Adult firefly abundance is linked to weather during the larval stage in the previous year

T.R. Evans [1], *, D. Salvatore[2], M. van de Pol[3] and C.J.M. Musters[4]

[1] Illinois State Museum Research and Collections Center, 1011 E. Ash Street, Springfield, Illinois 62703, USA

[2]Museum of Science, Science Park, Boston, MA 02114

[3]Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Droevendaalsesteeg 10,6708PB, Wageningen, The Netherlands

[4]Institute of Environmental Sciences, van Steenisgebouw, Einsteinweg 2, 2333 CC Leiden University, Leiden, The Netherlands

;

*Corresponding author: Tel.: 001-217-498-0345; e-mail: tracy.evans62545@gmail.com

Abstract.

1. Much is known about the brief adult phase of fireflies. However, fireflies spend a relatively long developmental period under the soil surface. Climatic and soil conditions may directly affect the eggs, larvae and pupae and indirectly affect them through predators, competitors and prey items. Climatic conditions during the early life stages of this iconic species are therefore relevant to their hypothesized decline within the context of global warming.

2. We extracted data on the abundance of fireflies from the publicly available citizen data set across North America over a period of nine years. We document the effects of weather in the 24 months prior to the observations of firefly abundance based on 6761 observations.

3. Climatic conditions during both the larval and adult phases have a non-linear effect on adult firefly abundance. Maximum winter and spring temperatures and mean precipitation in the 20-month period prior to the observations had the greatest impact on the abundance of firefly adults. Low maximum soil moisture during the 5-19 months preceding the observations affected the adult abundance negatively, and high maximum soil moisture positively.

4. After correcting the firefly abundance for these weather effects, we estimate that the abundance of fireflies increased over the time period of this study.

5. Our study suggests that early life climatic conditions have a small but significant impact on adult firefly abundance with a total R^2 of 0.017.

Key words. Beetles, citizen science, climate change, Coleoptera, Lampyridae, life history, lightning bugs.

Running title: Firefly abundance and weather

Introduction

Fireflies (*Coleoptera, Lampyridae*) are among the most charismatic insect species. They are the focus of ecotourism around the world (Jusoh & Hashim, 2012; Foo & Dawood, 2016), education programs (Kaufman *et al*., 1996) and citizen science projects. Anecdotally, we hear about the decline in firefly abundance, as elders tell grandchildren tales of their youth (Lewis, 2016). Environmental threats include pesticide use, light pollution, commercial harvest, and habitat loss (Lewis, 2016; Faust, 2017).

The importance of weather on adult behavior has been well documented, allowing the prediction of emergence and peak display by individual species in a particular locality (Faust & Weston, 2009; Faust, 2017). Characteristics such as flash pattern (i.e. Moiseff & Copeland, 2010; Ohba, 2004) and bioluminescence (i.e. White *et al.*, 1971; Martin *et al*., 2017) are the subject of numerous investigations. Less studied is the impact of weather on a large spatial scale during the period when much of the development occurs out-of-sight, in the soil or under bark and logs (Faust, 2017). We took the opportunity provided by the citizen science program, "Firefly Watch" (Museum of Science, Boston), to examine data collected over a large part of the United States.

Fireflies spend a relatively long developmental period under the soil surface. Climatic and soil conditions may directly affect the eggs, larvae and pupae and indirectly affect them through predators, competitors and prey items. The larval phase of fireflies is an "eating-machine" with transitions through one instar to the next requiring a steady food supply. Prey species during the larval phase include snails, slugs, earthworms and con-specifics (Lewis, 2016). The transition from egg to adult may be completed in one or two, and rarely more, years, and probably depends on latitude, elevation, climate and local weather conditions (Lewis, 2016; Faust, 2017). Prey availability is also most likely dependent on these factors as well as the densities of predators and competitors. There is evidence that some larvae within a single population may postpone pupation for an additional season (Faust, 2017). In this way they emerge as adults with greater reproductive potential (Faust, 2017).

All this suggests that changes in the environmental conditions during firefly development ultimately result in changes in abundance of adult fireflies. Here, we study the impact of weather during early life phases on adult firefly abundance. We examine the effect of weather variables beginning 24 months before the abundance observations. Our hypothesis is that variation in weather changed the abundance of fireflies through changes in the conditions of larval development. Since many insect groups have long larvae phases, our study could be regarded as an example for studying the impact of weather on adult abundance in many other insect groups.

Temperature and precipitation are obvious weather variables to consider. However, climate encompasses more than just average temperature and precipitation. Changes in precipitation may not result in an overall increase or decrease in the amount of precipitation, but rather a change in the patterns of rain events and dry periods (Fay *et al*., 2008; Intergovernmental Panel on Climate Change, 2014). For that reason, we include a variable for soil moisture in our analyses (the Palmer Drought Severity Index, PDSI, see Methods for further explanation; Van de Pol *et al*., 2016).

We conducted a pilot study with a subset of the Boston Museum of Science (MOS) database. From this we concluded that climatic conditions in the previous years (the period of larval development) could affect adult firefly abundance. We expected firefly abundance to increase after high temperatures but also expected abundance to be highest with an optimal amount of precipitation and soil moisture. Finally, we investigated whether firefly abundance decreased over the 9-year study period and whether this could be attributed to the observed climate effects.

Methods

Study system

We used the publicly available data set gathered by the MOS (accessed 14 February 2017). This data set includes citizens observations of firefly abundance from 40 US states over a period of nine years (2008-2016) and is currently archived with Mass Audubon (https://www.massaudubon.org). We selected only the information needed for our study, i.e., the maximum observed abundance per year, which is the first date the maximum number of fireflies were seen, latitude, longitude, and state. When enrolling in the Firefly Watch program, citizen scientists were asked to make observations once a week at a non-specified time of the day.

Number of observations are measured as a range and placed in categories. No distinctions between firefly species are made. The abundance of fireflies is recorded in the data set as the number of spatially distinct flashes in a 10 second period in categories: 0 (none seen); 0+ (none seen during the 10 second period but some before or after; 1; 2-5; 6-20; and >20 (more than 20). We were interested in peak numbers only and eliminated the first two categories from our analysis. Our measure of abundance had therefore a 4-level scale (1: 1; 2: 2-5; 3: 6-20; and 4: >20) and will be called Bin hereafter.

Climate variables

We selected monthly weather data for all locations within the USA that had multiple yearly firefly observations over the period 2008-2016. The mean temperature, mean precipitation and

Palmer Drought Severity Index (PDSI) were obtained from the National Oceanic and Atmospheric Administration through the Midwestern Regional Climate Center (https://mrcc.illinois.edu/CLIMATE, accessed February 2017). For soil moisture we selected the Palmer Drought Severity Index (PDSI). PDSI is based on water supply, water demand and other factors such as evapotranspiration and recharge rates (Dai, 2004). It is a standardized index that spans -10 (dry) to +10 (wet) and able to capture the basic effect of temperature and precipitation on drought through potential evapotranspiration (Dai, 2011).

Statistical analysis

We performed statistical analysis using R software 3.4.4 (R Core Team, 2017). We used the package *climwin 1.2.0* (van de Pol *et al*. 2016; Bailey & van de Pol, 2016) to analyze the effects of weather (temperature, precipitation and soil moisture) in the months before firefly observation on firefly abundance. *Climwin* uses a sliding window to systematically evaluate all possible climate windows and subsequently uses Akaike's information theoretic criterion corrected for small sample size (AICc) to compare their relative importance.

