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Climate change is leading to an ecological trap in a migratory insect

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Many insect migrants rely on favorable seasonal winds to carry out long-range latitudinal migrations. In East China, the annual advance and retreat of the East Asian summer monsoon produces ideal conditions for seasonal range expansion and contraction of many migratory crop pests. However, climate-induced changes in the strength, timing, and location of the monsoon are impacting wind systems which may, in turn, affect migration patterns. We investigated these questions in the rice leafroller (RLR) moth, a severe pest of rice that annually invades the Lower Yangtze River Valley (LYRV) of China from winter-breeding areas further south. Using a 24-y dataset of RLR population dynamics from 31 monitoring stations across Southeast China, we investigated the impact of changes in monsoon wind regimes on fall migration patterns of the pest. Historically, RLR emigrated from the LYRV to South China on the favorably directed winds produced by the retreat of the monsoon at the end of the outbreak season (from mid-August onward). We show that in the recent 12-y period, prevailing late-season winds remain northward for longer than previously, preventing locally produced moths from emigrating southward. Additionally, winds now facilitate mass late-season immigrations into the LYRV, creating an ecological trap, as immigrants do not have time to produce another generation. As a consequence of the changing wind patterns, pest pressure is declining, and climate-induced changes to the East Asian summer monsoon result in seasonal migration becoming a riskier strategy. Such changes in insect migration patterns have severe implications for the population dynamics of windborne migrants, ecosystem functioning, and pest management strategies.

rice leafroller | *Cnaphalocrocis medinalis* | East Asian summer monsoon | windborne insect migration | crop pests

Significance

Many of the world's most important crop pests and disease vectors are small migratory insects that depend upon windborne transport to invade seasonally favorable regions. In East China, atmospheric conditions are generally favorable for bidirectional transport (northward in the spring and southward in the fall) due to wind regimes associated with the spring advance and fall retreat of the East Asian summer monsoon system. However, climate change has delayed the retreat of the monsoon and, in the case of the rice leafroller (RLR) moth, has led to an absence of favorable winds for fall return migrations. Climate change has thus tipped the balance such that migration is now a less favorable strategy for the RLR and potentially many other insects.

Long-range animal migration is a risky and energetically expensive life-history trait, often considered to cause lower survival and fecundity in a wide range of taxa, including insects (1–3). Despite these costs, annual migration between lower and higher-latitude zones is a widespread, successful, and ecologically important strategy among many insect species inhabiting the northern hemisphere (4–9). Every spring across Eurasia and North America, mass migrations of many hundreds of insect species, comprising trillions of individuals (10–13), move poleward and exploit the seasonal progression of suitable habitats to produce subsequent generations (5).

Due to the relatively slow flight speeds and short adult lifespans of most insect migrants (5), the existence of these enormous insect flyways is dependent on rapid transport in high-altitude airstreams blowing in the appropriate seasonal direction. In spring, this is relatively easily achieved on poleward winds that are reasonably frequent and warmer than winds from other directions which encourages insect flight. However, for long-range migrations to be maintained in the population, at least some of the resulting progeny must return to lower latitudes to successfully produce the next generations during the winter months; otherwise, long-range migratory phenotypes will rapidly disappear (5, 9). Despite ample observations of northward spring movements of many species, evidence of these return migrations during fall was originally lacking (5), generating the theory that poleward migration leads to an ecological trap for many species (14–16). This concept, known as the "Pied Piper" phenomenon, posits that insects will be led poleward in the spring on warm southerly winds to higher-latitude temperate regions from where there is little chance of return in the fall, as northerly winds will be infrequent and/or cool enough to suppress flight.

This notion has been somewhat overturned, at least among larger insect migrants (those with body masses >10 mg), because it has transpired that large-scale returns of these insects are, in fact, frequent. For example, the availability of long-term entomological radar data,

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plus systematic monitoring at mountain passes, has revealed the apparent ubiquity of massive return movements hundreds of meters above the ground among a wide range of larger migrants, including Lepidoptera, Diptera, and Odonata (5, 11, 12, 17). These larger insects have comparatively fast self-propelled airspeeds, and so while they partly rely on favorable winds, they are not entirely dependent upon them. Southward return movements are achieved by employment of a complex suite of related behaviors, including selection of days/nights with favorable tailwinds and adaptive orientation to maximize travel speed in the preferred direction (18–20).

In addition to the intensively studied larger migrants discussed above, numerous smaller species (with body masses <10 mg, hereafter "small insects") also engage in mass windborne migrations. Small insects are vastly more numerous than the larger species, making up 97 to 99% of the total windborne insect fauna (11, 12). Important components of the small migrant insect fauna include aphids, planthoppers, small Diptera (e.g., mosquitoes), parasitic wasps, and crambid moths (12, 21–23). Small insect migrants have self-powered airspeeds <1 m/s, and thus flight behaviors are likely to be much less important than for larger insects, as their flight vector will have a negligible impact on their movement track due to the typical windspeeds experienced by the migrants. Consequently, small insects do not exhibit common orientation during high-altitude flights (21, 22), and migration directions simply track the prevailing winds (11). Bidirectional latitudinal migrations of such species are thus most likely to evolve in regions where seasonal wind patterns facilitate transport in beneficial directions, for example along the Mississippi Flyway in North America (10, 24).

