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Migration patterns and winter population dynamics of rice planthoppers in Indochina: new perspectives from field surveys and atmospheric trajectories

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ABSTRACT:

Rice planthoppers (RPH) are the most serious insect pests of rice production in East Asia, frequently out-breaking in China, Korea and Japan each summer. They are unable to overwinter in temperate East Asia, and summer populations arise anew each year via northward spring migration from south-east Asia. The annual migration cycle is generally believed to be a closed loop with mass returns to south-east Asia in the autumn, but this leg of the journey and the overwintering dynamics are much less studied than the spring immigrations. Previous studies have indicated that the north-central Vietnam (NCV) region is a key location for both the spring colonisation of China and for receiving return migrants from southern China each autumn. However, NCV experiences a three-month rice-free fallow period during mid-winter, and so it cannot be the principal over-wintering region for RPH populations. In this study, the continental-scale migration patterns of RPH in East Asia were explored using data from light trap catches, field surveys and atmospheric trajectory simulations. Our results confirmed that large numbers of return migrants arrive in NCV from southern China each autumn, but that they are unable to survive there over winter. The NCV region is recolonised in the early-spring (mid-February to mid-March) of each year by migrants from winter rice-growing regions in north-east Thailand, southern Laos and south-central coastal Vietnam, which are transported on favourable high-altitude synoptic winds. The following generation initiates the colonisation of East Asia from a large source population in NCV. Our results provide a new perspective on RPH migration patterns and over-wintering dynamics in East Asia, which is governed by crop production, environmental conditions and synoptic wind patterns at a continental scale.

Keywords:

Rice planthoppers; Brown planthopper *Nilparvata lugens*; white-backed planthopper *Sogatella furcifera*; Spatio-temporal trajectory analysis; Weather factors; Indochina Peninsula

1. Introduction

The most important pests of rice in East Asia are the brown planthopper (*Nilaparvata lugens* [Stål]) and white-backed planthopper (*Sogatella furcifera* [Horváth]) (Hemiptera, Delphacidae), collectively known as rice planthoppers (RPH) (Cheng et al., 1979; Kisimoto, 1976; Kisimoto and Rosenberg, 1994; Zhai, 2011). These highly migratory pests frequently outbreak in this region, where they can cause significant losses to rice crops; in China alone, for example, up to 20 million hectares of rice crop can be lost in a single year during serious RPH outbreaks (Hu et al., 2011, 2014, 2018; Lu et al., 2017), largely due to virus transmission (Cheng, 2009, 2015; Zhou et al., 2010; Heong et al., 2015). RPH cannot overwinter in the temperate regions of East Asia (Korean Peninsula, Japan and all but extreme southern China), and this region is annually colonized by a series of northward migrations throughout the spring and summer (Cheng et al., 1979; National Coordinated Research Group for white-backed planthoppers, 1981; Kisimoto and Sogawa, 1995; Hu et al., 2011, 2017; Otuka et al., 2013; Wu et al., 2018b). The annual migration is generally believed to take the form of a closed loop, but in contrast to the well-studied spring migrations to the north, the autumn return movements and over-wintering dynamics within Indochina are poorly known. There is some evidence of southward autumn migrations within China (Riley et al., 1991; Hu et al., 2013), but while the ultimate destination of these return migrants is often considered to be the Indochina Peninsula (Hu et al., 2013, 2018; Wu et al., 2017), the precise destination of the autumn return migrants, and the regions where they persist throughout the winter, remain poorly understood.

The timing and extent of crop damage in China and the rest of temperate East Asia will be partly determined by conditions and source populations in the winter-breeding areas (Cheng et al., 1979; Otuka et al., 2006, 2008; Shen et al., 2011; Zheng et al., 2014). Thus to understand the migration circuit and annual population dynamics of these pests, and develop mitigation strategies for rice crops in East Asia, a thorough understanding of RPH winter population dynamics is required. Winter rice crops are present over much of Indochina, so there are many potential areas for RPH to persist through the winter months. Recent work has identified the north-central Vietnam region (NCV; Fig. 1) as potentially a key area, as it appears to be the principal source of migrants colonizing southern China each spring (Hu et al., 2017; Wu et al., 2018b), and it is an important destination for returning migrants from southern China during autumn (Wu et al., 2017).

This poses the question of whether the NCV region forms part of the main overwintering area, as its geographical location (Fig. 1) makes it ideally placed to receive large numbers of return migrants from southern China, and it lies to the south of the northern winter-breeding limit (around the Tropic of Cancer; Cheng, 1979; Luo et al., 2013). However, field surveys conducted as part of this study (Plates S1–S5) in NCV confirmed that there is a 3-month fallow period during November to January when no rice crops are grown, as previously reported (Wu et al., 2017), and rice at a suitable developmental stage for RPH colonization is not present until late-February at the earliest. As rice is the only food source of RPH, the absence of suitable hosts will disrupt the population cycle leading to an apparent gap in the migration loop. Clearly, RPH must recolonize the rice paddies in NCV during late-February to mid-March in order to provide the source of the immigrants to southern China later in the spring, thus closing the loop.

There are clear gaps in our understanding of the RPH recolonization process in NCV. Firstly, where do the re-colonizers come from? Secondly, as RPH are weak flyers and their migrations are completely windborne (Deng, 1981; Rosenberg and Magor, 1983), what is the influence of synoptic wind patterns and atmospheric temperatures on the colonization process? In this study we used population data from large-scale light-trapping and field surveys from the regions of north-central and south-central coastal Vietnam (NCV and SCV, respectively), in combination with atmospheric trajectory simulations and meteorological analyses across Indochina and southern China, to elucidate the winter population dynamics and identify the source regions for the recolonization process.

2. Materials and methods

2.1. Study region and period

The study region encompassed the southern Chinese provinces of Guangdong, Guangxi and Hainan, and the Indochina Peninsula (Fig. 1). The main rice-growing regions in Vietnam, Laos, Cambodia and Thailand discussed in this study (Fig. 1) were identified following the scheme of Hu et al. (2017). Rice planthopper light-trap catches were collected in southern China during every October of 2004 to 2013, intensive field surveys and light-trapping were carried out in the two main study regions of north-central and south-central coastal Vietnam (NCV and SCV, respectively; Fig. 1, inset) during the early-spring of 2010 to 2013, while large-scale trajectory analyses were conducted over the 10-year period from 2004 to 2014.

2.2. Light trap and field survey data

Daily light-trap RPH catch data from seven sites in southern China (two in Guangdong Province, four in Guangxi Province, and one in Hainan Province) were collected every morning during October of 2004-2013, and obtained from the China National Agro-Tec Extension and Service Center (NATESC). At all stations, 20-W blacklight traps (Jiaduo Science, Industry and Trade Co. Ltd., Henan Province, China) were used to catch planthoppers. The blacklight traps were switched on daily at 19:00 h and switched off at 07:00 h Beijing Time (UTC+8) the following morning. The specific locations of the trapping sites were as follows: Qujiang (QJ) and Yangchun (YC) in Guangdong Province; Babu (BB), Hepu (HP), Longzhou (LZ) and Zhaoping (ZP) in Guangxi Province; and Sanya (SY) in Hainan Province. However, there were periods of missing data: October of 2004, 2010 and 2013 at QJ; of 2004-2008 at ZP; of 2004-2009 at BB; of 2011-2013 at LZ; and of 2004-2006 at SY.

Daily light trap RPH catch data from three sites in Vietnam, one in NCV (Nghệ An (NA)) and two in SCV (Quảng Nam (QNa) and Phú Yên (PY); Fig. 1, inset), were collected every morning during 1 February to 20 March 2010, and obtained from the Department of Plant Protection, Ministry of Agricultural and Rural Development, Vietnam. The backlight traps at NA and QNa were the same design as those deployed in southern China, while a traditional light trap with a 75-W electric lamp was deployed at PY. The Vietnamese light traps were switched on daily at 18:00 h and off at 06:00 h Ho Chi Minh Time (UTC+7) the following morning. The relationships among light-trapping population dynamics of the three sites (NA, QNa and PY; see Fig. 1, inset) were tested by Pearson correlation analysis for each pair. Calculations were performed using R software 3.4.1 (R Core Team, 2017; https://www.R-project.org/).

Field surveys of RPH population and rice growth stage in NCV and SCV were conducted by Nanjing Agricultural University staff in November 2011 and 2012, February and March 2012 and 2013. Paddy fields located every 30-50 km apart were chosen for surveys, and in each survey site, 2-3 rice paddies were sampled. In each paddy, at least 5 plots were randomly checked. RPH population size was estimated by the plant-shaking method (Hu et al., 2011) with a white plate (39 cm×29.5 cm× 2 cm) inserted at the base of the rice plants or stubble. At each plot, 10-20 rice plants were shaken and the individuals falling onto the white plate were counted; the total was extrapolated to give a mean value from 100 plants, which was then used as a relative estimate of population size. In NCV we found only rice stubble, ratoon rice and self-seeding rice from fallen grain during the post-harvest period from November until January (Plates S1-S2), and the population dynamics of RPH were studied by the same method of shaking rice stubble or very young plants.

2.3. Atmospheric trajectory models

2.3.1. Atmospheric model

In order to obtain detailed models of RPH migration pathways, we implemented the Weather Research and Forecasting (WRF) Version 3.8 model (Skamarock et al., 2008; www.wrf-model.org) in this study. This next-generation mesoscale numerical weather research system consists of fully compressible non-hydrostatic equations and a range of meteorological variables (including three-dimensional wind, air temperature, precipitation, and surface pressure variables). The hourly initial and boundary conditions simulated by the WRF model were obtained to run the RPH three-dimensional trajectory program, which had a spatial resolution of 30 km. The region modelled is shown in Fig. 1 and the detailed model setup and parameterizations are listed in Table S1. The terrestrial data used in the WRF processing system included Moderate Resolution Imaging Spectroradiometer (MODIS) and Gravity Wave Drag by Orography (GWDO) data with a resolution of 2′, and these data cover the entire globe (180°W – 180°E and 90°S – 90°N) (http://www2.mmm.ucar.edu/wrf/users/download/get_sources_wps_geog.html). We used National Centers for Environmental Prediction (NCEP) Final Analysis (FNL) Operational Global Analysis data (prepared every 6 hours on a 1° by 1° grid; http://rda.ucar.edu/datasets/ds083.2/) as the initial and boundary conditions to drive the WRF model.