To implement *climwin*, we created two data files; firefly observations (n=6761) which included the variables location identification number, state, date, year, month and Bin; and monthly weather observations (n=4620) which included the state, mid-point date of each month, year, month, mean temperature (C°), mean precipitation (cm) and soil moisture. The time periods we considered were 24 months prior to the firefly observation, with firefly observations in any given month linked to the weather conditions during all possible windows in the 24 previous months (see Supplemental Information). Firefly abundance at a given location were linked to the weather data of the USA state in which the sampling site was located. We followed the systematic stepwise approach as proposed by Van der Pol *et al*. (2016) for selecting the best fitting climate window for each weather variable. We first set a baseline model without climate variables as our null model. For our baseline we applied a linear mixed effects model (function *lmer()* from the package *lme4*, Bates *et al*., 2017) with the dependent variable ‘Bin’ which we considered to be a proxy for peak abundance. As random effect variables we included year and location in order to correct for dependency among observations due to the same year and location. Because we expected that the effect of weather on firefly abundance could be dependent on latitude and longitude, e.g., in southern regions high temperature could negative, while in northern regions it could be positive, we included the interaction between latitude and longitude with weather in our baseline models. So our baseline model for selecting the first window was _lmer(Bin~climate*(Lat+Long)+(1|Year)+(1|Location), REML=False)._

We then selected the statistical measures of maximum, minimum and mean per time window for each of our climate variables. From previous research (unpublished data) we believed that the relationship of firefly abundance to climate variables may be non-linear and decided to test linear and quadratic response curves. This resulted in six combinations that were to be tested for each of our climate variables to find the best fitting climate window. To avoid a type I error of identifying a false climate window due to multiple testing of many possible windows (van de Pol *et al.* 2016), we compared the results of the best fitting window with that of the window from a randomized data set (data with no relationship between climate and firefly abundance). We then calculated the P-value based on 10 or 100 repeats (see Supplemental Information).

We used the “nsj” function of the R package *r2glmm* (Jaeger, 2017) to partition the variance of the final model in semi-partial R^2 to give a measure of the relative importance of the windows for purposes of discussion.

Results

Study system

Extracted firefly observations were located in 35 states with a heavier concentration of observations in the northeast United States (**Fig. 1a**). Most observations were done around June, 28th (**Fig. 1b**, median Julian day: 178, mean Julian day: 181.7). Firefly abundance has significantly increased over the years of this study (**Fig 1c**; LRT: Chi Sq=13.532, df=1, $p< 0.001$).

Climate variables

To test whether the yearly increase of firefly abundance observed in the raw data was due to the effect of weather changes on larval development, we constructed the best fitting model for predicting firefly abundance based on weather in the 24 months period before the firefly abundance observations. For that we used 4620 observations of 3 weather variables. Correlations between monthly averages of the weather variables were generally weak and were as follows: precipitation and temperature = 0.31; precipitation and soil moisture = 0.32; and temperature and soil moisture = -0.17. Temperature ($F_{1, 4618} = 0.098$, $p = 0.754$, precipitation ($F_{1,4618} = 0.210$, $p= 0.885$), and soil moisture ($F_{1, 4618} = 1.454$, $p = 0.228$) showed no trend over the 11 years of weather data included in our study.

Statistical analysis

For each of our weather variables, the best fitting window within the 24 months period before the firefly abundance observations was stepwise selected (complete information on the stepwise selection is in the Supplementary Information). The first best fitting window turned out to be that of temperature. Then the stepwise approach was repeated to check which climate window should be added to our baseline model next. That turned out to be that of precipitation. The last window to be added was the best fitting window for soil moisture (**Table 1**). The best temperature window was between 6 and 2 months, while that of precipitation was between 20 and 0 months and that of soil moisture between 19 and 5 months before adult observation (**Fig. 2**). In all three weather variables, a quadratic model fit the best, that of the maximum temperature, mean precipitation and maximum soil moisture (**Fig. 3**). We use loess lines to show how the models behave in relation to the climate variables. To summarize, climatic conditions during both the larval and adult phases have a non-linear affect adult firefly abundance. Maximum winter and spring temperatures and mean precipitation in the 20-month period prior to the observations had the greatest impact on the abundance of firefly adults. Low maximum soil moisture during the 5-19 months preceding the observations affected the adult abundance negatively, and high maximum soil moisture positively.

The best fitting model of the weather variables had a R^2 of 0.201 (**Table 2**). The summed R^2 of the fixed effect variables was 0.017, showing that most of the explained variance was actually explained by the random effect variables year and location. The weather variables, including their interactions with latitude and longitude, had a small, though significant effect on firefly abundance.

Adding year as a fixed effect variable to the best fitting weather model increased the R^2 to 0.221 (**Table 3**), a significant improvement of the model (LRT: Chi Sq=13.473, df=1, $p < 0.001$). The effect of the weather variables, including their interactions with latitude and longitude, on firefly abundance did not change because of the inclusion of year (**Table 3**). The summed R^2 of the fixed effect variables increased to 0.026, an increase of 0.009 which is exactly the partial R^2 of year. The abundance of the fireflies predicted by the best fitting model are increasing over the years in the same rate as they are in the null model (slope of regression line in both **Fig. 1c** and **Fig. 4**: 0.0732).

Summary of weather impacts on firefly abundance:

- Weather variables have an impact on firefly abundance during early development more than 12 months before the observations.
- High maximum temperatures winter and spring months immediately before the observation result in lower firefly abundance.
- Precipitation has an optimal amount through several instars, over or under which has a significant negative impact on firefly abundance.
- Low and high maximum PDSI scores result in lower firefly abundance.

Discussion

It is important to put the impacts of weather data in a biological perspective. First of all, it should be recognized that the effect of pre-eclosure weather on the abundance of the adult fireflies is small in terms of the amount of variance in the observations that is explained by the weather variables (1.7% for all three weather variables together). Therefore, our model explains only a small part of the variation in abundance of adult fireflies. Flashing activity may be affected by many other factors, e.g. the time of day the observation was made. Variance in data from public science can be expected to be huge, but the large amount of data enabled us to show that the effect of weather is real, though small.

Temperature has the greatest impact during the window 6-2 months before the adult observations; precipitation 20-0 months; and soil moisture 19-5 months prior to the observations. The impact of temperature as measured in degree days has been thoroughly documented for most firefly species found in north America (Faust & Weston, 2009; Faust, 2016). This method begins temperature measurement most commonly on March 1st. This is accurate for predicting when adult fireflies will emerge and achieve peak abundance, but does not predict what the abundance will be. Our study shows a longer period of impact by temperatures in the months prior to the observation. Precipitation and soil moisture have an impact throughout much of the larval phase as the beetles pass through several instars. Surprisingly, our results also indicate increasing firefly abundance, unrelated to weather, in the nine years of our study. The use of non-linear categorical data ('Bin') creates the impression of small differences in abundance when in fact the differences were sometimes quite large.

Our study suggests that using climate variables 24 months before the adult observation will add critical information in species specific studies and studies that are undertaken in a more local geographical area. Not all of the 125 firefly species found in North America are well-studied. And our study did not differentiate between species. The pattern of our data indicates that there is a two-year development cycle for most of the observed species and locations (**Fig. 2**). While our data showed statistically different weather over the years of our study, there were no evident trends. Shifts in temperature and precipitation on a global level have been well documented (Boggs, 2016).

