ECOLOGY

Long-term insect censuses capture progressive loss of ecosystem functioning in East Asia

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Insects provide critical ecosystem services such as biological pest control, in which natural enemies (NE) regulate the populations of crop-feeding herbivores (H). While H-NE dynamics are routinely studied at small spatiotemporal scales, multiyear assessments over entire agrolandscapes are rare. Here, we draw on 18-year radar and searchlight trapping datasets (2003–2020) from eastern Asia to (i) assess temporal population trends of 98 airborne insect species and (ii) characterize the associated H-NE interplay. Although NE consistently constrain interseasonal H population growth, their summer abundance declined by 19.3% over time and prominent agricultural pests abandoned their equilibrium state. Within food webs composed of 124 bitrophic couplets, NE abundance annually fell by 0.7% and network connectance dropped markedly. Our research unveils how a progressive decline in insect numbers debilitates H trophic regulation and ecosystem stability at a macroscale, carrying implications for food security and (agro)ecological resilience during times of global environmental change.

INTRODUCTION

Standardized inventories have uncovered 41 to 67% drops in arthropod biomass over the past decade in Germany's terrestrial ecosystems—driven by anthropogenic factors (e.g., habitat loss and agrochemical pollution), agricultural intensification, and climate change Arthropod decline in grasslands and forests is associated with landscape-level drivers (*1*–*4*). Similar phenomena have been recorded through long-term surveys or comparative historical studies in other settings, primarily in Western Europe or North America (*5*, *6*). Considering how insects feature prominently within trophic webs and act as prime ecosystem service (ES) providers (*7*, *8*), long-term insect declines are expected to negatively affect societal well-being. Regrettably, published datasets mainly record temporal patterns in insect abundance, diversity, or biomass (*9*, *10*) but rarely document trends in ecosystem function. Food webs capture the extent to which energy flow and species diversity shape ecosystem function (*11*–*13*), thus constituting unique analytical lenses to assess the broader social-environmental consequences of the current (insect) biodiversity crisis.

Insect biodiversity support the delivery of ES such as biological pest control and pollination (*7*). Both ES underpin food and nutrition security and human welfare and they are (conservatively) valued at a respective \$24 $\mathrm{ha}^{-1}\mathrm{year}^{-1}$ and \$14 $\mathrm{ha}^{-1}\mathrm{year}^{-1}$ globally (*14*). In the Asia-Pacific region, insect natural enemies (NE) mitigate invasive pest attack—reconstituting crop yields by 73 to 100% and annually generating on-farm benefits of \$14.6 billion to \$19.5 billion year^{-1} in a (small) set of food crops (*8*). However, the strength and stability of these ES is negatively affected by land-use change (*1*, *15*), ecosystem simplification (*16*), and agrochemical inputs, i.e., pesticides and fertilizers (*17*, *18*). Given the pace of agricultural intensification and extent of pesticidal pollution in Asia, these effects could be locally exacerbated. However, so far, broad-scale impacts on insect numbers, ecological interactions, or ensuing ES have not been quantitatively assessed.

Each year, countless insects take to the air to undertake long-distance windborne migration (*19*). Large numbers of (crop-feeding) herbivores (H) and NE undertake migratory flight with their movements in par or temporally lagged (*20*, *21*), thus contributing to energy flows and ES delivery over extensive spatial scales. For example, the specialist parasitoid *Cuphocera varia* Fabricius disperses together with its lepidopteran host, *Mythimna separata* (Walker) (*22*). Similarly, the predatory bug *Cyrtorhinus lividipennis* (Reuter) exhibits synchronized migration with its prey, the rice brown planthopper *Nilaparvata lugens* (Stål) (*23*). The sheer numbers of codispersing H and NE reflect the magnitude of the related ES. For instance, up to 4 billion hoverflies (80 tons of biomass) annually undertake migratory flight between the United Kingdom and Europe, with their offspring consuming 6 trillion crop-infesting aphids and visiting billions of (crop and noncrop) flowers (*24*).

Organisms that act at higher trophic levels can exert powerful indirect impacts on lower trophic levels through so-called "trophic cascades." These phenomena shape the overall structure and functioning of entire ecosystems (*25*), although large-bodied predators, e.g., vertebrates may have stronger (per capita) impacts on trophic regulation, H release and food web biomass than smaller ones such as insects (*26*). Irrespective of the above and despite large variability between ecosystems, individual biota, or trophic levels (*27*, *28*), insect biological control in agricultural systems is often predicated on the concept of trophic cascades (*29*). Empirical research has also linked biodiversity to ecosystem function (BEF) and has covered themes such as top-down trophic regulation (*30*), yet this work is primarily restricted to small spatial scales (*31*, *32*). BEF studies have shown how insect species are connected through multiple feeding linkages, with insect parasitoids and predators adding to the ecological regulation of crop-feeding H at the field or farm scale. Food webs with more modular

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architecture have a higher diversity of functional group, and food web size, complexity, and assemblage all shape functional diversity (*33*). As a result, insect biodiversity and food web structure jointly mediate natural biological control in agricultural fields (*13*, *16*).

