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The East Asian Insect Flyway: Geographical and Climatic Factors Driving Migration Among Diverse Crop Pests

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Abstract

The East Asian Insect Flyway is a globally important migration route stretching from the Indochina Peninsula and the Philippines through East China to Northeast China and northern Japan, although most migrants utilize only part of the flyway. In this review, we focus on long-range windborne migrations of lepidopteran and planthopper pests. We outline the environment in which migrations occur, with emphasis on the seasonal atmospheric circulations that influence the transporting wind systems. Northward movement in spring is facilitated by favorable prevailing winds, allowing migrants to colonize vast areas of East Asia. Migrants may be subject to contemporary natural selection for long flights as succeeding generations progressively advance northward. Overshooting into far northern areas from which there is little chance of return seems common in planthoppers. Moths are less profligate and have evolved complex flight behaviors that can facilitate southward transport in autumn, although timely spells of favorable winds may not occur in some years.

INTRODUCTION

Every spring in the Northern Hemisphere, trillions of insects migrate to higher latitudes, expanding their range northward from overwintering areas to colonize temporary summer breeding grounds (11, 37, 48, 58, 109). These migrations involve a wide variety of species and are predominantly windborne, taking place hundreds of meters above ground and assisted by favorable large-scale seasonal airflows (26, 104). At the end of summer, the migrants' ranges contract southward again as temperatures at higher latitudes fall and the growing season comes to an end. Seasonal insect migrations of this type have been documented in North America (128); Europe and the Middle East (40, 48, 53); and, particularly, East Asia (30–34, 37, 58, 74, 92, 133). In the latter region, the East Asian monsoon system (1, 21, 59) facilitates windborne movements of insects northward in spring and, to a lesser extent, southward at the end of summer, along what we refer to below as the East Asian Insect Flyway (EAIF). The EAIF covers a vast region, ranging in latitude from Mainland Southeast Asia and the Philippines in the south, through East China and adjacent parts of Mongolia, to the Russian Far East and Japan in the north (**Figure 1**), constituting the most extensive area of intensive agriculture on Earth. Many of the species undertaking these migrations are pests, and consequently, these poleward and return bioflows are of the greatest economic and societal importance, directly impacting the food security and health of the >2 billion people that reside in this region (38, 41, 63, 135).

East Asian Insect Flyway (EAIF): geographical corridor from Indochina to Northeast Asia along which many migrant insects move

Due to a happenstance of suitable seasonal climates, favorable wind regimes, and abundant and varied food resources, the EAIF exceeds all other insect flyways in terms of the diversity, abundance, and biomass of migrants transferred. For example, a searchlight trap situated on Beihuang Island in the Bohai Sea, North China, caught 119 species of larger nocturnal migrants (79% of which were Lepidoptera) during a 15-year period, the majority being pest species (38). The addition of smaller species (e.g., aphids, parasitoid wasps, tiny Diptera, many beetle families) and day-active species (e.g., butterflies) not routinely sampled or processed in light-trap catches, plus species largely restricted to the south of the region (e.g., many rice pests), would likely increase the list of regular migrants to >200 species. The migrants include beneficial biocontrol agents

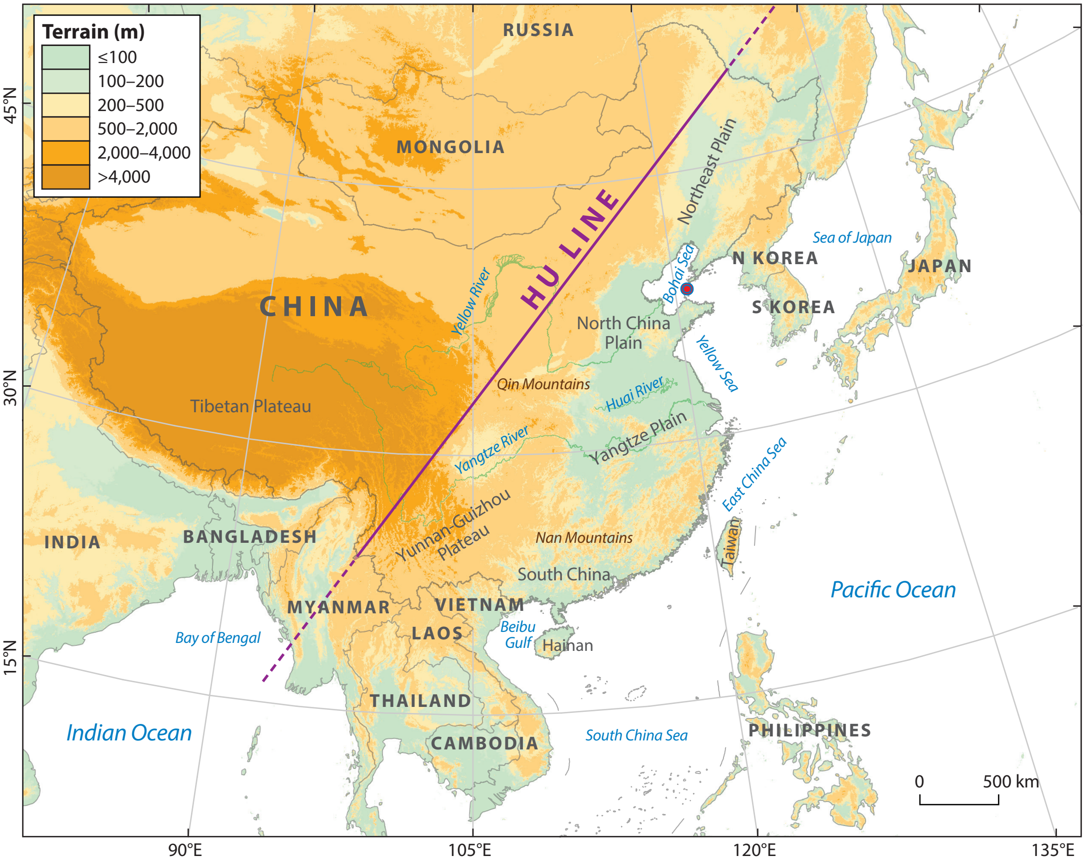

Figure 1

Map of the East Asian Insect Flyway (EAIF) migration arena showing features discussed in the text and the Hu Line (*purple*). The location of Beihuang Island (*red dot*) at the entrance to the Bohai Sea is indicated.

