Reconstruction of a 1,910-y-long locust series reveals consistent associations with climate fluctuations in China

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It is becoming increasingly clear that global warming is taking place, however, its long-term effects on biological populations are largely unknown due to lack of long-term data. Here, we reconstructed a 1,910-y-long time series of outbreaks of Oriental migratory locusts (Locusta migratoria manilensis) in China, on the basis of information extracted from >8,000 historical documents. First by analyzing the most recent period with the best data quality using generalized additive models, we found statistically significant associations between the reconstructed locust abundance and indexes of precipitation and temperature at both annual (A.D. 1512–1911) and decadal (A.D. 1000–1900) scales: There were more locusts under dry and cold conditions and when locust abundance was high in the preceding year or decade. Second, by exploring locust–environment correlations using a 200-y moving window, we tested whether these associations also hold further back in time. The locust–precipitation correlation was found to hold at least as far back as to A.D. 500, supporting the robustness of this link as well as the quality of both reconstructions. The locust–temperature correlation was weaker and less consistent, which may reflect this link being indirect and thus more easily moderated by other factors. We anticipate that further analysis of this unique time series now available to the scientific community will continue to provide insights into biological consequences of climate change in the years to come.

Outbreak of Oriental migratory locusts (Locusta migratoria manilensis) was, together with drought and flood, considered one of the three most severe natural disasters causing damage to crop production in ancient China and has long been noted and consistently recorded in historical documents (1). The earliest known written record of locusts was found inscribed on an ox bone in Oracle Script (Jiaguwen, the earliest Chinese script) 3,500 y ago, asking: “Will locusts appear in the field; will it not rain?” (2). Starting from the History of the Former Han Dynasty (Hanshu) (B.C. 206–A.D. 25), locust records frequently appeared in standard histories (official dynastic histories) (3), and during the Ming-Qing period (A.D. 1368–1911), with the flourishing of gazetteers (local historical chronicles), thousands of detailed locust records were preserved (4).

Using locust records collected from historical documents by Chen (4) and Chen (5), Ma constructed a 1,000-y-long locust series (6). The locust index was derived by summing the reported intensity (ranked 0–5) and spatial extent (ranked 0–5) of locust outbreaks. On the basis of the reconstructed locust series, Ma reported that locust outbreaks in China show no obvious periodicity and that outbreaks generally occurred in drought years or years after floods. For the Hongze Lake region during the period 1913–1962, Ma et al. found that the largest locust outbreaks often occurred in warm and dry years (7). It was supposed that warm temperatures may benefit locusts by increasing winter survival of nymphs, whereas dryness can supply more suitable habitats along riverbanks and lakesides. Using Ma’s 1,000-y locust series (6), Stige et al. (8) found that decadal mean locust abundance was negatively associated with temperature and positively associated with the frequencies of droughts and floods. Using wavelet analysis to explore Ma’s locust series further, Zhang et al. (9) suggested that 160- to 170-y periodic cooling promotes locust outbreaks by enhancing temperature-associated drought/flood events. In contrast to the studies of Stige et al. (8) and Zhang et al. (9), using more local-scale climate data reconstructed by a general circulation model (GCM), Yu et al. (10) found positive associations between Ma’s locust index and temperature at both interannual and interdecadal scales.

These contradictory results have incited us to study the relationship of locusts and temperature further, and a crucial step is to make sure the reconstructed locust series is reliable. The reconstruction method used by Ma (6) has shortcomings that can potentially generate an increasing trend in the locust series. For example, there are higher numbers of local historical documents in more recent periods (especially during the Ming and Qing dynasties) and thus, possibly, higher chance for locust outbreaks to be reported. The territory and its administration units (province, prefecture, or county) also changed from dynasty to dynasty, which may also bias the locust estimation. When studying long-term variation in locust occurrences, such biases should be minimized.

Zhang (11) published a meteorological records compendium based on 8,228 Chinese historical documents. This compendium contains almost the entire available historical records of weather-related phenomena from the 23rd century B.C. until A.D. 1911 and includes >8,000 records of locust occurrence [twice the number Ma (6) used]. The compendium provides a unique opportunity for reconstructing a more reliable locust series for the last two millennia. In this paper, we present the reconstruction of a 1,910-y-long (A.D. 2–1911) locust abundance series and analyze its relationship with different climate proxies. As the association between temperature and precipitation in China may be scale dependent in space, we considered temperature in-...
indexes ranging from local (Beijing) to eastern China, entire China, and the northern hemisphere. To draw robust inferences, we first analyzed the more recent and reliable data at both annual and decadal scales using generalized additive models (GAMs) and then tested whether the correlations hold in the earlier parts of the period.

