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Recurrent Insect Outbreaks Caused by Temperature-Driven Changes in System Stability

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Insects often undergo regular outbreaks in population density but identifying the causal mechanism for such outbreaks in any particular species has proven difficult. Here, we show that outbreak cycles in the tea tortrix *Adoxophyes honmai* can be explained by temperature-driven changes in system stability. Wavelet analysis of a 51-year time series spanning more than 200 outbreaks reveals a threshold in outbreak amplitude each spring when temperature exceeds 15°C and a secession of outbreaks each fall as temperature decreases. This is in close agreement with our independently parameterized mathematical model that predicts the system crosses a Hopf bifurcation from stability to sustained cycles as temperature increases. These results suggest that temperature can alter system stability and provide an explanation for generation cycles in multivoltine insects.

One of the fundamental tenants in insect ecology is that temperature is a pace-maker of all vital rates (*1*, *2*). Temperature has a direct impact on ontogenetic development, survival, and reproduction and, through these, an indirect impact on generation time and population growth rate (*3*, *4*). The reliability by which temperature can predict development in insects is used to predict the number of generations per year (voltinism), and the timing at which different life stages appear (*5*, *6*). The latter is a critical component for scheduling pest control. While the influence of temperature on individual-level life-history traits is well understood, the impact on population-level dynamics, such as population cycles or outbreak frequency, is less clear. For multivoltine insects, temperature is thought to contribute to insect outbreaks early in the season when climate has helped synchronize the population stage

structure through either induction of diapause (*7*, *8*) or differential winter mortality (*9*). Mathematical theory suggests that temperature could also destabilize dynamics of ectotherms (*10*–*13*); however, the role that temperature plays in sustained cycles or overall dynamics in real systems is poorly understood.

The smaller tea tortrix, *Adoxophyes honmai*, is a multivoltine lepidopteran that undergoes multiple outbreak cycles each year (*14*). The insect is a pest on tea plantations and of significant economic concern throughout Japan. Outbreak densities are higher at the peaks than the troughs by a rate between 100- and 4000-fold (Fig. 1). Our previous work (*15*) showed that summer outbreaks are most consistent with intraspecific mechanisms that involve the strongly stage-structured nature of the insect life cycle. The outbreak dynamics themselves, however, are highly variable throughout a season (Fig. 1), with outbreaks occurring during the warmer months of the season (typically May to September) but not during the cooler months. The classic explanation for such a pattern is that cool winter temperatures synchronize population stage-structure, which leads to transient generation cycles (*5*). This mechanism

generally results in cohort synchrony and outbreak amplitudes that are greatest at the start of the season and decay through time. The decay in cohort synchrony through time is observed in other structured systems (*16*) and occurs because developmental plasticity and environmental variability cause development to become increasingly uncorrelated. However, in the smaller tea tortrix, developmental synchrony is enhanced rather than eroded through the season. We, therefore, studied an alternative explanation, motivated by mathematical models, whereby sustained cycles are the result of temperature-dependent changes in system stability—seasonal temperature increases cause the system to destabilize each spring, and cooling temperatures cause the system to restabilize each fall.

To test this idea, we studied the relation between temperature and stability in a stage-structured model of the tortrix life cycle (supplementary text). The model, which is a set of coupled integral delay-differential equations parameterized with individual-scale laboratory data, provides theoretical predictions that are fully independent of the time-series data and so can be used for a rigorous test of the hypotheses. Our model represents a dynamic description of life history that incorporates a more realistic nonlinear function for ontogenetic development than is found in the classic degree-day model from insect ecology (*17*). We studied local stability of the models using characteristic equations (supplementary text). The model predicts that the population dynamics should be strongly temperature-dependent with decay to extinction at low temperatures, transient fluctuations around a stable equilibrium at intermediate temperatures, and sustained generation cycles at higher temperatures (Fig. 2 and supplementary text). The predicted transition from stability to cycles is via a supercritical Hopf bifurcation at 12.6°C. This class of bifurcation generates a smooth increase in amplitude with increasing temperature once past the critical temperature threshold. The model provides two testable predictions that can be used to evaluate if the dynamics are driven by temperature-dependent destabilization: (i) cycle amplitude should show a threshold response to temperature, and (ii) above the thresh-

