability of coordinated movement (MacMillan & Sinclair, 2011). Between the optimal developmental temperature and where development ceases, the relationship between developmental rate and temperature is usually close to linear ($\hat{d} = a + b \cdot t$; where a is the intercept, b is the slope, t is the temperature and $\hat{d}$ is the model estimate of development rate) (Ludwig, 1928) for ectothermic organisms (Trudgill et al., 2006). This linear relationship is used to calculate BDT by finding the temperature where development rate is equal to zero (BDT = -a/b; Arnold, 1959; Jarošík et al., 2011). Despite knowledge that thermal reaction norms are not linear (von Schmalensee et al., 2021), this linear approach remains the most popular method of estimating BDT (Rebaudo & Rhabi, 2018).

2.3. Species-specific BDT data

To build growing degree-days for the hybrid models, I used species-specific BDT data compiled by Jarošík et al. (2011). Briefly, Jarošík et al. (2011) calculated BDT for 152 Lepidoptera species based on developmental data from published articles. Jarošík et al. (2011) often further processed or recalulated BDT from the published articles so that it was based only on the range of temperatures for which the relationship between the rate of development and temperature was linear, as discussed previsouly (see Section 2.2; Figure 1).

Of the 152 Lepidopteran species in the Jarošík et al. (2011) database, 35 were native to Canada and the United States, and 30 of them fit the criteria for this study, as discussed below (see Section 2.4.1). The final list of species included species from 9 families and 28 genera (Table 1), with the Tortricidae family being best represented (n=9 species).

For these 30 species, there were three main types of source studies whose data Jarošík et al. (2011) used to estimate BDT: (1) lab experiments (n=21 species); (2) field experiments (n=5); and (3) unknown (n=4) (Table S1). In the lab experiments, the study organism was reared at a range of constant temperatures and the mean developmental time per temperature for each life stage was measured. In the field experiments (e.g., Potter and Timmins, 1983; Lysyk, 1989), counts of each life stage and/or larval instar were recorded periodically and combined with daily temperature data collected from a field site over the growing season. These data were used to model the relationship between developmental rate and temperature, and then estimate BDT. If both types of experiments were done for a species, I took the BDT estimated from the lab experiment to keep the methods underlying the estimation of BDT as consistent as possible between species. For four species, I was unable to obtain the source study, and classified the type of study as ‘unknown’.

There were a few other decisions I made based on the data available. If BDT was estimated for both sexes, I took the average BDT (n=2 species). If there were multiple BDT estimates for a species from different lab experiments, I selected one of the studies at random (n=1 species).

For most of the lab experiments (17/21), the developmental rate of three or more life stages were used (i.e., egg, larva, prepupa, pupa; Table S1). One study only measured the developmental rate of one life stage (i.e., egg; Mendel et al., 1989), and three studies measured the developmental rate of two life stages (Johnson et al., 1983; Haughen et al., 1984; Cardwell et al., 2001; Table S1). However, since the BDT of a species doesn't change between life stages (Jarošík et al., 2002), only one BDT was provided for each source study, regardless of how many life stages were included in the source study.

In the final list of species' BDT, the mean BDT was 8.76°C (ranging between 3°C and 13.65°C; Table 1).

2.4 Species Distribution Modelling

2.4.1 Species data:

Occurrence data was extracted from the Global Biodiversity Information Facility (GBIF) for the period 1980-2010 in June 2022 (GBIF.org). To prevent spatial biases (i.e., over-representation of occurrence data in regions that have higher levels of sampling) I first thinned the occurrence data to 1 km resolution (*thin* function from the package *spThin* v0.2.0; Aiello-Lammens et al., 2015). Spatial biases are common in non-systematically sampled occurrence records, and if not accounted for, can result in over-representation of environmental conditions from areas that have been more heavily sampled (Aiello-Lammens et al., 2015). To define the species' background extent used for the species distribution modelling (explained in more detail in section 2.4.3), I created a minimum convex polygon (MCP) using 95% of the occurrence points using the *mcp* function from the package *adehabitatHR* v0.4.19 in R (Calenge, 2006). The MCP is a commonly used approach that approximates the range that a species could have colonized while establishing its range (Phillips 2008; Lee-Yaw et al., 2016). I excluded 5% of the records from the MCP to attempt to remove potential outliers from the occurrence dataset (e.g., incorrect taxonomic identification, occurrences in sink habitat or unsuitable climate).

Of the native North American Lepidoptera species with BDT estimates from Jarošík et al., (2011), there were 30 moth species with at least 10 occurrence records available after this processing (Table 1). For this final list of species, I further included the occurrence data filed under their synonymous names (based on GBIF and the BugGuide), and all types of GBIF records except for "unknown". On average, there were 136 occurrence records per species (ranging between 11-386; Table 1)

2.4.2 Climate data:

I considered 19 bioclimatic variables modelled for the period 1980-2010 (Table 2). These environmental variables were estimated based on monthly minimum and maximum temperature, and precipitation at a resolution of ~10 km^2 using historical monthly climate data from the Canadian Forest Service of Natural Resources Canada (McKenney et al., 2006; Foster et al., 2022).

To estimate growing degree-days across North America for 1980-2010, I used daily maximum and minimum temperature data from Daymet (1 km^2 resolution; Thornton et al., 2020). I first calculated daily mean maximum and minimum temperature across years. I then calculated the mean daily degree-days across years (DD = [tmax-tmin] – BDT) and summed the degree-days across days to get annual growing degree-days (hereby referred to as growing degree-days). I calculated growing degree-days on an annual time frame rather than just including the growing season (e.g., May-September in Canada) because some of the species are widespread across North America and have different growing seasons depending on their geographic location. Annual growing degree-days are also typically included in species distribution models for butterflies (e.g., Hill et al., 2002; Luoto et al., 2006; Buckley et al., 2011).

For each species, I estimated growing degree-days three-ways based on a: i) species-specific BDT (for the hybrid model); ii) BDT of 10°C (for DD10 correlative model); and iii) BDT of 5 °C (for DD5 correlative model). I rescaled the extent and resolution of the growing degree-day layers to the bioclimatic layers using the *resample* function in R (*raster* package v3.5.15; Hijmans et al., 2022). All environmental variables were manipulated in R using the *raster* package v3.5.15 (Hijmans et al., 2022).

2.4.3 Species distribution models

To build the SDMs, I used Maxent (version 3.4.4, Phillips et al., 2006) with the *dismo* package (v1.3-5; Hijmans et al., 2021). Maxent is a commonly used approach for species distribution modelling for presence-only data (Phillips et al., 2006) across diverse taxa (e.g, Lee-Yaw et al., 2016; Connor et al., 2019; Newman et al., 2022), and has been shown to outperform other methods of distribution models for presence-only data (Elith et al., 2006). Maxent uses a maximum entropy approach to relate the species' presences and pseudo-absences (random background points restricted to the background extent) to the environmental variables to predict where the habitat is suitable across geographic space (Merow et al., 2013).

To assess collinearity among the 20 climatic variables across North America, I conducted a variance inflation factors (VIF) analysis with a threshold of five to balance reducing collinearity among variables but not be overly restrictive (O'Brien, 2007). I conducted a VIF analysis for the combination of environmental variables in both of the correlative models (DD5, DD10), and each hybrid model (32 VIF analyses total) and removed variables that did not meet the threshold of independence (i.e., VIF=5). The least-collinear climatic variables were the same in all cases (Table S2). Therefore, I used the same variables for the correlative and the hybrid models (n=7, Table 2) which also allowed for a direct comparison of variable contribution across species.

To explore potential overfitting of the models for species with fewer occurrence records, I also ran all three models with only three climatic variables (i.e., the two least correlated bioclimatic variables plus growing degree-days, hereby known as "reduced model") for the species with fewer than 35 occurrence points (i.e., 'data-poor species'; n=4). The accuracy of the full model was almost always higher than the reduced model for these species (difference in AUC: 3.2-42.7%, TSS: 20-173%, kappa: 0.5-18.7%; Table S3). Given this decline in accuracy for the reduced model for the data-poor species, I also conducted a sensitivity analysis where I excluded the four species from the analysis. Upon removing the data-poor species, there were slight changes in average model accuracy (changes in average percent difference of < 1.5% for all accuracy metrics; Table S4, Table S5, Table S6), and average percent contribution of the environmental variables (< 3% change for all variables; Table S7, Table S8, Table S9) but the overall results remained the same so only the results from full model is presented in the main text.

For ease of computation at this scale, I kept all model settings at default. Pseudo-absence point selection was restricted to the MCP for each species (i.e., the background extent). I built all models using all available occurrence points. I used the log-log (cloglog) transformed output from Maxent. Cloglog is now the default transformation in Maxent, replacing logistic, since it does a better job of estimating probability of occurrences (Phillips et al., 2017). All climatic variables and occurrence points were reprojected into a Lambert Conformal Conic projection before modelling.

To create climatic suitability predictions in geographic space, I used the *predict* function in the *dismo* package (v1.3-5; Hijmans et al., 2021). This function produces continuous prediction maps from 0-1, with 1 being a perfectly suitable climate and 0 being completely unsuitable. To create binary prediction maps (suitable vs. not-suitable), I used the maximum training sensitivity plus specificity threshold (Liu & White, 2016).

2.5 Evaluating predictive performance of models

To evaluate model performance, I evaluated each model using five-fold cross-validation (e.g., Lee-Yaw et al., 2016). This evaluation method randomly selected 80% of the available occurrence records to train the model and used the remaining 20% of the records to test the model (Fielding & Bell, 1997). This process was repeated five times, using different records as the testing and training data, and resulted in five values for each of the evaluation metrics measured. To get the performance for each model, I took the mean of the five values.

I calculated three measures of model performance: Area under the ROC curve (AUC; Fielding & Bell, 1997), True Skill Statistic (TSS) and Kappa (Allouche et al., 2006). AUC is a threshold-independent score between 0-1 that evaluates the model's ability to correctly discriminate if a presence or absence is a true presence or absence (Fielding & Bell, 1997; Yackulic et al., 2013). An AUC value of 1 indicates that the model discriminates all presences and absences and an AUC value of 0.5 indicates that the model cannot discriminate presences and absences better than chance. An AUC value above 0.80 is generally considered a 'good' model (Swets, 1988; Fielding & Bell, 1997). Despite being widely used, AUC can be influenced by the number of background points and does not always perform well with smaller sample sizes (Yackulic et al., 2013). I obtained the AUC scores for each species and model type using the *evaluate* function in the *dismo* package (v1.3-5; Hijmans et al., 2021).

TSS is based on model sensitivity (i.e., proportion of observed presences correctly predicted as suitable) and specificity (i.e., proportion of observed absences correctly predicted as not suitable; Allouche et al., 2006). To determine the binary threshold (i.e., suitable, not-suitable) for the TSS calculation, I used the 90th percentile cut-off of Maxent's presence predictions. This method attempts to remove records in areas of lower suitability (i.e., sink habitats; Lee-Yaw et al., 2016). For TSS, a score above 0.75 indicates 'excellent' model performance while a score between 0.4 and 0.75 indicates 'good' model performance (Allouche et al., 2006). I obtained the TSS for each species and model using the equation: TSS = sensitivity + specificity – 1. Sensitivity and specificity were obtained using the *presence.absence.accuracy* function in the *PresenceAbsence* package (v1.1.10; Freeman & Moisin, 2008).

Kappa is another commonly used statistic in evaluating the performance of SDMs that uses confusion matrices to assess a model's ability to correctly predict occurrences (Allouche et al., 2006). Unlike TSS, kappa can be sensitive to prevalence (i.e., the proportion of the background extent that is occupied by the occurrence records; Allouche et al., 2006). Generally, kappa scores above 0.75 indicate 'strong' agreement with the model, while scores below 0.4

indicate ‘poor’ agreement, and values between 0.4-0.75 indicate ‘fair’ to ‘good’ agreement (Monserud and Leemans, 1992). I obtained kappa for each species and model using the *threshold* function in the *dismo* package (v1.3-5; Hijmans et al., 2021).

To reduce the extent of results I report in the main text, I assessed whether the three evaluation metrics (i.e., AUC, kappa and TSS) were correlated. The AUC scores were highly correlated with TSS in all three model types (Table S10). Kappa was not highly correlated with AUC or TSS, but it can be sensitive to prevalence and is less reliable in cases of low prevalence (Allouche et al., 2006). Given the lower prevalence of my species (Table S11), I did not include kappa in the main text. As a result of these considerations, I only report AUC as the metric of model performance in the main text.

Additionally, I examined how similar the performance was between the two correlative models. Since the evaluation scores were highly correlated between the DD5 and DD10 models (r=0.932 for AUC) and there were more species with a BDT that was different from 5°C (n=30) than 10°C (n=26), only the results of the DD5 model are reported in the main text. For all model performance metrics, see Appendix (Table S4, Table S5, Table S6).

2.6 Analysis

The analysis consisted of three sections. First, to determine whether growing degree-days was the most important climatic predictor of these species’ distributions at broad scales, I compared the contribution of growing degree-days to the other climatic variables included in the hybrid model. Second, to determine whether the species-specific estimate of growing degree-days improved the predictive performance of SDMs, I took three approaches: (1) I quantitatively compared the performance of the hybrid and correlative models; and (2) I examined the relationship between growing degree-days and climatic suitability using response curves; and (3) qualitatively compared the model predictions using suitability maps. I also examined the change in contribution of growing degree-days for each species in the correlative and hybrid models. Finally, to determine whether the quality of experiments used to estimate BDT influenced the performance of the hybrid models, I examined correlations between metrics of experimental quality and hybrid model performance.

2.6.1 Evaluating importance of climatic variables

To determine which climatic variable was the most important in predicting these species' distributions, I took two approaches. I first determined which variable had the highest mean percent contribution to climatic suitability for the greatest number of species in the hybrid model. In Maxent, this is represented by the percent increase in regularization gain (Philips, 2017). For each species, I ranked the variables based on their contribution to the hybrid model. I then tallied the number of times each variable had the highest percent contribution to the model (i.e., was the first contributor). The variable that was the first contributor for the greatest proportion of the 30 species was considered the best predictor on average. Second, I calculated the mean percent contribution of each environmental variable to the model across all species.

To get mean percent contribution for each environmental variable I took the mean of the five values of percent contribution values for each model given by the 5-fold cross-validation (see section 2.5).

I also conducted both analyses for the correlative model to use as an additional comparison between the performance of the two models.

2.6.2 Comparing model performance

To determine whether a more accurate estimate of BDT (i.e., the lab-estimated species-specific BDT) increased hybrid model performance, I took five approaches. First, I calculated an effect size to compare predictive performance between model types. I used the percent difference in AUC: (correlative AUC - hybrid AUC)/hybrid AUC. Second, I compared the difference in percent contribution of growing degree-days between the hybrid and DD5 model. Third, I examined whether the percent contribution of the environmental variables were correlated between the models to determine whether incorporating species-specific growing degree-days changed the contribution of other environmental variables included in the models. Fourth, I evaluated whether there was a correlation between the percent difference in AUC between the DD5 and hybrid models, and the absolute difference between the BDTs used in the two models (i.e., species-specific BDT (°C) - 5°C).

Lastly, I qualitatively compared the relationship between growing degree-days and climatic suitability between the two models using response curves. I also qualitatively compared the suitability maps for areas of congruence and divergence between the two models.

2.6.3 Experimental quality analysis

I assessed the quality of the experiment using two metrics that were readily available from all laboratory-based studies: the number of constant temperature treatments included in the experiment and the difference between the lowest temperature treatment included in the experiment (LTM) and BDT. A greater number of experimental treatments increases the precision with which BDT is estimated. A negative difference between LTM and BDT indicates that BDT fell within the experimental treatment. A positive difference between LTM and BDT indicates that BDT fell outside of the experimental treatments, and the range of values used for the development of the linear model. Only the species with a positive value for the difference between LTM and BDT were included in the quality analysis because in these cases, the estimation of BDT was an extrapolation and thus reduces the operationalization of the BDT. If there was a different number of temperature treatments, or a different lowest temperature measured for different life stages within a study, I took the mean. Details provided by the authors on sample size in the original papers varied greatly between studies, and so I did not include it here.

To determine whether these two experimental quality metrics improved the performance of the hybrid models, I examined the strength of the relationship using a linear model and the Pearson correlation coefficient between each metric, and: (1) the AUC of the hybrid model, and; (2) the contribution of growing degree-days to the hybrid model. In this analysis, I only included the source studies that were lab experiments (n=21) because the field experiments did not have comparable quality metrics to the lab experiments and the sample size was too small to conduct a quality analysis specific to the field experiments (n=5). The species with unknown experiment types (n=4) were also not included in this analysis because there was no information provided on how the BDT was measured.

3. Results

3.1 Variable contribution

In the hybrid model, temperature annual range (max temperature of the warmest month – min temperature of the coldest month) was the best predictor of climatic suitability across species. It was ranked as the first contributor for 50% (15/30) of the species and had a mean contribution of 33.97% (4.32SE) to the models (Figure 2, Table 3). Next, precipitation seasonality was the first contributor for 20% (6/30) of the species and had a mean percent contribution of 15.21% (2.38SE). Mean temperature of the wettest quarter was the third best predictor, being the first contributor for 10% (3/30) of the species and having a mean percent contribution of 11.86% (2.34SE).

