Entomologia Generalis, Vol. 43 (2023), Issue 2, 325–335
Published online 17 January 2023

Article

The contrasting response of crop production and pest damage to ENSO cycles

Leyun Wang[1,2], Gadi V. P. Reddy[3], Su Wang[4], and Zihua Zhao[1,*]

[1] Department of Plant Biosecurity & Key Laboratory of Surveillance and Management for Plant Quarantine Pests, China Agricultural University, Beijing 100193, China;
[2] Guangxi Key Laboratory of Agro-Environment and Agric-Product Safety, College of Agriculture, Guangxi University, Nanning 530004, China;
[3] USDA-ARS-Southern Insect Management Research Unit, 141 Experiment Station Road, PO Box 346, Stoneville, MS 38776, USA;
[4] Institute of Plant and Environment Protection, Beijing Academy of Agriculture and Forestry Sciences, Beijing 100097, China.
* Corresponding author: zhzhao@cau.edu.cn

With 6 figures

Abstract: El Niño-Southern Oscillation (ENSO) is a large-scale climatic phenomenon that has fundamental effects on the terrestrial environments and ecosystem functions. Based on observed crop production and pest damage of a 41-y time series from 1980-2020 in China, the present study examined ENSO's long-term effects on agroecosystems and found that changing crop yields per hectare and pest outbreaks can ultimately be connected to ENSO cycles by comparing the effect sizes of respective responses across different ENSO phases. The El Niño phases (the warming phases) and La Niña phases (the cooling phases) have had opposite effects on crop yields and damage of arthropod pests in most cases, and such effects were climatic-region-dependent. Our evidence demonstrates that the climatic origin of a crop could associate with its responses to ENSO phases: wheat benefited from La Niña phases when planted in subtropical climates and from El Niño phases when planted in the middle temperate climate; rice were resilient to El Niño phases in warmer areas, while La Niña phases significantly increased the rice yield in the subtropical climate. Corn yields were significantly lower during El Niño phases in all four climatic regions, while La Niña phases significantly increased corn yields only in the Tibetan Plateau. Additionally, we found higher pest damage occurring during El Niño phases and lower damage occurring during La Niña phases for many arthropod species. Our improved understanding of crops and arthropod herbivore responses to ENSO phases can contribute to predicting global impacts of climate changes on agriculture and food security.

Keywords: El Niño-Southern Oscillation, agroecosystem, insect pest, crop yield, climate change

1 Introduction

Climate change involves both global warming and increases in extreme climatic events, and it has tremendous impacts on ecosystem functions and services (Pounds et al. 1999, Timmermann et al. 1999, Easterling et al. 2000). Examining how individuals and populations respond to climatic factors and large climatic phenomena is key to predicting the effects of climate change on ecosystem functions (Karl & Trenberth 2003, Hance et al. 2007, Jeffs & Lewis 2013, Pacifici et al. 2015).

Climate variables (e.g., temperature) have been monitored and described by specific climatic indices of ocean conditions, which can be good indicators of variation in both oceanic and terrestrial ecosystems (Holmgren et al. 2001, Hallett et al. 2004). El Niño-Southern Oscillation (ENSO), which comprises three phases, the warming phase (El Niño), the cooling phase (La Niña), and the neutral phase in between, is a common and important large-scale climatic phenomenon that reflects the variation in the ocean surface temperature in the central and eastern tropical Pacific Ocean that has fundamental effects on the atmosphere and the surrounding terrestrial environment. Cases of oceanic oscillation-induced regulation of the population dynamics of terrestrial organisms have been detected in various natural ecosystems (Holmgren et al. 2001, Hallett et al. 2004). Some insect populations have been found in long-term studies to respond sensitively to large-scale climate effects (Vandenbosch 2003,

DOI: 10.1127/entomologia/2022/1688
www.schweizerbart.de
0171-8177/2022/1688 $ 4.95

Pardikes et al. 2015, Pardikes et al. 2017). For example, 15 years of evidence revealed that Rocky Mountain (Alberta, Canada) populations of the butterfly *Parnassius smintheus* (Doubleday) showed a sharp decline in abundance in years with extreme winter Pacific Decadal Oscillation. Similarly, the population dynamic of a corn pest, *Spodoptera* (Guenée), was found to be more affected by ENSO than seasonal changes and host plant availability in a Brazilian Savanna (Piovesan et al. 2018).

In agroecosystems, such associations between biotic communities and large-scale climatic indices are rarely explored due to the limited availability of long-term data sets. ENSO phases are critical drivers of climate changes and extreme climatic events, which are likely to affect crop production globally, and these effects can be climate type-dependent. Understanding the potential cascading effects of climate patterns on site-level ecological processes of agroecosystem components, i.e., crops and pests, could help in exploring the complex interconnections among global climate changes and ecosystem functions. Generally, the warming effects of El Niño events could benefit both crops and insects by enhancing developmental rates, while La Niña events could decrease the development and growth of ectotherms, such as insect pests (e.g. Porter & Gawith 1999, Aluja et al. 2012, Bai et al. 2021). Simultaneously, it is still largely unknown whether extreme climate events exhibit impacts on organisms depending on their thermal tolerances, resulting from different evolutionary histories.

In the present research, we investigated whether ENSO effects on these ecosystem functions were detectable in different climatic regions based on a 41-year large-scale database including crop production and arthropod pest data from China and tested our hypotheses. We hypothesize that (1) the response patterns of crops and arthropod pests to ENSO events can be the outcome of their previous thermal adaptation and optimal thermal performance ranges: i.e., whether heat-acclimated crops (corn and rice) benefit from the warming phase in cool climates, and whether cold-acclimated crops (wheat) benefit from the cooling phase in hot climates; (2) the stabilities of crop production differ across different crop types and climate types in responses to ENSO events. Our findings could be used to explore the climate-dependent driving forces on crop production and pest damage with global changes of climate.

2 Material and methods

2.1 Crop yield data

The data on crop yields of wheat, corn, and rice and their respective cultivation areas in each province in China were obtained from the *China Agriculture Yearbook*s of 1980 to 2020 (released by the China Ministry of Agriculture, http://www.stats.gov.cn/). Thus, the crop yield per unit area in each province in China was calculated from the total yield and total cropland area for each year. Most of the time series for crop yields in China were available, but unfortunately data in 1998 had no records. Therefore, a popular method of mean imputation was used to complete missing data of the time series (Nakagawa & Freckleton 2008). We categorized all provinces into four different types of climatic regions: middle temperate (M-temperate), warm temperate (W-temperate), Tibetan Plateau (Tibet), and subtropical regions to investigate the climate-dependent responses of ecosystem functions to ENSO events (see the map in Fig. 2a). The comprehensive records of crop yield data and cropland area were included in our dataset. Thus, 2,480 records of total crop yield per province and cropland area were obtained for all recorded provinces in China, and crop yield per hectare was calculated accordingly. We separately examined the responses of crop yield per hectare to ENSO events in each climatic region of China.