**Results**

**Reconstructed Time Series.** The annual locust index for A.D. 1368–1911 was constructed by multiplying the reported spatial extent (number of counties) and intensity (ranked 1–3) of locust outbreaks and then adjusting for trends in recording effort; locust index values for A.D. 2–1367 were first calculated as the number of prefectures having locust reports and then converted to the same unit as the locust index for A.D. 1368–1911. The annual locust index was natural logarithm transformed for statistical convenience. A decadal index was constructed by averaging the values. These missing values are most frequent in the period A.D. 1000–1200, and a predominant 110-y cycle was found around A.D. 1300. Missing values are most frequent in the late 15th century, where there is the number of years with locust records in a given decade. The spatial distribution of locust records and the reconstructed locust series are shown in Fig. 1. As seen from the dashed lines in Fig. 1 B and C, the reconstructed locust series contains many no-report years (hereafter referred to as missing values). These missing values are most frequent in the first 1,000 y, probably due to poor recording effort. For drawing robust inferences, we first focused the analysis on periods with few missing values: A.D. 1512–1911 for annual-scale analysis and period A.D. 1000–1910 for decadal-scale analysis. Periodicity analysis for these time periods shows that the annual series displayed a 30-y cycle around A.D. 1512–1660 and 1850 and a 10-y cycle intermittently across the whole period; for the decadal series, a predominant 110-y cycle was found around A.D. 1500–1700, together with shorter-period cycles around A.D. 1350, 1500, and 1650 (Fig. 2).

**Locusts and Climate. Correlation analysis.** Correlations between locust and climate indexes (Table 1) were calculated using both original and detrended series (SI Appendix, Fig. S6). Results revealed positive associations between locust abundance and dryness at both annual and decadal scales, although the correlation with the decadal index was statistically significant only after detrending the time series (Table 2, “dryness” and “precipitation” indexes). Further, there was a negative association between locust abundance and annual temperature (Table 2, “temp.”: Beijing, but it was statistically significant at P < 0.05 only before detrending. The decadal-scale analysis further suggested that the locust–temperature association was stronger when a temperature index representative of entire China (Table 2, “temp.Y”) was used, both compared with a regional-scale index (Table 2, “temp.W”: eastern China) and compared with indexes for northern hemisphere temperature (Table 2, “temp. M” and “temp.L”).

**Regression analysis.** Fig. 3 shows the combined effects of previous year’s locust abundance, dryness, and temperature on current year’s locust abundance, estimated using the GAM on annual-scale data for the last 400 y. This model (baseline model) explained 47.0% of the variance in the locust series. In comparison, a model with no climate predictor variable (only previous decade’s locust abundance) explained 30.8%, a model with temperature as the only climate variable explained 32.7%, and a model with only precipitation explained 45.9% (SI Appendix, Table S1). The model shows that the previous year’s locust abundance and dryness have generally positive but somewhat nonlinear effects on the current year’s locust abundance, whereas temperature has a weaker, negative effect (Fig. 3 A–C). The nonlinearities in the estimated effects suggest that the previous year’s locust abundance has an effect only after reaching a threshold value of ~1–2 on the locust index scale and dryness after reaching a value of ~2.5 on the dryness index scale. That is, there appears to be less difference in abundance of locusts between wet and normal years than between normal and dry years. Residual diagnostics (Fig. 3 D–F) show that the residuals are approximately normally distributed and independent. Results were qualitatively similar when all time series were detrended before analysis (SI Appendix, Fig. S7), suggesting that the effects were not artifacts of low-frequency trends in the data.

Fig. 4 shows the combined effects of the previous decade’s locust abundance, precipitation, and temperature on locust abundance, estimated using the GAM on decadal-scale data for A.D. 1000–1900. This model explained 25.6% of the variance in the decadal locust series. In comparison, a model with no climate predictor variable (only the previous decade’s locust abundance) explained 10.8%, a model with temperature as the only climate variable explained 17.1%, and a model with only precipitation explained 21.3% (SI Appendix, Table S1). All variables in the model showed a significant effect: previous decade’s locust abundance has a positive linear effect, precipitation has a negative nonlinear effect, and temperature has a linear negative effect on decadal mean locust abundance (Fig. 4 A–C). Residual diagnostics showed that residuals are nearly normally distributed, but not independent (significant autocorrelation at lag 3 decades, Fig. 4F), which means that some of the low-frequency variation in the response was not captured by the model. For example, there were negative anomalies in locust abundance in the two to three first centuries not captured by the predictor variables in the model (Fig. 4D). When detrending the data before analysis, the temperature effect was estimated to be nonlinear, whereas the other results remained qualitatively similar (SI Appendix, Fig. S8). The functional form of the temperature effect is therefore questionable, as the reliability of the
linear effect shown in Fig. 4 depends on how well the temperature and locust series preserve the low-frequency variation. **Correlation back to first 1,000 y.** To evaluate the consistency of the locust–climate correlations through the 1910-y period, we computed correlations between decadal locust and climate indexes using a 200-y moving window (Fig. 5). We found that the correlation between locusts and precipitation was consistently negative throughout the period investigated (A.D. 500–1900), except for a short period around AD 1200 (Fig. 5A). The correlation between locusts and temperature in China (“temp.Y,” Fig. 5B) was generally negative, but both weaker and less consistent than the locust–precipitation correlation. For example, around A.D. 0–300, A.D. 700–900, A.D. 1100, and A.D. 1400 the correlations were weak or positive. Also the correlations between locusts and two larger-scale temperature indexes varied through time (Fig. 5C and D), partly in parallel with those shown in Fig. 5B, suggesting that this variation was not solely an artifact of the temperature reconstruction method.

