Thousand-year-long Chinese time series reveals climatic forcing of decadal locust dynamics

Leif Christian Stige*, Kung-Sik Chan†, Zhibin Zhang‡§, David Frank¶, and Nils C. Stenseth*§

*Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, P.O. Box 1066 Blindern, 0316 Oslo, Norway; †Department of Statistics and Actuarial Science, University of Iowa, 263 Schaeffer Hall, Iowa City, IA 52242; ‡State Key Laboratory of Integrated Management of Pest Insects and Rodents in Agriculture, Institute of Zoology, Chinese Academy of Sciences, Tatun Road, Chao Yang District, Beijing 100101, People's Republic of China; and ¶Swiss Federal Research Institute for Forest, Snow, and Landscape Research, Zuercherstrasse 111, 8903 Birmensdorf, Switzerland

Communicated by Hans R. Herren, Millennium Institute, Arlington, VA, July 20, 2007 (received for review March 16, 2007)

For >1,000 years, Chinese officials have recorded the annual abundance of the oriental migratory locust *Locusta migratoria manilensis*, with the ultimate aim of predicting locust outbreaks. Linking these records with temperature and precipitation reconstructions for the period 957-1956, we show that decadal mean locust abundance is highest during cold and wet periods. These periods coincide with above-average frequencies of both floods and droughts in the lower Yangtze River, phenomena that are associated with locust outbreaks. Our results imply differential ecological responses to interdecadal and interannual climatic variability. Such frequency-dependent effects deserve increased attention in global warming studies.

agricultural pest | ecological response | frequency dependence | global warming | *Locusta migratoria manilensis*

Migratory locusts are widespread throughout Asia, Africa, Australia, and New Zealand (1, 2), potentially causing severe damage to food crops. At low densities, locusts are solitary insects that cause little damage to agriculture. However, as densities increase, the locusts may change morphologically and behaviorally into a gregarious phase, aggregating into dense and devastating swarms that can move far from the normal breeding areas of the locusts (1–4). In China, the main source of locust plagues has historically been the marshland associated with the overflow channels and flood lakes connecting the lower reaches of the Yellow and Yangtze River systems (Fig. 1), until wetland management measures from the 1950s onward reduced this breeding area (5, 6). These and other control measures largely checked locust outbreaks in China for several decades (1, 6). However, in a trend probably linked with climatic changes, locusts have again become a serious problem in China (6). As the global climate continues to change, there is a need to understand how locusts and other species respond to such low-frequency climatic variability.

Temperature and moisture are key factors affecting the biology of *Locusta migratoria manilensis*, the subspecies of *L. migratoria* dominating the productive southeastern regions of China (1) (Fig. 1). Warm temperatures enhance winter survival (7), nymph aggregation, and adult flight (1), whereas egg development is critically dependent on soil moisture being within a restricted range (1). For the period 1913–1962, in the Hongze Lake region, it was found that the largest outbreaks occurred in warm and dry years (7). For the periods 200 B.C. to A.D. 1900 (8) and A.D. 957-1956 (7–9), it has been shown that locust outbreaks typically occurred in years reported as drought years or in years after floods. In drought years, suitable habitat for the locusts to lay eggs existed along riverbanks and lakesides as the water level receded (6). Similarly, in years after floods, suitable habitat was provided in formerly flooded areas (6). These contrasting interannual responses call into question the low-frequency climatic forcing of locust populations, because both low and high precipitation seemed to facilitate locust outbreaks, but through different causal links. It is therefore difficult to predict the effects of the generally wetter and warmer East Asian climate projected by the Intergovernmental Panel on Climate Change (10). Evidence for low-frequency variability in locust abundance derives from the observation that the power spectrum of the 1,000-year locust time series (A.D. 957-1956) is red-shifted (i.e., increasing variability at longer time scales) (11), but it is not known whether the low-frequency variability in locust abundance is climatically driven. Beyond the original studies by Tsao (8) and Ma *et al.* (7, 9) and the spectral analysis by Sugihara (11), these unique locust data have until presently remained unexplored. Here we analyze the 1,000-year locust time series (9), together with newly available temperature (12) and precipitation (13) reconstructions, to explore the effects of low-frequency climatic variability on locust abundance. Analysis of millennial-length ecological and climate proxy time series allows for the discovery of dynamics that could not be revealed by shorter instrumental records.