2.2 Pest damage data

We collected pest damage data for three main crops (wheat, rice, and corn) to determine their responses to climate events. Due to the species-specific characteristics, several main arthropod pests of rice, maize, and wheat in China were separately selected to examine their responses to ENSO phases and determine their potential mechanisms. In total, 18 species of arthropod pests were included in the current research: 7 species (*Nilaparvata lugens* (Stål), *Chilo suppressalis* (Walker), *Tryporyza incertulas* (Walker), *Chloethrips oryzae* (Williams), *Laodelphax striatellus* (Fallén), *Sogatella furcifera* (Horvath) and *Cnaphalocrocis medinalis* (Guenée)) in rice, 5 species (*Tetranychus truncatus* (Ehara), *Rhopalosiphum padi* (Linnaeus), *Ostrinia furnacalis* (Guenée), *Anaphothrips obscurus* (Müller), and *Holotrichia oblita* (Falderman)) in corn, and 6 species (*Sitobion miscanthi* (Takahashi), *Pleonomus canaliculatus* (Faldermann), *Dolerus tritici* (Chu), *Petrobia latens* (Müller), *Sitodiplosis mosellana* (Géhin), and *Pentfaleus major* (Duges)) in wheat. The crop pest outbreak data were collected from the *China Yearbooks of Plant Protection Statistics* (the National Agricultural Technology Extension Service Center of China) from 1980 to 2020. The total cropland area that was infested by a crop pest whose population density exceeded the economic threshold indicated the annual outbreak area of that pest. The economic thresholds for each pest species used by data collectors were determined by the Ministry of Agricultural and Rural Affairs of the People's Republic of China (the latest version (2022) of *Monitoring and Prediction of Crop Disease and Pest Management Guidelines* can be found in https://www.moa.gov.cn/). The pest damage levels were indicated by the ratios of the outbreak area of a pest to the total area of its host crop planted in the study region for a year (Meehan et al. 2011, Wang et al. 2016, Zhao et al. 2015). We separately examined the responses of the pest outbreak level to ENSO events for different crops as well as in different climatic regions of China.

2.3 Temperature anomaly

The World Ocean Database was extracted from the website of the National Centers for Environmental Information (https://www.nodc.noaa.gov/). A time series of sea surface temperature (SST) of the Peru Current was constructed from 1900 to 2020. Thus, the anomaly of SST (T'_i) was calculated using the following equation: $T'_i=(T_i-\overline{T}_i)$. T_i and $\overline{T}_i$ are the observed and mean values of the temperature variables in year i, respectively.

The ENSO cycles were identified by defining an El Niño event followed by a La Niña event, which is also a typical pattern of climate fluctuation. There were 8 typical ENSO cycles in the past 4 decades. To define the different ENSO phases, an individual year whose yearly mean temperature was ≥ 0.5 °C ($T'_i \geq 0.5$ °C) higher than the overall mean temperature was considered an El Niño year, while an individual year whose yearly mean temperature was ≤ 0.5 °C ($T'_i \leq 0.5$ °C) lower than the overall mean temperature was considered a La Niña year. The remaining years were considered neutral years when the SST anomaly (T'_i) was between –0.5 °C and 0.5 °C.

2.4 Statistical analysis

To examine the effects of climate change on crop production and pest damage, a detrending analysis of the time series was used to remove linear trends before analysis. The detrended data consisted of the residuals from the linear regression of each time series as a smooth function of year. Then, we divided the time series of all crop production and pest damage into three categories for each province: El Niño years, La Niña years, and neutral years. The crop production and pest damage of each study species was compared between neutral years and El Niño/La Niña years by using Hedge's d.

Hedge's d is a popular metric that is commonly used to examine effect size in ecological and evolutionary meta-analyses due to a low Type I error rate and high within-study precision. Additionally, the random effects caused by small sample sizes can be corrected by a weighting factor in Hedge's d analysis. Hedge's d was used to calculate effect size as the standardized mean difference in crop production or pest damage between ENSO events and neutral years. Each data point consisted of one effect size, the difference between the mean performance measure of El Niño/La Niña years ($\overline{X}_{el/la}$) and the neutral year ($\overline{X}_{ny}$), normalized by the pooled standard error (S) and a sample-size weighting factor and was calculated as follows:

$$d=\frac{(\overline{X}_{el/la}-\overline{X}_{ny})}{S}J$$

where S is the pooled standard deviation and was calculated as

$$S=\sqrt{\frac{(N_{el/la}-1)S^2_{el/la}+(N_{ny}-1)S^2_{ny}}{N_{lel/la}+N_{ny}}}.$$

where $S_{el/la}$ and S_{ny} are the standard deviations of crop production or pest damage in ENSO and neutral years, respectively.

J is a weighting factor based on the number of replicates (N) in each case for the two groups and was calculated as follows:

$$J=1-\frac{3}{4(N_{el/la}+N_{ny}-2)-1}$$

The variance of Hedges' d (Vd) was calculated as follows:

$$V_d=\frac{N_{el/la}+N_{ny}}{N_{el/la}N_{ny}}+\frac{d^2}{2(N_{el/la}+N_{ny})}$$

Zero d values indicate no difference in the variable measured, and positive values indicate better performances in ENSO years. When a confidence interval (CI) does not include zero, it indicates a statistically significant effect size. The calculation of effect size was performed by using the function 'rma' of the package 'metafor' in R (R Core Team 2021). This method is a generally unbiased and efficient estimator to test whether the mean effect sizes of each variable type differ significantly from zero.

We separately calculated the mean effect size of crop production and pest damage for the M-temperate, W-temperate, Tibet, and subtropical regions. Additional tests were performed to examine the heterogeneity (Q_T) of the mean effect sizes. The Q_T was tested with Cochran's Q-test. The percentage of variation across studies due to Q_T (I^2 statistic) was also obtained to summarize Q_T importance and was classified as low, moderate, high and very high Q_T (I^2 values <25%, 25–50%, and 50–75%, >75%, respectively) among study groups.

For the different climate phases, we calculated the coefficient of variation (CV) of crop production, which was the ratio of the standard deviation divided by the means. The CV of crop production was calculated at two levels: the crop production of climatic regions and the crop production of particular crop types. The CV of crop production for the different climatic regions was calculated as the variation in crop production in different years within a particular climate phase, while the CV of crop production for a particular crop was calculated as the variation in the average production of different years within a particular climate phase. Then, one-way ANOVA was used to examine the differences in the CVs for crop production among El Niño years, La Niña years, and neutral years. In addition, to evaluate the CV differences in crop production of the different climate phases, one-way ANOVA was conducted using the ‘aov’ function of the R package “stats”, and all data analyses were performed in R (R Core Team 2021), and all the figures were constructed with Origin 2021.

3 Results

3.1 ENSO cycles

The sea surface temperature (SST) of the Peru Current (Niño 34) has varied dynamically over the last 120 years, fluctuating from its minimum temperature (24.09 °C) to its maximum temperature (28.96 °C) (Fig. 1a). The average yearly SST of El Niño/La Niña years was significantly higher/lower than that of neutral years (Fig. 1a and Fig. 1c). These temperature patterns were consistent across each of the 4 seasons in a year (Fig. 1d and 1e), and temperature differences were greatest in winter and spring (Fig. 1e).