**Discussion**

China is the only nation with historical documents systematically recorded and well preserved, covering the past two millennia. These documents contain not only valuable information about history and culture, but also important meteorological, agricultural, and biological information. In this study we reconstructed a nearly 2,000-y locust abundance series, which is, to our knowledge, the longest observation-based time series of biological populations. The source material used in our reconstruction (11) is a long-term, systematic collection of meteorology-related records from thousands of historical documents, which contain twice the number of locust records used in the previous locust dynamic reconstruction by Ma (6). Moreover, our reconstruction has strived to overcome potential shortcomings of Ma’s locust series caused by variation in recording effort and administrative division from dynasty to dynasty. Our locust series (natural-logarithm transformed) correlates well with Ma’s for A.D. 960–1911 ($r = 0.79$), suggesting that the reconstructed locust abundance is not very sensitive to the choice of reconstruction method.

The uncertainty of the reconstruction varies between periods. During the last 400 y, recording frequency was consistently high, and we believe that both the decadal and the annual locust series have optimal quality. Before this period, recording frequency was lower, especially for the first 1,000 y. Although we have used the most comprehensive material available, many years have no locust reports at all, in some periods for >40 y in a row. Given this limitation, it is noteworthy that the negative correlation between the precipitation index and the locust index held at least back to A.D. 500 (no precipitation data were available before this time), suggesting that there is indeed a biological signal in the locust series also in the earlier periods.

The periodicity of locust outbreaks has attracted ecologists for a long time (8, 9, 19–21). Our reconstructed locust series failed to reveal consistent periodicity, but predominant periods of 10 y, 30 y, and 110 y showed transient significance in the global wavelet power spectrum (Fig. 2). Further, previous decade’s locust abundance was found to have a positive effect on decadal mean locust abundance. This finding is consistent with the periodicity analysis, which showed several time periods with cycles of ~10 y. Also the residual autocorrelation at lag 3 decades is consistent with the periodicity analysis, showing a predominant period around 30 y. As locust abundance may respond rapidly to climate conditions, such transient periodicities seem likely to result from the superimposition of several somewhat irregular climate cycles affecting rainfall and temperature (22). Other examples of possible climate-linked, transient population cycles are oscillations of budmoths in the Alps (23) and lemmings in Scandinavia (24) having disappeared with the recent warming.

**Table 1.** Climate variables used in this study

<table>
<thead>
<tr>
<th>Variable</th>
<th>Location</th>
<th>Period (A.D.)</th>
<th>Resolution</th>
<th>Seasonality</th>
<th>Data type</th>
<th>Ref.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dryness</td>
<td>Eastern China (103°–125°E, 25°–43°N)</td>
<td>1470–2000</td>
<td>Annual</td>
<td>Spring–autumn</td>
<td>Historical documents, mean of 65 stations</td>
<td>(12)</td>
</tr>
<tr>
<td>Temp.T</td>
<td>Beijing, China (40°N, 116°E)</td>
<td>1–1985</td>
<td>Annual</td>
<td>Summer</td>
<td>Stalagmite layer thickness</td>
<td>(14)</td>
</tr>
<tr>
<td>Temp.W</td>
<td>Eastern China (106°–127°E, 23°–42°N)</td>
<td>1000–1999</td>
<td>Decadal</td>
<td>Annual</td>
<td>Composite of 7 proxies</td>
<td>(15)</td>
</tr>
<tr>
<td>Temp.Y</td>
<td>China (20°–42°N, 80°–130°E)</td>
<td>1–1999</td>
<td>Decadal</td>
<td>Annual</td>
<td>Composite of 9 proxies</td>
<td>(16)</td>
</tr>
<tr>
<td>Temp.M</td>
<td>Northern Hemisphere (18°–90°N)</td>
<td>1–1979</td>
<td>Annual</td>
<td>Annual</td>
<td>Composite of 18 proxies</td>
<td>(17)</td>
</tr>
<tr>
<td>Temp.L</td>
<td>Northern Hemisphere (30°–90°N)</td>
<td>1–1999</td>
<td>Decadal</td>
<td>Annual</td>
<td>Composite of 30 proxies</td>
<td>(18)</td>
</tr>
</tbody>
</table>

