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

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12

13 **Abstract.**

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

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

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

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

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

31

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

34 Running title: Firefly abundance and weather

35 **Introduction**

36 Fireflies (*Coleoptera, Lampyridae*) are among the most charismatic insect species. They are
37 the focus of ecotourism around the world (Jusoh & Hashim, 2012; Foo & Dawood, 2016),
38 education programs (Kaufman *et al.*, 1996) and citizen science projects. Anecdotally, we hear
39 about the decline in firefly abundance, as elders tell grandchildren tales of their youth (Lewis,
40 2016). Environmental threats include pesticide use, light pollution, commercial harvest, and
41 habitat loss (Lewis, 2016; Faust, 2017).

42 The importance of weather on adult behavior has been well documented, allowing the
43 prediction of emergence and peak display by individual species in a particular locality (Faust &
44 Weston, 2009; Faust, 2017). Characteristics such as flash pattern (i.e. Moiseff & Copeland,
45 2010; Ohba, 2004) and bioluminescence (i.e. White *et al.*, 1971; Martin *et al.*, 2017) are the
46 subject of numerous investigations. Less studied is the impact of weather on a large spatial scale
47 during the period when much of the development occurs out-of-sight, in the soil or under bark
48 and logs (Faust, 2017). We took the opportunity provided by the citizen science program,
49 “Firefly Watch” (Museum of Science, Boston), to examine data collected over a large part of the
50 United States.

51 Fireflies spend a relatively long developmental period under the soil surface. Climatic and soil
52 conditions may directly affect the eggs, larvae and pupae and indirectly affect them through
53 predators, competitors and prey items. The larval phase of fireflies is an “eating-machine” with
54 transitions through one instar to the next requiring a steady food supply. Prey species during the
55 larval phase include snails, slugs, earthworms and con-specifics (Lewis, 2016). The transition
56 from egg to adult may be completed in one or two, and rarely more, years, and probably depends
57 on latitude, elevation, climate and local weather conditions (Lewis, 2016; Faust, 2017). Prey

58 availability is also most likely dependent on these factors as well as the densities of predators and
59 competitors. There is evidence that some larvae within a single population may postpone
60 pupation for an additional season (Faust, 2017). In this way they emerge as adults with greater
61 reproductive potential (Faust, 2017).

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

69 Temperature and precipitation are obvious weather variables to consider. However, climate
70 encompasses more than just average temperature and precipitation. Changes in precipitation may
71 not result in an overall increase or decrease in the amount of precipitation, but rather a change in
72 the patterns of rain events and dry periods (Fay *et al.*, 2008; Intergovernmental Panel on Climate
73 Change, 2014). For that reason, we include a variable for soil moisture in our analyses (the
74 Palmer Drought Severity Index, PDSI, see Methods for further explanation; Van de Pol *et al.*,
75 2016).

76 We conducted a pilot study with a subset of the Boston Museum of Science (MOS) database.
77 From this we concluded that climatic conditions in the previous years (the period of larval
78 development) could affect adult firefly abundance. We expected firefly abundance to increase
79 after high temperatures but also expected abundance to be highest with an optimal amount of

80 precipitation and soil moisture. Finally, we investigated whether firefly abundance decreased
81 over the 9-year study period and whether this could be attributed to the observed climate effects.

82

83 **Methods**

84 *Study system*

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

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

99

100 *Climate variables*

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

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

110

111 *Statistical analysis*

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

118 To implement *climwin*, we created two data files; firefly observations (n=6761) which
119 included the variables location identification number, state, date, year, month and Bin; and
120 monthly weather observations (n=4620) which included the state, mid-point date of each month,
121 year, month, mean temperature (C°), mean precipitation (cm) and soil moisture. The time periods
122 we considered were 24 months prior to the firefly observation, with firefly observations in any
123 given month linked to the weather conditions during all possible windows in the 24 previous
124 months (see Supplemental Information). Firefly abundance at a given location were linked to the
125 weather data of the USA state in which the sampling site was located. We followed the

126 systematic stepwise approach as proposed by Van der Pol *et al.* (2016) for selecting the best
127 fitting climate window for each weather variable. We first set a baseline model without climate
128 variables as our null model. For our baseline we applied a linear mixed effects model (function
129 *lmer()* from the package *lme4*, Bates *et al.*, 2017) with the dependent variable ‘Bin’ which we
130 considered to be a proxy for peak abundance. As random effect variables we included year and
131 location in order to correct for dependency among observations due to the same year and
132 location. Because we expected that the effect of weather on firefly abundance could be
133 dependent on latitude and longitude, e.g., in southern regions high temperature could negative,
134 while in northern regions it could be positive, we included the interaction between latitude and
135 longitude with weather in our baseline models. So our baseline model for selecting the first
136 window was *lmer(Bin~climate*(Lat+Long)+(1/Year)+(1/Location), REML=False)*.