3.2 Crop yield in response to ENSO cycles

Wheat, corn, and rice were widely planted across China in middle temperate (M-temperate), warm temperate (W-temperate), Tibet Plateau (Tibet), and subtropical regions, which had different compositions of these three main crops (Fig. 2a). In general, the annual total yields of corn, wheat, and rice increased in 2001-2020 compared with those in 1981-1990 (Fig. 2b-e). Meanwhile, the yields per hectare of each of the three crops also generally increased in all 4 climatic regions from 1980 to 2020 (Fig. S1).

In comparison with the neutral phase, the La Niña phase did not affect crop yields per hectare of these three crops in average in the M-temperate, W-temperate, and Tibet regions, while they significantly benefited from the La Niña phase in the subtropical region (Fig. 3a). During the El Niño phase, the yields per hectare of all 3 crops in average were significantly lower in the M-temperate, W-temperate, and subtropical regions, and they were unaffected in Tibet Plateau (Fig. 3a).

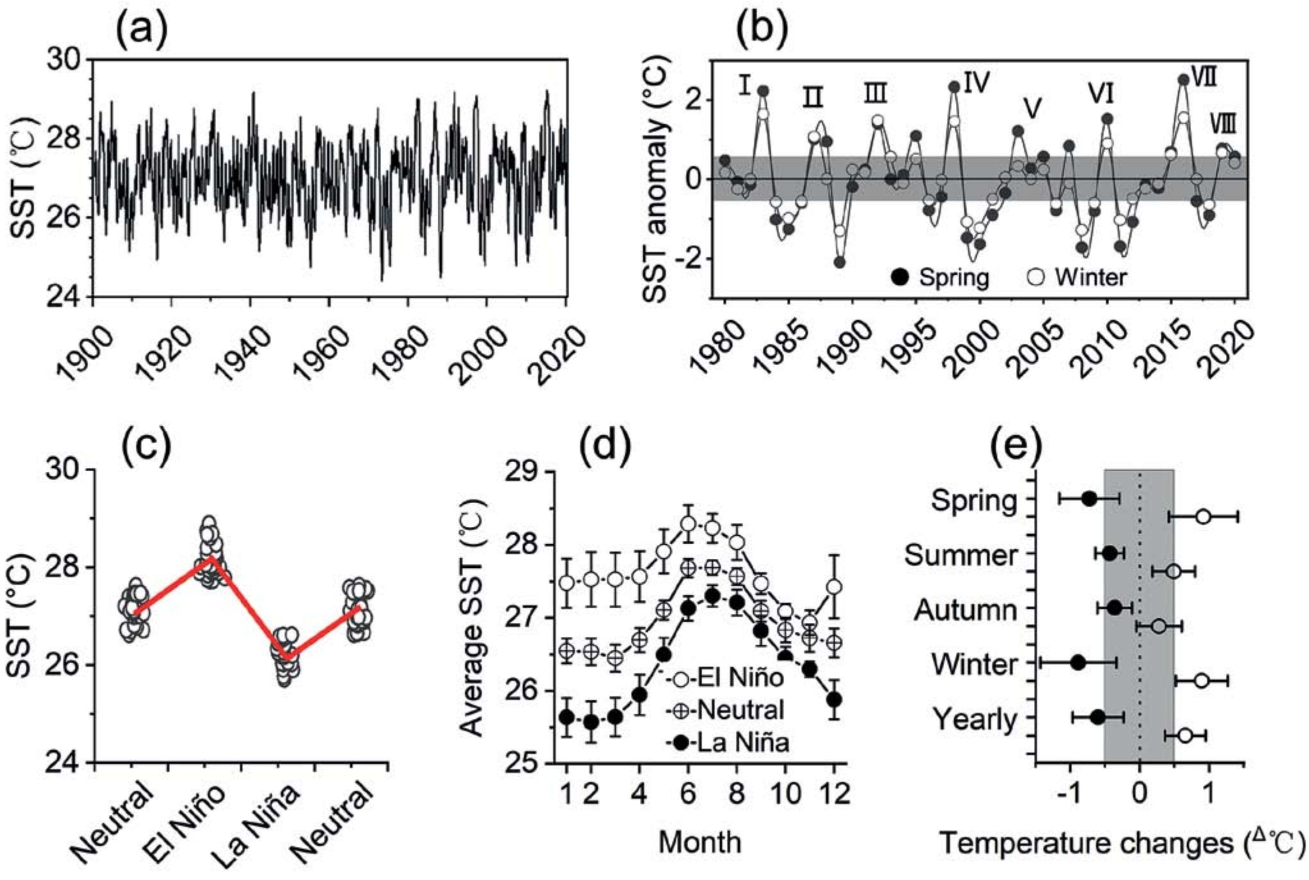

Fig. 1. El Niño-La Niña cycles mediate temperature variations. **(a)** Time series of sea surface temperature (SST) in Peru Current from 1900 to 2020; **(b)** El Niño-La Niña cycles from 1980 to 2020. The Roman numerals indicate individual El Niño-La Niña cycles. **(c)** the typical SST fluctuation during El Niño-La Niña cycles; **(d)** the monthly average SST during El Niño, neutral and La Niña years from 1980 to 2020 (error bars indicate standard errors); **(e)** the temperature differences in four seasons of El Niño (empty circles) and La Niña (black circles) years from 1980 to 2020

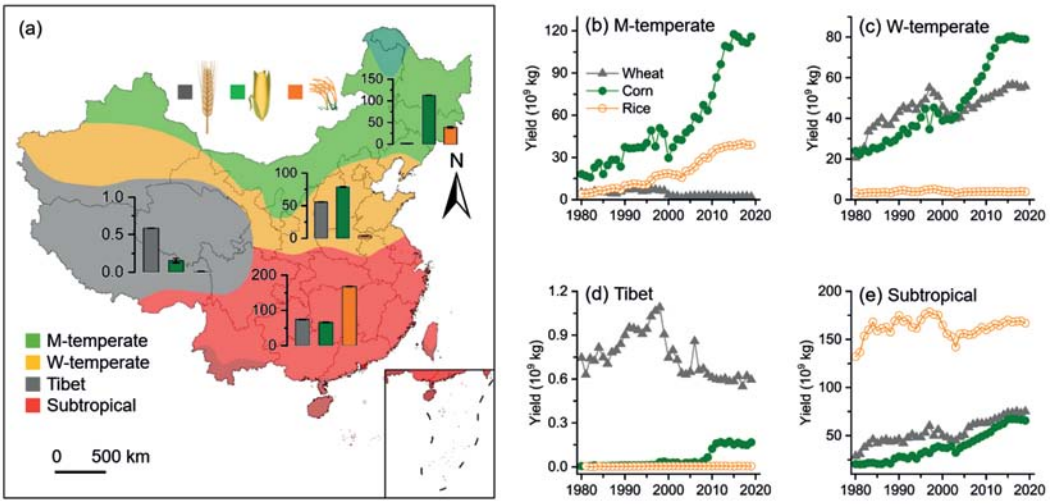

Fig. 2. The time series and distribution of crop yields in China from 1980 to 2020. **(a)** The spatial distribution of the main grain-producing regions (bars indicate annual mean yields (× 10^9 kg) of each crop in 2016-2020 in each climatic region). The annual total yields of wheat, corn, and rice in **(b)** the middle-temperate (M-temperate), **(c)** the warm-temperate (W-temperate), **(d)** the Tibet Plateau (Tibet), and **(e)** the subtropical region (Subtropical).