A novel finding of our study, is the increase in firefly abundance over the period of our study. We have noted three areas that may be related to this finding. The first is related to the weather variables. Each of these three parameters, i.e. temperature, precipitation and soil moisture, did not significantly change over our study period. It should be noted however, that over much of the study area, 2012 was considered a "drought year", with higher than normal temperatures and lower than normal precipitation (Cook *et al*., 2014). That being said, climate is warming and larval development might speed up resulting in higher larval survival and higher abundance of adults. Firefly larvae, like other soft bodied soil inhabitants, are dependent on soil moisture with eggs laid in an area with sufficient moisture over the coming weeks to prevent desiccation. (Curry, 2004). Weather variables may also increase food availability. As "eating-machines" firefly larvae are dependent on prey species such as snails (Sasakawa, 2016), slugs (Kaufman, 1965), and earthworms (Seric & Symondson, 2016) for nourishment.

Our results do not necessarily conflict with other studies documenting a decline in insect abundance (Vogel, 2017), if we can assume that the changes in the firefly abundance are lagging behind an earlier, long-term change of climate. In view of the complex food web of which the fireflies are part, and the physiological changes the species might need to establish, such a time lag is not unlikely.

An alternative explanation, at least for the increase of fireflies over the years, may relate to shifts in the micro-environment. We noted that firefly development is often associated with trees. The 12 genera described in Faust (2017) are all found in close proximity to trees and several species use trees for much of their reproduction. Forests provide greater microhabitat stability than other habitat types. We speculate that trees keep the micro-environmental traits, such as soil moisture and temperature (Pastor & Post, 1986), more stable for the larval phase of development. Examination of pre-settlement North American forest cover suggests fireflies may have utilized the forested area for the early phase of the life-cycle and more open areas for adults for breeding display (**Fig. 5a & b**). A recent increase in forested areas in the United States, provided by conservation programs and field abandonment, may therefore, provide additional habitat for fireflies (Brown *et al.*, 1999; Drummond & Loveland, 2010).

A third explanation involves the nature of citizen science. Fireflies are so charismatic, that people may have gone to where they could see fireflies rather than where fireflies once were seen and that this effect has increased over the years.

While the abundance of fireflies appears to have increased, we note firefly abundance is dependent on weather several seasons prior to the observation of adult mating behavior. Further increase of temperature or drought conditions may push some species of fireflies past the "tipping point" of survivability (Van Nes *et al.*, 2016).

Ecological studies are delving into more complex areas with reported coefficients of determination (R^2) becoming smaller (Low-Décarie *et al.*, 2014). We seek to develop a deeper understanding of the unseen larval life stage and point future research beyond the "low hanging fruit".

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Contribution of authors

Evans: statistical analysis, writing; Salvatore: Firefly Watch Data; van de Pol: statistical analysis, writing; Musters: statistical analysis, writing.

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Figure legends:

Fig. 1. Firefly observations in the USA. a: distribution of the firefly observations in the publicly available data set gathered by the Museum of Science in Boston; b: distribution of the firefly observations over day numbers; c: change of adjusted firefly abundance over the years. Purple line: linear regression line; red line: loess line, red broken lines: one-sided standard deviation of the loess line. Boxplots along axes: 50% of the observations lie within the boxes; whiskers show 1.5 times box range; open dots are outliers.

Fig. 2. Three climate windows of best fitting model. Yellow: temperature; blue: precipitation; green: soil moisture. Windows are illustrated in months before the observation. Gray shading indicates life stage of the firefly: Dark: egg; lighter: larva; middle: diapause; lightest; pupa/adult.

Fig. 3. Relationship between firefly abundance and weather variables in the best fitting weather model. a: temperature, b: precipitation, c: soil moisture. Solid lines: loess lines; broken lines: one-sided standard deviation of the loess line. Boxplots along axes: 50% of the observations lie within the boxes; whiskers show 1.5 times box range; open dots are outliers.

Fig. 4. Change in adjusted abundance of fireflies predicted by the best fitting weather model between 2008 and 2016. Purple line: linear regression line; red line: loess line, red broken lines: one-sided standard deviation of the loess line. Boxplots along axes: 50% of the observations lie within the boxes; whiskers show 1.5 times box range; open dots are outliers.

Fig. 5. Present, 2011 (a) and past, 1620 (b) coverage of forest in the USA

Table legends:

Table 1. Three best climate windows, one for each climate variable. Model support for the best time window (ΔAICc) compared to a baseline model using different aggregate statistics and response curves (see Supplementary Information).

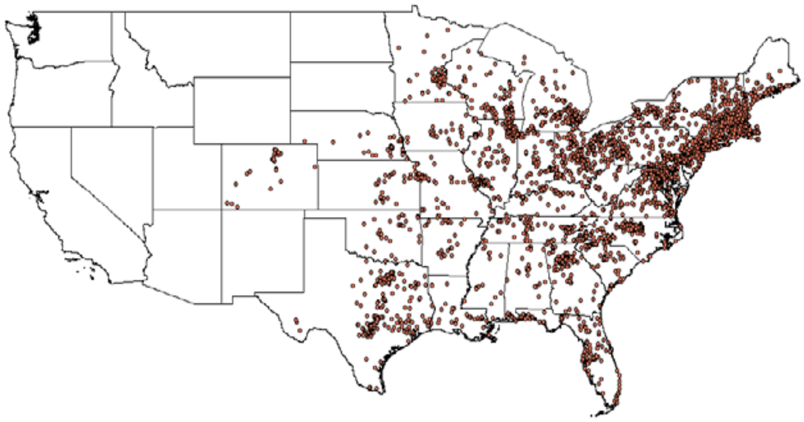
Table 2. Final complete model. MaxTE_{6-2}: maximum temperature of window 1, being the 6th to the 2nd month before observation; MeanPR_{20-0}: mean precipitation of window 2, being the 20th to 0th month before observation; MaxPD_{19-5}: maximum soil moisture of window 3, being the 19th to 5th month before observation.

Table 3. Final complete model plus Year. $MaxTE_{6-2}$: maximum temperature of window 1, being the 6th to the 2nd month before observation; $MeanPR_{20-0}$: mean precipitation of window 2, being the 20th to 0th month before observation; $MaxPD_{19-5}$: maximum soil moisture of window 3, being the 19th to 5th month before observation.