2.3.2. Three-dimensional trajectory analysis

Landing areas of emigrating insects and likely source populations can be estimated by constructing forward and backward trajectory analysis, respectively (Westbrook et al., 2016; Wang et al., 2017; Wu et al., 2018a). This method has been successfully used to study the migration of rice planthoppers in previous studies (Otuka et al., 2005; Furuno et al., 2005; Hu et al., 2013, 2017; Wu et al., 2018b). The downwind trajectory analysis of RPH in the present study is based on the following assumptions: (i) RPHs migrate downwind (Deng, 1981; Rosenberg and Magor, 1983) at heights of 300–2500 m above ground level (Deng, 1981; Riley et al., 1991, 1994); (ii) take-off is predominantly at dusk (and partly at dawn) (Chen and Cheng, 1980; Liu et al., 1982; Riley et al., 1991, 1994; Luo et al. 2011); (iii) migrants have a one-way journey and can land at any time along the route (Rosenberg and Magor, 1983, 1987; Zhai and

Zhang, 1997; Feng et al., 2001; Wang and Zhai, 2004); and (iv) RPH cannot fly when the air temperature at flight altitude is below 16.5°C (Ohkubo, 1973; Rosenberg and Magor, 1983; Riley et al., 1991; Otuka et al., 2005). In this study, take-off at dawn was not considered in the forward trajectory analyses, because the amount of RPH initiating flight at this time is rather low (Chen and Cheng, 1980; Riley et al., 1991).

Specifically, the forward trajectories from each start point were calculated at the start time of 19:00 h (after mean local sunset time in Indochina during the studied period; local time, same thereafter), at seven initial heights of 500, 750, 1000, 1250, 1500, 1750 and 2000 m above mean sea level (AMSL). The calculation framework for the backward trajectory analyses was the same as the setup for the forward trajectory analyses, except that: (i) start times of backward trajectories were every hour from 19:00 h the previous day to 07:00 h the following morning (both local time, 13 start times in total), which were consistent with operating time of the light-traps; (ii) the locations of calculated endpoints where RPH took-off at dusk (19:00 h local time) were selected as source areas if the location was in a rice planting area (Lu et al., 2013), and plotted with R software 3.4.1. The trajectories were run for up to a maximum of 36 h (Rosenberg and Magor, 1983, 1987; Chen et al., 1984; Wang and Zhai, 2004). Both forward and backward trajectories were terminated when the air temperature at flight altitude fell below 16.5°C, the hourly precipitation was ≥ 0.1 mm, or the trajectory extended beyond the grid-spaced region of the WRF model. The program for calculating trajectories was designed in FORTRAN (Hu et al., 2013, 2014) and run under UBUNTU 14.04. The migration trajectory pathways were plotted with ArcGIS (ESRI® 2012). In this study, we present the results of the forward trajectory analyses as the number of trajectory pathways which cross grid cells of 100 x 100 km, whereas backward trajectory analyses are presented as endpoints (which represent the take-off locations).

2.3.3. Departure points for forward and backward trajectories

To model the autumn return migration to Indochina, forward trajectories were started at every

0.2° grid in the southern Chinese provinces of Hainan (71 departure locations), Guangdong (386) and Guangxi (520) (Fig. 1) at 19:00 h on every date in October during 2004–2013, comprising >2.1 million forward trajectories in total. To identify source areas of the recolonization of the NCV region, backward trajectories were run from 114 grid points in NCV for each hour of every night during 21 February to 20 March of 2005 to 2014, comprising >2.9 million backward trajectories in total. To confirm the identification of the source areas for the spring recolonization, and investigate general spring migration patterns within Indochina, forward trajectories were also run during the same time period from the 8 regions which have year-round rice planting (Fig. 1). Trajectories were started from 1,013 departure points at every 0.2° grid in all 8 regions: i) southern Laos (S Laos); (ii) south-central coastal Vietnam (SCV); (iii) Central Highlands of Vietnam (Central Highlands); (iv) south-eastern Vietnam (SE Vietnam); (v) Mekong River Delta of Vietnam (Mekong); (vi) Tonlé Sap Lake Region of Cambodia (Tonlé Sap); (vii) north-eastern Thailand (NE Thailand); and (viii) eastern Thailand (E Thailand) (Fig. S1), comprising >2.0 million forward trajectories. Thus in total, >7 million migration trajectories were calculated, making this the largest study of RPH migration pathways conducted.

2.4. Meteorological data

To investigate the long-term atmospheric conditions (wind speeds and directions, and air temperatures), within which the RPH migrate, we plotted meteorological conditions at 850 hPa (approximately 1500 m above ground level, the height at which RPH typically fly; Deng, 1981). Long-term data were extracted and calculated from the daily NCEP/National Centre for Atmospheric Research (NCAR) Reanalysis data, with a spatial resolution of 2.5° by 2.5° global grids (Kalnay et al., 1996), and displayed using the Grid Analysis Display System (GrADS) 2.0.1. Detailed daily wind field and temperature data for the spring recolonization period (21 February to 20 March) during 2010 to 2014 were plotted for the regions identified as the principal sources, using twice-daily data from the 850 hPa level obtained from the FNL dataset.

Using the Rayleigh test of uniformity for circular data (Fisher, 1993), mean downwind directions (plus associated circular statistics) at 850 hPa were calculated for: (i) the autumn return migration period (October of 2004-2013) for winds from the 3 southern Chinese provinces of Hainan, Guangdong and Guangxi; and (ii) the spring recolonization period (21 February – 20 March of 2005-2014) for winds from the 8 rice-growing regions (excluding NCV) in Indochina. For each period/region, the Rayleigh test was used to calculate the following three parameters for the distributions of downwind directions: (i) the mean direction; (ii) the mean vector length 'r' (a measure of the clustering of the angular distribution of headings or tracks ranging from 0 to 1, with higher values indicating tighter clustering around the mean) for each distribution; and (iii) the probability that the distribution of downwind directions differed from a uniform distribution (a P-value of < 0.05 indicates that the distribution is significantly unimodal, and hence there is a significant bias in that region/period for downwind directions to blow toward a particular compass sector).

3. Results

3.1. Autumn mass return migration to Indochina

Mean October light-trap catches of RPH from the three southern Chinese provinces of Guangdong, Guangxi and Hainan, over the 10-year study period, demonstrated that large populations of flight-capable RPH were present throughout this region. Mean catches ranged from about 1500 – 80,000 RPH per month (Fig. 2), with a maximum nightly catch of 13,248 RPH per trap. These large catches indicated that there were substantial RPH populations in late-autumn, and as rice crops are not grown throughout the winter in most of southern China, these RPH populations must emigrate further south or crash.

Examination of the 10-year average wind fields in October at ~1500 m AMSL (typical RPH flight height) across the whole region showed the presence of fast (5–10 m s^{-1}), suitably-directed winds for south-westward/westward transport from southern China towards the east coast of

Indochina (Fig. 3a). Winds from the southern Chinese provinces studied in detail were consistent with the general pattern (Rayleigh tests; Guangdong: N = 119,660, mean downwind direction (DWD) = 236°, r = 0.726, $P < 0.0001$, mean wind speed (WS) = 6.3 m s^{-1}; Guangxi: N = 161,200, DWD = 272°, r = 0.607, $P < 0.0001$, MS = 5.6 m s^{-1}; Hainan: N = 22,010, DWD = 250°, r = 0.788, $P < 0.0001$, WS = 7.3 m s^{-1}; Fig. 3b). The suitability of the wind fields for transport was confirmed by forward trajectory analyses over a 10-year period from southern China, which showed a high proportion of trajectories reaching eastern Indochina (Fig. 4). Trajectories from Guangdong (Fig. 4a) indicated that many emigrants will have reached northern Vietnam/NCV after 36 hours, with smaller numbers travelling further west to rice-growing regions in S Laos and NE Thailand (Fig. 1). Emigration patterns from Guangxi (Fig. 4b) were similar to that from Guangdong, but with slightly fewer trajectories reaching central Indochina. In contrast, trajectories from Hainan (Fig. 4c) travelled further west into Indochina, and numbers reaching NCV were substantially higher than from the two other provinces. These results confirm that NCV is the key area for receiving return migrants as the southern China population retreats each autumn.

3.2. Winter population dynamics of RPH in NCV

Field surveys of RPH densities were carried out through autumn to spring of 2011-2012 and 2012-2013 in six locations in NCV and six in SCV (Fig. 1, inset). In both autumn periods, there were large populations of RPH in some sites in NCV (Fig. 5a), but there were consistently lower densities in the SCV locations in the same period (Fig. 5b), indicating that substantial emigration from southern China to NCV had occurred. The autumn surveys in 2011 were carried out in late-November, by which time the NCV population consisted mostly of nymphs (Fig. 5a), indicating that the original immigrants arriving earlier in the autumn had already produced the next generation. By contrast, in 2012 the autumn surveys were carried out 3 weeks earlier (in early-November), when populations in NCV were dominated by macropterous (long-winged) adults (Fig. 5a) indicating the arrival of immigrants. By the time of the winter surveys (in February), the rice crops in NCV had been harvested and the fields ploughed, and only a very few plants of ratoon and self-seeding rice were present (Plates S2). Consequently, RPH populations almost completely crashed in the NCV survey sites during February (Fig. 5a); by contrast, there was some evidence that small RPH populations were able to persist through the winter in the southern SCV sites (Fig. 5b). Despite the population crash during mid-winter, RPH populations in NCV had rebounded by the surveys in March (Fig. 5a), by which time the rice plants had grown to the tillering/jointing stage suitable for RPH development.

In contrast to the complete crash of RPH populations on rice plants in NCV during mid-winter, light-traps catches during February 2010 from Nghệ An (NA) in the north of NCV (Fig. 1, inset) demonstrated that flying macropterous adults (i.e. potential immigrants) were present in good numbers every night (Fig. 6), despite no hoppers being present on rice plants this far north. The patterns of nightly light trap catches at three sites spanning 800 km distance, from NA in northern NCV, via Quảng Nam (QNa) in northern SCV to Phú Yên (PY) in southern SCV (Fig. 1, inset) were very similar (Fig. 6). Pairwise comparisons between the three sites showed positive and significant correlations in all cases (Pearson correlations; NA and QNa: $N = 48$, $r^2 = 0.104$, $P = 0.025$; NA and PY: $N = 47$, $r^2 = 0.502$, $P < 0.0001$; QNa and PY: $N = 48$, $r^2 = 0.803$, $P < 0.0001$; Fig. S2). This indicates that migratory activity was highly correlated over very large spatial scales. As there were no other suitable host plants in the NCV region through the winter period, the rapid resurgence in the spring indicates that RPHs must have immigrated into NCV from elsewhere in Indochina, such as SCV, where rice crops are grown throughout the winter.