Growing degree-days and mean diurnal range were tied as the fourth best contributor to the models, being ranked as the highest contributor for 6.67% (2/30) of the species. Growing degree-days was the best predictor for *Choristoneura fumiferana* and *Plathypena scabra* (Table S7, Table S8, Table S9). Growing degree-days had a mean percent contribution of 10.91% (1.63SE). Climatic suitability typically increased with annual degree-days (Figure 4).

3.2 Comparing model performance

The mean AUC score for the hybrid and correlative models was 0.785 (0.16SE) and 0.784 (0.016SE), respectively, indicating that both models had ‘fair’ performance. The performance of the hybrid model was indistinguishable from the correlative model (Figure 3; Table S4, Table S5, Table S6). On average, the correlative model was 0.10% (0.54SE) better than the hybrid model.

There was also no difference between models in the contribution of growing degree-days to climatic suitability (Figure 3). For 60% (18/30) of the species, growing degree-days contributed more to climatic suitability in the hybrid model than in the correlative model, but on average only contributed 0.49% more (n=30, Figure 3; Table S12).

The percent contribution for each of the seven climate variables was highly correlated between the hybrid, DD5 and DD10 model (Table 3). A species-level breakdown of the contribution of each environmental variables for each model can be found in the Appendix (Table S7, Table S8, Table S9).

The lab-estimated BDT for 97% (29/30) of the species was higher than the standard 5°C threshold that is commonly used. Despite this difference, the lab-estimated BDT did not result in improved predictive performance of the hybrid models (Figure 5). No relationship was found between the difference in the contribution of growing degree-days between the two models and the absolute difference between the BDT used in the two models (i.e., species-specific BDT (°C) - 5°C; r=-0.127, p=0.5; Figure 5a). There was also no relationship found between the percent difference in AUC between the correlative and hybrid model and the absolute difference between the BDT used in the two models (r=0.172, p=0.36; Figure 5b).

The type of relationship between climatic suitability and growing degree-days was similar between the correlative and hybrid models, though it differed substantially across species (Figure 4). There was also high spatial congruence between the suitability predictions from the hybrid and correlative models (Figure 6). Generally, spatial divergence in predictions only occurred along the margins of the core areas of congruence (Figure 6). There were no consistent patterns in spatial divergence between models across species (Figure 6). For example, hybrid models did not consistently predict greater suitability at higher latitudes.

3.3 Experimental quality analysis

The quality of the metrics of the experiments that I measured here were not related to the performance of the hybrid models, or to the contribution of growing degree-days in the hybrid model (Table 4, Figure 7). There was no relationship between the AUC scores of the hybrid model or the number of temperatures measured in the lab experiment (Figure 7A) or difference between the lowest temperature treatment included in the experiment and BDT (Figure 7B). There was also no relationship found between the contribution of growing degree-days in the hybrid model and the number of temperatures measured in the lab (Figure 7C) or the difference between the lowest temperature treatment and BDT (Figure 7D).

4. Discussion

Despite the potential importance of growing degree-days in moderating the influence of climate on species' geographic distributions, its importance has been poorly tested at broad scales. Using species-specific estimates of BDT to calculate growing degree days, I did not find support for the hypothesis that growing degree-days are an important climatic factor for predicting moth species' distributions in North America. I also did not find support for the hypothesis that a more accurate estimate of growing degree-days would improve the performance of SDMs. This suggests that lab-estimated biological thresholds may not always scale up to be predictive at a broad scale. Finally, I found that there was no link between the quality of the lab experiments used to estimate BDT and the performance of hybrid models. Together my results suggest that future studies can use standard BDTs when incorporating growing degree-days into broad scale SDMs of lepidopteran species distributions without compromising their predictive performance.

4.1 Importance of growing-degrees

Growing degree-days was not an important predictor of the geographic distribution for the majority of these species. Instead, temperature annual range was the best predictor for half of the moth species' distributions. Temperature annual range describes the difference between the maximum temperature of the warmest month and the minimum temperature of the coldest month. This metric likely best encapsulated the temperature extremes that can constrain Lepidoptera species at broad scales. All ectotherms have upper and lower thermal limits above and below which they cannot tolerate– the critical thermal maximum and minimum, respectively (Trudgill et al., 2005; Figure 1). Indeed, thermal limits have been shown in the past to accurately predict insect species' distributions (Overgaard et al., 2014; Andersen et al., 2015; but see Tremblay et al., 2021).

My result that growing degree-days was not an important predictor of climate suitability is inconsistent with studies that found it to be the best predictor of the distribution of many Lepidopteran species (e.g., Luoto et al., 2006; Buckley et al., 2011; Tremblay et al., 2021). My result is also unexpected considering that growing degree-days models are commonly used in integrated pest management to predict the timing of insect phenology and facilitate more precise control strategies (Pruess, 1983; but see Whitworth, 1979; Lysyk, 1989; Fettig & Barisford, 1999; Crimmins et al., 2020 for examples), and have been used to accurately predict the first emergence and peak abundance of Lepidopteran species (Cayton et al., 2015).

Some of these discrepancies in the importance of growing degree-days in determining Lepidopteran distributions could be explained by differences in methodologies between studies. For example, differences in the number, type, and potential collinearities between climatic variables included in the models will also influence the relative contribution of growing-degree days (e.g., Buckley et al 2011 only considered influence of three variables). Modelling approaches might also affect the relative contribution of climatic predictors. For example, Eskildsen et al. (2013) showed that the variable importance of growing degree-days changed depending on the type of model used (i.e., GAM vs boosted regression tree). The geographic scale at which the relationship between climatic suitability and growing degree-days was assessed may also have influenced which climatic variables were found the most important. My study assessed these relationships on a continental scale, which means that I likely captured the entire distribution of these species, while others quantified the relationship in a specific country (e.g., the UK in Buckley et al., 2011; Finland in Luoto et al., 2006 & Eskildsen et al., 2013), which could result in an underestimation of the range of climatic conditions their study species experience on an ecological scale.

Finally, it may also have been more difficult to accurately assess the relationship between climatic suitability and growing degree-days at this scale for two reasons. First, all the species considered here were agricultural or forest pests (i.e., species that cause significant damage to plants of human interest) to different degrees, and thus are often heavily managed and found in human-modified landscapes. Consequently, the occurrence data available for these species may represent a small, and potentially biased, proportion of the suitable niche space for the species. Potential spatial and environmental biases in occurrence records used to create SDMs is not unique to this study, however. Previous studies have recommended using independent datasets, when possible, to test SDMs to help with these biases (Elith & Burgman, 2002; Lee-Yaw et al., 2021). The species in this study also had low prevalence (small number of samples per unit area; Royle et al., 2012) on average. Both of these factors could make it more difficult to accurately estimate the full realized niche of these species (Loiselle et al., 2007; Lee-Yaw et al., 2021) and thus the contribution of growing degree-days in limiting the geographic distribution of the species. However, it could also be the case for these species that human intervention in their distributions has occurred for such a long period of time that the publicly available occurrence records from GBIF represent an unbiased sampling of their niche. Indeed, the predictive performance of these models is similar to models for native non-pest species based on similar climate variables (Buckley et al., 2011; Enriquez-Urzelai et al., 2019).

Second, as is typically used at broad scales and based on the lack of data available for all species, I used a simplistic calculation of growing degree-days: I used an averaging method based on daily temperature and did not include the upper developmental threshold for these species. Combined, this reduces the accuracy of my estimate of growing degree-days. However, more complex calculations of annual degree-days used in the literature (e.g., sine curve, hourly temperature) still only assume a linear relationship between development rate and temperature (Roltsch et al., 1999). Yet, both theory and empirical data show that species' thermal response curves are not usually linear (Figure 1). This non-linearity can become increasingly important when making predictions into areas that experience conditions at the upper end of the thermal response curves, such as the warmer range edge of species' distributions. However, recent work demonstrates that in environments where temperature variation is primarily in the approximately linear region of the thermal performance curve, average temperatures or linear degree-day models should be sufficient (von Schmalensee et al., 2021). Given the severe projections of climatic warming (IPCC 2021) and the greater vulnerability of species at lower latitudes (Deutsch et al., 2008), future research should investigate whether more complex calculations of growing degree-days would improve our understanding of the role of growing degree-days in limiting species' distributions.

4.2 Improving SDMs

Incorporating species-specific estimates of growing degree-days did not significantly improve the performance of the SDMs. These results are consistent with other comparisons of the performance of hybrid and correlative SDMs for the current distributions of species when species-specific thermal thresholds are included (Buckley et al., 2011; Enriquez-Urzelai et al., 2019; Tremblay et al., 2021). The predictions of correlative and hybrid models have been shown to typically only significantly diverge when being used to forecast future species' distributions (Buckley et al., 2011; Brotons et al., 2012; Enriquez-Urzelai et al., 2019). However, given the way Maxent models suitability across geographic space—by discriminating differences in suitability between presences and pseudo-absences—it is not actually unexpected that the predictive performance of these two models was so similar. In this context, the geographic structure of different estimations of growing degree-days is very similar: more degree-days in the south, fewer in the north (Figure S1). In other words, Maxent finds similar associations between the species' presences and growing degree-days regardless of the differences in the absolute values of growing degree-days between models.

Instead, comparing the contribution of growing degree-days to predicted climate suitability between models is a more informative way to compare the usefulness of hybrid Maxent models relative to correlative models (Enriquez-Urzelai et al., 2019). More accurately estimated growing degree-days should have resulted in greater contribution in the hybrid model than the correlative model. In this study, the contribution of growing degree-days to climate suitability did not substantially increase in the hybrid models compared to the correlative models. This finding is inconsistent with the assumption that lab-estimated species-specific thermal thresholds better characterize the underlying climatic mechanism constraining species' distributions than a standard thermal threshold. However, the lack of improvement of hybrid models is likely because growing degree-days was not an important predictor of these species' geographic distributions.

4.3 Using lab estimates of BDT in SDMs

I found that available metrics of experimental quality did not influence the performance of hybrid models or the contribution of growing degree-days to the hybrid models. It could be that other study differences I did not consider, such as species' life history traits and extent of data collected on a given species, influenced the accuracy of BDT. For example, given that the vast majority of the source studies measured the developmental rate at more than one stage (i.e., egg, larval and pupal life stages (Table S1), more work could be done to determine whether life stage influenced the performance of the hybrid models.

Alternatively, challenges associated with the methods used to estimate BDT and the biological relevance of BDT likely contributes more to the lack of improvement to the SDMs than study differences in experimental design. Effectively, while the lab-estimated species-specific estimates of BDT are more accurate than the standard 5°C threshold that is commonly used in ecological modelling, these estimates still only approximate the true BDT experienced by the species at ecological scales. First, BDT was estimated based on a linear regression extrapolation method which has been shown not to give biologically accurate estimates of BDT (Rebaudo & Rabhi, 2018). This is because the developmental curve is not actually linear at low temperatures (Campbell et al., 1974; Lamb 1992). Despite this being well known, linear extrapolation of the development curve remains the most popular method of estimating BDT (Rebaudo & Rabhi, 2018).

Second, the estimates of BDT are also likely to be less accurate than other thermal thresholds because it is difficult to distinguish between slow development and no development at low temperatures. Organisms developing at low temperatures are more likely to have a higher mortality so researchers may determine there is no development at those temperatures rather than slow development (Jarošík et al., 2011; Rebaudo & Rabhi, 2018), thus potentially leading to an overestimation of BDT (i.e., 'true' BDT should be lower) (Jarošík et al., 2011). Ideally, monitoring schedules should be proportional to the development time expected (Jarošík et al., 2011; Shaffer 1983, van Rijn et al. 1995) and/or include dissections or closer examination to confirm development (e.g., Haugen & Stephen, 1984; Mendel et al., 1989).

Third, as is typically done in these experiments, most of the source experiments only measured developmental rates at constant temperatures and humidity. This is not reflective of natural conditions where organisms experience fluctuating temperatures (Howe 1967; von Schmalensee et al., 2021) and relative humidity (Tochen et al., 2016). For example, relative humidity can interact with temperature to influence developmental rate (Chen et al., 2015). Moreover, these laboratory estimates of BDT do not consider periods of time where an organism exists above its BDT but may not be developing (e.g., diapause initiated by photoperiod) or may be developing but may have lower fitness than when not developing (e.g., due to predation). Since the species-specific BDTs used in the hybrid models may still not be a true reflection of what insects experience in their natural environments, we may not be accurately capturing the functional relationship between climate suitability and degree-days in the SDMs.

4.4 Moving forward: Improving our understanding of the role of growing season length on moth species' distributions

The importance of growing degree-days in predicting moth species' distributions may increase towards the species' range edge, at different spatial scales and for different types of species. Growing degree-days may play a more important role closer to the poleward range limit where the length of the growing season can be limiting (Luoto et al., 2006; Buckley et al., 2011), a spatial scale that is difficult to capture with this broad-scale approach. Correlative SDMs built based on a species' entire distribution perform better than those restricted to a portion of the distribution (Connor et al., 2019; VanDerWal et al., 2009; Tremblay et al., 2021). The thermal thresholds of insects have also been shown to change across a species' range due to local adaptation (Uvalov, 1933; Sinclair et al., 2012) which could result in different patterns of dependency on growing degree-days across a species range.

Growing degree-days may also contribute more to the geographic distribution of species at smaller spatial scales. Modelling at broad scales does not typically account for behavioural responses to temperature, such as thermoregulation, which could result in increased developmental rates and underestimate the role of growing degree-days on more local scales (Bryant et al., 2002; Buckley et al., 2011). Indeed, estimations of BDT have been shown to be more accurate for non-mobile life stages, such as egg and pupal stages, because mobile organisms are able to thermoregulate (Honek and Kocourek 1990; Jarosik et al. 2002). Researchers interested in more accurately incorporating growing degree-days in SDMs at broad scales should consider how to better incorporate these local-scale processes (e.sg., including microclimatic variables) into SDMs.

Species' life history strategies and phenological traits could also influence the importance of growing degree-days on species' distributions at broad scales. Traits such as facultative diapause, and overwintering stage can greatly affect how a species experiences climate (Bale & Hayward, 2010), while others such as voltinism, are closely tied to the length of the growing season (Forrest, Cross & Caradonna, 2019). For example, annual degree-days contributed more to suitability for *Choristoneura fumiferana* (i.e., eastern spruce budworm), a uni-voltine or semi-voltine species depending on climatic conditions (Marshall & Roe 2021) than *Amyelois transitella* (i.e., navel orangeworm), a multi-voltine species (Bragard et al., 2021; Table S8, Table S7, Table S8, Table S9). Given the reduces thermal sensitivity of metabolism during diapause and the role of non-thermal cues in diapause initiation and termination for many insects (Tauber & Tauber 1976; Bale & Hayward 2010), growing degree-days may play a less important role in predicting species' distributions for species that undergo diapause. However, given that some life history traits like voltinism change across a species' geographic distribution, it may be challenging to meaningfully incorporate their role in mediating this functional relationship at these scales.

5. Conclusions

Despite long knowing that climate is important in limiting insect species distributions at broad scales (Merriam, 1894; Good, 1931; Gaston, 2003; Chuine, 2010), we still do not always know which climatic variables or seasons are the most limiting of species' distributions. My results were inconsistent with the hypothesis that growing degree-days play an important role in limiting the geographic distributions of native moth species in North America. My results also suggest that future broad scale SDMs of lepidopteran species distributions can use standard

BDTs to estimate growing degree-days without compromising their predictive performance, and that species-specific estimates from lab experiments are not required.

To improve the predictive performance of SDMs, future studies should focus on the scalability of lab-measured species' traits by considering biological thresholds that are directly measured (e.g., CT_{min}, CT_{max}) rather than estimated (e.g., BDT) and traits that are more predictive at broad scales (e.g., temperature annual range). Given the variation in life history strategies even within a single taxonomic group like moths, a single physiological threshold may not be equally predictive across all species. More work is needed to determine how we can refine our predictions for species with different life histories so that we can maximize our ability to accurately predict how species ranges will shift under a changing climate.

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Tables

Table 1. Summary data for the species included in the analysis (n=30), in alphabetical order of genus. Shown is the family, species-specific base development temperature (BDT), number of occurrence records used in the species distribution models, and size of geographic range based on the minimum convex polygon.