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Fig. 1. Adult densities of the smaller tea tortrix, *Adoxophyes honmai*, over 51 years from light-trap census at the Kagoshima tea experiment station in Japan. (**A** and **B**) Adult densities. Sqrt, square root. (Right) Sample dynamics for years with relatively low-amplitude (**C**) and high-amplitude (**D**) outbreak cycles. Horizontal green bars show periods of time when different pest control strategies were used at the tea station (starting from the bottom: organophosphorus, carbamate, pyrethroid, insect growth regulator, *Bacillus thuringiensis*, and/or mating disruption compounds).
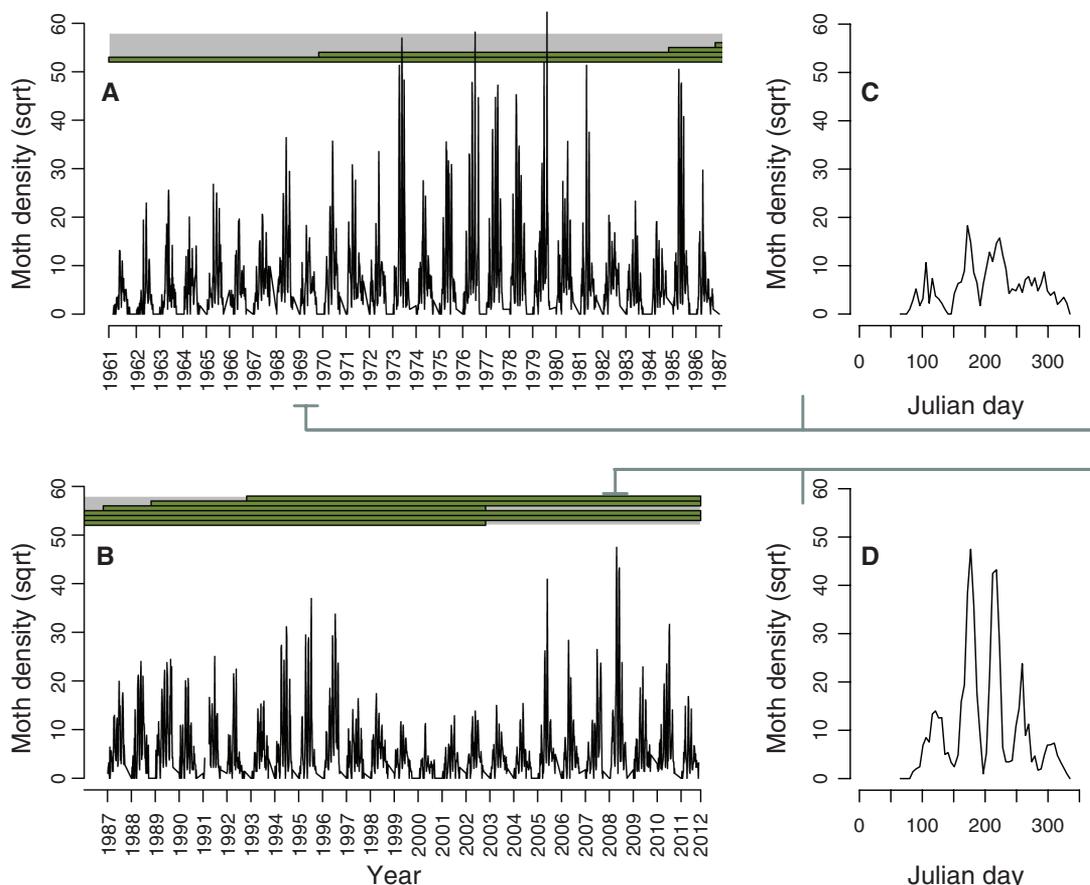