3.3. Identification of the source areas for the recolonization of NCV

To identify potential source areas of the RPH which recolonize NCV in the early-spring, we examined the mean 10-year wind field patterns during the recolonization period (21 February to 20 March) at RPH flight altitudes (Fig. 7a). At the synoptic scale, wind patterns were complex and varied across the region; on average there was a tendency for winds to blow towards the northeast over much of Indochina, but at relatively slow speeds (often <5 m s^{-1}; Fig. 7a). This indicates that wind directions were generally suitable for transport of RPH to the NCV region from the rest of Indochina, but the slow speeds will have restricted the distances over which RPH could have travelled (Fig. 7a). Analysis of wind directions and speeds for the 8 rice-growing regions indicated that 5 of the regions (Central Highlands, SE Vietnam, Mekong, Tonlé Sap and E Thailand) could not be the source area for recolonization of NCV (Fig. 8). Wind conditions were however favourable in the 2 important rice-growing regions of central Indochina, which both had a high proportion of south-westerly winds which would have transported RPHs to NCV (Fig. 7b; Rayleigh tests; NE Thailand: N = 100,110, DWD = 347°, $r = 0.490$, $P < 0.0001$, WS = 3.5 m s^{-1}; S Laos: N = 39,198, DWD = 333°, $r = 0.259$, $P < 0.0001$, WS = 3.4 m s^{-1}). The situation was different in SCV, which had relatively few favourable winds for transport to NCV (i.e. southerly winds were scarce; N = 17,484, DWD = 255°, $r = 0.454$, $P < 0.0001$, WS = 4.4 m s^{-1}; Fig. 7b), but given its close proximity to NCV and highly correlated light-trap catches (Fig. S2), we assumed that it may still be an important source area for the recolonization of NCV. While the general pattern was favourable for transport to NCV from central Indochina (Fig. 7), examination of detailed daily wind conditions and air temperatures shows a highly dynamic situation, with good transport opportunities interspersed with periods when migration would not have been possible (Fig. 9). The position of the 16.5°C isotherm at 1500 m AMSL during the recolonization period will have encouraged fallout of emigrants in the NCV region and prevented migration onwards into northern Vietnam and southern China where the rice was also so young during the recolonization period that it would have been tough for RPH to survive locally (Fig. 7a and S3).

The importance of NE Thailand, S Laos and SCV as source areas was further investigated by running backward trajectories from every 0.2° grid in NCV during the recolonization period (Fig. 10). The results demonstrated that each of these regions were frequent potential source areas of RPHs arriving in NCV (proportion of backward trajectories originating from beyond the NCV in each of the 3 regions after 12 h, 24 h and 36 h respectively were as follows: NE Thailand: 18%, 46% and 41%; S Laos: 11%, 13% and 10%; SCV: 4%, 5% and 5%; the other

5 regions had values between 1% and 4% in total; Fig. 10). The importance of these 3 regions as potential sources for recolonizing NCV was confirmed by calculating forward trajectories from all 8 winter rice-growing regions throughout Indochina, which showed that relatively high proportions of trajectories from NE Thailand (10%), S Laos (15%) and SCV (21%) pass through NCV (Figs. 11 and S4-6), but only 7% in total reached NCV from the other 5 regions (Fig. 11).

4. Discussion

The northern winter-breeding boundary of RPHs is limited by the requirement for winter temperatures to remain >12°C, which in East Asia tends to be south of the Tropic of Cancer (Cheng et al., 1979; Luo et al., 2013), and the widespread availability of rice crops. This effectively limits large-scale winter-breeding to no further north than the Indochina Peninsula. Thus the large populations which outbreak in southern and eastern China each summer (Hu et al., 2011, 2013, 2014, 2018; Lu et al., 2017) must return to Indochina during the autumn in order for the migratory populations to persist. Direct evidence for these southward return migrations was relatively scant until recently, and limited to a few observations of movements within China (Riley et al., 1991; Hu et al., 2013), but the current paper and recent work of Wu et al. (2017) indicate that wind conditions suitable for transport from southern China to Indochina are frequent in the autumn. In particular, we identify the NCV region as a key area for the return migrants, with a high proportion of trajectories from the southern Chinese provinces of Guangdong, Guangxi, and especially Hainan, reaching NCV (Fig. 4). Field surveys demonstrated that large populations of RPHs were present in rice crops in NCV during November (Fig. 5), consistent with large-scale arrivals of emigrants from southern China in the previous month.

Our work indicates that large-scale returns to Indochina occur each autumn, and that NCV is both the start point for spring colonization of southern China and the destination for autumn return migrants. In order for the migration loop to be closed however, it is necessary to explain how RPH populations returning from China persist over the winter despite the fact that their reproductive cycle is broken during the 3-month fallow period in NCV. The immigrants arriving in NCV in the autumn produce a new generation, as evidenced by the large proportion of nymphs we found in late-November 2011 on rice (Fig. 5). However, by February, RPH populations in NCV have completely crashed, so what has happened to the immigrant populations? There are two possible scenarios, which are not mutually exclusive. Firstly, the November generation may have completed development and produced macropterous (long-winged) adults, which departed on mass to colonize other areas to the south or west where rice is grown through the winter. Secondly, the rice crop may have been harvested before development was complete, resulting in local extirpation of RPHs in NCV. Further research is required to test these assumptions. If the latter scenario is the sole explanation for the mid-winter crash, then there would appear to be a paradox, as the migratory loop would apparently experience a complete break in the NCV region during mid-winter.

This apparent paradox can be explained by the small proportion of autumn migration trajectories which overfly NCV and reach continuous rice-growing areas in central Indochina, specifically the NE Thailand and S Laos winter rice-growing regions (Figs. 1 and 4). Even though the proportion of the emigrants from southern China which reach these distant regions is small, they may be disproportionally important in maintaining the migratory loop, as r-selected species such as RPHs have extremely rapid population growth (Cheng, 2009). The progeny of these winter generations in central Indochina therefore constitute an important source for the recolonization of NCV during early-spring, ensuring that the migration is a closed loop. Field surveys should be carried out in these regions to demonstrate the existence of winter-breeding populations there.

Our data provides further evidence to refute the so-called ‘pied piper’ syndrome: a long-standing idea which posits that many insect migration systems are non-adaptive, because large-scale returns to winter-breeding areas are apparently absent, leading to mass mortality in the progeny of immigrants (Stinner et al, 1983). This idea made little evolutionary sense (McNeil, 1987; Cardé, 2008; Chapman et al., 2012), and has been refuted in recent years by the widespread demonstration of autumn return migrations in multiple species (e.g. Showers, 1997; Feng et al., 2005; Chapman et al., 2008, 2010, 2015; Hu et al., 2016). The data we provide in the current paper provides evidence that the migration loop in RPHs is complete, with successful return of the progeny of spring migrants to breed over the winter in Indochina, and so provides another blow to the ‘pied piper’.

As RPHs are small, weak-flying insects, with a mean flight-speed of only 0.3 m s^{-1} (Chen et al., 1984), their long-range migration patterns will be completely determined by wind fields (Chapman et al., 2011b). Our results thus underline the importance of synoptic wind patterns in the annual cycle of expansion and subsequent retreat of RPH populations in the Indo-China/East Asia region. The advance and retreat of the monsoon over East Asia through spring to autumn provides highly favourable winds (Hu et al., 2018) for carrying RPHs northwards into southern China each spring, on to East China, Korea and Japan by late-summer, and back to Indochina during the autumn. Our trajectories confirm that October winds facilitate return of RPHs from southern China to eastern Indochina (particularly NCV), and also that rice-growing regions in central Indochina (especially NE Thailand and S Laos) receive frequent favourable winds for recolonization of NCV during February to March. However, it is also very clear from our results that the important over-wintering region of the Mekong Delta, where very large RPH populations exist during winter (Chen and Zhai, 2006; Sakamoto et al., 2006; Otuka et al., 2014), is not the source for the spring recolonization. Forward trajectories show that migrant RPHs from the Mekong only achieve short-range dispersal to the W/NW (to the Tonlé Sap region of Cambodia; Fig. 11) due to the prevalence of easterly winds (Fig. 7), confirming previous results (Chen and Zhai, 2006; Otuka et al., 2014). The short-range movements observed in the Mekong and SE Vietnam (Fig. 11) are not maladaptive in this case, as these regions have year-round rice-growing with 2-3 harvests per year (Sakamoto et al., 2006), so long-range movements to track seasonally available resources are not necessary. The lack of selection pressure has resulted in much shorter migration distances in tropical populations (Riley et al., 1987) than typically seen in populations which expand into temperature areas. This difference is partly caused by shorter ‘migratory windows’ (i.e. shorter pre-reproductive periods) and lower migratory tendencies in response to starvation in tropical populations (Wada et al., 2007, 2008), and partly due to less favourable winds.

In summary, our analyses confirm the importance of NCV as both the source of migrants colonizing southern China each spring and the destination of return migrants leaving southern China each autumn. The 3-month winter break in rice cropping in this region leads to a mid-winter population crash here, but this important region is recolonized during February-March by immigrants from central Indochina, particularly from rice-growing regions of NE Thailand and S Laos. The winter fallow period in NCV does not break the RPH annual migratory loop, due to the high mobility and rapid development of RPHs. However, the absence of suitable habitat and hosts probably does lead to crashes in the local populations of natural enemies over the winter (Schonely et al., 2010; Wada, 2015), which will lead to higher population growth among RPHs when they recolonize NCV in the early-spring, with knock-on effects on the size of immigrant populations reaching southern China. Thus winter rice fallows in NCV, which are designed to reduce local RPH population densities (Dyck et al., 1979; Nozaki et al. 1984), may have the opposite effect. Prediction of outbreaks of migratory pests such as RPHs, which are too small to be directly tracked and are strongly influenced by weather conditions, remains challenging. Further work is required to fully understand the biometeorological aspects of small insect pest movements; long-term radar monitoring to quantify the numbers of migrants, using both special-purpose entomological radars (Chapman et al., 2011a) and continental-scale networks of weather radars (Bauer et al., 2017), in combination with atmospheric trajectory analyses and traditional field monitoring of populations, would increase our predictive abilities in relation to migratory pests.

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Appendix A. Supplementary Data

Supplementary data associated with this article can be found, in the online version, at http://.....