ECOLOGY

Results and Discussion

The locust and climate proxy data are shown in Fig. 1. The highest levels of locust abundance were recorded for the 16th and 17th centuries, coinciding with unusually low temperature levels but variable levels of precipitation. The lowest locust levels were recorded for the warm and wet 12th century. On average, the abundance of locusts seems to have increased during the millennium. This increasing trend may be due to environmental forcing or increasingly better monitoring of locust activities or a combination of both. For conservativeness and for statistical stationarity considerations in modeling, we accounted for the linear trend in the statistical analysis.

The data were analyzed at a decadal scale, which was the highest possible resolution, given the temperature reconstruction and slight temporal uncertainties in the extracted locust records. After adjusting for serial residual correlation by using a subset autoregressive integrated moving average (ARIMA) (0, 0, 7) model (14), we found that decadal mean locust abundance depended negatively on temperature and that there was an interaction between precipitation and temperature: Precipitation affected locust abundance positively in cold, but not in intermediate to warm periods, whereas temperature had a negative effect at most precipitation levels, and most pronouncedly during wet periods (Fig. 2). We found no evidence for nonlinear (quadratic) climate effects.

Author contributions: L.C.S. and N.C.S. designed research; L.C.S., K.-S.C., Z.Z., and D.F. performed research; L.C.S. and K.-S.C. analyzed data; and L.C.S., K.-S.C., Z.Z., D.F., and N.C.S. wrote the paper.

The authors declare no conflict of interest.

Abbreviation: ARIMA, autoregressive integrated moving average.

§To whom correspondence may be addressed. E-mail: n.c.stenseth@bio.uio.no or zhangzb@ioz.ac.cn.

This article contains supporting information online at www.pnas.org/cgi/content/full/0706813104/DC1.

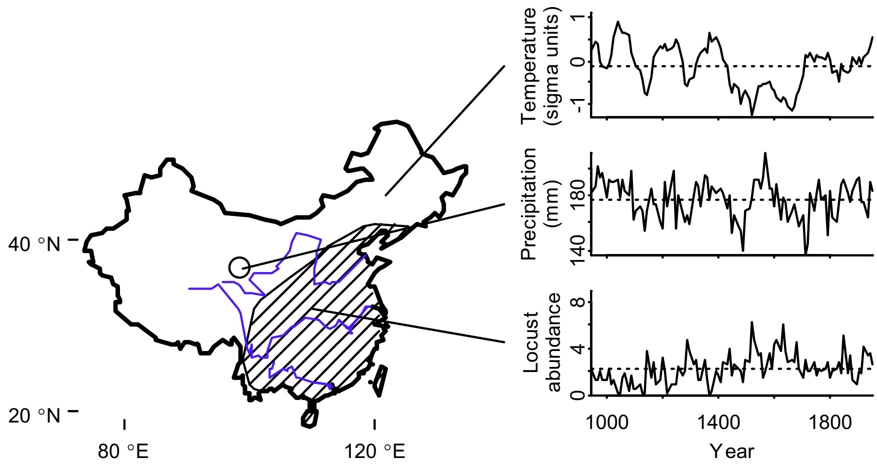

Fig. 1. One thousand years of Chinese locust and climate data, shown to the right at decadal scales. The temperature proxy (12) is a composite index for all of China. The precipitation data (13) are from northeastern Qinghai (circle). The locust data (9) are for all of China. The present distribution of *Locusta migratoria manilensis* (1) is shown by oblique lines on the map (China, excluding off-shore areas unrelated to the locust data studied in the present contribution). Large rivers are shown by blue lines and are, from north to south, the Yellow, Yangtze, and Pearl Rivers.

Spectral analysis (15, 16) was used to identify the temporal scales at which locusts and climate showed the highest (co-)variability. We found that decadal mean locust abundance possessed significant power at periods of ≈25–30, 50, and 100 years, temperature with periods of ≈40, 70, and 150–200 years, and precipitation with a period of ≈20–30 years (Fig. 3). Locusts and temperature had greatest coherence (see Fig. 3 legend) at periods of ≈50, 70, and 200 years, whereas coherence between locusts and the product of temperature and precipitation was greatest at periods of 30, 50, and 200 years (Fig. 3). These results imply that the climatic effects reported here account mainly for variability in locust abundance at time scales longer than 50 years (30 years for the interaction effect).