**Table 2.** Correlations between reconstructed locust abundance and climate indexes

<table>
<thead>
<tr>
<th>Climate index</th>
<th>Period</th>
<th>Original</th>
<th>Detrended</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dryness</td>
<td>1512–1911</td>
<td>0.49****</td>
<td>0.48****</td>
</tr>
<tr>
<td>Precipitation</td>
<td>1000–1900</td>
<td>–0.19</td>
<td>–0.30***</td>
</tr>
<tr>
<td>Temp.T</td>
<td>1512–1911</td>
<td>–0.23**</td>
<td>–0.09</td>
</tr>
<tr>
<td>Temp.W</td>
<td>1000–1900</td>
<td>–0.16</td>
<td>–0.08</td>
</tr>
<tr>
<td>Temp.Y</td>
<td>1000–1900</td>
<td>–0.32**</td>
<td>–0.20*</td>
</tr>
<tr>
<td>Temp.M</td>
<td>1000–1900</td>
<td>–0.26</td>
<td>–0.06</td>
</tr>
<tr>
<td>Temp.L</td>
<td>1000–1900</td>
<td>–0.29</td>
<td>–0.03</td>
</tr>
</tbody>
</table>

Original: correlations between original time series. Detrended: correlations between detrended time series. P values were adjusted for autocorrelation following ref. 30.

* *P < 0.10; **P < 0.05; ***P < 0.01; ****P < 0.001.
The analysis of interannual locust dynamics for the last 400 years showed that locust abundance in a given year depends mainly on the previous year’s locust abundance and the current year’s precipitation and to a lesser extent on temperature. The effect of the previous year’s locust abundance was nonlinear, with a low effect at low values (annual locust index < 2), suggesting that it is only intermediate and large outbreaks that increase locust outbreaks in a following year. We hypothesize that this result may be related to the life history of locusts, as they form migratory swarms only after reaching a certain threshold density (5). Further, the dryness index showed a nonlinear effect, consistent with droughts (dryness index > 3) leading to more locust outbreaks through effects on the

![Fig. 3](image-url)

**Fig. 3.** Regression analysis of the effects of climate on annual-scale locust dynamics. (A–C) Estimated effects of previous year locust index, dryness ("dryness", Table 1; average of regional values ranging from 1 (very wet) to 5 (very dry)), and temperature ("temp." Table 1, unit is °C) on locusts, respectively. Points: partial residuals. Shaded areas: 95% confidence bands. Residual diagnostics reveal no residual trend (D), approximate normal distribution of residuals (E; the quantile plot of residuals forms a nearly straight line), and no significant autocorrelation function (ACF) of residuals (F: autocorrelation marginally surpassed the 5% critical limits indicated by the dotted lines for one out of the 25 time lags considered (lag = 19 y), which is roughly as expected to arise from chance alone).

![Fig. 4](image-url)

**Fig. 4.** Regression analysis of effects of climate on decadal-scale locust dynamics. (A–C) The effects of previous decade’s locust abundance, precipitation (Table 1, α-unit), and temperature (“temp.”, Table 1; α-unit), respectively, on decadal mean locust abundance. (D) Time series of residuals suggest that reconstructed locust abundance tended to be lower than predicted during the first centuries. (E) Residuals were approximately normally distributed. (F) Autocorrelation function of residuals (ACF) reveals significant positive autocorrelation at lag 3 decades.
breeding habitat, whereas current year floods (dryness index <3) have no effect on locusts compared with normal years (6).

The results of the analysis of interdecadal locust dynamics largely conformed to the results of the annual-scale analysis, showing a strong, negative effect of precipitation and a weaker, negative effect of temperature. Temperature may affect locusts in an indirect way (8, 9), as cooling decreases summer monsoon rainfall through reduced moisture transport from the surrounding oceans to the Asian continent (25, 26). The fact that it was the temperature index representative of entire China that provided the highest explanatory power, rather than the temperature index for eastern China, from where the locust data derive, is consistent with the locust–temperature association not reflecting a direct, causal link. Across the 1910 y, we found that the correlation between temperature and locusts alternated between positive and negative values (although being negative on average), which may also be more easy to explain if the effect is indirect. Other explanations for the changing temperature–locust correlation could be inaccuracies in either index or the relationship being spurious.

Global climate change has been a focus of both scientists and the public. In general, studies on climate change based on long-term biological data are extremely rare (27, 28), and our newly reconstructed locust series of 1910 y is among the longest time series of biological populations. Global warming is thought to increase the frequencies of several meteorological, agricultural, and biological disasters, for example through temperature-driven increases in insect outbreaks (29). Our study on long-term locust dynamics highlights that other climate factors than temperature per se may be driving biological populations and that predicting global warming effects on precipitation patterns should receive increased attention. As more and better proxies of the historical fluctuations in climate are becoming available to the scientific community, we anticipate that further analysis of this unique locust index (SI Appendix, Datasets S1 and S2) will provide unique insights into the biological consequences of global climate change in the years to come. In particular, we believe the locust series provides a unique opportunity to explore how climate and intrinsic population processes jointly shape population fluctuations at different timescales.