Up until present, insect biodiversity studies have largely centered on (comparatively) small sets of taxa within one single trophic level, e.g., diurnal butterflies, (managed) bees, or dung beetles (*3*, *34*, *35*). Meanwhile, surveys that encompass multiple trophic levels or that cover developing countries are rare. Also, given the demands on time and taxonomic expertise, most long-term insect censuses have focused on a subset of terrestrial or aquatic ecosystems (*6*, *36*). One notable exception is the multidecadal survey of migratory H and associated biota within the East Asia monsoon system (*20*). This atmospheric circulation system lays at the intersection of the Pacific Ocean and the Eurasian continent, spanning temperate and (subtropical) ecological zones. Beihuang Island (BH; 38°24′N, 120°55′E), a small island located within China's Bohai Bay, is positioned within one prime (insect) migration corridor and constitutes a unique setting to assess insect BEF over space and time (*37*).

In this study, we use long-term migration datasets from BH to assess temporal trends in the abundance of individual insect taxa or feeding guilds (i.e., H and NE) and to record the NE/H abundance ratio for established bitrophic (NE-H) couplets. Our work provides unprecedented insights into insect population dynamics, H-NE coevolution, and the overall strength and stability of core ecosystem functions, i.e., predation and parasitism. Our work thus constitutes an important stepping stone toward systematically gauging and remediating (agro)ecological resilience in the face of biodiversity loss and pervasive environmental change.

RESULTS

Temporal trends in insect abundance

Over 2003–2020, a total of 3,124,778 individual insects (including ants, flies, and aphids; Fig. 1, A and C, and fig. S2, I and J) were captured with searchlight traps at BH while radar observations recorded 9,183,601 migratory individuals (Fig. 1B). The H, NE, and "neutral" guilds primarily consisted of Noctuidae, Libellulidae, and Tipulidae, respectively (table S2). However, all 2007 radar readings were lost, and mechanical issues resulted in incomplete radar records for the spring of 2003, 2009, 2011, 2014, and 2020 and the fall of 2011 and 2014. Radar data were thus not as complete as searchlight trap records and were not included in subsequent analyses. As aphids, Tachinid flies and ants were not systematically monitored over the 18-year study period (Fig. 1C and fig. S2, I and J), these taxa were excluded from further analyses. Searchlight trapping and radar data revealed a (marginally) substantial decline in total migratory insect abundance over the past 18 years (Fig. 1, A and B). More specifically, overall insect abundance decreased by 0.4% per annum or 7.6% over the entire study period (Fig. 1A). While searchlight trapping and radar monitoring detected significant interannual variation in insect population size (searchlight: $F_{2,51} = 126.63$, $P < 0.001$; Fig. 1A; radar: $F_{2,34} = 3.66$, $P = 0.04$; Fig. 1B), overall insect abundance within a given year was highest during summer (Fig. 1, A and B). Over the course of 7 years, a total of 18,969 aphids were captured, and this H taxon attained higher abundance during spring than in summer ($F_{1,7} = 7.039$, $P = 0.033$; Fig. 1C).

Coarse-grained H-NE population trends

After removing neutral insects (e.g., reproductive Formicidae), unidentified species, and aphids, we retained a database of 2,856,434 individuals involving 80 H species (five orders: 20 families) and 18 NE species (five orders: 8 families; table S1). In this database, overall NE abundance progressively declined at a rate of 0.85% per year over the 18-year time period ($F_{1,16} = 15.66$, $P = 0.001$; Fig. 2A) and the NE/H abundance ratio followed a 2.5-year oscillation cycle [$y = 0.20 + 0.12\sin[2.55(x - 84.08)]$, $R^2 = 0.29$; Fig. 2A]. Meanwhile, NE dominance declined ($F_{1,16} = 6.75$, $P = 0.02$; Fig. 2B), and NE diversity increased markedly ($F_{1,16} = 24.28$, $P < 0.001$; Fig. 2C). Summer abundance of H and NE (i.e., Hsu and NEsu) consistently declined over the survey period (Hsu: $F_{1,16} = 5.61$, $P = 0.031$; NEsu: $F_{1,16} = 15.55$, $P = 0.001$; Fig. 2D), with the steepest declines in NEsu (i.e., 1.07% per annum; Fig. 2D). Overall population abundance equally declined for seven main NE families (fig. S2, A and C to H) except Carabidae (fig. S2B), with the sharpest decline for the (single-species) Libellulidae at 1.03% per annum ($F_{1,16} = 8.03$, $P = 0.01$; fig. S2A).