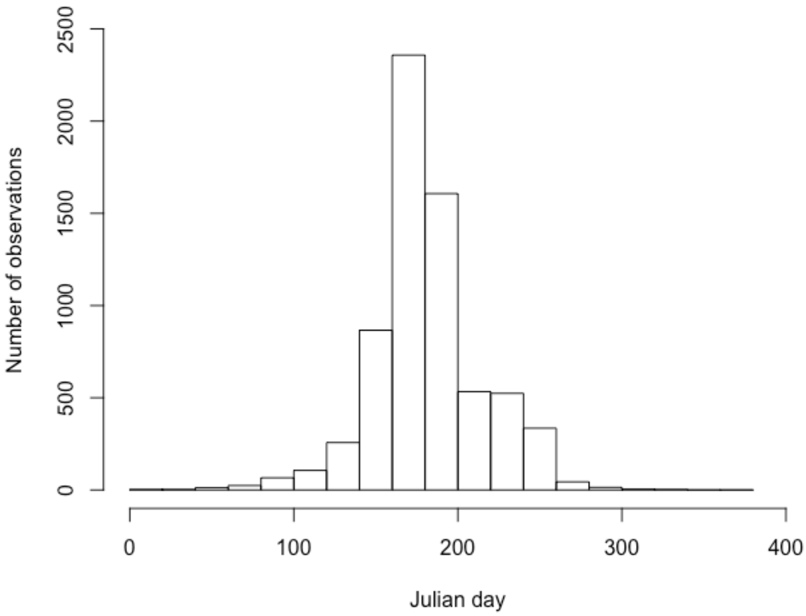
Fig. S1. Diagnostics of best model for the first climate window. a: heat plot of the maximum temperature in a quadratic function; b: weight plot of the maximum temperature in a quadratic function; c: scatter plot of the quadratic model predictions against the maximum temperature of the window between month 6 and 2 before the firefly observations; d: the comparison of 10 random null models (right hand) and the best model for the first climate window (broken vertical line).

Fig. S2. Diagnostics of best model for the second climate window. a: heat plot of the mean precipitation in a quadratic function; b: weight plot of the mean precipitation in a quadratic function; c: scatter plot of the quadratic model predictions against the mean precipitation of the window between month 20 and 0 before the firefly observations; d: the comparison of 10 random null models (right hand) and the best model for the first climate window (broken vertical line).

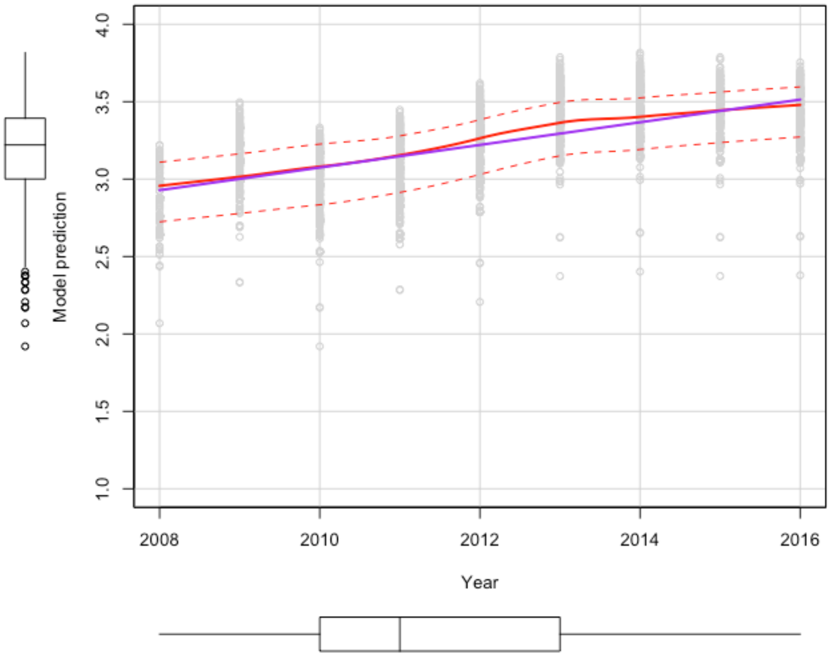
Fig. S3. Diagnostics of best model for the third climate window. a: heat plot of the maximum soil moisture in a quadratic function; b: weight plot of the maximum soil moisture in a quadratic function; c: scatter plot of the quadratic model predictions against the maximum soil moisture of the window between month 19 and 5 before the firefly observations; d: the comparison of 100 random null models (right hand) and the best model for the first climate window (broken vertical line).



[Fig. 1a]


Number of observations
0
500
1000
1500
2000
2500
0
100
200
300
400
Julian day

[Fig. 1b]



[Fig. 1c]

Fig. 1. Firefly observations in the USA. a: distribution of the firefly observations in the publicly available data set gathered by the Museum of Science in Boston; b: distribution of the firefly observations over day numbers; c: change of adjusted firefly abundance over the years. Purple line: linear regression line; red line: loess line, red broken lines: one-sided standard deviation of the loess line. Boxplots along axes: 50% of the observations lie within the boxes; whiskers show 1.5 times box range; open dots are outliers.

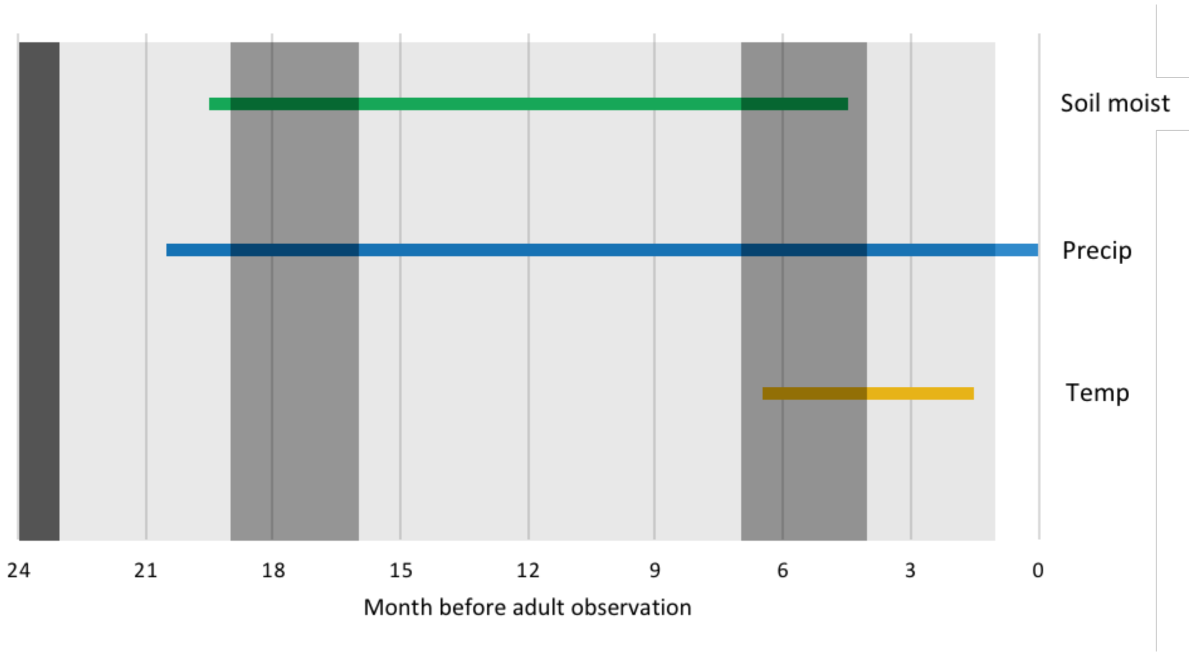
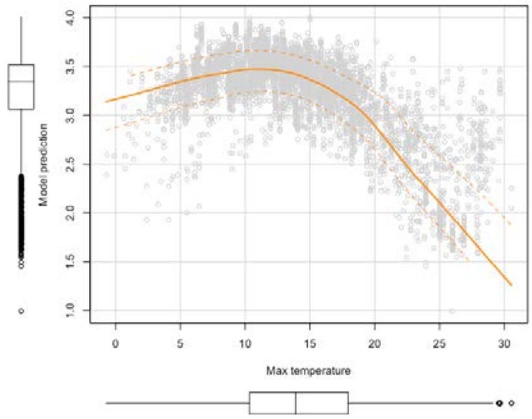
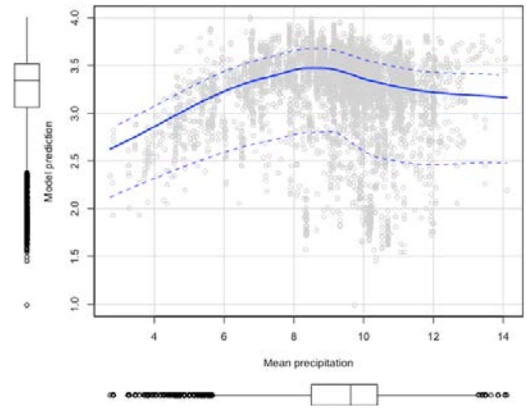