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Figure legends

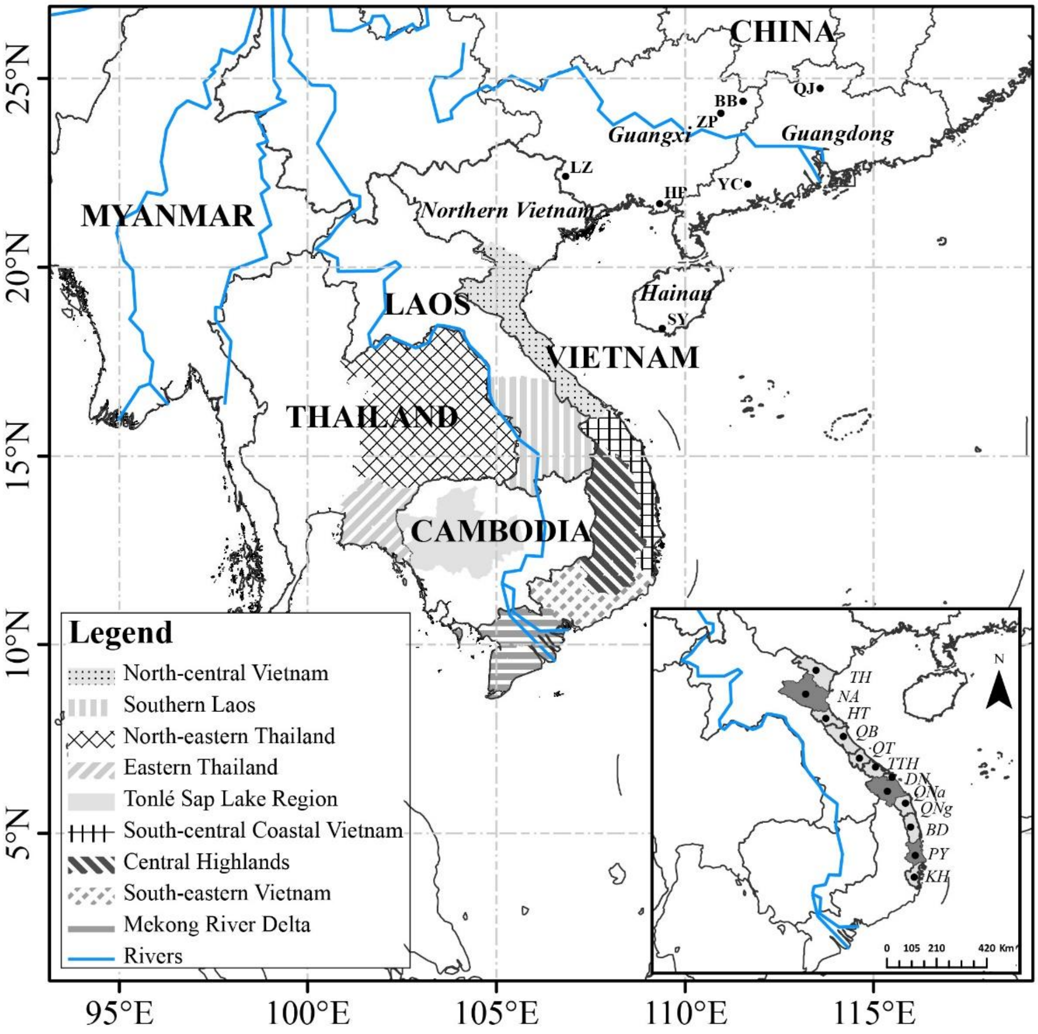


Fig. 1. Locations of winter rice-growing regions in Indochina and provinces of southern China discussed in the text, and, in the inset, the field survey sites in north-central Vietnam (NCV) and south-central coastal Vietnam (SCV). In October of 2004-2013, light traps in southern China were routinely operated at seven sites: Qujiang (QJ) and Yangchun (YC) in Guangdong Province; Babu (BB), Hepu (HP), Longzhou (LZ) and Zhaoping (ZP) in Guangxi Province; and Sanya (SY) in Hainan Province. During 2011-2013, field surveys of RPH infestation levels were conducted at 6 sites in NCV: Thanh Hóa (TH), Nghệ An (NA), Hà Tĩnh (HT), Quảng Bình (QB), Quảng Trị (QT) and Thừa Thiên-Huế (THH); and 6 sites in SCV: Đà Nẵng (DN),

Quảng Nam (QNa), Quảng Ngãi (QNg), Bình Định (BD), Phú Yên (PY) and Khánh Hòa (KH). Three of these sites (NA, QNa and PY, highlighted in darker grey) were locations where light traps were also run in 2010.

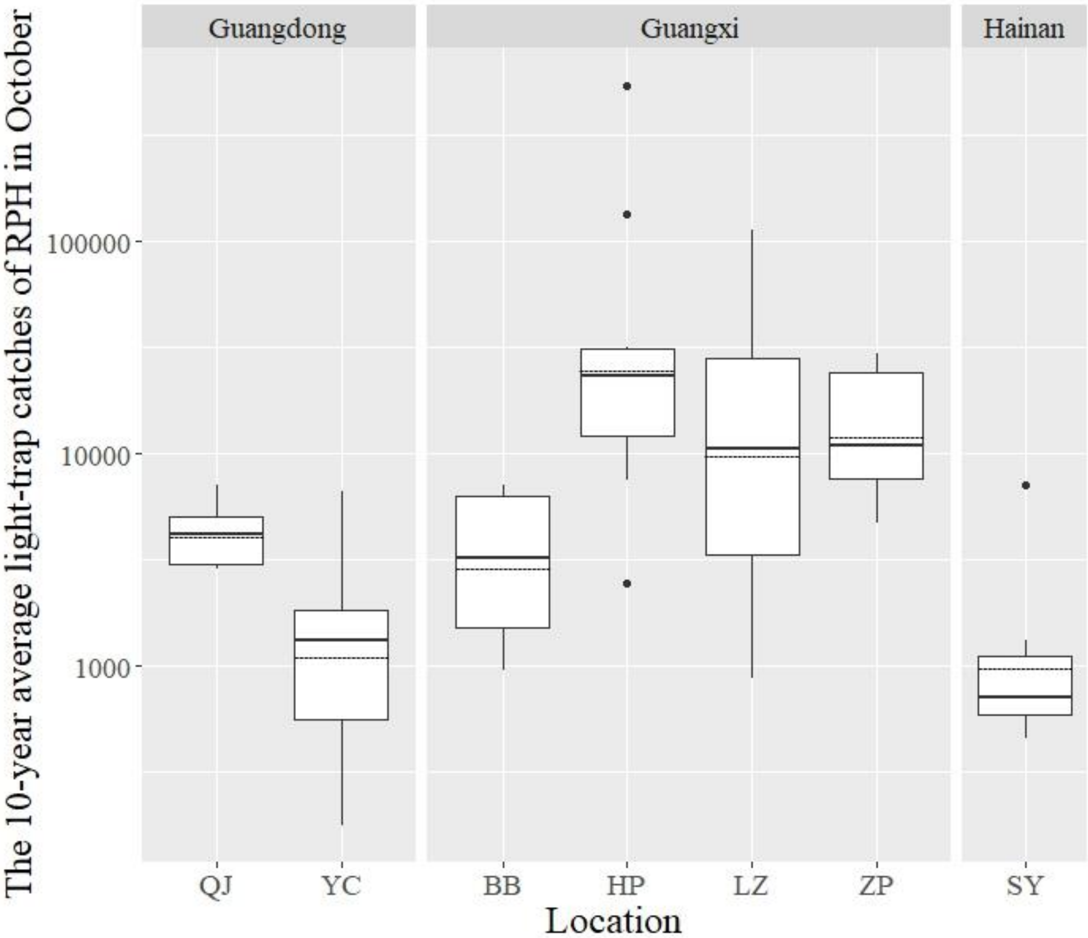


Fig. 2. Mean monthly light-trap catches of RPH during October of 2004-2013 at seven locations in three southern Chinese provinces. The bottom and top of the box indicate the lower and upper quartile values, respectively. The horizonal solid black line shows the median for each location, and the black dashed line represents the mean. Whiskers indicate the 5th and 95th percentiles, while the black circle represents the outlier. (See Fig. 1 for station names and locations.)

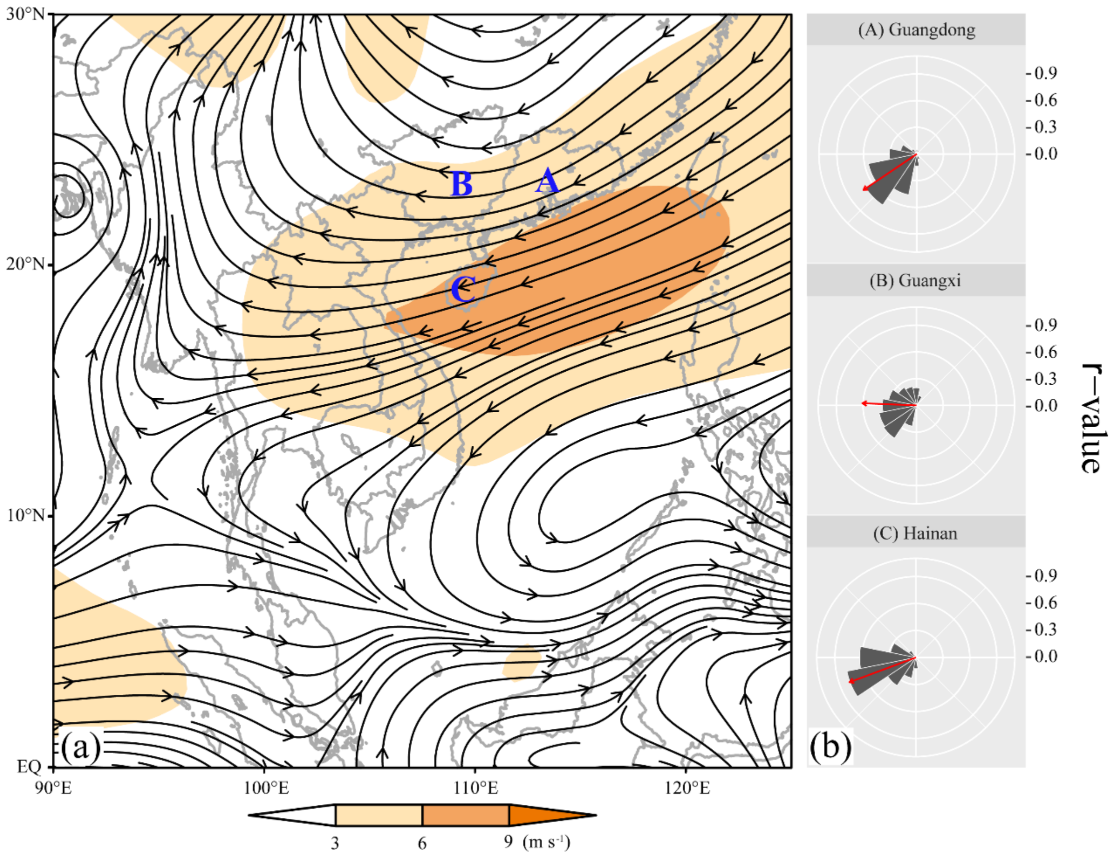


Fig. 3. (Left) The 10-year mean synoptic wind conditions at 850 hPa for October of 2004-2013 over southern China and Indochina. The colour scale shows the mean wind speed in m s^{-1}. (Right) Circular histograms of downwind directions at 850 hPa during October 2004 to 2013 for the southern Chinese provinces of (A) Guangdong, (B) Guangxi and (C) Hainan. (For easy comparison with insect displacements, the *downwind* direction is shown rather than the (conventional) direction from which the wind is blowing). The area of the dark grey segments is proportional to the number of occasions when downwind directions fell within each 22.5° sector. The bearing of the red arrow indicates the mean downwind direction, while its length is proportional to the clustering of the dataset around the mean direction (the 'r-value' shown on the y-axis).

