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Summer Heatwaves Produce Divergent Responses of Migratory Crop Pests in East China

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Highlights

- Contrary to the global insect decline consensus, 130 migratory pest species in east-central China showed an overall abundance increase over 12 years, with 23% increasing, 69% stable, and only 8% declining.
- Summer heatwave intensity was the dominant driver of divergent population trends, benefiting some species but harming others.
- Agricultural pest insects in this region are not just tolerating but thriving under warmer, more extreme summer temperatures.
- Our work fills critical gaps for East Asia and aerial migratory pests.

Abstract

Background Insect populations globally are declining, and climate change is one of the most important drivers of population trends of insects. A threat which has been increasingly recognised to have negative impacts on a wide range of insects is the extreme temperatures that occur in summer heatwaves, which are becoming more intense and lasting longer. However, there are important knowledge gaps in our understanding of insect population trends across taxa and global regions, as many insect groups and important parts of the world have not been assessed. This study aims to explore the population trends of a functional group of insects (migratory pests) and a region (East Asia) which have hardly featured in previous global syntheses of insect population trends, and clarify the role of climate, especially summer heatwaves in driving the divergent population trajectories of these insect species. A community of 130 species of nocturnal aerial migrants (predominantly crop pests) over a 12-year period during their migration over east-central China were sampled by searchlight trap to identify the climatic factors associated with species showing positive and negative abundance trends.

Results In contrast to most studies of insect trends, we found that there was a moderate increase in the combined abundance of the 130 species, even though extreme summer temperatures were frequent, and increased in duration and intensity over the period. Among the 130 species, 23% significantly increased in abundance, 69% remained stable, and only 8% declined significantly. Species which exhibited significant trends consisted mainly of agricultural pests, including species capable of local overwintering as well as those immigrating from southern regions. The most important driver of the divergent trends was the effect of summer heatwave intensity, which was positively associated with the population trends of increasing species but negatively associated with the population trends of decreasing species.

Conclusions Despite increasing extremes of summer heatwave conditions, the community of migratory pests in East China are not only coping with changing environmental conditions, but many species are actually thriving in response to warming temperatures.

Keywords Summer heatwave intensity; Nocturnal insects; Migratory group; Divergent trends; Global climate change

Background

In the past few years, a plethora of studies, meta-analyses and reviews have reported pervasive and often precipitous declines in terrestrial insect populations around the globe [1–6]. These declines are concerning due to the central role insects hold in food webs and in providing a range of beneficial ecosystem services including pollination, transfer of nutrients, and pest control [7–10]. Anthropogenic habitat degradation and agricultural intensification have long been known to be key drivers of biodiversity loss [5, 11], but increasingly climate change is implicated as a driver of population trends and local extinctions [12–17]. Insects, being poikilothermic, typically respond positively to warmer temperatures, at least in temperate regions. However, some recent studies have indicated that the extreme temperatures which occur in summer heatwaves have negative effects on insect abundance, even in taxa which are otherwise stable or increasing [18–20]. Given that summer heatwaves have recently increased in frequency, severity and duration, and are predicted to continue to do so [21–23], this is expected to become an increasing threat to insect populations. Thus, the commonly accepted consensus is that insect populations around the world are declining in abundance and diversity – imperilling the vital roles insects play in ecosystem functioning – and that climate change is becoming a key driver of these changes [24–27].

In contrast to this widely held view, a few studies have reported stable or even increasing populations in some regions and in some taxa. For example, one study found no evidence of an overall net decline in insect abundance or diversity from samples collected at a network of Long-Term Ecological Research sites distributed across the USA [28], although the conclusions of this study have been debated [19, 29, 30]. Furthermore, there is growing evidence that crops are facing increasing levels of pest damage and disease caused by insects, in response to warming climates [31–34]. Increasing pest damage indicates that communities of insect pests may be faring better than non-pests and thus will presumably have positive or at least stable abundance trends. However, evidence for this from large-scale studies of aphids (a group containing many important crop pests) is mixed, with some studies finding increases [20, 35, 36], but another study finding moderate to large declines in the same group [37].

One of the challenges in trying to draw general conclusions from these studies is that knowledge gaps exist in some key regions and some important functional groups of insects. For example, there is very unequal coverage across the terrestrial globe: the datasets used in the meta-analyses and global syntheses discussed above come predominantly from Europe and North America. One stark omission is data from East Asia, particularly China, which is almost entirely absent from the major regional and global assessments [2–4, 6, 14, 15]. We therefore know little about how insect populations are faring in one of the largest, most densely populated and biodiverse countries in the world, where impacts of insects on agricultural productivity are of huge importance [33, 38]. Another key knowledge gap is the population trends of aerial migrants, many of which are also important crop pests [38–40]. Communities

of aerial migrants are relatively species poor compared to general insect communities on the ground, but they often include extremely abundant species and are disproportionately important in agricultural landscapes [38, 41–44]. However, very few studies have assessed abundance and biodiversity trends in communities of aerial migrants, as they are a challenging group to continuously monitor for long periods.

One method that can be used to assess long-term trends in nocturnal migratory species is monitoring with searchlight traps. These are powerful, upward-pointing lights that effectively sample communities of high-flying nocturnal insect migrants, and they have been used to directly monitor migratory activity of a range of night-flying species in locations across China for the past two decades [38–40, 45]. The most intensively studied location is Beihuang Island in the Bohai Gulf (38°N), situated on the migratory route between North China and Northeast China (Fig.1), where a searchlight trap has been continuously operated since 2002 [39, 46]. Data from this trap indicates that the community of 98 species of nocturnal aerial migrants flying over this island have shown a moderate decline in combined abundance of 0.4% per annum over the 18-year period from 2003–2020 (ref 10), with six times as many species declining (19 species) as increasing (3 species) in this period [39]. Declines were consistent across all guilds but were more pronounced in natural enemies (particularly dragonflies) than in crop pests. The Bohai Gulf is towards the northern fringe of the East Asian Insect Flyway [38] and thus may not be representative of the main part of the flyway further south (Fig.1). The northern location may be of particular relevance over the past decade, when changes to the seasonal wind patterns over East Asia have started to impact insect migration patterns with negative consequences for population trends [47, 48]. Indeed, there is some evidence that return migration to the winter-breeding region is challenging for populations produced in Northeast China over the summer [49, 50] and this is likely to result in smaller numbers of nocturnal migrants passing over the Bohai Gulf and thus being caught in the Beihuang Island searchlight trap.

