Population dynamics of rice planthoppers, *Nilaparvata lugens* and *Sogatella furcifera* (Hemiptera, Delphacidae) in Central Vietnam and its effects on their spring migration to China

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Abstract

Rice planthopper (RPH) populations of *Nilaparvata lugens* and *Sogatella furcifera* periodically have erupted across Asia. Predicting RPH population dynamics and identifying their source areas are crucial for the management of these migratory pests in China, but the origins of the migrants to temperate and subtropical regions in China remains unclear. In particular, their early migration to China in March and April have not yet been explored due to a lack of research data available from potential source areas, Central Vietnam and Laos. In this study, we examined the population dynamics and migratory paths of *N. lugens* and *S. furcifera* in Vietnam and South China in 2012 and 2013. Trajectory modeling showed that in March and April in 2012 and 2013, RPH emigrated from source areas in Central Vietnam where rice was maturing to the Red River Delta and South China. Early migrants originated from Southern Central Vietnam (14–16°N), but later most were from Northern Central Vietnam (16–19°N). Analysis of meteorological and light-trap data from Hepu in April (1977–2013) using generalized linear models showed that immigration increased with precipitation in Southern Central Vietnam in January, but declined with precipitation in Northern Central Vietnam in January. These results determined that the RPH originate from overwintering areas in Central Vietnam, but not from southernmost areas of Vietnam. Winter precipitation, rather than temperature was the most important factor determining the number of RPH migrants. Based on their similar population dynamics and low population densities in Central Vietnam, we further speculated that RPH migrate to track ephemeral food resources whilst simultaneously avoiding predators. Migrations do not seem to be initiated by interspecific competition, overcrowding or host deterioration. Nevertheless,

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S. furcifera establishes populations earlier than *N. lugens* South China, perhaps to compensate for interspecific competition. We provide new information that could assist with forecasting outbreaks and implementing control measures against these migratory pests.

Introduction

Rice planthopper (RPH) populations of *Nilaparvata lugens* (Stål) and *Sogatella furcifera* (Horváth) have periodically erupted across Asia. In outbreak years, this can result in heavy rice loss and almost total crop failure in many paddies (Zhai, 2011; Bottrell & Schoenly, 2012; Otuka, 2013; Ma *et al.*, 2015). In China, RPH (refers to both studied species hereafter) are currently the most important agricultural insect pest and are responsible for damaging an area of about 20,000,000 ha rice each year (Hu *et al.*, 2011, 2014; Cheng, 2015). Predicting RPH population dynamics and identifying their source areas are crucial for the management of this migratory pest in China. The origins of migratory RPH populations, both in temperate and subtropical regions, remain unclear (Zhai, 2011; Zhai *et al.*, 2011; Otuka, 2013; Otuka *et al.*, 2014). This is also a common problem for other migratory insects, due to very low population densities in one or more generations in the seasonal cycle (e.g. after overwintering) (Flockhart *et al.*, 2013; Stefanescu *et al.*, 2013; Chapman *et al.*, 2015).

Nilaparvata lugens and *S. furcifera* (Hemiptera, Delphacidae) are insect pest species that cannot overwinter in temperate climates. In China, only a few individuals can survive during winter in areas of Southern Yunnan, Southern Guangxi and Hainan (Cheng *et al.*, 1979; Hu & Xie, 1988; Otuka *et al.*, 2008, Otuka, 2013; Hu *et al.* (2015*a*, *b*);). Instead, infestations in temperate zones are initiated by windborne spring/summer migrants from the southern areas (Cheng *et al.*, 1979; Otuka *et al.*, 2008, Otuka, 2013). A northward migration of *N. lugens* and *S. furcifera* begins in March every year, and migrant progeny further expand population distributions to cover the rice-growing regions in China, Japan and the Korean Peninsula (Cheng *et al.*, 1979; National Coordinated Research Group for White Backed Planthopper, 1981; Hu & Xie, 1988; Kisimoto & Sogawa, 1995; Hu *et al.*, 2011). DNA sequence analysis of mitochondrial genes (*cox*1, *cox*2) of both RPH species did not show much genetic differentiation among Asia populations, and this indicated a wide extent of genetic mixing between RPH populations in East and Southeast Asia (Matsumoto *et al.*, 2013).

Based on the rice-planting schedule, seasonal wind direction and topographic features, the Mekong River Delta was hypothesized to be the first source of *N. lugens* populations, whose flight to the Central Indochina Peninsula arrives in the Red River Delta in February and March (Wu *et al.*, 1997). However, evidence from RPH biotype data and trajectory analysis showed that RPHs in the Mekong River Delta do not undertake northward migration into Central or Northern Indochina Peninsula (Li *et al.*, 1999; Zhai *et al.*, 2011; Otuka *et al.*, 2014). An alternative, and long-standing hypothesis, was that Northern Vietnam is a source region for RPH population outbreaks in China and other temperate

regions. This hypothesis was supported by field investigations carried out in the Red River Delta in May (Otuka *et al.*, 2008; Zhai, 2011; Zhai *et al.*, 2011). However, light-trap catches recorded RPH in South China as early as March (Hu *et al.*, 2010). The immigration of RPH in South China before May has been termed as 'early migration', but the source of these immigrants has not yet been identified. Several field investigations have been carried out during March and April by Cheng in 1988 and Zhai in 2008–2013 (Zhai, 2011; Zhai *et al.*, 2011). These studies concluded that Northern Vietnam could not be the initial source area of early immigrants of RPH to China because during these two months the growth stage of rice plants in paddies in Northern Vietnam and South China were similar. Recently, backward trajectory analyses indicated that possible sources of the early migrations of *N. lugens* and *S. furcifera* in March and April were from Hainan Province, Northern and Central Vietnam and Southern Laos (Qi *et al.*, 2010, 2011; Shen *et al.*, 2011; Wang *et al.*, 2011; Jiang *et al.*, 2012). Hitherto, there was a lack of research data available from Central Vietnam and Laos to explore these questions. Furthermore, there is little knowledge about RPH population dynamics and migrations in these overwintering areas. Thus, the first source area of the migrants to subtropical regions, such as China and Japan, remains unclear.

To investigate linkages between RPH population dynamics in China and Vietnam, a joint monitoring project was established in 2010 between the two countries (China–Vietnam Joint Project of Monitoring and Controlling Rice Migratory Pest). As part of this research framework, the present study aims to investigate early migration patterns of these pests from their purported overwintering ground. Early migration of RPH and population dynamics were investigated and analyzed in Vietnam and South China in 2012 and 2013 (March–April). Historical climate data recorded between 1977 and 2013 from Hepu (Guangxi Province, China) were analyzed to try to identify important factors potentially associated with RPH outbreaks.