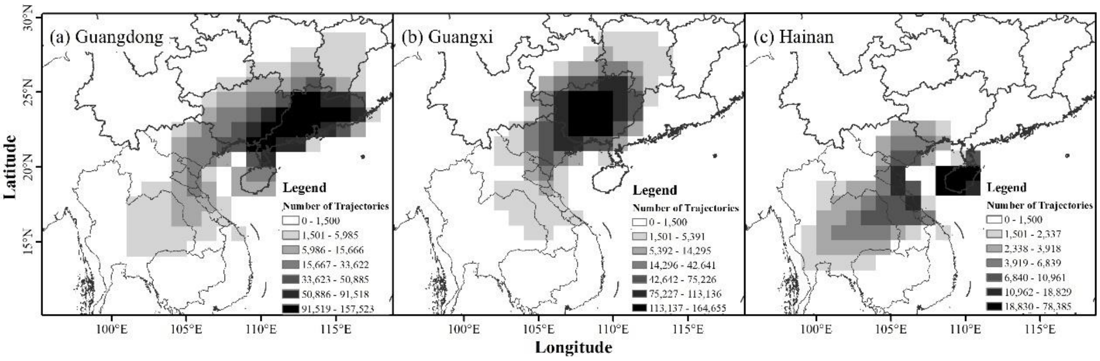


Fig. 4. The number of forward trajectory pathways starting from the southern Chinese provinces of (a) Guangdong, (b) Guangxi and (c) Hainan which crossed every 100 x 100 km grid cell in the region. Trajectories were run for every night in October of the 10 years 2004-2013.

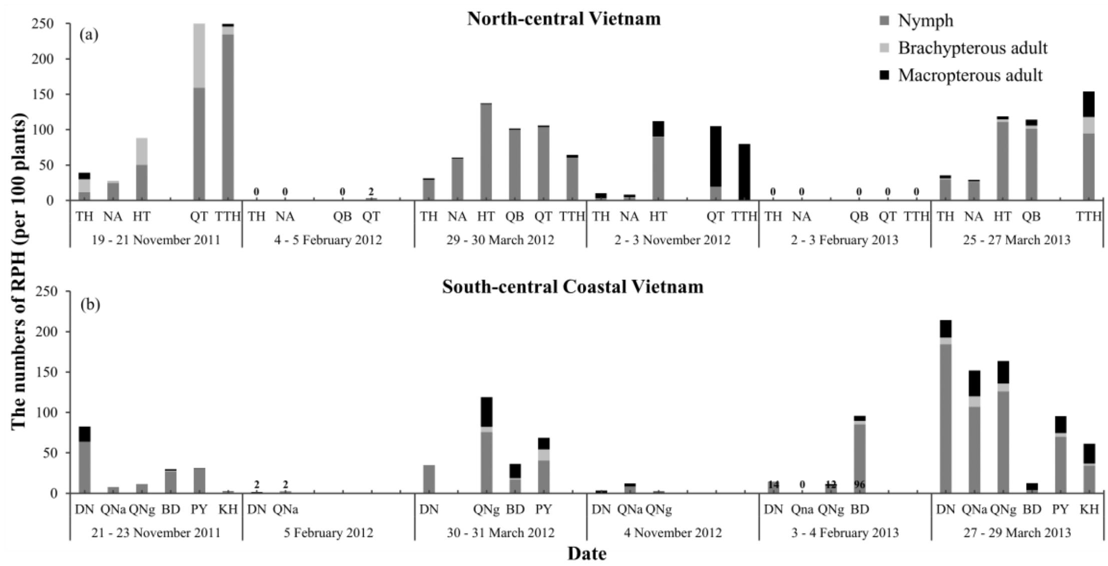


Fig. 5. Population densities of RPH estimated during field surveys in (a) north-central Vietnam (NCV) and (b) south-central coastal Vietnam (SCV). Site codes are the same as in Fig. 1.

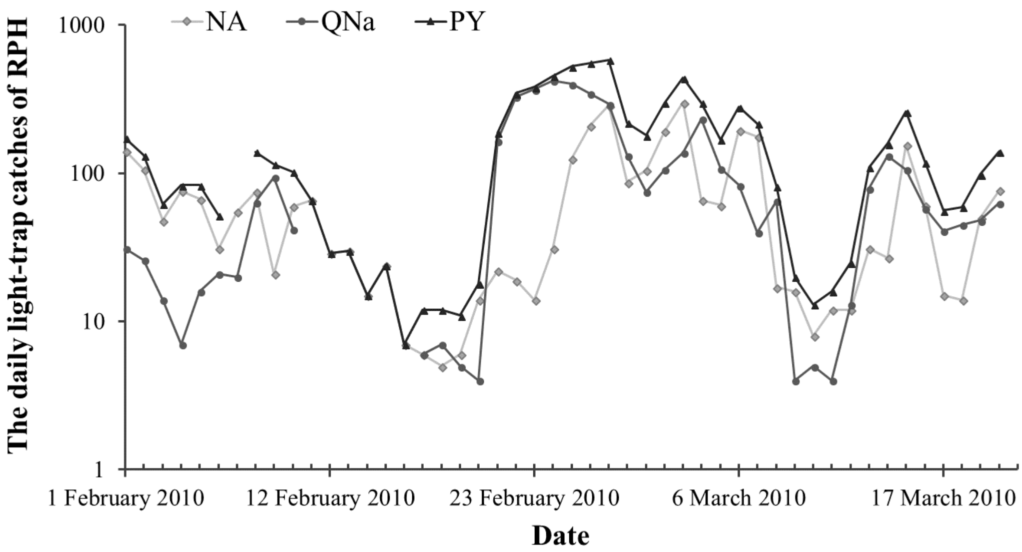


Fig. 6. The daily light trap catches of RPH at Nghệ An (NA) in the NCV region, and at Quảng Nam (QNa) and PhúYên (PY) from the SCV region, during February to March 2010. Correlations between these datasets are shown in Fig. S2.

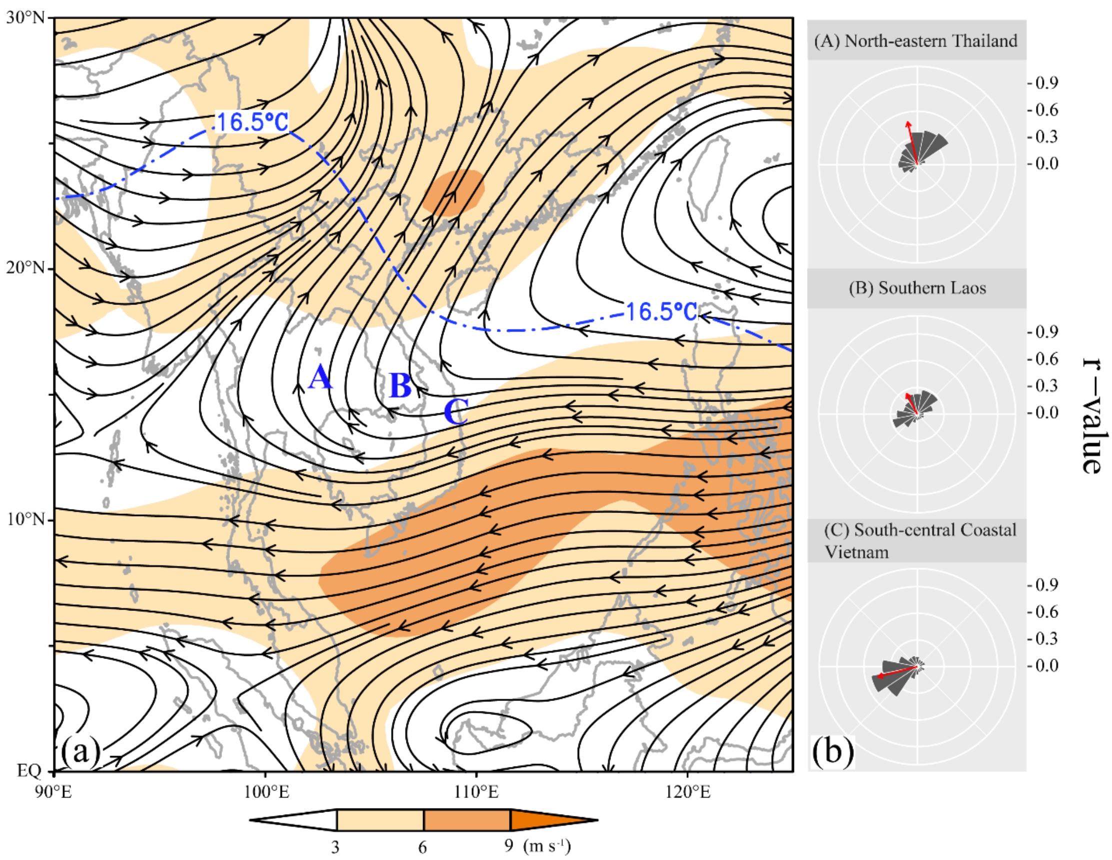
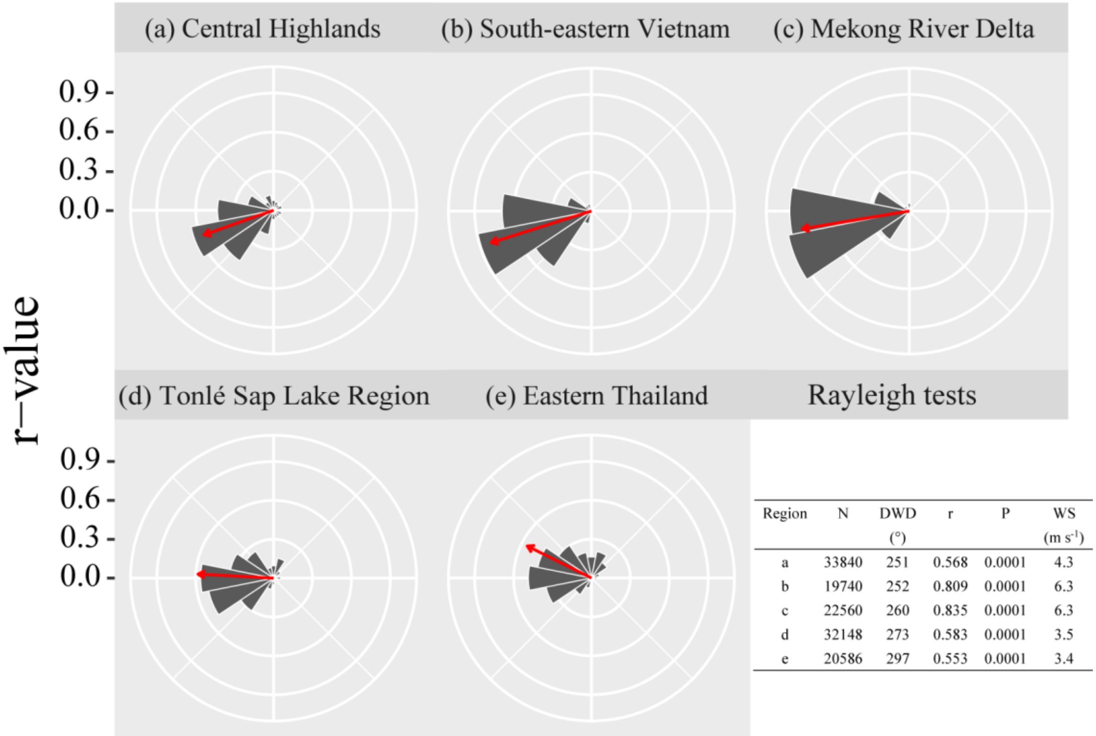