Genus	**Species**	**Family**	**Number of records**	**BDT (°C)**	**Range size (km^2)**
Amyelois	*transitella*	Pyralidae	12	12.8	181,851.60
Anticarsia	*gemmatalis*	Erebidae	75	11	448,215.86
Argyrotaenia	*citrana*	Tortricidae	52	6.1	40,782.14
Argyrotaenia	*velutinana*	Tortricidae	149	8.1	288,623.26
Choristoneura	*fumiferana*	Tortricidae	114	8	892,712.52
Choristoneura	*rosaceana*	Tortricidae	297	10.5	915,803.42
Cydia	*latiferreana*	Tortricidae	134	10.55	737,671.66
Diatraea	*grandiosella*	Crambidae	11	9.8	62,056.89
Egira	*curialis*	Noctuidae	113	7.6	268,623.25
Hemileuca	*oliviae*	Saturniidae	39	12.5	56,03.88
Hyphantria	*cunea*	Erebidae	386	10.8	1,022,024.60
Lacanobia	*subjuncta*	Noctuidae	130	9.5	757,955.53
Mamestra	*configurata*	Noctuidae	81	5	265,706.08
Manduca	*sexta*	Sphingidae	241	10	829,359.50
Nomophila	*nearctica*	Pyralidae	247	10.9	1,223,035.66
Orgyia	*pseudotsugata*	Lymantriidae	46	8.2	235,851.75
Orthosia	*hibisci*	Noctuidae	281	3	1,106,040.64
Pandemis	*pyrusana*	Tortricidae	18	5	176,283.30
Papaipema	*nebris*	Noctuidae	57	4.8	226,731.82
Pediasia	*trisecta*	Crambidae	149	10	716,929.09
Peridroma	*saucia*	Noctuidae	315	4.6	1,109,329.01
Plathypena	*scabra*	Noctuidae	276	8.5	471,164.11
Platynota	*flavedana*	Tortricidae	77	9	203,810.25
Podosesia	*syringae*	Sesiidae	65	10	541,191.23
Pseudaletia	*unipuncta*	Noctuidae	374	8.1	1,163,029.86
Rhyacionia	*frustrana*	Tortricidae	41	9.4	143,003.18
Simyra	*henrici*	Noctuidae	49	10.1	473,172.07
Spodoptera	*frugiperda*	Noctuidae	145	13.65	676,187.80
Synanthedon	*exitiosa*	Sesiidae	93	10	907,974.15
Zeiraphera	*canadensis*	Tortricidae	17	5.32	340,236.22

Table 2. Climatic variables considered in the modelling process. BIO1-BIO19 are bioclimatic variables as defined by WorldClim (Fick & Hijmans, 2017). These annual variables were derived from monthly precipitation and temperature values. All 20 variables were included in the variance inflation factor (VIF) analysis (threshold = 5) to assess collinearity amongst climatic variables. Bolded variables (n=7) passed the VIF analysis and were included in the Maxent models for all species.

BIO1 = Annual Mean Temperature
BIO2 = Mean Diurnal Range (Mean of monthly (max temp - min temp))
BIO3 = Isothermality (BIO2/BIO7) (×100)
BIO4 = Temperature Seasonality (standard deviation ×100)
BIO5 = Max Temperature of Warmest Month
BIO6 = Min Temperature of Coldest Month
BIO7 = Temperature Annual Range (BIO5-BIO6)
BIO8 = Mean Temperature of Wettest Quarter
BIO9 = Mean Temperature of 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 (Coefficient of Variation)
BIO16 = Precipitation of Wettest Quarter
BIO17 = Precipitation of Driest Quarter
BIO18 = Precipitation of Warmest Quarter
BIO19 = Precipitation of Coldest Quarter
Annual degree-days* = accumulated degrees across the year above a base developmental temperature threshold

* Three variations: (1) based on species-specific BDT; (2) based on a BDT of 5°C; (3) based on a BDT of 10°C

Table 3. Summary of the contribution of each climate variable to the three species distribution models (hybrid, DD5, DD10), ordered by rank in the hybrid model. Shown for each variable is the percentage of species for which this variable was the first contributor, mean and standard error of the percent contribution across species. Temperature annual range (bolded) was the highest contributor for the greatest proportion of species. I also highlight the ranking of growing degree days (bolded) as I hypothesized it to be the best contributor. Details about variables are found in Table 2. The ranking based on the first contributor proportion and mean percent contribution of the seven environmental variables in the hybrid model is depicted in Figure 2.

		Hybrid			DD5			DD10		
Variable	Ranking	First contributor percentage (n=30)	Percent Contribution	SE	First contributor percentage (n=30)	Percent Contribution	SE	First contributor percentage (n=26)	Percent Contribution	SE
Temperature Annual Range	**1**	**50.00%**	**33.97**	**4.33**	**50.00%**	**33.15**	**4.31**	**53.85%**	**33.30**	**4.78**
Precipitation Seasonality	2	20.00%	15.21	2.38	20.00%	15.25	2.42	7.69%	13.32	2.08
Mean Temperature of Wettest Quarter	3	10.00%	11.86	2.34	6.67%	12.78	2.73	7.69%	13.56	2.79
Growing degree-days	**4**	**6.67%**	**10.91**	**1.63**	**6.67%**	**10.42**	**1.57**	**7.69%**	**11.10**	**1.73**
Mean Diurnal Range	4	6.67%	10.98	1.73	10.00%	11.02	1.76	11.54%	11.46	2.02
Precipitation of Warmest Quarter	5	3.33%	8.45	1.57	3.33%	8.92	1.77	3.85%	9.16	1.88
Precipitation of Wettest Month	6	3.33%	8.62	1.46	3.33%	8.45	1.48	7.69%	8.09	1.59

Table 4. Strength of linear correlations and associated p values between the experimental quality metrics and the measures of model performance. Strength of the relationships was determined using the Pearson correlation coefficient (r). The two measures of experimental quality were the number of constant temperatures measured (NTM) and the difference between the lowest temperature treatment measured in the experiment (LTM) and the BDT used to calculate annual degree-days in the hybrid model (LTM-BDT; °C). The two measures of model performance were the AUC score of the hybrid model and the contribution of growing degree-days to the hybrid model.

		Experimental quality metrics			
		NTM		LTM-BDT (°C)	
		r	p	r	p
Measures of model accuracy	AUC	-0.109	0.64	-0.342	0.19
	Percent contribution of growing degree-days	-0.189	0.41	0.052	0.85

Figures

Figure 1. The theoretical developmental curve, showing changes in the developmental rate (DR) of an ectotherm at different temperatures (t; in °C or °F). The red dotted line represents the slope of the line from a linear model used to estimate the lower or base development temperature (BDT, or x-intercept). The critical thermal minimum and maximum (CT_{min} and CT_{max}) are a species' lower and upper developmental limits, respectively, while t_{opt} indicates a species' optimal developmental temperature.

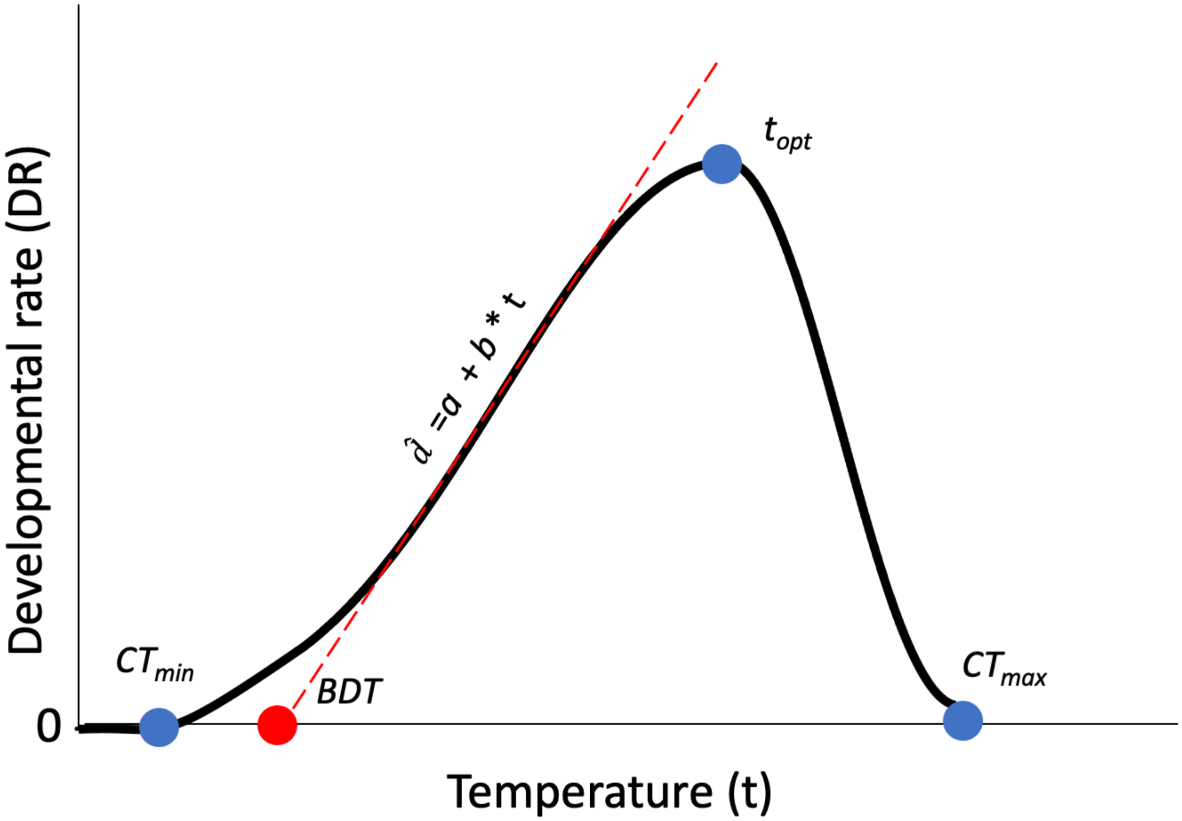


Figure 2. Relative importance of climatic variables (n=7) in the hybrid model. Shown is the rank order of variables based on the proportion of species for which each climatic variable was the first contributor to the model (a) and the mean percent contribution of the climatic variables across all species (b). Error bars in panel b are SE (n=30). Raw values are shown in Table 3.

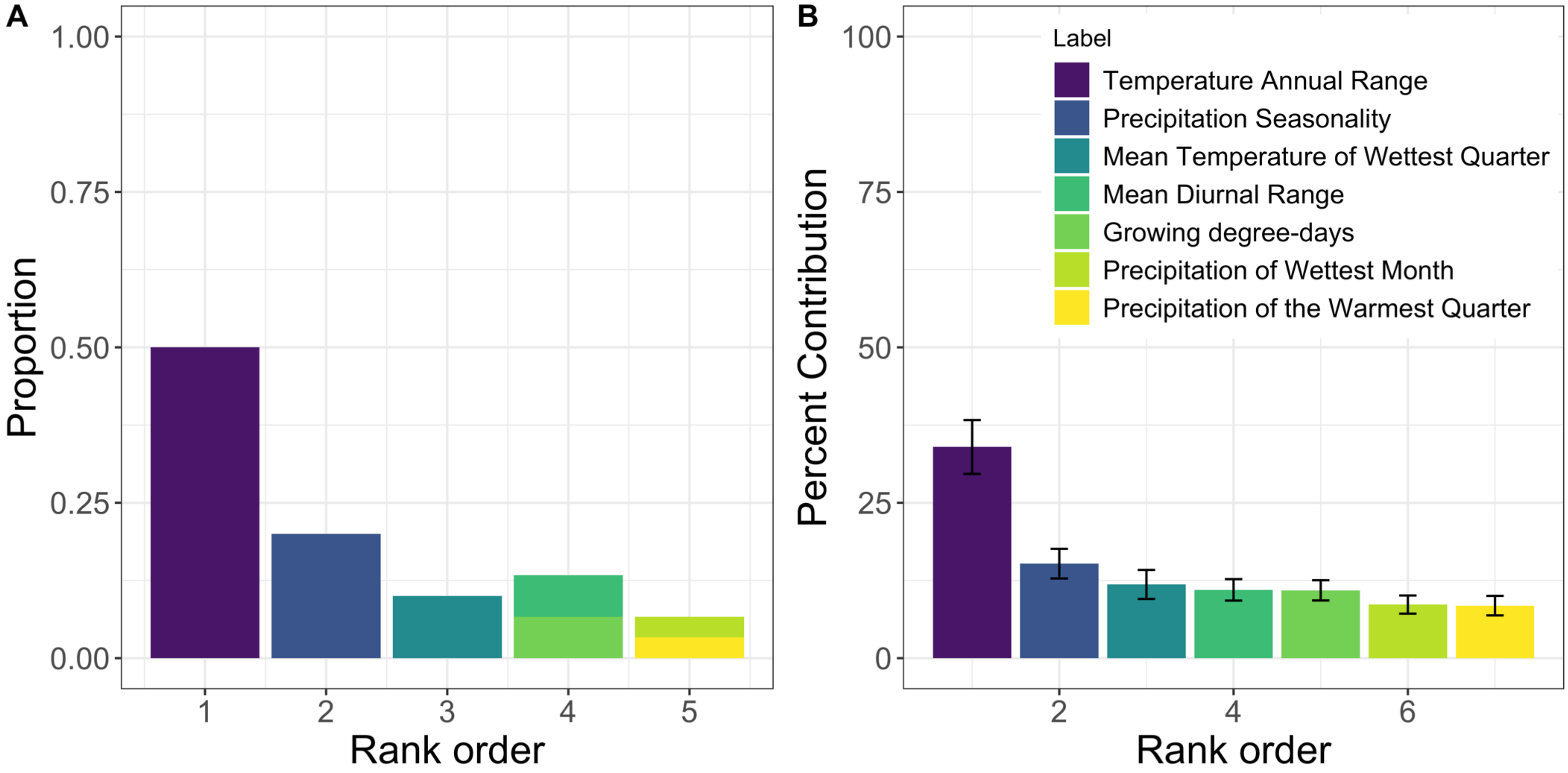


Figure 3. Comparison of the percent difference in AUC (a) and difference in percent contribution of growing degree-days (b) between the hybrid and correlative (DD5) model for each species (n=30). Species are listed in decreasing order of absolute percent difference in AUC ((correlative AUC – hybrid AUC) / hybrid AUC). Negative values indicate that the hybrid model performed better than the correlative, while positive values indicate that the correlative model performed better than the hybrid. The difference in percent contribution of growing degree-days was calculated as: percent contribution in correlative model – percent contribution in hybrid model. Negative values indicate that growing degree-days contributed more to model suitability in the hybrid model, while positive values indicate that growing degree-days contributed more to model suitability in the correlative model.