and pollinators (32, 60), but the great majority are serious agricultural pests or disease vectors (38, 63, 135, 151). According to the National Agro-Technical Extension and Service Centre of China, the seven most important groups of crop pests in that country are all long-range migrants (63). These are (*a*) the migratory locust (*Locusta migratoria*), (*b*) cereal aphids (three species), (*c*) rice planthoppers (RPHs) (three species), (*d*) the rice leafroller (RLR) (*Cnaphalocrocis medinalis*), (*e*) the beet webworm (*Loxostege sticticalis*), (*f*) the Oriental armyworm (OAW) (*Mythimna separata*), and (*g*) the invasive fall armyworm (FAW) (*Spodoptera frugiperda*) (see **Supplemental Table 1**). Cumulatively, these pests inflict a yield loss of >6 million tons each year in China alone, leading to East Asia suffering among the highest crop losses across the globe and being the largest consumer of pesticides (63, 135). Although there has been a long history of research projects on migratory pests, dating back to the 1960s in China and Japan (2, 72) (see **Supplemental References**), the EAIF has not previously been examined as an integral phenomenon. In this review, by focusing on a few key pest species, we examine this system from the perspective of integrative biology, linking the geographic and climatic bases of the flyway to the migratory adaptations of the various species and drawing on diverse disciplines ranging from genetics to behavior to biometeorology.

Supplemental Material >

Rice planthoppers (RPHs): three species of planthopper in the family Delphacidae (brown planthopper, white-backed planthopper, and small brown planthopper), which are important migratory pests of rice crops

MIGRATION FLYWAYS AND ARENAS

Migration Flyways

Flyways are geographical corridors along which migrating species of animals move. The concept is usually applied to bird migrants (5, 141) and occasionally to butterflies such as the monarch butterfly, *Danaus plexippus* (43). The most relevant bird flyway for this review is the East Asian-Australasian Flyway (110, 141), which partially overlaps with the EAIF. The EAIF is less extensive than the bird flyway, as it does not extend northward much beyond 50°N (Northeast China) or southward much beyond 10°N (mainland Southeast Asia and the Philippines) (**Figure 1**). A key difference between characterizations of flyways for birds and those for insects arises because generation times of insect migrants are nearly always shorter than the annual cycle. Therefore, in contrast to the seasonal to-and-fro movements of individual birds, individual insects will complete only part of each circuit; i.e., migratory circuits are multigenerational in most insect species (11, 22, 25, 37). The flyway concept is a means of integrating knowledge of disparate migration systems, and in the case of birds, the cross-border perspective helps promote cooperation to conserve migrant populations across the several countries within the flyway. For insects migrating along the EAIF, the integrative approach will be mostly concerned with improving the effectiveness of pest forecasting and management, including recognition that pest populations are not confined by international borders (38, 63, 92, 135).

East Asian-Australasian Flyway: flyway for hundreds of species of migratory birds between Arctic Russia and Alaska at one extreme and Australasia at the other

Migration arena: the region over which migratory flights of the various species occur and in which habitats exploited by the migrants are located

Hu Line: an imaginary line between Heihe city on the northeast border of China and Tengchong on the southwest border, splitting the country into western and eastern regions

The East Asian Migration Flyway and Its Arena

The primary geographical features defining the flyway's migration arena are the high mountainous regions to the west and the East Asian coastline to the east (**Figure 1**). From 10°N (southern Vietnam) to 50°N (Heilongjiang Province, Northeast China), a belt of highly fertile land extends inland from the mainland coastline for hundreds of kilometers, forming an axis running southwest to northeast, corresponding to the direction of movement of the East Asian monsoon, described below. The coastline exhibits two major indentations, due to the South China Sea and Beibu Gulf in the south and the Yellow Sea and Bohai Sea in the north, and one major projection, the Korean peninsula. Three major offshore island groups—the Philippines, Taiwan, and Japan—extend the border of the flyway's migration arena eastward, as insects frequently migrate between them and the mainland across hundreds of kilometers of ocean. While many areas are hilly, there are few elevations above 1,500 m (**Figure 1**). On the Asian mainland, there are four extensive low-elevation areas important for crop production: (*a*) the lowlands of Thailand, Cambodia, and southern Vietnam; (*b*) the river deltas of northern Vietnam and South China; (*c*) the Yangtze Plain and adjacent North China Plain; and (*d*) the Northeast Plain (**Figure 1**). To the west, rising terrain, drier climates, and the associated transition from cropping to pastoralism provide an imprecisely defined western border to the flyway, corresponding approximately to the Hu Line (**Figure 1**) demarcating the boundary between humid and arid climates in China (145). The area east of the Hu Line contains 43% of China's land area but 96% of its human population. The arena axis is approximately 4,000 km long; its width on the Asian mainland varies between 500 and 1,000 km.

Arena climates become progressively cooler with increasing latitude, from (*a*) tropical savannah with wet and dry seasons in Indochina and the Philippines; to (*b*) temperate regions with a hot summer, and either no dry season or a dry winter, in southern and central China and southern Japan; to (*c*) cold regions with a hot summer and dry winter in the Northeast Plain, most of the Korean Peninsula, and northern Japan (4). Other forms of cold climate are found on much of the western flank, although in the warmer, lower-latitude regions of South China and Indochina, the inland boundary is less defined as temperate and savannah climates (respectively) extend westward. Easterly trade and westerly monsoon winds predominate in southern Indochina (133)