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

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

149

150 **Results**

151 *Study system*

152 Extracted firefly observations were located in 35 states with a heavier concentration of
153 observations in the northeast United States (**Fig. 1a**). Most observations were done around June,
154 28th (**Fig. 1b**, median Julian day: 178, mean Julian day: 181.7). Firefly abundance has
155 significantly increased over the years of this study (**Fig 1c**; LRT: Chi Sq=13.532, df=1, p<
156 0.001).

157

158 *Climate variables*

159 To test whether the yearly increase of firefly abundance observed in the raw data was due to
160 the effect of weather changes on larval development, we constructed the best fitting model for
161 predicting firefly abundance based on weather in the 24 months period before the firefly
162 abundance observations. For that we used 4620 observations of 3 weather variables. Correlations
163 between monthly averages of the weather variables were generally weak and were as follows:
164 precipitation and temperature = 0.31; precipitation and soil moisture = 0.32; and temperature and
165 soil moisture = -0.17. Temperature ($F_{1, 4618} = 0.098$, $p = 0.754$, precipitation ($F_{1,4618} = 0.210$, $p =$
166 0.885), and soil moisture ($F_{1, 4618} = 1.454$, $p = 0.228$) showed no trend over the 11 years of
167 weather data included in our study.

168

169 *Statistical analysis*

170 For each of our weather variables, the best fitting window within the 24 months period before the
171 firefly abundance observations was stepwise selected (complete information on the stepwise

172 selection is in the Supplementary Information). The first best fitting window turned out to be that
173 of temperature. Then the stepwise approach was repeated to check which climate window should
174 be added to our baseline model next. That turned out to be that of precipitation. The last window
175 to be added was the best fitting window for soil moisture (**Table 1**). The best temperature
176 window was between 6 and 2 months, while that of precipitation was between 20 and 0 months
177 and that of soil moisture between 19 and 5 months before adult observation (**Fig. 2**). In all three
178 weather variables, a quadratic model fit the best, that of the maximum temperature, mean
179 precipitation and maximum soil moisture (**Fig. 3**). We use loess lines to show how the models
180 behave in relation to the climate variables. To summarize, climatic conditions during both the
181 larval and adult phases have a non-linear affect adult firefly abundance. Maximum winter and
182 spring temperatures and mean precipitation in the 20-month period prior to the observations had
183 the greatest impact on the abundance of firefly adults. Low maximum soil moisture during the 5-
184 19 months preceding the observations affected the adult abundance negatively, and high
185 maximum soil moisture positively.

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

191 Adding year as a fixed effect variable to the best fitting weather model increased the R^2 to
192 0.221 (**Table 3**), a significant improvement of the model (LRT: Chi Sq=13.473, df=1, $p < 0.001$).
193 The effect of the weather variables, including their interactions with latitude and longitude, on
194 firefly abundance did not change because of the inclusion of year (**Table 3**). The summed R^2 of

195 the fixed effect variables increased to 0.026, an increase of 0.009 which is exactly the partial R^2
196 of year. The abundance of the fireflies predicted by the best fitting model are increasing over the
197 years in the same rate as they are in the null model (slope of regression line in both **Fig. 1c** and
198 **Fig. 4**: 0.0732).

199 Summary of weather impacts on firefly abundance:

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

207

208 **Discussion**

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

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

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

237 A novel finding of our study, is the increase in firefly abundance over the period of our study.
238 We have noted three areas that may be related to this finding. The first is related to the weather
239 variables. Each of these three parameters, i.e. temperature, precipitation and soil moisture, did

240 not significantly change over our study period. It should be noted however, that over much of the
241 study area, 2012 was considered a “drought year”, with higher than normal temperatures and
242 lower than normal precipitation (Cook *et al.*, 2014). That being said, climate is warming and
243 larval development might speed up resulting in higher larval survival and higher abundance of
244 adults. Firefly larvae, like other soft bodied soil inhabitants, are dependent on soil moisture with
245 eggs laid in an area with sufficient moisture over the coming weeks to prevent desiccation.
246 (Curry, 2004). Weather variables may also increase food availability. As “eating-machines”
247 firefly larvae are dependent on prey species such as snails (Sasakawa, 2016), slugs (Kaufman,
248 1965), and earthworms (Seric & Symondson, 2016) for nourishment.

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

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

263 conservation programs and field abandonment, may therefore, provide additional habitat for
264 fireflies (Brown *et al.*, 1999; Drummond & Loveland, 2010).

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

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

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

276

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283 their creation of Firefly Watch. The authors declare no conflict of interest.

284

285 **Contribution of authors**

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

288

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367

368 **Figure legends:**

369 **Fig. 1.** Firefly observations in the USA. a: distribution of the firefly observations in the publicly
370 available data set gathered by the Museum of Science in Boston; b: distribution of the firefly
371 observations over day numbers; c: change of adjusted firefly abundance over the years. Purple
372 line: linear regression line; red line: loess line, red broken lines: one-sided standard deviation of
373 the loess line. Boxplots along axes: 50% of the observations lie within the boxes; whiskers show
374 1.5 times box range; open dots are outliers.

