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RESEARCH ARTICLE

Changing patterns of the East Asian monsoon drive shifts in migration and abundance of a globally important rice pest

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Abstract

Numerous insects including pests and beneficial species undertake windborne migrations over hundreds of kilometers. In East Asia, climate-induced changes in large-scale atmospheric circulation systems are affecting wind-fields and precipitation zones and these, in turn, are changing migration patterns. We examined the consequences in a serious rice pest, the brown planthopper (BPH, *Nilaparvata lugens*) in East China. BPH cannot overwinter in temperate East Asia, and infestations there are initiated by several waves of windborne spring or summer migrants originating from tropical areas in Indochina. The East Asian summer monsoon, characterized by abundant rainfall and southerly winds, is of critical importance for these northward movements. We analyzed a 42-year dataset of meteorological parameters and catches of BPH from a standardized network of 341 light-traps in South and East China. We show that south of the Yangtze River during summer, southwesterly winds have weakened and rainfall increased, while the summer precipitation has decreased further north on the Jianghuai Plain. Together, these changes have resulted in shorter migratory journeys for BPH leaving South China. As a result, pest outbreaks of BPH in the key rice-growing area of the Lower Yangtze River Valley (LYRV) have declined since 2001. We show that these changes to the East Asian summer monsoon weather parameters are driven by shifts in the position and intensity of the Western Pacific subtropical high (WPSH) system that have occurred during the last 20 years. As a result, the relationship between WPSH intensity and BPH immigration that was previously used to predict the size of the immigration to the LYRV has now broken down. Our results demonstrate that migration patterns of a serious rice pest have shifted in response to the climate-induced changes in precipitation and wind pattern, with significant consequences for the population management of migratory pests.

KEYWORDS

brown planthopper, East Asian monsoon, migration trajectories, pest management, Western Pacific subtropical high-pressure system, windborne insect migration

Hua Lv and Meng-Yuan Zhai contributed equally to this work.

1 | INTRODUCTION

Long-distance insect migration occurs on an enormous scale (Bauer & Hoye, 2014; Chapman et al., 2015; Hu et al., 2016). This has implications for predator-prey interactions and ecosystem function (Krauel et al., 2017; Satterfield et al., 2020), transport of biomass and essential nutrients (Hu et al., 2016), pollination in natural and agricultural landscapes (Wotton et al., 2019), the transmission of human pathogens (Huestis et al., 2019; Reynolds et al., 2006; Yaro et al., 2022), and, perhaps most significantly, positive and negative impacts on agricultural productivity (Chapman et al., 2004; Hu et al., 2019; Li et al., 2020; Wotton et al., 2019). Most insect migrants engage in windborne movements high above the ground, where their self-propelled flight speeds are considerably slower than typical windspeeds, and thus they are transported more-or-less downwind (Chapman et al., 2010, 2015; Reynolds et al., 2017). With such transport on fast-moving airstreams, even minute insects can cover hundreds of kilometers in a single day or night of continuous flight, and thousands of kilometers over several successive days or nights of migration (Chapman et al., 2012; Florio et al., 2020; Gao et al., 2020; Hedlund et al., 2021; Huestis et al., 2019; Hu et al., 2019, 2021). In addition to the fundamental importance of winds, migration can be terminated by weather events such as heavy rainfall, downdrafts, and cold temperatures (Drake & Farrow, 1988; Drake & Reynolds, 2012; Wainwright et al., 2022; Westbrook & Isard, 1999); thus, meteorological factors have a critical influence on insect migration patterns (Chapman et al., 2015; Drake & Farrow, 1988; Reynolds et al., 2017).

Global climate change is a key issue of our times (Ou et al., 2021; Sippel et al., 2020). Climate change is projected to affect migration patterns of many aerial migrants (La Sorte et al., 2019), but the effects of global warming on insect populations are particularly acute because insects are heterothermic, and as such they are highly sensitive and respond rapidly to changes in temperature (Deutsch et al., 2018; Ma et al., 2021). For example, insects' metabolic rate and development time accelerates with temperature, and increased development rates lead to more generations per year as climates warm (Culbertson et al., 2022; Deutsch et al., 2018; Ma et al., 2021). In addition, migratory insects are arriving earlier to their summer breeding areas (Colom et al., 2022; Hu et al., 2010; Liu et al., 2018; Roy & Sparks, 2000; Zeng et al., 2020), and shifting their higher-latitude range margins poleward (Bebber, 2015; Bebber et al., 2013; Tu et al., 2020), while increased winter temperatures may result in larger overwintering areas leading to a larger source of potential migrants (Hu et al., 2010). As so many of the world's most damaging crop pests are migrant insects (Drake & Gatehouse, 1995; Drake & Reynolds, 2012), these potential climate-induced changes in timing, location and abundance are of serious concern to food security in temperate regions of the world.

In addition to rising temperatures, climate change is also altering precipitation and atmospheric circulation patterns (An et al., 2015), which can significantly influence regional climates. In East Asia the climate is strongly affected by the East Asian summer monsoon, which in turn is linked to global atmospheric circulation patterns (An et al., 2015; Ding et al., 2018; Yang, Cai, et al., 2022). Winds associated with the East Asian monsoon over China generally blow from the southwest in spring and summer, but from the north in autumn (Ding & Chan, 2005; Li et al., 2021), and this seasonal reversal will be beneficial for the windborne transport of migratory insects that exploit the seasonal glut of resources in temperate East Asia. The water vapor transported by the summer monsoon originates from the tropical Indian and Pacific Oceans (Ding & Chan, 2005; Zhou & Yu, 2005), and thus the intensity and location of the East Asian summer monsoon is closely linked with large-scale tropical and subtropical atmospheric systems, such as the Intertropical Convergence Zone (ITCZ) and the Western Pacific subtropical high (WPSH). The ITCZ is a band of low pressure circling the Earth which lies generally close to the equator; it moves north into East Asia during the northern summer, bringing warm and wet air from the southwest and producing the summer monsoon. Global warming, via increased equatorial surface temperatures, is reducing this northward shift of the ITCZ during summer, which in turn alters key features of the East Asian monsoon including the intensity and latitude of the southwesterly jet and the rain band (Sooraj et al., 2015; Zhou et al., 2019; Zhu et al., 2012). The position and intensity of the WPSH also impacts the summer monsoon (Yang, Cai, et al., 2022), as the location of the western edge of the circulation determines the longitude of the southwesterly jet and rainfall zone (Ding et al., 2018; Wang et al., 2013). The effects of these changes to the East Asian monsoon on insect migration patterns in this region have not been determined.