Materials and Methods
Locust Series. See SI Appendix for more detailed descriptions of the materials and reconstruction of the 1,910-y-long locust index. The annual locust abundance index was constructed on the basis of >8,000 locust records compiled in A Compendium of Chinese Meteorological Records of the Last 3000 Years (11). The total period considered (A.D. 2–1911) can be separated into two periods, A (A.D. 2–1367) and B (A.D. 1368–1911, i.e., the Ming and Qing dynasties). In period A, 598 of 639 locust records derive from standard histories (e.g., Twenty-Four Histories, Comprehensive Mirror to Aid in Government), whereas in period B, 7,519 of 7,677 locust records derive from local gazetteers (provincial, prefectural, and district gazetteers). To ensure consistent spatial coverage throughout the period studied we restricted the study area to eastern China (25–43°N, 103–125°E; Fig. 1), which is the most important agricultural region and also coincides with the core distribution area of Oriental migratory locusts in China.

The descriptions of locust outbreaks in period A are relatively simple, and the number of prefectures where locust outbreaks were recorded was chosen as the initial locust index unit for this period. Locust records in period B contain more detailed descriptions on extent and intensity of locust outbreaks, and we used county as a spatial unit and assigned each record an intensity grade ranked 1–3 according to the description of the outbreak. Initial locust index values for period B were calculated by summing the intensity grade values across all counties with recorded locusts in Y. The reconstructed locust series for period B displayed a significant increasing trend (P < 0.05), possibly because of bias from increased recording effort. The locust index for period B was therefore adjusted for recording effort, using the total number of historical records in the source archive (11) as recording effort proxy. The initial locust index values for periods A and B cannot be compared directly due to the different units. We therefore converted the initial locust index unit of period A into the recording effort-corrected unit of period B using regressive models, resulting in the 1,910-y-long annual locust time series ( Locust proxy temp.W matches our research region best, temp.Y represents the temperature of entire China, and temp.M and temp.L are two temperature proxies representing the northern hemisphere.
Statistical Analysis. Detrending. The detrended versions of the time series were residuals from GAMs of each time series as a smooth function of year (natural cubic spline with the number of knots fixed at 4, that is, with 3 df).

Correlation analysis. Ecological time series are often autocorrelated, which violates assumptions of independence in correlation tests. To deal with this issue, the effective number of degrees of freedom in significance tests of correlations was adjusted following a method proposed by ref. 30 and implemented in the package mgcv (version 1.6-2) (31, 32) in the program R (version 2.12.0) (33). The model formula we used for both annual and decadal data was

$$L_f = a + f(L_{t-1}) + g(P_T) + h(T_T) + e_t,$$

where \( L_f, P_T, \) and \( T_T \) are, respectively, reconstructed locust abundance (\( L_{\text{wm}} \) or \( L_{\text{bm}} \)), precipitation index (dryness or precipitation), and temperature index (temp.W or temp.T) for year (or decade) \( T \). The scalar \( a \) is the intercept, \( f, g \), and \( h \) are smooth functions (natural cubic splines with maximally 4 knots); and \( e_t \) is an independent and normally distributed error term.

Wavelet. Decomposition is in many respects an ideal approach for investigating the nonstationary periodicity of ecological time series. Unlike Fourier decomposition, wavelet analysis performs local timescale decomposition of a time series and thus can track the change of its periodicity over time (34, 35). In this study, we adopted the widely used “Morlet” wavelet as the mother wavelet. The significance levels (\( P = 0.05 \)) were calculated on the basis of 2,000 “Beta-Surrogate” series: surrogates of analyzed time series with similar histogram distributions and autocorrelation features (35–37).

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Supporting Information to


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Part A. Reconstruction of locust abundance series

1. Locust records in historical documents.

There are 8343 locust records in *A Compendium of Chinese Meteorological Records of the Last 3000 Years* (1), most of which derive from two types of historical documents: standard histories and local gazetteers. Standard histories, such as *Twenty–four Histories, Comprehensive Mirror to Aid in Government* and *Draft History of Qing Dynasty*, were stringently organized and compiled by the succeeding dynasty and are generally considered authoritative and credible sources of Chinese history (2). Local gazetteers (including provincial, prefectural and district gazetteers) were compiled and produced by local officials, which embrace various types of information concerning historical, geographical, economic, administrative, natural and other aspects of a locality in China. The earliest locust records appeared in *The Spring and Autumn Annals* in BC 707. However, systematic and continuous recording of locust outbreaks only starts from the year AD 2 in the *History of the Former Han Dynasty*. From then on, locust records frequently appeared in standard histories. In AD 1418, the Yongle Emperor (AD 1360–1424) ordered all counties of China to compile gazetteers, and decreed *The Guideline of Gazetteers Compilation* (3). By the end of
the Ming dynasty (AD 1368–1644), almost every county or prefecture had its own gazetteer (4) and numerous locust records were preserved.