Materials and methods

Population dynamics of RPH in Vietnam and South China

Systematic field investigations and light-trap monitoring were carried out between 2011 and 2013 at three sites in Vietnam (Thang Binh, Nam Dan and Hai Hau) and three in China (Hepu, Longzhou and Leizhou; see fig. 1). Field investigations were performed by the Department of Plant Protection, Vietnam and the China National Agro-Tec Extension and Service Center, China. At each experimental site, one or two paddies were selected that were moderately fertile and at least 600 m^2 in area. Routine agricultural
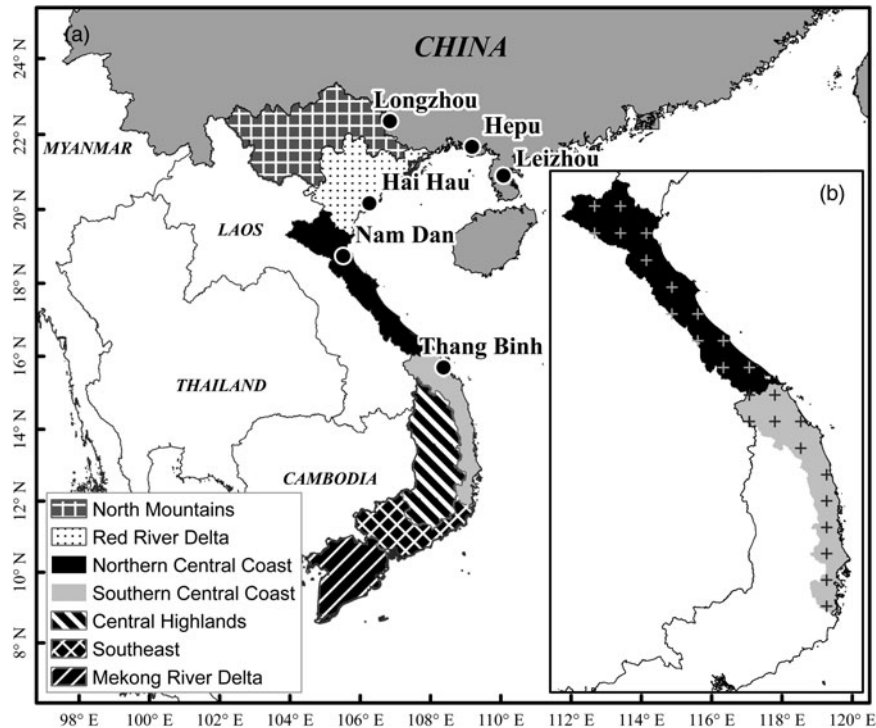
Fig. 1. Location of experimental sites and list of regions of Vietnam (a). Starting points (+) of forward trajectories from Central Vietnam are presented in the inset (b).

practices were carried out at the chosen sites, and ideally, no pesticides were applied during the rice-growing season. Field investigations of RPH populations were performed once every 5 days using the plant-shaking method. This entailed inserting a plate $(39 \times 29.5 \times 2$ cm$)$ at the base of the rice plants, shaking the plant and collecting any RPH samples that fell from the plant (Hu *et al.*, 2011). Individuals were counted and the number of *N. lugens* and *S. furcifera* per square meter was estimated.

At each experimental site, a black light-trap with 20 W fluorescent lamps (Jiaduo Science, Industry and Trade Co. Ltd., China) was used to monitor the population dynamics of RPH from 1 January to 15 November (2011–2013). In China, the black light traps were switched on at 19:00 h and off at 07:00 h the next morning (Beijing Time). In Vietnam, black light traps were switched on at 18:00 h and off at 06:00 h the next morning (Ho Chi Minh Time). Light-trap catches were collected every morning at 09:00 h and insects were identified using a stereomicroscope. To identify migration patterns, an abrupt (more than tenfold) increase in the daily light-trap catches was defined as the beginning of a peak period. Similarly, we determined that the peak period had ended when there was an abrupt decrease in catch (<1/10). All the days during a peak period were regarded as peak days.

In this study, early spring migration was the focus of our investigation, therefore only catch data from March and April were analyzed. The population dynamics of RPH could not be examined in 2011, because so few individuals were observed that year; thus, only data from 2012 and 2013 were considered. Population dynamics of *N. lugens* in Thang Binh and Dan Dam were similar with that of *S. furcifera*, but

numbers of *N. lugens* in Hai Hau and Hepu were much smaller than that of *S. furcifera*. Trajectory analysis and regression models are based on the sum of both species.

Historical light-trap data from Hepu

Daily light-trap data were collected at Hepu between 1979 and 2013 by the China National Agro-Tec Extension and Service Center. Prior to 2005, traditional black light traps (20 W black light lamp) were used to catch RPH. From 2005 onwards, a new Jiaduo black light-trap with a fluorescent lamp was used instead. To our knowledge, no comparative studies for the efficacy of the two types of light traps for catching planthoppers have been carried out. Thus, the type of light trap was also included as a variable in the regression model to predict migration volume at Hepu with all data (1979–2013). Only data between 2005 and 2009 were selected to calculate migration trajectories.

Meteorological data and modeling

We implemented the Weather Research and Forecasting (WRF) Model in this study (Skamarock *et al.*, 2005). The WRF is a mesoscale numerical weather prediction system designed to serve both atmospheric research and operational forecasting needs. We elected not to use the PSU/NCAR mesoscale model (MM5), because it was not supported since 2006 and the WRF now has all the capabilities that the MM5 system had. The WRF model provided hourly meteorological background data necessary for the trajectory analysis. The dimensions of the model domain were 99×84 grid points at a horizontal resolution of 30 km. Thirty-three vertical layers

were available and the model ceiling was 100 hPa. The scheme selection and parameters used for the WRF are listed in table S1. National Centers for Environmental Prediction (NCEP) Final Analysis (FNL) Data were used as the meteorological data for the model input. FNL is a 6-hourly, global, 1-° grid meteorological dataset. The model forecast time is 72 h with data outputs at 1 h intervals, for horizontal and vertical wind speeds, temperature and precipitation.

Trajectory analysis

Likely population sources and landing areas of migrating RPH were estimated by constructing both backward and forward flight trajectories. The trajectory analysis had the following assumptions: (i) RPH are displaced downwind (Deng, 1981; Riley *et al.*, 1991, 1994; Furuno *et al.*, 2005; Hu *et al.*, 2013); (ii) take-off occurs mostly at dusk and partly at dawn (Chen & Cheng, 1980; Riley *et al.*, 1991, 1994; Furuno *et al.*, 2005; Hu *et al.*, 2013); (iii) migrants are likely to land at any time; and (iv) RPH cannot fly in an atmospheric temperature below 16.5°C (Riley *et al.*, 1994; Furuno *et al.*, 2005; Otuka *et al.*, 2005; Hu *et al.*, 2013). During the peak days of light-trap catches, backward trajectories from light-trap locations were calculated hourly from 07:00 to 06:00 h the previous day, using seven different initial heights above mean sea level: 500, 750, 1000, 1250, 1500, 1750 and 2000 m. A total of 168 trajectories (24 h × 7 heights) were calculated for each location in 1 day. Backward trajectories were terminated at the take-off time of RPH (about 18:00 h) or when the air temperature fell below 16.5°C. Dawn take-off was not considered because the number of RPH flying at this time is much lower compared with at dusk (Chen & Cheng, 1980; Riley *et al.*, 1991). Trajectories were calculated for a flight duration of up to 36 h, but the total time was condition dependent (Cheng *et al.*, 1979; Hu *et al.*, 2013). Flight duration was considered to be: (i) below 13 h if migrants took off at dusk of the same night; (ii) 13–24 h if migrants took off at the previous dusk and landed during daytime; and (iii) above 24 h if migrants took off at the previous dusk and landed at night. A trajectory endpoint was considered a likely source if it was located in a place that satisfied the following two conditions. First, it had fine weather at dusk with an air temperature at 2 m above ground >17°C, an hourly precipitation <0.1 mm and a wind speed at 10 m above ground <4 m s^{-1}, based on the WRF data (Chen & Cheng, 1980; Riley *et al.*, 1991). Second, if it was located in a rice planting area where the crops were at a late growth stage (Cheng *et al.*, 1979).