Here, we study the brown planthopper (BPH) *Nilaparvata lugens*, the most important global insect pest of rice. This pest undertakes seasonally predictable, long-range movements in East Asia on an annual basis (Bottrell & Schoenly, 2012; Heong et al., 2015; Hu et al., 2019; Otuka, 2013; Yang, Bao, et al., 2022). It cannot survive overwinter in temperate regions of China, Korea and Japan, so summer outbreaks in these regions are initiated by a series of about five long-range windborne migrations originating from winter-breeding areas in the Indochina Peninsula (Cheng et al., 1979; Kisimoto & Sogawa, 1995; Otuka, 2013; Yang, Bao, et al., 2022), particularly Central Vietnam (Hu et al., 2017; Wu et al., 2019). In this study, we focus on just one of the BPH migration legs—that which occurs from the northern South China (NSC) region into the Lower Yangtze River Valley (LYRV) region of East China (Figure 1). We focus on this immigration into the LYRV because it is the largest northward movement (Hu et al., 2019) and because it has the greatest economic impact as it determines the size of the pest population in this nationally important rice-producing region (Hu et al., 2011, 2014). The arrival of the summer monsoon leads to: (i) development of nocturnal low-level jets (LLJs), comprised of warm southwesterly winds blowing from the NSC region to the LYRV, providing frequent transport opportunities for migrating BPH; and (ii) a zone of heavy rainfall forming in the LYRV, promoting the aerial concentration and deposition of planthoppers from the atmosphere (Chen et al., 2019; Crummay & Atkinson, 1997; Feng et al., 2002; Watanabe & Seino, 1991). Based on a 26-year dataset (1978–2003), preliminary studies indicated that serious BPH summer outbreaks in

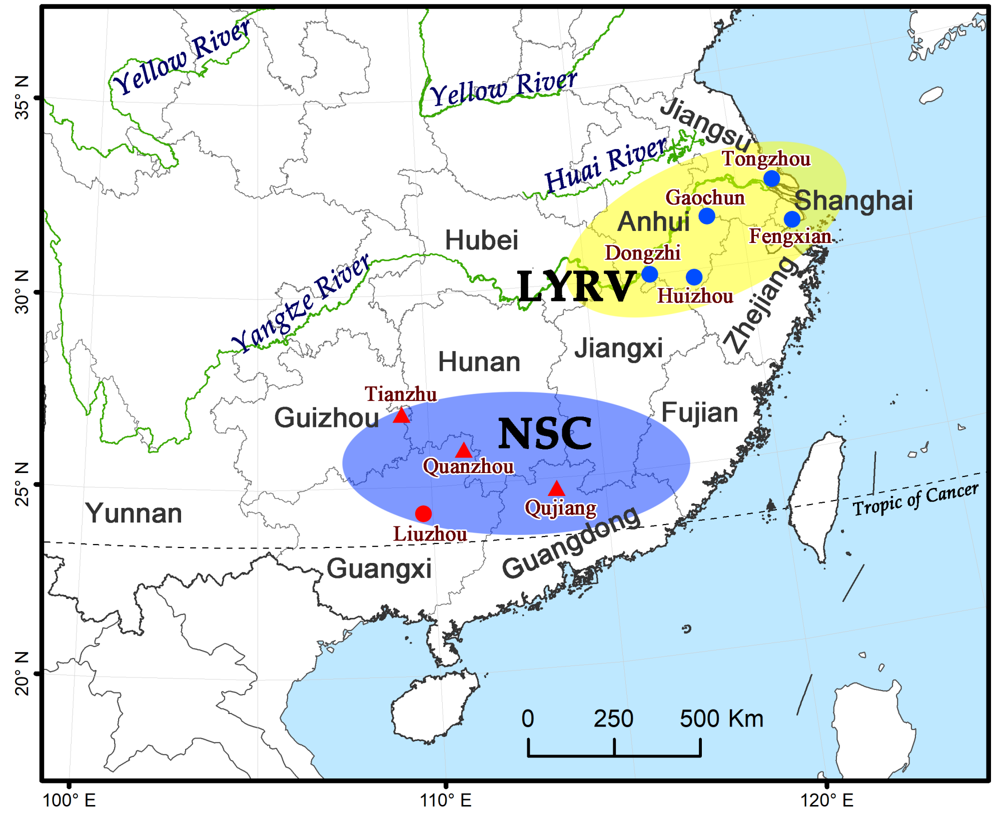

FIGURE 1 Map of the study area in South and East China, with provincial names and major rivers indicated. The three red triangles represent the plant protection stations (PPS) in the northern South China (NSC) region (the blue oval), whose light trap catches were selected to assess emigration from this region. The five blue dots indicate the locations of PPS light-traps used to assess immigration into the Lower Yangtze River Valley (LYRV) region (the yellow oval) in July. Liuzhou, indicated by the red circle, was defined as the hypothetical starting point for calculating migration distance. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

the LYRV are associated with strong WPSH conditions the preceding spring (Hu et al., 2019). Such conditions promote large immigrations from the NSC region into the LYRV during early-summer, due to the high frequency of suitable LLJs for rapid transport, and the location of the rain belt that terminates BPH migration in the LYRV (Hu et al., 2019; Lu et al., 2017). In the current study, we first investigated the relationships between the WPSH and the spatiotemporal distribution of LLJ winds blowing from the southwest, and precipitation patterns above the LYRV, during a period when the East Asian monsoon has moved equatorward due to the effects of global climate change (Zhou et al., 2019). Secondly, we used a 42-year dataset (1978–2019) to explore the impacts of changes to the WPSH on BPH migration patterns and population size in the LYRV.

2 | METHODS

2.1 | Light trap data

Daily planthopper catch data from 341 standardized 20-W 'black light' (UV) traps located at the plant protection stations of more than 300 counties (Figure S1) in China were obtained from the National Agro-Tech Extension and Service Centre (NATESC), which has been continuously collecting data since 1977. In this study, data from eight stations (Figure 1), which have complete data coverage from 1978 to 2019, were used in the correlation analyses.

2.2 | Regression models for BPH migration intensity against distance

We focused on the fifth migration wave of BPH in East China, in which BPH migrate from the NSC into the LYRV during July (Hu et al., 2019). The relationship between the BPH immigration volume at each station in July and the migration distance from southern China was explored using regression models. Immigration volumes for 5-day periods were log-transformed with a log base of 10 to follow a normal or near-normal distribution before modeling. Liuzhou city (109.75°E, 24.30°N; the red dot in Figure 1) in the north of South China, was defined as the hypothetical starting point for the migrations. The 229 stations located northeast of Liuzhou were selected as the potential BPH landing areas. The migration distances from Liuzhou to each site were calculated using the simple spherical law of cosines formula (Gellert et al., 1989), see the following equations:

$$C = \sin(\text{LatA}) \times \sin(\text{LatB}) \times \cos(\text{LatA} - \text{LonB}) + \cos(\text{LatA}) \times \cos(\text{LatB}), \quad (1)$$

$$\text{Distance} = R \times \text{Arccos}\,(C) \times \pi / 180, \quad (2)$$

where (LonA, LatA) represents the longitude and latitude of the first site A (i.e., Liuzhou), (LonB, LatB) represents the longitude and latitude of another site B, and R is the radius of the earth (6371 km).