375

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

379

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

384

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

389

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

391

392 **Table legends:**

393 **Table 1.** Three best climate windows, one for each climate variable. Model support for the best
394 time window ($\Delta AICc$) compared to a baseline model using different aggregate statistics and
395 response curves (see Supplementary Information).

396

397 **Table 2.** Final complete model. $MaxTE_{6-2}$: maximum temperature of window 1, being the 6th to
398 the 2nd month before observation; $MeanPR_{20-0}$: mean precipitation of window 2, being the 20th
399 to 0th month before observation; $MaxPD_{19-5}$: maximum soil moisture of window 3, being the
400 19th to 5th month before observation.

401

402 **Table 3.** Final complete model plus Year. MaxTE₆₋₂: maximum temperature of window 1, being
403 the 6th to the 2nd month before observation; MeanPR₂₀₋₀: mean precipitation of window 2, being
404 the 20th to 0th month before observation; MaxPD₁₉₋₅: maximum soil moisture of window 3,
405 being the 19th to 5th month before observation.

406

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

413

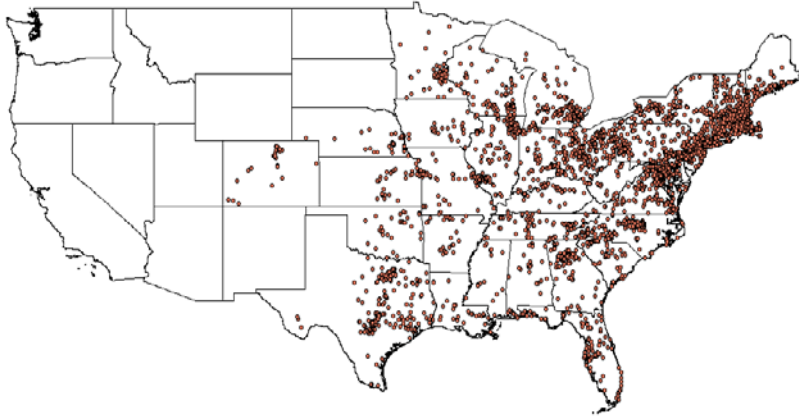
414 **Fig. S2.** Diagnostics of best model for the second climate window. a: heat plot of the mean
415 precipitation in a quadratic function; b: weight plot of the mean precipitation in a quadratic
416 function; c: scatter plot of the quadratic model predictions against the mean precipitation of the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

419

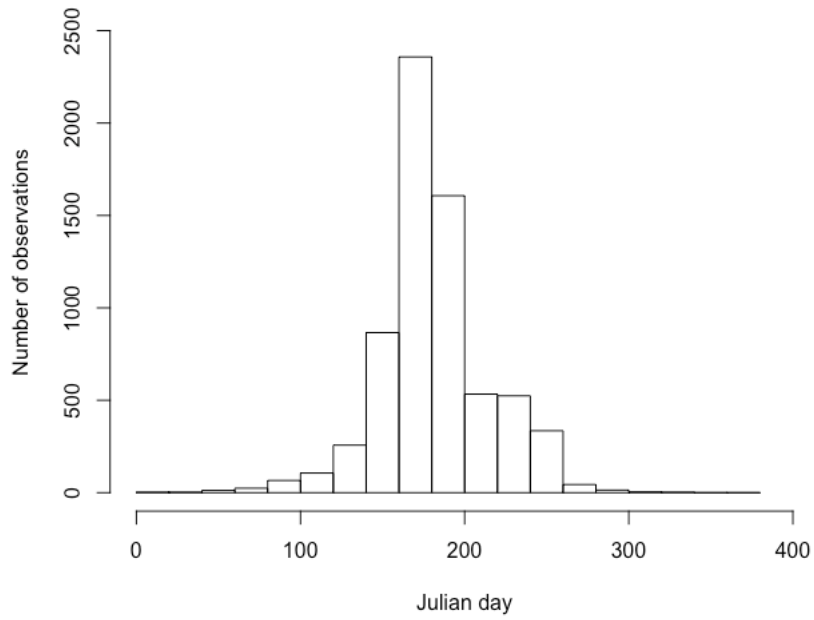
420 **Fig. S3.** Diagnostics of best model for the third climate window. a: heat plot of the maximum
421 soil moisture in a quadratic function; b: weight plot of the maximum soil moisture in a quadratic
422 function; c: scatter plot of the quadratic model predictions against the maximum soil moisture of
423 the window between month 19 and 5 before the firefly observations; d: the comparison of 100

424 random null models (right hand) and the best model for the first climate window (broken vertical
425 line).