It is in East Asia, however, that this situation reaches its zenith; here, the East Asian Insect Flyway (EAIF) constitutes the largest and most diverse insect flyway on the planet (9, 12). The annual poleward progression and subsequent retreat of the East Asian summer monsoon generates consistent winds blowing from southwest to northeast in the spring and summer, and then reversing direction in the fall (25, 26). This reliable wind pattern facilitates the mass transport of >200 species each spring northeastward from Southeast Asia along the East Asian coastal plain (9, 12), including many harmful crop pests and disease vectors (6, 27), but also some beneficial biocontrol agents and pollinators (7, 28). The most important small insect migrants in this region are several species of rice planthoppers (Hemiptera: Delphacidae) and the rice leafroller (RLR) moth *Cnaphalocrocis medinalis* (Lepidoptera: Crambidae; hereafter RLR), that collectively constitute the world's most serious rice pests (9, 29–31). Their annual expansion into East Asia from more southern winter-breeding regions is dependent on the northward progression of the East Asian summer monsoon and its associated southwesterly winds; they return south in the fall when the winds reverse (21, 22, 32), although the proportion reaching the winter-breeding areas is unknown (19, 33).

Given the complete dependence on favorable seasonal wind regimes, it seems highly likely that global climate change will modify and potentially disrupt the migratory patterns of these small weak-flying insects. We investigate this important topic by analyzing long-term changes in the annual population dynamics and migration patterns of the RLR moth in the East China provinces of Anhui, Jiangsu, Jiangxi, and Zhejiang, an area known as the Lower Yangtze River Valley (LYRV; Fig. 1*A*), and compare these changes with variations in regional meteorological patterns. The RLR is a major migratory rice pest across Asia, exhibiting a multigenerational migration that takes it from Southeast Asia northward into East Asia (34) during spring and summer, reaching as far as Northeast China by crossing the Bohai Sea (35). By mid-August to early September, the general movement direction reverses and the RLR moves south-westward (22, 34, 36); this species must retreat to Southeast Asia and extreme South China where rice is grown year-round, and temperatures are suitable for larval development through the winter months (9). The RLR is a small weak-flying moth, with an average body mass of about 8 mg (22) and self-powered airspeed of 0.8 m/s (37), and thus achieving seasonal movements covering thousands of km is entirely dependent on suitable wind systems. In China, its average occurrence area exceeds 16 million hectares (66.3% of the rice planting

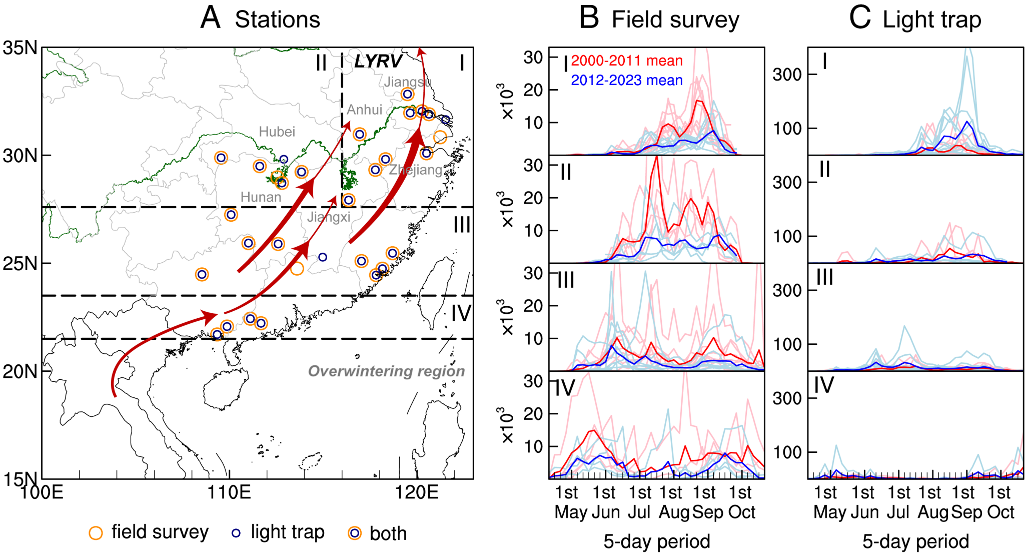

Fig. 1. Monitoring stations and population trends of RLR in southern China. (*A*) Locations of the 28 field survey sites and 28 light traps (31 stations in total) for monitoring RLR moths, grouped into 4 geographical regions: the LYRV (I), the Middle Yangtze River Valley (II), the region north of the Nan Mountains (III), and the region south of the Nan Mountains (IV). The Yangtze River is indicated by the green line, and key provinces named in the text are indicated. Thick red arrows show the major migratory trajectories, and thin red arrows show the minor migratory trajectories. Regional division and migratory trajectories are based on historical investigations (34). (*B*) Mean annual density of RLR moths in each 5-d period per hectare of rice paddy across the occurrence season, for each of the 4 regions in (*A*). (*C*) Mean numbers of RLR moths caught in light traps in each 5-d period across the occurrence season, for each of the 4 regions in (*A*). Red lines show the annual mean for Period I (2000 to 2011), and blue lines show the annual mean for Period II (2012 to 2023). Faint lines show annual means for each station, and thick lines show the annual means for the whole region.

area) during its peak abundance in late summer, when it can reduce rice production by >60% and yield by >500,000 tons (30, 38, 39).