The dataset was split into two subgroups, that is, Period I (1978–2000) and Period II (2001–2019), based on several factors, most importantly the distinct change in the WPSH intensity that occurred at this time (see Section 3). We built two linear models for these two periods, and the slope of these models was compared to explore the difference between these two periods. Further, we built a series of linear models for each year (1978–2019), and the changes in the slope of all models against year were explored. Moreover, smoothed curves of BPH migration level against distance for Period I and Period II were fitted by using generalized additive models. The position of 'humps' on these two fitted curves indicated that migrating planthoppers are being concentrated by atmospheric processes and subsequently landing at specific migration distances.

2.3 | BPH concentration zones

To represent BPH migration activity, light trap catch data from all 341 stations (Figure S1) from 1 April to 10 August of each year from 1978 to 2019 were extracted, and the summed catch for each 5 days for each station was calculated. To assign any given station as a "concentration and landing zone" (i.e., a station which received a major immigration of BPH), we calculated the 90th percentile value of catches (termed "BPH90th") in each of the 26 five-day periods from 1 April–10 August.

To explore the seasonal variation in the position of BPH concentration and landing zones, the latitude-time cross-section of the relative 2-D binned kernel density of stations in a concentration zone was estimated. A heat map showing the intensity of BPH outbreaks by latitude and seasonal period (see Figure 4c) was generated from raw count data for 5-day periods from all 341 recording sites, using a 2-dimensional kernel smoother to produce density estimates on a regular grid from the irregularly spaced raw data. An outbreak was flagged if a count exceeded the 90th percentile value for the seasonal period and year in question. The densities shown on the heat map are the probability of an outbreak at the specified time and latitude, minus the probability of any relevant data being available, to allow for uneven data collection. Only outbreak densities that are greater than data availability densities are shown, to filter out unreliable density peaks.

2.4 | Meteorological data and WPSH indices

Monthly and hourly global-gridded meteorological data with a spatial resolution of 0.25° from 1978 to 2019, including the geopotential height, precipitation and u- and v-winds, were derived from ERA5 data. ERA5 is the fifth-generation ECMWF reanalysis for the global climate and weather, and it provides hourly estimates of a large number of atmospheric, land and oceanic climate variables. The data cover the Earth on a 30-km grid and resolve the atmosphere using 137 levels from the surface up to a height of 80 km (Hersbach et al., 2018a, 2018b, 2019a, 2019b). These ERA5 data were downloaded from the Copernicus Climate Change Service (C3S) Climate Data Store (https://cds.climate.copernicus.eu).

The monthly indexes of WPSH (110°–180°E) from 1951 to 2019 were obtained from the China Meteorological Data Sharing Service System (https://cmdp.ncc-cma.net/). WPSH is described using five indices: (VA7, VI7, VR7, VN7 and VW7 to represent the area, intensity, mean ridge, northern edge, and westward extension of the WPSH, respectively).

2.5 | Migration trajectory simulations

To assess the migration distance of BPH in the two periods (1978–2000 and 2001–2019), a numerical trajectory model was used. This model has been previously employed to accurately predict the migration pathways of other insect migrants (Hu et al., 2017, 2021; Li et al., 2020; Wu et al., 2018, 2019).

Rice planthoppers are small insects, with self-propelled airspeeds of only ~0.3 m/s (Chen et al., 1984), much slower than the wind speeds at flight height; hence, their movement pathways can be assumed to be precisely downwind (Wu et al., 2019). BPH can migrate at a range of altitudes (300–2500 m above ground level), but often concentrate at ~1000 m (Dung, 1981; Riley et al., 1991). Rice planthopper migrants mostly take off at dusk (and partly at dawn) under calm weather conditions. Individuals take a one-way journey, can land at any time along the route, and the flight time is typically <24 h (Chen et al., 1984; Ohkubo, 1973). The planthoppers cannot fly when the air temperature at flight altitude is below 16.5°C (Ohkubo, 1973; Riley et al., 1991; Wu et al., 2019).

We calculated potential forward migration trajectories daily for July 1978–2019 from all 28 potential departure points at every 1° grid in the NSC (24°–27°N, 109°–115°E). Forward trajectories from each departure point were calculated at a start time of 19:00 h (after local sunset time), at the initial height of 1000 m above ground level (i.e., at the level of 850 hPa) whenever there were calm dry weather conditions at take-off time (surface temperature ≥16.5°C, wind speed at 10 m above ground ≤4 m/s, and hourly precipitation ≤0.1 mm). In total, 31,317 BPH migration trajectories were calculated. The program for calculating trajectories was designed in Fortran and run under CentOS 7.4 on a server platform (IBM system x3500 M4; Wu et al., 2019). ERA5 hourly data at 850 hPa and surface levels were used as high-resolution atmospheric backgrounds for the trajectory calculations.

2.6 | Statistical analysis

All variables associated with the light trap catch data (i.e., daily BPH catches, monthly catches, and catches of 5-day periods) were log-transformed with a log base of 10 to follow a normal or near-normal distribution before further statistical analysis. A one-tailed *t*-test ('greater' or 'less') was used to test the variables from two periods (Period I: 1978–2000, Period II: 2001–2019). These variables included the BPH catches in May in the NSC region, the BPH catches in July in the LYRV region, the BPH catches in the late season in the LYRV, and the indices of WPSH. The linear temporal trends of these variables were tested by using a linear model. Pearson's correlation coefficients were calculated to test the correlation between two variables, including BPH catches in the LYRV in July with other variables and WPSH indices in July with other variables. The spatial maps of correlation coefficients between the number of BPH catches in the LYRV with precipitation and v-winds in July were calculated by *tcorr*() function in Grid Analysis and Display System (GrADS, version 2.2.1). All other statistical analyses were conducted using R (R Version 3.6.2; R Core Team, 2021).

3 | RESULTS

3.1 | BPH immigration levels into the LYRV have declined strongly

Our results confirm the finding of Hu et al. (2019), that the major immigration of BPH into the LYRV region occurs in July and the timing has not changed over the study period (Figure 2a). During 1978–2000, the size of the July immigration into the LYRV remained high and stable, with no temporal trend in abundance ($F = 3.9$, $p = .0605$), but since 2001 the abundance of immigrants has dramatically declined ($F = 11.6$, $p = .003$; Figure 2b, middle panel). The mean annual catch of BPH in the LYRV during July was an order of magnitude smaller in 2001–2019 than in 1978–2000 (790 vs. 8152; $t = 5.2$, df = 33.7, $p < .0001$), and by the end of the second period, catches had declined by two orders of magnitude compared to the first period (Figure 2b). Our previous studies (Hu et al., 2019) indicated that the size of the July immigration determines the population size in the LYRV in the late season (after mid-August), when the pest is most damaging to rice crops. We found this was indeed the case, as the two datasets were significantly correlated across the entire period (1978–2000: df = 21, $r = .65$, $p < .001$; 2001–2019: df = 17, $r = .71$, $p < .001$; Figure S2b). Accordingly, the BPH population size in the late season also decreased since 2001 ($F = 6.3$, $p = .022$), and was significantly smaller in 2001–2019 than in 1978–2000 (4982 vs. 15,341; $t = 2.1$, df = 25.6, $p = .021$; Figure 2b, bottom panel); in other words, BPH has become a progressively less important pest in the LYRV.