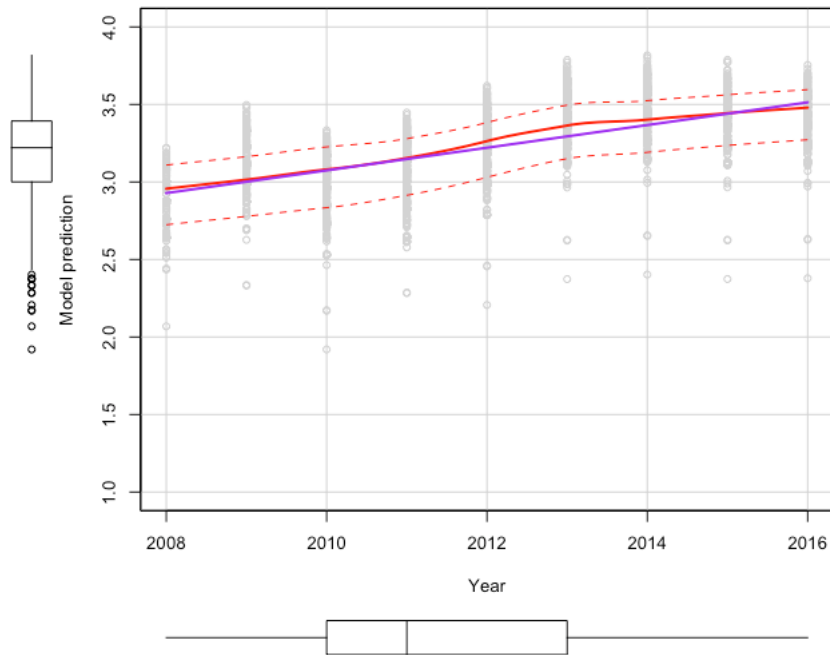
426



[Fig. 1a]



[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.

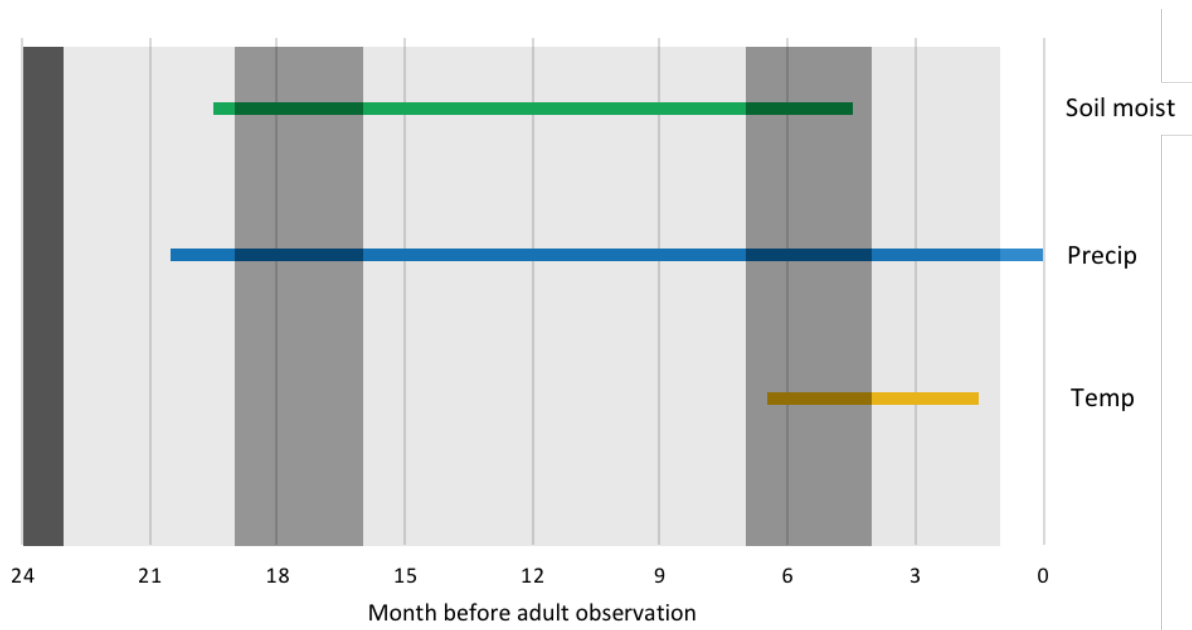
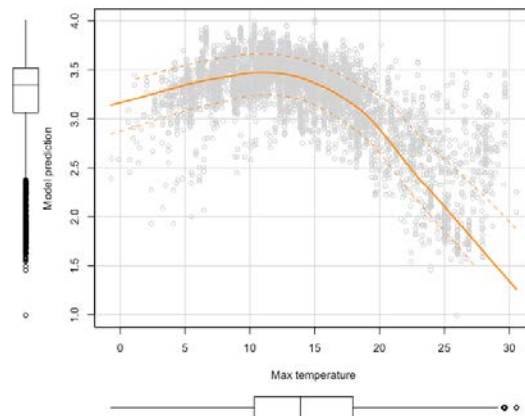
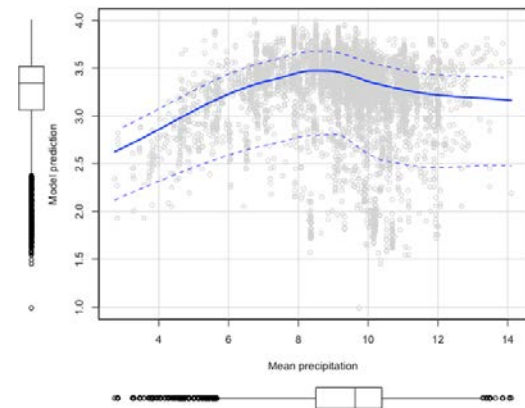