The calculation setup for the forward trajectory was the same as that for the backward trajectory except that the initial time for the forward trajectory was at dusk (about 19:00 h). The starting points of forward trajectories from Central Vietnam formed a grid at equal distance of 0.5° (see fig. 1b). During emigration periods, forward trajectories were calculated on each day except some rainy and/or windy days. Based on rice growth stage and RPH population dynamics at Thang Binh and Nan Dam, the emigration periods were from March to April in Southern Central Vietnam and from late March to late April in Northern Central Vietnam (see the *Results* section, fig. 5). Endpoints with a flight duration <4 h were regarded as short-distance dispersal and were ignored. The number of forward trajectories that arrived in Nam Dan, Hai Hau and Hepu were estimated by counting trajectories that passed through a circle with its center at these sites and within a radius of 100 km.

Backward and forward trajectories were calculated based on the method introduced by Zhu & Liao (1992) with wind field and temperature data from the WRF output (for more details, see Hu *et al.*, 2013; Lu *et al.*, 2013). The program for calculating trajectories was written in FORTRAN and run using Fedora 13, the Linux-based operating system (Fedora Project, http://fedoraproject.org/).

Regression models with meteorological data

Based on the results of the trajectory analyses, Central Vietnam was identified to be a key source area for the RPH immigrating to South China in March and April (see the *Results* section). We explored the relationship between monthly cumulative light-trap catches at Hepu in April and weather factors in Central Vietnam, including Southern Central Vietnam (SCV) and North Central Vietnam (NCV). Our aim was to determine which factors had the most effect on immigration rates. Temperature is thought to be the most important factor for determining RPH population dynamics (Chen & Wang, 1996; Hu *et al.*, 2010, 2011). A previous study recorded that the winter migration rates increased as temperature increased at Longzhou, Guangxi province in Central Indochina Peninsula (Hu *et al.*, 2010). Average monthly temperatures recorded from January to April in Central Vietnam were used in the analysis as potential variables. Previous studies also determined that the southerly wind was another very important factor for determining long distance windborne northward migration (Syobu *et al.*, 2012; Hu *et al.*, 2013). Thus, the number of days of southerly wind with speed of >4 m s^{-1} were summed for April and used as a variable in the analysis. The Indochina Peninsula is located in a tropical zone and the dry season extends roughly from November to April. In the dry season, precipitation is a major limiting factor on rice planting (Chang *et al.*, 2005; Phan *et al.*, 2009; Zhai, 2011), and thus it might also have influence on the growth of RPH population. Wu *et al.* (1997) attempted to predict the occurrence of RPH in China based on the precipitation in the Mekong River Delta. Monthly precipitation recorded from January to April in Central Vietnam was also included as potential variables for the analysis. The type of light trap was also included as a variable in the regression model to rule out any difference between the two different light traps used in this study. This last variable was included because comparative studies for the efficacy of the two types of light traps for catching planthoppers were unavailable.

The monthly Climate Prediction Center (CPC) Merged Analysis of Precipitation (CMAP) data are available from 1979. The monthly temperature data and monthly days of southerly wind were derived from the NCEP/National Center for Atmospheric Research (NCAR) Reanalysis data from 1948 to 2011. The CMAP and NCEP/NCAR data, with a spatial resolution of 2.5° (i.e. 144 points in longitude and 72 points in latitude) are presented in the NETCDF format, which is self-explanatory and machine-independent.

Data exploration were carried out following the protocol described by Zuur *et al.* (2010). The data were examined for the presence of outliers, auto-correlation in the response variable, collinearity and the type of any relationships identified. The variance inflation factor (VIF) was used to measure the multicollinearity, and a potential variable was excluded if its VIF value was >5 (Rogerson, 2001; Zuur *et al.*, 2010). As the initial analysis indicated that the residuals and the response variables were not auto-correlated, a Poisson General Linear
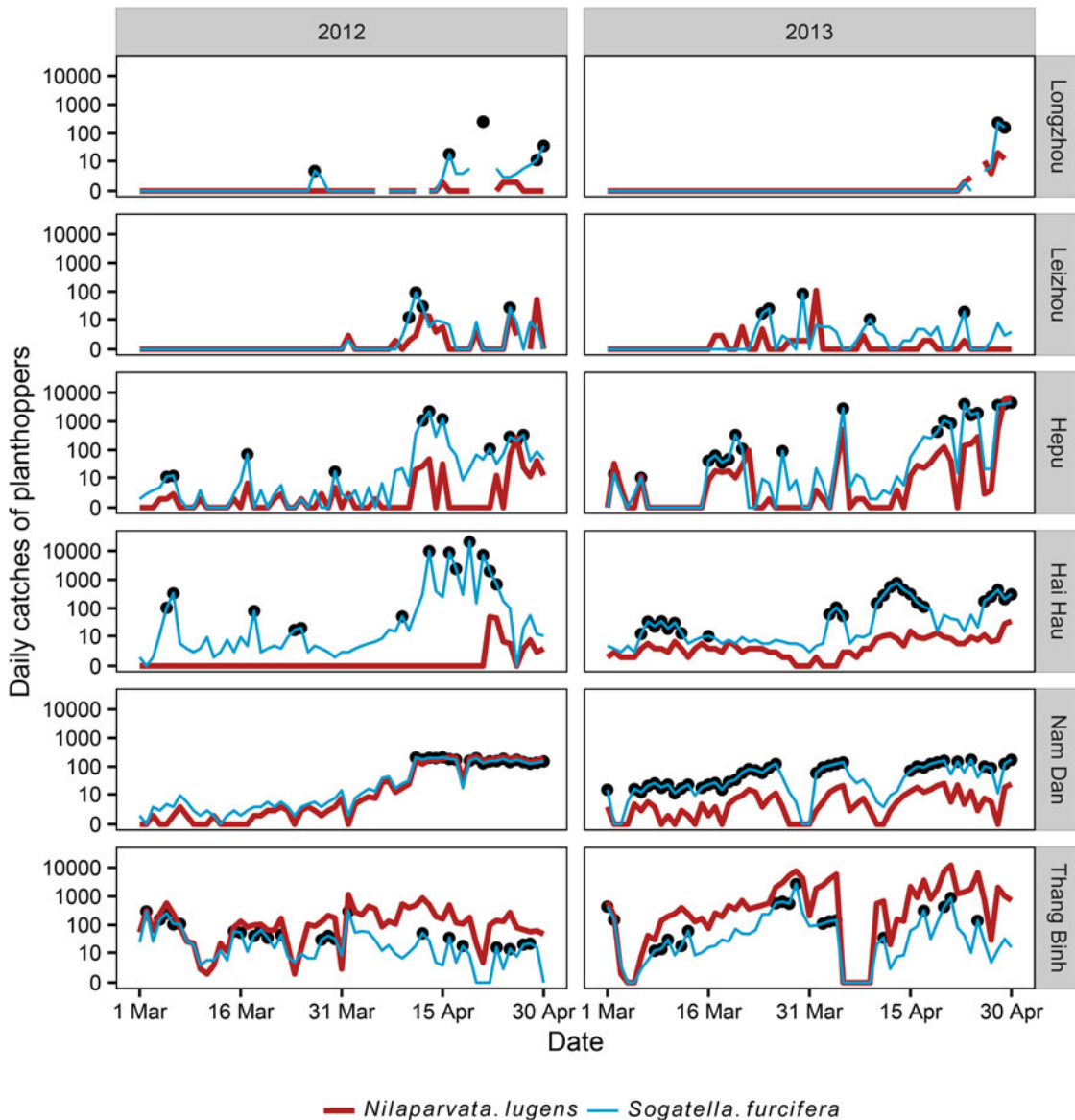
Fig. 2. Number of *Nilaparvata lugens* and *Sogatella furcifera* caught by light trap at experimental sites in 2012 and 2013. The *Y*-axes are on log10 scale. Peak days of catches are indicated by dot symbols (for details see the Methods section). Some data at Longzhou were not collected due to technical problems with the light trap (discontinuous line).