The principal geographical source area of the BPH arriving in the LYRV during July is the NSC region (Cheng et al., 1979; Hu et al., 2011, 2019). Thus, as expected, in the first period (1978–2000) the size of the spring population in the NSC was significantly positively correlated with the size of the arrival in the LYRV (df = 21, $r = .56$, $p = .006$; Figure S2a). However, this relationship broke down from 2001 onwards, and there is no longer a correlation between abundance in the source and destination areas in the second period (df = 17, $r = -.192$, $p = .430$; Figure S2a). These changes in the LYRV were not brought about by a similar decrease in spring populations in the NSC, as populations here were stable across the entire period

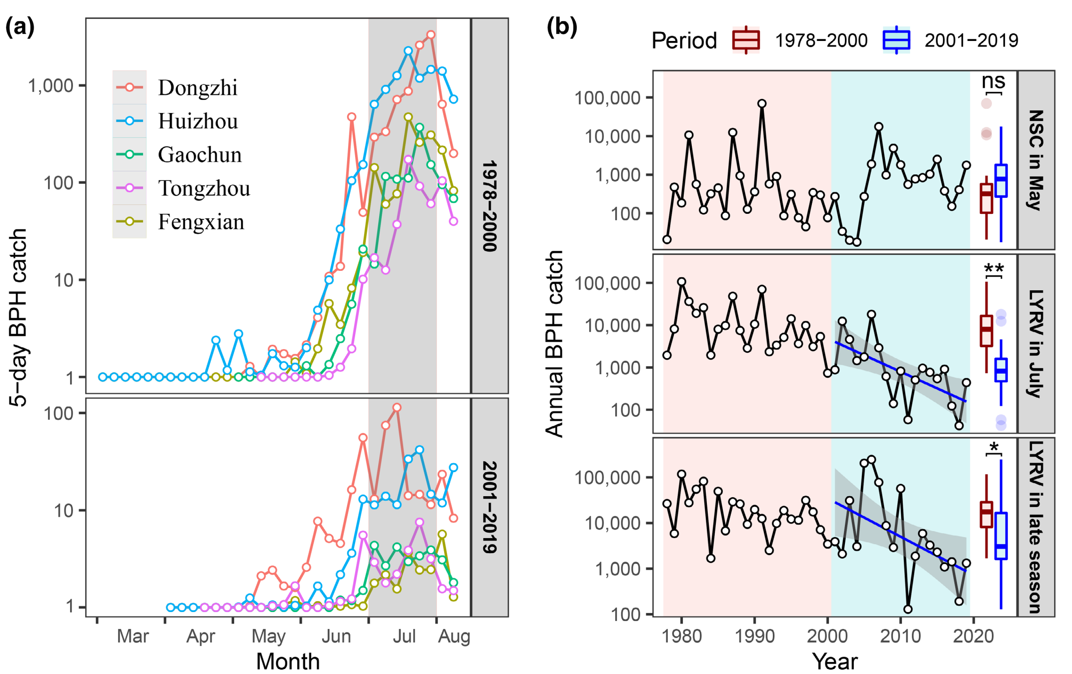

FIGURE 2 (a) Mean 5-day catches of BPH for each selected PPS light-trap in the LYRV region. The grey shaded bar indicates the major immigration period. (b) Mean annual catches of BPH in the two study regions (NSC and LYRV) during the two time periods: 1978–2000 (shaded in pink) and 2001–2019 (shaded in blue). Significant linear trends in any time period/location are indicated by trend lines (solid blue lines). Significant differences between the two time periods are indicated above the boxplots: ns = not significant; *$p < .05$; **$p < .01$.

(whole period: $F = 0.60$, $p = .445$; 1978–2000: $F = 0.29$, $p = .598$; 2001–2019: $F = 2.6$, $p = .124$; Figure 2b, top panel) and the population size did not differ between the two time periods (382 vs. 546; $t = 0.6$, df = 39.2, $p = .267$). These results show that the source population for immigration into the LYRV has not changed in size, and the timing of the immigration into the LYRV (July) has also remained constant (see Figure 2a). Thus, the reduction in the number of BPH reaching the LYRV must have another cause than changes to the size of the source population.

3.2 | Changes to rainfall and wind patterns since 2000 are less conducive for BPH migration into the LYRV

Major zonal rainfall belts, and their associated downdrafts, rain and cold temperatures, provide a serious impediment to BPH flight, and thus they promote concentration and landing at their location (e.g., Chen et al., 2019; Crummay & Atkinson, 1997). Over the entire study period, the mean location of the major rainfall belt ran west-to-east along the northern shore of the Yangtze River (Figure 3a), an area termed the Jianghuai Plain. July precipitation levels along this belt are positively correlated with BPH immigration to the LYRV during July (blue band in Figure 3d). This is due to the rainfall belt providing a natural barrier to migration, causing migrating BPH to be deposited from the atmosphere; as the LYRV is located at the southern fringe of the rain belt, the migrants will be 'rained-out' predominantly into this region. We investigated the relationship between the annual July rainfall intensity in a part of the Jianghuai Plain located on the northern fringe of the LYRV (purple rectangle in Figure 3) and the size of the BPH immigration to the LYRV that same July. Over the entire study period, there was a significant and positive correlation between these two factors (df = 40, $r = .536$, $p = .003$; Figure 3d). This relationship was strongly positive during 1978–2000 (df = 21,