Thus, there is a knowledge gap concerning the long-term trends of migratory species moving along the central part of the East Asian Insect Flyway, further south in China. We therefore conducted a regional survey in east-central China from an intensively agricultural region in Henan province, about 700 km southwest of Beihuang Island (Fig.1). Four sites were sampled over 12 years (2013–2024) using searchlights to monitor nocturnal high-flying insects. We analysed trends in the community of nocturnal aerial insect migrants, which are predominantly crop pests, caught by a searchlight trap in this region [38–40]. We then determined individual population trends for all species of migratory insects, and further we identified the climatic factors (including extreme summer weather events) associated with species showing positive and negative abundance trends (Table S1). Our results provide important insights into the population trends of an important guild of insects (nocturnal migratory crop pests) in a region that has been chronically understudied from the perspective of biodiversity trends, and identifies the role of climate, particularly summer heatwaves, in driving the divergent population trajectories observed in this study.

Results

Overall trends in insect abundance

The total abundance of insects captured with the searchlight traps at four sites over the 12-year period from 2013-2024 was 2,910,896 individuals for all 262 species. After quality control, 130 species were retained, with a total abundance of 2,857,564 individuals, including 1,787,477 individuals (100 species) in XX, 545,256 individuals (23 species) in LH, 465,214 individuals (4 species) in HY, and 59,617 individuals (3 species) in MZ. Overall combined annual abundance of insects captured with the searchlight trap showed a significant increasing trend over the 12-year period ($F_{10} = 9.40$, slope = 0.040, $p = 0.012$; Fig. 2A). At the seasonal level, the trend was significantly positive in spring ($p = 0.004$; Fig. 2B) and autumn ($p = 0.001$; Fig. 2D), but with no overall trend in summer ($p = 0.501$; Fig. 2C). The majority of these 130 species were Lepidoptera (98 species, predominantly pest noctuid and crambid moths) and Coleoptera (17 species), with single-digit numbers of species from 8 other orders (Table S1). They are predominantly migrant crop pests that move along the East Asian Insect Flyway [10, 38–40]. Given that this community of migratory crop pests has shown a marginal increase over time, it may be expected that pest problems in the region will have similarly increased. This is indeed the case, as both the area of crops in which pests occur, and the area that requires control, have increased in three of the major crops that these pests attack in Henan (Fig.S1).

Among the 130 individual species, the 30 defined as “increasing species” exhibited significant positive trends, the 10 “decreasing species” exhibited significant negative trends, and the remaining 90 “stable species” had non-significant trends (Fig. 3A). Increasing species (n=30) had a mean combined annual abundance of 78,179 individuals which increased by 2.3% per year ($F_{10} = 30.14$, slope = 0.110, $p<0.001$; Fig. 2E); stable species (n=90) had a mean combined annual abundance of 150,825 and showed no overall trend ($F_{10} = 1.96$, slope = 0.023, $p = 0.192$; Fig. 2I); and decreasing species (n=10) had a mean combined annual abundance of 9,156 and decreased by 1.5% per year ($F_{10} = 31.78$, slope = -0.060, $p<0.001$; Fig. 2M).

Among the 30 increasing species, known migratory pest species predominated (n=24), most of which were able to overwinter locally (n=18). Both migratory and non-migratory taxa were included among the 90 stable species, and the majority overwintered locally (n=77). For the 10 decreasing species, declines occurred mainly in certain agricultural pest species (*Mythimna separata*，*Peridroma saucia*), which were also predominantly migratory (n=7), yet most of these taxa were capable of local overwintering (n=8) (Fig. 3B).

Seasonal trends

The increasing, stable, and decreasing species exhibited fundamentally different seasonal patterns. Increasing species had a distinct peak in abundance in August-September (Fig. 4A), stable species

maintained high abundance throughout June-August (Fig. 4B), and decreasing species peaked at the beginning of June (Fig. 4C). Increasing species had consistently positive seasonal trends (Fig. 2F-H), that were significantly positive through the year (p<0.001; Fig. 4D). Stable species also had significant positive trends in spring and autumn (Fig. 2J,L), that were most positive in May (F_{10} = 12.82, slope = 0.080, p=0.005; Fig.4E), but a negative trend in summer (Fig. 2K) that was most pronounced in July (F_{10} = 1.46, slope = -0.024, p = 0.254; Fig. 4E). Decreasing species had consistently negative trends in summer and autumn (Fig. 2O,P), declining most strongly in June (F_{10} = 17.51, slope = -0.074, p=0.002; Fig. 4F) and July (F_{10} = 49.16, slope = -0.081, p<0.0001; Fig. 4F) and only marginally positive in April (Fig. 4F). Thus, there was a consistent pattern, across all groups, of population trends being more positive early and late in the year (especially spring), but most negative in the summer (particularly July; Fig. 2 and Fig. 4).

Summer Climate Trends

June and July are the hottest months in the local area, with a mean temperature across the 24-hour period of 27.6°C (XX: 27.8°C, LH: 27.6°C, MZ: 27.3°C, HY: 27.6°C); the mean daily maximum was 33.1 (XX: 33.0°C, LH: 33.1°C, MZ: 33.4°C, HY: 32.9°C), the mean daily minimum was 22.8°C (XX: 23.1°C, LH: 23.0°C, MZ: 21.8°C, HY: 23.1°C), and the mean temperature during night-time hours (20:00–04:00) was 25.7°C (XX: 25.4°C, LH: 26.2°C, MZ: 25.6°C, HY: 25.7°C). Summer heatwaves (daily maximum temperature ≥35°C) occurred on over 236 (XX: 210, LH: 242, MZ: 275, HY: 216) days in total across the 12 years (average 121 days in June, 115 days in July; Fig. 5A,D,G,J), with an annual average of 19.7 days of heatwave per year. Trend analysis revealed significant intensification of heatwave conditions; they tended to increase in duration (XX: F_{10} = 2.369, increase = 0.832 d yr^{-1}, p=0.155; LH: F_{10} = 0.772, increase = 0.601 d yr^{-1}, p=0.400; MZ: F_{10} = 0.746, increase = 0.500 d yr^{-1}, p=0.408; HY: F_{10} = 0.395, increase = 0.364 d yr^{-1}, p=0.544; Fig. 5B,E,H,K) and became significantly hotter (XX: F_{10} = 15.36, increase = 0.119°C yr^{-1}, p=0.003; LH: F_{10} = 8.761, increase = 0.080°C yr^{-1}, p=0.014, MZ: F_{10} = 14.921, increase = 0.076°C yr^{-1}, p=0.003, HY: F_{10} = 3.525, increase = 0.035°C yr^{-1}, p=0.090; Fig. 5C,F,I,L).