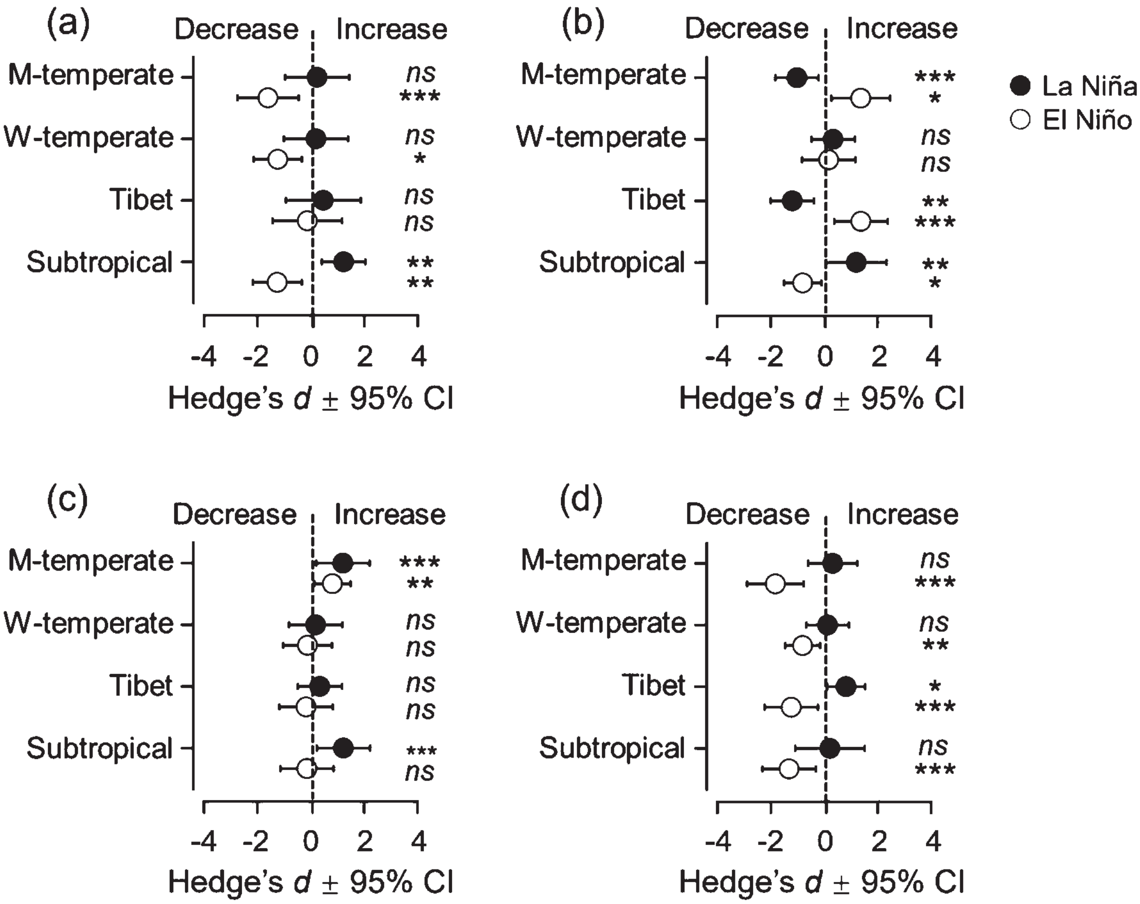

Fig. 3. Effects of El Niño phases and La Niña phases on the crop yield per hectare in comparison to those of neutral phases on crop production in China from 1980 to 2020. (**(a)** yields per hectare of wheat, rice, and corn in average; **(b)** yields per hectare of wheat; **(c)** yields per hectare of rice; and **(d)** yields per hectare of corn). The error bars are the 95% confidence intervals (*CI*s) of the mean effect sizes.

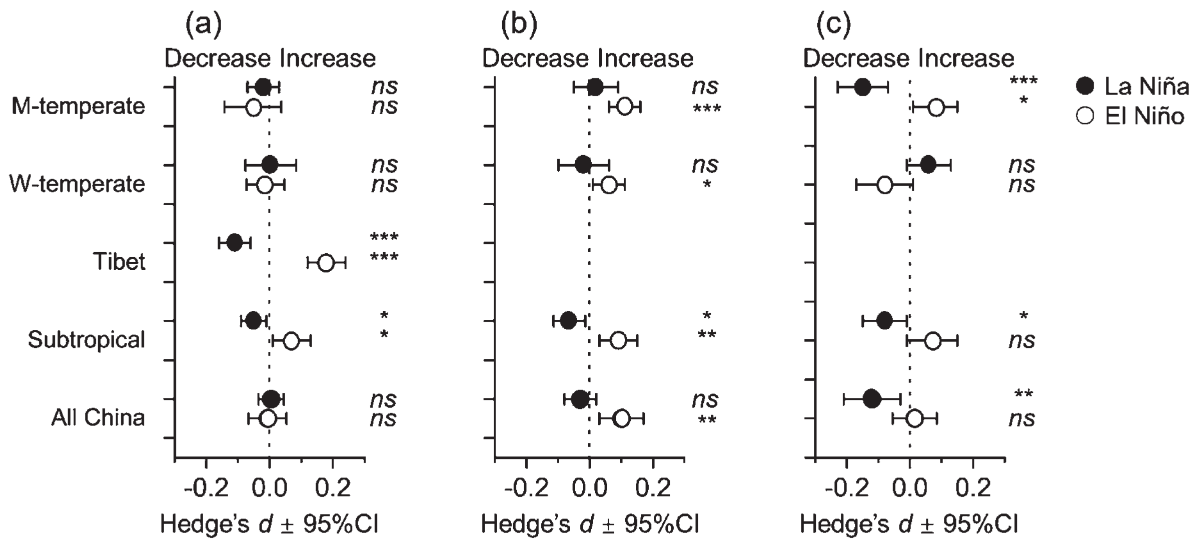

Fig. 4. Pest outbreak responses to El Niño phases and La Niña phases in different climatic regions in comparison with those to neutral phases in China from 1980 to 2020 (**(a)** wheat pests, **(b)** corn pests, and **(c)** rice pests). The error bars are the 95% *CI*s of the mean effect sizes.

There were significant differences in the yield per hectare of specific crops during El Niño and/or La Niña phases in comparison to those during the neutral phases in the 4 climates (Fig. 3). The La Niña phase caused significant decreases in wheat yields per hectare in the M-temperate and Tibet, but significantly enhanced the yields per hectare in the subtropical region. The El Niño phase caused significant increases in wheat yields per hectare in the M-temperate and Tibet, and significant decreases in the yields per hectare in the subtropical region. However, neither the El Niño nor La Niña phase had significant effects on wheat yields per hectare in the W-temperate (Fig. 3b). Rice yield per hectare was significantly higher during both El Niño and La Niña in the M-temperate, while La Niña significantly increased the rice yield per hectare in the subtropical region. Additionally, the rice yields per hectare were unaffected by either phase in the W-temperate and Tibet (Fig. 3c). For corn, its yield per hectare was significantly lower during the El Niño phase in all four climates, while the La Niña phase significantly increased corn yields per hectare in only Tibet (Fig. 3d).