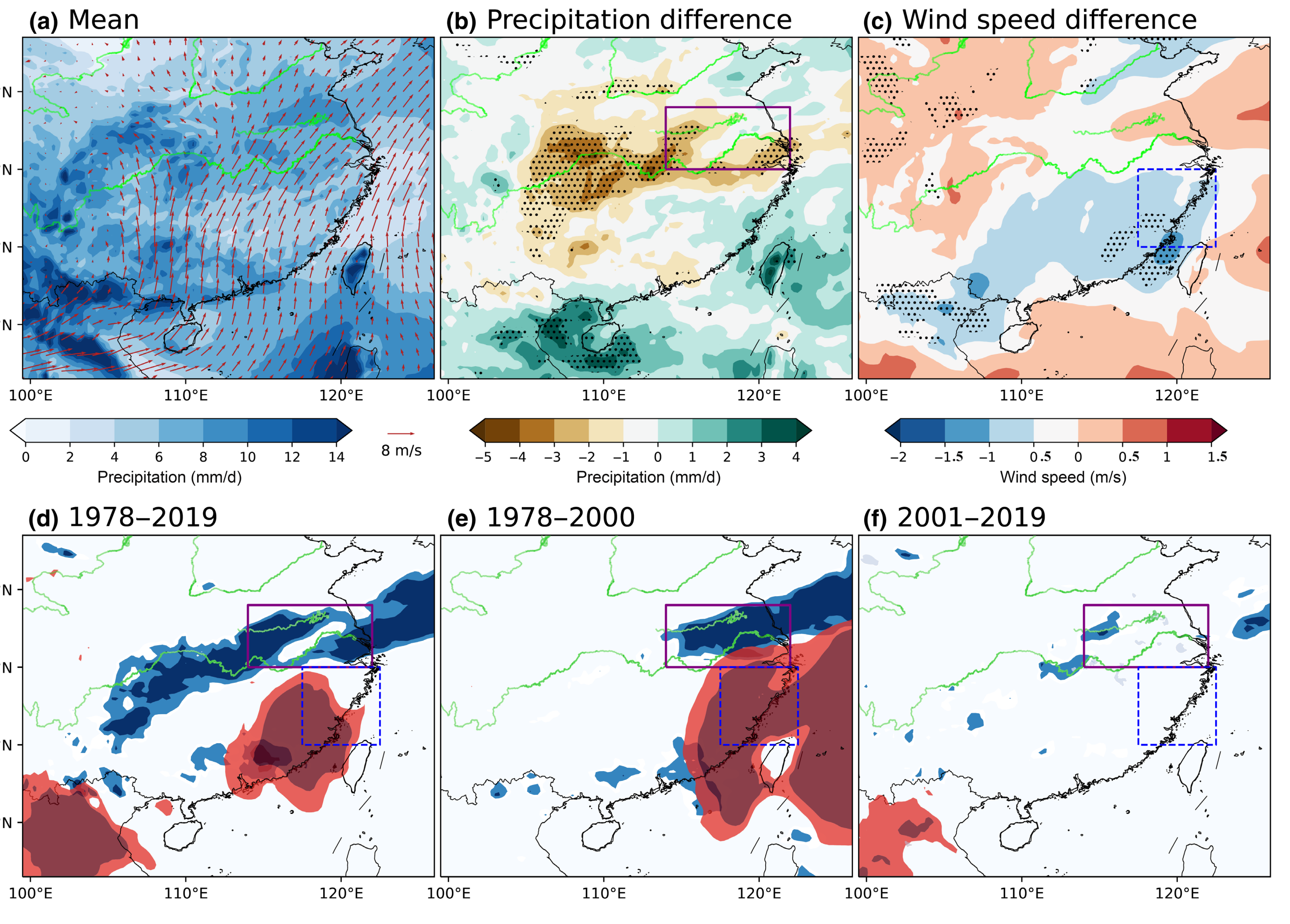

FIGURE 3 The migration pattern of BPH is significantly affected by northward windspeed and rainfall intensity. (a) Mean precipitation and wind vectors at 850 hPa in 1978–2019. (b, c) The difference in (b) precipitation and (c) windspeed between 1978–2000 and 2001–2019. The stippled areas in (b) and (c) indicate areas that were significantly different at the .1 level of a two-tailed Student's *t*-test. The purple rectangle indicates the Jianghuai region (30°–34°N and 112°–122°E) identified as being important for rainfall, and the dashed blue square is a region of southeast China (25°–30°N, 117.5°–122.5°E) identified as being important for wind speed. (d–f) Simultaneous correlation map between immigration levels of BPH to the LYRV and precipitation (blue), and velocity of the v-component (northward-blowing component) of the wind (red), in July. The BPH immigration level is defined as the cumulative sum of light trap catches from five plant protection stations. The light and dark blue/red areas in (d)–(f) indicate significance at 1% and 5% levels, respectively.

$r = .55$, $p = .008$; Figure 3e), but it disappeared during 2001–2019 (df = 17, $r = .38$, $p = .107$; Figure 3f), likely due to changing precipitation patterns. Rainfall was particularly intense in the Jianghuai Plain during 1978–2000, but in 2001–2019 the intensity of rainfall here decreased significantly (brown area in Figure 3b) while increasing slightly to the south of the Yangtze (pale green area in Figure 3b). This shift in rainfall to the south will have caused some BPH to be deposited before reaching the LYRV, while the decrease in rainfall on the northern fringe of the LYRV will have reduced the concentration of BPH that had previously occurred, with the result being fewer BPH arriving in the LYRV and the loss of the correlation with July precipitation on the Jianghuai Plain (Figure 3f).

In addition to the effect of rain, the northward migration process is facilitated by the development of strong southwesterly winds (Feng et al., 2002; Hu et al., 2019; Watanabe & Seino, 1991), which blow from the NSC region and transport planthoppers northeastwards towards the LYRV (Figure 3a). We identified a region of southeast China (the dashed blue square in Figure 3) where the velocity of the v-component (northward-blowing component) of the wind was significantly correlated with BPH immigration to the LYRV in July (df = 40, $r = .383$, $p = .012$; Figure 3d). However, northward windspeed in the region south of the Yangtze River has significantly weakened since 2001 (blue areas in Figure 3c), reducing the probability of long-distance planthopper migration. Indeed, there is evidence of this, as the relationship between the northward windspeed and the BPH immigration was very strong in 1978–2000 (df = 21, $r = .641$, $p = .001$; dark red area in Figure 3e) but had completely disappeared during 2001–2019 (df = 17, $r = .411$, $p = .080$; Figure 3f). Taken together, the changes to rainfall and wind patterns have significantly reduced the opportunities for BPH immigrants to reach the LYRV.

3.3 | Migration distances of BPH have reduced since 2000

Our results clearly show that regional weather patterns have undergone substantial changes since 2001, and neither the location of the rain belt nor the wind patterns are currently favorable for the long-distance migration of BPH into the LYRV. We therefore assumed that the mean migration distances of BPH from 2001 onwards will be shorter than they were in the first period. We compared the migration distances in the two periods by analyzing the abundance of BPH in light-trap catches at each of the 229 stations located along the northeastward migration pathway (Figure S1). As expected, BPH catches at individual stations significantly decreased as distance from the source increased, in both time periods (Figure 4a). However, the rate of decrease in 2001–2019 (slope = $-9.7\times10^{-4} \pm 2.9\times10^{-5}$, $t = 32.82$, $p < .0001$) was steeper than the rate of decrease in 1978–2000 ($-4.1\times10^{-4} \pm 3.0\times10^{-5}$, $t = 13.60$, $p < .0001$). Additionally, we built separate linear models for catch against distance in each year, and the mean slope during 1978–2000 was significantly shallower than the mean slope in 2001–2019 (-5.7×10^{-4} vs. -9.8×10^{-4}; $t = 3.940$, df = 34.9, $p = .0002$; Figure 4b). The model outputs confirm that BPH migration distance was significantly shorter in the second period. Accordingly, by July, the zone of concentration of BPH population had reached 30°N in during the first period, but only as far as 28°N in 2001–2019 (Figure 4c). This reduction in migration distance was supported by the outputs of our simulated migration trajectories, as the mean distance of the modelled trajectories was indeed significantly shorter in the second period compared to the first (Figure 5a). After 24 h of windborne transport, the mean trajectory distance in 2001–2019 was 823.9 ± 3.2 km, significantly shorter than the mean of 867.1 ± 2.9 km in 1978–2000 (difference = 43.2 km, $t = 9.937$, df = 30759, $p < .0001$; Figure 5a). The peak value of the probability curves of distance travelled appeared at 980.0 km in 1978–2000 compared to 783.1 km in 2001–2019, a difference of 196.9 km (Figure 5b).