We separated the locust records into two periods characterized by different recording frequencies as well as different types of source documents: period A (AD 2–1367) and period B (AD 1368–1911). In period A, 598 out of 639 locust records derive from standard histories, while in period B, 7519 out of 7677 locust records derive from local gazetteers. Eastern China, mainly covering the Yellow River basin and the Yangtze River basin, is the most important agricultural region in China. Almost all of the locust records are from this region, although some records appeared from areas further south in period B (Fig. S1A, B). In order to ensure consistent spatial coverage throughout the period studied we restricted our study area to the area around the middle and lower parts of the Yellow River and Yangtze River basins (yellow polygon in Fig. S1A, B). This area also coincides with the core distribution area for Oriental migratory locusts (*Locusta migratoria manilensis*) in China (5).

The descriptions of locust outbreaks in period A are quite diverse in the level of detail, and some of them are ambiguous especially in its earlier period. For example: "summer, locust"; "12 provinces had locust"; "6 states had locust"; "Province Si, Ji, Qing and Yong had locust". Period B contains more detailed descriptions of locust outbreaks. For example: "Locusts ate up all crops"; "Flying locusts darkened the sky and seriously injured crops"; "Locust outbreak from spring to autumn". Further, the spatial extent of the outbreaks in period B can generally be inferred from the information in the various local gazetteers.
Fig. S1. Spatial extent of locust records in China in period A (AD 2–1367; panel A) and period B (AD 1368–1911; panel B). The yellow polygon shows the area considered in this study. The mean frequency of locust records is indicated by background colors ranging from light-yellow (low frequency) to dark-red (high frequency). (C) Initial reconstructed locust abundance index for period A ($L_{\text{orig}}$; scale: number of prefectures with locust reports). The index is comparable within but not among four sub-periods due to variation in administrative boundaries: Han–Sui, AD 2–618; Tang, AD 618–960; Song, AD 960–1206 and Yuan, AD 1206–1368. (D) Initial reconstructed locust abundance index for period B ($L_{\text{orig}}$; scale: number of counties with locusts multiplied with outbreak intensity, ranked 1–3). (E) Final reconstructed locust abundance index for AD 2–1911 ($L_{\text{adj}}$) before log-transformation.

2. Reconstruction method

The number of prefectures with reports of locusts per year was chosen as the initial locust index ($L_{\text{orig}}$) for period A because most of locust records referred to the number or list of prefectures having locust outbreaks. For ambiguous records, the numbers of prefectures were assigned by author’s comprehension of the historical context.

Since the administrative divisions of China were not fixed but changed from dynasty to dynasty, prefecture numbers in different periods cannot be compared directly. For example, the numbers of prefectures in Later Han (AD 25–220), Three
Kingdoms (AD 220–280), Jin (AD 265–420), South and North Dynasties (AD 240–589) and Sui (AD 581–618) are 105, 158, 172, 628 and 190, respectively (6). To partly address this problem, period A was divided into four sub–periods with relatively stable administrative divisions (Fig. S1C), and prefecture numbers were standardized within each sub–period. For example, the first sub–period (AD 2–618) includes a unified and stable period Han (AD 2–220) and several divided and chaotic periods (Three Kingdoms – Sui dynasty, AD 220–618). Locust index values for this sub–period were standardized to Later Han prefecture number units by comparing outbreak locations on maps from around the time of the outbreak with a map of the administrative division of the Later Han dynasty. Note that the initial locust index values are thus comparable within but not among sub–periods.

The majority of locust records in period B come from district gazetteers (about 5700) and the rest are mainly from prefecture gazetteers (about 1400). There were 179 and 276 prefectures in Ming and Qing dynasties, respectively, and this difference could potentially bias a locust index based on numbers of prefectures with locust outbreaks (period A). However, the total number of counties changed proportionately less (being 1427 and 1579, in Ming and Qing dynasties, respectively) (6). Moreover, prefectural gazetteers were generally compiled by summarizing the information in district gazetteers under their jurisdiction, and areas of counties were relatively stable in imperial era of China (6). Thus, county was used as spatial unit for period B. Locust records in period B contain detailed descriptions about the intensity of locust outbreaks. An intensity grade ranked 1–3 was assigned to each record according to its context. Grade 1 was used for commonly occurring records, such as: “Locusts”; “Nymphs”; “Locusts ate crops”. Grade 2 was used for records of serious outbreaks, such as: “Serious locust outbreak”; “Flying locusts darkened the sky and seriously injured crops”; “Locusts ate up all crops”. Grade 3 was used for records of extreme upsurge, such as: “Locust outbreak all the year”; “Locusts covered the land nearly one foot deep”; “Serious locust outbreak from summer to autumn, locusts ate up crops, grass and small branches, darkened the sun and filled up all lower places wherever they arrived, thus causing men and horses trouble to walk”. The original locust index \( L_{\text{org}} \) for period B (Fig. S1D) was calculated by summing the intensity grade values across all counties with recorded locusts in a year (the highest grade was used if there were several locust records for a county in one year). The locust index for period B
thus integrates information about spatial extent and intensity of locust outbreaks.