3.3 Pest responses to ENSO cycles

In China, the damage to wheat caused by all of its arthropod pest species studied in average was not significantly different among the El Niño, La Niña or the neural phases, and which to corn was not significantly affected by the La Niña phase but was significantly enhanced by the El Niño phase. Overall, the arthropod pests in rice were significantly suppressed by the La Niña phase but did not respond significantly to the El Niño phase at the national scale (Fig. 4, Fig. 5).

In the M-temperate, the El Niño phase significantly facilitated pest damage in both corn and rice, and the La Niña phase significantly suppressed pest damage levels in rice. In the W-temperate, the El Niño phase significantly facilitated pest damage in corn only, while for the three crops, the effects of La Niña on pest damage were not significant (Fig. 4). In the Tibet region, pest damage in wheat increased during the El Niño phase but declined during La Niña phases (only data on wheat pests were available) (Fig. 4). In the subtropical region, the El Niño phase significantly increased the pest damage in wheat and rice, and the La Niña phase showed significantly opposite effects on all three crops (Fig. 4).

3.4 Crop yield stability mediated by ENSO phases

Crop yield per hectare was mediated by ENSO phases and exhibited different stability patterns during the three different phases as well as in the four climatic regions (Fig. 6a). The coefficient of variation (CV) of crop yield per hectare was significantly higher during La Niña phases than during the neutral phases and El Niño phases in the W-temperate, subtropical, and Tibet regions (Fig. 6a). Crop yields per hectare in the neutral phase were the most stable among the three phases in the W-temperate and subtropical regions (Fig. 6a). In the M-temperate, crop yield stability did not differ significantly across the three ENSO phases (Fig. 6a). At the national scale, the wheat, corn, and rice yields per hectare were significantly most stable in the neutral phase and significantly least stable during La Niña phases, and the yields per hectare during El Niño phases were moderately stable (Fig. 6b).

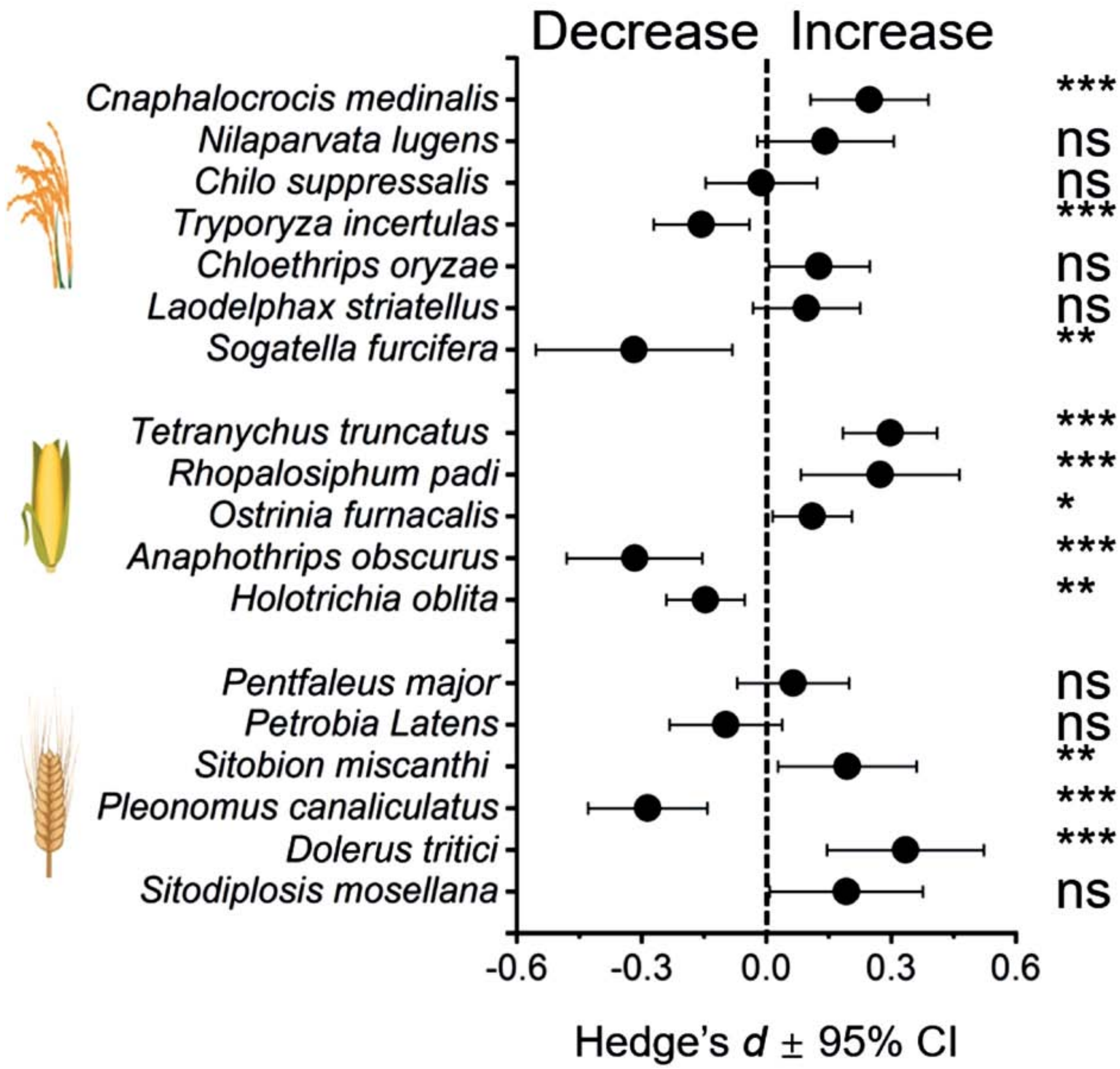

Fig. 5. Species-specific pest outbreak responses to the El Niño phase in comparison with those to neutral phases (from the top, they are rice pests, corn pests, and wheat pests) in China from 1980 to 2020. The error bars are the 95% *CI*s of the mean effect size.

4 Discussion

Climate extremes and changes in climate variability are important components of climate change, and their effects on biological systems, including on agroecosystems, are noticeable and variable (Lobell et al., 2011; Thornton et al., 2014). In addition to changes in climatic factor means inevitably altering ecosystem responses, climate change might result in shifts in the frequency and magnitude of unusually cold and heat events that can affect plants and other participants in agroecosystems in a more complex way (IPCC, 2012). For example, increases in heavy rainfall or droughts are likely to have direct impacts on agroecosystems; furthermore, climatic disasters can also play an important role in affecting crop production (Lobell et al., 2011). It is difficult to quantify extreme climate effects on ecosystems in a systematic way, given that climate extremes are historically rare (Lobell et al., 2011); however, the use of large climatic indices might potentially be a good method for capturing the climate extremes and examining their effects (Hallett et al., 2004).