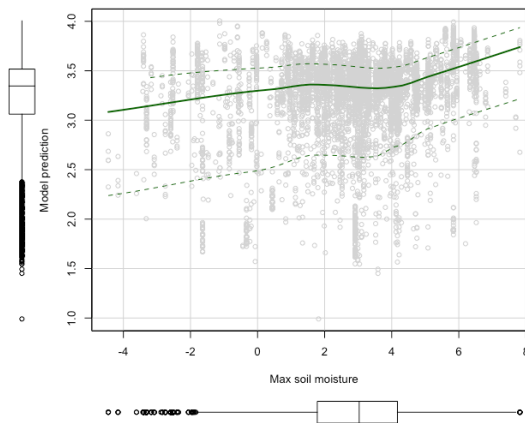
Fig. 2. Three climate windows of best fitting model. Yellow: temperature; blue: precipitation; green: soil moisture. Windows are illustrated in months before the observation. Gray shading indicates life stage of the firefly: Dark: egg; lighter: larva; middle: diapause; lightest; pupa/adult.



[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.

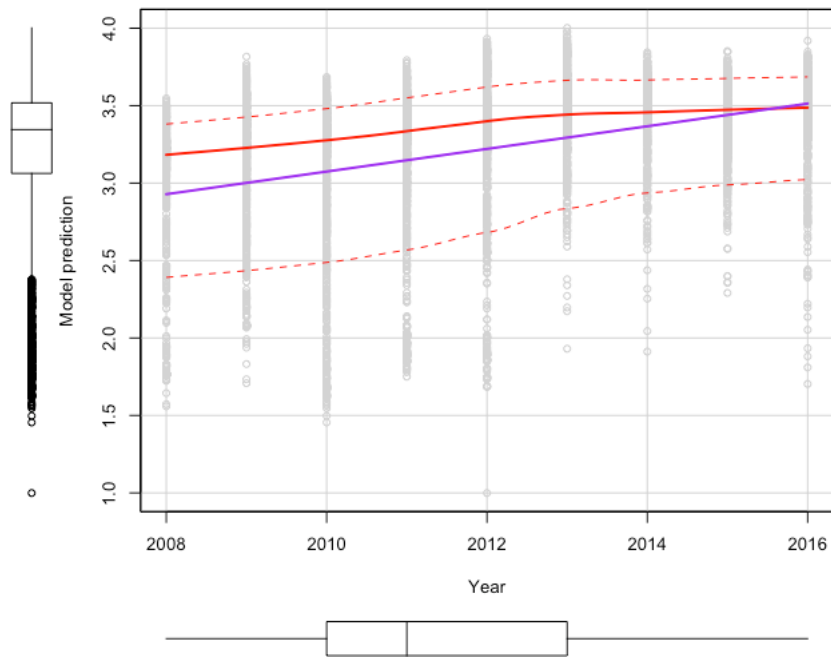
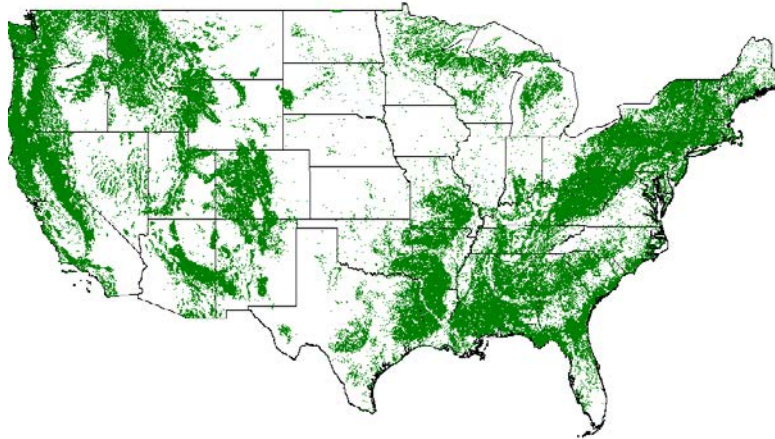
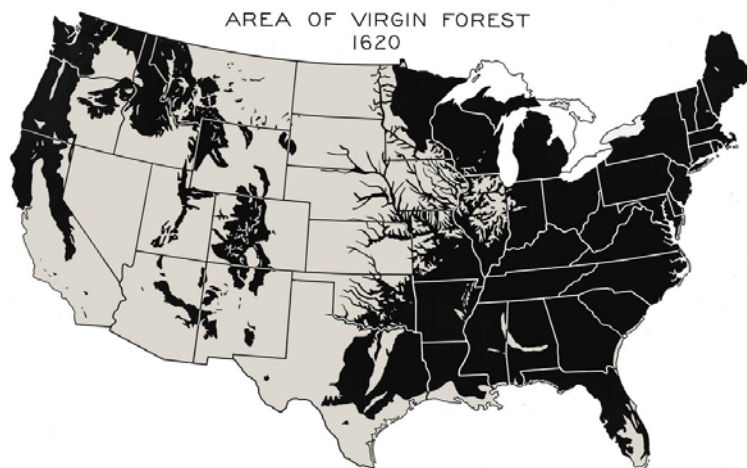