The region also experiences frequent summer heavy rain events. Heavy rain (daily precipitation ≥10 mm) predominantly occurred in June-August during 2013-2024, account for over 80% of the total (Fig. S2). The mean daily precipitation for June-July is 4.6 mm/day (XX: 5.2 mm/day; LH: 4.8 mm/day; MZ: 3.9 mm/day; HY: 4.4 mm/day), with extreme events reaching 250.2 mm/day (XX: 250.2 mm/day; LH: 163.3 mm/day; MZ: 139.5 mm/day; HY: 157.2 mm/day). Trend analysis revealed slight significant increases in duration in MZ (F_{10} = 4.672, increase = 0.360 d yr^{-1}, p=0.056) and HY (F = 7.299, increase = 0.338 d yr^{-1}, p=0.024) and non-significant changes in intensity of heavy rain events (Fig. S2).

Climate Impacts on Insect Population Trends

To assess the impact of climate on seasonal insect population dynamics, we employed stepwise regression to develop optimal models for all 130 species, to evaluate the contributions of climate factors across the three trend groups (increasing, stable and decreasing species) and seasons. The contributions of each factor was assessed by two criteria: (1) the magnitude of the standardized regression coeficients (β in Fig. 6, S3 and S4; factors were considered to have greater contributions if the 95% interval does not include zero), and (2) frequency of selection among all optimal species models (indicated by the number of species above each variable label in Fig. 6, S3 and S4). We focus primarily on population dynamics during summer (Fig. 6) as this is when trends were most divergent. Spring and autumn population dynamics are discussed in less detail and the model outputs can be found in the supplemental material (Fig. S3 and S4).

1. Increasing Species

The 30 increasing species had positive trends throughout the year (Fig. 4D). The principal driver of abundance of these species in each season was the abundance in the previous season, which always had a strong positive relationship (median β = 0.51, 0.71, and 0.79 for spring, summer and autumn abundance, respectively; Fig. 6A, S3A and S4A). The most important climate effects on spring abundance were a positive effect of spring maximum temperature (median β = 0.57; Fig. S3A), plus negative effects of average minimum winter temperature (median β = -0.24; Fig. S3A) and winter precipitation (median β = -0.74; Fig. S3A). Summer heatwave intensity (which significantly increased over time; Fig. 4C) was the most important climate driver of abundance in both summer (median β = 0.41; Fig. 6A) and autumn (median β = 0.53; Fig. S4A). The important climate effects of autumn abundance were a positive effect of the mean summer temperature (median β = 0.32; Fig. S3A). Thus the positive trends of the increasing species were largely driven by hot and dry conditions, particularly the increasing intensity of summer heatwaves (Fig. 6).

2. Stable Species

The 90 stable species had positive population trends in the spring but this was counterbalanced by negative trends in the summer (Fig. 4E). Not surprisingly, only a few climatic factors had strong effects on abundance of stable species. The only consistent one was a positive effect of the previous seasonal abundance in each season (median β = 0.36, 0.62, and 0.52 for spring, summer and autumn abundance, respectively; Fig. 6B, S3B and S4B). Additionaly, spring populations responded positively to maximum spring temperatures (median β = 0.48) and spring precipitation (median β = 0.26) (Fig. S3B), while autumn abundance responded negatively to the minimum autumn temperature (median β = -0.39; Fig. S4B).

3. Decreasing Species

The ten decreasing species had almost conistently decreasing populations trends, which were strongest in summer (Fig. 4F). Once again, the previous season's abundance had a conistently positive effect on abundance in the present season (median β = 0.36, 0.62, and 0.79 for spring, summer and autumn abundance, respectively; Fig. 6C, S3C and S4C). There were many and complex effects of climate factors on decreasing species, especially temperature variables which tended to have positive effects in spring but negative effects in summer and autumn. Warmer spring minimum temperatures (median β = 0.57) and mean temperatures (median β = 0.34) had a positive effect on spring abundance (Fig. S3C), whereas hotter summer mimmum temperatures had a negative effect on summer abundance (median β = -0.50; Fig. 6C) and hotter summer and autumn mean temperatures had a negative effect on autumn abundance (summer: median β = -1.29; autumn : median β = -0.57; Fig. S4C). Additionally, the intensity of summer heatwaves had strongly negative effects on summer abundance (median β = -0.64; Fig. 6C) and autumn abundance (median β = -0.75; Fig. S4C) and the minimum temperature of summer (median β = -0.50; Fig. 6C) or autumn (median β = -0.29; Fig. S4C) also had a negative effects on its summer or autumn abundance. Thus negative trends of the decreasing species are a result of sensitivity to hotter temperatures in the latter part of the year, especially duriung summer heatwaves (Fig. 6C).

Discussion

There is growing concern that warming climates are negatively effecting population trends of insects worldwide [12–15]. In particular, summer heatwaves have recently been implicated in the declines of several groups of insects [18–20]. Given that in the past few decades, summer heatwaves have increased in frequency, severity and duration, and are predicted to continue to do so [21–23], they are expected to have increasingly adverse influences on insect population trends. We show that in line with these global patterns of warming, summer heatwaves (days with maximum temperatures ≥35°C during June and July) in east-central China increased in severity and duration over the 12-year study period (2013-2014), with heatwave conditions typically occurring on about 20 days and with a mean daily maximum of >37°C by the end of the study period. We therefore expected that insect population trends in the region would largely respond negatively to these extreme summer temperatures, which are becoming hotter and are occurring more frequently.

However, in contrast to expectations, the community of 130 species of nocturnal migratory insects caught by a searchlight trap in an intensively agricultural region of east-central China showed a moderate (marginally significant) increase in annual combined abundance over the 12-year study period. At the seasonal level, the combined abundance of the 130 species significantly increased during spring and autumn, but this pattern broke down in the summer, when the overall population trend was flat (albeit with a very slight downward trend). These contrasting seasonal trends indicate that, on average, the community of nocturnal species responded positively to warming temperatures during the start and end of the annual cycle, but not to the extreme temperatures which occur during the middle of the year, like other studies from Europe and North America [18–20]. Analysis of trends at the community level

masks the range of individual responses, however, and some species in our study have indeed declined sharply over the study period in response to changing climate, including *Tipula sinica* (Diptera), all unidentified Chrysopidae (Neuroptera), *Aloa lactinea* (Lepidoptera), and *Maladera ovatula* (Coleoptera). Declining species were in the minority though (only 8% had significant negative annual trends), with more two times as many species (23%) having significant positive annual trends, and most species (69%) had effectively stable populations with non-significant annual trends.