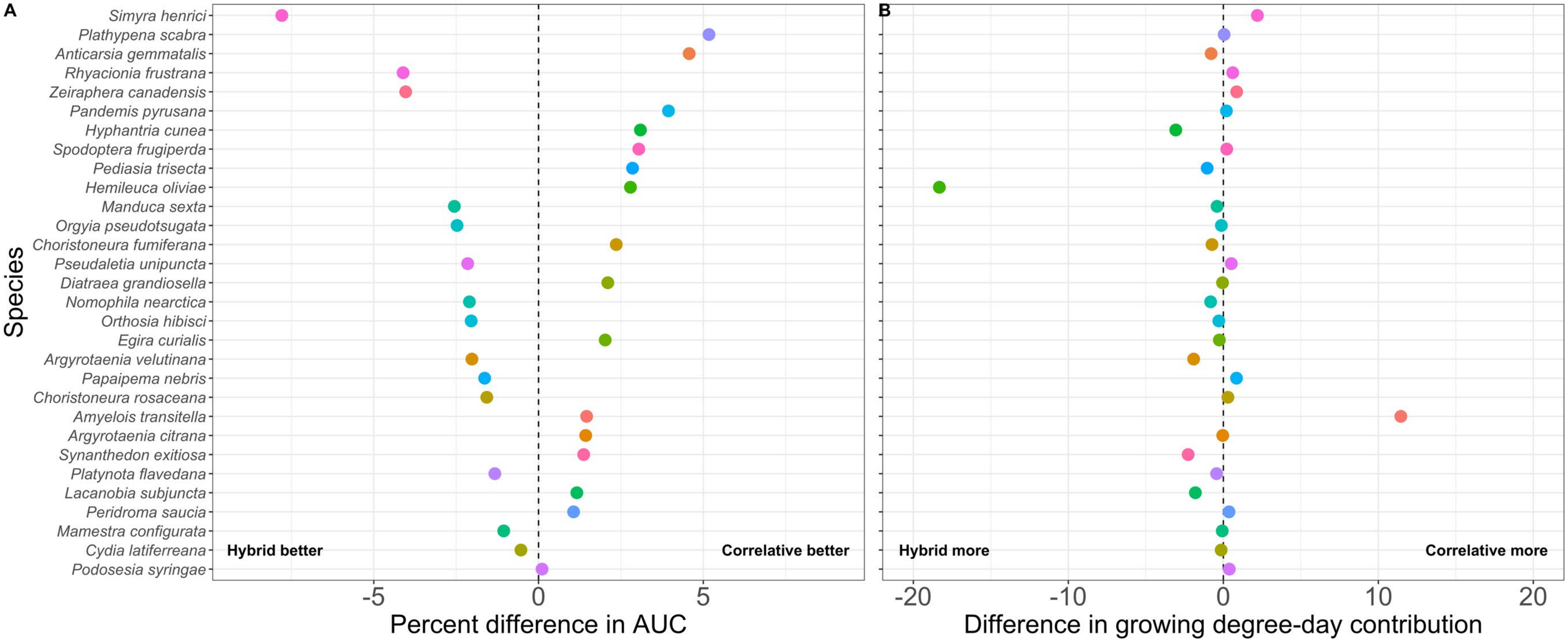
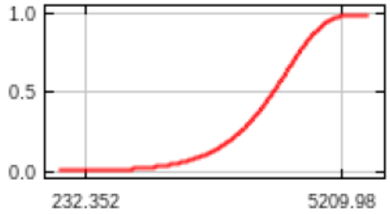
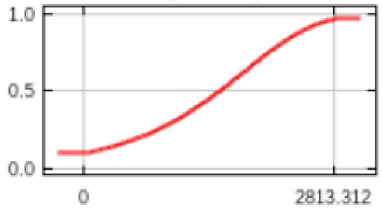
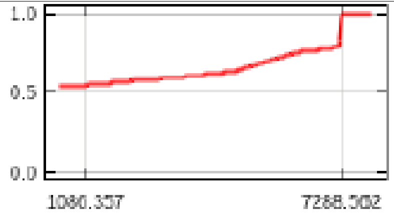
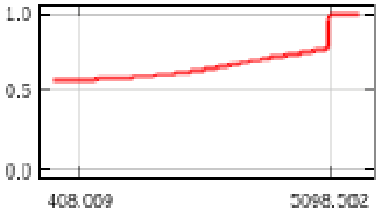
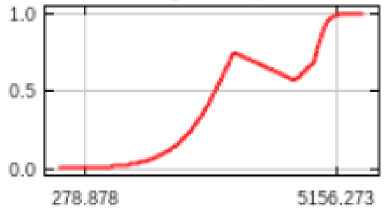
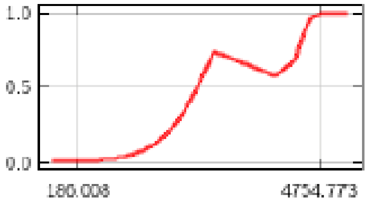
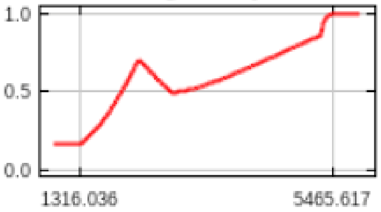
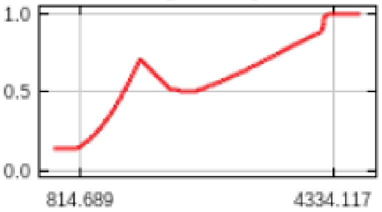
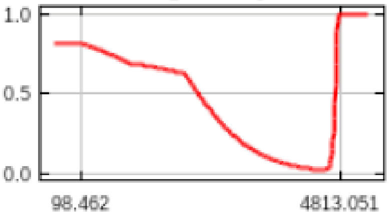
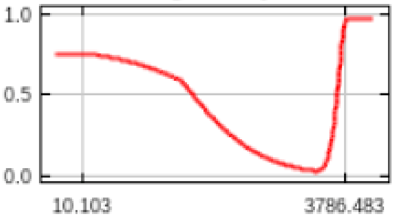
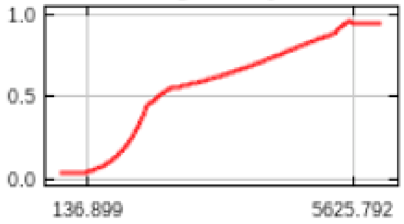
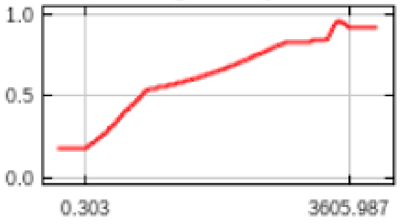
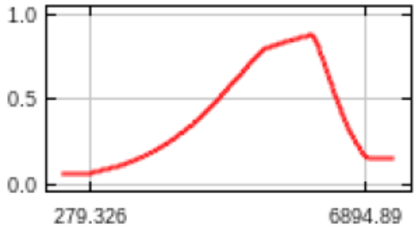
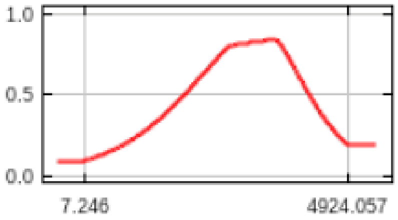
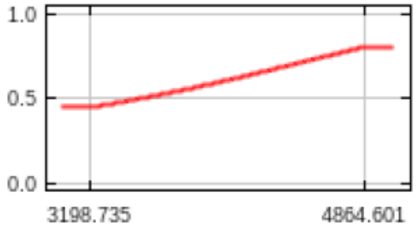
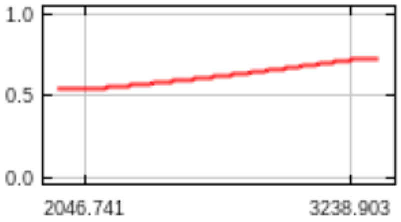
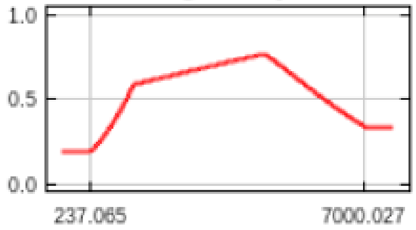
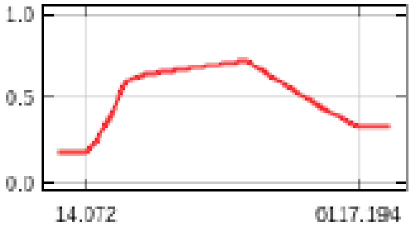
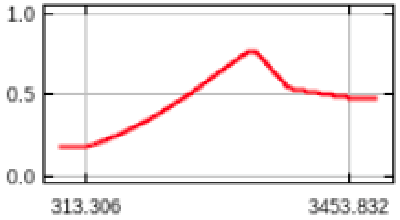
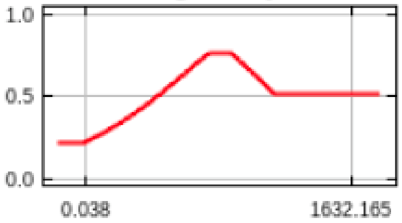
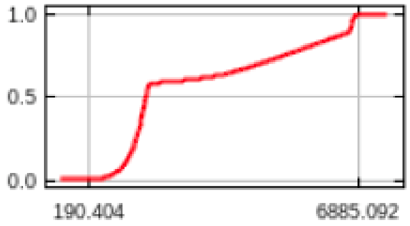
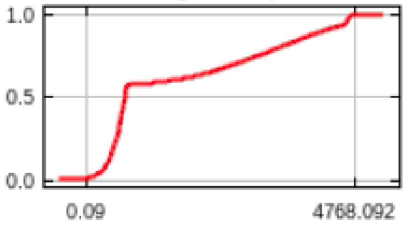
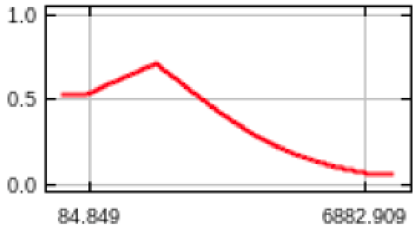
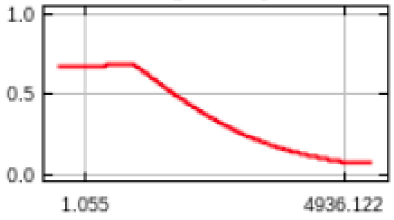
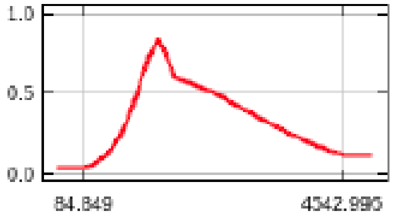
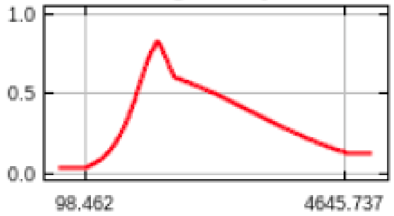
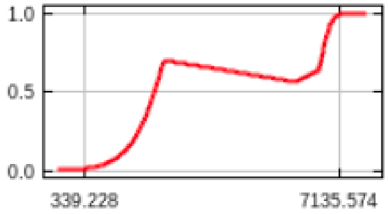
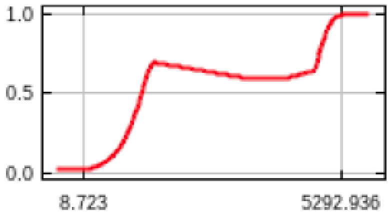
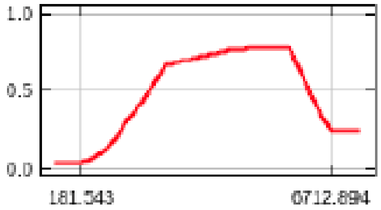
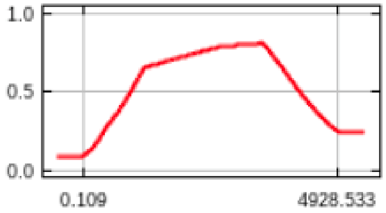
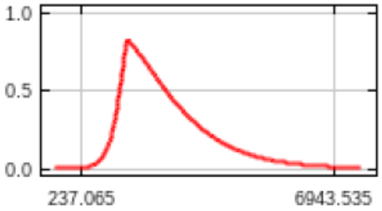
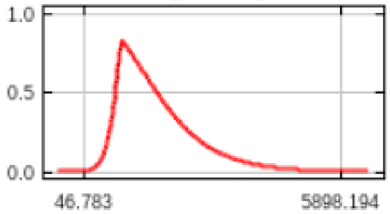
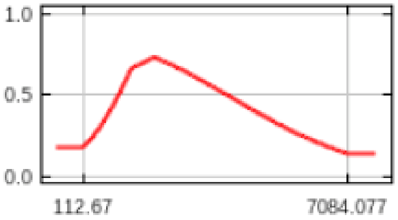
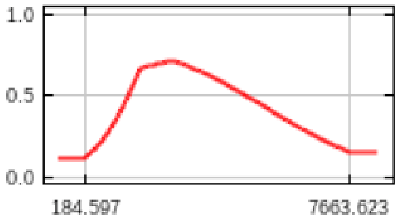
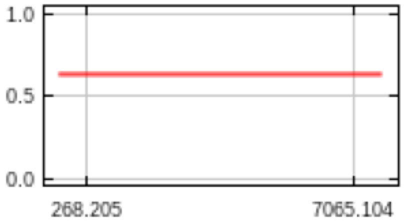
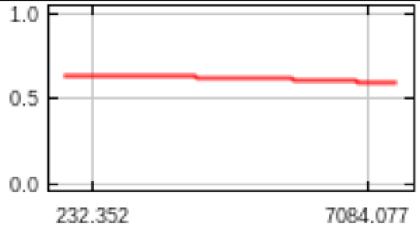
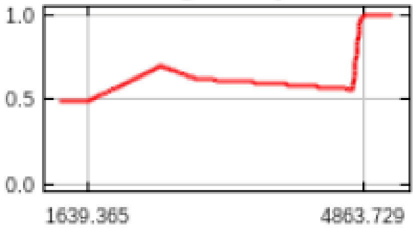
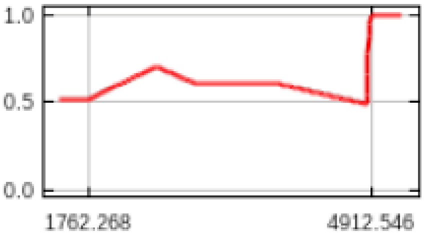
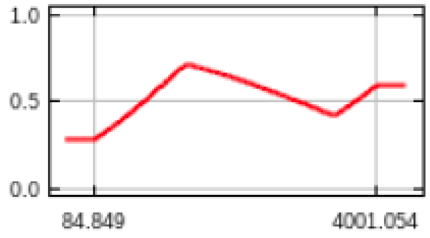
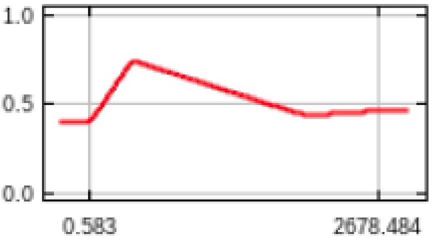
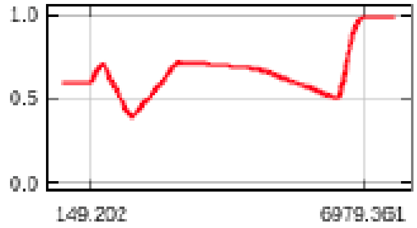
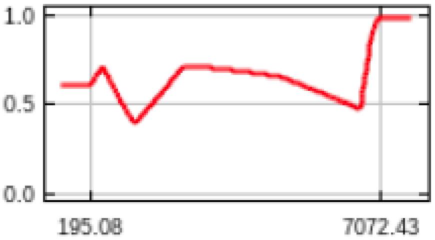
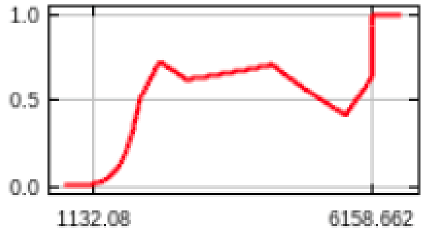
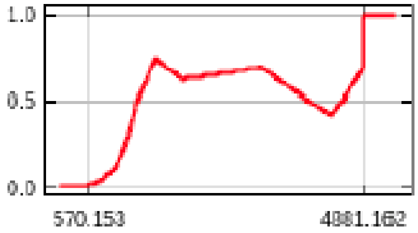
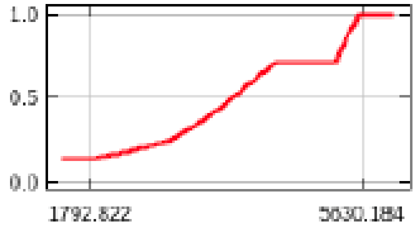
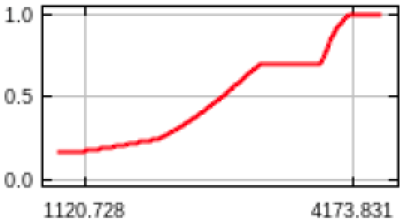
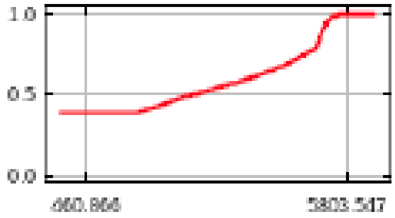
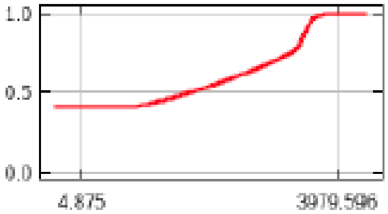
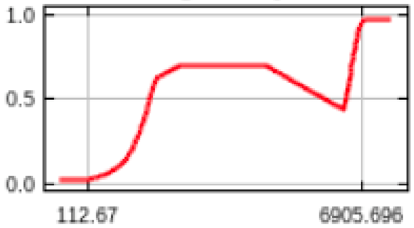
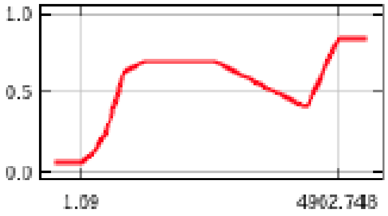

A
B
Species
Simyra henrici
Plathypena scabra
Anticarsia gemmatalis
Rhyacionia frustrana
Zeiraphera canadensis
Pandemis pyrusana
Hyphantria cunea
Spodoptera frugiperda
Pediasia trisecta
Hemileuca oliviae
Manduca sexta
Orgyia pseudotsugata
Choristoneura fumiferana
Pseudaletia unipuncta
Diatraea grandiosella
Nomophila nearctica
Orthosia hibisci
Egira curialis
Argyrotaenia velutinana
Papaipema nebris
Choristoneura rosaceana
Amyelois transitella
Argyrotaenia citrana
Synanthedon exitiosa
Platynota flavedana
Lacanobia subjuncta
Peridroma saucia
Mamestra configurata
Cydia latiferreana
Podosesia syringae
Hybrid better
Correlative better
-5
0
5
Percent difference in AUC
Hybrid more
Correlative more
-20
-10
0
10
20
Difference in growing degree-day contribution

Figure 4. Response curves based on the predicted probability of presence as a function of growing degree-days (n=30). Axes labels are the same across species. Figures in the first column are from the DD5 models and the second column are from the hybrid models. Each row is a species. Figures were produced by Maxent and models were built using only annual degree-days. days.