Our recent research has found that climate-induced changes in the East Asian summer monsoon have led to alterations of the spring migrations of small windborne insect migrants in this region (31). However, little is known about the critical fall return migrations, and whether they are also being impacted by recent climate change. Here, we use a 24-y dataset on RLR abundance in the LYRV to investigate the impact of changes to the monsoon wind regimes on the late-season population dynamics and fall migration patterns of this critically important rice pest. Further, we test the idea that changing wind patterns associated with later retreat of the summer monsoon may be increasingly leading this species into an ecological trap from which there is a reduced chance of progeny returning to lower-latitude winter-breeding areas. Finally, we discuss the implications of the changing patterns observed in the RLR for the wider community of small insect migrants and the ecosystems they link.

Results and Discussion

RLR Annual Population Trends in the LYRV. Over the 24-y study period, monitoring data indicate that there have been substantial changes to RLR population abundance and phenology in the LYRV region (Fig. 1*A*, Region I). Field surveys show that in Period I (2000 to 2011), annual mean densities of RLR in rice paddies were very high: At the peak density (in the 3rd to 6th 5-d periods of August), there was an average of 16,690 moths per hectare across all 10 stations, with a maximum of 39,424 at one location (Fig. 1 *B*, *Top*). During this peak period (mid- to late August), when rice is at the panicle stage, infestations of RLR have a significant impact on rice yield (40). More recently, in Period II (2012 to 2023), moth density in rice paddies has shown a significant decline ($t_{21.1} = -2.4$, $P = 0.012$): Annual mean density peaked at 7,785 RLR moths per hectare, only 46.6% of the Period I density (Fig. 1 *B*, *Top*). The peak density was also delayed in Period II, from the 3rd to 6th 5-d periods of August to the 1st to 2nd 5-d periods of September (Fig. 1 *B*, *Top*) when the rice growing stage is less suitable for RLR development (41) and so less crop damage will occur, as densities in the key period (mid- to late August) were lower still (Fig. 1 *B*, *Top*). The Middle Yangtze River Valley (Fig. 1*A*, Region II) and the region north of the Nan Mountains (Fig. 1*A*, Region III) are the major source areas of RLR infesting rice crops in the LYRV (34). Both regions have also seen significant declines in RLR densities in rice paddies between Periods I and II, particularly in the Middle Yangtze (Region II: 29,240 vs. 7,360, $t_{21.0} = -2.5$, $P = 0.009$; Region III: 10,958 vs. 5,910, $t_{22.0} = -2.3$, $P = 0.016$; Fig. 1 *B*, *Central*). These results clearly show that in the most recent 12-y period, RLR densities in rice paddies in the LYRV are reduced and delayed. Consequently, pest outbreaks in the LYRV are less severe than historically, and this is supported by significantly lower densities of eggs in the rice paddies and reduction in the crop area attacked by RLRs between Periods I and II (eggs: 156 vs. 57, $t_{21.9} = -4.0$, $P < 0.0001$, *SI Appendix*, Fig. S1*A*; area: 31% vs. 19%, $t_{20.8} = -6.6$, $P < 0.0001$, *SI Appendix*, Fig. S1*C*). Field surveys indicate the abundance of moths breeding in the rice crop, and thus pest pressure in rice paddies, have seemingly reduced in the LYRV during the most recent period.

Given these field survey results, it is thus initially surprising that light-trap catches in the LYRV during Period II were significantly higher than in Period I (peak 5-d period catches of 131 moths vs. 36 moths averaged across all stations; $t_{20.2} = 2.6$, $P = 0.008$; Fig. 1 *C*, *Top*). As in the field survey data, the peak was also delayed in Period II, from the 3rd to 6th 5-d periods of August to the 1st to 2nd 5-d periods of September (Fig. 1 *C*, *Top*). This change in light-trap catches was not replicated in the other regions in China, where catches were typically low throughout the season and similar in both Periods I and II (Fig. 1 *C*, *Lower* 3). Light traps monitor the population abundance of RLR moths in the general area (rather than the numbers developing in the rice crop), and thus are composed of both locally emerging moths and recent immigrants arriving in the region. The substantial increase of moths caught at light during Period II in the LYRV, particularly in the late season, thus strongly indicates that mass migrations into the region now regularly occur in early September. Historically, RLR populations would have largely left the LYRV region during this period, on westward and south-westward winds toward Regions II and III (22, 36). Late-season arrival of moths (in September) is not beneficial for RLR as the growing stage of rice crops in the LYRV is no longer suitable for mass insect development in this period (41) and few other food sources are available; these late-arriving moths are thus likely doomed to have few or no surviving progeny. This is supported by the fact that field surveys find evidence that late-arriving moths lay eggs in the rice crop (*SI Appendix*, Fig. S1*A*), but very few larvae are found in September (*SI Appendix*, Fig. S1*B*). Furthermore, our model of RLR development indicates that the progeny of late-season immigrants would have only been able to develop into adults in 3 of the 12 y of Period II (*SI Appendix*, Fig. S2). We therefore focused our investigations on the source of these late-season immigrants and the meteorological causes of the phenological change observed in the LYRV.