The divergence between the increasing and decreasing species categories is primarily driven by summer heatwave conditions. Considering the 10 species that significantly decreased over the whole year, they had negative trends in each season, but the magnitude of the decline was considerably stronger in the summer than in spring and autumn. The greatest climate contributor to their declines was summer heatwave intensity and higher temperatures, which had strong negative effects on both summer and autumn population trends, so this category is particularly sensitive to hotter summer conditions. The 90 stable species responded positively to warmer spring conditions (maximum temperature in spring) and had a positive trend in this season; however, trends were non-significant in summer and autumn. This indicates that these species are currently coping with the extreme summer temperatures, and any negative impacts are offset by the positive effect of warming springs. However, the balance may shift as summers continue to warm and heatwaves become more extreme [23, 51], resulting in more species declining in the summer. Contrary to expectations, almost one-quarter of the species (30) had consistently significant positive trends, even in summer, and in this category summer heatwave intensity was positively associated with abundance in both summer and autumn. Thus, even though maximum daytime temperatures during summer heatwaves are quite considerable (averaging >37°C by the end of the study period), these species have responded positively to the rising temperatures and must be pre-adapted to consistently hot temperatures.

The overall generally positive response to increasing extreme summer temperatures we observed in our study is intriguing, as they are not consistent with insect trends in response to climate reported elsewhere [12–17] and also at the northern end of the flyway in the Bohai Gulf of NE China [10, 39]. Of particular relevance to our study (which was conducted in an expansive area of intensive agriculture), the global analysis of Outhwaite et al [15] produced sharply contrasting results in relation to impacts of climate warming on insects inhabiting regions of intensive agriculture. Their models indicated that recent warming has resulted in a 49% reduction in insect abundance in intensive agriculture when compared to primary vegetation with no warming, and this decline is present in both tropical and temperate zones. The severity of declines occurring in intensive agricultural lands is believed to be driven by the reduced availability of microhabitats that can buffer the effect of hotter temperatures, such as shady locations in which insects can behaviourally thermoregulate, and thus insects in these habitats will be more sensitive to increasing temperatures [15, 52, 53]. How can we explain the contradictory results of our study, in which there has been a general increase in insect abundance alongside sharply

rising summer temperature extremes, in a region that already had hot summers with little natural habitat to buffer those climate extremes?

One potential explanation is that our study was restricted to insects that, as adults at least, are active solely or predominantly at night. Nocturnal species may partly buffer the effects of hotter daytime temperatures by carrying out energetically expensive activities such as flight in the cooler night-time period. Additionally, adults and immature stages of nocturnal species can avoid exposure to extreme daytime temperatures by avoiding activity and seeking out cooler micro-habitats. The predominantly nocturnal nature of this community of insects perhaps partly explains the differences between the two studies. However, in many regions and habitats, insect activity is often greater at night than during the day, especially for the larger species we have focussed on here [54]. Thus, most other studies of insect trends that have reported declines in response to climate change will have contained many nocturnal species. Hence, nocturnal activity cannot be the sole explanation of this disparity.

A more plausible reason for the contradictory results is that the community of 130 species studied here is largely comprised of migratory crop pests [10, 39, 40]. Compared to the generality of declining trends reported in many studies, several strands of evidence suggest that migrant insects seem to be faring more positively than non-migratory species. Firstly, insect migrations often occur on an enormous scale, involving millions of individuals moving overhead [40–41, 55–60]. Secondly, while consistent and systematic long-term monitoring of aerial migrants has not yet been achieved, there are indications that aerial migrant populations are stable or even increasing [36, 56, 61]. Thirdly, many migratory species are also crop pests [38], and several meta-analyses have found evidence that the incidence of crop pests is increasing in response to warming [31–34]. Thus, migratory crop pests are likely pre-adapted to a warming world and can not only cope but flourish under conditions of summer heatwaves, even in intensive agriculture with its absence of climate-buffered microhabitats and with decades of chemical control.

An important aspect of this study is the focus on insect trends in China, a region which has been largely missing from the abundance of recent syntheses of insect trends [2, 3, 4, 6, 15, 17]. A commonly held perception is that the intense conversion of natural habitat to agricultural land and urbanisation will have severely depleted the insect fauna of East China, but data is lacking to support this contention. While we believe this will undoubtedly be the case for many specialist and sedentary species, the evidence from Huang et al [40] and the current study indicates that a (relatively depauperate) subset of nocturnal migratory species has adapted to the changing environment and climate, and these generalists are faring rather well. It seems quite plausible that, due to the very long history of extensive and intensive agriculture in this region, that many of the species we assessed have become preadapted to thriving in agricultural landscapes [38]. Surveys of other groups, such as day-flying insects and non-migratory species are urgently needed to assess their population trends in China.

Conclusion

In summary, our analysis demonstrates fundamentally divergent thermal adaptations between increasing and decreasing species in response to summer heatwaves. Increasing species benefit from both spring demographic carry-over effects and positive responses to most spring-summer climate variables, especially summer heatwaves, demonstrating successful thermotolerance that facilitates population growth. By contrast, declining species demonstrate contrasting responses, where the contributions of populations from the previous seasons are offset by the negative spring-summer climate effects, especially summer heatwaves, resulting in consistent population declines under increasing heatwave stress.