Our work indicates that crop yields per hectare and pest outbreak levels varied significantly during ENSO phases. The underlying mechanism of ENSO-driving factors affecting crop yields can be complex (Porter & Gawith, 1999; Iizumi et al., 2014). A study investigating global crop yield anomalies in relation to ENSO found that such associations

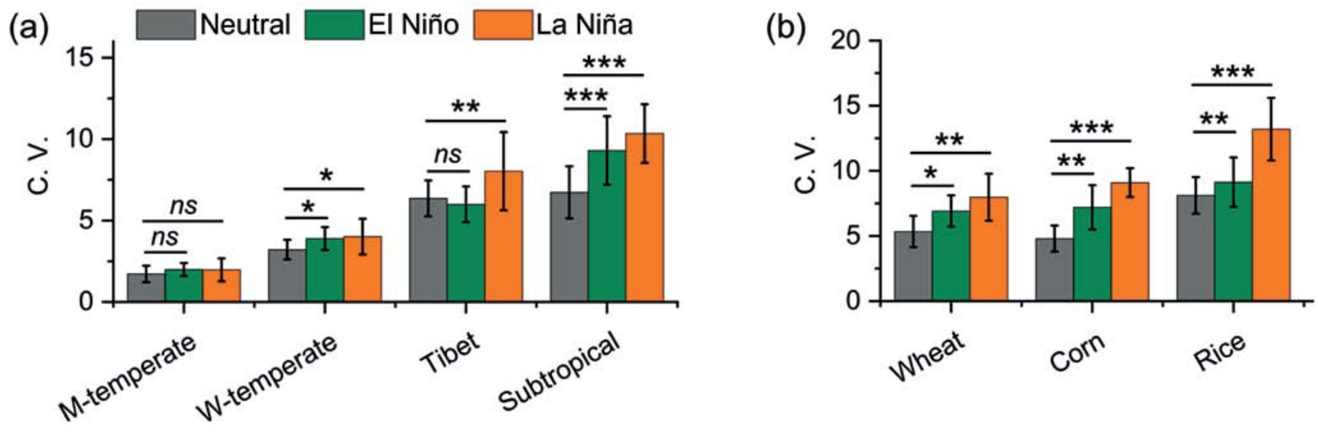

Fig. 6. Effects of El Niño-La Niña cycles on crop yield stability in different **(a)** climatic regions and **(b)** crop types, in China from 1980 to 2020. Error bars indicate standard errors.

vary among geographical locations, crops, and ENSO phases, as well as different seasons (Iizumi et al., 2014), while the underlying mechanisms of such associations are still largely unknown. In humid ecosystems, where El Niño events often cause heat and drought, such as the Amazonian ecosystem, a net positive emission of carbon to the atmosphere occurs, while in other ENSO phases, an ecosystem can serve as a global carbon sink (Tian et al., 1998). These results suggest that ENSO-driving changes could potentially alter the net biomass assimilated in ecosystems, and this pattern might potentially be reflected in varying crop yields during different ENSO phases in agroecosystems, which was found in the present study. Furthermore, these effects can also be climatic region-dependent (Holmgren et al., 2001), which was again demonstrated by our comparisons among four distinct climatic regions in China.

The geographical origins of our study crops, which indicate their thermal acclimation, might explain the climatic region-dependent responses of yield per hectare to ENSO phases: the closer the optimal thermal temperature range of the crop to the local temperatures resulting from an ENSO phase, the better the crop could perform (Hatfield et al., 2011; Lobell & Gourdji, 2012). Temperature effects on crops can be complex in that different plant physiological processes, growth, and development, and plant phenological stages have unique thermal requirements and limits (Porter & Gawith, 1999; Eyshi Rezaei et al., 2015).

Wheat originated from a temperate region, which is likely to explain why it has a lower tolerance to heat and a lower temperature for optimal yield (an elevated temperature can shorten its grain-filling period (Sofield et al., 1977)) that is lower than that for vegetative growth (Porter & Gawith, 1999; Eyshi Rezaei et al., 2015; Hatfield et al., 2011). These factors might explain the reduced wheat yield per unit area during El Niño phases and the opposite effect during La Niña phases in warm regions. At the same time, in cool regions, the warmer conditions during the El Niño phase enhance wheat yields. Rice, on the other hand, has long been domesticated in subtropical and tropical regions, so its inherent tolerance and utilization of heat throughout growing seasons might contribute to its resilience to El Niño in warmer areas (Hatfield et al., 2011). Corn is also a heat-acclimated crop, but with an optimal temperature for yield that is generally lower than that of rice (Hatfield et al., 2011). It is cultivated only in warmer seasons in our study areas, and the El Niño phase is more likely to impose heat stress in these growing seasons as opposed to promote growth in cold seasons, which results in yield losses, as shown in our results.

Crop yield stabilities that we examined, indicated by yield variances, showed significant differences across different ENSO phases, climatic regions, and crop types, which is consistent with the results of other studies (Iizumi et al., 2014; Anderson et al. 2017). The underlying mechanisms of the associations between ENSO events and the above noted factors might be the coupled outcomes of changed climatic conditions/events and the phenology and adaptation of organisms, which should be further examined in detail. Based on the asymmetrical responses to climatic changes by organisms native to different climatic regions, we hypothesize that global warming can severely disrupt ecosystems in warmer areas in earlier waves before similar effects are gradually imposed in cooler areas.

The magnitudes of the impacts of ENSO cycles on overall pest outbreaks were host crop-dependent as well as climatic region-dependent. Similarly in a Kansas prairie, climate change cycles were found to play an important role in changes in grasshopper abundance (Welti et al., 2020). A five-month delayed El Niño effect could lead to temporary emigration and the subsequent return of females of the Amazonian butterfly *Nessaea hewitsoni* (Felder & Felder) (Kajin et al., 2017). Field population dynamics of *Anastrepha* species (fruit flies) infesting grapefruit were also found to be affected by both ENSO events and North Atlantic Oscillation (NAO) in Veracruz, Mexico (Aluja et al., 2012). Based on dendrochronological reconstruction of *Dendrolimus punctatus* (Walker) outbreaks that affected the host plant *Pinus massoniana* (Lamb.), researchers detected the associations between insect outbreaks with the La Niña phase that induced hot and dry conditions in the study site in humid subtropical eastern China (Bai et al., 2021).

Furthermore, climate changes are likely to influence the arthropod populations through altering the number of generations per year, disrupting their life cycles (Altermatt 2010, Teder 2020, Hill et al. 2021) and/or population sizes (Vandenbosch 2003, Roland & Matter 2013, Pardikes et al. 2015). Voltinism of arthropod pests might participate in determining their responses to ENSO phases. Among our study species, *Pleonomus canaliculatus* and *H. oblita* are univoltine and semivoltine pests, and *A. obscurus* is bivoltine: they exhibited significantly negative responses to El Niño phases; while the pest damage of the majority of multivoltine species were unaffected or significantly increased by El Niño phases (Table S1, Fig. 5). Similarly, it was found that the abundance of bivoltine butterfly species within longer flight seasons was more likely to associate with NAO than univoltine species in a study mining 34 years' butterfly monitoring data in the UK (Westgarth-Smith et al. 2012).