Within a given year, both H and NE communities underwent population growth: Fall H abundance ($\mathrm{H_f}$) was consistently higher than spring abundance ($\mathrm{H_s}$; $t_{17} = -11.06$, $P < 0.001$; fig. S3A), and similar patterns were recorded for NE ($t_{17} = -5.43$, $P < 0.001$; fig. S3B). $\mathrm{NE_f/H_f}$ was lower than $\mathrm{NE_s/H_s}$ ($t_{17} = 2.86$, $P = 0.011$; fig. S3C), reflecting how NE populations respond to H population buildup within a given year. Also, relative NE spring abundance ($\mathrm{NE_{sn}/H_{sn}}$) negatively related to H fall abundance ($\mathrm{H_{fn}}$; Table 1). Last, $\mathrm{H_{fn}/H_{sn}}$ (i.e., H fall abundance divided by H spring abundance) exhibited a 2.2-year oscillation cycle (Fig. 3A), 0.5 year shorter than the respective $\mathrm{NE_{fn}/NE_{sn}}$ (Fig. 3A).

Between years, $\mathrm{H_{sn}/H_{fn-1}}$ (i.e., H spring abundance divided by H fall abundance in the preceding year, Fig. 3B) followed a 2.8-year oscillation cycle, 0.3 years longer than the respective $\mathrm{NE_{sn}/NE_{fn-1}}$ (Fig. 3B). The interannual NE ratio $\mathrm{(NE/H)_{sn}/(NE/H)_{fn-1}}$ (i.e., NE/H ratio of spring versus fall of the preceding year) was higher than the interseasonal ratio $\mathrm{(NE/H)_{fn}/(NE/H)_{sn}}$ ($t_{16} = -2.93$, $P = 0.01$; Fig. 3C), mirroring how NE and H are also linked between years. Absolute NE abundance during a given season mediated H population growth [i.e., $\mathrm{GRH_n}$ representing $\mathrm{(H_n - H_{n-1})/H_{n-1}}$] over the subsequent one ($\mathrm{GRH_n}$: $F_{1,33} = 26.51$, $P < 0.001$; Fig. 4A). However, while absolute NE fall abundance positively related to H population growth during the following spring ($\mathrm{GRH_{sn}}$: $F_{1,15} = 5$, $P = 0.041$; Fig. 4B), these patterns were not recorded intra-annually, i.e., for spring-time NE populations affecting H population growth during fall (Fig. 4C). At both an inter- and intra-annual basis, H and NE abundance in the preceding season negatively related to H abundance—possibly reflecting intraspecific competition or NE-mediated population regulation (Table 1).

Correlation analysis showed how annual H and NE abundance follow a binomial distribution. NE abundance thus rapidly increases with H up to a certain value, to then exhibit a gradual decline ($y = 14.29x - 1.36x^2 - 33.08$, $R^2 = 0.26$; fig. S4A). Within a given year, monthly NE abundance also increased with that of H ($F_{1,109} = 122.14$, $P = 0.00$; fig. S4B). Both H and NE abundance thus showed clear seasonality (H: $F_{6,111} = 68.03$, $P = 0.00$; NE: $F_{6,105} = 40.79$, $P = 0.00$; fig. S4C), although the respective population dynamics differed markedly ($t_{110} = 16.586$, $P = 0.00$; fig. S4C). Peak monthly H abundance levels in September was 308-fold higher than that in April, and peak monthly NE abundance in August was 389-