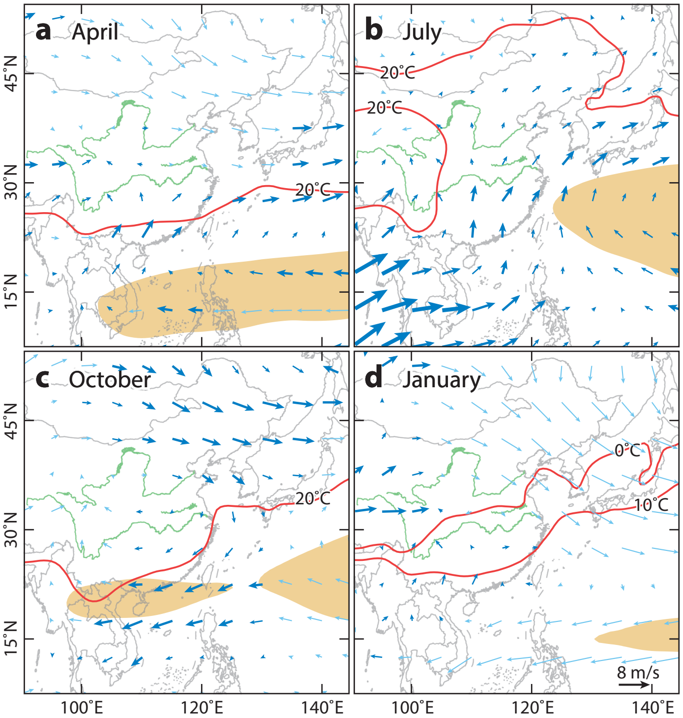

Figure 2

Seasonal synoptic weather conditions in the East Asian Insect Flyway (EAIF). Air temperature isotherms at 2 m above ground (*red lines*) and average monthly downwind directions at the 850 hPa level are shown for each season; downwind directions that are seasonally favorable for wind-assisted migration (*dark blue arrows*) are separated from unfavorably directed winds (*light blue arrows*). In (*a*) spring and (*b*) summer, southwesterly winds prevail in the southern part of the flyway and expand northward over time, while temperatures rise and the Western Pacific Subtropical High (WPSH) (*beige regions*) advances northward. (*c*) In autumn, the prevailing winds along the EAIF become more northerly as temperatures fall and the WPSH retreats. (*d*) In winter, the temperate and subtropical regions are too cold for most migratory insects to survive. All long-term monthly means are derived from a 30-year data set (1991–2020) of NCEP-DOE Reanalysis II (**https://psl.noaa.gov/**).

(**Figure 2**), reducing opportunities for northward transport in spring from south of 15°N. The cold winters in China (except the far south), Korea, and Japan (**Figure 2**) generally preclude overwintering for most migratory pests, while high temperatures, good rains, and extensive areas of crops make these same areas highly favorable for summer breeding.

Winds and precipitation within the arena are influenced by three major factors: (*a*) the Tibetan Plateau, which diverts westerly airflows to its north or south; (*b*) the Western Pacific Subtropical High (WPSH), which produces favorable tailwinds along the flyway axis in spring and summer (52, 78) (**Figure 2**); and (*c*) the Siberian Anticyclone, which produces northerly winds over East Asia from late autumn onward (21). These factors combine to produce not only a tropical monsoon, bringing heavy rains to Indochina from May to October, but also a subtropical monsoon, a phenomenon unique to this region. The subtropical monsoon occurs as a frontal band of heavy rainfall, locally called Meiyu in China, Baiu in Japan, and Changma in Korea, located across first South China (May–June), then the Yangtze Plain and Japan (June–July), and finally the North China Plain and Korea (July), remaining stationary at one latitude for a few weeks before rapidly

Western Pacific Subtropical High (WPSH): a persistent anticyclone situated on the eastern flank of East Asia, which moves northward as the summer progresses, bringing summer monsoon rains to East Asia moving to the next. The large-scale circulation systems produce persistent warm and moist southwesterly airflows from the Indian Ocean and southeasterly airflows from the Pacific, both of which bring moisture-laden air to the rain front, the longitude of which is controlled by the position of the WPSH (21, 52, 78). These flows do not persist into autumn, when rainfall occurs more generally as the cool continental air advances southward, and typhoons develop in the South China Sea and adjacent low-latitude regions of the Pacific Ocean. Variability in the intensity and timing of these monsoons, recent and future changes due to climate warming, and the resulting impacts on insect population trends, are topics of active current research (78, 138, 139).

Siberian Anticyclone: a persistent high-pressure system sitting above the North Asian landmass over winter

Qin Mountains: a mountain range aligned west to east through southern Shaanxi province in central China

Huai River: called the Huai He in Chinese, runs across East China approximately midway between the Yellow River to the north and the Yangtze River to the south

Supplemental Material >

From an agricultural perspective, the arena is separated into southern and northern sectors by the Qinling-Huaihe Line, an imaginary line running west to east along the Qin Mountains and Huai River valley at about 34°N (**Figure 1**), approximately corresponding to the January 0°C isotherm (**Figure 2**). South of the dividing line, crop production predominantly consists of rice cultivation (**Supplemental Table 2**), and thus, the major pest insects in this region are rice-feeding RPHs and RLRs (63, 135). In China alone, rice pests require control measures to be employed on 50 million ha of land and cause an average annual yield loss of 1.4 million tons (**Supplemental Table 1**). In the northern section of the arena, the principal crops are maize and wheat (89) (**Supplemental Table 2**), with vegetables, legumes, and peanuts also being important. Rice cultivation is also significant in some parts of the northern region, namely Northeast China (Heilongjiang), Japan, and the Korean Peninsula (89) (**Supplemental Table 2**). The major migratory insects in this region are cereal and legume pests, falling primarily into three classes that differ in size, flight capacity, and migratory behaviors: (*a*) microinsects, e.g., aphids; (*b*) medium-sized insects, e.g., crambid moths such as the Asian corn borer (*Ostrinia furnacalis*) and the beet webworm; and (*c*) large insects, e.g., multiple species of noctuid moths, such as the OAW, FAW, and beet armyworm (*Spodoptera exigua*), the black cutworm (*Agrotis ipsilon*), and the cotton bollworm (*Helicoverpa armigera*). Over the past 20 years in China, there have been geographical shifts in crop production, with maize overtaking rice and wheat to become the most extensively planted crop along the EAIF (primarily driven by the increased requirement for fodder for livestock production) and the movement of cotton production out of the EAIF region, primarily to Xinjiang in Northwest China (88, 89) (**Supplemental Table 2**). This has resulted in changes in the importance of the major pests; for example, the OAW and (increasingly) FAW are now considered the most important moth pests due to their prevalence in maize, while cotton bollworm has decreased in its significance (63).