Fig. 2. Predicted temperature-driven changes in stability. (**A**) The system heads toward extinction at low temperature (gray), followed by stable population dynamics with densities that increase as temperature warms (yellowish white), followed by outbreak cycles at high temperatures with amplitudes that increase with temperature (blue). Solid black line denotes the stable equilibrium, dashed black line the unstable equilibrium. The solid blue line shows the minimum and maximum of outbreak cycles. Mean monthly temperature for the Kagoshima tea station is shown in red. (**B**) An example of predicted moth densities through time from the independently parameterized model driven with observed temperatures.
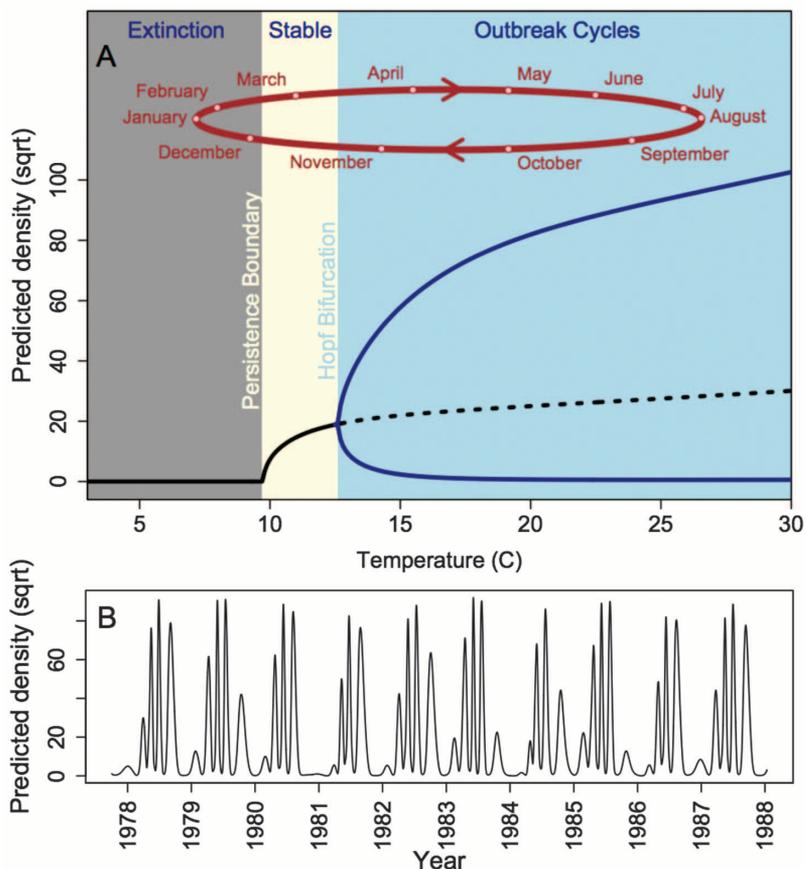
Fig. 3. Observed changes in moth density. Observed changes in moth density at the annual (**A** and **B**) and subannual (**C** and **D**) frequencies based on wavelet reconstruction. Scaled moth dynamics are shown with black lines, and smoothed mean daily temperature is shown in orange. Annual changes in moth dynamics are in phase with the observed temperature dynamics. The subannual cycles reveal striking nonstationary dynamics, with no cycles during the cold periods and large-amplitude outbreak cycles during the warm periods.
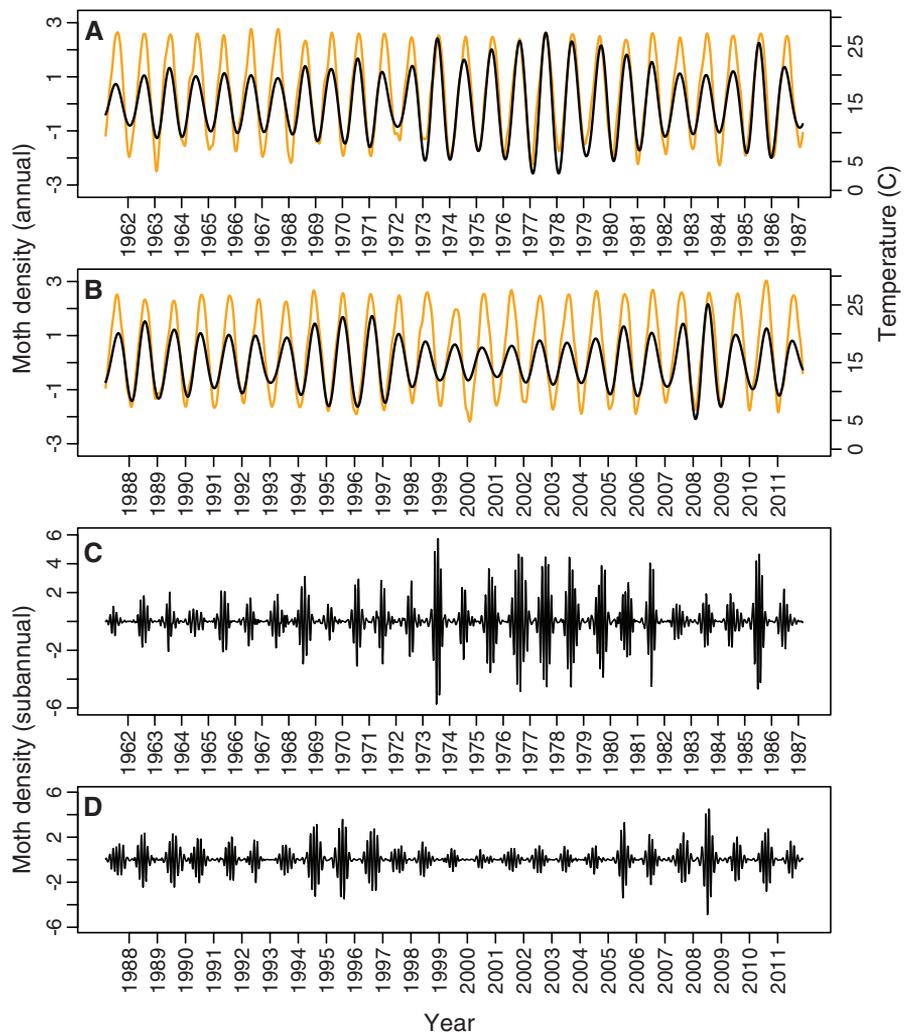
old, the cycle amplitude should increase roughly proportionally to temperature (Fig. 2). In contrast, if the cycles are simply due to the classic explanation of seasonally transient developmental synchrony, there should be no threshold relation between amplitude and temperature, and the amplitude should decrease with increasing temperature through the spring as cohorts smear into each other.