The negative association between low-frequency temperature variability and locust abundance contrasts with results of annual-scale analyses (7) and is not easily explainable solely in terms of temperature. The most plausible explanation is that the effect is indirect and reflects larger-scale covariation of temperature and precipitation regimes (17). An indirect effect of temperature at multidecadal scales is consistent with temperature having an opposite direct effect at annual scales, because low-frequency effects would not be detectable in short-term studies. To explore the link between the new findings and the previously established effects of floods and droughts (7–9), we assessed the association between locust abundance, the climatic proxies (temperature and precipitation) and the frequencies of floods and droughts in

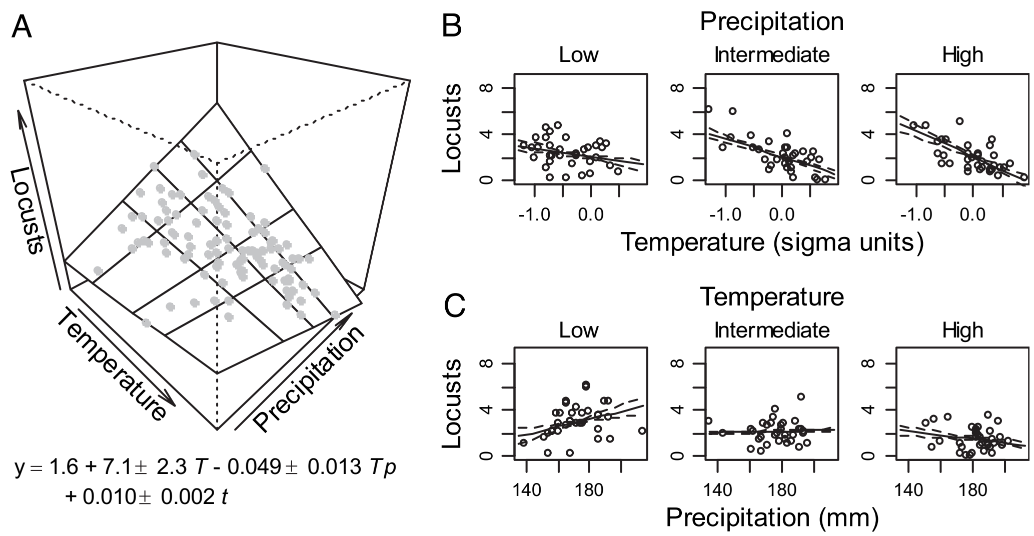

Fig. 2. Effects of climate on locust abundance (mean decadal values, scale 0–9). (*A*) The fitted effects of reconstructed temperature (T, in σ units, dimensionless units that are derived from normalizing individual proxy records before averaging; see *Materials and Methods*) and precipitation (p, in millimeters) combined. The points show the locations of the covariates. The model formula was coefficients ± SE. A linear time effect (t, range 1–101) is included as covariate. Both the included climatic effects were significant when using a sequential bootstrap test (temperature, $P = 0.005$; temperature × precipitation, $P = 0.04$), whereas precipitation had no significant main effect ($P > 0.1$). The climatic variables explained 27% of the variance in detrended locust abundance. (*B*) The observed and fitted (±1.96 SE) effects of temperature for the driest, intermediate, or wettest thirds of the decades. (*C*) The observed and fitted (±1.96 SE) effects of precipitation for the coldest, intermediate, or warmest thirds of the decades. Model predictions for the median year within each group are shown (also shown by lines in *A*).