PEST POPULATIONS AND THEIR MIGRATIONS

Due to the diversity, abundance, economic impact, and societal effect of crop pests migrating along the EAIF, a huge research effort has been directed at these migrations over the past 60 years. Southeast and East Asian entomologists, particularly in China, Japan, and South Korea, have endeavored to document the seasonal population dynamics, elucidate the migration pathways, monitor and forecast pest outbreaks, and limit the yield loss resulting from these annual movements for a wide array of pest species. This effort has resulted in many hundreds of research publications, especially from China and Japan (see the **Supplemental References**); in this review, we focus on a few key species of migratory crop pests to illustrate the salient issues, highlighting similarities and differences in the various migratory adaptations.

Historical Perspectives

Outbreaks of migratory pests have been recorded for thousands of years in China (153), but confirmation of long-range migratory movements was only obtained from the 1960s, when the migratory system of the OAW in East China was documented. Evidence that this species migrates between the North China Plain and the Northeast Plain, crossing a sea in the process, came from the capture of >1,000 OAWs on board ships in the Bohai Sea during May–September 1960 (44). This early indication led to pioneering large-scale mark-release-recapture programs with OAWs across nine provinces of East China during 1961–1963, when the release of two million individuals led to 12 recaptures of marked moths at distances of 600–1,400 km from their release sites. Based on these results, Li et al. (72) mapped the migration pathway of the OAW in China, laying the foundation for the vast research effort described in this review.

By the 1970s, national monitoring and research efforts were launched for the most important rice pests in China, i.e., RPHs and RLRs. Pest population dynamics and seasonal distributions have been monitored by coordinated trapping of pests with blacklight traps (18) and by aerial sampling in mountain passes, from aircraft and on board ships (27, 76, 90). Combining these results with outputs from experimental work, including mark-release-recapture (87), several groups determined the migration pathways and their environmental drivers for the RPH and RLR (7, 18, 55, 91, 107).

Aeroecological studies have played a pivotal role in the study of insect migration along the EAIF, ever since a scanning entomological radar was deployed to study pest moth migration in Jilin, Northeast China in 1982 (17). Numerous radar studies followed, providing many insights that have been reviewed extensively elsewhere (9, 26, 29, 104, 143). In this section, we briefly mention that entomological radar studies, in conjunction with searchlight trapping and high-altitude aerial sampling, have revealed the scale and timing of aerial movements, altitudinal distributions, in-flight orientation behaviors, and the role of wind transport for many high-flying migrant pests utilizing the EAIF. Notable studies include those concerning RPHs in the Philippines (106) and East China (103, 105, 108), mosquito vectors above East China (83), and numerous species of pest moths in North and Northeast China (17, 30, 31, 34, 35, 115, 116).

Contemporaneously, Japanese researchers were carrying out extensive studies of transoceanic migrations from China to Japan, especially of RPHs (2, 66–68). Immigrations of RPHs from China during the Baiu rainy season were proposed to be the source of infestations on the Japanese mainland as early as 1929 (86). This hypothesis was revived following the observation of a mass of RPHs swarming around a weather ship in the Pacific Ocean (29°N, 135°E) in July 1967 (2) and subsequently confirmed by field investigations, trajectory simulations, and meteorological analyses (66, 67, 69).

Rice Pests

The most serious migratory rice pests in the EAIF fall into two categories: (*a*) delphacid RPHs, especially the brown planthopper (BPH), *Nilaparvata lugens*, and white-backed planthopper, *Sogatella furcifera*, and (*b*) the RLR, a crambid moth (**Supplemental Tables 1 and 3**). These three primary species are important pests throughout the rice-planting regions of Asia and Oceania and cumulatively are responsible for rice yield losses of approximately 1.4 million tons per year in China alone (**Supplemental Table 1**), amounting to approximately 70% of all losses due to pests, diseases, and weeds (63). Adult and nymphal RPHs cause physical damage (hopperburn) via the sucking of sap (3) and, more importantly, transmit several serious diseases of rice (92, 144). Caterpillars of the RLR, in contrast, only cause physical damage. The northern boundaries of winter breeding areas are delimited by various January isotherms, as follows: 12°C (approximately 23.5°N) for the BPH, 10°C (approximately 26°N) for white-backed planthopper, and 4°C (approximately 30°N) for the RLR (77); thus, all of these species can survive winters in South China (**Figures 2*d*** and **3*a***; **Supplemental Table 3**). However, these species are monophagous

Supplemental Material >

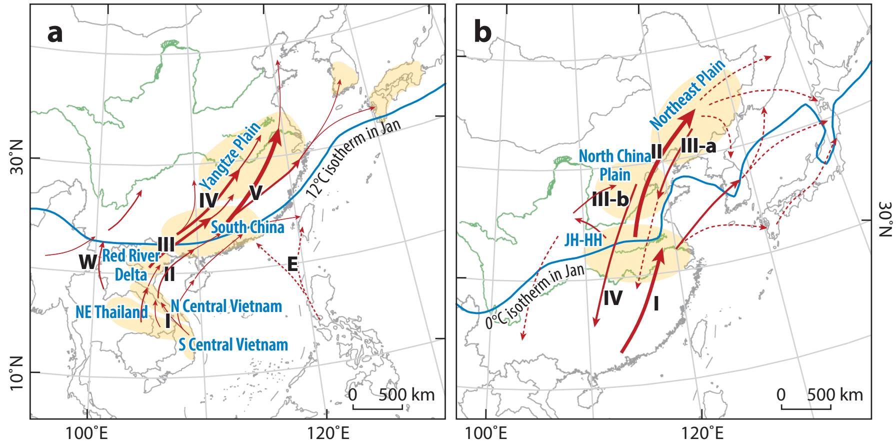

Figure 3

Migration pathways of (*a*) the brown planthopper (BPH) and (*b*) the Oriental armyworm (OAW) along the East Asian Insect Flyway. For both species, thick red arrows show the major routes, thin red arrows show less important routes, dashed red arrows show possible routes, and yellow ovals approximate the breeding locations of each generation. The Jianghuai & Huanghuai (JH-HH) region is the region between the Yellow River (also known as the Huang River) and the Yangtze River, including the Huai River valley. Information on BPH migration pathways was taken from References 18, 51, 52, 92, 131, and 133, and information on OAW pathways was taken from References 61, 71, and 72.

or oligophagous herbivores, feeding almost exclusively on rice crops; as winter rice is not grown in South China except in southern Hainan Island, the major winter breeding area is in Southeast Asia, where rice is grown year round (51, 52, 78, 133). In general, the migration patterns of the BPH, white-backed planthopper, and RLR along the EAIF are rather similar (7, 13, 18, 91, 107, 131), so we focus on the most important species (BPH) as an exemplar migratory rice pest.