Model (GLM) was therefore applied. Initial Poisson GLMs indicated overdispersion, thus we decided to apply a quasi-Poisson GLM. Due to the small sample size, a forward selection was applied using the quasi-AIC (QAIC) method (Burnham & Anderson, 2002).

Results

Population dynamics of RPH in Vietnam in 2012 and 2013

Thang Binh

There were many peak days of light-trap catches of RPH at Thang Binh in March and April of 2012 and 2013. These peak days can be divided into five periods each year, namely in early March, middle March and early April, late March,

middle April and late April. The interval between each periods was about 15 days (fig. 2). *N. lugens* and *S. furcifera* showed similar trends in their population dynamics. In paddies, rice was at booting stage in early March, and began to mature and harvested in late March (fig. 3). Late instar nymph (instar IV–V) and adults consistently accounted for a considerable proportion of the RPH population catches in the paddies during this time (fig. 3). Given the age structures of RPH and the maturity of the rice, this may indicate that many adults emerged from late instar nymphs and catches from light traps might be potential emigrants to other areas.

Results of the backward trajectories from Thang Binh also suggested that the macropterous catches from the light traps were from the surrounding area. A total of 56.04% (506/903) endpoints of the backward trajectories were located in the
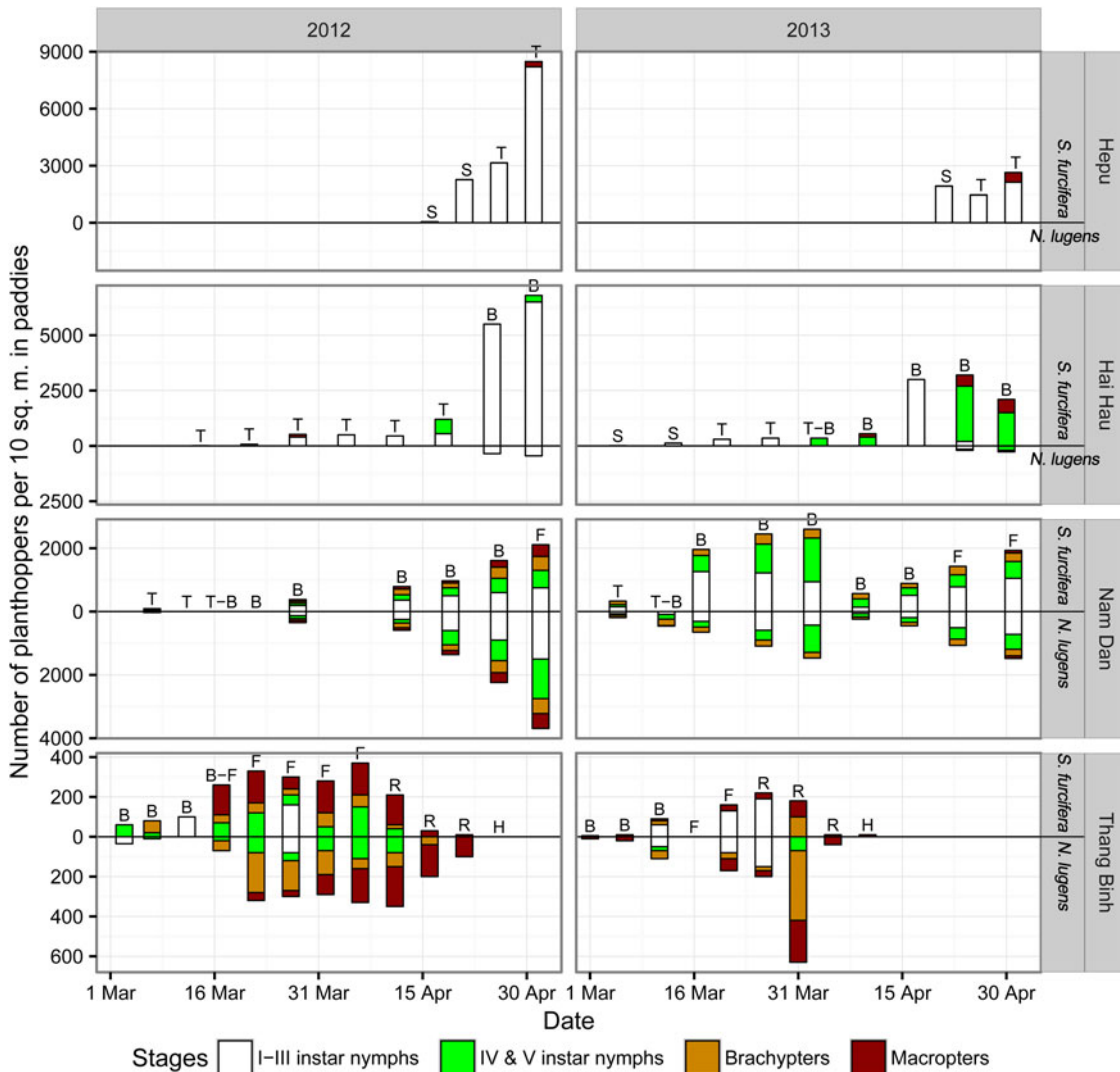
Fig. 3. Numbers of *Nilaparvata lugens* and *Sogatella furcifera* in paddies counted at experimental sites in Vietnam in 2012 and 2013. The letters on the top of each bar indicate the growth stage of rice: S-Seedling, T-Tillering, B-Booting, F-Flowering, R-Ripening and H-Harvest. In South China, only data from Hepu are shown. Population abundance of rice plant hoppers at Longzhou and Leizhou showed similar patterns to Hepu, but actual numbers of individuals were much fewer.

south part of Central Vietnam within a flight duration of 10.06 ± 0.59 h (95% confidence interval (CI)) (fig. 4). No backward trajectory could be traced back to Southern Vietnam, including the Mekong River Delta or Southeast Vietnam (fig. 4), but 59 trajectories (6.53%) on 13 peak days (32.5%, 13/40) had endpoints in Cambodia within 24.59 ± 2.44 h (95% CI). These results also suggest there was no direct exchange between RPH populations in Central and Southern Vietnam, but RPH in the Cambodian source area may have been the progeny of migrants from Southern Vietnam.