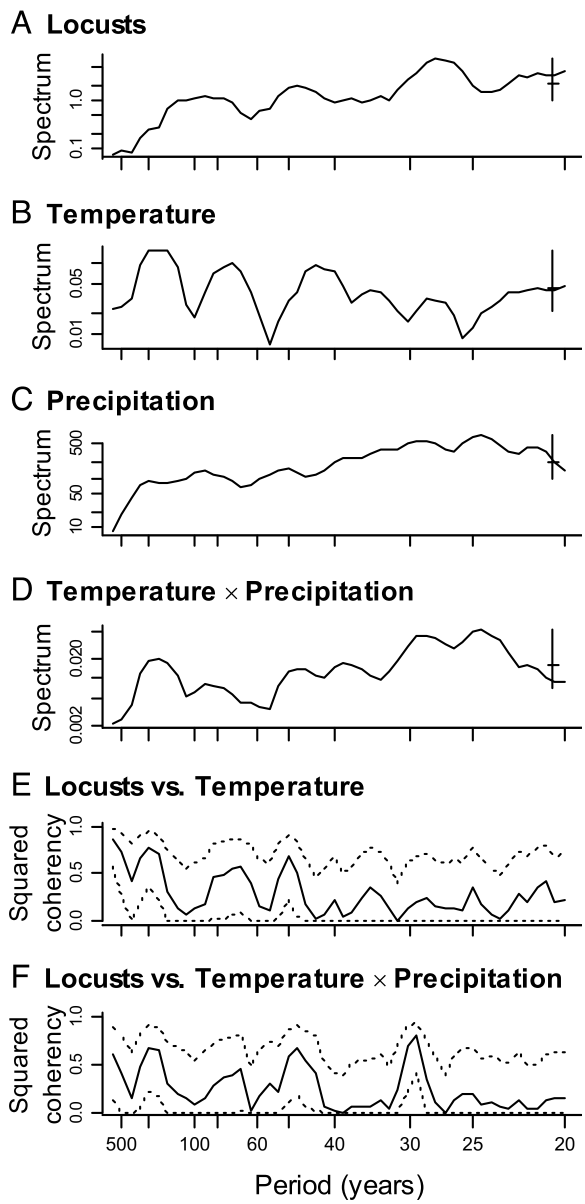

Fig. 3. Spectral analysis of differenced decadal locust and climate data. Differencing is required to render all processes stationary, and it preserves any linear relationship among the variables. (*A–D*) Periodograms smoothed by using modified Daniell smoothers (15, 16) of widths 5, with 95% confidence bars (34). (*E* and *F*) Coherency between time series, with 95% confidence bands. Temperature × precipitation represents the product of the two variables standardized to scales from 0 to 1. The coherency spectrum of two variables is a measure of the strength of their association in frequency domain, which is a function of frequency that is defined as the squared magnitude of the cross-spectrum divided by the product of the spectra of the variables (16).

the Yangtze delta since A.D. 1000 (18). We found that decadal frequencies of droughts and floods had a multiplicative effect on locust abundance: locust abundance is highest in periods with high frequencies of both floods and droughts (Fig. 4). This result is consistent with droughts and floods leading to locust outbreaks during the same or one of the subsequent years (7–9). High frequencies of both floods and droughts occur in cold and wet periods (18) (Fig. 5), exactly the same conditions that were found to enhance locust outbreaks (Fig. 2). The predictions from the two models presented in Figs. 5 and 2, having either locust abundance or the product of the frequencies of floods and droughts as response and temperature and precipitation as predictors, are highly correlated (Pearson's coefficient of correlation, $r = 0.88$), underlining this similarity. It thus appears that the effects of temperature and precipitation may be mediated through floods and droughts. A model that includes temperature, precipitation, floods, and droughts as predictor variables is slightly better than a model including only temperature and precipitation [change in Akaike's information criterion (ΔAIC) of 2.4], which is better than a model including only floods and droughts (ΔAIC = 15.9). This ranking of the models suggests that neither the temperature and precipitation nor the flood and drought reconstructions capture all of the relevant environmental variability, but that the temperature and precipitation proxies provide the strongest and clearest result. Note that because of regional differences in precipitation trends (19–21), neither the precipitation index nor the drought or flood frequencies are likely to represent rainfall across China. Droughts and floods in the Yangtze River affect the breeding habitat of locusts directly, however. The variability in the precipitation index is associated with large-scale atmospheric circulation anomalies, the latitudinal positions of winter storms being shifted southward in wet years and northward in dry years (13). We hypothesize that the temperature and precipitation proxies combined track low-frequency variability in the East Asian monsoon, which is associated with changes in both temperature and precipitation patterns in China (22–24). In terms of locust ecology, we hypothesize that temperature is negatively associated with locust abundance at a decadal and regional scale because of increases in suitable breeding habitats during cold and wet periods (with frequent droughts and floods). The positive temperature–locust association previously documented at an annual and local scale within a 50-year period (7) may be related to more direct, positive effects of temperature on, for example, survival, aggregation behavior, or migration (1, 7).