Each spring, most rice-growing regions of East Asia (i.e., South China and the Yangtze Plain, the Korean Peninsula, and Japan) are colonized anew by waves of BPH migration from their winter breeding grounds in Southeast Asia and southern Hainan Island. These waves are generally considered to occur along three separate pathways into South China during early spring (131) before coalescing in the northern sector of the EAIF later in the season (**Figure 3*a***). The Western Pathway begins with migration from Myanmar and northwest Thailand into Southwest China (Yunnan and Guizhou provinces); the population using this route was long thought to be separate from BPH populations in South Asia, but recent genomic studies have discovered a degree of gene flow between India and East Asia via admixture in Myanmar and Yunnan (37, 42), indicating frequent interchange between the South, Southeast, and East Asian regions (37, 56). The Eastern Pathway is postulated to originate from winter populations in the Philippines that regularly migrate to coastal Southeast China (Guangdong, Fujian, and Taiwan) (**Figure 3*a***). Population genomics evidence recently demonstrated a lack of connectivity between samples from the Philippines and Southeast China (42), indicating that this migration route is less important than initially thought, although migrations may occasionally occur via transport on typhoon winds or winds around the edge of the WPSH during the summer monsoon period (59, 75, 94, 97).

The most important migration pathway is the Central Pathway (**Figure 3*a***), which starts with emigration from winter breeding areas on the Indochina Peninsula into coastal South China (Hainan, Guangxi, and Guangdong). The Mekong River Delta region in southern Vietnam, the largest rice production area in Indochina, was originally considered to be the primary origin of this migratory pathway (131). However, a paucity of favorably directed (southerly) winds from this region during winter and spring prevents mass emigration northwards (**Figure 2*a*,*d***). Different insecticide susceptibility between the population in the Mekong River Delta and other East Asian populations also indicates that it is not the source (81). It is now thought that the first migration wave originates primarily from winter breeding populations in central Indochina, especially Northeast Thailand, South Laos, and South-Central Vietnam (96, 133) (**Figure 3*a***). The first wave of migrants along the Central Pathway are transported on favorable high-altitude winds to North-Central Vietnam and the Red River Delta; subsequent migrations (second to fifth waves) along this pathway progressively reach South China, the Yangtze Plain, and ultimately Korea and Japan (13, 18, 51, 52, 69, 121, 122, 133), with smaller numbers of migrants on the Western and Eastern Pathways joining en route (**Figure 3*a***). During August and September, southward return movements within China have been documented (18, 47, 50, 105, 108), and atmospheric trajectory simulations indicate that large numbers of return migrants may travel from South China to North-Central Vietnam during October (133).

The two other major rice pests (white-backed planthopper and RLR) show similar migration patterns to the BPH, but due to a combination of wintering further north and stronger flight capability, small numbers of these species travel through the North China Plain and cross the Bohai Sea, reaching as far as Heilongjiang (36, 45). A third planthopper species, the small brown planthopper, *Laodelphax striatellus*, was formerly considered to be nonmigratory, as it can overwinter as far north as Jilin and is also capable of breeding in China year-round, developing on wheat when rice is not available (114). However, the small brown planthopper is now known to have a strong migratory capability, and there is clear evidence of transoceanic migration from China to Korea and Japan (95, 99, 150), where its immigrations are of economic significance.

Pests of Wheat and Maize

A huge array of lepidopteran pest species, predominantly Noctuidae and Crambidae (**Supplemental Table 3**), undergo long-range migrations along the EAIF (38, 58, 63, 71, 93, 118, 132, 134, 151). The larvae of many of these species are polyphagous and can thus attack many crops; these, along with aphids (which we do not consider further), are the major pests of wheat and maize in China. Many of these species are capable of overwintering further north than the rice pests, so they can exploit the rich seasonal resources of the northern parts of the EAIF, regularly causing substantial problems as far north as Northeast China, Korea, and Japan (61–63, 70, 71, 118). The migration patterns of these species are broadly similar, so we focus on the economically most important pest, the OAW, as our exemplar migratory noctuid moth (**Figure 3*b***).

Supplemental Material >

The OAW is a polyphagous pest of grain and legume crops, causing substantial damage and economic losses, especially in maize, wheat, and rice, throughout Asia and Australasia (61, 70–72, 119, 152). In China, it causes substantial yield losses every year (**Supplemental Table 1**), and in outbreak years, it can be extremely serious, as in 2012, when it occurred over an area of approximately 9 million ha and caused almost 1 million tons of yield loss (62, 63). Prior to 1985, damage was mostly concentrated on wheat in East-Central China, but after 1995, it shifted to maize crops, principally in North and Northeast China during late summer (62, 63, 146); in Korea and Japan, the main damage occurs to pasture and rice crops (70, 71). The northern overwintering limit for the OAW is the January 0°C isotherm around 33°N (61), south of the Huai River valley (**Figures 1** and **2**), and thus, long-range migration is required to colonize the northern section of the EAIF each summer. Overwintering in mainland Japan is possible in warm areas where the mean January temperature is over 4°C (70). However, as early season trap catches in Japan are small, it seems likely that immigration from overseas is important for recolonization each summer (93).