Wavelet analysis decomposes variability in a time-series into oscillations at different frequencies. In contrast to more traditional methods of spectral analysis, the wavelet also quantifies changes in cycle amplitude through time and accommodates nonstationarity in the data (*18*). Hence, it provides a useful framework to test our predictions. We applied the wavelet analysis to light-trap counts of adult moths recorded every 5 or 6 days from 1961 to 2012 at the Kagoshima tea station, Japan (*15*). The 51-year time series comprises more than 2500 observations and around 250 outbreaks. The analysis identifies two dominant patterns: a strong and relatively stationary signal that reflects an annual cycle and a pronounced, but punctuated, nonstationary signal that reflects

the four to six distinct outbreak cycles that occur from late April through early October each year (Fig. 3 and supplementary text).

To test the predictions of the "classic" seasonal hypothesis versus the new temperature-induced destabilization hypothesis, we regressed outbreak amplitude against temperature using a mixed-effects linear and thresholded piecewise linear model. We modeled year as a random effect and used a first-order moving-average error structure to accommodate the serial dependence inherent in wavelet amplitudes (supplementary text). The thresholded regression model strongly outperforms the linear model for both spring and fall [likelihood ratio test: $\chi^2(24) = 689.6$, $P < 0.0001$, and $\chi^2(24) = 1338.8$, $P < 0.0001$, respectively]. Moreover, the best-fit model predicts a highly significant positive slope of amplitude against temperature above the threshold [spring slope ($\pm$ SE): 34.3 ± 2.9; fall slope: 34.8 ± 3.8]. The profile likelihood for the threshold regression places the breakpoint at $15.0°C$ [confidence interval (CI): $14.5°$ to $15.5°C$] for spring transitions and at $19.7°C$ (CI: $19.3°$ to $20.1°C$) for fall transitions. These values are in good agreement but

somewhat larger than the theoretical, temperature-induced Hopf bifurcation point expected under constant temperature. To investigate whether the discrepancy might be due to transient dynamics from the relatively rapid seasonal changes in temperature during the spring and fall transitions, we applied the same statistical protocol to numerical simulations of the model driven with observed monthly temperature data at the tea station for the last 50 years (supplementary text and fig. S23). The resultant regression patterns for the data and model are very close in terms of both the estimated threshold [simulated data, spring: $17.2°C$ (CI: $16.7°$ to $17.6°C$), fall: $16.6°C$ (CI: $16.0°$ to $17.8°C$)] and the estimated slope (Fig. 4). The analysis thus strongly supports the hypothesis that temperature destabilizes population dynamics and sustains recurrent outbreaks in this system.