3.4 | Changes to the characteristics of the WPSH and impact on BPH migration parameters

Previous studies have shown that the development of southwesterly airstreams and the location of rain belts in East Asia is regulated by the WPSH system (e.g., Ding et al., 2018; Ding & Chan, 2005; Wang et al., 2013). Our analyses show that two key characteristics of the WPSH have changed from 2001 onwards: the intensity of the WPSH system has become significantly stronger in the second period compared to the first ($t = 2.0$, df = 36.4, $p = .028$; Figure 6a), and there has been a marginally significant westward shift of the WPSH in the same period ($t = 1.5$, df = 36.6, $p = .070$; Figure 6b). We hypothesized that these changes to the WPSH characteristics will have impacted the meteorological factors and ultimately the immigration of BPH to the LYRV region. This was indeed the case, as during the first period, both July precipitation in the Jianghuai Plain and the v-component of July windspeed in southeast China were significantly positively correlated with the WPSH intensity (rainfall: df = 21, $r = .45$, $p = .035$; v-component of windspeed: df = 21, $r = .43$, $p = .041$; Figure 6c,d). These relationships broke down after 2001, as neither were correlated with WPSH intensity in the second period (rainfall: df = 17, $r = .33$, $p = .163$; windspeed: df = 17, $r = .17$, $p = .475$). As a result, the location of the rainfall belt and wind pattern has changed since 2001 (Figure 3), and this has changed BPH migration patterns: BPH immigration level was significantly positively correlated with WPSH intensity in July during 1978–2000 (df = 21, $r = .57$, $p = .004$), but not during 2001–2019 (df = 17, $r = .06$, $p = .814$; Figure 6e).

4 | DISCUSSION

Our study reveals that the population abundance of BPH in the key rice growing region of East China (the LYRV region) has significantly declined, due to shifts in the migration patterns of the planthoppers during the immigration period (July) in response to changing climate patterns over the past 40 years. These changes were enacted via two

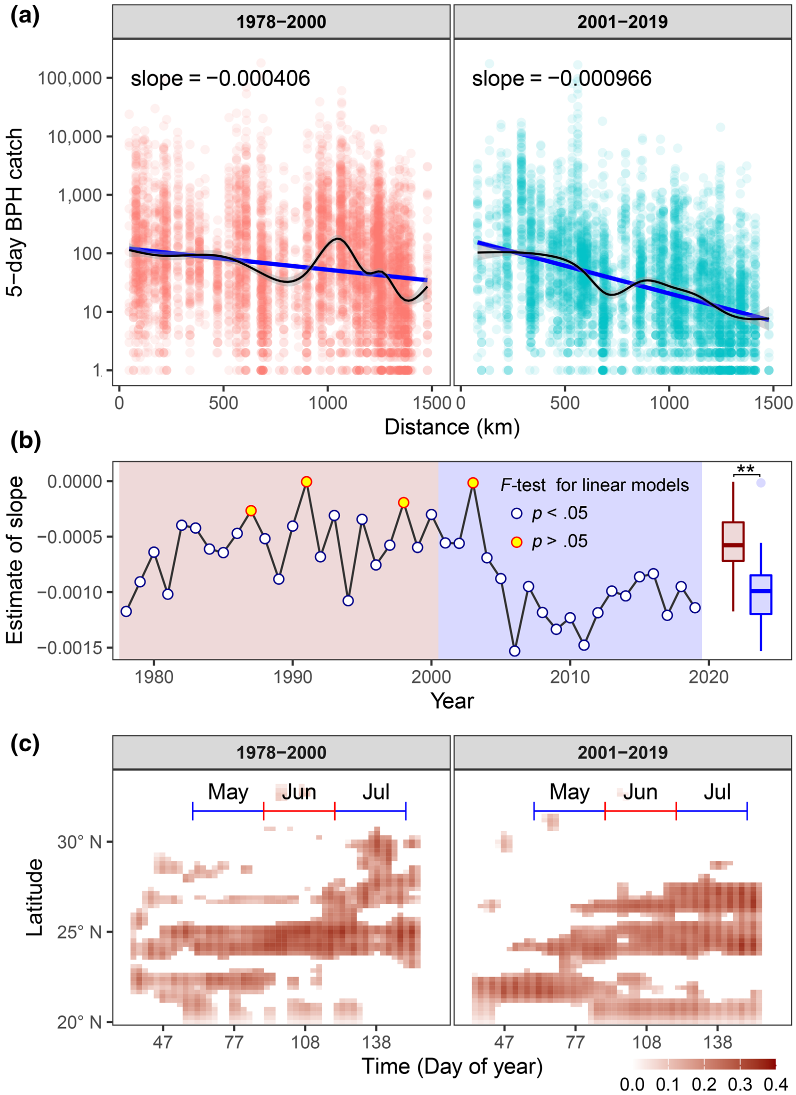

FIGURE 4 The migration distance of BPH has decreased. Parts (a) and (b) show the relationship between 5-day BPH catches at each of the 229 stations along the migration route and the distance from the hypothetical start point of the migration (Liuzhou City, 109.75°E, 24.30°N, in the NSC region). (a) The relationship between BPH catches and distance from Liuzhou in each time period. In 1978–2000, the linear model (blue line) had a shallower slope than in 2001–2019, indicating that BPH migrated further in the first period than the second period. In the general additive model (black line), there was a peak around the migration distance of 1000 km in the first period, corresponding to the LYRV that was absent in the second period. (b) The slope values of the fitted linear model from (a) but built separately for each year. The slopes were typically steeper in each year from 2001 onwards, and the overall mean values were significantly steeper in the second period than in the first period. (c) Latitude date cross-section of the relative 2-D binned kernel density of the 341 trapping stations (relative density of traps per unit of latitude for each 5-day period) in a BPH concentration zone, based on the data from more than 300 county plant protection stations between 1978 and 2019. Any given BPH trapping station in any 5-day period was defined as a planthopper 'concentration and landing zone' if the number of BPH in the 5-day catches was greater than or equal to the BPH90th (i.e., the 90th percentile value in that period of that year).

processes related to the position and strength of the East Asian summer monsoon and WPSH. Firstly, the major rainfall belt produces less precipitation over the Jianghuai Plain and more rain south of the Yangtze in the recent 20-year period compared to the preceding one, resulting in decreased concentration and deposition of migrating BPH in the LYRV region. Secondly, in the same time period there has been a significant reduction in the strength of southwesterly winds blowing from the BPH source (the NSC region) towards the LYRV during July, reducing opportunities for windborne transport. Together, these processes have significantly shortened the migration distance and resulted in deposition of BPH before they reach the main rice production region of the LYRV. These changes in precipitation and wind patterns are consistent with other studies that have found that key characteristics of the East Asian summer monsoon have changed in response to the effect of global climate change on atmospheric circulation patterns such as the WPSH and ITCZ (Lin et al., 2014; Ma et al., 2017; Preethi et al., 2017; Sooraj et al., 2015; Zhou et al., 2019).