Weather during peak days of light-trap catches in Thang Binh were sunny and calm in 2012 and 2013, providing suitable conditions for RPH to take-off. Between March and April (2005–2013), average wind speeds on the 850 hPa level (at altitude of about 1400 m) were <8 m s^{-1} during 526 days (95.81%) and <4 m/s during 372 days (67.76%), wind conditions that were not conducive for long-distance flight migrations. Nevertheless, nine years (2005–2013) of forward

trajectory analyses suggested that RPH from Southern Central Vietnam can arrive in Northern Central Vietnam, the Red River Delta and South China. Many forward trajectories from South Central Vietnam arrived in China at Hepu, Hai Hau and Nam Dan in about 24 h (table S2).

Nam Dan

At Nam Dan, the curve of daily catches of RPH flattens out gradually and there were no distinctive peaks in March and April 2012, especially in *S. furcifera* populations. The number of *S. furcifera* changed gradually from several to 500 individuals (fig. 2). In paddies, rice was at tillering stage in early March and began booting in middle March and was matured by middle April (fig. 3). Brachypterous adults were predominant in the paddies population (fig. 3) thereby indicating that the rice habitat was suitable for the population growth of both planthoppers. However, as brachypterous adults cannot
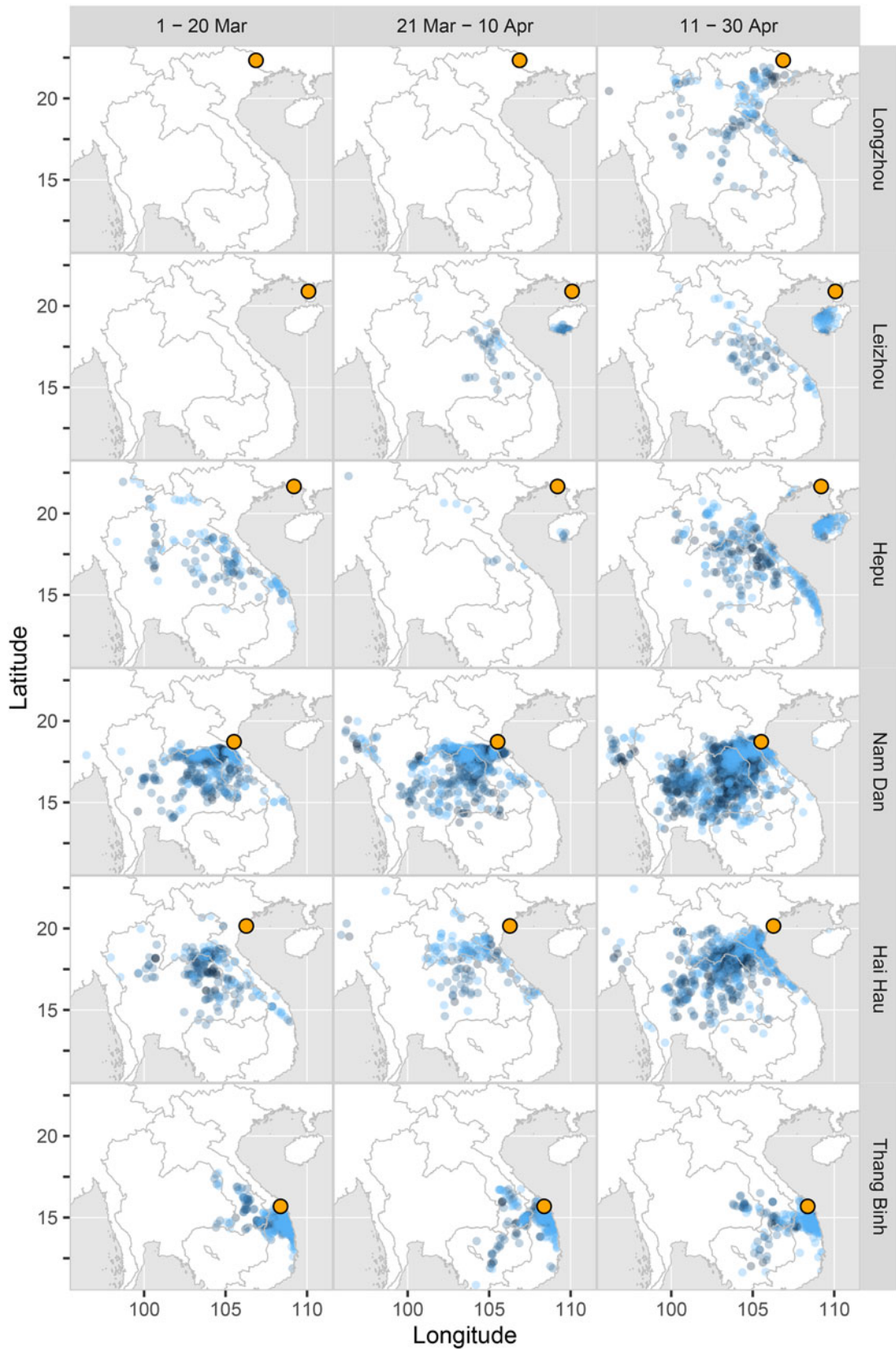
Fig. 4. Distribution of endpoints of backward trajectories from experimental sites in 2012 and 2013 in Vietnam and South China (○).
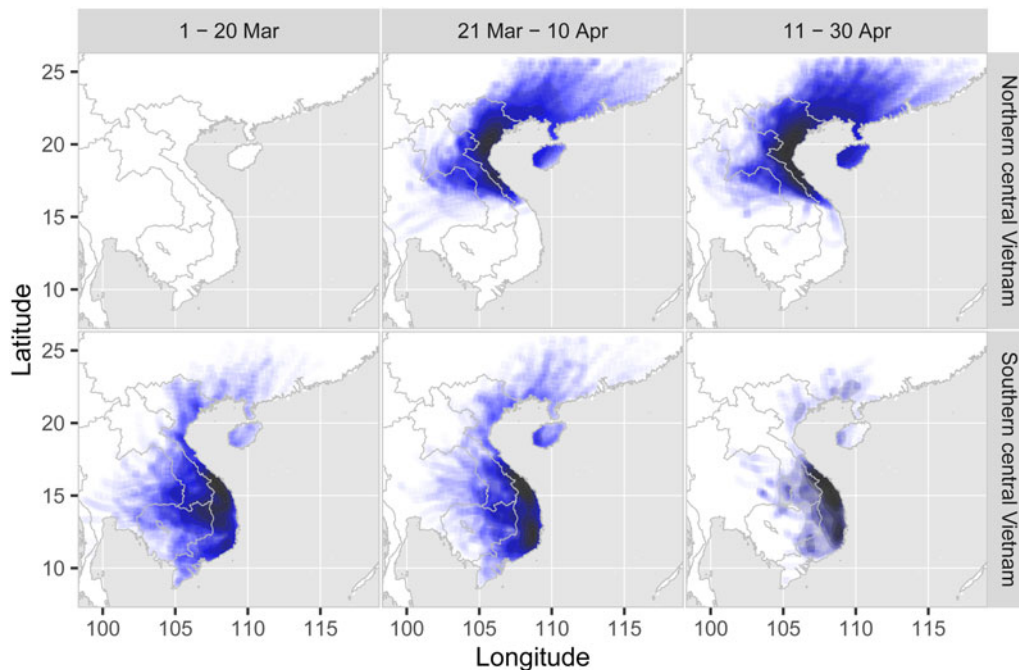
Fig. 5. Distribution of endpoints of forward trajectories from Northern and Southern Central Vietnam in 2005–2013.