Reduced Linkage Between Local Breeding and Late-Season Light-Trap Catches in the LYRV. To further understand the causes of the increased and delayed peak in late-season light-trap catches in the LYRV, we examined long-term trends in the monitoring data from the late-season period only (data from 15 August onward). Late-season light-trap catches have shown a consistent gradual increase in RLR numbers throughout the whole study period (2000 to 2011: $F = 7.99$, slope = 0.13, $P = 0.018$; 2012 to 2023: $F = 6.24$, slope = 0.08, $P = 0.032$; Fig. 2*A*), resulting in the mean annual late-season total being significantly greater in Period II than it was in Period I (530 vs. 143, $t_{14.6} = 2.74$, $P = 0.008$; Fig. 2*A*). By contrast, late-season field surveys were stable in Period I and then significantly declined in Period II (2000 to 2011: $F = 0.28$, slope = 0.01, $P = 0.607$; 2012 to 2023: $F = 5.06$, slope = -0.05, $P = 0.048$; Fig. 2*B*), and the mean density of RLR in rice crops was significantly lower in Period II than it was in Period I (30,322 vs. 63,218, $t_{21.5} = -2.73$, $P = 0.006$; Fig. 2*B*).

Given these divergent trends, we predicted that locally emerging RLR moths now comprise a decreasing component of the late-season light-trap catches in the LYRV; we tested this by correlating early-season field surveys with abundance in light traps, first at the regional level. In Period I, early-season field survey data were strongly positively correlated with light-trap catches in both the early season ($r = 0.78$, $P = 0.002$) and late season ($r = 0.79$, $P = 0.002$) when averaged across all stations in the LYRV. However, by Period II this relationship had broken down: Early-season field survey density was slightly positively correlated (but not significantly) with early-season light-trap catches ($r = 0.43$, $P = 0.160$), and by late season, there was no relationship ($r = -0.10$, $P = 0.752$) at the regional level. This trend was also clear when monitoring data from individual stations in the LYRV were analyzed separately: Early-season field surveys were significantly positively correlated with late-season light-trap data at 7 of the 9 stations in

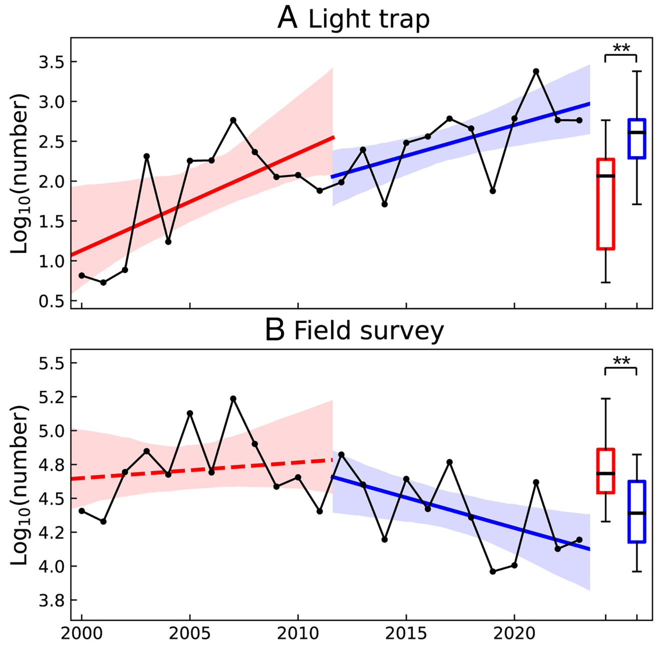

Fig. 2. Late-season population trends of RLR in the LYRV in the two periods. (*A*) Log-transformed total catches of RLR moths caught in light traps on every night from 15 August onward. (*B*) Log-transformed total field survey counts of RLR moths in the rice paddies from every 5-d period after 15 August. Red lines show the linear trends and 95% CI in Period I (2000 to 2011), and blue lines show trends and 95% CI in Period II (2012 to 2023). Solid lines indicate significant linear trends, while the dashed line indicates a nonsignificant trend. Significant differences in mean totals of the two periods are indicated above the box plots: $^{**}P < 0.01$.

Period I, implying a strong contribution from local breeding, but at only one of these stations in Period II (Fig. 3), and there was a decrease in the mean value of these correlations between the two periods, although it was not significant (paired t test; Period I mean: 0.50; Period II mean: 0.16; $t_8 = 1.64$; $P = 0.069$). These results show that the linkage between local breeding in the early-season and light-trap catches in the late season has broken down in the LYRV region in Period II, supporting our contention that the late-season peak in light-trap catches occurring here in recent years primarily results from mass immigrations into the LYRV, which historically did not occur so late in the year.