Methods

Searchlight Traps and Insect Trends

Long-term monitoring of larger, actively migrating nocturnal insects was carried out nightly (18:00 to 06:00 h local time) from 15 March to 31 October each year, during 2013 to 2024, with a searchlight trap network at four sites in Henan Province, Xinxiang city (XX, 35.02°N, 113.69°E) , Luohe city (LH, 33.63°N, 113.98°E), Mengzhou city (MZ, 34.91°N, 112.85°E) and Huaiyang city (HY, 33.68°N, 114.99°E) (Fig.1). Those regions are dominated by extensive areas of intensive agricultural land [38, 40]. The searchlight trap comprised a 1000 W metal halide lamp and parabolic reflector (model GT70, Shanghai Yayuan Light Electronic Company, Shanghai), which projects a light beam vertically up to more than 500 m height, and a large metal funnel and net for collecting insects. Searchlight traps are an established method for monitoring nocturnal migrant insects, as their powerful upward-pointing beam preferentially attracts and captures individuals engaged in active migratory flight high above the ground [10, 38–40, 45]. Night-flying migrants can travel hundreds of km in a single night's flight [62, 63]. Thus, catches from a searchlight trap are indicative of populations of migrants moving through the wider region, rather than simply representing populations in the immediate vicinity of the trap, in much the same way as has been demonstrated for the Rothamsted Insect Survey 12-m tower suction traps [35] and for vertical-pointing radar systems [40, 64]. Nocturnal insect migrants are often concentrated in temperature and wind-speed maxima in the atmosphere which typically occur several hundred meters above ground [45, 46, 64, 65], providing further evidence that captures in the searchlight traps are unlikely to be predominantly local in origin.

Over the study period, we collected insects at four different locations, and we treat these as a distinct collection for each species in each region. All together 262 species were recorded at least once. Nightly catches were hand-sorted and identified to species every day through the study period (253 species in location XX, 35 species in LH, 4 species in HY and 3 species in MZ; among these, 33 species were recorded in at least two sites), and all individuals of larger species (i.e., excluding small species such as aphids and rice planthoppers) were systematically counted. After quality control to remove species with low abundance throughout the period (average annual abundance <25 individuals), 130

species with adequate data in each year were retained for further analysis (Table S1). This species pool is predominantly comprised of migrant crop pests [40]. For each species, total abundance, annual population trend over the 12-year period, and monthly population trends (for April - October) over the 12-year period were calculated. Species with significantly positive annual trends were categorised as "increasing"; species with significantly negative annual trends were categorised as "decreasing"; and all other species were categorised as "stable" (Table S1).

Climate Data

Meteorological data for climate impact assessment were obtained from the China national basic meteorological observation station close to each of the searchlight traps, covering 2013-2024. We collated daily mean (T_{mean}), maximum (T_{max}) and minimum (T_{min}) daily temperatures, and precipitation (P), in four seasons – spring (March-May), summer (June-July), autumn (August-October), and winter (November-February), which correspond to distinct migratory periods of insects in this region [38–40] – for comparison with insect population trends.

Summer Extreme Weather Events

We examine two types of summer extreme events: heatwaves and heavy rainfall. Following meteorological definitions and considering their distinct biological impacts, we employed absolute thresholds rather than relative percentiles (e.g., 95th percentile) to classify summer extreme events. Heatwaves (HT) were defined as days with daily $T_{max} \geq 35°C$, characterized by both duration (HTD, total number of days with $T_{max} \geq 35°C$ during June-July) and intensity (HTI, mean T_{max} across heatwave days). Similarly, heavy rainfall (HR) events were defined as days with daily precipitation ≥ 10 mm, characterized by both duration (HRD, total occurrence days during June-July) and intensity (HRI, mean daily precipitation across heavy rain days).

Stepwise Regression

We performed forward stepwise regression modelling to assess how insect populations respond to climate factors, systematically evaluating predictors from three categories: (1) population abundance of insects in the previous season; (2) climatic conditions in previous seasons; and (3) climatic conditions in the current season. Modelling incorporated distinct predictor sets for each season: spring models included autumn population abundance with winter and spring temperatures (T_{mean}, T_{max}, and T_{min}) and precipitation; summer models included spring population abundance with spring and summer temperatures and precipitation, plus summer extreme weather event indices (HTD, HTI, HRD and HRI); autumn models included summer population abundance with summer and autumn temperatures and precipitation, plus summer extreme weather event indices. We performed stepwise regressions for the 130 individual species in three seasons, with model selection proceeded iteratively by sequentially

adding predictors to minimize the Akaike Information Criterion (AIC value), with maximum step limits set as half of the sample size to prevent overfitting (maximum 2-6 predictors depending on season and species). The optimal models demonstrated strong explanatory power (mean R^2= 0.78 across all species-season combinations). We quantified the importance of each predictor based on how many species had it selected in its optimal model, and assessed individual contributions of each predictor by the standardized regression coefficients (β), enabling cross-species-seasons comparison of climate response patterns.

Declaration of competing interests

The authors declare no competing interests.

Ethics statement

Investigations involving insects followed institutional regulations and no human subject was involved in this study.

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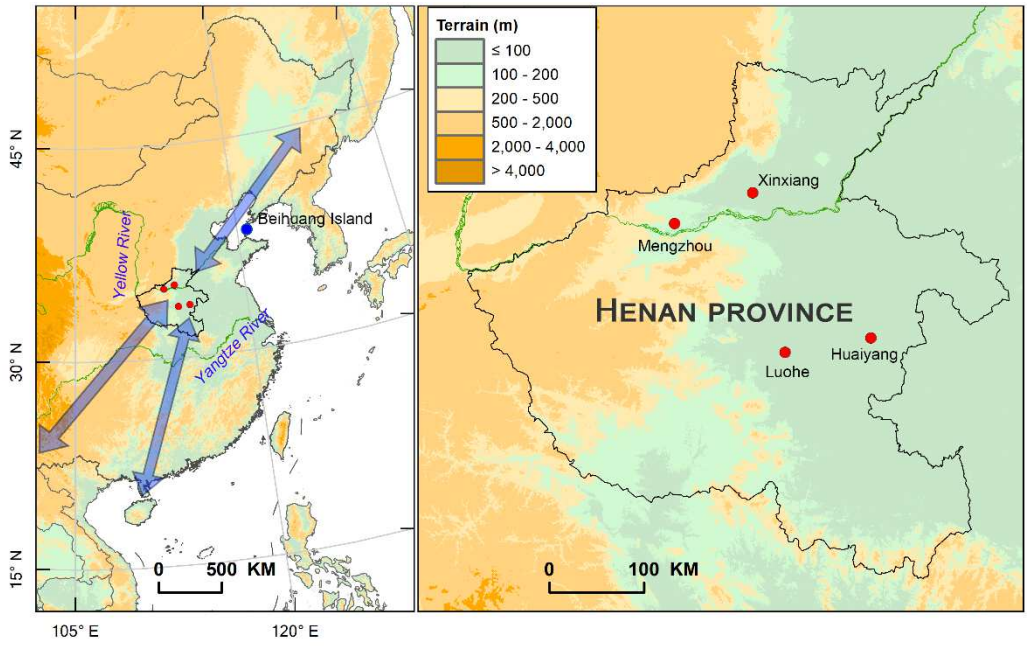

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611 **Fig.1** Map of East China, showing the main migration routes of the East Asian Insect Flyway [38]. Our
612 field survey region is in Henan Province in east-central China; the four searchlight sampling sites (red
613 dots) are in Xinxiang city, Luohe city, Mengzhou city, and Huaiyang city. The other long-term
614 searchlight trap site we refer to (Beihuang Island) is indicated by a blue dot.