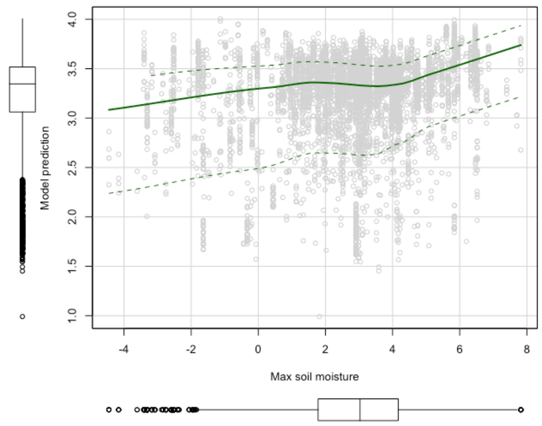
Fig. 2. Three climate windows of best fitting model. Yellow: temperature; blue: precipitation; green: soil moisture. Windows are illustrated in months before the observation. Gray shading indicates life stage of the firefly: Dark: egg; lighter: larva; middle: diapause; lightest; pupa/adult.



[Fig 3a]



[Fig 3b]



[Fig 3c]

Fig. 3. Relationship between firefly abundance and weather variables in the best fitting weather model. a: temperature, b: precipitation, c: soil moisture. Solid lines: loess lines; broken lines: one-sided standard deviation of the loess line. Boxplots along axes: 50% of the observations lie within the boxes; whiskers show 1.5 times box range; open dots are outliers.

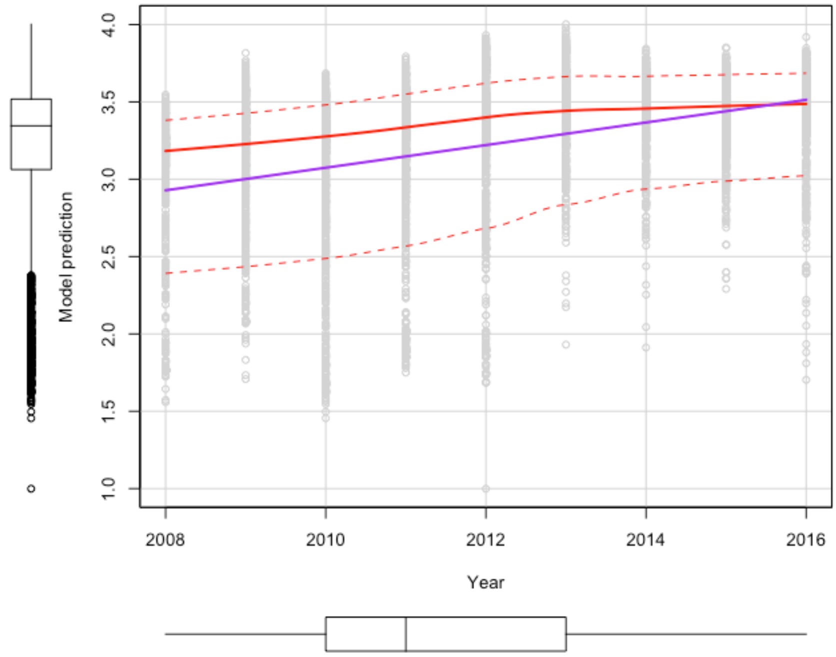
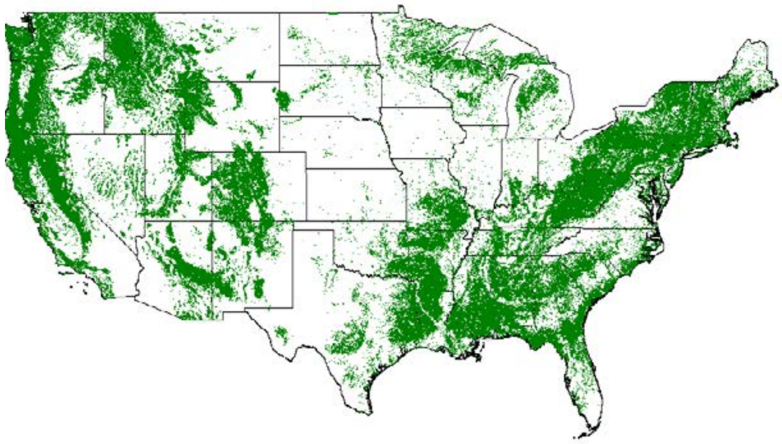
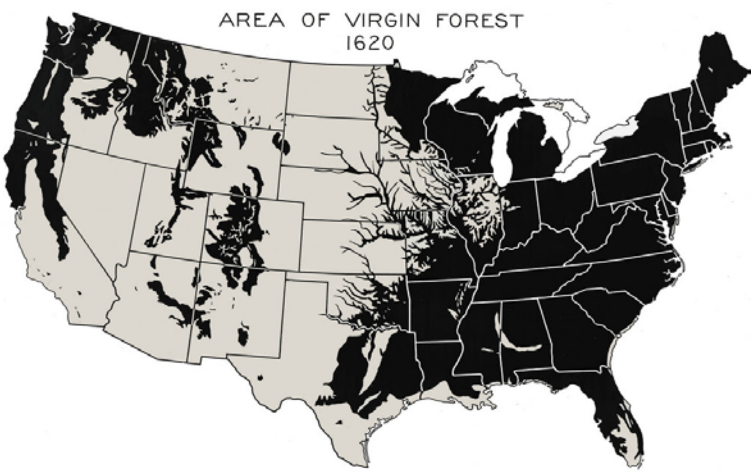


Fig. 4. Change in adjusted abundance of fireflies predicted by the best fitting weather model between 2008 and 2016. Purple line: linear regression line; red line: loess line, red broken lines: one-sided standard deviation of the loess line. Boxplots along axes: 50% of the observations lie within the boxes; whiskers show 1.5 times box range; open dots are outliers.

Forested areas 2011



[Fig. 5a]



[Fig 5b]

Fig. 5. Present, 2011 (a) and past, 1620 (b) coverage of forest in the USA

Table 1. Three best climate windows, one for each climate variable. Model support for the best time window (ΔAICc) compared to a baseline model using different aggregate statistics and response curves (see Supplementary Information).