The reconstructed locust series for period B displayed a significant increasing trend (P < 0.05), and its first one third seems to be abnormally lower than the rest (Fig. S1D). One likely reason for this trend is bias from increased recording effort (number of available gazetteers). The total number of meteorology–related records (including records of locusts, flood, drought, rainfall etc.) of each year in the source compendium for the locust data (1), which can be taken as a proxy of recording effort, also showed increasing trend (P < 0.001) and was abnormally low during the first one third of period B (Fig. S2A). The locust abundance series was first attempted corrected for recording effort by using the formula:

\[ L_{\text{rect}} = \left( \frac{G_{\text{max}}}{G} \right) \cdot L_{\text{orig}} \]  \hspace{1cm} (1),

where \( L_{\text{rect}} \) is the rectified locust index, \( L_{\text{orig}} \) is the original (uncorrected) locust index for period B, \( G \) is smoothed meteorological record number (Fig. S2A) and \( G_{\text{max}} \) is the maximum of \( G \) (smoothing: natural cubic spline function of year in a generalized additive model, as implemented using the \textit{gam} function in the \textit{mgcv} package (7) of the program R (8). However, \( L_{\text{rect}} \) decreased significantly (P < 0.05), indicating that this method over–compensated for lower sampling effort in the earliest period. Thus we used the formula:

\[ L_{\text{adj}} = \frac{L_{\text{rect}} + L_{\text{orig}}}{2} \]  \hspace{1cm} (2),

to balance the rectified and the original locust abundance. In contrast to \( L_{\text{orig}} \) and \( L_{\text{rect}} \), \( L_{\text{adj}} \) (Fig. S2B) showed no significant linear trend (P > 0.1).
As mentioned above, the initial locust index values for different sub–periods in period A are not comparable with each other or with locust index values for period B. These values were therefore transformed to the same unit used for period B. To do so, a regression equation was developed for each of the four sub–periods, to convert from numbers of locust–infested prefectures (the initial locust unit for period A) to the $L_{adj}$ index scale of period B. The regression equations were developed by transposing maps of period A prefecture boundaries on the county–resolved maps of locust reports in AD 1512–1911 (relative stable recording effort, see Fig. S2A), counting how many period A prefectures were infested by locusts for each of these years (i.e., given the older administrative divisions), and finally regressing these calculated prefecture numbers on the $L_{adj}$ index values for the same years. For example, given that the locations of locust outbreaks in a year in period B with $L_{adj} = 150$ fell inside of 30 prefectures in Later Han’s map (the first sub–period of period A), then the locust index value 30 in this sub–period of period A corresponds to a locust index value of 150 in period B. The maps for the four sub–periods of period A were selected from the Later Han, Tang, Song and Yuan dynasties, respectively (9). The regression equations were developed using generalized additive models of $L_{adj}$ as natural cubic spline functions of calculated prefecture number, shown in Fig. S3A–D. By combining the transformed locust index values for period A with those from period B, a 1910–years long (AD 2–1911) annual locust series was constructed (Fig. S1E, Dataset S1, Dataset S2). The reconstructed annual locust series was highly skewed, and for the convenience of statistical analysis, the final annual locust index was log–transformed: $L_{ann} = \ln(L_{adj} + 1)$. 

Fig. S2. (A) Number of all meteorology–related records in period B and smoothed line ($G$, eq. 1) used as indicator of recording effort. (B) Locust abundance index for period B adjusted for recording effort ($L_{adj}$).
Fig. S3 Regression lines used to transform locust index values (L_{orig}) for the four sub–periods in period A to the scale used in period B (L_{adj}). (A) Han–Sui, AD 2–618; (B) Tang, AD 618–960; (C) Song, AD 960–1206 and (D) Yuan, AD 1206–1368 (see Fig. S1C). Response: locust index values for years 1512–1911. Predictors: calculated numbers of locust–infested prefectures using maps for each of the four sub–periods. Deviances explained by the four regression models are: 0.936, 0.957, 0.963, and 0.911, respectively.