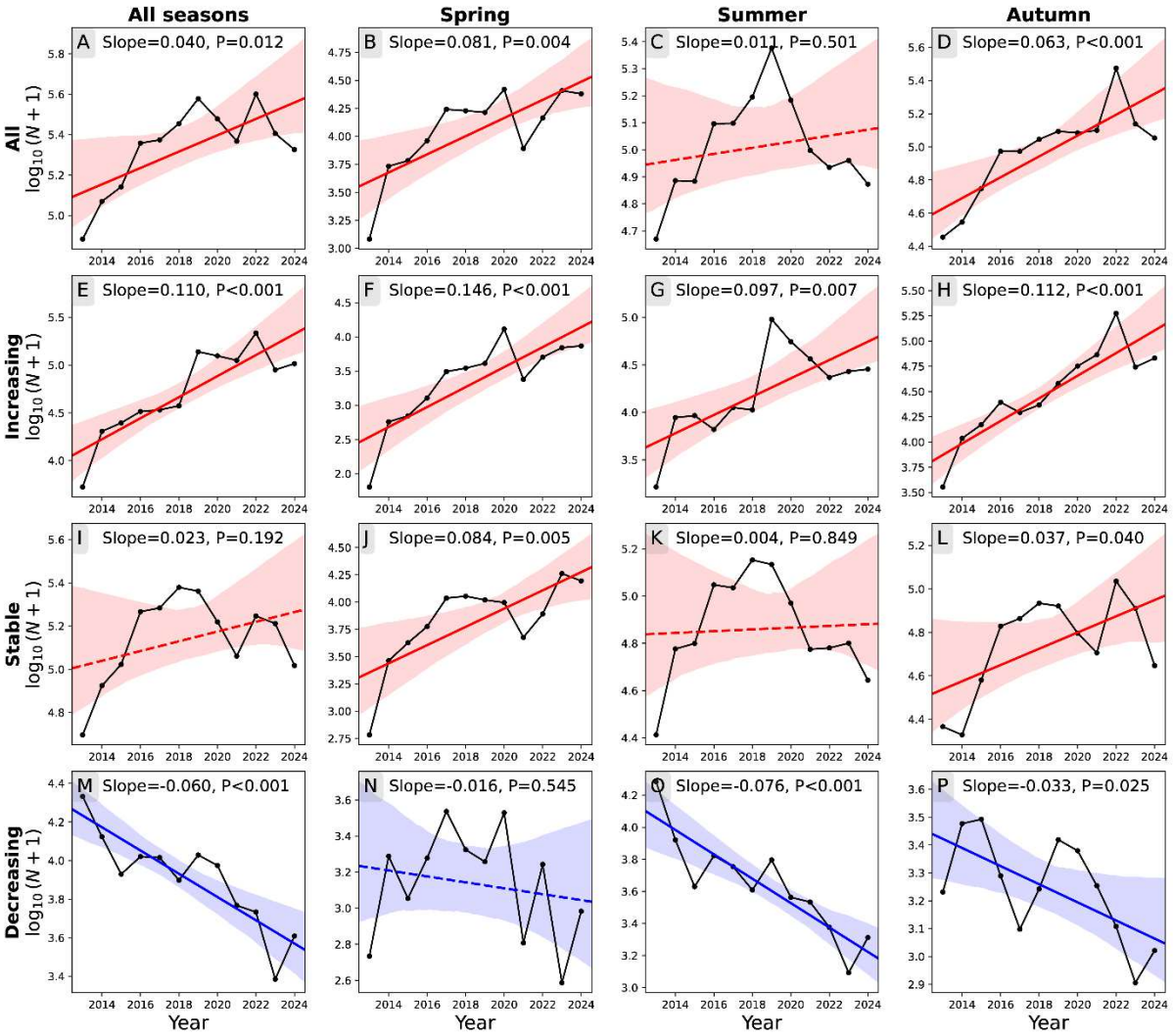

Fig.2 Community abundance trends of migratory insect from 2013 to 2024 for the whole year and each season. (**A-D**) Annual log combined abundance of 130 species; (**E-H**) Combined abundance of 30 species with increasing trends; **(I-L**) Combined abundance of 90-species with stable trends; (**M-P**) Combined abundance of 10 species with decreasing trends. Regression lines are solid if they are significant and dashed if they are not significant; red indicates a positive trend and blue indicates a negative trend.

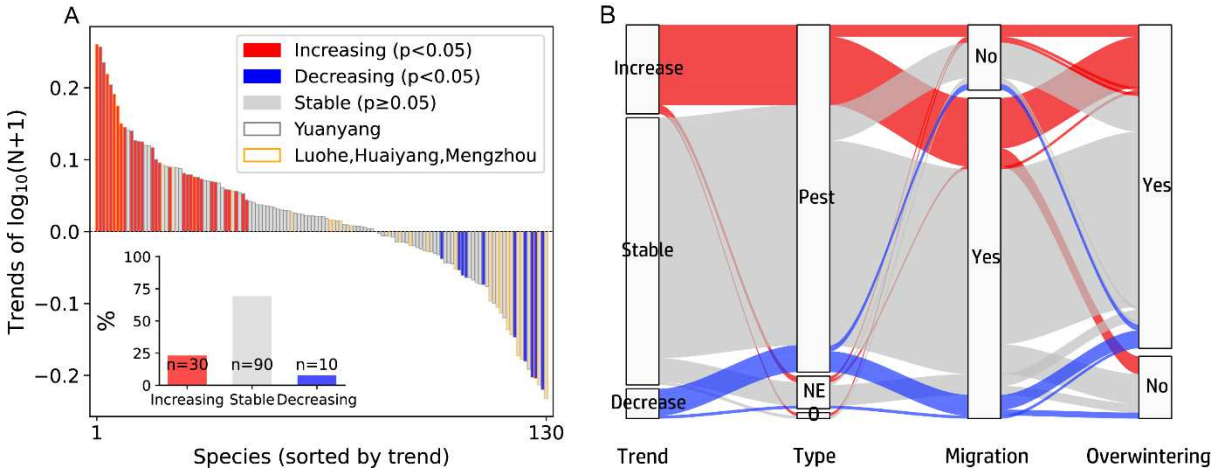

Fig.3 Abundance trends of individual species associating with its local biological characteristics. (**A**) Species' trends distribution; (**B**) The relationship between species' trends, agriculture interaction, and local overwintering. Red bars indicate significant positive trends ("increasing species"), grey bars indicate non-significant trends ("stable species"), and blue bars indicate significant negative trends ("decreasing species"). The inset plot in (A) shows the numbers and percentage of each group.