Fig. 4. Change in adjusted abundance of fireflies predicted by the best fitting weather model between 2008 and 2016. Purple line: linear regression line; red line: loess line, red broken lines: one-sided standard deviation of the loess line. Boxplots along axes: 50% of the observations lie within the 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 ($\Delta AICc$) compared to a baseline model using different aggregate statistics and response curves (see Supplementary Information).

Climate	Statistic	Function	$\Delta AICc$	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 being the 6th to the 2nd month before observation; MeanPR being the 20th to 0th month before observation; MaxPD window 3, being the 19th to 5th month before observation.

being maximum temperature
 2 0- 0 : mean precipitation
 1 9- 5 : maximum soil moisture

		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	2 0- 0	-1.3550	0.8444	-1.604	0.0009	Window 2 (Mean precipitation)
(MeanPR	2 0- 0	0.0903	0.0516	1.750		
MaxPD	1 9- 5	0.5407	0.2258	2.394	0.0009	Window 3 (Max soil moisture)
(MaxPD	1 9- 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 :Lat	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	2 0-	0.0358	0.0145	2.473	0.0023	Interaction Window 2 - Latitude
MeanPR	2 0	-0.0054	0.0066	-0.818	0.0001	Interaction Window 2 - Longitude
(MeanPR	2 0	-0.0026	0.0009	-2.924		
(MeanPR	2 0	0.0002	0.0004	0.552		
MaxPD	1 9- 5	-0.0136	0.0032	-4.176	0.0032	Interaction Window 3 - Latitude
MaxPD	1 9-	0.0015	0.0017	0.838	0.0005	Interaction Window 3 - Longitude
(MaxPD	1 9-	0.0011	0.0006	1.895		
(MaxPD	1 9-	0.0005	0.0003	1.632		
					0.0167	Fixed effect variables

Table 3. Final complete model plus Year. MaxTE₆₋₂: maximum temperature of window 1, being the 6th to the 2nd month before observation; MeanPR₂₀₋₀: mean precipitation of window 2, being the 20th to 0th month before observation; MaxPD₁₉₋₅: 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