Fig. 7. (Left) The 10-year mean synoptic wind conditions at 850 hPa for 21 February to 20 March of 2005–2014 over southern China and Indochina. The colour scale shows the mean wind speed in m s^{-1}. The 16.5°C isotherm for the period 21 February to 20 March of 2005–2014 is also plotted. (Right) Circular histograms of downwind directions at 850 hPa during 21 February to 20 March of 2005–2014 for the 3 central Indochinese rice-growing regions of (A) NE Thailand, (B) S Laos and (C) SCV. (For easy comparison with insect displacements, the *downwind* direction is shown rather than the (conventional) direction from which the wind is blowing). See Fig. 3 for a description of the circular plots.



Region	N	DWD (°)	r	P	WS ($m\ s^{-1}$)
a	33840	251	0.568	0.0001	4.3
b	19740	252	0.809	0.0001	6.3
c	22560	260	0.835	0.0001	6.3
d	32148	273	0.583	0.0001	3.5
e	20586	297	0.553	0.0001	3.4

Fig. 8. Circular histograms of downwind directions at 850 hPa during 21 February to 20 March of 2005–2014 for the 5 Indochinese winter rice-growing regions which were not potential source areas for the recolonization of NVC. (For easy comparison with insect displacements, the *downwind* direction is shown rather than the (conventional) direction from which the wind is blowing). See Fig. 3 for a description of the circular plots.

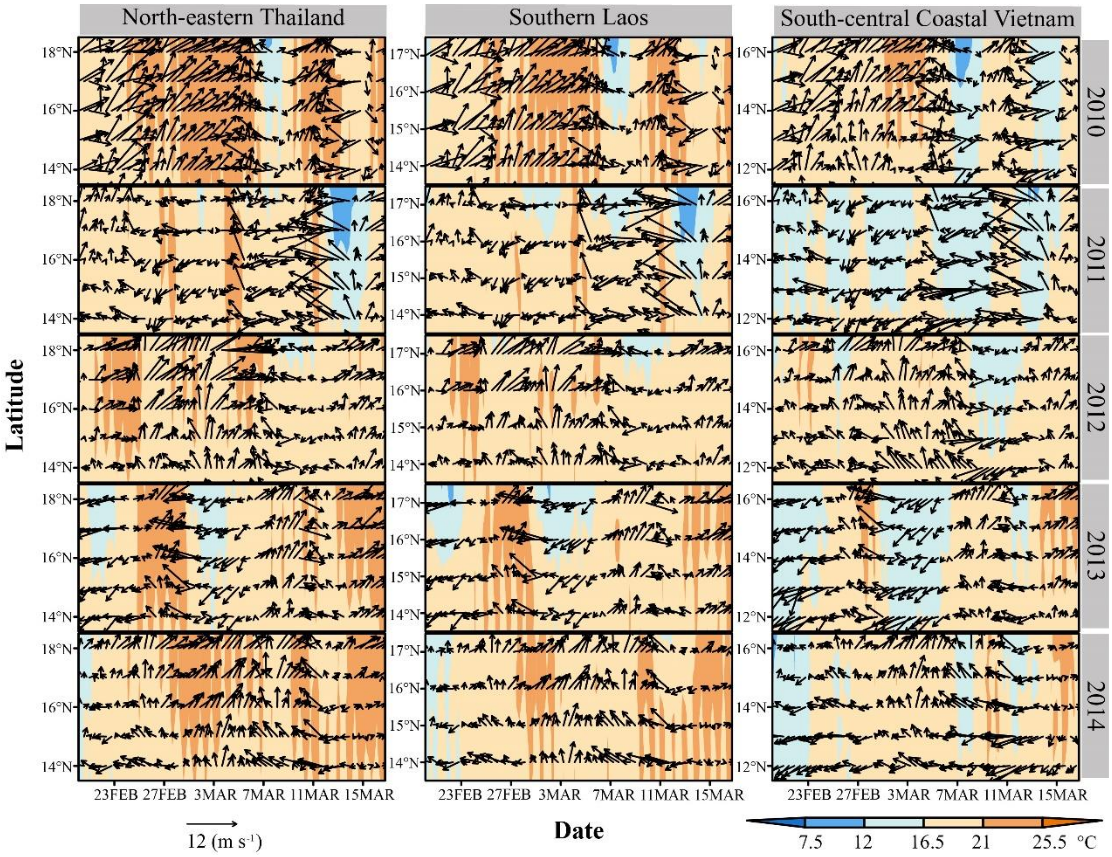


Fig. 9. Twice daily wind vectors and air temperatures for 5 example years at 850 hPa above the three main source regions for the recolonization of NCV during 21 February to 20 March. The arrows show wind directions, with the length of the arrow proportional to the wind strength; while the background is colour coded for the air temperature.

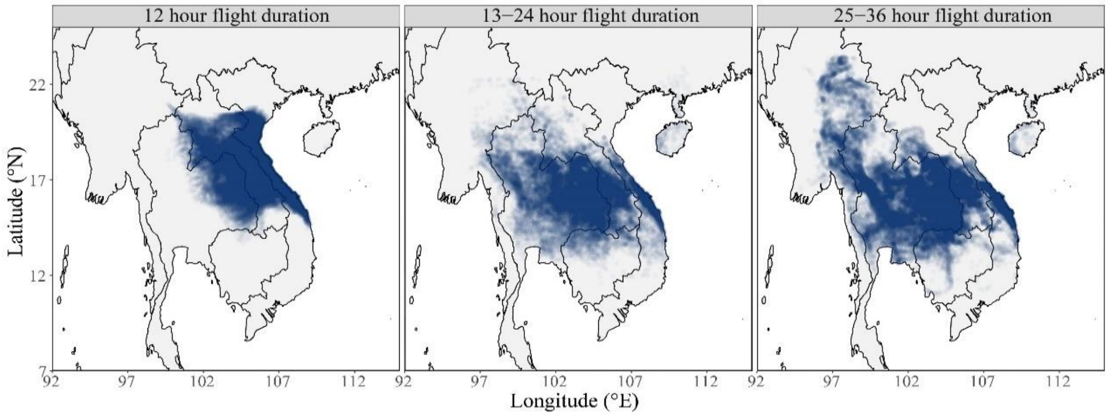


Fig. 10. Endpoints of backward trajectories (i.e. the potential start points of migrations) from NCV during every night of 21 February to 20 March of 2005–2014 for maximum flight durations of 12 hours, 24 hours and 36 hours. The more intense the blue colour, the greater the density of endpoints at any location.

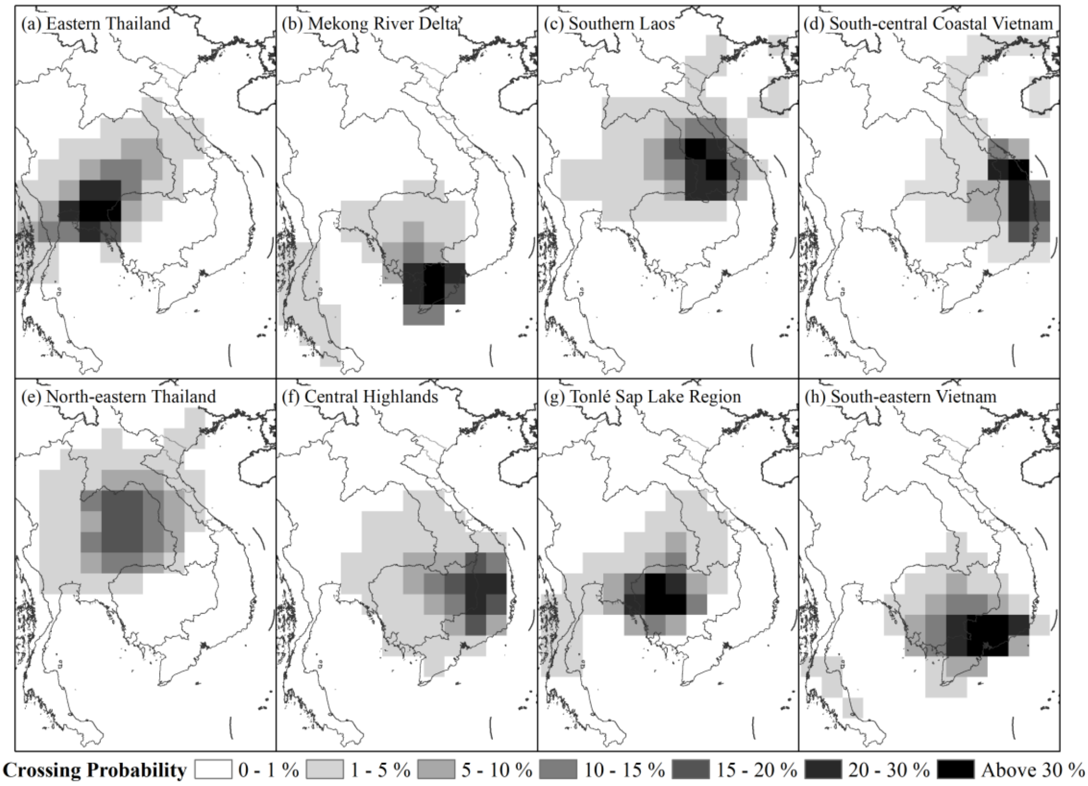


Fig. 11. The proportion of forward trajectory pathways starting from each of the 8 winter rice-growing regions of Indochina which crossed every 100 x 100 km grid cell in the region. Trajectories were run for every night during 21 February to 20 March of the 10 years 2005–2014. The start points of the trajectories are shown in Fig. S1.