Changing Wind Patterns Facilitate Late-Season Immigration into the LYRV. Having demonstrated that the increased and delayed peak in the general population of RLR within the LYRV region is associated with large-scale late-season immigration, we hypothesized that this has been caused by changing wind regimes over the study period. Immigration of RLR moths to the LYRV (dashed blue boxes in Fig. 4) is believed to primarily originate from a source area to the west and southwest (42), in the provinces of Hubei, Hunan, and Jiangxi (Fig. 1*A*), and thus, we analyzed wind patterns at 900 hPa (1,000 m above sea level) from this key source region (dashed magenta boxes in Fig. 4). We used the annual pattern of the ratio of late-season light-trap to late-season field survey data, which has significantly increased over the study period ($F = 56.07$, slope = 0.019, $P < 0.0001$; Fig. 4*A*), to identify two subsets of years for subsequent analyses. Years where the light-to-field ratio was >1 SD below the mean ("low-ratio" years, namely 2000, 2001, 2002, and 2004) were assumed to have much lower rates of late-season immigration than the long-term mean, whereas years with ratios >1 SD above the mean ("high-ratio" years, namely 2020, 2021, 2022, and 2023) were assumed to have much higher rates of late-season immigration (Fig. 4*A*).

Late-season wind patterns in low-ratio years were favorable for southward return migration but not conducive to northward immigration (Fig. 4*B*). In the key source area (magenta box), the mean direction of late-season winds suitable for transport (>8 m/s) was toward the southwest (Rayleigh test: mean = 247°, $n = 4{,}110$, $r = 0.43$, $P < 0.0001$; Fig. 4 *B*, *Inset*) in the low-ratio years. Thus, the largely westward and south-westward winds would have facilitated return migration of RLR moths emerging in the LYRV to Regions II and III (Fig. 1*A*), and prevented any further immigration into the LYRV, during this period. By the end of the study period, in the high-ratio years, there had been a distinct interdecadal shift in the late season; winds were no longer favorable for return migration but highly conducive to fresh immigration into the LYRV (Fig. 4*C*) from Regions II and III (Fig. 1*A*). The mean direction of late-season winds suitable for transport (>8 m/s) in the key source area has switched toward a more northerly direction (Rayleigh test: mean = 327°, $n = 3{,}768$, $r = 0.39$, $P < 0.0001$; Fig. 4 *C*, *Inset*), facilitating northward transport and preventing southward return. There is a striking disparity in the difference in the mean v-component (i.e., the northward-blowing component) of the winds between these two subsets in the key source area; late-season winds are much more northerly in high-ratio years than they were in the low-ratio years at the start of the study period (dark-red shaded area in Fig. 4*D*), and the circular distributions are significantly different (Watson–Wheeler test: $W = 3{,}643$, $P < 0.0001$). Taken together, the wind direction data strongly indicate that in Period II, prevailing late-season winds will lead to locally emerged populations becoming trapped in the LYRV and unable to return south, as well as conditions highly favorable for additional mass immigration into the LYRV.

Associations with Changes to the East Asian Summer Monsoon Retreat. The changing wind patterns in the late-season period are likely associated with changes to the retreat of the East Asian summer monsoon from the LYRV, as this large-scale atmospheric system produces the prevailing winds over East Asia. Our analysis of the summer monsoon retreat from the LYRV region shows that there is a trend for delayed retreat date although it was not significant ($F = 2.165$, slope = 0.13, $P = 0.155$; Fig. 5), consistent with similar changes since the mid-2000s shown in climatological studies (43, 44). Our data show that the mean date of the retreat is about 10 d later in 2023 than it was in 2000 (2nd 5-d period of September vs. 6th 5-d period of August; Fig. 5). Perhaps more importantly, the retreat date is not only delayed but the Coefficient of Variation has become substantially more variable in Period II compared to Period I (27.9% vs. 17.4%; Fig. 5), with some years (i.e., 2017, 2021, and 2023) experiencing delays into late September or early October. These late-retreat years also experienced large late-season immigrations (Fig. 2*A*) which made a substantial contribution to the local population (Fig. 4*A*).

Increased Late-Season Migration is Leading to an Ecological Trap for the RLR. Our data clearly show that RLR migration patterns and population dynamics in the LYRV major rice-growing provinces (Anhui, Jiangsu, and Zhejiang) have undergone substantial recent changes, likely in response to climate-induced modifications to the regional wind patterns. In the RLR and similar small windborne insects, both the spring/summer northward advance and the fall return migration are highly dependent on appropriate climate conditions, including beneficially directed winds, favorable zones of rainfall, and suitable temperatures (9, 29, 31, 36). Thus, it is to be expected that as various aspects of the East Asian climate are changing, in association with modifications to the intensity, position, and timing of the East Asian summer monsoon, that windborne insect migration patterns in East Asia will also be affected (31).