	DD5	**Hybrid**
Amyelois transitella		
Anticarsia gemmatalis		
Argyrotaenia citrana		
Argyrotaenia velutinana		
Choristoneura fumiferana		

Choristoneura rosaceana		
Cydia latiferreana		
Diatraea grandiosella		
Egira curialis		
Hemileuca oliviae		
Hyphantria cunea		
Lacanobia subjuncta		

Mamestra configurata		
Manduca sexta		
Nomphila nearctica		
Orgyia pseudotsugata		
Orthosia hibisci		
Pandemis pryusana		
Papaipema nebris		

Pediasia trisecta		
Peridroma saucia		
Plathypena scabra		
Platynota flavedana		
Podosesia syringae		
Pseudaletia unipuncta		

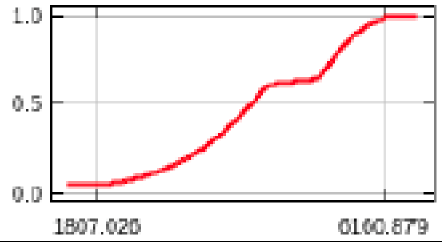
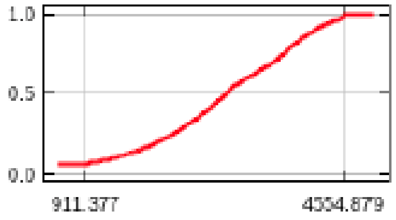
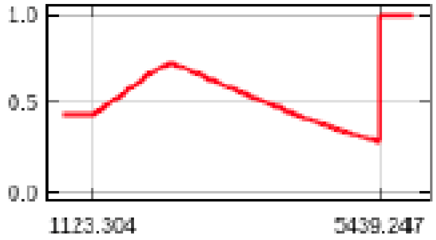
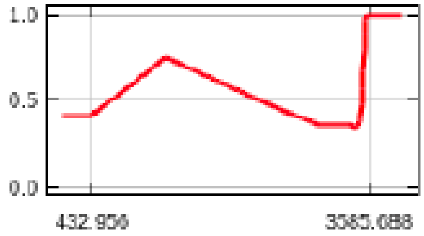
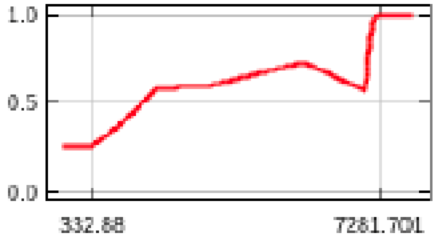
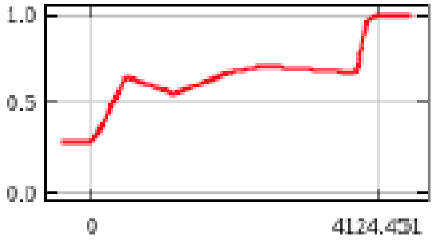
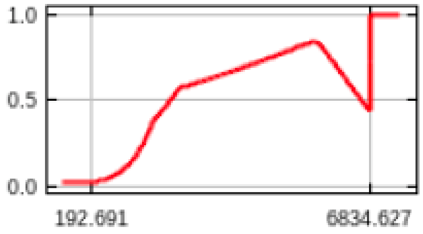
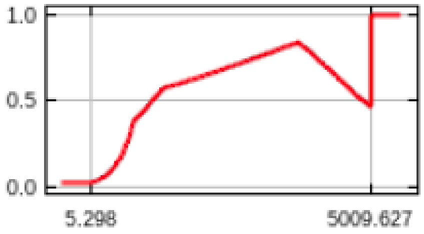
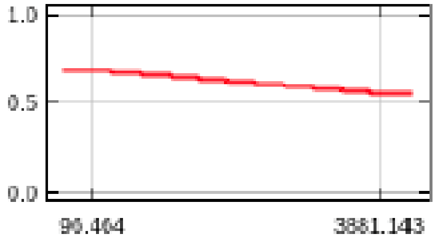
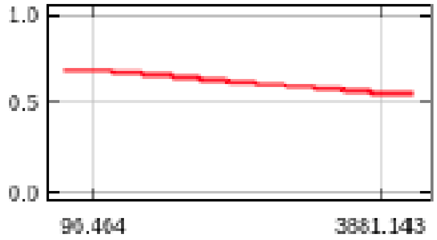
Rhyacionia frustrana		
Simyra henrici		
Spodoptera frugiperda		
Synanthedon exitiosa		
Zeiraphera canadensis		

Figure 5. Correlations between the absolute difference between the BDT used in the two models (i.e., species-specific BDT (°C) - 5°C) and; a) the difference in contribution of growing degree-days (GDD) between the hybrid and correlative model (n=30) and; b) percent difference in AUC between the hybrid and correlative models (n=30). The difference in percent contribution of growing degree-days was calculated as: percent contribution in correlative model – percent contribution in hybrid model. The percent difference in AUC (Diff AUC) was calculated using: [(correlative AUC – hybrid AUC)/hybrid AUC] *100. Shown are data points at the species level, and associated Pearson correlation coefficients (r) and p values.

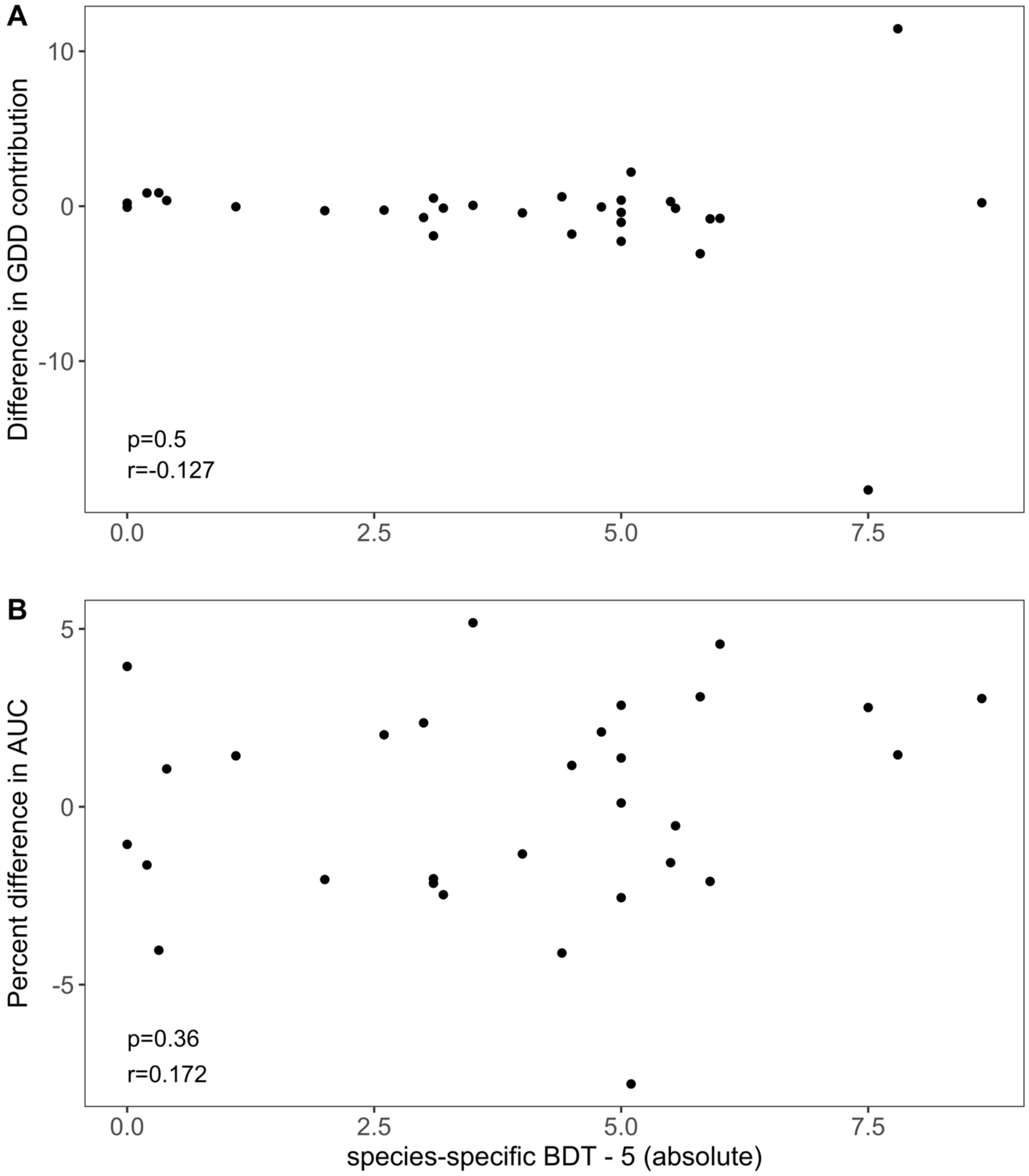
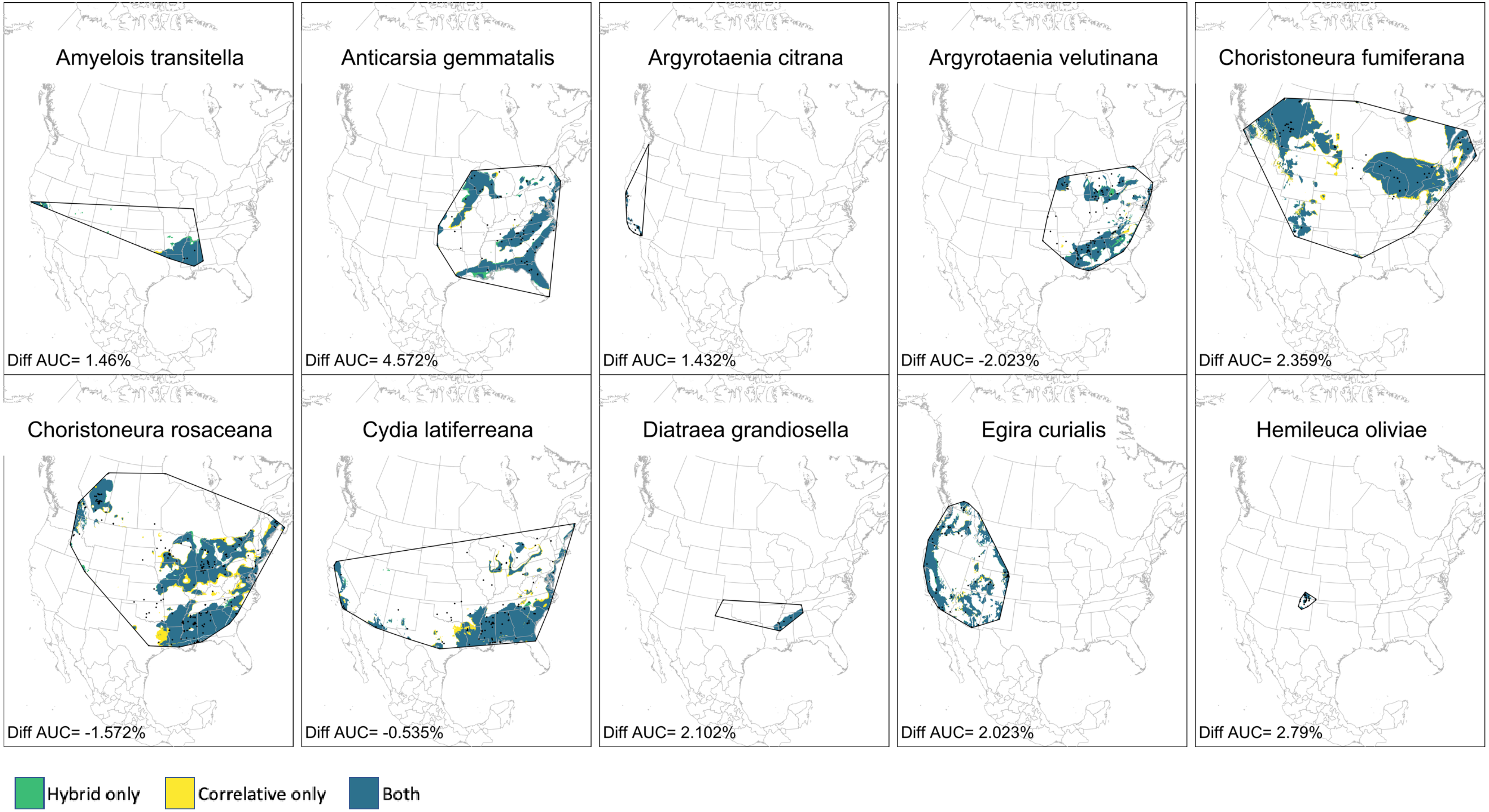
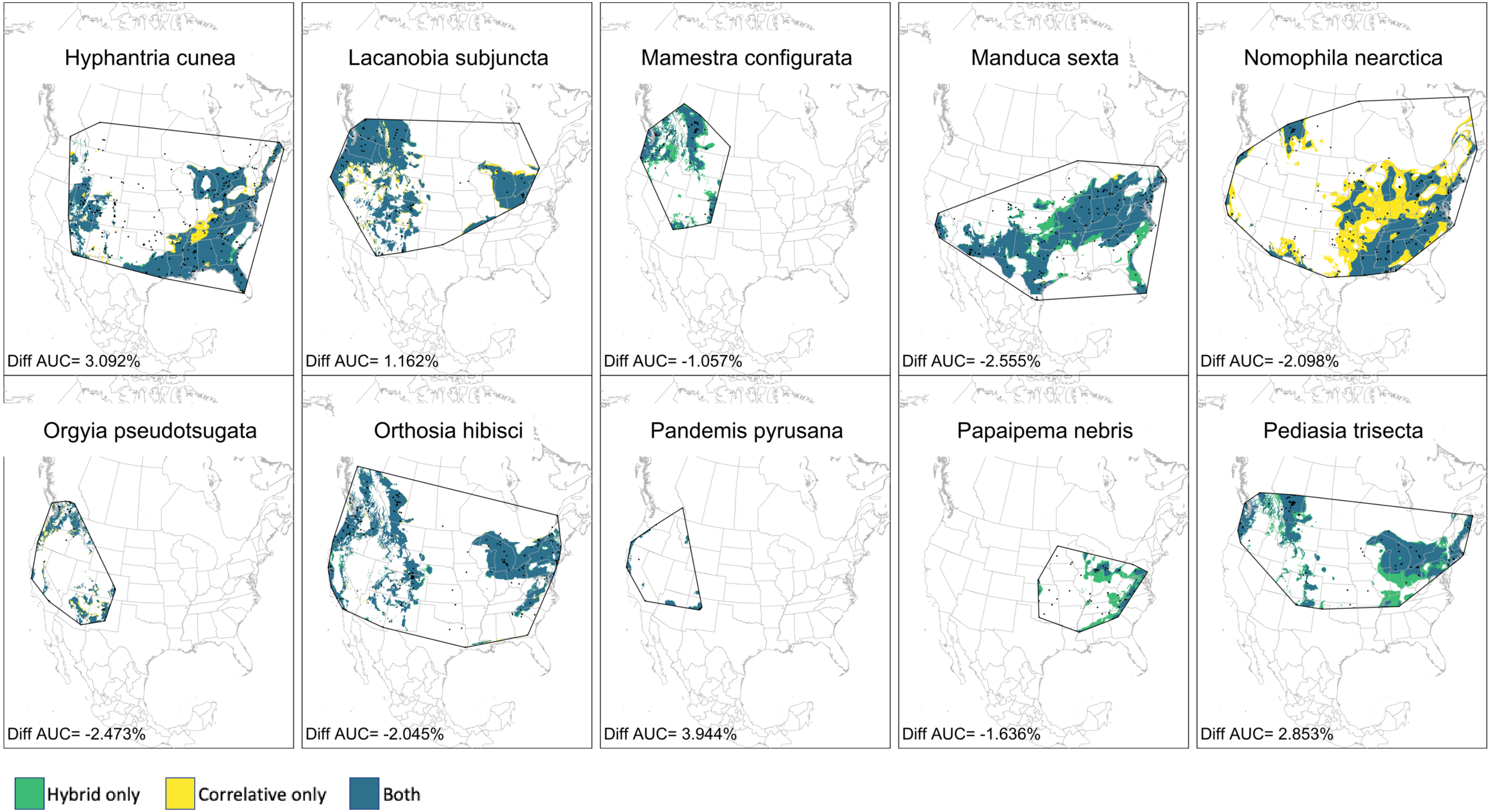


Figure 6. Area predicted as suitable by the DD5 and hybrid model for each species (n=30). Species are presented in alphabetical order. Shown in blue is the concordance in suitability predictions between the two models. The green and yellow represent areas predicted as suitable by only the hybrid or correlative model, respectively. The solid black line is the species' MCP, and the black points are occurrence records. The percent difference in AUC (Diff AUC) was calculated using: [(correlative AUC – hybrid AUC)/hybrid AUC] *100. Positive values indicate that the correlative value was larger than the hybrid, and vice versa.