Our conclusion relating to locust dynamics and low-frequency climatic forcing should certainly be treated as an impetus for further empirical work. However, residual diagnostics showed that the presented model properly accounted for autocorrelation and nonstationarity in the data (Fig. 6), suggesting that the statistical inference is robust. We also obtained qualitatively similar results regarding the effect of temperature by using an independent warm-season temperature reconstruction for Beijing (25) [supporting information (SI) Figs. 7 and 8], suggesting that the main findings do not rely critically on the use of a particular climate index. It should also be kept in mind that the locust index represents a large area with heterogeneous locust dynamics (e.g., the number of generations per year decreases from 3–4 in the south to 1–2 in the north; refs. 1 and 4), and data of higher spatial resolution would be needed to assess how local and regional dynamics interact. It would be particularly instructive to explore to what extent the reported decadal and regional locust–climate association reflects the effects of environmental factors triggering locust outbreaks or effects of factors responsible for allowing swarming locusts to maintain their populations outside the outbreak areas.

Our analyses have found that cold climatic conditions are associated with high frequencies of both droughts and floods and, hence, with more locust outbreaks in China. Our findings thus suggest that the projected warmer East Asian climate, with increased risk of extremely wet and decreased risk of extremely dry seasons (10), will lead to unfavorable breeding conditions for locusts. However, because regional downscaling of model-based rainfall projections remains uncertain (10), and because the hydrological responses to anthropogenically and naturally forced temperature increases may differ (26), our findings add a further impetus to the urgency of assessing the direct and indirect effects of global warming on ecological systems.

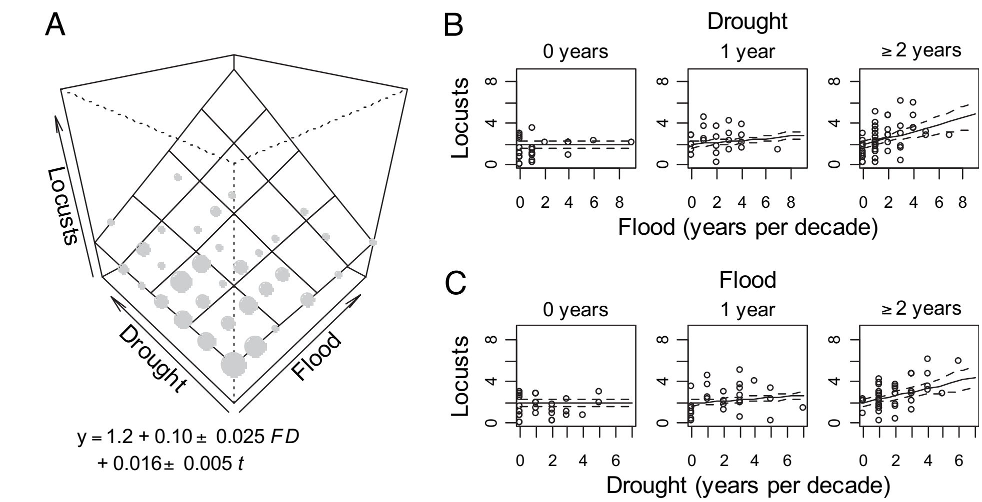

Fig. 4. Effects of droughts and floods on locust abundance (mean decadal values, scale 0–9). (*A*) The fitted effects of flood (*F*, number of flood years per decade) and drought (*D*, number of drought years per decade). Droughts and floods may occur in the same year. Point sizes reflect the number of decades the given combinations of the covariates occur. The model formula was coefficients ± SE. A linear time effect (*t*, range 1–96) is included as covariate. The drought × flood interaction effect is highly significant ($P < 0.0001$, bootstrap test; neither the main effect of drought nor flood remained in the model). The data were analyzed by using a subset ARIMA (0, 0, 7) model, including moving average (MA) parameters 1, 2, 7 (estimated, respectively, as 0.22 ± 0.11 SE, 0.26 ± 0.09 SE, and −0.16 ± 0.09 SE; residual variance of 0.99). Droughts and floods explained 20% of the variance in detrended locust abundance. (*B*) The observed and fitted (±1.96 SE) effects of flooding for decades with 0, 1, or 2–7 years with drought. (*C*) The observed and fitted (±1.96 SE) effects of drought for decades with 0, 1, or 2–9 years with flood.

It was the Emperor of China who initiated the annual recording of locust abundance >1,000 years ago, aiming at using the acquired knowledge to obtain warnings of future locust outbreaks. Today, the Emperor's initiative may help us in preparing for the ecological effects of future climate change. The evidence for opposing biological responses to short- and long-term climatic variation may alter the picture of climatic forcing mechanisms. This frequency-dependent response deserves attention in ecological studies, particularly in those dealing with long-term projections.