Previous studies have shown that the population dynamics of some insect, fish, bird, and mammal species can be explained by single-species (*19*) or few-species (*20*) interactions even though they are embedded in complex food webs. Our results suggest that the outbreaks of the smaller tea tortrix share a similar level of dynamical sim-

Fig. 4. Subannual cycle amplitude as a function of temperature. Observed cycle amplitude increases with increasing temperature (black circles) in the spring (**A**), with a fit threshold of 15°C (dashed blue line), and decreases with decreasing temperature in the fall (**B**), with a fit threshold of 20°C (dashed blue line). These compare very well with the theoretically predicted critical threshold temperatures of around 17°C for spring (**C**) and fall (**D**) from the independently parameterized model under seasonally driven temperatures (dashed blue line). Predicted constant temperature threshold is shown with the light blue solid line. Horizontal bars denote the mean and 95% confidence intervals from a variant of the model with year-specific transition points (supplementary text). Solid thin lines show fit of the piecewise regression model for each year (spring: green lines, fall: red lines).
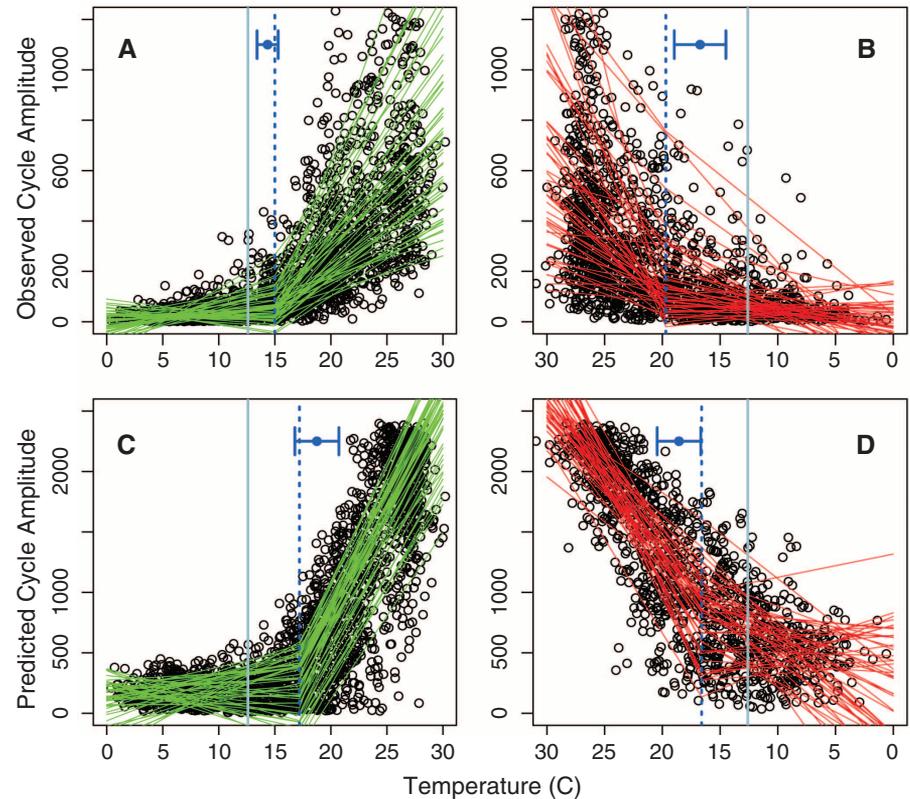
plicity despite being part of a complex food web that includes parasitoids, predators, and competitors (*14*, *16*). We note, however, that the outbreak amplitudes are more variable between years than predicted by the model. This may be the signature of other interactions not included in our model that are of subdominant importance relative to the overall temperature pacemaker.

Theory predicts that environmentally induced changes in life-history traits can scale up to alter population and community dynamics, such that a system may be stable under certain conditions yet undergo cyclic or erratic dynamics in other environments (*21–24*). Various laboratory experiments manipulating productivity and mortality in consumer-resource systems provide essential proof-of-concept that dynamics can indeed undergo abrupt changes toward system instability in the face of gradual environmental gradients (*25–28*). Similar to other environmental drivers, mathematical models predict that temperature may cause abrupt changes in the stability of ectotherms through its ubiquitous influence on life-history rates (*10–13*). Despite these theoretical predictions and the enormous focus on contemporary and anticipated climate change, no previous studies have demonstrated that increased temperature may induce population cycles. Indeed, warming is linked to the loss of cyclicity in the larch budmoth in the Alps (*29*) and various other herbivores in northern latitudes (*30*). The smaller tea tortrix, however, demonstrates temperature-induced destabilization in a natural insect population.

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Supplementary Materials
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Supplementary Text
Figs. S1 to S24
Tables S1 and S2
References (*31–42*)