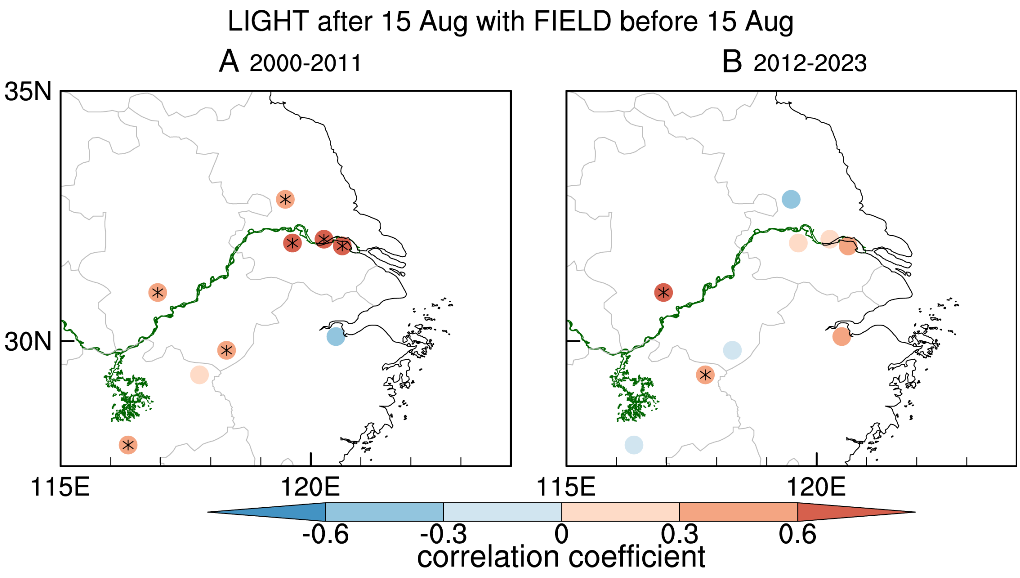

Fig. 3. The linkage between local breeding and late-season light-trap catches of RLR has broken down in the LYRV. The maps of the LYRV region show correlation coefficients between early-season field survey data and late-season light-trap catches from the 9 monitoring stations in the LYRV that have continuous time-series of both data, for Periods I (*A*) and II (*B*). Red symbols indicate locations with positive correlations, blue symbols indicate locations with negative correlations, and stars indicate that the correlation is significant. The green line shows the course of the Yangtze River.

We have found this to be the case with the RLR populations annually invading the LYRV region. Due to the recent switch in wind direction during the late-season period (mid-August to mid-September), locally emerging moths are often no longer able to return to suitable lower-latitude breeding areas. Thus, mass fall migrations of RLR to the south historically observed by radar (22) have been replaced by substantial immigration from the south. This combination of increased immigration and entrapment of locally bred moths leads to substantially elevated late-season RLR populations in the LYRV. By this season the rice crop is at the heading stage (41), and no longer suitable for development of healthy RLR larvae (45). The large numbers of late-season adult

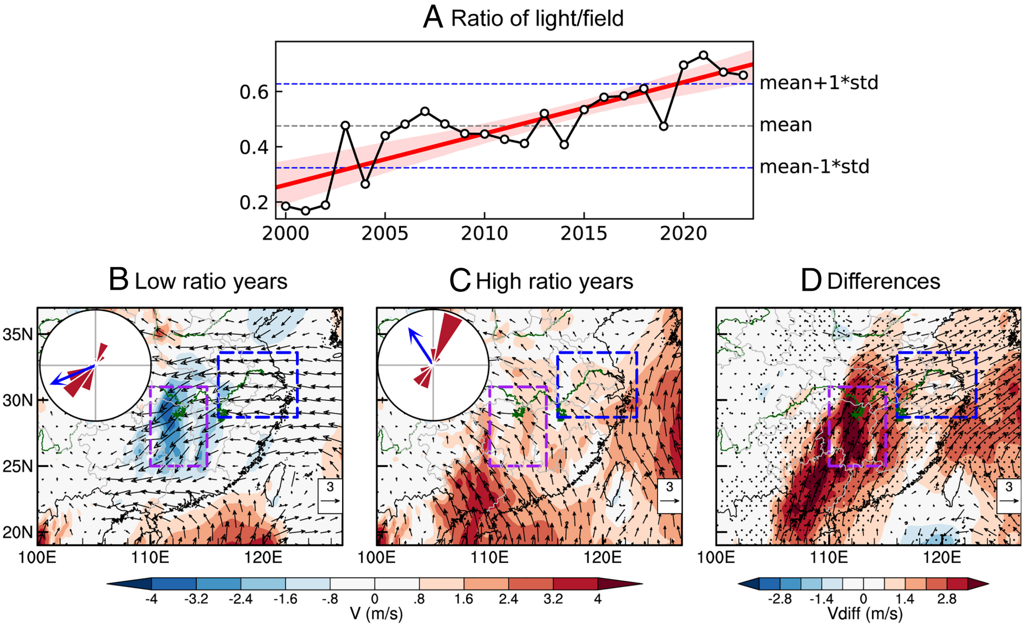

Fig. 4. Changing wind directions during the study period. (*A*) The mean ratio of light-trap catches to field survey data of RLR moths during the late season (after 15 August) in the LYRV, which has significantly increased. The solid red line shows the significant linear trend and 95% CI. Low ratios indicate that late-season immigration was not an important component of the local population, while high ratios indicate late-season immigration was a major contributor to the local population. The 4 y >1 SD below the long-term mean (2000, 2001, 2002, and 2004) were defined as "low-ratio" years, and the 4 y >1 SD above the long-term mean (2020, 2021, 2022, and 2023) were defined as "high-ratio" years, for subsequent analyses. (*B*) Mean downwind vectors at 900 hPa in the low-ratio years (little immigration). (*C*) Mean downwind vectors at 900 hPa in the high-ratio years (much immigration). (*D*) The difference in the mean wind vectors between these two subgroups. On each map, the dashed blue box indicates the LYRV, and the dashed magenta box indicates the presumed source/destination area used for the wind comparisons. The inset circular plots show the distribution of downwind directions >8 m/s from the magenta box, with the blue arrow indicating the mean. The small black arrows on the maps indicate the direction and speed of the mean downwind vector at 900 hPa at each location. The colors superimposed on the maps indicate the strength of the V-component of the wind, i.e., how strong the north/south component is: Red colors (positive values) indicate winds with a northward component (suitable for late-season immigration), blue colors (negative values) indicate winds with a southward component (suitable for late-season return migration). Regions with dots in (*D*) indicate that the difference between the two periods is significant ($P < 0.05$).