3. **Comparison of our locust series with Ma’s 1000–years–long locust series**

The number of locust records used to construct the new locust index is twice of that used by Ma (5), thus the new locust index should be more reliable. We here extracted Ma’s locust series for AD 960–1959 from Fig. 9A in (5) by consulting the literature sources (10, 11) used by Ma to obtain accurate temporal resolution. We can see that the two locust indices matched very well and that they have similar trends (Fig. S4A, B). The frequency distributions of the two locust series have similar patterns, although our series contain a higher proportion of intermediate values. The correlation between the two locust series is 0.79, which shows that reconstructed locust abundance is not very sensitive to reconstruction method. Periodicity analysis shows that the two locust series have similar wavelet decomposition and global spectrum pattern: two predominant frequencies appeared around periods of 110 years and 30 years, but our new locust series shows somewhat smoother frequency spectrum (Fig. S4C, D).
Fig.S4 Comparison between our newly constructed locust series and Ma’s locust series (5). The two locust series and their frequency distributions (A: newly constructed, Lann; B: Ma’s locust series). Wavelet decomposition and global power spectra of the two series (C: newly constructed; D: Ma’s locust series). See legend of Fig. 2 for wavelet decomposition.

4. Decadal locust series

A decadal locust series was constructed as described in the main text. The assumption behind the construction of this index is that years without locust reports are a random subset of the years. Alternatively, one could hypothesize that years with locusts reports were years with heavy locust outbreaks. Period A has a higher proportion of years having no locust report than period B (73% compared to 12%). If data were missing at random, one would expect similar frequency distributions of non-missing locust index values for periods A and B, whereas if missing values generally
represented low locust abundance one would expect a distribution skewed towards high values in period A. The frequency distributions for the two periods appear similar (except for a higher proportion of very low values in period A; Fig. S5), providing support for the assumption of randomness. Mean and standard deviation of the normalized decadal locust index (\(L_{dec}\)) did not differ significantly between periods A and B (P>0.10; A: Mean = –0.13, SD = 1.37; B: Mean = –0.09, SD =1.55), providing additional support for the assumption of randomness being approximately correct.

![Fig. S5 Distribution histograms of annual locust index in periods A and B.](image)

Fig. S5 Distribution histograms of annual locust index in periods A and B.
Fig. S6 Original data series with low–frequency trend imposed (left column) and their detrended version (right column). Trends were estimated using generalized additive models of the climate variable as a smooth function of year (natural cubic spline with the number of knots fixed at 4).
Fig. S7. Regression analysis of effects of climate on annual-scale locust dynamics using detrended data (shown in the right column of Fig. S6). Panels A, B and C show the effects of previous-year’s locust abundance, dryness and temperature, respectively, on locust abundance. Residual diagnostics reveal no residual trend (D), approximate normal distribution of residuals (E, the quantile plot of residuals forms a nearly straight line), and a significant negative autocorrelation function (ACF) of residuals at lag 16 (F), which is, however, unlikely to invalidate statistical inferences. The model explained 43.2 % of the variance in the detrended locust series. Estimated effects of predictor variables are qualitatively similar to results obtained using the original (not detrended) data (Fig. 3).
Fig. S8 Regression analysis of effects of climate on decadal–scale locust dynamics using detrended data (shown in Fig. S6). Panels A, B and C show the effects of previous–decade’s locust abundance, precipitation and temperature, respectively, on current decade’s locust abundance. Time–series of residuals reveals no residual trend (D). Residuals were approximately normal distributed (E). Autocorrelation function of residuals (ACF) reveals significant positive auto–correlation at lag 3 decades and negative autocorrelation at lag 4 and 7 decades (F), which are not thought to have large influence on statistical inferences. The model explained 26.3 % of the variance in the detrended locust series. Estimated effects of previous–decade locust abundance and precipitation are qualitatively similar to results obtained using the original (not detrended) data (Fig. 4), whereas the estimated temperature effect is nonlinear instead of linearly negative.
Table S1. Summary of alternative regression models of locust dynamics. Model: generalized additive model, as described in main text or with one or both climate terms removed. $L_{\text{ann}}$: annual locust index. $L_{\text{dec}}$: decadal locust index. $P$: precipitation index (annual analysis: “dryness”; decadal analysis: “precip”). $T$: temperature index (annual analysis: “temp.T”; decadal analysis: “temp.Y”). Effect: general sign of effect and approximate statistical significance (+: positive, -: negative, ~: wave–shaped; *: P<0.05, **: P<0.01, ***: P<0.001; the assumptions of independence of residuals not checked in all models). Dev.expl: proportion of deviance explained by the models.

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Dataset S1. Reconstructed annual locust time series for period A (AD 2–1367). Sub-period: Han–Sui, AD 2–618; Tang, AD 618–960; Song, AD 960–1206 and Yuan, AD 1206–1368. \( L_{\text{orig}} \): initial locust index (unit: number of prefectures with locusts). \( L_{\text{orig}} \) is comparable within, but not between the four sub-periods. \( L_{\text{adj}} \): final locust index, scaled to the same unit used for period B. The annual locust index used in the analysis and for the construction of a decadal index was log-transformed, \( L_{\text{ann}} = \ln(L_{\text{adj}} + 1) \).

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