really fly they will settle locally. On the other hand, the light-trap catches also were increasing as the RPH population in paddies grew over time (figs 2 and 3). In 2012, the population density of both species of planthoppers remained low in March, but grew quickly in April (fig. 3). Correspondingly, light-trap catches increased with the course of time until they reached a maximum in the middle of April, 2012 (fig. 2). In 2013, the population density in paddies showed two growth phases during these two months and two peaks occurred in late March and late April (fig. 3). Results from the light-trap catches based on increasing catches, could be divided into two stages, before and after early April (fig. 2). Parallel trends between population dynamics inferred from light traps and those in paddies suggested that the light-trap catches might come from local populations. Nevertheless, it cannot be ruled out that these catches may have comprised of both local residents and immigrants from distant sources. However, based on the host plant status, most catches in early and middle March were probably immigrants, because as the rice was so young it would have been difficult for RPH to complete its nymph stage locally.

Backward trajectories suggested that the probable source of light-trap catches were located in Central Laos and Northeastern Thailand (fig. 4). Among the 58 peak catch days, 1038 trajectories (36.73%) on 41 days (70.69%) could be traced to Central Laos, and 1557 trajectories (55.10%) on 41 days (70.69%) to Northeastern Thailand, and the flight durations for each were 9.54 ± 0.40 and 16.51 ± 0.42 h (95% CI), respectively. Only 11 trajectories (0.39%) on 6 days (10.34%) had endpoints in the south part of Central Vietnam with flight durations of 24.09 ± 4.48 h. No trajectories had endpoints in the Mekong River Delta and Southeast Vietnam, and only 27 trajectories (0.96%) on 8 days (19.51%) had endpoints in Cambodia (fig. 4).

The weather during peak days of light-trap catches at Nam Dan were mostly sunny and calm in 2012 and 2013, suitable conditions for RPH to take-off. Forward trajectories from North and South Central Vietnam suggested that most migrants arrive in Central Laos, the Red River Delta and South China (fig. 5, table S2). A number of endpoints were located at Hepu, Hai Hau and Nam Dan with flight duration <18 h (Table S2).

Hai Hau

At Hai Hau, rice was at the seedling stage in March and at the tillering stage in April. The population density of RPH was very low before late April of 2012 and 2013, and mainly comprised early instar nymphs (fig. 3). Thus, it can be assumed that the large number of adults caught by light traps, especially in mid to late April, were probably immigrants (fig. 2). Backward trajectories suggested that these adults might come from Central Laos, Northeastern Thailand and the north part of Central Vietnam (fig. 4). Analysis for previous subareas suggested that macropterous adults emigrated from Central Vietnam (see the Results sections – 3.1.1, 3.1.2). Among the 37 peak days of light-trap catches, 177 backward trajectories (17.05%) on 18 peak days (48.65%) arrived in Northern Central Vietnam and the flight durations were 9.03 ± 0.88 h (95% CI; fig. 4). Only 15 trajectories (1.45%) on 6 peak days (16.22%) arrived in Southern Central Vietnam, and the flight durations were 28.00 ± 1.59 h (95% CI; fig. 4). Results seem to suggest that in these cases, RPH could have come from Northern Central Vietnam. The forward trajectories also confirmed that RPH arrived in Northern Central Vietnam in the Red River Delta (fig. 5, table S2). However, a greater number of backward trajectories arrived in Laos and Northeastern Thailand (fig. 4). In all, a total of 37.86% (393/1038) of trajectories on 24 days (64.86%) arrived in Laos within 13.00 ± 1.32 h (95% CI), while 40.17% (417/1038) of trajectories
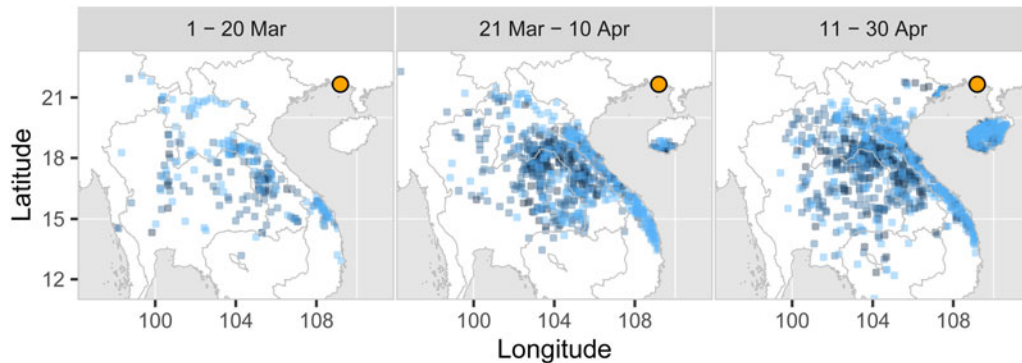
Fig. 6. Distribution of endpoints of backward trajectories from Hepu (○) in 2005–2013.

on 23 days (62.16%) arrived in Northeastern Thailand within 21.32 ± 0.71 h (95%) of flight duration (fig. 4).