The seasonal movement of the OAW in East Asia involves a multigenerational migratory loop consisting of four separate waves of migration extending from South China to as far north as Korea and northern Japan (**Figure 3*b***), with individual migratory legs of up to 1,400 km in length (72). The first wave in March and April takes migrants from southern winter breeding regions into the winter wheat growing region north of the Huai River valley. The second wave involves emigration of the progeny in May and June, primarily moving into North and Northeast China (17, 61) but also with some westward movement into central China and eastward movement into Korea and Japan (61, 71, 93). The traditional view is that the third wave in July and August is the start of the fall return migration (61), with emigrants departing Northeast China toward the North China Plain (**Figure 3*b***). However, the situation seems more complex than this, as winds are often unfavorable for return migration (i.e., blowing mostly from the southwest; **Figure 2*b***), and there is evidence that most moths emerging in the northeast as autumn approaches are unable to leave the region (101, 152). However, the warming climate now allows this third generation of moths to develop as far north as Jilin in Northeast China, where they are causing severe late-season crop losses (62, 115). The fourth wave occurs from late August through September, with moths heading southward from the North China Plain toward the wintering region (61, 72), but again, it is unclear how many can return, as winds are still only marginally favorable during this period, and there is evidence that many moths are trapped at high latitudes as winter approaches (6, 116); this topic is discussed further in the section titled Evolution of Migration Systems.

The migratory flights of the OAW are typical of noctuid moth migrants, i.e., taking off at dusk and ascending to high altitude, migrating for up to 10 h if conditions are suitable, and landing by dawn (17, 34). Migrating moths over the mainland are often concentrated into narrow altitudinal layers where conditions are optimal for flight (130), and radar observations of the OAW have recorded layers at a variety of altitudes between 200 and 1,000 m above the ground (17, 34, 115, 147). High-flying migrant OAWs crossing the Bohai Sea traveled at speeds of approximately 4–12 m/s (34); thus, with a flight duration of up to 10 h, maximum movement distances more than 400 km per night are likely. Assuming that migrants are capable of several nights of sustained migratory flight within their pre-reproductive window, which may last for 2 weeks in Northeast Chinese populations (39), total migration distances could easily exceed 1,000 km in a single generation. At least a few nights of seasonally favorable wind directions during the fall migration window, and mechanisms by which moths can select favorable nights and altitudes and at least partially correct for marginal winds are required for substantial movement in the seasonally appropriate direction; radar observations from North China indicate that these mechanisms do indeed exist (6, 17, 34). Additionally, the OAW also takes overseas migrations in the early summer from the Korean Peninsula, Northeast China, and East China to northern Japan, and their flight duration and distance per single flight are estimated to be considerably longer than migratory flights above the Asian mainland (93).

In addition to the many native migratory insects, the invasive FAW, a pest from the Americas that became established in East Asia in 2018, now exhibits a seasonal migration pattern (65). The FAW has rapidly adapted (14) to utilize favorable tailwinds to expand, each spring and summer, from year-round breeding areas in the Indochina Peninsula and South China as far north as the North China Plain, its major occurrence region, with a few individuals reaching Northeast China, the Korean Peninsula, and Japan before returning south during the autumn (74, 132, 134).

EVOLUTION OF MIGRATION SYSTEMS

Interactions between environmental factors and the underlying genetic complex continuously mold migratory syndromes (22, 25). A key environmental factor promoting migrations over vast areas in the Northern Hemisphere is the exploitation of the seasonal resources at higher latitudes, which become available every spring to individuals able to reach them. In the case of the EAIF, these resources are both abundant and predictable. Crops providing food supplies for the principal migratory pests have been extensively cultivated in East Asia for thousands of years, and the monsoonal winds that take migrants northwards in spring are reliable. There are some geographical barriers, such as the Qinling Mountains of China in the west of the EAIF, that can obstruct the movement of the smaller, weak-flying species (137) but not the larger, strong-flying pests (134). These topographical barriers are less challenging than those faced along flyways in the Western Palearctic, however, where migrants potentially face the Sahara, the Mediterranean, and high mountain ranges (e.g., the Pyrenees, Alps, or Taurus Mountains). Some of the poleward migrations in East Asia are simply expansions from the winter range (e.g., the BPH) and can be considered facultative, but in other species, e.g., the OAW (61), black cutworm (111), and diamondback moth (*Plutella xylostella*) (136), spring migrants are escaping from unfavorably high summer temperatures in the southernmost areas of their distributions. These are therefore obligate migrants for which temperatures are an important driver of both the spring–summer and the fall movements. The combination of extensive cropping areas, seasonally favorable climates, suitable transport opportunities, and lack of major geographical barriers to movement has led to many species exploiting the EAIF on an annual basis. Such large-scale movements will typically result in extensive mixing and lack of population differentiation; genomic analyses have indeed demonstrated that this is the case in RPHs and a wide variety of pest moths (12, 56, 73, 80, 113, 114, 119, 137, 140).

While food resources and temperature variation are likely the primary drivers of the invasions into the North Temperate zone, avoidance of predation and parasitism may also be a factor (11, 22). For example, Wada (123, p. 86) observed that, “because BPH populations were always low in ancient tropical paddy fields, a risk of population decline caused by natural enemies seems to be more critical than deterioration of rice damaged by planthoppers themselves.” However, some important predators and parasitoids of RPHs, such as the mirid bug *Cyrtorhinus lividipennis*, frequently migrate along with their prey (105, 106, 149), and dryinid parasitoid wasp larvae can be transported long distances inside their hosts (84). Nevertheless, escaping from natural enemy attacks may have preadapted the BPH and other flyway species for the massive modern-era migrations that appear to be associated with widespread intensive agriculture.

Due to the low self-powered airspeeds of small migrant insects, for example, only 0.3 m/s for the BPH (16) and 0.8 m/s for the RLR (102), active flight will have negligible influence on migration direction, and movement will essentially be downwind. Consequently, it is unsurprising that these species do not exhibit common heading directions during windborne migration (105, 107, 108). Their annual expansion from the south of the flyway into the major rice-growing areas along the Yangtze and Huai Rivers of China, as well as to Korea and Japan, relies, therefore, on the northward progression of the WPSH and its associated southerly airflows over the eastern seaboard of China. The advance of this atmospheric system produces an aerial highway of favorably directed winds and determines the location of the major rainfall belt (21, 124), which transports and then concentrates the migrants in intense zones of fallout in major rice-growing regions, with the advance occurring in a series of jumps across the growing season (20, 28, 52, 127). Thus, the position and intensity of the WPSH throughout the season are of critical importance for forecasting the arrival of BPHs into the major rice-producing regions (52, 78, 98). For these small migrants, the northward expansion is facilitated by the large-scale meteorological conditions during spring and summer.