We found that oscillating crop yields and pest outbreaks can ultimately be related to ENSO cycles, whose global effects arise from variation in ocean surface temperatures in the central and eastern tropical Pacific Ocean and have fundamental impacts on the atmosphere. Our evidence demonstrates that crops with origins from different climatic regions can exhibit optimal thermal performance range-dependent responses to ENSO events. A cold-acclimated crop (wheat) benefits from the cooling ENSO phase in hot climates as well as from the warming ENSO phase in cold climates. Rice, a heat-acclimated crop, showed an inherent ability to use heat throughout growing seasons and was resilient to El Niño phases in the W-temperate, Tibet, and subtropical regions. Corn, the other heat-acclimated crop, was cultivated only in warmer seasons, and El Niño phases were more likely to cause heat stress in the growing seasons rather than promote growth in cold seasons, which resulted in net decreases in yields.

We also show a universal pattern of greater pest damage in El Niño years and less pest damage in La Niña years for many pest species. Additionally, pest responses can be further mediated by voltinism and climate types. Understanding how host plants and arthropod herbivores mutually influence each other during ENSO events can be key to predicting the global changes in climate impacts on agriculture and food security. Climate change might also increase the instability and unpredictability of ecosystem dynamics, which should be further considered in future studies.

Acknowledgements: This research is supported by the National Key R&D Program of China (No. 2021YFC2600401) and the Natural Science Foundation of the Guangxi Zhuang Autonomous Region (No. 2022GXNSFBA035623). This research is also supported by the China National Tobacco Corporation of Science and Technology Major Project (110202101049[LS-091]). We thank the graduates, Dr. Hongying Cui, and Mr. Huanyi Wang for assistance in data collection, compilation, and processing.

References

Altermatt, F. (2010). Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological Sciences, 277*(1685), 1281–1287. https://doi.org/10.1098/rspb.2009.1910

Aluja, M., Ordano, M., Guillen, L., & Rull, J. (2012). Understanding long-term fruit fly (Diptera: Tephritidae) population dynamics: Implications for areawide management. *Journal of Economic Entomology, 105*(3), 823–836. https://doi.org/10.1603/EC11353

Anderson, W., Seager, R., Baethgen, W., & Cane, M. (2017). Crop production variability in North and South America forced by life-cycles of the El Niño Southern Oscillation. *Agricultural and Forest Meteorology, 239*, 151–165. https://doi.org/10.1016/j.agrformet.2017.03.008

Angilletta, M. J. (2009). *Thermal Adaptation: A Theoretical and Empirical Synthesis*. UK: Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198570875.001.1

Baho, D. L., Futter, M. N., Johnson, R. K., & Angeler, D. G. (2015). Assessing temporal scales and patterns in time series: Comparing methods based on redundancy analysis. *Ecological Complexity, 22*, 162–168. https://doi.org/10.1016/j.ecocom.2015.04.001

Bai, M. W., Yao, Q. C., Camarero, J. J., Hu, H. Q., Dong, Z. P., Li, Y. J., … Fang, K. Y. (2021). El Niño-Southern Oscillation modulates insect outbreaks in humid subtropical China: Evidences from tree rings and carbon isotopes. *Dendrochronologia, 66*, 125815. https://doi.org/10.1016/j.dendro.2021.125815

Cochran, W. G. (1954). The combination of estimates from different experiments. *Biometrics, 10*(1), 101–129. https://doi.org/10.2307/3001666

de Andres, E. G., Blanco, J. A., Imbert, J. B., Guan, B. T., Lo, Y. H., & Castillo, F. J. (2019). ENSO and NAO affect long-term leaf litter dynamics and stoichiometry of Scots pine and European beech mixedwoods. *Global Change Biology, 25*(9), 3070–3090. https://doi.org/10.1111/gcb.14672

Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). Climate extremes: Observations, modeling, and impacts. *Science, 289*(5487), 2068–2074. https://doi.org/10.1126/science.289.5487.2068

Eyshi Rezaei, E., Webber, H., Gaiser, T., Naab, J., & Ewert, F. (2015). Heat stress in cereals: Mechanisms and modelling. *European Journal of Agronomy, 64*, 98–113. https://doi.org/10.1016/j.eja.2014.10.003

Haddad, N. M., Crutsinger, G. M., Gross, K., Haarstad, J., & Tilman, D. (2011). Plant diversity and the stability of foodwebs. *Ecology Letters, 14*(1), 42–46. https://doi.org/10.1111/j.1461-0248.2010.01548.x

Hallett, T. B., Coulson, T., Pilkington, J. G., Clutton-Brock, T. H., Pemberton, J. M., & Grenfell, B. T. (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature, 430*(6995), 71–75. https://doi.org/10.1038/nature02708

Hance, T., van Baaren, J., Vernon, P., & Boivin, G. (2007). Impact of extreme temperatures on parasitoids in a climate change perspective. *Annual Review of Entomology, 52*(1), 107–126. https://doi.org/10.1146/annurev.ento.52.110405.091333

Hatfield, J. L., Boote, K. J., Kimball, B. A., Ziska, L. H., Izaurralde, R. C., Ort, D., … Wolfe, D. (2011). Climate impacts on agriculture: Implications for crop production. *Agronomy Journal, 103*(2), 351–370. https://doi.org/10.2134/agronj2010.0303

Hedges, L., & Olkin, I. (1985). *Statistical Methods in Meta-Analysis*. San Diego, CA: Academic Press.

Higgins, J. P., Thompson, S. G., Deeks, J. J., & Altman, D. G. (2003). Measuring inconsistency in meta-analyses. *BMJ (Clinical Research Ed.), 327*(7414), 557–560. https://doi.org/10.1136/bmj.327.7414.557

Hill, G. M., Kawahara, A. Y., Daniels, J. C., Bateman, C. C., & Scheffers, B. R. (2021). Climate change effects on animal ecology: Butterflies and moths as a case study. *Biological Reviews of the Cambridge Philosophical Society, 96*(5), 2113–2126. https://doi.org/10.1111/brv.12746

Holmgren, M., Scheffer, M., Ezcurra, E., Gutierrez, J. R., & Mohren, G. M. (2001). El Niño effects on the dynamics of terrestrial ecosystems. *Trends in Ecology & Evolution, 16*(2), 89–94. https://doi.org/10.1016/S0169-5347(00)02052-8

Iizumi, T., Luo, J. J., Challinor, A. J., Sakurai, G., Yokozawa, M., Sakuma, H., … Yamagata, T. (2014). Impacts of El Niño Southern Oscillation on the global yields of major crops. *Nature Communications, 5*(1), 3712. https://doi.org/10.1038/ncomms4712

IPCC. (2012). *Managing the Risks of Extreme Events and Disasters to Advance Climate Change Adaptation: A Special Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press.

Jeffs, C. T., & Lewis, O. T. (2013). Effects of climate warming on host–parasitoid interactions. *Ecological Entomology, 38*(3), 209–218. https://doi.org/10.1111/een.12026

Kajin, M., Penz, C. M., & DeVries, P. J. (2017). Large-scale climate effects meet an Amazonian butterfly: Which population parameters respond to El Niño? *Environmental Entomology, 46*(6), 1202–1211. https://doi.org/10.1093/ee/nvx170

Karl, T. R., & Trenberth, K. E. (2003). Modern global climate change. *Science, 302*(5651), 1719–1723. https://doi.org/10.1126/science.1090228

Lobell, D. B., & Gourdji, S. M. (2012). The influence of climate change on global crop productivity. *Plant Physiology, 160*(4), 1686–1697. https://doi.org/10.1104/pp.112.208298

Lobell, D. B., Torney, A., & Field, C. B. (2011). Climate extremes in California agriculture. *Climatic Change, 109*(S1), 355–363. https://doi.org/10.1007/s10584-011-0304-5

Meehan, T. D., Werling, B. P., Landis, D. A., & Gratton, C. (2011). Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proceedings of the National Academy of Sciences of the United States of America, 108*(28), 11500–11505. https://doi.org/10.1073/pnas.1100751108

Nakagawa, S., & Freckleton, R. P. (2008). Missing inaction: The dangers of ignoring missing data. *Trends in Ecology & Evolution, 23*(11), 592–596. https://doi.org/10.1016/j.tree.2008.06.014

OriginLab (2021). Origin (Version 2021): Northampton, MA, USA.