Amyelois transitella
Diff AUC= 1.46%
Anticarsia gemmatalis
Diff AUC= 4.572%
Argyrotaenia citrana
Diff AUC= 1.432%
Argyrotaenia velutinana
Diff AUC= -2.023%
Choristoneura fumiferana
Diff AUC= 2.359%
Choristoneura rosaceana
Diff AUC= -1.572%
Cydia latiferreana
Diff AUC= -0.535%
Diatraea grandiosella
Diff AUC= 2.102%
Egira curialis
Diff AUC= 2.023%
Hemileuca oliviae
Diff AUC= 2.79%
🟩 Hybrid only
🟨 Correlative only
🟦 Both


Hyphantria cunea
Lacanobia subjuncta
Mamestra configurata
Manduca sexta
Nomophila nearctica
Diff AUC= 3.092%
Diff AUC= 1.162%
Diff AUC= -1.057%
Diff AUC= -2.555%
Diff AUC= -2.098%
Orgyia pseudotsugata
Orthosia hibisci
Pandemis pyrusana
Papaipema nebris
Pediasia trisecta
Diff AUC= -2.473%
Diff AUC= -2.045%
Diff AUC= 3.944%
Diff AUC= -1.636%
Diff AUC= 2.853%
🟩 Hybrid only
🟨 Correlative only
🟦 Both

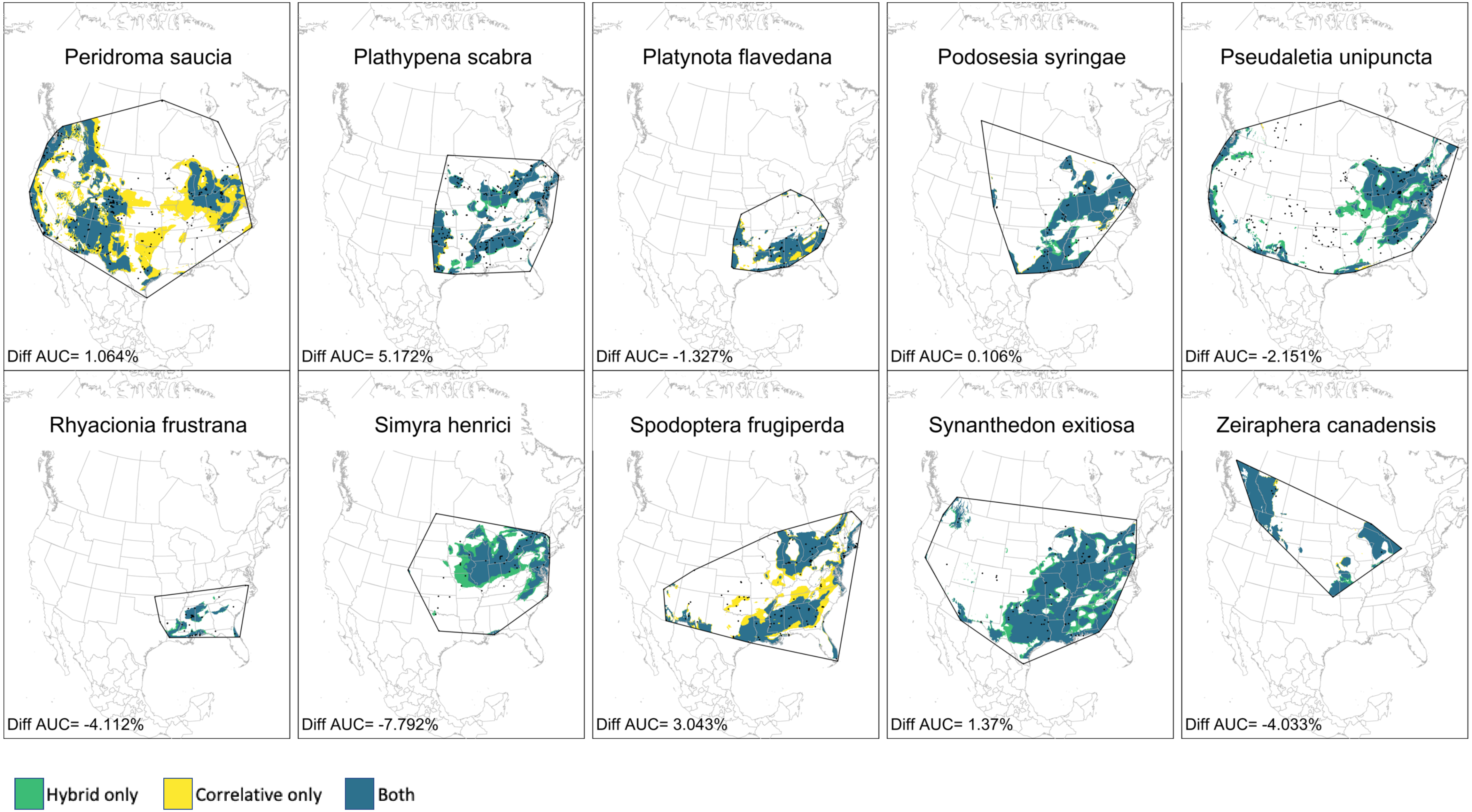
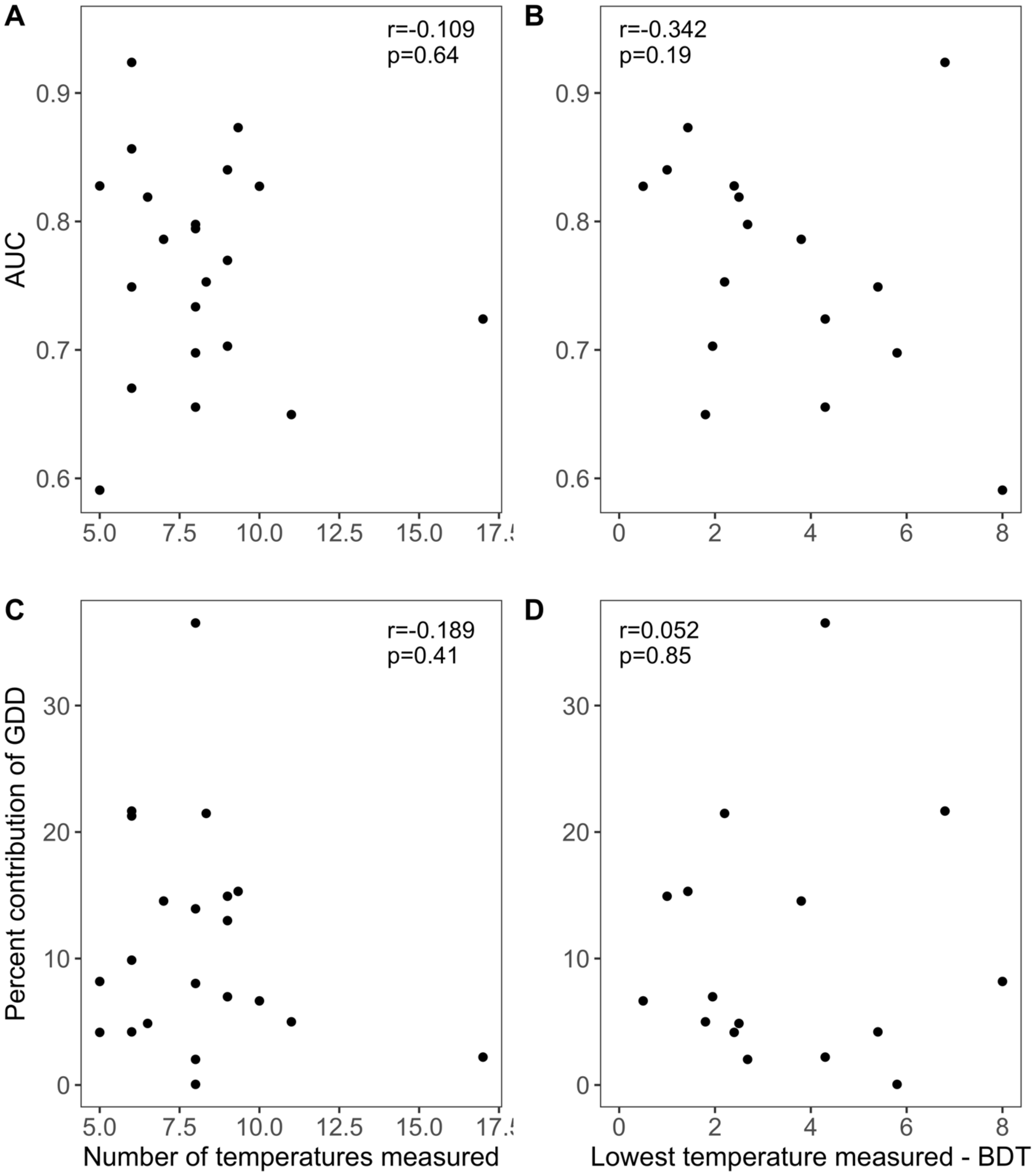

Peridroma saucia
Diff AUC= 1.064%
Plathypena scabra
Diff AUC= 5.172%
Platynota flavedana
Diff AUC= -1.327%
Podosesia syringae
Diff AUC= 0.106%
Pseudaletia unipuncta
Diff AUC= -2.151%
Rhyacionia frustrana
Diff AUC= -4.112%
Simyra henrici
Diff AUC= -7.792%
Spodoptera frugiperda
Diff AUC= 3.043%
Synanthedon exitiosa
Diff AUC= 1.37%
Zeiraphera canadensis
Diff AUC= -4.033%
Hybrid only
Correlative only
Both

Figure 7. Correlations between metrics of experimental quality and model performance (n=21) for panels A, C, n=16 for panels B,D). Shown in the first column (panels A, C) is the number of constant temperatures included in the experiment and in the second column (panels B, D) is the difference between the lowest temperature treatment in the experiment and the BDT used to calculate annual degree-days in the hybrid model (°C). The influence of experimental quality on (A,B) the AUC of the hybrid model; and (C, D) the percent contribution of growing degree-days (GDD) to the hybrid model. For panels B & D, only species whose BDT was outside the experimental treatments (i.e., lowest temperature treatment - BDT > 0) were included. Shown are data points at the species level, and associated Pearson correlation coefficients (r) and p values.



Appendices

Table S1. Summary of species-specific base development temperatures used to calculate growing degree-days for hybrid models (from Jarošík et al., (2011)), and the associated source studies. Data collected from the source studies included a) type of experiment (i.e., field (F), lab (L) or unknown (U)), lowest temperature measured (LTM), number of constant temperature treatments measured (NTM) and number of life stages measured (LS).

Species	**BDT**	**Type of experiment**	**LTM**	**NTM**	**LS**	**Author**	**Year**	**Name**
Amyelois transitella	12.8	F	NA	NA	NA	Sanderson, J. P., M. M. Barnes, et al.	1989	Synthesis and validation of a degree-day model for navel orangeworm (Lepidoptera: Pyralidae) development in California almond orchards
Anticarsia gemmatalis	11	L	12.8	11	2	Johnson, D. W., C. S. Barfield and G. E. Allen	1983	Temperature-dependent developmental model for the velvetbean caterpillar (Lepidoptera: Noctuidae)
Argyrotaenia citrana	6.1	U	NA	NA	NA	Bettiga, L. J., H. Kido, and N. F. McCalley	1992	Orange Tortrix
Argyrotaenia velutinana	8.1	L	5	8	3	Hawthorne D.J., Rock G.C., Stinner R.E.	1988	Redbanded leafroller (Lepidoptera: Tortricidae): thermal requirements for development and simulation of within-season phenology in North Carolina
Choristoneura fumiferana	8	F	NA	NA	NA	Lysyk, T. J.	1989	Stochastic model of eastern spruce budworm (Lepidoptera: Tortricidae) phenology on white spruce and balsam fir
Choristoneura rosaceana	10.5	L	13	6.5	3	Gangavalli, R. R. and M. T. AliNiazee	1985	Temperature requirements for development of the obliquebanded leafroller, Choristoneura rosaceana (Lepidoptera: Tortricidae)
Cydia latiferreana	10.55	U	NA	NA	NA	AliNiazee, M.T.	1983	A Degree-Day Method for Predicting the Filbertworm Emergence
Diatraea grandiosella	9.8	L	15.6	8	3	Whitworth, R.J. and Poston, F.L.	1979	A thermal unit accumulation system for the Southwestern Corn Borer
Egira curialis	7.6	L	10	5	2	Grafton Cardwell, E. E., G. H. Montez, et al.	2001	Lower developmental threshold and degree-day prediction of larval emergence of citrus cutworm, Egira curialis (Grote) (Lepidoptera: Noctuidae)
Hemileuca oliviae	12.5	L	10	6	1	Mendel M.J., Shaw P.B., Owens J.C., Richman D.B.	1989	Developmental rates, thresholds and thermal constants of the egg parasitoid Anastatus semiflavidus (Hymenoptera: Eupelmidae) and its host Hemileuca oliviae (Lepidoptera: Saturniidae).
Hyphantria cunea	10.8	L	13	8.33	3	Ito, Y., Miyashita, K. and Yamada, H.	1968	Biology of Hyphantria cunea Drury (Lepidoptera: Arctiidae) in Japan. VI. Effect of temperature in development of immature stages.
Lacanobia subjuncta	9.5	L	10	10	3	Doerr, M. D., J. F. Brunner, et al.	2002	Temperature-dependent development of Lacanobia subjuncta (Lepidoptera: Noctuidae).
Mamestra configurata	5	L	6	9	3	Bailey, C.G.	1976	Temperature effects on non-diapause development in Mamestra configurata (Lepidoptera: Noctuidae).
Manduca sexta	10	F	NA	NA	NA	Bossart, J. L. and S. H. Gage	1990	Biology and seasonal occurrence of Manduca quinquemaculata and M. sexta (Lepidoptera: Sphingidae) in southwestern Michigan

Nomophila nearctica	10.9	L	10	6	3	Miller, F. D., Jr. and J. V. Maddox	1991	Effect of temperature on development rate and survival of Nomophila nearctica (Lepidoptera: Pyralidae)
Orgyia pseudotsugata	8.2	L	15	6	3	Beckwith, R.C.	1982	Effects of constant laboratory temperatures on the Douglasfir tussock moth (Lepidoptera: Lymantriidae).
Orthosia hibisci	3	L	4.43	9.33	3	Judd, G.J.R, Cossentine, J.E., Gardiner M.G.T., and Thompson D.R	1994	Temperature-dependent development of the speckled green fruitworm, Orthosia hibisci Guenee (Lepidoptera: Noctuidae)
Pandemis pyrusana	5	U	NA	NA	NA	Brunner, J.	1991	Leafroller pests of fruit crops in Washington State
Papaipema nebris	4.8	L	12.8	5	3	Levine, E.	1983	Temperature requirements for development of the Stalk Borer, Papaipema nebris (Lepidoptera: Noctuidae)
Pediasia trisecta	10	F	NA	NA	NA	Tolley, M. P. and W. H. Robinson	1986	Seasonal abundance and degree-day prediction of sod webworm (Lepidoptera: Pyralidae) adult emergence in Virginia
Peridroma saucia	4.6	L	10	6	3	Shields E.J.	1983	Development rate of variegated cutworm (Lepidoptera: Noctuidae).
Plathypena scabra	8.5	L	12.8	8	3	Hammond, R. B., F.L. Poston and L. P. Pedigo	1979	Growth of the green cloverworm and a thermal-unit system for development.
Platynota flavedana	9	L	12.8	7	3	David, P. J. , Horsburgh, R. L. , Holtzman, G. I.	1989	Development of Platynota flavedana and P. idaeusalis (Lepidoptera: Tortricidae) at constant temperatures in the laboratory
Podosesia syringae	10	F	NA	NA	NA	Potter, D. A. and G. M. Timmons	1983	Forecasting emergence and flight of the lilac borer (Lepidoptera: Sessiidae) based on pheromone trapping and degree-day accumulations
Pseudaletia unipuncta	8.1	L	5	8	3	Guppy, J.C.	1969	Some effects of temperature on the immature stages of the armyworm, Pseudaletia unipuncta (Lepidoptera: Noctuidae), under controlled conditions.
Rhyacionia frustrana	9.4	L	9	9	2	Haughen, D. A. & F. M. Stephen	1984	Development rates of Nantucket Pine Tip Moth, Ryhacionia frustrana (Comstock) (Lepidoptera: Torticidae), life stage in relation to temperature
Simyra henrici	10.1	L	14.4	17	3	Decker, G.C. and Maddox, J.V.	1971	Effect of temperature on rate of development and survival of Simyra henrici.
Spodoptera frugiperda	13.65	L	15.6	9	3	Barfield C.S., Mitchell, E.R. an Poe, S.L.	1978	A temperature-dependent model for fall armyworm development
Synanthedon exitiosa	10	U	NA	NA	NA	Johnson, D. T. and R. L. Mayes	1984	Studies of larval development and adult flight of the peachtree borer, Synanthedon exitiosa (Say), in Arkansas
Zeiraphera canadensis	5.32	L	8	8	3	Regiere, J. and J. J. Turgeon	1989	Temperature-dependent development of Zeiraphera canadensis and simulation of its phenology

Table S2. Environmental variables that passed the variance inflation factor (VIF) analysis (threshold =5) to assess collinearity, and the associated collinearity scores.

	BIO2	**BIO15**	**BIO7**	**Degree-days**	**BIO8**	**BIO13**	**BIO18**
Average	1.80	1.84	2.86	3.13	3.18	3.46	4.38
BDT used to calculate degree-days							
BDT = 5	1.88	1.83	2.86	3.51	3.17	3.52	4.49
BDT = 10	1.70	1.80	2.91	3.01	3.09	3.62	4.49
Amyelois transitella	1.75	1.87	2.73	2.64	3.13	3.30	4.19
Anticarsia gemmatalis	1.79	1.86	2.78	2.76	3.09	3.47	4.33
Argyrotaenia citrana	1.89	1.87	2.77	3.37	3.35	3.20	4.34
Argyrotaenia velutinana	1.80	1.79	2.83	3.24	3.27	3.38	4.16
Choristoneura fumiferana	1.81	1.84	2.83	3.24	3.20	3.37	4.26
Choristoneura rosaceana	1.78	1.84	2.86	2.94	3.24	3.57	4.38
Cydia latiferreana	1.77	1.85	2.81	2.92	3.15	3.52	4.56
Diatraea grandiosella	1.79	1.80	2.76	3.02	3.16	3.34	4.17
Egira curialis	1.81	1.79	2.84	3.21	3.21	3.32	4.18
Hemileuca oliviae	1.70	1.84	2.90	2.70	3.08	3.74	4.62
Hyphantria cunea	1.73	1.83	2.86	2.94	3.12	3.63	4.55
Lacanobia subjuncta	1.76	1.91	2.86	3.00	3.07	3.37	4.31
Mamestra configurata	1.86	1.96	2.83	3.54	3.23	3.22	4.29
Manduca sexta	1.77	1.76	2.94	3.10	3.30	3.48	4.33
Nomophila nearctica	1.72	1.82	2.88	2.96	3.20	3.58	4.50
Orgyia pseudotsugata	1.83	1.90	2.85	3.02	3.02	3.59	4.59
Orthosia hibisci	2.00	1.77	2.96	3.84	3.39	3.52	4.28
Pandemis pyrusana	1.83	1.89	2.97	3.59	3.21	3.48	4.39
Papaipema nebris	1.94	1.96	3.04	3.50	3.23	3.62	4.45
Pediasia trisecta	1.81	1.84	2.91	3.05	3.22	3.51	4.37
Peridroma saucia	1.91	1.85	2.93	3.60	3.25	3.44	4.35
Plathypena scabra	1.84	1.82	2.87	3.25	3.25	3.48	4.47
Platynota flavedana	1.77	1.85	2.82	3.01	3.08	3.47	4.44
Podosesia syringae	1.78	1.84	2.89	2.93	3.11	3.53	4.42
Pseudaletia unipuncta	1.77	1.81	2.81	2.91	3.14	3.58	4.58
Rhyacionia frustrana	1.72	1.83	2.84	3.10	3.23	3.16	4.05
Simyra henrici	1.78	1.81	2.88	3.05	3.14	3.60	4.54
Spodoptera frugiperda	1.75	1.84	2.73	2.56	3.13	3.40	4.42
Synanthedon exitiosa	1.75	1.90	2.78	2.94	3.20	3.54	4.63
Zeiraphera canadensis	1.91	1.81	2.83	3.54	3.18	3.20	4.10

Table S3. Comparison of model accuracy for the full and reduced models for data-poor species (i.e., < 35 occurrence records). Full models included all seven environmental variables that passed VIF analysis. Reduced models included the two least correlated bioclimatic variables, plus annual degree-days.