Materials and Methods

Annual locust abundance records for the period 957-1956 were extracted from fig. 9*A* of Ma (9), who obtained the data by consultation with various sources of the older Chinese literature (e.g., refs. 27 and 28). The locust index is assumed to refer only to the subspecies *L. migratoria manilensis* (9). The index was derived by summing (*i*) the reported intensity of locust outbreak (ranked 0–5) based on locust reports and/or damages (e.g., no reports of locusts, reports of locusts, medium or heavy damage, sky full of locusts, or no harvest of crops) and (*ii*) the spatial

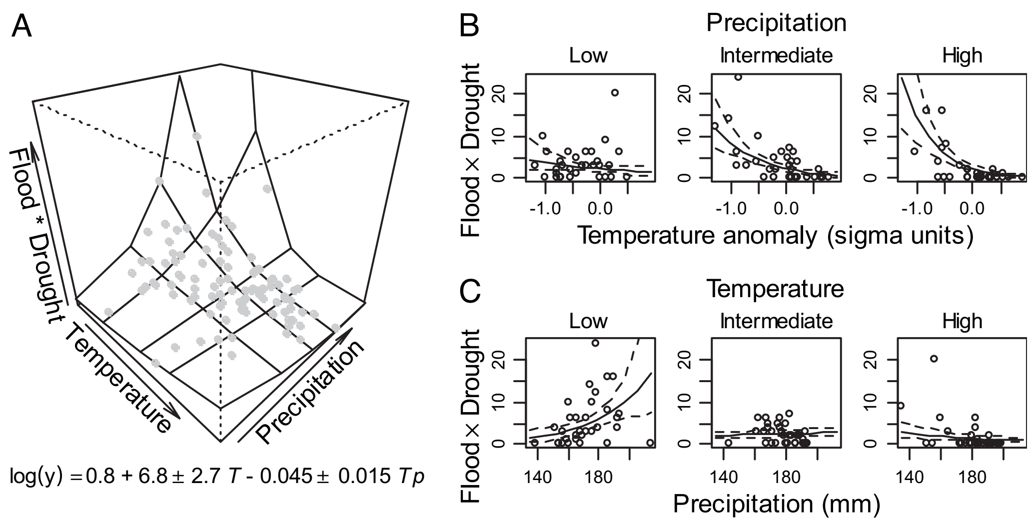

Fig. 5. Effects of climate on the occurrence of flood and drought (the product of their decadal frequencies). (*A*) The fitted effects of reconstructed temperature (*T*, in σ units) and precipitation (*p*, in millimeters) combined. The points show the locations of the covariates. The model formula was coefficients ± SE. Both the included climatic effects were significant (temperature: $\chi^2_{94} = 97.0$, $P < 0.0001$; temperature × precipitation: $\chi^2_{93} = 43.1$, $P < 0.01$; sequential test), whereas precipitation had no significant main effect ($\chi^2_{93} = 0.28$, $P > 0.1$). The model was fitted by using a generalized linear model with log link (family quasipoisson) and explained 27% of the null deviance. (*B*) The observed and fitted (±1.96 SE) effects of temperature for the driest, intermediate, or wettest thirds of the decades. (*C*) The observed and fitted (±1.96 SE) effects of precipitation for the coldest, intermediate, or warmest thirds of the decades. Model predictions for the median year within each group are shown (also shown by lines in *A*).