Population dynamics of RPH in South China

In South China at Longzhou, Hepu and Leizhou, rice was seeded in the middle of March and transplanted in early April. In 2012 and 2013, early instar nymphs of both RPH species were predominant in paddies in April and this suggested that the adults caught by light trap were immigrants to South China (fig. 3). Backward trajectories suggested that these adults might come from Central Vietnam, Central Laos, Hainan Island or Northeastern Thailand (fig. 4). Among the 30 peak days of light-trap catches at Hepu in March and April of 2012 and 2013, 13.51% (67/496) backward trajectories on 16 days (3.33%) arrived in Southern Central Vietnam within 25.22 ± 1.62 h (95% CI) flight duration (fig. 4). A further 10.89% (54/496) trajectories on 12 days (40%) arrived in Northern Central Vietnam. In early and middle March, 17.32% (24/127) backward trajectories on 6 days (60%, 6/10) arrived in Southern Central Vietnam, while 12.82% (45/351) trajectories on 11 days (73.33%, 11/15) arrived there in middle and late April. Only 1.71% (6/351) backward trajectories on 3 days (20.00%, 3/15) arrived in the Red River Delta in middle and late April. These results suggested that migrants from Central Vietnam could arrive in South China. Results of the forward trajectories further confirmed this finding (fig. 5). Interestingly, a greater proportion of backward trajectories could be traced to Laos and Northeastern Thailand. Among 30 peak catch days, 32.86% (163/496) trajectories on 22 days (73.33%) had endpoints in Laos within 22.82 ± 1.15 h (95% CI), while 20.36% (101/496) trajectories on 17 days (56.67%) arrived in Northeastern Thailand in 29.76 ± 1.12 h (95% CI) flight duration (fig. 4).

At both Leizhou and Longzhou, there were fewer peak catch days than at Hepu (fig. 2). The endpoints' distributions of back trajectories from Hepu were similar to the results for Leizhou, but differed from Longzhou (fig. 4). At Longzhou, 27.40% (40/146) backward trajectories on 4 days (57.14%, 4/7) arrived in the Red River Delta (fig. 4). This suggests that the Red River Delta was potentially an important source area of migrants to Longzhou.

Results for the backward trajectory analysis of 9 years data (2005–2013) from Hepu were similar and also suggested that the macropterous adults migrated from Central Vietnam, central Laos, Hainan Island or Northeastern Thailand (fig. 6, table

S3). In early and middle March, migrants most likely come from Southern Central Vietnam within 23.62 ± 2.51 h (fig. 6, table S3). In late March and early April, migrants most likely come from Northern Central Vietnam within 16.67 ± 1.07 h and the south part of Central Vietnam within 23.39 ± 1.21 h (fig. 6, table S3). Finally, in middle and late April migrants probably come from the north part of Central Vietnam within 17.22 ± 1.04 h (fig. 6, table S3). The forward trajectories also confirmed that RPH arrived from Central Vietnam to South China (fig. 5, table S2).

GLM regression

We explored the relationship between monthly cumulative light-trap catches at Hepu in April and weather factors in the Indochina Peninsula using regression models. Model covariates included monthly temperature and monthly precipitation in all potential source areas from January to April, and days of southerly wind with speed >4 m s^{-1} over the migration area in April. Results indicated that precipitation was the most important covariate at predicting the immigration volume of RPH at Hepu in April. Immigration volume in Hepu in April increased with increasing precipitation in Southern Central Indochina in January, and declined with increasing precipitation in Northern Central Indochina in January (table 1). The GLM model results suggested that wind did not have a significant influence on the RPH migration rates at Hepu in April.

Discussion

Our trajectory analyses results corroborate previous findings and support the hypothesis that RPH migrants in South China during March and April came from Central Vietnam (Shen *et al.*, 2011; Wang *et al.*, 2011). Many endpoints of backward trajectories from Nam Dan, Hai Hau and Hepu were located in Southern Laos, Central Laos and Northeastern Thailand. This suggested that the Central Indochina Peninsula may be the main source area of early spring migrants. RPH population dynamics and migration are poorly understood in Laos and Thailand. Northeastern Thailand is an essential production area for high-quality fragrant rice. The Chao Phraya River runs through this large rice-planting area and provides irrigation during the dry season (Zhai, 2011; Thanawong *et al.*, 2014). Lots of rice is also planted on the Vientiane Plain in Central Laos, and in the dry season this area is irrigated by reservoirs built near the Nan Ngum

Table 1. Results of the GLM model based on a quasi-Poisson distribution testing the effect of regional climatic parameters and light-trap type on cumulative light catches at Hepu in April.

Dependent variable	Independent variable	Estimate	S.E.	t	P
Cumulative light catches in Hepu in April	Intercept	6.061	0.583	10.392	<0.0001
	Light-trap type	3.125	0.518	6.036	<0.0001
	Precipitation. NCV. Jan	−1.638	0.384	−4.262	<0.0001
	Precipitation. SCV. Jan	1.083	0.103	10.511	<0.0001

Note: The type of light trap was a logical variable and it has two values, TRUE and FALSE. TRUE value means the black light trap with a fluorescent lamp and FALSE value means the traditional black light trap. Other variables included precipitations in Central Vietnam (NCV – Northern Central Vietnam, SCV – Southern Central Vietnam) in January.

River (Zhai, 2011). In addition, our results indicated that RPH in the Mekong River Delta likely could not migrate to Central Vietnam directly, as the backward trajectory analysis from Central Vietnam showed no endpoints with an origin in the Mekong River Delta. These findings are in agreement with previous studies (Li *et al.*, 1999; Zhai *et al.*, 2011; Otuka *et al.*, 2014).

The population dynamics and migration of RPH in Southern Central Vietnam were investigated in detail for the first time in this study. Many macropterous adults emerged and emigrated in March as rice matured (see Thang Binh in fig. 3). Both forward and backward trajectories suggested that these migrants arrived in Northern Central Vietnam, Northern Vietnam and South China. Thus, Southern Central Vietnam was one of the first source areas of migratory RPH. In Southern Central Vietnam, RPH always had shorter flight distance simulations due to the weak winds during the sunny weather conditions, characteristic of this and other tropical areas like the Mekong River Delta and the Philippines (Riley *et al.*, 1987; Otuka *et al.*, 2014). In tropical areas, RPH has a shorter pre-ovipositional period and seems to have less migratory tendencies (Wada *et al.*, 2007; Wada, 2014). However, our results revealed that planthoppers located in tropical areas do undertake long-distance migration over sea areas. We recorded simulated migration from Southern Central Vietnam over the South China Sea to South China. Similarly, tropical populations of *N. lugens* in the Philippines are estimated to migrate across the sea to Taiwan (Otuka *et al.*, 2005, 2012). Radar observation also showed that a small number of RPH detected at night may have the potential to migrate longer distances (Riley *et al.*, 1987). The ecological and evolutionary drivers for long-distance migration of RPH remain a key question to answer. Similar population dynamics of *N. lugens* and *S. furcifera* at Thang Binh suggested that interspecific competition was not a factor to force them to emigrate. Previous studies suggested that macropterous migratory adults emerge under crowding or deteriorating host conditions (Kisimoto, 1956; Chen & Cheng, 1980; Sogawa, 1982; Xu *et al.*, 2015). In tropical areas, the maximum density of the two RPH species was 810 per 10 m² at Thang Binh and 5800 per 10 m² at Nan Dam (fig. 3). These densities of RPH are relatively low compared with the subtropical Yangtze River Delta area, where numbers of *N. lugens* were frequently greater at 13,500–16,500 per 10 m² (Hu *et al.*, 2014). Our results concurred with the observation that RPH population density in tropical regions was always much lower than that in subtropical regions (Wada, 2014). Hence, population densities and overcrowding during emergence did not appear to be a factor forcing emigration of RPH from tropical areas.