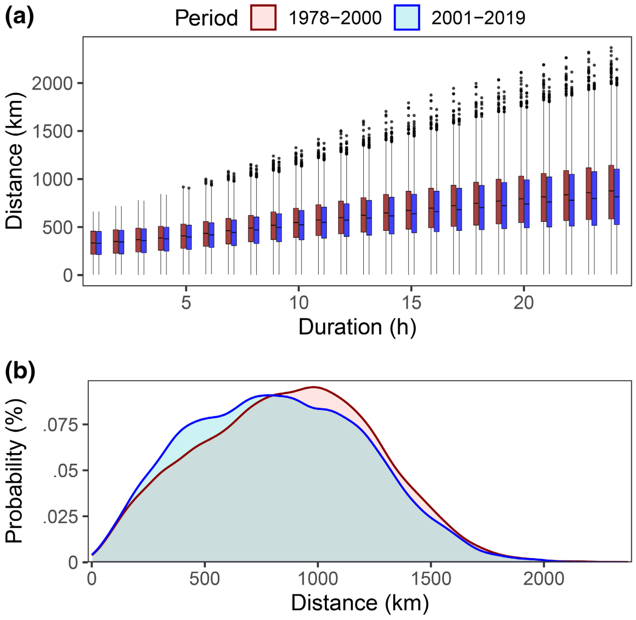

FIGURE 5 Distance of simulated migration trajectories. (a) Distance of simulated trajectories against flight duration (1–24 h) in each period. (b) Probability distribution of the maximum migration distance of each simulated trajectory with a 24-h flight duration.

The data from the long-term monitoring stations in the LYRV demonstrate two surprising facts: the timing of arrival of immigrant BPH has remained constant over the past 40 years, and the population size is significantly smaller in the recent 20-year period compared to the previous 20 years. As a result, pest problems arising from the annual immigration of BPH to the LYRV have ameliorated in the past 20 years, as they have also done so in Taiwan (Huang et al., 2022). The patterns we observed in BPH migrations and population change are in stark contrast to the typical patterns of earlier arrival, increases in population abundance, range expansions, and/or invasions of new regions, that have been observed in many other migratory insects that are important crop pests (e.g., Bebber, 2015; Bebber et al., 2013; Jones et al., 2019; Kenis et al., 2022; Tu et al., 2020; Zeng et al., 2020). The changes in BPH population dynamics that have occurred in the LYRV are thus a rare example of climate change having an ameliorative effect on a major crop pest problem, and thus it is instructive to examine the drivers of these changes in pest status of BPH in East Asia.

Rainfall is one of the key factors that cause migrating insects to terminate their journey, and a band of heavy precipitation will lead to concentration and deposition of migrants along the fringe of the rain belt (Drake & Reynolds, 2012; Westbrook & Isard, 1999). Our study reveals that precipitation patterns in East China have undergone an important shift that contributes to the changing migration patterns of BPH during the past two decades. There was significantly less precipitation from the rain belt situated along the Jianghuai Plain during the second period (2001–2019) than during the first period (1978–2000), and as rainfall in this region forms a natural barrier, it means that there will be less concentration and landing of migrants in the LYRV lying immediately to the south of the Jianghuai Plain. In addition, there was a (non-significant) increase in precipitation south of the Yangtze River during the same period, which will tend to increase the 'raining out' of emigrants from the NSC region before they reach the LYRV. Thus, the changes in rainfall in this region that we have documented are one of the key drivers of the reduced immigration of BPH to the LYRV. However, global warming is increasing the frequency and intensity of extreme weather events (Robinson et al., 2021), and as a result the summer monsoon rainfall in the LYRV is more variable from year-to-year (Li et al., 2021; Ma et al., 2017; Yang, Cai, et al., 2022). It will therefore be harder to predict the future effects of rainfall on BPH migration parameters and population dynamics in the region.

The second meteorological factor we found to be an important driver of the changes was the reduction in the northward windspeed component of the circulation patterns south of the Yangtze. Fast-moving airstreams are of critical importance in the transport of insect migrants, particularly for very small insects like BPH that have comparatively slow self-powered airspeeds. Thus, it is not surprising that the reduction in northward speed of suitable winds leads to shorter migration distances and ultimately fewer BPH immigrants reaching as far as the LYRV region from their source in the NSC. Our simulated migration trajectories indeed showed that migration distance was shorter in 2001–2019 than that in 1978–2000 but only by an average of 42 km after 24 h of windborne transport. Considering the average total trajectory length was >800 km after 24 h, this difference may seem rather inconsequential. However, it arises solely from the effect of slower windspeed, as the numerical trajectory model incorporates this factor but does not take account of the effect of changes in rainfall and downdrafts that will tend to halt the migration earlier as discussed above. Thus, we can conclude that reduced windspeed will have an additive effect on reducing migration distance, that is not as powerful as the effect of changing rainfall patterns.

However, the region that showed the strongest positive correlation between the northward windspeed and the intensity of BPH immigration to the LYRV is actually located in southeast China (the dashed blue box in Figure 3), and thus not on the direct migration route of BPH from the NSC region to the LYRV. This suggests that the most important effect of the reduced northward component of the windspeed is not the direct effect of wind on transport distance, but an indirect effect on rainfall. The rainfall belt of the East Asian summer monsoon results from an atmospheric convergence of winds carrying moisture from the southwest, originating over the Indian Ocean, and the southeast, originating from the South China Sea and the tropical Pacific Ocean west of the WPSH (Ding et al., 2018; Zhou & Yu, 2005). The meridional transport of water vapor from these ocean regions into East China is vital for the development of the monsoonal rainfall belt, and a reduction in the northward windspeed from these regions will tend to weaken the water vapor transport to this region, resulting in the major rainfall zone moving southwards. The correlation that we observed between reduced windspeed and BPH immigration is thus largely indirect, via reduced moisture