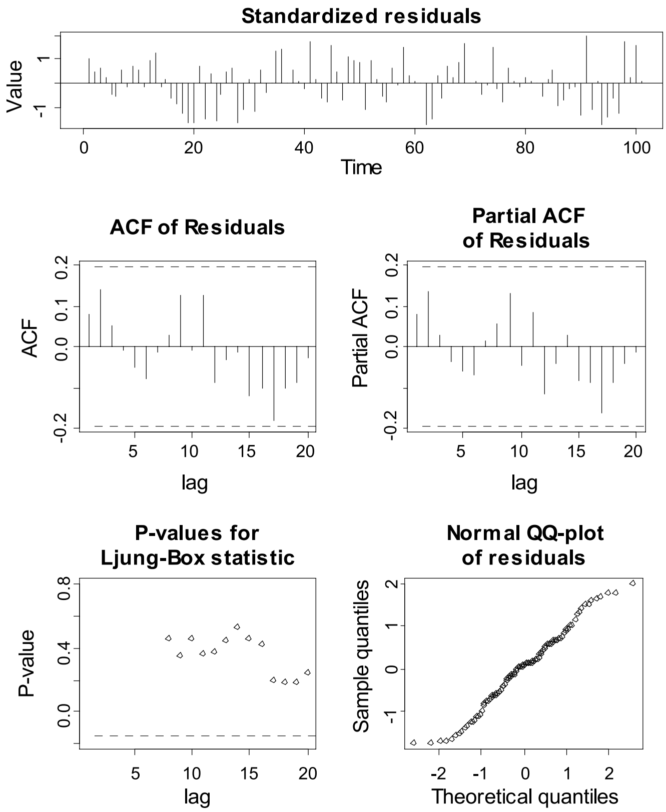

Fig. 6. Residual diagnostics for the subset ARIMA (0, 0, 7) model of decadal mean locust abundance in response to temperature and precipitation. There are no evident trends or patterns in the standardized residuals. The standardized residuals are not significantly autocorrelated, as evidenced by the fact that the autocorrelation function (ACF), the partial ACF, and the Ljung-Box statistic do not reach significance (stippled lines). The normal quantile–quantile (QQ) plot shows that the residuals are approximately normally distributed.

extent of the reported occurrence of locusts in China (ranked 0–5) based on the extent of counties reporting locusts (9).

Decadal mean temperature for the same period was reconstructed by combining multiple area weighted paleoclimate proxy records obtained from ice cores, tree rings, lake sediments, and historical documents (12, 29). Before averaging, individual proxy records were first normalized to zero mean unit variance by 12, thus yielding a dimensionless temperature index expressed in σ units. The index is representative for all of China and shows good agreement with temperature reconstructions for the Northern Hemisphere (Pearson's coefficient of correlation, r, ranging from 0.45 to 0.56) (12). Annual precipitation for the same period was reconstructed from living and archeological juniper samples from northeastern Qinghai province, China (13). This index correlates with observed annual (July–June) precipitation in the area (r = 0.70), and its low-frequency variability matches reasonably well a historic moisture index (19) for semiarid regions of China (13).

In the analyses, decadal mean locust abundance was treated as the response variable, and decadal mean temperature and precipitation were considered explanatory variables along with their squared and interaction terms. The optimal correlation structure of the subset ARIMA model (14, 15) was chosen by minimizing AIC, first selecting autoregressive (AR) and moving average (MA) orders and then removing nonsignificant AR and MA parameters. The final subset ARIMA (0, 0, 7) model only included MA parameters for lags 4 and 7 (estimated as -0.30 ± 0.12 SE and -0.32 ± 0.11 SE, respectively; residual variance of 0.81), with the other MA coefficients set to zero. Subset ARIMA models are often used to obtain parsimonious models that may be more interpretable than nonsubset ARIMA models (see refs. 15, 30, and 31). The significant MA coefficients at lags 4 and 7 suggest the presence of residual cyclical patterns beyond those induced by the covariates in the model, which reflects the fact that the climatic proxies used herein did not completely capture the past climatic conditions. Also note, however, that resonance between external forcing and intrapopulation processes might induce population oscillations of lower frequencies than those of the climatic forcing factors (32). Time was included as a covariate to account for nonstationarity in the time series: locust abundance increased significantly, by ≈0.2 unit per 100 years (P = 0.001, bootstrap test) (with climatic variables in the model the estimated increase was 0.1 unit per 100 years, P = 0.05). There were no significant quadratic or cubic trends ($P > 0.1$, bootstrap tests). In bootstrap tests, null distributions for model coefficients were generated from 10,000 sets of randomly generated, independent locust and climate time series, each having trends (except in tests of time effects) and autocorrelated errors similar to the observed data. ARIMA models were fitted by using the ARIMA function of the base package of the program R (www.R-project.org) (33). The spectrum function in the base package of R was used for spectral analysis (34).

We thank G. Sugihara for the initial interaction with N.C.S. regarding the 1,000-year-long locust series, J. Esper for help with our evaluating and accessing of climate data, and P. Tarasov (Institut für Geologische Wissenschaften, Freie Universität Berlin, Berlin, Germany) for providing the precipitation reconstruction. A. Hassanali and H. Herren provided constructive comments on the manuscript, as did four anonymous reviewers on an earlier version of the paper. The work reported in this paper was made possible through core-funding to the Centre for Ecological and Evolutionary Synthesis (CEES), the Swiss National Science Foundation (National Centre of Competence in Research, Climate), and the Chinese Academy of Science Albert Einstein Professorship.