DD5						
	Reduced			Full		
	AUC	TSS	kappa	AUC	TSS	kappa
Amyelois transitella	0.875	0.481	0.923	0.904	0.718	0.810
Diatraea grandiosella	0.408	-0.016	0.511	0.712	0.050	0.762
Pandemis pyrusana	0.790	0.463	0.965	0.933	0.599	0.900
Zeiraphera canadensis	0.680	0.165	0.762	0.766	0.481	0.766
DD10						
	Reduced			Full		
	AUC	TSS	kappa	AUC	TSS	kappa
Amyelois transitella	0.817	0.239	0.879	0.781	0.593	0.790
Diatraea grandiosella	0.474	-0.047	0.670	0.722	0.064	0.612
Pandemis pyrusana	0.785	0.463	0.832	0.914	0.579	0.949
Zeiraphera canadensis	0.696	0.131	0.747	0.726	0.429	0.794
Hybrid						
	Reduced			Full		
	AUC	TSS	kappa	AUC	TSS	kappa
Amyelois transitella	0.791	0.287	0.834	0.891	0.678	0.798
Diatraea grandiosella	0.455	-0.036	0.651	0.698	0.072	0.801
Pandemis pyrusana	0.791	0.432	0.975	0.898	0.596	0.961
Zeiraphera canadensis	0.739	0.231	0.736	0.798	0.586	0.795

Table S4. AUC scores for each species and model. Negative percent difference values indicate that the hybrid model was more accurate than the correlative model, and vice versa.

Species	**DD5 (correlative)**	**DD10 (correlative)**	**Hybrid**	**Percent difference***	
				DD5 and hybrid	**DD10 and hybrid**
Amyelois transitella^{x}	0.904	0.781	0.891	1.46%	-12.35%
Anticarsia gemmatalis	0.679	0.663	0.650	4.57%	2.11%
Argyrotaenia citrana	0.988	0.976	0.974	1.43%	0.20%
Argyrotaenia velutinana	0.719	0.702	0.734	-2.02%	-4.35%
Choristoneura fumiferana	0.860	0.837	0.840	2.36%	-0.35%
Choristoneura rosaceana	0.806	0.826	0.819	-1.57%	0.89%
Cydia latiferreana	0.841	0.820	0.846	-0.53%	-2.99%
Diatraea grandiosella^{x}	0.712	0.722	0.698	2.10%	3.54%
Egira curialis	0.844	0.855	0.828	2.02%	3.30%
Hemileuca oliviae	0.689	0.712	0.670	2.79%	6.27%
Hyphantria cunea	0.776	0.760	0.753	3.09%	0.92%
Lacanobia subjuncta	0.837	0.825	0.827	1.16%	-0.34%
Mamestra configurata	0.831	0.845	0.840	-1.06%	0.59%
Manduca sexta	0.717	NA	0.735	-2.56%	NA
Nomophila nearctica	0.839	0.839	0.857	-2.10%	-2.07%
Orgyia pseudotsugata	0.901	0.913	0.924	-2.47%	-1.13%
Orthosia hibisci	0.855	0.860	0.873	-2.05%	-1.49%
Pandemis pyrusana^{x}	0.933	0.914	0.898	3.94%	1.74%
Papaipema nebris	0.581	0.590	0.591	-1.64%	-0.08%
Pediasia trisecta	0.873	NA	0.849	2.85%	NA
Peridroma saucia	0.757	0.757	0.749	1.06%	1.03%
Plathypena scabra	0.689	0.656	0.655	5.17%	0.10%
Platynota flavedana	0.776	0.788	0.786	-1.33%	0.26%
Podosesia syringae	0.724	NA	0.723	0.11%	NA
Pseudaletia unipuncta	0.777	0.781	0.794	-2.15%	-1.63%
Rhyacionia frustrana	0.738	0.750	0.770	-4.11%	-2.60%
Simyra henrici	0.668	0.751	0.724	-7.79%	3.79%
Spodoptera frugiperda	0.724	0.714	0.703	3.04%	1.58%
Synanthedon exitiosa	0.747	NA	0.737	1.37%	NA
Zeiraphera canadensis^{x}	0.766	0.726	0.798	-4.03%	-8.94%
Average	**0.785**	**0.783**	**0.784**	**0.10%**	**-0.46%**
Reduced average**	**0.778**	**0.783**	**0.779**	**-0.01%**	**0.18%**

* Percent difference = (correlative score – hybrid score) / hybrid score *100

** Excludes species that have fewer than 35 occurrence records (indicated by ^{x}

Table S5. TSS scores for each species and each model type. Negative percent difference values indicate that the hybrid model was more accurate than the correlative model, and vice versa.

Species	**DD5 (Correlative)**	**DD10 (Correlative)**	**Hybrid**	**Percent difference***	
				DD5 and hybrid	**DD10 and hybrid**
Amyelois transitella$^{\times}$	0.718	0.593	0.678	5.90%	-12.59%
Anticarsia gemmatalis	0.258	0.262	0.213	21.04%	23.01%
Argyrotaenia citrana	0.865	0.843	0.822	5.21%	2.52%
Argyrotaenia velutinana	0.270	0.243	0.303	-10.65%	-19.83%
Choristoneura fumiferana	0.613	0.532	0.552	11.15%	-3.68%
Choristoneura rosaceana	0.399	0.432	0.438	-8.82%	-1.33%
Cydia latiferreana	0.489	0.492	0.506	-3.49%	-2.85%
Diatraea grandiosella$^{\times}$	0.050	0.064	0.072	-30.56%	-11.11%
Egira curialis	0.494	0.521	0.509	-2.95%	2.27%
Hemileuca oliviae	0.213	0.313	0.247	-13.80%	26.39%
Hyphantria cunea	0.376	0.350	0.354	6.04%	-1.13%
Lacanobia subjuncta	0.489	0.438	0.488	0.16%	-10.31%
Mamestra configurata	0.457	0.440	0.467	-2.08%	-5.79%
Manduca sexta	0.191	NA	0.261	-26.70%	NA
Nomophila nearctica	0.477	0.487	0.507	-5.82%	-4.03%
Orgyia pseudotsugata	0.647	0.618	0.637	1.61%	-2.90%
Orthosia hibisci	0.536	0.534	0.534	0.31%	-0.13%
Pandemis pyrusana$^{\times}$	0.599	0.579	0.596	0.56%	-2.80%
Papaipema nebris	-0.039	0.027	-0.023	68.23%	-216.93%
Pediasia trisecta	0.523	NA	0.480	9.02%	NA
Peridroma saucia	0.292	0.276	0.262	11.68%	5.29%
Plathypena scabra	0.201	0.215	0.183	10.02%	17.77%
Platynota flavedana	0.354	0.363	0.371	-4.63%	-2.16%
Podosesia syringae	0.355	NA	0.287	23.53%	NA
Pseudaletia unipuncta	0.319	0.303	0.347	-7.88%	-12.53%
Rhyacionia frustrana	0.288	0.283	0.336	-14.31%	-15.73%
Simyra henrici	0.146	0.270	0.296	-50.63%	-8.72%
Spodoptera frugiperda	0.255	0.268	0.261	-2.42%	2.69%
Synanthedon exitiosa	0.339	NA	0.383	-11.44%	NA
Zeiraphera canadensis$^{\times}$	0.481	0.429	0.586	-17.97%	-26.85%
Full average	**0.389**	**0.391**	**0.398**	**-1.32%**	**-10.82%**
Reduced average**	**0.377**	**0.387**	**0.385**	**0.09%**	**-10.37%**

* Percent difference = (correlative score – hybrid score) / hybrid score *100

** Excludes species that have fewer than 35 occurrence records (indicated by $^{\times}$)

Table S6. Kappa scores for each species and model. Negative percent difference values indicate that the hybrid model was more accurate than the correlative model, and vice versa.

Species	**DD5** **(Correlative)**	**DD10** **(Correlative)**	**Hybrid**	**Percent difference***	
				DD5 and hybrid	**DD10 and hybrid**
Amyelois transitella$^{\times}$	0.810	0.790	0.798	1.39%	-1.03%
Anticarsia gemmatalis	0.647	0.674	0.669	-3.25%	0.64%
Argyrotaenia citrana	0.704	0.706	0.641	9.89%	10.17%
Argyrotaenia velutinana	0.597	0.751	0.688	-13.18%	9.21%
Choristoneura fumiferana	0.649	0.566	0.579	12.11%	-2.32%
Choristoneura rosaceana	0.559	0.535	0.557	0.47%	-3.89%
Cydia latiferreana	0.611	0.504	0.545	12.15%	-7.55%
Diatraea grandiosella$^{\times}$	0.762	0.612	0.801	-4.89%	-23.65%
Egira curialis	0.731	0.692	0.783	-6.67%	-11.59%
Hemileuca oliviae	0.805	0.893	0.842	-4.43%	6.03%
Hyphantria cunea	0.575	0.572	0.514	11.93%	11.26%
Lacanobia subjuncta	0.699	0.702	0.703	-0.69%	-0.25%
Mamestra configurata	0.861	0.770	0.890	-3.24%	-13.50%
Manduca sexta	0.654	NA	0.598	9.38%	NA
Nomophila nearctica	0.570	0.422	0.456	25.11%	-7.48%
Orgyia pseudotsugata	0.671	0.733	0.801	-16.28%	-8.51%
Orthosia hibisci	0.528	0.544	0.499	5.74%	8.94%
Pandemis pyrusana$^{\times}$	0.900	0.949	0.961	-6.40%	-1.26%
Papaipema nebris	0.852	0.822	0.841	1.23%	-2.27%
Pediasia trisecta	0.648	NA	0.746	-13.16%	NA
Peridroma saucia	0.508	0.511	0.495	2.45%	3.18%
Plathypena scabra	0.663	0.557	0.651	1.85%	-14.50%
Platynota flavedana	0.804	0.849	0.904	-11.10%	-6.06%
Podosesia syringae	0.696	NA	0.502	38.50%	NA
Pseudaletia unipuncta	0.552	0.667	0.567	-2.78%	17.50%
Rhyacionia frustrana	0.846	0.819	0.819	3.28%	-0.07%
Simyra henrici	0.727	0.826	0.687	5.83%	20.28%
Spodoptera frugiperda	0.689	0.690	0.554	24.28%	24.49%
Synanthedon exitiosa	0.810	NA	0.736	10.01%	NA
Zeiraphera canadensis$^{\times}$	0.766	0.794	0.795	-3.58%	-0.06%
Average	**0.696**	**0.690**	**0.688**	**2.86%**	**0.30%**
Reduced average**	**0.679**	**0.673**	**0.664**	**3.82%**	**1.53%**

* Percent difference = (correlative score – hybrid score) / hybrid score *100

** Excludes species that have fewer than 35 occurrence records (indicated by $^{\times}$)

Table S7. Percent contribution of the seven environmental variables to each species in the hybrid model (n=30). Percent cont = the mean percent contribution of each environmental variable across the five rounds of internal cross validation. Bolded values indicate the top contributor for each species. The reduced average (n=26) excludes data-poor species (i.e., < 35 records, indicated by $^{\times}$).

	Temperature annual range		Precipitation seasonality		Mean temperature of the wettest quarter		Growing degree-days		Mean diurnal range		Precipitation of the warmest quarter		Precipitation of the wettest month	
Species	Percent cont	SE	Percent cont	SE	Percent cont	SE	Percent cont	SE	Percent cont	SE	Percent cont	SE	Percent cont	SE
Amyelois transitella$^{\times}$	**92.56**	5.313	0.00	0	0.98	0.969	6.43	5.3	0.03	0.03	0.00	0	0.00	0
Anticarsia gemmatalis	9.46	2.2303	**30.79**	3.246	12.70	1.526	5.00	1.58	3.19	1.33	16.70	4.61	22.17	4.72
Argyrotaenia citrana	**72.32**	2.2322	1.99	0.382	14.13	2.343	0.22	0.16	0.94	0.33	10.27	0.81	0.13	0.1
Argyrotaenia velutinana	**27.92**	3.8866	1.29	0.685	21.09	4.26	13.93	3.15	22.22	2.2	4.61	0.69	8.94	1.64
Choristoneura fumiferana	27.67	1.8656	7.21	1.852	8.94	2.183	**29.04**	1.45	4.47	1.61	22.67	1.98	0.02	0.01
Choristoneura rosaceana	**46.63**	0.4628	9.44	1.049	6.71	0.234	4.87	0.63	19.97	0.82	2.66	0.7	9.71	1.2
Cydia latiferreana	**64.09**	1.9461	3.04	0.663	5.95	0.489	5.84	0.69	3.89	1.25	1.18	0.3	16.01	1.37
Diatraea grandiosella$^{\times}$	34.65	21.622	0.00	0	**65.30**	21.66	0.05	0.05	0.00	0	0.00	0	0.00	0
Egira curialis	13.48	3.7922	8.55	1.683	**30.91**	2.211	4.16	1.02	15.54	2.14	5.47	0.63	21.89	1.99
Hemileuca oliviae	0.23	0.2288	18.06	4.702	13.29	7.013	21.27	4.99	7.85	3.45	**33.86**	5.86	5.44	1.1
Hyphantria cunea	**41.04**	3.5835	20.98	2.138	2.01	0.641	21.47	1.39	5.15	0.53	3.51	1.3	5.84	0.31
Lacanobia subjuncta	**57.90**	1.9404	9.55	1.049	11.69	1.273	6.65	1.08	3.94	0.67	7.61	1.7	2.66	0.39
Mamestra configurata	**24.79**	1.028	19.51	2.024	4.43	0.814	14.92	1.32	14.59	3.21	14.10	2.75	7.65	1.99
Manduca sexta	13.67	1.3233	**26.45**	2.624	4.40	0.624	20.68	1.74	7.75	1.29	13.75	2.48	13.30	1.24
Nomophila nearctica	**35.31**	2.3321	27.46	1.236	3.12	0.395	9.87	2.42	9.93	0.36	6.84	1.31	7.46	1.71

Orgyia pseudotsugata	3.82	1.0813	2.96	0.546	5.83	0.821	21.66	1.37	21.41	1.65	21.82	2.1	**22.50**	2.19
Orthosia hibisci	**48.98**	1.2131	9.52	0.782	8.26	1.135	15.31	0.76	6.09	0.41	2.79	0.65	9.05	0.86
Pandemis pyrusana$^{\times}$	7.35	5.0538	**29.20**	5.631	14.19	4.211	1.33	0.61	0.00	0	25.70	6.43	22.22	10.4
Papaipema nebris	20.08	2.5708	**24.82**	1.6	1.98	1.478	8.19	2.59	12.96	1.03	8.33	1.65	23.64	3.01
Pediasia trisecta	38.20	1.7114	**42.31**	2.004	3.53	0.649	4.30	0.9	6.74	1.28	4.20	0.39	0.71	0.48
Peridroma saucia	**62.57**	2.5837	9.60	1.746	9.62	0.904	4.20	0.28	4.28	0.39	4.81	0.95	4.93	0.47
Plathypena scabra	2.24	0.4198	22.65	2.136	11.09	1.376	**36.53**	0.77	16.84	1.91	8.17	0.71	2.47	0.28
Platynota flavedana	**38.47**	6.2352	3.42	0.867	28.24	4.987	14.55	2.4	11.99	1.04	0.73	0.62	2.61	0.61
Podosesia syringae	27.04	5.8632	**51.85**	3.578	1.01	0.531	7.82	2.68	5.50	0.96	2.36	0.45	4.43	1.87
Pseudaletia unipuncta	**44.59**	1.7027	20.24	1.504	3.47	0.606	8.03	0.76	19.57	1.34	1.37	0.36	2.73	0.8
Rhyacionia frustrana	22.59	1.799	15.07	2.159	**24.16**	3.671	13.00	1.01	21.47	4.74	3.61	1.02	0.11	0.07
Simyra henrici	8.01	1.7179	18.12	1.259	14.75	2.391	2.21	0.75	**28.64**	3.31	17.19	3.56	11.08	2.66
Spodoptera frugiperda	17.27	2.7887	19.20	2.709	11.09	1.068	6.98	1.13	**38.30**	4.15	5.26	0.21	1.91	1.31
Synanthedon exitiosa	**39.70**	1.8455	2.91	0.752	0.97	0.235	16.68	1.22	15.79	2.14	3.87	1.7	20.08	2.95
Zeiraphera canadensis$^{\times}$	**76.49**	6.2388	0.00	0	12.04	4.927	2.02	2.02	0.48	0.48	0.00	0	8.96	2.95
Average	33.97	4.33	15.21	2.38	11.86	2.34	10.91	1.63	10.98	1.73	8.45	1.57	8.62	1.46
Reduced average	31.08	3.95	16.42	2.48	10.13	1.61	12.21	1.73	12.65	1.78	8.76	1.59	8.75	1.53

Table S8. Percent contribution of the seven environmental variables to each species in the DD5 model (n=30). Percent cont = the mean percent contribution of each environmental variable across the five rounds of internal cross validation. Bolded values indicate the top contributor for each species. The reduced average (n=26) excludes data-poor species (i.e., < 35 records, indicated by $^{\times}$).