APPENDIX A.

SUPPLEMENTAL MATERIAL

Table S1. Parameters of the WRF (Weather Research and Forecasting) model used for calculating RPH migration trajectories.

Item	Simulated domain
Location	10°N / 20°N, 105°E
The number of grid points	100*98
Distance (km) between grid points	30
Layers	27
Map projection	Mercator / Lambert
Microphysics scheme	WSM3
Longwave radiation scheme	RRTM
Shortwave radiation scheme	Dudhia
Surface layer scheme	Revised MM5 Monin-Obukhov
Land/water surface scheme	Noah
Planetary boundary layer scheme	YSU
Cumulus parameterization	Kain-Fritsch (new Eta)
Turbulence and mixing option	Simple diffusion
Eddy coefficient option	2d Deformation
Simulated time	Every 72h

MM5 is short for the Fifth-Generation Penn State/NCAR Mesoscale Model.

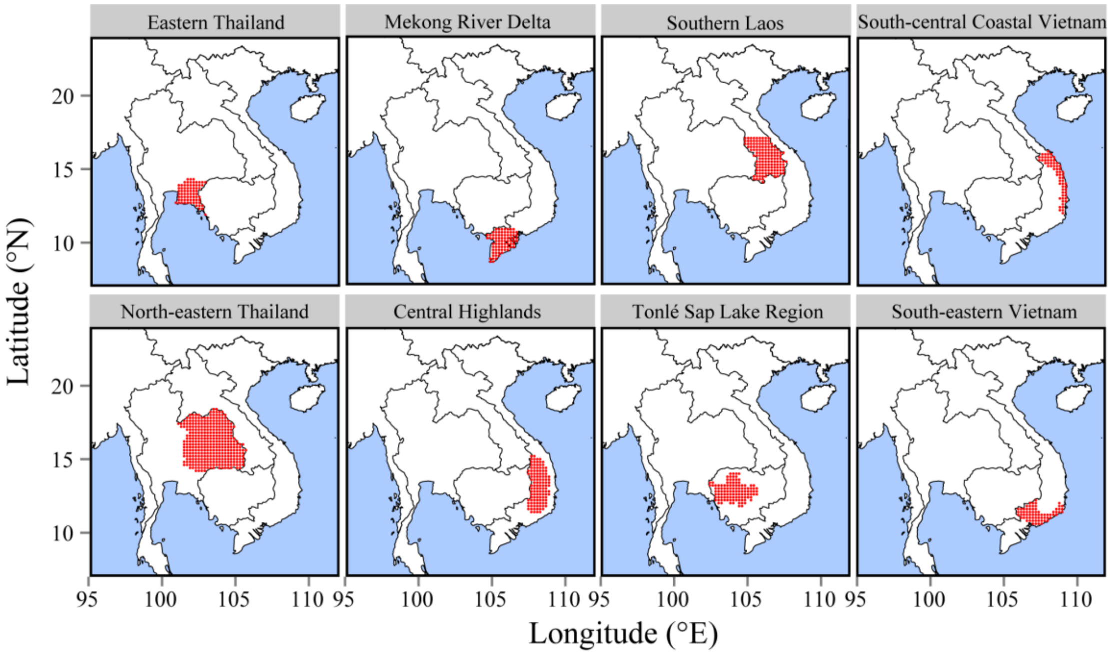


Fig. S1. Start points of forward trajectories from the 8 winter rice-growing regions of Indochina. The red points represent the 0.2° by 0.2° grid point location of each start point: 139 sites in southern Laos, 62 in south-central coastal Vietnam, 120 in Central Highlands, 70 in south-eastern Vietnam, 80 in Mekong River Delta, 73 in eastern Thailand, 355 in north-eastern Thailand, and 114 in Tonlé Sap Lake Region of Cambodia.

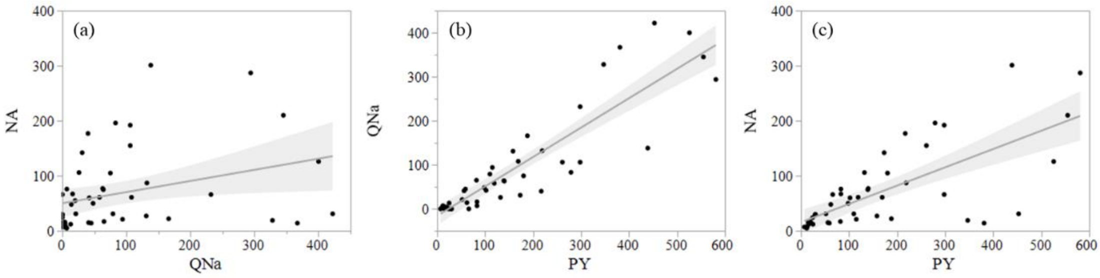


Fig. S2. The relationships between daily light-trap catches of RPH among three locations. Pearson correlation analysis indicated a significant positive correlation among the light-trap catches in these regions (NA and QN: N = 47, $r^2 = 0.104$, P = 0.025; NA and PY N = 46, $r^2 =$ 0.502, P < 0.0001; QN and PY: N = 47, $r^2 = 0.803$, P < 0.0001.)

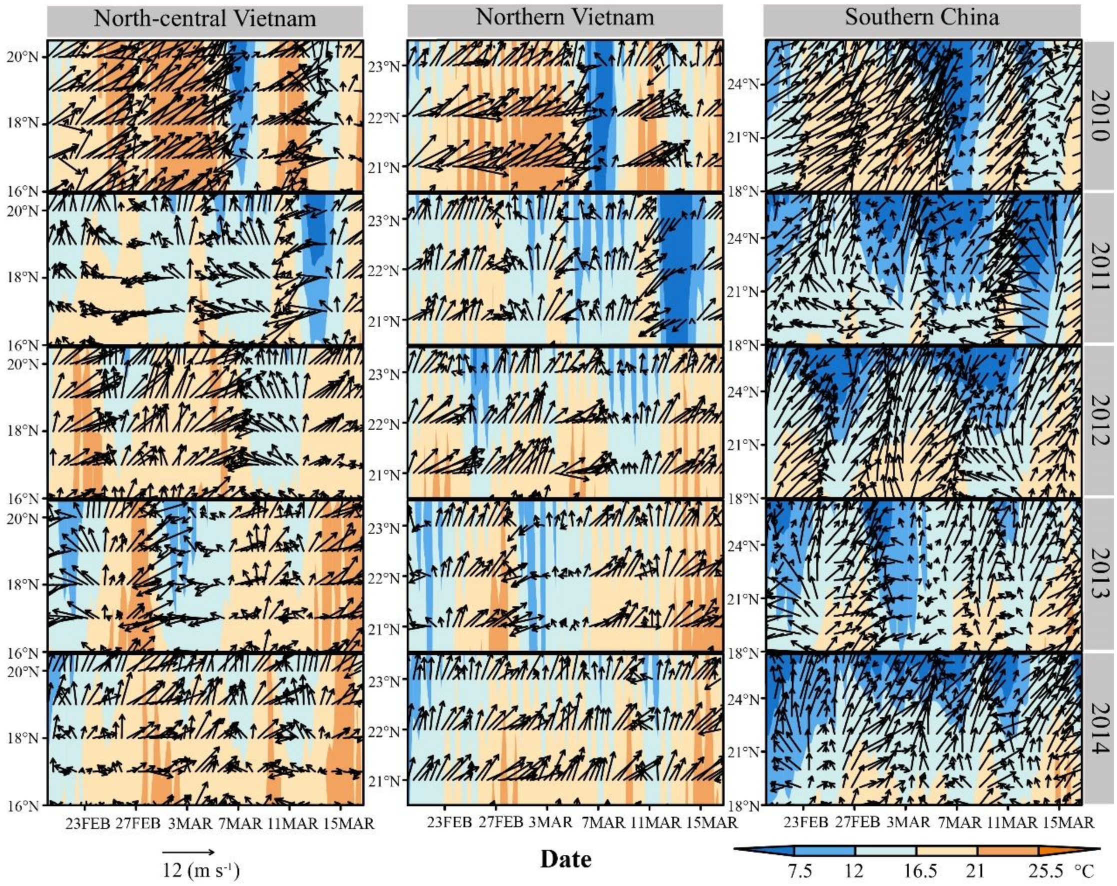


Fig. S3. Twice daily wind vectors and air temperatures for 5 example years at 850 hPa above NCV, northern Vietnam and southern China during 21 February to 20 March. The arrows show wind directions, with the length of the arrow proportional to the wind strength; while the background is colour coded for the air temperature.