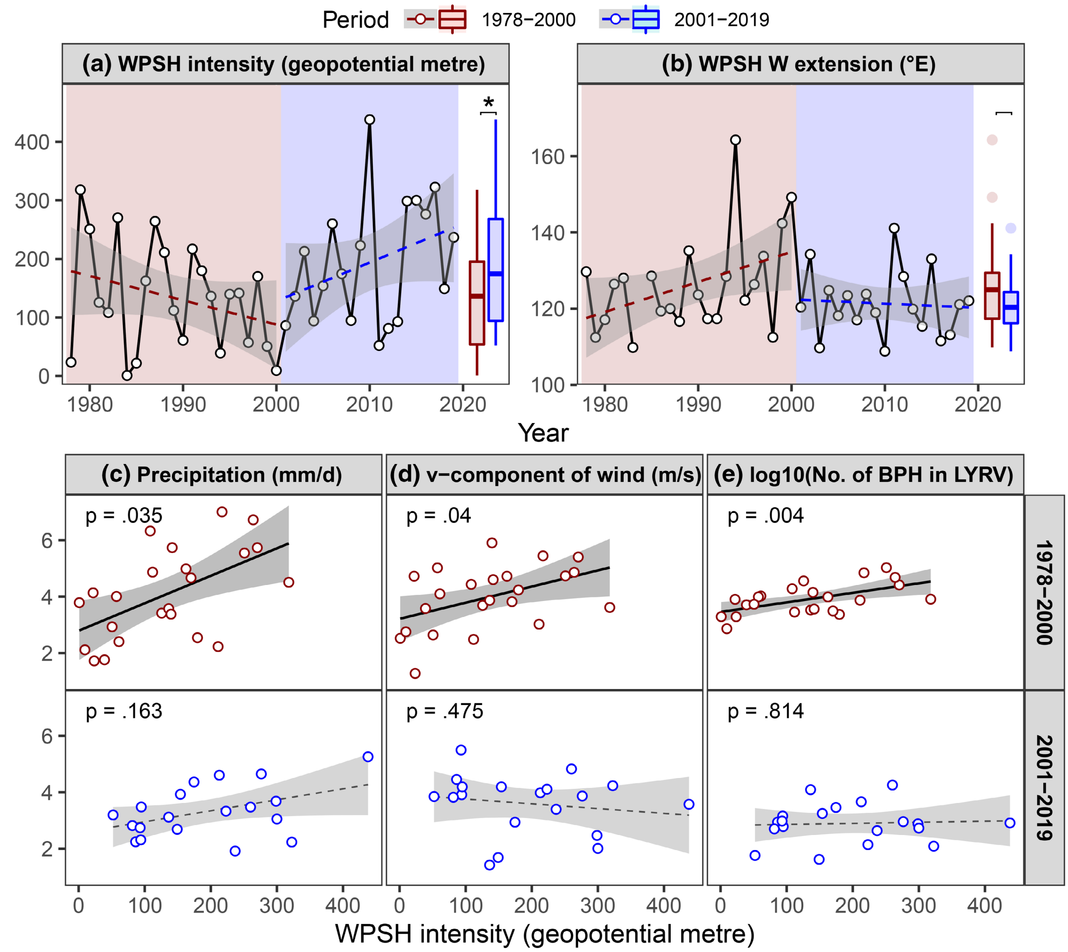

FIGURE 6 The characteristics of the WPSH have changed. (a) The intensity of the WPSH declined during the first period (pink shading) and then increased during the second period (blue shading), although none of these trends were significant (indicated by dashed trend lines); the box plots show that the overall mean intensity was significantly greater in the second period compared to the first ($p = .028$). (b) The westward extension of the WPSH tended to occur further to the west during the second period than in the first period, and this difference was marginally significant ($p = .070$). (c–e) Relationships between the intensity of the WPSH and other factors associated with BPH population changes. During the first period (top row), the amount of rain in the Jianghuai Plain in July (c), the speed of the v-component (northward) of the wind in SE China in July (d), and the immigration of BPH to the LYRV (e), were all significantly positively correlated (solid trend lines) with WPSH intensity. However, in the second period (bottom row), all of these relationships broke down and there was no trend with WPSH intensity (dashed lines).

transport and changing rainfall patterns, rather than a direct effect on windborne transport.

The fact that winds blowing from the Pacific Ocean in the region of the WPSH are important drivers of BPH immigration indicates that the changes we have witnessed are likely driven by changes to the WPSH system. This does indeed seem to be the case, as supported by the current results and our previous studies of this system (Hu et al., 2019; Lu et al., 2017). The WPSH transports water vapor into East Asia via southerly winds blowing along its western flank, and also anchors the rain belt on its northwestern periphery where the moist southerly winds meet the cold air mass to the north (Ding et al., 2018; Ding & Chan, 2005; Wang et al., 2013). Therefore, WPSH indices are very important for weather forecasting in East Asia and have also been used to build predictive models for migrating pests, such as BPH (Hu et al., 2019). We found that the strength, westward extension and area of China covered by the WPSH all increased in the second period compared to the first period, and this has changed the relationship between WPSH parameters and BPH levels in the LYRV: in the first period, there was a strong, positive correlation between WPSH intensity and BPH immigration, but this completely disappeared in the recent 20-year period. Previous studies have established that variation in the WPSH is primarily controlled by central Pacific cooling/warming and that there is a positive atmospheric-oceanic feedback between the WPSH and the Indo-Pacific warm pool ocean (Wang et al., 2013). It seems likely, therefore, that changes in intensity and position of the WPSH are linked with the recent warming of the equatorial Pacific due to global climate change (He et al., 2015; Huang et al., 2020). Taken together, it is clear that global warming is changing atmospheric circulation patterns, which impact regional weather factors such as precipitation and wind patterns, and these changes will inevitably alter the migration patterns of small migratory insects such as BPH.

To conclude, the migration patterns of BPH have shifted in response to changes in precipitation and wind patterns in East China, resulting in an amelioration of pest problems in the key rice-producing region of the LYRV, and this has been driven by global warming. These changes may have shifted the pest problems to other regions, via increased retention of BPH in the NSC region or migration to southwest China, rather than ameliorated them everywhere, and these possibilities require further study. The consequences of global warming on atmospheric circulation patterns and regional weather will also be felt in other regions of the world (An et al., 2015; Annamalai et al., 2013; Zhang & Zhou, 2019), such as in North America, South Asia, and North Africa. Given that these regions, along with East Asia, constitute the most important insect migration arenas in the world, with many important windborne insect pests and disease vectors (Drake & Gatehouse, 1995), further studies of the impacts on global climate change on migration patterns of windborne insects are urgently required.

AUTHOR CONTRIBUTIONS

Gao Hu and Juan Zeng designed the research, Hua Lv and Meng-Yuan Zhai performed research and analyzed data, Yi-Yang Zhang, Feng Zhu, Hui-Mei Shen, and Kun Qiu provided data and expertise on how to analyze the data. Hua Lv, Don R. Reynolds, Jason W. Chapman, and Gao Hu wrote the paper. All authors reviewed the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from Dryad Digital Repository: (Lv et al., 2023), https://doi.org/10.5061/dryad.gxd2547qv.

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