	Temperature annual range		Precipitation seasonality		Mean temperature of the wettest quarter		Growing degree-days		Mean diurnal range		Precipitation of the warmest quarter		Precipitation of the wettest month	
Species	Percent cont	SE	Percent cont	SE	Percent cont	SE	Percent cont	SE	Percent cont	SE	Percent cont	SE	Percent cont	SE
Amyelois transitella$^{\times}$	**81.30**	8.65	0.00	0.00	0.82	0.82	17.88	8.46	0.00	0.00	0.00	0.00	0.00	0.00
Anticarsia gemmatalis	7.29	1.65	**32.40**	4.43	12.26	2.15	4.21	1.07	4.07	1.09	17.69	4.77	22.09	2.96
Argyrotaenia citrana	**72.79**	3.02	2.12	0.55	14.49	3.05	0.19	0.16	0.88	0.42	9.52	0.49	0.02	0.02
Argyrotaenia velutinana	**25.10**	2.59	1.61	0.46	19.39	1.64	12.01	3.11	25.00	2.51	6.69	1.96	10.20	1.94
Choristoneura fumiferana	26.24	0.69	7.42	0.90	9.25	2.61	**28.30**	2.58	5.74	1.10	22.89	1.94	0.15	0.05
Choristoneura rosaceana	**46.12**	1.46	10.51	1.68	6.70	0.63	5.17	0.69	20.44	0.84	2.60	0.54	8.47	1.85
Cydia latiferreana	**64.33**	4.06	4.00	1.03	4.77	0.57	5.70	1.31	3.46	1.01	1.65	0.39	16.09	2.20
Diatraea grandiosella$^{\times}$	23.44	19.43	0.00	0.00	**76.56**	19.43	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Egira curialis	10.54	1.41	7.36	1.76	**31.80**	2.59	3.90	0.53	18.12	3.11	5.22	1.21	23.04	4.05
Hemileuca oliviae	0.50	0.47	12.95	1.55	29.62	3.97	2.95	2.77	6.74	2.71	**42.08**	1.38	5.15	1.73
Hyphantria cunea	**43.35**	1.46	20.84	0.96	1.71	0.33	18.40	0.68	6.12	0.50	2.91	0.29	6.66	0.26
Lacanobia subjuncta	**58.53**	2.47	9.78	1.16	14.25	1.85	4.85	0.46	3.12	0.67	6.28	0.71	3.18	0.56
Mamestra configurata	**25.93**	1.33	19.83	3.65	3.22	0.51	14.85	1.53	11.94	1.77	16.45	2.02	7.77	3.12
Manduca sexta	13.55	1.77	**25.79**	3.07	4.45	0.37	20.27	1.38	8.20	1.16	14.85	2.25	12.89	2.10
Nomophila nearctica	**37.13**	2.00	25.80	1.60	3.48	0.64	9.05	2.35	8.45	0.52	8.69	0.74	7.40	1.33
Orgyia pseudotsugata	2.78	0.72	3.69	0.29	5.69	1.06	21.53	1.11	21.46	2.23	20.37	4.33	**24.47**	3.28
Orthosia hibisci	**50.17**	0.80	8.82	0.64	8.81	0.75	15.02	0.71	5.43	0.56	2.74	0.36	9.02	1.60

Pandemis pyrusana[×]	5.46	2.88	**33.54**	5.72	17.43	6.14	1.53	0.62	0.00	0.00	26.14	2.83	15.89	6.20
Papaipema nebris	20.66	5.96	**24.05**	3.09	2.20	0.88	9.04	3.04	13.80	1.32	7.45	2.86	22.80	2.09
Pediasia trisecta	39.11	1.02	**43.47**	2.17	2.93	0.30	3.26	0.73	5.87	0.64	5.23	0.83	0.14	0.04
Peridroma saucia	**61.63**	2.26	9.24	2.01	9.65	0.61	4.57	1.55	4.69	0.51	4.72	0.64	5.51	0.42
Plathypena scabra	1.98	0.52	20.79	2.83	12.71	1.45	**36.58**	1.39	17.44	3.21	7.70	1.04	2.80	0.34
Platynota flavedana	**37.35**	1.82	3.01	1.89	32.54	2.60	14.11	2.89	10.18	2.40	0.26	0.19	2.55	0.76
Podosesia syringae	26.63	6.67	**52.26**	6.18	0.95	0.40	8.20	2.30	5.11	0.58	3.54	1.58	3.31	0.51
Pseudaletia unipuncta	**46.12**	2.85	18.16	2.25	3.35	0.12	8.55	0.99	19.42	1.40	1.89	1.18	2.52	0.21
Rhyacionia frustrana	22.41	4.12	15.96	2.55	19.07	5.20	13.60	1.78	**25.59**	5.88	3.27	1.78	0.10	0.06
Simyra henrici	9.21	1.54	18.66	3.13	14.15	2.97	4.40	2.36	**25.17**	2.39	20.12	5.26	8.29	3.01
Spodoptera frugiperda	15.23	2.28	21.30	3.28	11.53	2.19	7.20	1.11	**38.23**	2.75	5.14	0.49	1.37	0.34
Synanthedon exitiosa	**38.64**	2.91	4.26	1.13	1.76	0.48	14.41	0.70	15.36	2.63	1.40	0.67	24.17	4.31
Zeiraphera canadensis[×]	**80.99**	8.22	0.00	0.00	7.93	4.86	2.88	2.88	0.61	0.38	0.00	0.00	7.59	4.39
Average	**33.15**	**4.31**	**15.25**	**2.42**	**12.78**	**2.73**	**10.42**	**1.57**	**11.02**	**1.76**	**8.92**	**1.77**	**8.45**	**1.48**
Reduced average	30.90	4.04	16.31	2.49	10.80	1.82	11.17	1.68	12.69	1.82	9.28	1.84	8.85	1.61

Table S9. Percent contribution of the seven environmental variables to each species in the DD10 model (n=26). Percent cont = the mean percent contribution of each environmental variable across the five rounds of internal cross validation. Bolded values indicate the top contributor for each species. The reduced average (n=22) excludes data-poor species (i.e., < 35 records, indicated by $^{\times}$).

	Temperature annual range		Precipitation seasonality		Mean temperature of the wettest quarter		Annual degree-days		Mean diurnal range		Precipitation of the warmest quarter		Precipitation of the wettest month	
Species	Percent cont	SE	Percent cont	SE	Percent cont	SE	Percent cont	SE	Percent cont	SE	Percent cont	SE	Percent cont	SE
Amyelois transitella$^{\times}$	**77.72**	19.34	12.61	12.61	0.54	0.54	3.68	1.58	0.00	0.00	5.47	5.47	0.00	0.00
Anticarsia gemmatalis	6.28	1.72	**32.71**	2.84	13.59	2.84	6.22	1.67	2.49	0.88	15.05	2.34	23.66	3.25
Argyrotaenia citrana	**71.65**	3.19	2.11	0.90	14.88	2.98	0.08	0.04	1.30	0.41	9.96	1.24	0.02	0.02
Argyrotaenia velutinana	**23.19**	3.85	2.60	0.89	21.00	3.06	16.25	3.76	22.39	1.92	4.10	0.97	10.47	0.61
Choristoneura fumiferana	27.28	1.39	5.19	1.21	7.64	2.37	**32.18**	2.21	4.91	2.03	22.76	1.27	0.03	0.03
Choristoneura rosaceana	**45.64**	1.70	9.67	0.89	7.16	0.42	5.66	0.29	19.43	1.38	2.90	0.40	9.54	2.43
Cydia latiferreana	**65.55**	2.04	3.07	0.62	6.40	0.41	5.74	0.57	3.31	0.58	1.22	0.40	14.72	1.84
Diatraea grandiosella$^{\times}$	29.34	19.84	0.00	0.00	**70.66**	19.84	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Egira curialis	11.47	2.70	6.66	2.58	**31.56**	1.62	5.46	1.22	16.72	1.02	4.48	0.55	23.65	2.37
Hemileuca oliviae	0.00	0.00	16.59	4.94	16.26	5.11	13.85	5.57	7.90	4.01	**37.87**	2.33	7.54	2.55
Hyphantria cunea	**44.78**	1.46	19.67	1.14	1.43	0.32	19.97	1.01	5.63	0.40	2.59	0.53	5.93	0.63
Lacanobia subjuncta	**58.08**	1.35	10.91	0.84	13.61	1.48	6.20	0.88	2.82	0.54	5.44	0.63	2.93	0.59
Mamestra configurata	**26.00**	1.49	14.97	2.78	4.46	0.68	16.53	1.48	15.66	3.79	18.07	1.67	4.31	0.93
Nomophila nearctica	**38.35**	1.30	25.39	1.55	2.37	0.36	9.65	1.38	8.44	0.99	8.69	1.54	7.10	1.52
Orgyia pseudotsugata	2.93	0.80	2.83	0.71	5.57	0.47	21.84	0.82	21.16	1.58	21.21	2.92	**24.46**	2.89
Orthosia hibisci	**49.62**	1.30	8.19	0.81	7.54	0.55	18.36	1.31	5.04	0.22	2.20	0.12	9.05	0.35
Pandemis pyrusana$^{\times}$	2.07	1.26	**42.15**	8.84	12.12	4.50	5.48	2.18	0.04	0.04	26.87	6.19	11.27	5.62
Papaipema nebris	21.24	1.19	22.52	3.69	2.63	1.26	6.52	0.63	12.02	0.88	9.87	2.40	**25.20**	3.22

Peridroma saucia	**61.18**	2.15	9.64	1.78	9.90	1.14	4.15	0.32	3.97	0.24	5.98	0.61	5.18	0.29
Plathypena scabra	2.56	0.70	23.04	2.92	13.73	2.52	**34.26**	0.95	16.84	1.59	6.89	0.46	2.67	0.58
Platynota flavedana	**36.30**	3.74	2.28	0.97	32.68	2.89	14.35	4.89	11.73	3.02	0.25	0.15	2.41	0.17
Pseudaletia unipuncta	**44.02**	1.70	19.63	1.52	2.94	0.12	9.52	0.64	20.62	0.79	0.85	0.16	2.43	0.30
Rhyacionia frustrana	21.84	3.95	13.96	2.28	19.64	2.94	15.04	1.77	**26.03**	4.82	3.35	1.28	0.15	0.08
Simyra henrici	9.21	2.73	18.35	1.28	11.87	0.48	4.30	0.93	**28.86**	3.41	17.45	3.11	9.96	2.12
Spodoptera frugiperda	14.92	3.23	21.59	3.20	11.84	1.85	7.81	1.37	**38.06**	4.30	4.73	1.28	1.06	0.47
Zeiraphera canadensis[×]	**74.59**	14.66	0.00	0.00	10.42	9.72	5.65	5.65	2.63	2.63	0.00	0.00	6.71	4.79
Average	**33.30**	**4.78**	**13.32**	**2.08**	**13.56**	**2.79**	**11.10**	**1.73**	**11.46**	**2.02**	**9.16**	**1.88**	**8.09**	**1.59**
Reduced average	31.00	4.67	13.25	1.88	11.76	1.83	12.45	1.90	13.42	2.13	9.36	1.98	8.75	1.79

Table S10. Pearson correlation coefficients (r) representing the strength of linear relationships between the three metrics of model accuracy – area under the ROC curve (AUC), True Skill Statistic (TSS) and Kappa.

	Model		
	Hybrid	DD5	DD10
AUC vs TSS	0.944	0.951	0.891
AUC vs kappa	0.005	-0.073	-0.088
kappa vs TSS	0.023	-0.065	-0.039

Table S11. Prevalence (average probability of presence over background sites) for each species and each model.

Species	**DD5**	**SE**	**DD10**	**SE**	**Hybrid**	**SE**
Amyelois transitella	0.24366	0.012	0.21758	0.018	0.23304	0.022
Anticarsia gemmatalis	0.43614	0.012	0.44132	0.009	0.4299	0.012
Argyrotaenia citrana	0.05358	0.002	0.05348	0.003	0.05124	0.002
Argyrotaenia velutinana	0.43622	0.008	0.42378	0.007	0.42668	0.010
Choristoneura fumiferana	0.28514	0.006	0.28636	0.006	0.28024	0.004
Choristoneura rosaceana	0.29634	0.006	0.30058	0.005	0.30516	0.005
Cydia latiferreana	0.24364	0.008	0.24648	0.002	0.2368	0.010
Diatraea grandiosella	0.51618	0.044	0.5862	0.010	0.56278	0.026
Egira curialis	0.29092	0.010	0.2903	0.008	0.29362	0.004
Hemileuca oliviae	0.43724	0.012	0.441	0.016	0.42904	0.018
Hyphantria cunea	0.40132	0.002	0.3948	0.007	0.39872	0.005
Lacanobia subjuncta	0.28222	0.008	0.29316	0.005	0.27404	0.016
Mamestra configurata	0.23306	0.009	0.2307	0.008	0.23194	0.003
Manduca sexta	0.41668	0.005	*NA*	*NA*	0.41078	0.004
Nomophila nearctica	0.26996	0.003	0.26944	0.004	0.25972	0.004
Orgyia pseudotsugata	0.1293	0.011	0.12352	0.006	0.1205	0.006
Orthosia hibisci	0.2599	0.003	0.25714	0.003	0.2636	0.004
Pandemis pyrusana	0.2669	0.011	0.23398	0.014	0.24012	0.011
Papaipema nebris	0.47546	0.012	0.45942	0.014	0.44818	0.009
Pediasia trisecta	0.21796	0.010	*NA*	*NA*	0.21786	0.008
Peridroma saucia	0.35636	0.005	0.3565	0.006	0.3591	0.005
Plathypena scabra	0.4714	0.002	0.4715	0.005	0.46886	0.003
Platynota flavedana	0.31344	0.020	0.32178	0.003	0.32728	0.008
Podosesia syringae	0.36856	0.004	*NA*	*NA*	0.35672	0.009
Pseudaletia unipuncta	0.32586	0.008	0.32436	0.003	0.32554	0.003
Rhyacionia frustrana	0.29356	0.022	0.32802	0.017	0.33556	0.004
Simyra henrici	0.35448	0.016	0.3545	0.012	0.35716	0.011
Spodoptera frugiperda	0.4101	0.004	0.42104	0.010	0.40102	0.011
Synanthedon exitiosa	0.36982	0.005	*NA*	*NA*	0.37134	0.012
Zeiraphera canadensis	0.492	0.019	0.4831	0.022	0.47126	0.001

Table S12. Percent contribution of growing degree-days in the hybrid and correlative DD5 models, along with the difference in percent contribution between the two model types (correlative – hybrid). Negative values indicate that growing degree-days contributed more in the hybrid model than in the correlative (no shading), and vice versa (grey shading). The reduced average excludes species that have fewer than 35 occurrence records (indicated by ×)

Species	**Hybrid**	**Correlative**	**Difference**
Amyelois transitella×	6.43	17.88	11.45
Anticarsia gemmatalis	5.00	4.21	-0.79
Argyrotaenia citrana	0.22	0.19	-0.04
Argyrotaenia velutinana	13.93	12.01	-1.92
Choristoneura fumiferana	29.04	28.30	-0.73
Choristoneura rosaceana	4.87	5.17	0.30
Cydia latiferreana	5.84	5.70	-0.14
Diatraea grandiosella×	0.05	0.00	-0.05
Egira curialis	4.16	3.90	-0.26
Hemileuca oliviae	21.27	2.95	-18.32
Hyphantria cunea	21.47	18.40	-3.07
Lacanobia subjuncta	6.65	4.85	-1.80
Mamestra configurata	14.92	14.85	-0.07
Manduca sexta	20.68	20.27	-0.41
Nomophila nearctica	9.87	9.05	-0.82
Orgyia pseudotsugata	21.66	21.53	-0.13
Orthosia hibisci	15.31	15.02	-0.29
Pandemis pyrusana×	1.33	1.53	0.20
Papaipema nebris	8.19	9.04	0.85
Pediasia trisecta	4.30	3.26	-1.04
Peridroma saucia	4.20	4.57	0.37
Plathypena scabra	36.53	36.58	0.05
Platynota flavedana	14.55	14.11	-0.43
Podosesia syringae	7.82	8.20	0.39
Pseudaletia unipuncta	8.03	8.55	0.52
Rhyacionia frustrana	13.00	13.60	0.61
Simyra henrici	2.21	4.40	2.20
Spodoptera frugiperda	6.98	7.20	0.22
Synanthedon exitiosa	16.68	14.41	-2.27
Zeiraphera canadensis×	2.02	2.88	0.86
Average	**10.91**	**10.42**	**-0.49**
Reduced average	**12.21**	**11.17**	**-1.04**

Figure S1. Annual growing degree-days calculated based on a base development temperature of 5°C (a) and 10°C (b).