1. Chen Y-L (1999) *The Locust and Grasshopper Pests of China* (China Forestry Publishing House, Beijing).
2. Centre for Overseas Pest Research (1982) *The Locust and Grasshopper Agricultural Manual* (Centre Overseas Pest Res, London).
3. Tanaka S, Zhu D-H (2005) *Appl Entomol Zool* 40:257–263.
4. Uvarov B (1977) *Grasshoppers and Locusts: A Handbook of General Acridology* (Cambridge Univ Press, Cambridge, UK), Vol 2.
5. Farrow R (1984) *J Aust Inst Agric Sci* 50:161–166.
6. Zhang Z, Li D (1999) *Ecol Res* 14:267–270.
7. Ma S-C, Ting Y-C, Li D-M (1965) *Acta Entomol Sin* 14:319–338.
8. Tsao C (1950) *Chin J Agric Res* 1:57–66.
9. Ma S-C (1958) *Acta Entomol Sin* 8:1–40.
10. Christensen JH, Hewitson B, Busuioc A, Chen A, Gao X, Held I, Jones R, Kolli RK, Kwon W-T, Laprise R, *et al.* (2007) in *Climate Change 2007*: *The Physical Science Basis*, *Summary for Policy Makers*, *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (Cambridge Univ Press, Cambridge, UK).
11. Sugihara G (1995) *Nature* 378:559–560.
12. Yang B, Bräuning A, Johnson KR, Yafeng S (May 11, 2002) *Geophys Res Lett*, 10.1029/2001GL014485.
13. Sheppard PR, Tarasov PE, Graumlich LJ, Heussner K-U, Wagner M, Österle H, Thompson LG (2004) *Clim Dyn* 23:869–881.
14. Durbin J, Koopman SJ (2001) *Time Series Analysis by State Space Methods* (Oxford Univ Press, Oxford).
15. Cryer J, Chan KS (2007) *Time Series Analysis* (Springer, New York).
16. Priestley MB (1981) *Spectral Analysis and Time Series* (Wiley, London).
17. Treydte K, Schleser GH, Helle G, Frank DC, Winiger M, Haug GH, Esper J (2006) *Nature* 440:1179–1182.
18. Jiang T, Zhang Q, Blender R, Fraedrich K (2005) *Theor Appl Climatol* 82:131–141.
19. Gong G, Hameed S (1991) *Int J Climatol* 11:271–283.
20. Qian W, Zhu Y (2001) *Clim Change* 50:419–444.
21. Qian W, Lin X (2005) *Meteorol Atmos Phys* 90:193–207.
22. An Z (2000) *Quatern Sci Rev* 19:171–187.
23. Zhu J, Wang S (July 19, 2002) *Geophys Res Lett*, 10.1029/2001GL013997.

24. Shen C, Wang W-C, Gong W, Hao Z (February 1, 2006) *Geophys Res Lett*, 10.1029/2005GL024804.
25. Tan M, Liu T, Hou J, Qin X, Zhang H, Tieying Li T (June 19, 2003) *Geophys Res Lett*, 10.1029/2003GL017352.
26. Allen MR, Ingram WJ (2002) *Nature* 419:224–232.
27. Chen G (1939) *The Records of Disasters in Chinese History* (Jinan Univ Book Series, Jinan, China).
28. Chen J (1936) *Bull Zhejiang Entomol Bureau* 5:188–241.
29. Yang B, Bräuning A, Johnson KR, Yafeng S (2002) *Temperature Variation in China During the Last Two Millennia*, International Geosphere–Biosphere Programme PAGES/World Data Center A for Paleoclimatology (Natl Oceanic Atmos Admin/Natl Geophys Data Center Paleoclimatol Prog, Boulder, CO), Data Contribution Series 2002-061.
30. Box GEP, Jenkins GM, Reinsel GC (1994) *Time Series Analysis*: *Forecasting and Control* (Prentice Hall, Englewood Cliffs, NJ).
31. Tong H (1977) *J R Stat Soc A* 140:432–436.
32. Bjørnstad O, Fromentin J-M, Stenseth NC, Gjøsæter J (1999) *Proc Natl Acad Sci USA* 96:5066–5071.
33. R Development Core Team (2006) *R*: *A Language and Environment for Statistical Computing* (R Foundation Stat Comput, Vienna).
34. Venables WN, Ripley BD (2000) *Modern Applied Statistics with S-Plus* (Springer, New York), 3rd Ed, pp 405–412.