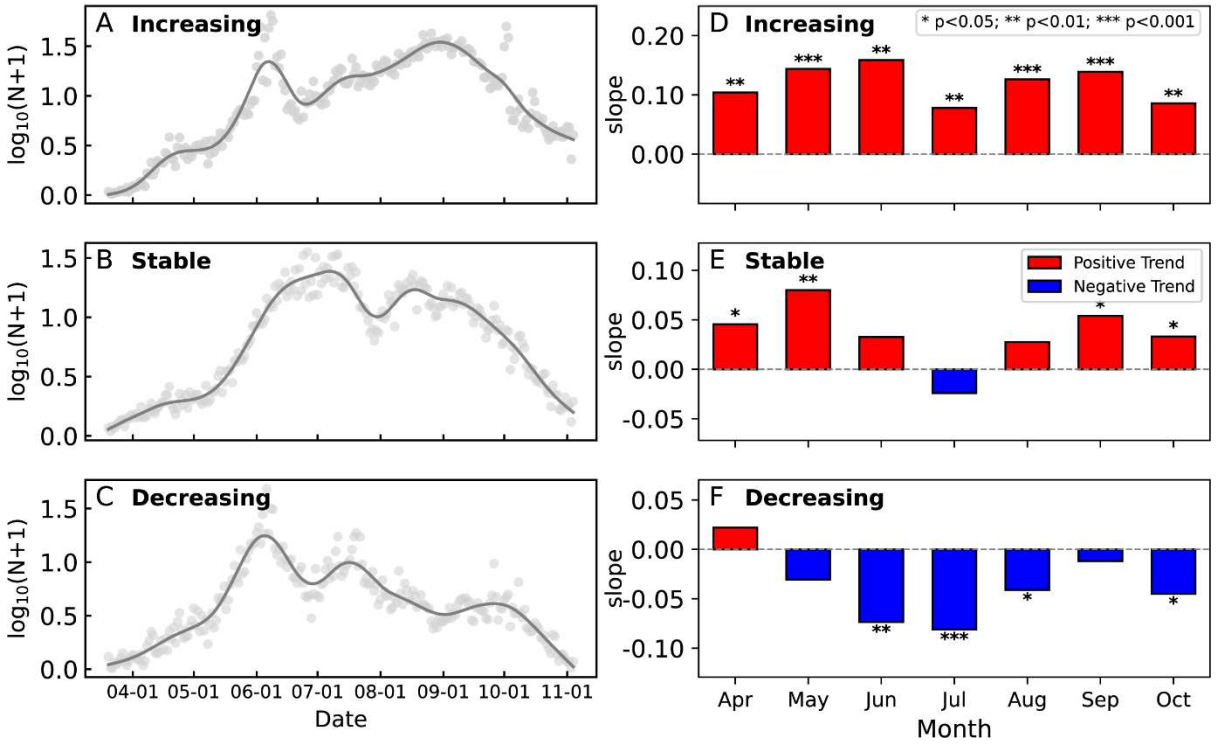

Fig.4 Daily averaged variations and monthly linear trends in abundance of increasing, stable, and decreasing species over 2013-2024. (**A**) Daily averaged variation of increasing; (**B**) Daily averaged variation of stable; (**C**) Daily averaged variation of decreasing; (**D**) Monthly linear trends of increasing; (**E**) Monthly linear trends of stable; (**F**) Monthly linear trends of decreasing. Light grey dots represent long-term averaged daily abundance values, and lines indicate generalized additive model (GAM) smoothing curves. Red and blue bars indicate positive and negative trends, with asterisks denoting significance levels (*p<0.05, **p<0.01, ***p<0.001).