Climate	Statistic	Function	ΔAICc	Window Open	Window Close
Temperature	maximum	quadratic	-971.34	6	2
Precipitation	mean	quadratic	-135.71	20	0
Soil moisture	maximum	quadratic	-47.92	19	5

Table 2. Final complete model. MaxTE$_{6-2}$ being the maximum tempera 6th to the 2nd month before observation; MeanPR$_{20-0}$: mean prec being the 20th to 0th month before observation; MaxPD$_{19-5}$: maximum window 3, being the 19th to 5th month before observation.

	Estimate	Std. Error	t value	Sum R^2	Explanation of sum R^2
(Intercept)	4.4140	3.9200	1.126	0.2010	Complete model
MaxTE$_{6-2}$	0.0855	0.1847	0.463	0.0002	Window 1 (Max temperature)
(MaxTE$_{6-2}$)^2	-0.0049	0.0055	-0.893		
MeanPR$_{20-0}$	-1.3550	0.8444	-1.604	0.0009	Window 2 (Mean precipitation)
(MeanPR$_{20-0}$	0.0903	0.0516	1.750		
MaxPD$_{19-5}$	0.5407	0.2258	2.394	0.0009	Window 3 (Max soil moisture)
(MaxPD$_{19-5}$)	0.0195	0.0390	0.501		
Lat	-0.0911	0.0622	-1.465	0.0003	Latitude
Long	0.0041	0.0311	0.133	0.0000	longitude
MaxTE$_{6-2}$:La	0.0081	0.0030	2.670	0.0047	Interaction Window 1 - Latitude
MaxTE$_{6-2}$:L	0.0028	0.0012	2.400	0.0036	Interaction Window 1 - Longitude
(MaxTE$_{6-2}$)	-0.0004	0.0001	-4.931		
(MaxTE$_{6-2}$	-0.0002	0.0000	-4.314		
MeanPR$_{20-}$	0.0358	0.0145	2.473	0.0023	Interaction Window 2 - Latitude
MeanPR$_{20}$	-0.0054	0.0066	-0.818	0.0001	Interaction Window 2 - Longitude
(MeanPR$_{2}$	-0.0026	0.0009	-2.924		
(MeanPR$_{2}$	0.0002	0.0004	0.552		
MaxPD$_{19-5}$	-0.0136	0.0032	-4.176	0.0032	Interaction Window 3 - Latitude
MaxPD$_{19-}$	0.0015	0.0017	0.838	0.0005	Interaction Window 3 - Longitude
(MaxPD$_{19}$	0.0011	0.0006	1.895		
(MaxPD$_{1}$	0.0005	0.0003	1.632		
				0.0167	Fixed effect variables

Table 3. Final complete model plus Year. $MaxTE_{6-2}$: maximum temperature of window 1, being the 6th to the 2nd month before observation; $MeanPR_{20-0}$: mean precipitation of window 2, being the 20th to 0th month before observation; $MaxPD_{19-5}$: maximum soil moisture of window 3, being the 19th to 5th month before observation.

	Estimate	Std. Error	t value	Sum R^2	Explanation of sum R^2
(Intercept)	-75.7800	15.6900	-4.831	0.2207	Complete model
Year	0.0401	0.0076	5.305	0.0087	Year
$MaxTE_{6-2}$	0.0904	0.1846	0.490	0.0002	Window 1 (Max temperature)
$(MaxTE_{6-2})^2$	-0.0053	0.0055	-0.955		
$MeanPR_{20-0}$	-1.4320	0.8425	-1.700	0.0010	Window 2 (Mean precipitation)
$(MeanPR_{20-0})^2$	0.0940	0.0515	1.826		
$MaxPD_{19-5}$	0.5304	0.2229	2.379	0.0009	Window 3 (Max soil moisture)
$(MaxPD_{19-5})^2$	0.0167	0.0388	0.431		
Lat	-0.0954	0.0621	-1.537	0.0004	Latitude
Long	0.0063	0.0310	0.204	0.0000	longitude
$MaxTE_{6-2}$:Lat	0.0083	0.0030	2.721	0.0048	Interaction Window 1 - Latitude
$MaxTE_{6-2}$:Long	0.0030	0.0012	2.522	0.0039	Interaction Window 1 - Longitude
$(MaxTE_{6-2})^2$:Lat	-0.0004	0.0001	-4.939		
$(MaxTE_{6-2})^2$:Long	-0.0002	0.0000	-4.446		
$MeanPR_{20-0}$:Lat	0.0359	0.0144	2.487	0.0022	Interaction Window 2 - Latitude
$MeanPR_{20-0}$:Long	-0.0061	0.0066	-0.924	0.0002	Interaction Window 2 - Longitude
$(MeanPR_{20-0})^2$:Lat	-0.0025	0.0009	-2.919		
$(MeanPR_{20-0})^2$:Long	0.0002	0.0004	0.652		
$MaxPD_{19-5}$:Lat	-0.0135	0.0032	-4.189	0.0033	Interaction Window 3 - Latitude
$MaxPD_{19-5}$:Long	0.0014	0.0017	0.824	0.0005	Interaction Window 3 - Longitude
$(MaxPD_{19-5})^2$:Lat	0.0011	0.0006	2.037		
$(MaxPD_{19-5})^2$:Long	0.0005	0.0003	1.651		
				0.0260	Fixed effect variables

Supplementary Information

Table S1a: Selection of the best model for the first climate window. Window Open gives the month before observation where the window starts and Window Close where the window ends. The Delta AICc of all possible combinations of Window Open and Window Close for a given combination of Climate, Statistic and Function have been calculated (see Figure S1a), but the one with the lowest Delta AICc, i.e., the one that differs mostly from the null model, is selected and given in this table. The bold model has the lowest Delta AICc of all combinations of Climate, Statistic and Function and is therefore regarded as the best first climate window.

Climate	Statistic	Function	Delta AICc	Window Open	Window Close
Temperature	mean	linear	-613.08	6	2
Precipitation	mean	linear	-133.48	10	6
Soil moisture	mean	linear	-211.06	6	0
Temperature	max	linear	-670.65	22	17
Precipitation	max	linear	-120.78	7	6
Soil moisture	max	linear	-264.9	5	1
Temperature	min	linear	-675.6	17	10
Precipitation	min	linear	-116.38	0	0
Soil moisture	min	linear	-215.03	6	5
Temperature	mean	quadratic	-937.46	4	2
Precipitation	mean	quadratic	-187.53	17	17
Soil moisture	mean	quadratic	-311.82	1	1
Temperature	**max**	**quadratic**	**-971.34**	**6**	**2**
Precipitation	max	quadratic	-187.53	17	17
Soil moisture	max	quadratic	-329.45	5	1
Temperature	min	quadratic	-921.83	2	2
Precipitation	min	quadratic	-187.53	17	17
Soil moisture	min	quadratic	-311.82	1	1

Table S1b: Model weights of the six best windows for quadratic maximum temperature as first window.