Pacifici, M., Foden, W. B., Visconti, P., Watson, J. E., Butchart, S. H., Kovacs, K. M., … Rondini, C. (2015). Assessing species vulnerability to climate change. *Nature Climate Change, 5*(3), 215–224. https://doi.org/10.1038/nclimate2448

Pardikes, N. A., Harrison, J. G., Shapiro, A. M., & Forister, M. L. (2017). Synchronous population dynamics in California butterflies explained by climatic forcing. *Royal Society Open Science, 4*(7), 170190. https://doi.org/10.1098/rsos.170190

Pardikes, N. A., Shapiro, A. M., Dyer, L. A., & Forister, M. L. (2015). Global weather and local butterflies: Variable responses to a large-scale climate pattern along an elevational gradient. *Ecology, 96*(11), 2891–2901. https://doi.org/10.1890/15-0661.1

Piovesan, M., Specht, A., Carneiro, E., Paula-Moraes, S. V., & Casagrande, M. M. (2018). Phenological patterns of *Spodoptera* Guenée, 1852 (Lepidoptera: Noctuidae) is more affected by ENSO than seasonal factors and host plant availability in a Brazilian Savanna. *International Journal of Biometeorology, 62*(3), 413–422. https://doi.org/10.1007/s00484-017-1450-x

Porter, J. R., & Gawith, M. (1999). Temperatures and the growth and development of wheat: A review. *European Journal of Agronomy, 10*(1), 23–36. https://doi.org/10.1016/S1161-0301(98)00047-1

Pounds, J. A., Fogden, M. P. L., & Campbell, J. H. (1999). Biological response to climate change on a tropical mountain. *Nature, 398*(6728), 611–615. https://doi.org/10.1038/19297

R Core Team (2021). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Roland, J., & Matter, S. F. (2013). Variability in winter climate and winter extremes reduces population growth of an alpine butterfly. *Ecology, 94*(1), 190–199. https://doi.org/10.1890/12-0611.1

Santoso, A., Mcphaden, M. J., & Cai, W. (2017). The defining characteristics of ENSO extremes and the strong 2015/2016 El Niño. *Reviews of Geophysics, 55*(4), 1079–1129. https://doi.org/10.1002/2017RG000560

Sazib, N., Mladenova, L. E., & Bolten, J. D. (2020). Assessing the impact of ENSO on agriculture over Africa using earth observation data. *Frontiers in Sustainable Food Systems, 4*, 509914. https://doi.org/10.3389/fsufs.2020.509914

Sinclair, B. J., Marshall, K. E., Sewell, M. A., Levesque, D. L., Willett, C. S., Slotsbo, S., … Huey, R. B. (2016). Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecology Letters, 19*(11), 1372–1385. https://doi.org/10.1111/ele.12686

Sofield, I., Evans, L., Cook, M., & Wardlaw, I. (1977). Factors influencing the rate and duration of grain filling in wheat. *Functional Plant Biology, 4*(5), 785–797. https://doi.org/10.1071/PP9770785

Teder, T. (2020). Phenological responses to climate warming in temperate moths and butterflies: Species traits predict future changes in voltinism. *Oikos, 129*(7), 1051–1060. https://doi.org/10.1111/oik.07119

Thornton, P. K., Ericksen, P. J., Herrero, M., & Challinor, A. J. (2014). Climate variability and vulnerability to climate change: A review. *Global Change Biology, 20*(11), 3313–3328. https://doi.org/10.1111/gcb.12581

Tian, H., Melillo, J. M., Kicklighter, D. W., McGuire, A. D., Helfrich, J. V. K., III, Moore, B., III, & Vörösmarty, C. J. (1998). Effect of interannual climate variability on carbon storage in Amazonian ecosystems. *Nature, 396*(6712), 664–667. https://doi.org/10.1038/25328

Tian, H., Stige, L. C., Cazelles, B., Kausrud, K. L., Svarverud, R., Stenseth, N. C., & Zhang, Z. (2011). Reconstruction of a 1,910-y-long locust series reveals consistent associations with climate fluctuations in China. *Proceedings of the National*

Academy of Sciences of the United States of America, 108(35), 14521–14526. https://doi.org/10.1073/pnas.1100189108

Timmermann, A., An, S.-I., Kug, J. S., Jin, F. F., Cai, W., Capotondi, A., … Zhang, X. (2018). El Niño–Southern Oscillation complexity. *Nature, 559*(7715), 535–545. https://doi.org/10.1038/s41586-018-0252-6

Timmermann, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M., & Roeckner, E. (1999). Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature, 398*(6729), 694–697. https://doi.org/10.1038/19505

Vandenbosch, R. (2003). Fluctuations of *Vanessa cardui* butterfly abundance with El Niño and Pacific Decadal Oscillation climatic variables. *Global Change Biology, 9*(5), 785–790. https://doi.org/10.1046/j.1365-2486.2003.00621.x

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor Package. *Journal of Statistical Software, 36*(3), 1–48. https://doi.org/10.18637/jss.v036.i03

Wang, L., Hui, C., Sandhu, H. S., Li, Z., & Zhao, Z. (2016). Population dynamics and associated factors of cereal aphids and armyworms under global change. *Scientific Reports, 5*(1), 18801. https://doi.org/10.1038/srep18801

Welti, E. A. R., Roeder, K. A., de Beurs, K. M., Joern, A., & Kaspari, M. (2020). Nutrient dilution and climate cycles underlie declines in a dominant insect herbivore. *Proceedings of the National Academy of Sciences of the United States of America, 117*(13), 7271–7275. https://doi.org/10.1073/pnas.1920012117

Westgarth-Smith, A. R., Roy, D. B., Scholze, M., Tucker, A., & Sumpter, J. P. (2012). The role of the North Atlantic Oscillation in controlling U.K. butterfly population size and phenology. *Ecological Entomology, 37*(3), 221–232. https://doi.org/10.1111/j.1365-2311.2012.01359.x

Zhao, Z. H., Ouyang, F., & Ge, F. (2015). Cropland expansion facilitated the outbreak of cereal aphids during 1951–2010 in China. *Science Bulletin, 60*(11), 1036–1037. https://doi.org/10.1007/s11434-015-0795-y

Manuscript received: 20 May 2022
Revisions requested: 1 August 2022
Modified version received: 20 September 2022
Accepted: 2 December 2022

The pdf version (Adobe JavaScript must be enabled) of this paper includes an electronic supplement: Supplementary Table S1, Supplementary Figure S1