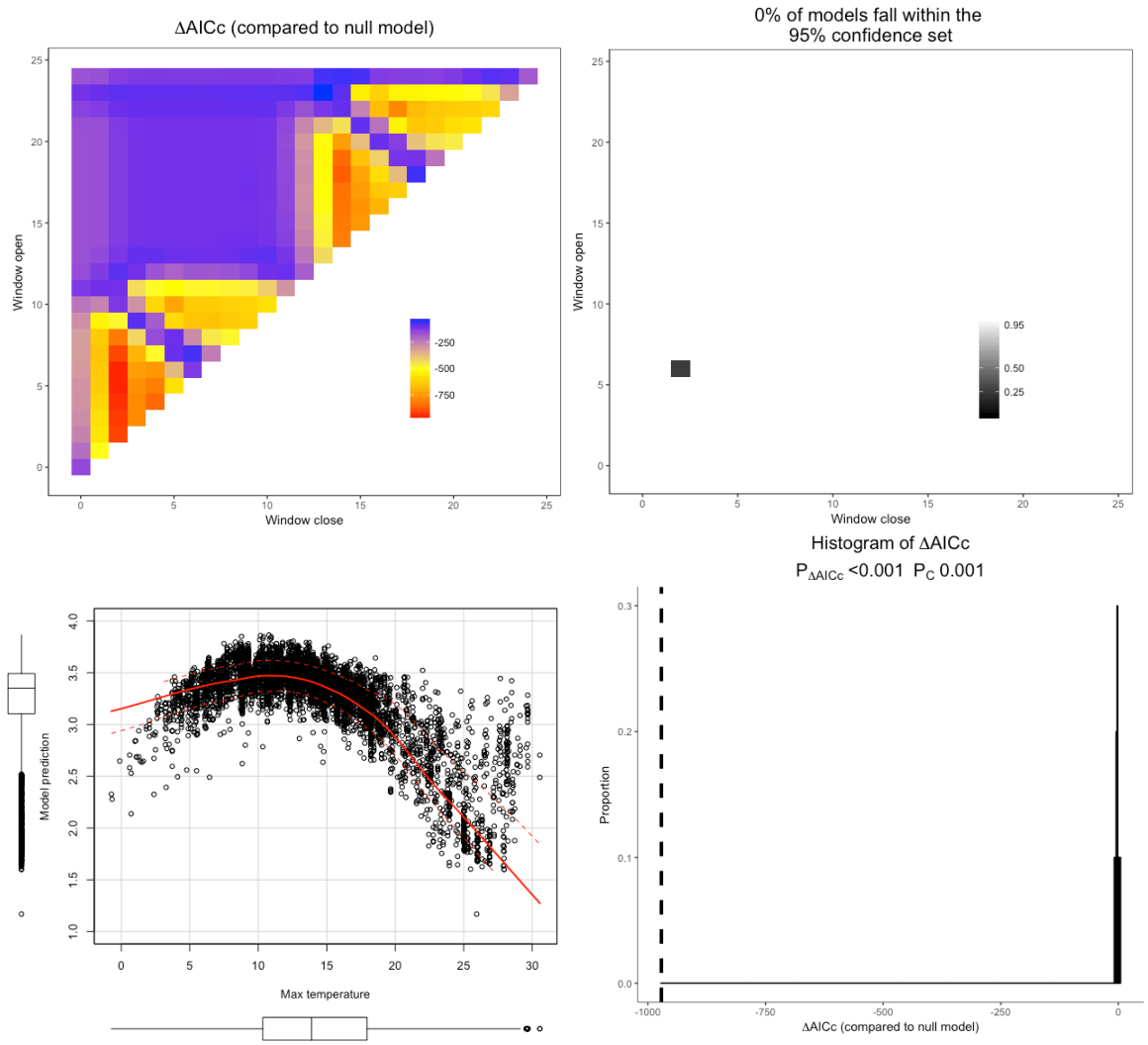


Figure S1: Diagnostics of best model for the first climate window. a: heat plot of the maximum temperature in a quadratic function; b: weight plot of the maximum temperature in a quadratic function; c: scatter plot of the quadratic model predictions against the maximum temperature of the window between 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