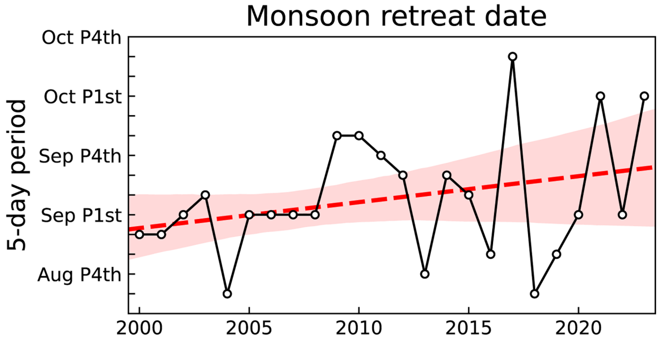

Fig. 5. The retreat date of the East Asian summer monsoon from the LYRV. There is a (nonsignificant) trend of delayed retreat over the study period. The dashed red line shows the linear trend and 95% CI.

moths in the LYRV during Period II do produce some eggs in the rice crop (*SI Appendix*, Fig. S1*A*), but very few manage to develop into large caterpillars (*SI Appendix*, Fig. S1*B*) and so consequently pest problems have ameliorated compared to Period I (*SI Appendix*, Fig. S1*C*). There are few other suitable hostplants in the region at this period, plus temperature conditions will rarely allow another generation to be completed in any case (*SI Appendix*, Fig. S2), so there are extremely limited chances to produce another generation. Additionally, adult moths are short-lived, and tethered flight experiments indicate that most individuals are only capable of engaging in migratory flight for 1 to 3 nights after emergence (*SI Appendix*, Fig. S3), greatly reducing the chance that late-season immigrants will be able to remigrate back south. Thus, these late-season moths are likely doomed to die without producing progeny or reaching locations suitable for producing the next generation. We therefore conclude that recent climate change and associated alterations in wind patterns have altered the tradeoff between costs and benefits of migration in the RLR, and now the extended period of southerly winds lead the late-season populations into an ecological trap (*SI Appendix*, Fig. S2) from which there is a much-reduced chance of escape.

Conclusions

The RLR is a small, weak-flying insect that makes use of favorable regional wind patterns to exploit seasonally available resources throughout the tropical, subtropical, and temperate rice-growing areas of Asia, Oceania, and Australia. Here, we are concerned with seasonal migrations between Southeast and East Asia, which also occur in many other insect migrants (9, 29). The susceptibility to climate-induced changes in wind patterns that we have documented in RLR moths is therefore highly likely to be replicated in a wide range of other migratory insects. These impacts will be most strongly felt in the smaller species with low self-powered airspeeds, but even the largest migrants are also at least partially dependent on windborne transport. While climate change impacts on migratory pest insects have been reasonably well documented in East Asia, they have typically focused on how warming temperatures may lead to increased population growth, northward expansions of the migratory range, and/or increased winter survival further north (41, 46–49). Results so far have indicated that migratory insect pests are tending to increase their range and abundance in China, with consequently an increase in severity of outbreaks and crop damage (50). However, Lv et al. (31) and the current study show that in the past decade, two of the most important regional crop pests (brown planthopper *Nilaparvata lugens* and RLR) have decreased in their abundance and pest severity in response to changes to the East Asian summer monsoon and its associated wind patterns. The brown planthopper has declined due to reduced northward migration in the spring, while the principal driver of the changes we have observed in the RLR is an ecological trap, resulting from increased late-season immigration to higher-latitude regions and an inability to escape before the Pied Piper's trap has closed. While the reduction in these two species may be beneficial for agricultural productivity and food security, similar changes in other (nonpest) species will have adverse effects on ecosystem functions such as provision of beneficial services and important food sources for higher trophic levels. There is already some evidence that migratory insect communities in North China are experiencing an element of decline with a consequent loss of ecosystem service provision (6, 7), but whether these patterns are being replicated in other regions remains to be determined. Climate change will lead to complex effects not only on the migratory insects themselves but also all aspects of the distant ecosystems they interact with and link (51), and so there is an urgent requirement to study these impacts in all terrestrial regions.