In Southern Central Vietnam, host rice plants are always available at different growth stages because rice is planted all year-round (Zhai *et al.*, 2011). Thus, in tropical areas RPH can easily find a suitable host plant within short dispersal distances and need not emigrate. Host deterioration should therefore not have been a factor to force RPH to commence long-distance migration. During the investigative periods at Thang Binh, it was noted that mirid bugs (*Cyrtorhinus lividipennis* Reuter), a natural enemy of RPH, were abundant in rice paddies. Previous studies have shown that unsprayed, irrigated rice fields can have relatively few insect pest problems (such as RPH), probably due to predation by their natural enemies such as spiders and *C. lividipennis* that occur in abundance under these conditions (Sigsgaard, 2002; Wada, 2014). Migration may confer benefits through the successive colonization of new habitats that temporarily provide an 'enemy-free space', or at least a significant reduction in predation, parasitism and/or pathogen infection compared with remaining permanently at the same location (Altizer *et al.*, 2011; Chapman *et al.*, 2015). RPH cannot completely escape their predators, however, because *C. lividipennis* migrate long distances to follow their food source (Riley *et al.*, 1987; Zhai, 2001). Nevertheless, the population abundance of spiders and *C. lividipennis* was much less in China than at the RPH source areas in tropical regions (Hu *et al.*, 2011; Wada, 2014). Predator avoidance may therefore have played an important role in driving the evolution of RPH to migrate long distances.

Previous studies have shown that *N. lugens* establishes its population on rice plants at the late stage of development after *S. furcifera* emigrates (Cheng *et al.*, 1979; National Coordinated Research Group for White Backed Planthopper, 1981; Hu & Xie, 1988; Yang *et al.*, 2011). In this study, *S. furcifera* consistently arrived and settled 1 month earlier in China than *N. lugens* did. The abundance of *N. lugens* was much less than *S. furcifera* at Hai Hau, Hepu, Longzhou and Leizhou in 2012 and 2013. This provides more evidence that *S. furcifera* established its population earlier than *N. lugens*. Conversely, in Central Vietnam both data from light traps and paddy surveys in 2012 and 2013 showed that *N. lugens* and *S. furcifera* had similar population dynamics in March and April. One possible explanation may be that *S. furcifera* has stronger migratory tendencies and capabilities than *N. lugens*. *S. furcifera* can fly for longer periods compared with *N. lugens* as demonstrated in flight mill experiments (Feng *et al.*, 2001; Wang & Zhai, 2004). Whilst both RPH species commence their northward migration at the same time from Central Vietnam or others parts of the Central Indochina Peninsula, it appears that *S. furcifera*'s longer-distance flight advantage provides it with the opportunity to establish its population in new habitats before *N. lugens* arrives. Interestingly, when both species are established in the same habitat *S. furcifera* is at a competitive disadvantage (Wang *et al.*, 1997, 1998; Cheng *et al.*, 2001; Yang *et al.*,

2011). It therefore seems likely that preemptive migration of *S. furcifera* before *N. lugens* to new habitats is to compensate for later interspecific competition.

Temperature is thought to be the most crucial factor for controlling brown planthopper population dynamics by its direct effects on survival, reproduction and foraging (Chen & Wang, 1996; Cheng & Zhu, 2006; Hu *et al.*, 2011). Similarly, temperature may regulate and control the population dynamics of both RPH species and a previous study has shown that catch sizes of *N. lugens* at Longzhou were positively correlated with winter temperature in the Central Indochina Peninsula, especially in May (Hu *et al.*, 2010). From November to April, most tropical areas of the Indochina Peninsula experience a dry season (Chang *et al.*, 2005; Phan *et al.*, 2009). Our weather data confirmed that during this period it was always warm and sunny, with only a few days of rain. Temperature does not appear to be a limiting factor for RPH in the Indochina Peninsula because during the study period it was always warmer than 10°C and hence above the survival threshold of both *N. lugens* and *S. furcifera* (Cheng *et al.*, 1979; Hu & Xie, 1988). For example, the mean temperature in January in Central Vietnam was 21.37°C during 1979–2013.

Our study revealed that winter precipitation in the Central Indochina Peninsula has the most influential role on migration volumes of *S. furcifera* at Hepu in April, as indicated by the GLM. In general, RPH prefer humid environments (Cheng *et al.*, 1979) and presumably, precipitation or humidity is a crucial factor for the survival of RPH, including overwintering populations. Rice plants do not grow well during dry winters and under these conditions few planthoppers were observed on rice plants from regeneration or fallen seeds in paddies in Guangdong, Yunnan and Sichuan Provinces (Yang *et al.*, 1982; Zhu & Wu, 1982; Gao *et al.*, 1988). Winter precipitation would be advantageous to RPH overwintering populations by providing a habitat with suitable and abundant rice plants and high humidity conditions that they prefer. Wu *et al.* (1997) proposed that the Mekong River Delta was the original source area of RPH emigrating to China. They suggested that precipitation might be very important in regulating RPH populations in this area, and that this information might be used to forecast RPH population abundance in China. Studies have shown that the *N. lugens* biotype in Southern Vietnam is different to that in Northern and Central Vietnam and China (Zhai et al., 2011; Li *et al.*, 1999). It is therefore assumed that *N. lugens* populations in Southern Vietnam do not frequently link to populations in Northern and Central Vietnam and China. Correspondingly, our study also provides strong evidence from the results of the trajectory analyses that the Mekong River Delta is not a source population for China. Furthermore, our study is reliable as it was both large in scope and time. The similarities in RPH population dynamics detected between the Mekong River Delta and Central Indochina regions by Wu *et al.* (1997) were probably due to a correlation in precipitation levels between the adjacent regions at that time that influenced local RPH population abundances, rather than any actual biological linkages between populations in these areas. The findings were based on limited data from 6 years only (1991–1996), thus we reject the conclusions drawn by Wu *et al.* (1997).

In summary, we provide new insights into RPH population dynamics and migration routes from source populations in Vietnam to South China. Some evidence suggested that Laos and Thailand might also be important source populations. We shed new light on our understanding of the interspecific relationships between RPH species, their establishment in new areas and the primary drivers that could have caused them to evolve their long-range insect migration. Our results provide valuable information for forecasting pest outbreaks, information that is necessary for implementing control measures against these migratory pests. Only Central and Northern Vietnam were studied here, further work across the whole Indochina Peninsula is required to deliver a more detailed and thorough migration map of RPH movements across the region. Future international joint pest monitoring programs between Eastern Asia countries might achieve this, as well as create further opportunities for information sharing relating to these pests.

Supplementary Material

The supplementary material for this article can be found at https://doi.org/10.1017/S0007485316001024

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