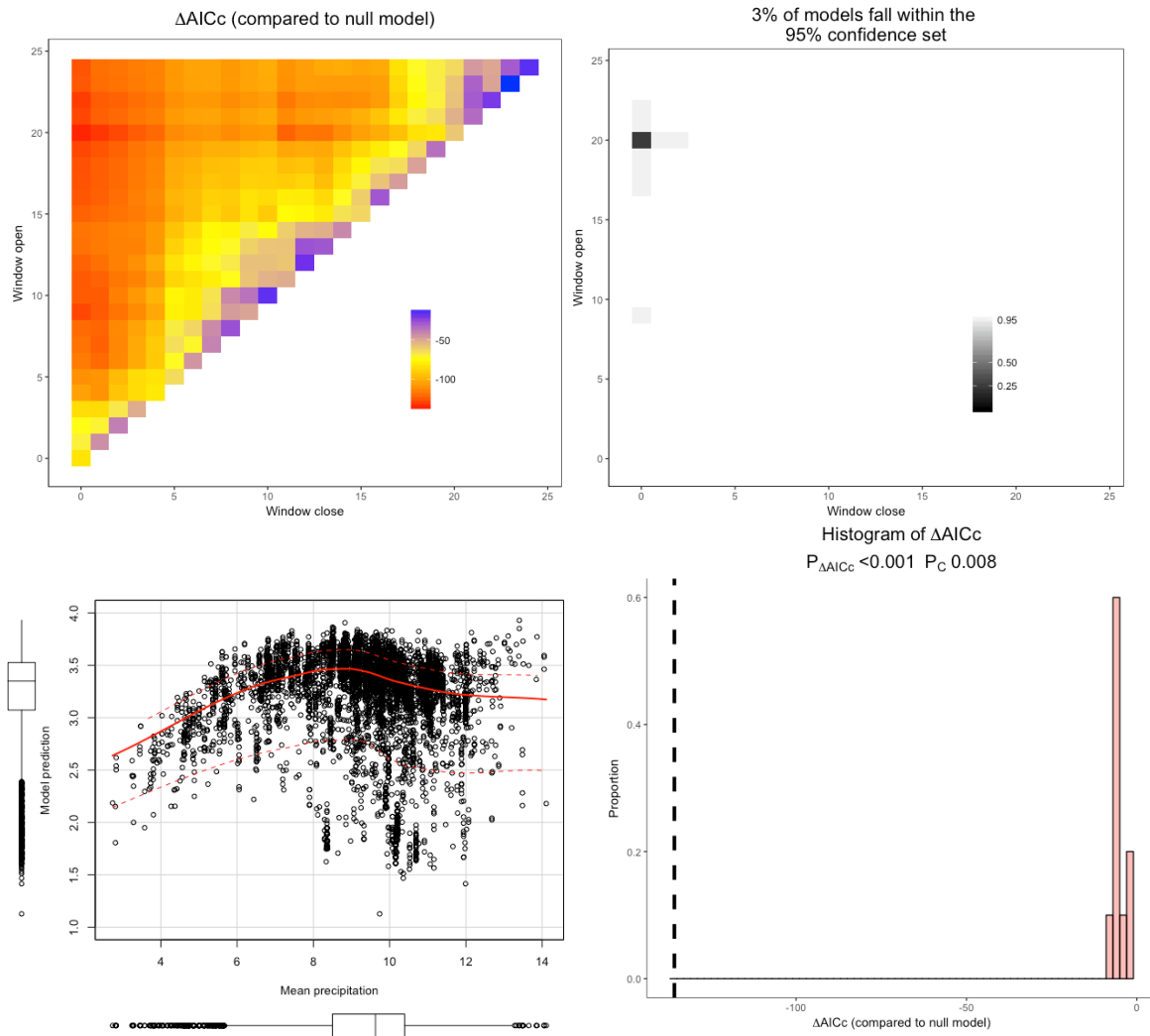


Figure S2: Diagnostics of best model for the second climate window. a: heat plot of the mean precipitation in a quadratic function; b: weight plot of the mean precipitation in a quadratic function; c: scatter plot of the quadratic model predictions against the mean precipitation of the window between 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

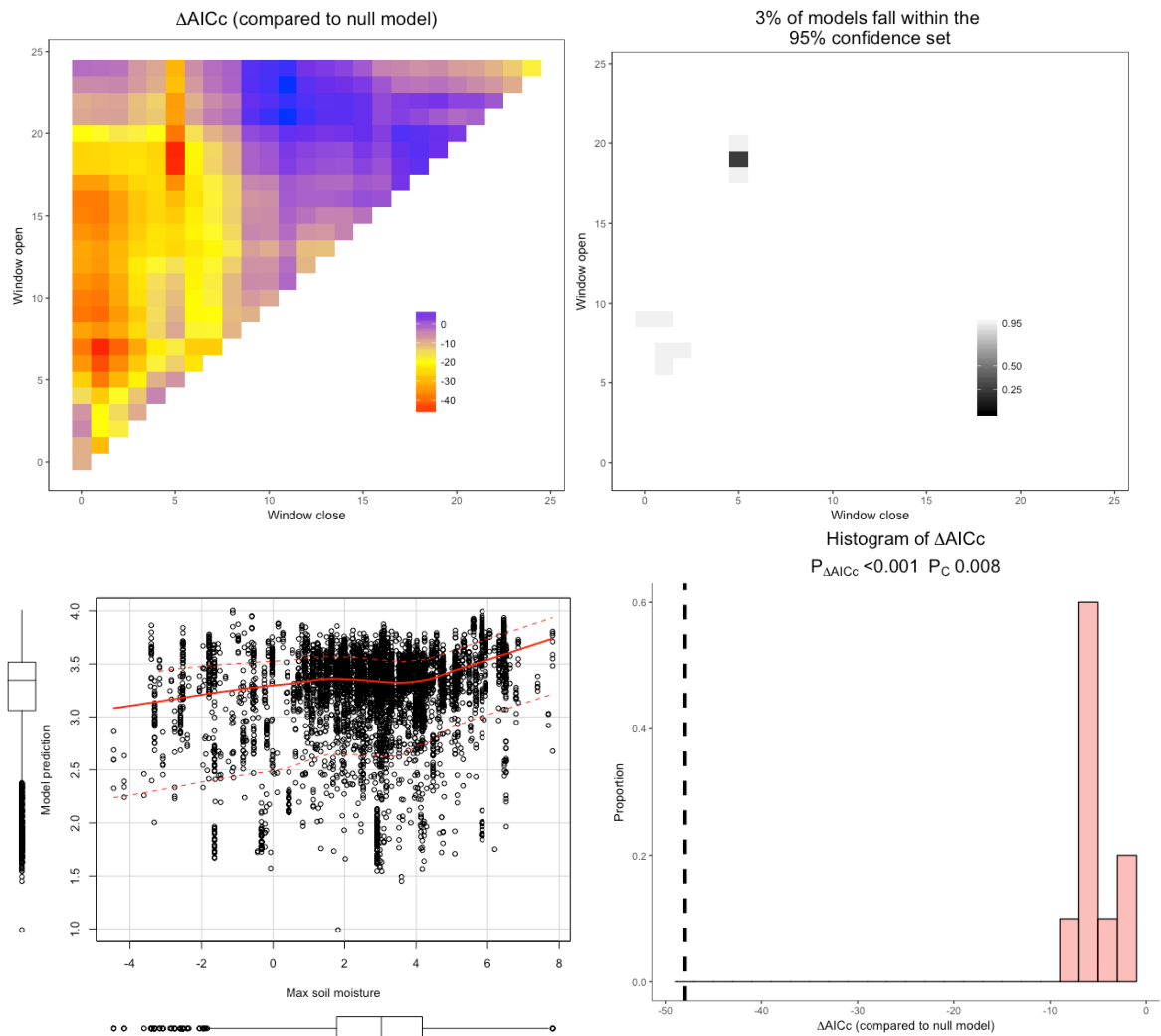


Figure S3: Diagnostics of best model for the third climate window. a: heat plot of the maximum soil moisture in a quadratic function; b: weight plot of the maximum soil moisture in a quadratic function; c: scatter plot of the quadratic model predictions against the maximum soil moisture of the window 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).