Methods

Field Survey and Light Trap Data. Field surveys and light-trap counts of RLR abundance were collected during the 24-y period of 2000 to 2023 from >300 plant protection stations located across a large area of southern China, coordinated by the National Agro-Tech Extension Service Center of China (NATESC). From this large dataset, a subset of monitoring stations where data were either complete, or <1% of the total time series was missing, were selected for further analyses (Fig. 1*A*). In total, there were 31 stations used in the study, as follows: 25 stations had field survey and light-trap data; 3 stations had only field survey data; and 3 stations had only light-trap data (Fig. 1*A*). The 31 stations were split into 4 geographical regions based on the different RLR regions identified by Chang et al. in their classic study of RLR population dynamics (34). Our main study area was the LYRV (Region I in Fig. 1*A*, mainly involving Anhui, Jiangsu, Zhejiang, and Jiangxi provinces), which contained 10 field survey and 10 light-trap stations (11 in total). We also assessed population trends in three regions to the west and south that are source and destination areas for RLR moths migrating into and out of the LYRV (Fig. 1*A*), namely: the Middle Yangtze River Valley (Region II, 5 field survey and 5 light-trap stations, 6 in total); the region north of the Nan Mountains (Region III, 9 field survey and 9 light-trap stations, 10 in total); and the region south of the Nan Mountains (Region IV, 4 field survey and 4 light-trap stations, 4 in total).

Field surveys involved plant protection station staff walking a standardized transect through a rice paddy every day during the season when moths are present in the area, and counting the number of adult RLR flushed from the crop. In addition, every 5 d, the number of RLR eggs and caterpillars in the crop was also recorded, and an index of crop area affected by RLR was calculated (*SI Appendix*, Fig. S1). These field survey data provide a quantitative measure of the abundance of moths and their immature stages in the crop and are a good measure of local breeding density and thus potential crop damage.

Nightly abundance of adult moths in the vicinity of the rice paddies where field surveys were conducted was monitored by counting the number of moths caught every night in standardized 20-W "black-light" (UV) traps. Capture rates from these traps will reflect a combination of local breeding/emergence plus recent immigration into the area of moths from further afield.

In this study, we are particularly interested in population dynamics and migration activity later in the season, as our focus is the factors driving the return fall migrations. In the LYRV, RLR moths produce 4 to 5 generations per year, based on data from historical studies (34, 52) and from the outputs of a time-series analysis (*SI Appendix*, Figs. S4 and S5). The 1st to 3rd generations from May to early August originate from a mixture of immigration from further south and west, and from local breeding within the region; historically, adult moths of the 4th generation, which start to appear from mid-August, start the southward migration toward the winter-breeding region. Thus, for the purposes of this study, we use a date of 15 August as the cutoff (*SI Appendix*, Fig. S5), after which we would typically expect to see the start of return migrations (34). We call the period before 15 August the "early season" and the period after 15 August the "late season" (*SI Appendix*, Fig. S5).

To understand temporal changes, we split the 24-y dataset into two equal-length periods, namely "Period I" (2000 to 2011) and "Period II" (2012 to 2023). The split point for the separation of the two periods was identified by carrying out a sliding-window correlation analysis between early-season field survey data and late-season light-trap catches (*SI Appendix*, Fig. S6) and was based on the stark change in the relationship that occurred between 2011 and 2012 (*SI Appendix*, Fig. S6).

Meteorological Data. Global-gridded meteorological data with a spatial resolution of 0.25° × 0.25° were derived from ERA5 data for the study period (every day between 2000 to 2023). ERA5 is the fifth-generation atmospheric reanalysis dataset from the ECMWF (European Centre for Medium-Range Weather Forecasts) (53). In this study, we used 2-h data for surface precipitation, temperature, specific humidity, and the wind vectors plus their u- and v-components (the east–west, and north–south, values respectively). Wind data used in these analyses were that at the 900 hPa level, corresponding to an altitude of approximately 1,000 m above sea level (typically 700 to 900 m above ground level in our study region). This height is used to represent the typical migration altitude range for RLR, which is generally between 100 and 1,800 m above ground (22, 54). Meteorological conditions at this altitude are considered important factors influencing the migration of the RLR (42, 55, 56). The East Asian summer monsoon retreat date is defined as the 5-d period when the northern boundary of the monsoon region has retreated from the LYRV for at least three consecutive 5-d periods. The monsoon region is determined at each grid in each 5-d period by satisfying three conditions: The 5-d period mean wind direction at 850 hPa must be from southwest to northeast, the 5-d period precipitation must be greater than 4 mm, and the 5-d period mean equivalent potential temperature at 850 hPa must be less than 335 K (57). The northern edge of the monsoon is then determined by averaging the northernmost latitude in each longitude over 110° to 120°E.

Statistical Analyses of Survey and Meteorological Data. Annual abundance of RLR in field surveys and light-trap catches in the LYRV during the late-season period (after 15 August) were compared with a range of other variables, including RLR numbers in other regions, and meteorological data, using Pearson correlations. All light-trap catches, and field survey data, were log transformed (base 10) to approximate to a normal distribution. One-tailed *t* tests were used to test the difference ("greater" or "less") between two periods (Period I: 2000 to 2011; Period II: 2012 to 2023). For wind direction comparisons, Rayleigh tests were performed to calculate the mean direction; the mean circular resultant length "*r*" is a measure of the clustering of the downwind direction distribution, with higher values indicating tighter clustering around the mean. A Watson–Wheeler test was used to test for a difference in the distributions of downwind directions in the low-ratio and high-ratio years.

Data, Materials, and Software Availability. Excel spreadsheets with 5-d RLR number in field and daily catch data from 11 stations in LYRV for 2000 to 2023, have been deposited in the Dryad repository, https://doi.org/10.5061/dryad.kd51c5bhh (58). ERA5 data are available at https://cds.climate.copernicus.eu/datasets (53). Other study data are included in the article and/or *SI Appendix*.

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