	Window 1		
Delta AICc	Open	Close	Model Weight
-971.3393	6	2	0.9919
-961.7269	5	2	0.0081
-942.4245	4	2	0.0000
-931.7863	3	2	0.0000
-921.8252	2	2	0.0000
-915.7598	7	2	0.0000

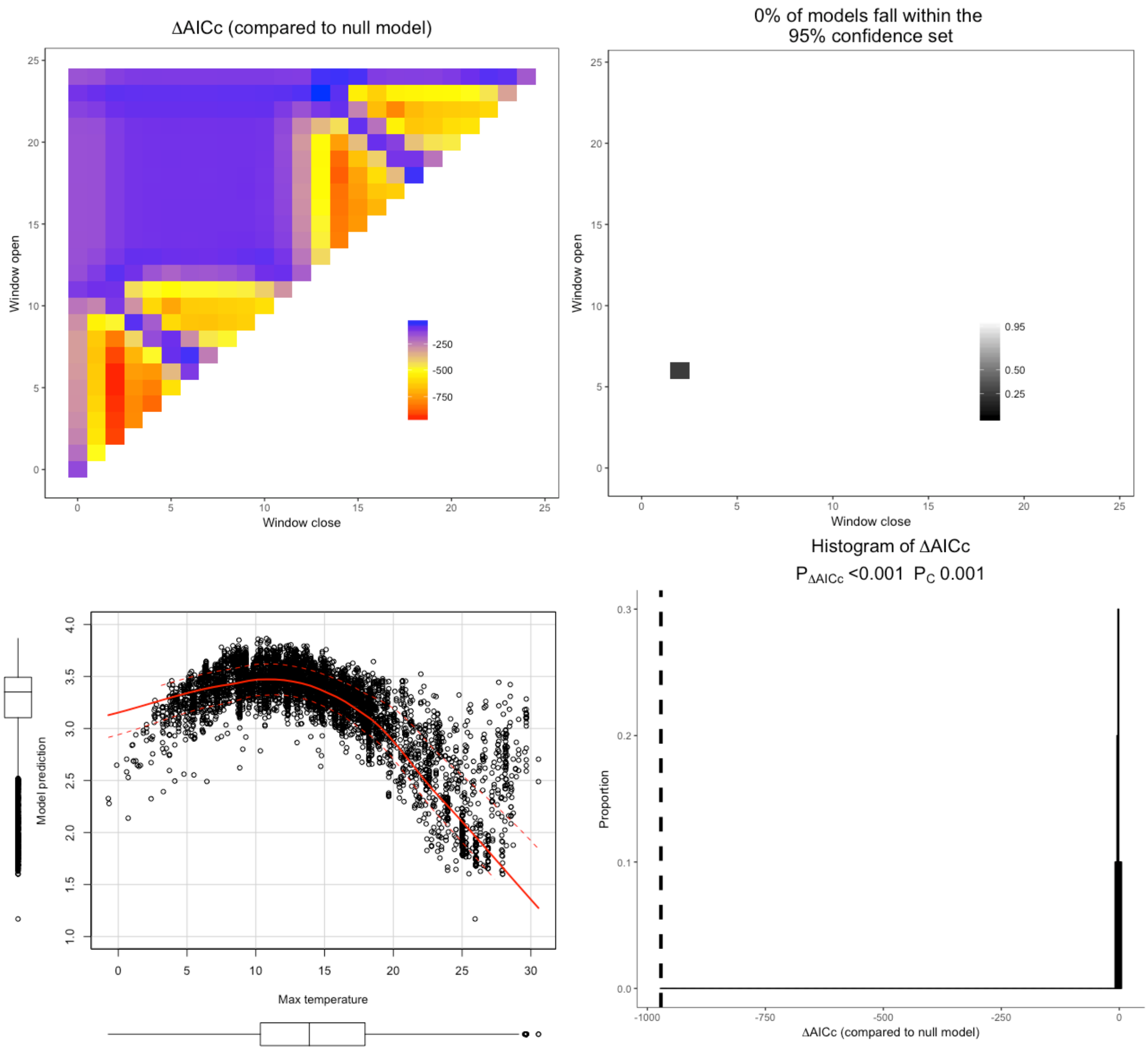


Figure S1: Diagnostics of best model for the first climate window. a: heat plot of the maximum temperature in a quadratic function; b: weight plot of the maximum temperature in a quadratic function; c: scatter plot of the quadratic model predictions against the maximum temperature of the window between month 6 and 2 before the firefly observations; d: the comparison of 10 random null models (right hand) and the best model for the first climate window (broken vertical line).

Table S2a: Selection of the best model for the second climate window. For more explanation see Table S1a. The bold model has the lowest Delta AICc and is therefore regarded as the best.

Climate	Statistic	Function	Delta AICc	Window Open	Window Close
Precipitation	mean	linear	-132.41	20	0
Soil moisture	mean	linear	-60.57	22	0
Precipitation	max	linear	-92.36	8	2
Soil moisture	max	linear	-80.23	7	1
Precipitation	min	linear	-79.93	20	17
Soil moisture	min	linear	-97.69	21	0
Precipitation	**mean**	**quadratic**	**-135.71**	**20**	**0**
Soil moisture	mean	quadratic	-78.77	1	1
Precipitation	max	quadratic	-129.19	6	2
Soil moisture	max	quadratic	-82.23	7	1
Precipitation	min	quadratic	-107.47	18	0
Soil moisture	min	quadratic	-97.29	21	0

Table S2b: Model weights of the six best windows for quadratic mean precipitation as second window.

	Window 2		
Delta AICc	Open	Close	Model Weight
-135.7115	20	0	0.7477
-130.8895	20	1	0.0671
-130.1198	22	0	0.0457
-128.4038	19	0	0.0194
-128.3964	9	0	0.0193
-128.3355	21	0	0.0187