In North America, the potato leafhopper (*Empoasca fabae*) shows enhanced emigration in weather conditions favoring southward movement in autumn (117), but there is no evidence that

Contemporary natural selection: natural selection acting on single or consecutive generations to rapidly develop a trait without necessarily leading to the trait becoming established

Pied piper: movement of a population on favorable winds into a region where winters are too cold for survival but from where return migrations are seldom possible

small insects in East Asia, such as the BPH, select favorable wind directions for migration (108). Catches made in autumn at weather station Tango, approximately 500 km south of the Japanese main islands (68), suggest that much of the progeny of RPHs that migrate into Japan will not get back to the species' winter breeding areas—they are displaced too far out into the Pacific and will perish. On the other hand, autumn immigrations into small islands east and west of Taiwan (68, 75) indicate that some successful overwater southward migrations do occur. On the Chinese mainland, southward RPH movements in the late summer or autumn are certainly observed (27, 87, 105, 108). Not surprisingly, migration pathways of RPHs back to regions of year-round reproduction are easier to demonstrate in populations that are relatively close to tropical China, e.g., southern Yunnan and Guangxi (57, 133). However, some areas where temperatures would be high enough for the survival of BPHs do not plant rice crops in winter (133), so any development there would be confined to ratooning rice plants.

Flight durations of BPHs in tropical source areas are highly skewed toward short flights (106). However, any individuals that are migratory enough to reach temperate areas of South China in spring will have experienced strong selection for longer-duration flight. In subsequent successive waves of northward migration, only the longest-flying individuals (representing a small proportion of each generation) will successfully colonize the next region of unexploited, natural enemy–free, seasonally developing rice. This process of contemporary natural selection (25) is posited to lead to a rapid increase in the proportion of alleles promoting long-distance windborne movement as the season progresses. The process begins anew each year and is not dependent on autumn return migrations; instead, it may lead to recurring fatal flights into a pied piper climatic trap without any substantial return of progeny south (82, 101). Alternatively, the within-year selection for longer-duration flight as the season progresses will also equip the fall generation with the capability to achieve long-distance return flights if winds are suitable; these returning individuals would provide a mechanism for maintaining the migratory trait through the winter generations.

In larger insects, there is evidence from China for orientation strategies and wind selectivity that facilitate migration in seasonally beneficial directions (32–34, 58, 115, 116). Spring and early summer migrations are assisted by prevailing southerly winds, so a better test for complex orientation strategies is provided by the southward movements necessary to prevent stranding at high latitudes at the onset of winter. For example, radar observations of cotton bollworm show that moths not only head toward the southwest but also partially compensate for wind drift away from this preferred migration direction (33). Some strong-flying migrants, such as the dragonfly *Pantala flavescens*, can compensate for wind drift and are able to maintain a displacement toward the southwest even in moderate headwinds (32). The above investigations were short-term case studies, but a recent multiyear radar study in East China revealed that larger species (including many pest moths) select beneficial tailwinds and flight headings that facilitate southward return migrations in the fall (58). Thus, we conclude that there is continued strong selection for take-off behaviors and orientation strategies that favor long southward movements in the autumn-emerging generation in various large insect species in China, as there is in other Northern Hemisphere regions (10, 37, 48, 100).

Nevertheless, for many species of EAIF migrants, evidence for or against return movements is not conclusive. Southward movements in the late summer or autumn certainly occur, e.g., in RPHs (see above), mosquitoes (83), dragonflies (32), and various pest moths (30, 31, 33, 34, 72, 107, 116). However, it is not always clear whether these flights will take migrants far enough south for successful overwintering (116, 147, 152); in some cases, migration by two or more successive generations would be required to reach the overwintering areas. Movements may be dependent on specific weather events and are likely to be more successful in some years than others (152). Populations of, for example, OAW that have invaded the far northeast of the flyway (e.g., Liaoning, Jilin, and Heilongjiang) are apparently unlikely to encounter wind fields favorable for a southward return (6, 101). This contrasts with observations in Western Europe, where, at least for the silver Y moth (*Autographa gamma*) and painted lady butterfly (*Vanessa cardui*), populations heading south after summer breeding, which can be four times more numerous than the spring immigrants, are highly likely to reach regions suitable for production of the next generation (8, 112). From inter-flyway comparisons of migratory patterns, we tentatively conclude that the annual population bottlenecks, which must occur somewhere if populations are not to perpetually increase, show interesting differences in different regions. For migrants between Europe and Africa, such as the silver Y moth and painted lady butterfly, bottlenecks occur during the winter generations in the (typically arid) south of the range (8, 53). By comparison, the evidence we have to date from East Asia indicates that the population bottleneck occurs during the fall migration, before individuals reach the southern winter breeding range (6, 152).

Successful return movements provide the most likely mechanism for maintenance of the genetic basis of annual long-distance migrations. If return migrations do not regularly occur, then movement across the widely distributed tropical range (e.g., populations in the Indochinese Peninsula and the Philippines) may be sufficient to maintain a capacity for long-distance migration and account for the genetic diversity observed in OAW populations at higher latitudes (116). Contemporary natural selection, as proposed above for RPHs, may also occur during the multigenerational northward migrations of pest moths, leading to the development each year of a genetic cline (24), with alleles associated with migratory potential, such as higher flight capacity and longer pre-reproductive periods (39, 129), becoming more prevalent at higher latitudes. Such latitudinal partitioning would again prime these populations for the long journey south in fall, provided that the mechanism for the reversal of the migration direction remains intact. It was shown 30 years ago that the pre-reproductive periods of OAW moths from Northeast China in summer are longer than those from intermediate latitudes (39), but apparently, these ideas have not been explored further.