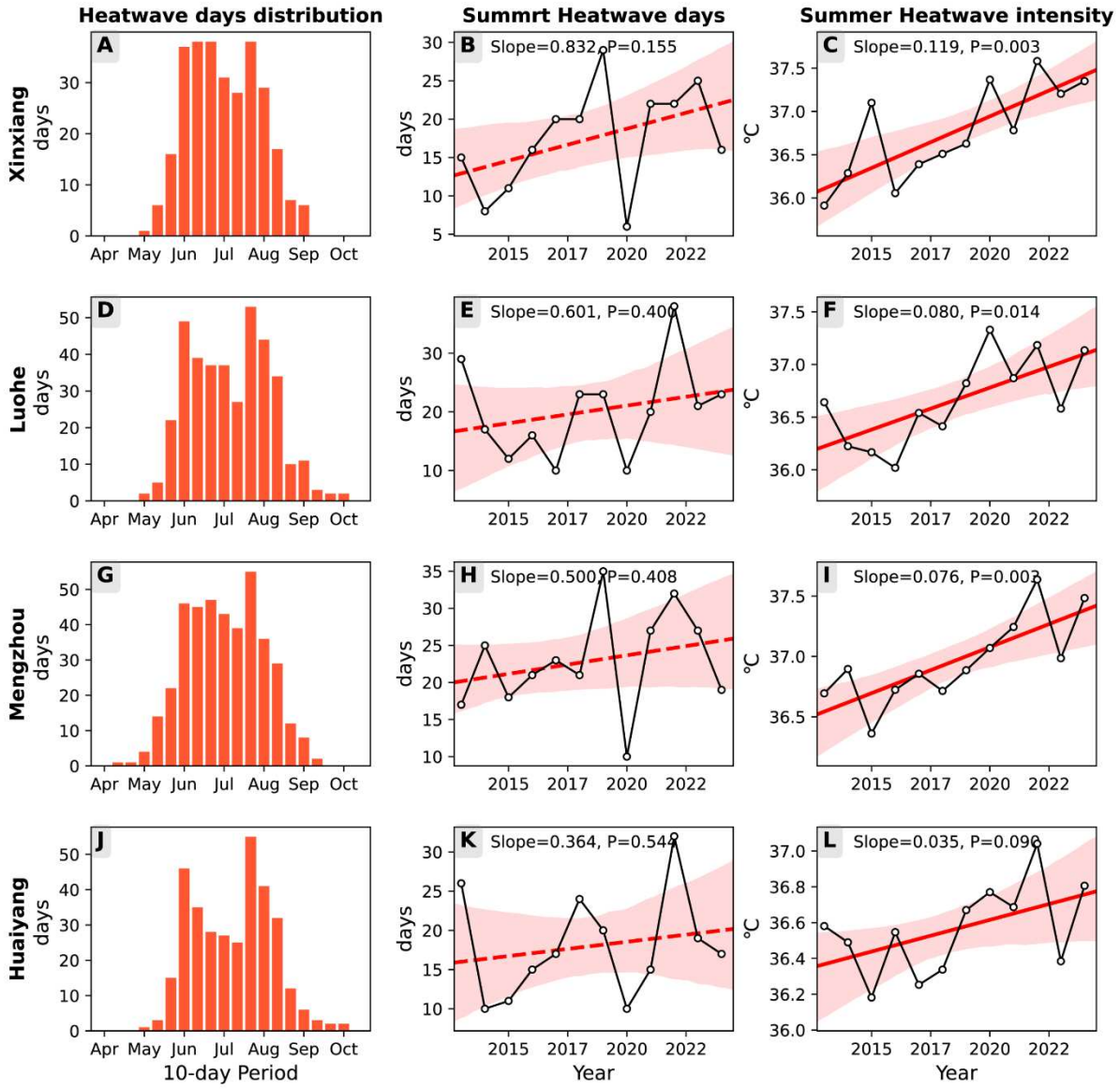

Fig.5 Heatwave daily distribution, summer heatwave duration and summer heatwave intensity during 2013–2024. (**A-C**) XX city; (**D-F**) LH city, (**G-I**) MZ city, **(J-L**) HY city. Heatwaves are defined as days with daily maximum temperature ≥35°C. summer heatwave days were the total days of up 35°C during June and July and summer heatwave intensity calculated as the mean daily maximum temperature across all heatwave days during June and July.

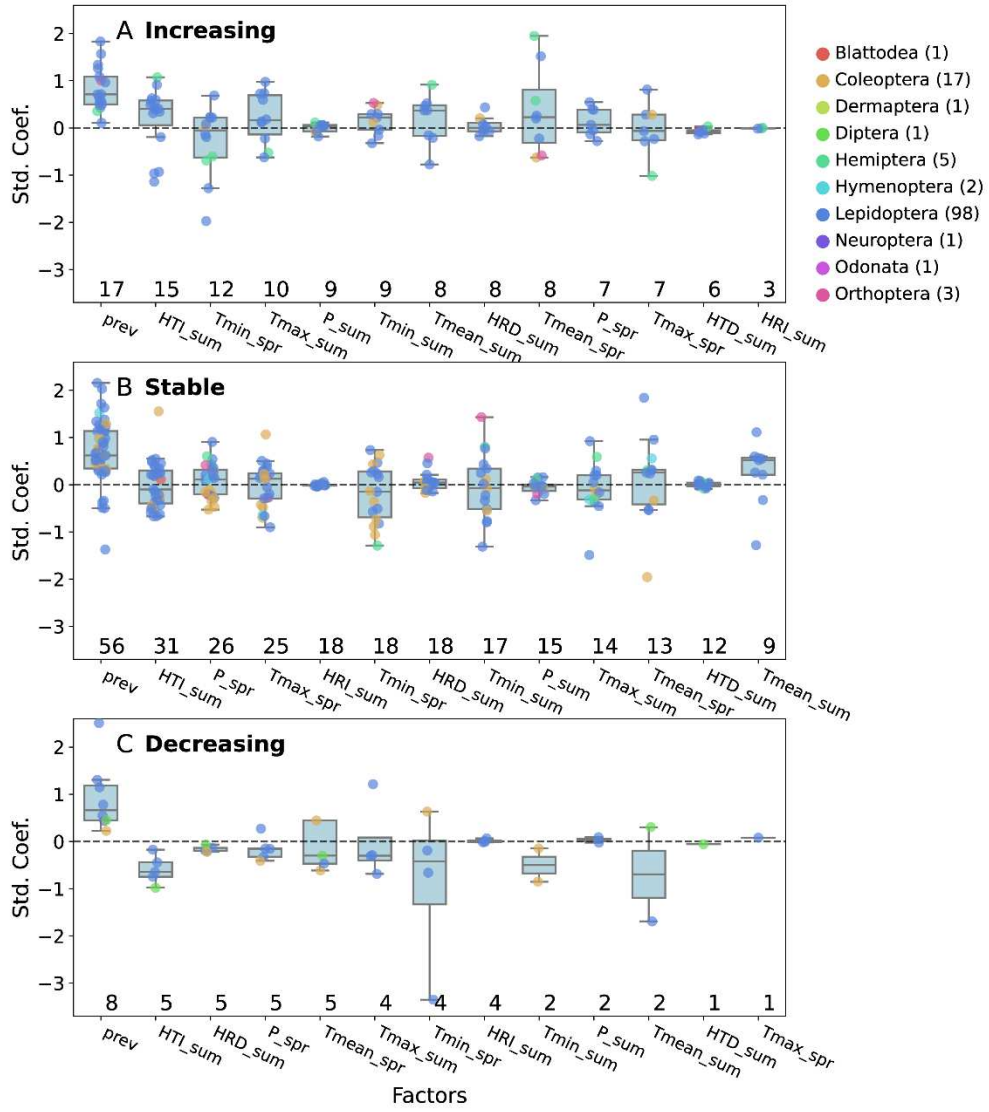

Fig.6 Contribution of different climatic factors to insect population trends in summer for (**A**) increasing species; (**B**) stable species; (**C**) decreasing species groups. Factors include: previous spring abundance (prev), temperature (T) indices, precipitation (P) indices, heatwave intensity (HTI) and duration (HTD), and heavy rain intensity (HRI) and duration (HRD), experienced in spring (spr) and summer (sum). Contributions quantified by standardized regression coefficients (β) from the optimal model selected through forward stepwise regression. Numbers above each factor indicate how many species' optimal models have selected that variable. The dots represent values of β for individual species, colour-coded by insect order, and values in parentheses are the total number of species in each order that have been assessed.

Supplementary Files

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