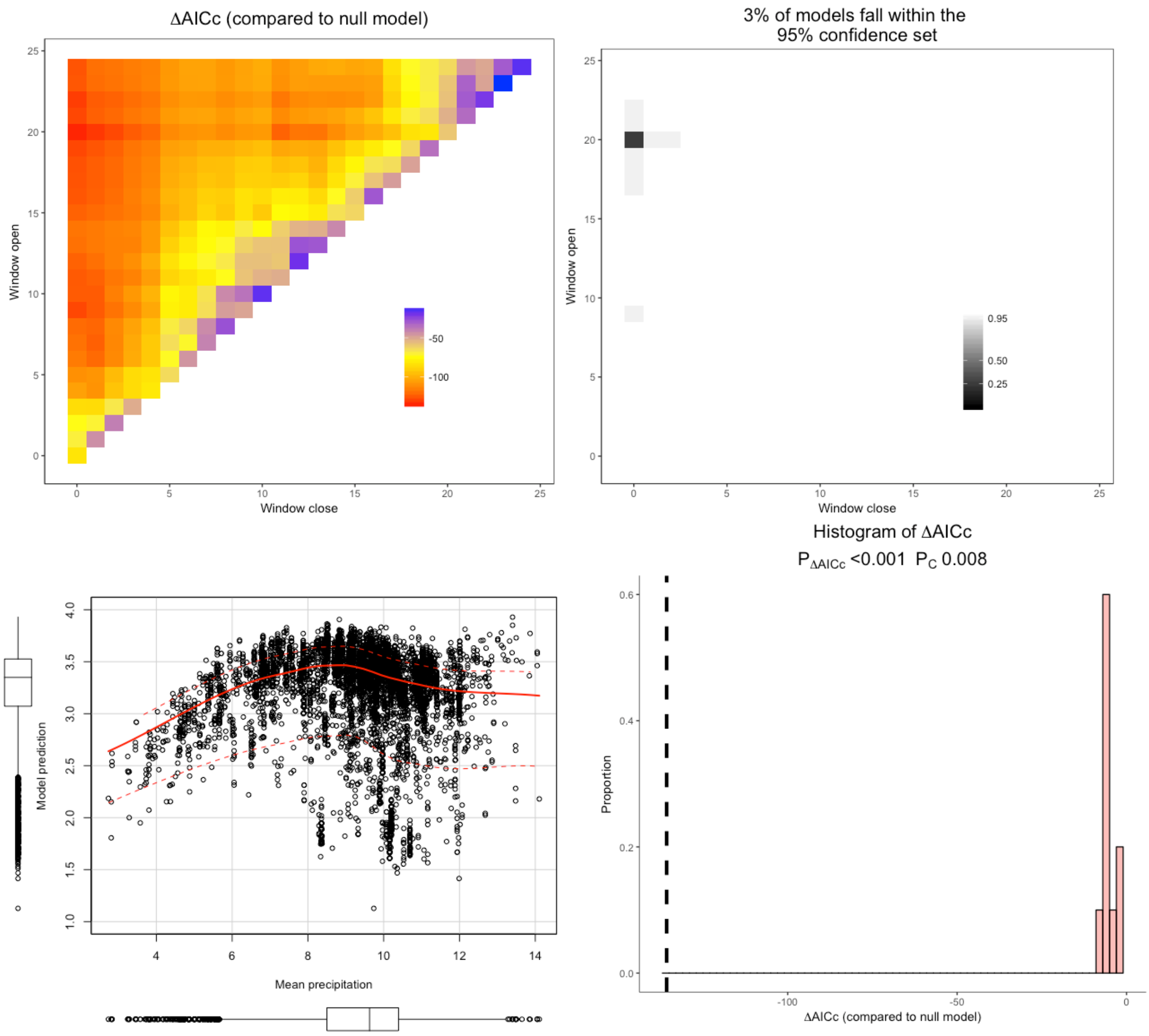


Figure S2: Diagnostics of best model for the second climate window. a: heat plot of the mean precipitation in a quadratic function; b: weight plot of the mean precipitation in a quadratic function; c: scatter plot of the quadratic model predictions against the mean precipitation of the window between month 20 and 0 before the firefly observations; d: the comparison of 10 random null models (right hand) and the best model for the first climate window (broken vertical line).

Table S3a: Selection of the best model for the third climate window. For more explanation see Table S1a. The bold model has the lowest Delta AICc and is therefore regarded as the best.

Climate	Statistic	Function	Delta AICc	Window Open	Window Close
Soil moisture	mean	linear	-27.82	10	0
Soil moisture	max	linear	-46.36	7	1
Soil moisture	min	linear	-31.43	21	0
Soil moisture	mean	quadratic	-29.73	1	1
Soil moisture	**max**	**quadratic**	**-47.92**	**19**	**5**
Soil moisture	min	quadratic	-34.14	3	0

Table S3b: Model weights of the six best windows for quadratic maximum soil moisture as third window.

	Window 3		
Delta AICc	Open	Close	Model Weight
-47.92352	19	5	0.4064
-46.89012	7	1	0.2424
-46.52598	18	5	0.2021
-43.98576	6	1	0.0567
-41.70100	7	2	0.0181
-40.84250	9	1	0.0118

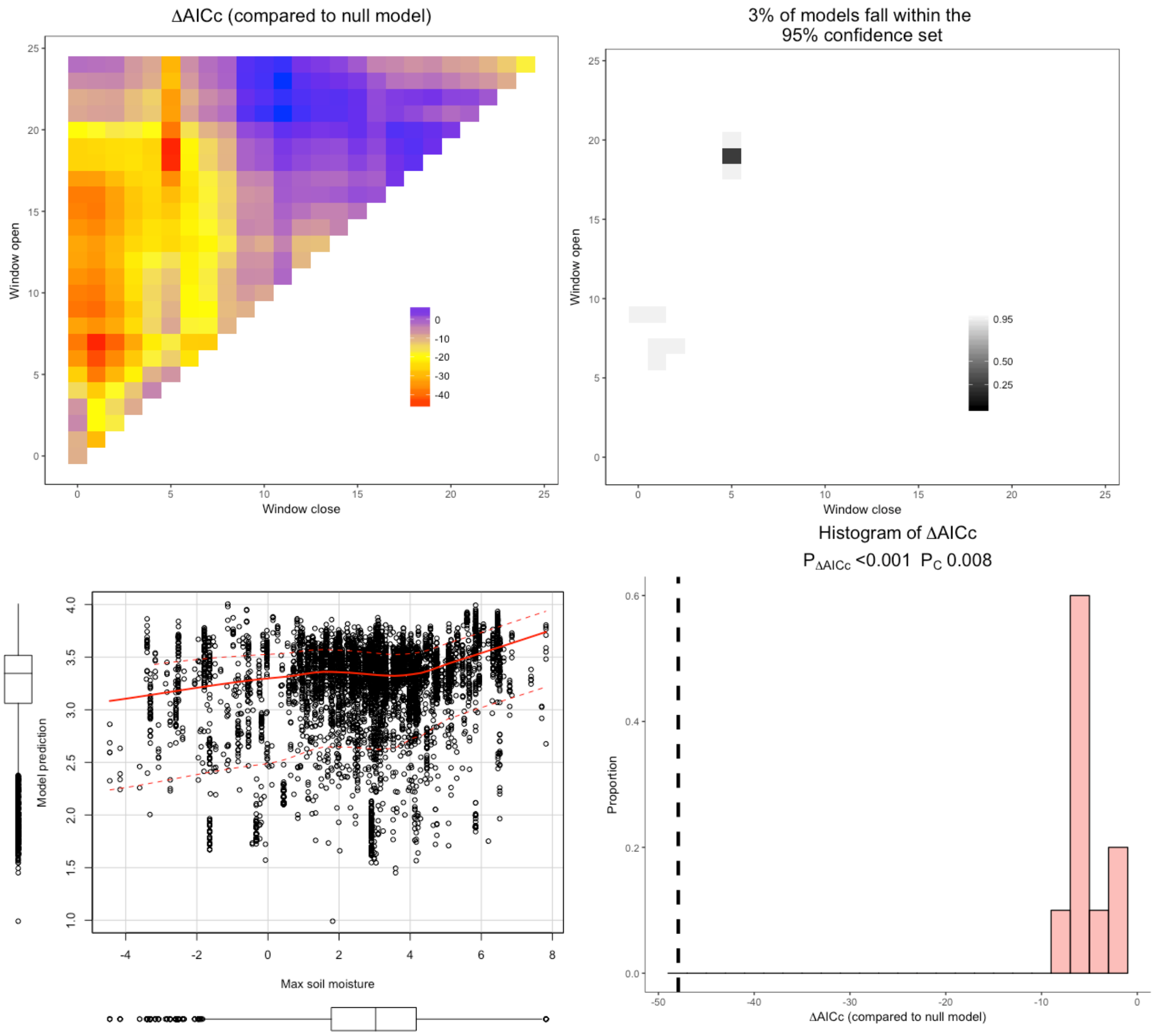


Figure S3: Diagnostics of best model for the third climate window. a: heat plot of the maximum soil moisture in a quadratic function; b: weight plot of the maximum soil moisture in a quadratic function; c: scatter plot of the quadratic model predictions against the maximum soil moisture of the window between month 19 and 5 before the firefly observations; d: the comparison of 100 random null models (right hand) and the best model for the first climate window (broken vertical line).