EFFECTS OF CLIMATE CHANGE ON FLYWAY MIGRANTS

The effects of anthropogenic climate change on EAIF migrants will no doubt be complex, but the obvious responses to rising temperatures include range expansions or latitudinal shifts (46, 120, 142); increased winter survival (54) and/or increased residency further north (15); and, eventually, even changes in the number of annual generations (46). Warmer nighttime temperatures (125) will stimulate increases in migration propensity of nocturnal migrants along the flyway. Climate change is also altering rainfall patterns, but there is much more uncertainty over these projections. Some studies have documented increasing intensity of summer frontal rainfall over East and Northeast China, the Korean Peninsula, and southern mainland Japan (85), but other reports found that less rainfall is occurring during the Meiyu season in the middle and lower reaches of the Yangtze and Huai River valleys, and there is more rainfall in the preflood season in South China (126). Accordingly, Lv et al. (78) reported that less precipitation from the rain belt located just north of the lower Yangtze River valley, combined with a weakening of the northward windspeed component of the circulation patterns south of the Yangtze River, has led to reduced concentration and deposition of planthopper migrants in the region. Global climate change is also increasing the frequency and intensity of extreme weather events, such as anomalous rainfall (138) and severe typhoons (148). For example, the intensity of typhoons affecting China has increased, and the tracks of typhoons are also moving northward, striking Japan and the Bohai Sea of China (148). As the movement of several pest species is significantly influenced by typhoons (49, 79, 94) this will inevitably affect long-range migratory movements along the EAIF in the future. Nonetheless, we believe that long-distance migratory behavior will tend to preadapt many migrants to changes in the distribution of their most favored habitats, making it unlikely that the dominant species of Lepidoptera and Hemiptera will suffer serious declines.

PERSPECTIVES AND FUTURE DIRECTIONS

In this review, we adapt the flyway concept, developed primarily in the context of bird migration, to provide a unified perspective on the remarkable insect migrations that occur along the eastern periphery of the Asian continent. While our designation of an East Asian Insect Flyway may be new, we recognize that the concept is implicit in many of the forecasting and control strategies developed since the 1960s and 1970s, particularly in China and Japan, against invasions of migratory pests such as rice pests and OAWs (see the section titled Historical Perspectives). Many of these pest problems persist, and new problems arise (19, 38, 63, 135); in each of the countries primarily affected (China, South Korea, and Japan), there are national or regional government organizations responsible for monitoring immigrations of pest species and issuing warnings and associated long-established and ongoing research programs (19, 135). Much of the research described in this review is focused on improving this operational effort and adapting it to changes in cropping and pest-management practices, new pest species, evolving insect behaviors and host preferences, and altered weather patterns associated with global warming. Beneficial species also migrate along the flyway and play important roles in biocontrol, pollination, and more general ecological services (32, 60, 149, 151), and we suggest that these species warrant a greater research effort than they currently receive.

The practical importance of protecting summer crops has led to a predominance of research on the northward migratory phase in spring and summer, but it was recognized early on that return migrations would apparently be needed to sustain the migratory adaptation from year to year. Return migrations are generally less evident than the early season range expansions, and for most species, evidence of a complete there-and-back annual cycle is still lacking. Establishing continuity and identifying population bottlenecks for additional species may reveal a variety of ways in which flyway migrations function and enable improved species-specific forecasting capabilities. Alternatively, pied piper dead-end migrations may sometimes occur, with contemporary natural selection perhaps producing populations with increasing migratory propensity at the flyway's northern limits. There is much scope for further exploration of these research topics, few of which have been conclusively demonstrated for any of the flyway species.

Insect flyways have previously been identified in North America and Europe. The Mississippi Flyway, which is associated with annual spring and summer invasions of leafhopper, aphid, and moth pests into the Great Plains states of the United States, was recognized as early as the 1960s (64). Frequent southerly winds, some in the form of nocturnal low-level jets, facilitate the northward movements of these pests, which cannot survive the region's harsh winters. Return movements in autumn have been documented for moth migrants during brief periods following the passage of a cold front, when the air is still not too cool, and the wind direction has become favorable (100). As with the EAIF, the phenomenon is of considerable agricultural importance. In western Europe, radar studies in the United Kingdom (10, 26, 48) and extensive studies of painted lady butterfly migrations (53, 112) indicate a likely Afro-European Insect Flyway, but more studies are required. These insect flyways all coincide with established bird migration corridors, suggesting that they represent similar adaptations to large-scale geographic features and climates. The lesser flight capacities of insects compared to birds reduce the distances covered and make them more dependent on prevailing winds, while their shorter lifetimes lead to annual cycles encompassing multiple insect generations rather than being completed by the same individuals. Unlike their bird counterparts, the insect flyways likely do not extend into the southern hemisphere. Such comparisons across major taxon groups may help to develop broader understandings of migration, and its associated life-history traits, as an adaptation to regional geography and resource availability. The EAIF, with its established and ongoing research programs, provides an exceptional natural laboratory for both broad investigations of the migration phenomenon and more focused studies of the movements of economically important crop pests.

FUTURE ISSUES

1. Evidence of a complete there-and-back annual cycle is still lacking for most species. Establishing continuity and identifying population bottlenecks for additional species may reveal a variety of ways in which flyway migrations function and enable improved species-specific forecasting capabilities. Cross-border and cross-regional research collaborations will be needed for many East Asian Insect Flyway (EAIF) migrants.
2. Winds favorable for return southward migrations to overwintering regions seem infrequent in the EAIF in autumn. Systematic observation of flight behavior of migrating insects with insect radars and other tools may further elucidate their adaptive strategies for enhancing migration success.
3. Migrants in the EAIF may be subject to contemporary natural selection for long flights, as succeeding generations progressively advance northward. Mechanisms for maintaining migratory traits need further study, perhaps employing novel technologies such as genomic analysis.
4. For many beneficial and benign EAIF migrants, there is little knowledge about annual life cycles, migration routes, and interactions with other organisms. A greater research effort on beneficial species is warranted in view of their valuable ecological roles.
5. Global climate change may lead to new migration patterns and require modifications to pest-management practices.
6. Long-distance oversea migration of insects between mainland Asia and peripheral islands appears to be an important part of the flyway, but the precise details of how these long oversea journeys are completed remain to be elucidated.

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