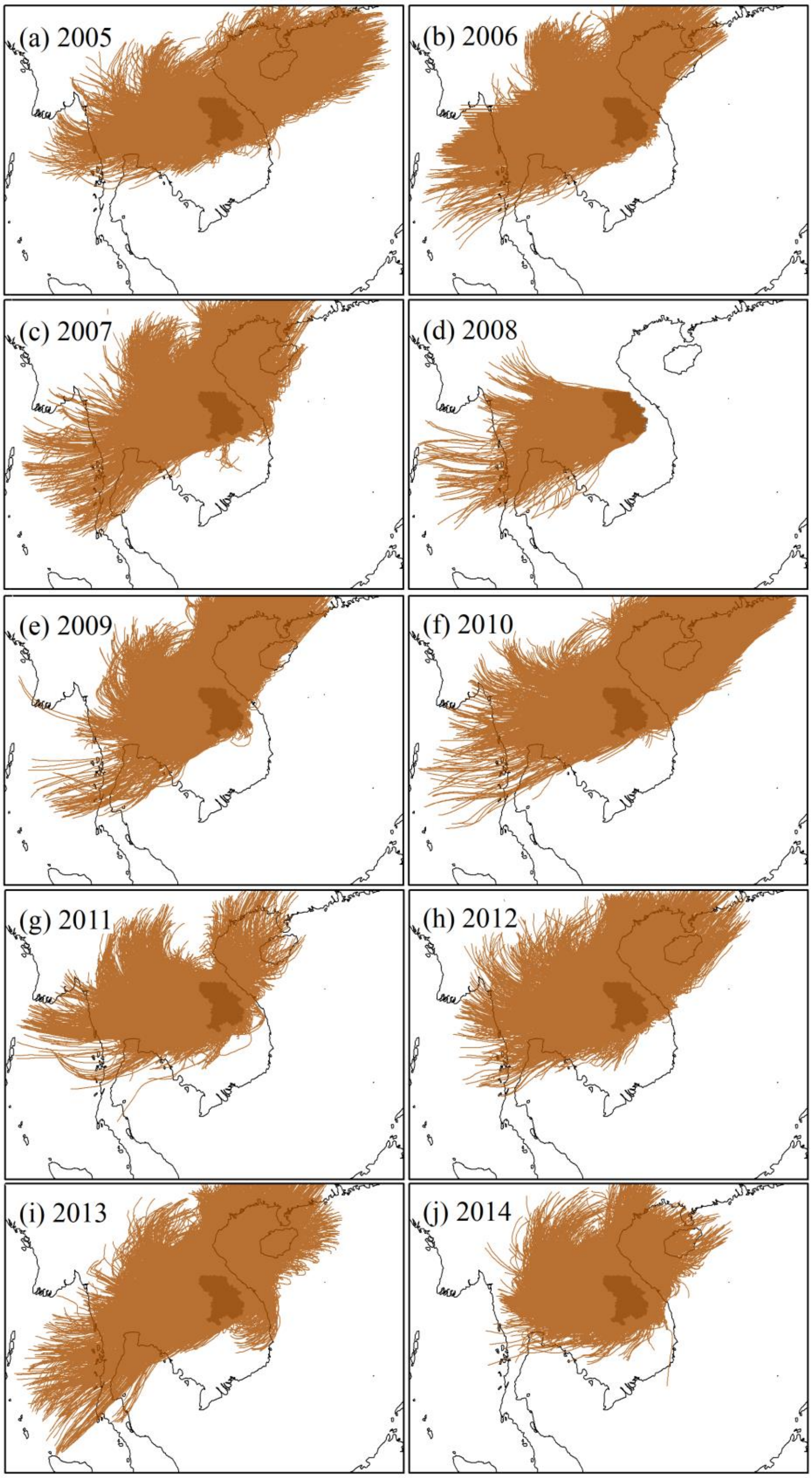


Fig. S4. All forward trajectories from 20 February to 21 March of the 10-year period 2005–2014 that departed from S Laos.

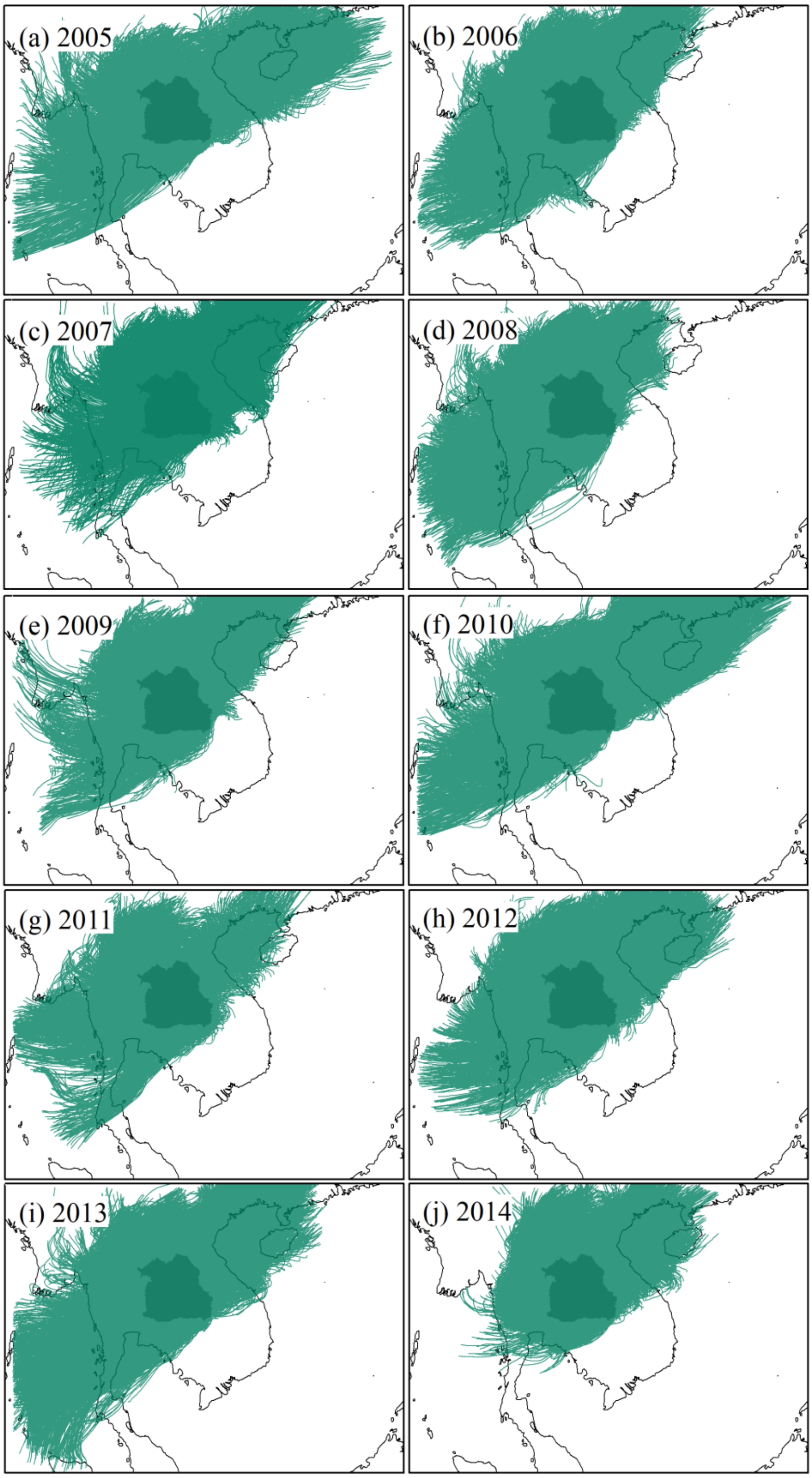


Fig. S5. All forward trajectories from 20 February to 21 March of the 10-year period 2005–2014 that departed from NE Thailand.

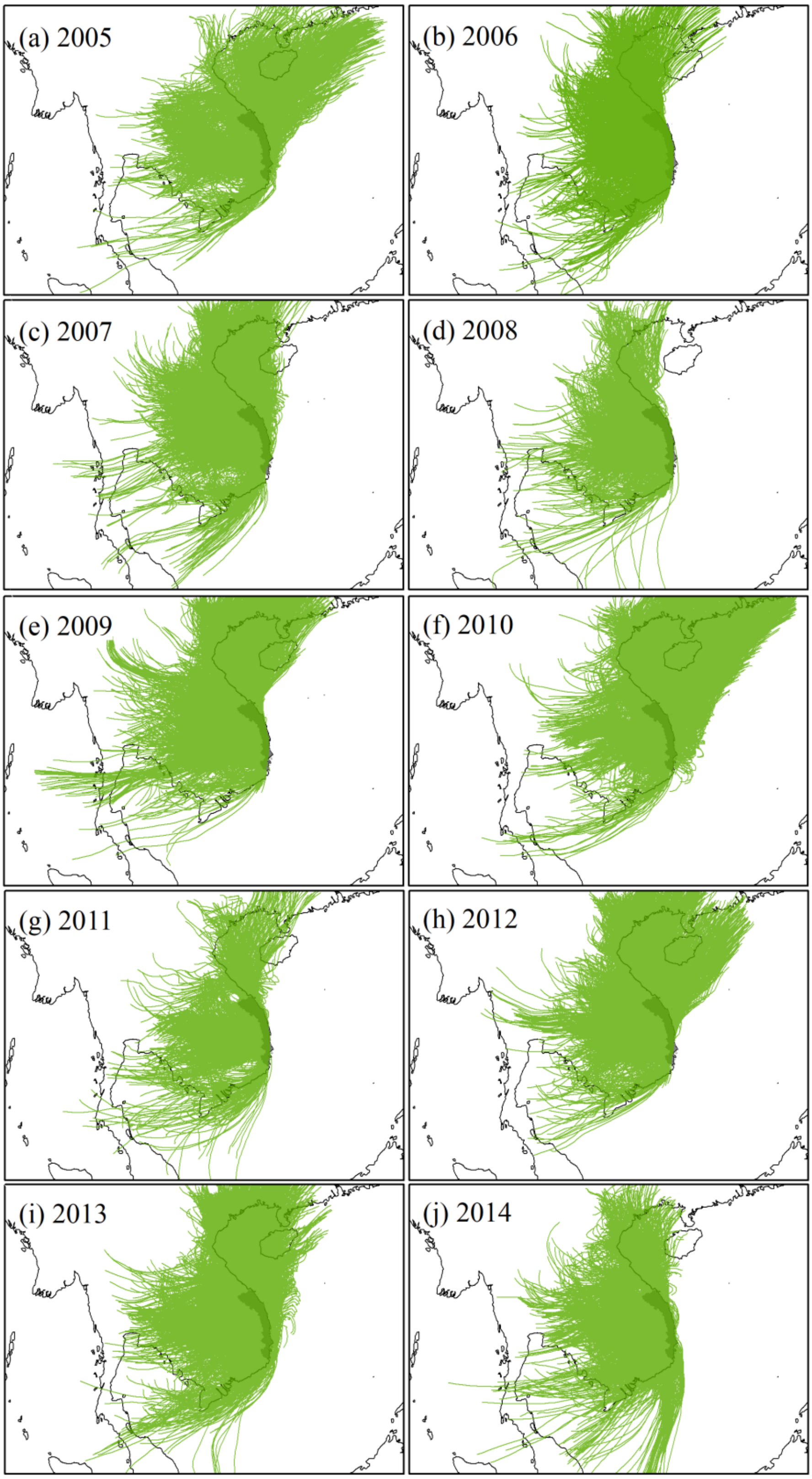


Fig. S6. All forward trajectories from 20 February to 21 March of the 10-year period 2005–2014 that departed from SCV.

Plate S1. The harvested rice paddy fields at northern Thanh Hóa (TH) in NCV on 19 November 2011.

Plate S2. The rice stubble, ratoon rice and self-seeding rice from fallen grain at northern Nghệ An (NA) in NCV on 20 November 2011.

Plate S3. The ploughed rice paddy fields at southern Hà Tĩnh (HT) in NCV on 20 November 2011.

Plate S4. The transplanting of rice at Thanh Hóa (TH) in NCV on 4 February 2012.

Plate S5. The rice plants at yellow ripe stage at Thanh Hóa (TH) in NCV on 3 November 2012.