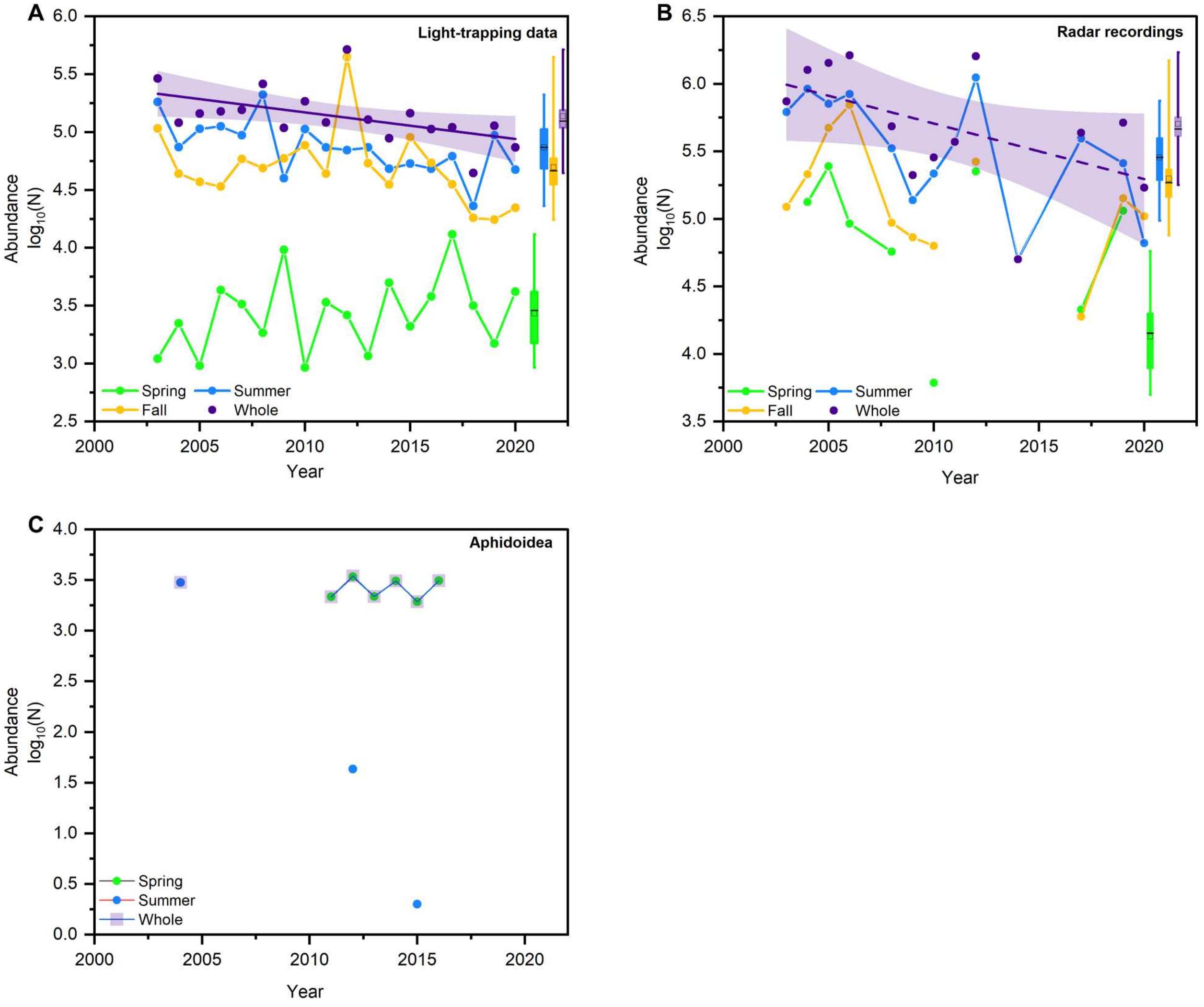

Fig. 1. Seasonal and annual abundance of migratory insects on BH over 2003–2020. (**A**) Temporal dynamics of all insect species that were sampled through high-altitude searchlight trapping ($F_{1,16}$ = 6.08, P = 0.03). (**B**) Temporal dynamics of insect species recorded with radar ($F_{1,11}$ = 4.09, P = 0.07). (**C**) Seasonal abundance data for Aphidoidea over a restricted time period, i.e., covering 7 of 18 years. Temporal dynamics are plotted for overall insect abundance during spring (green), summer (blue), fall (orange), and year-long (purple dots). Radar data are lacking for 2007, spring of 2003, 2009, 2011, 2014, and 2020, and fall of 2011 and 2014. In either panel, abundance values are log-transformed and boxplots represent interquartile ranges with medians (solid horizontal line) and means (small square). Whiskers indicate the 5th and 95th percentiles of the range. Solid and dashed lines with shaded 95% confidence interval (CI) indicate significant or marginally significant trends (0.05 < P < 0.1) in total annual abundance over time based on linear regression models, respectively.

fold higher than that in April. (fig. S4C). As a result, the NE/H abundance ratio equally demonstrated seasonality ($F_{6,111}$ = 39.383, P < 0.01; fig. S4D) and attained its peak values in July (fig. S4D).

Among the 98 trapped (H and NE) species, the coefficient of variation (CV) of annual abundance for 10 species exhibited significant variation over time—reflecting potential gains or losses in ecological stability or equilibrium. For a respective six and four H species, CV values either increased or decreased with time (Fig. 5). Overall abundance of the former (six) species accounted for 51.1% of all trapped H, out of which, four species (i.e., 66.6%) exhibited gradually declining abundance (Fig. 5).

Fine-grained patterns for H-NE couplets

Systematic literature reviews allowed us to establish 124 pairs of trophically linked (migrant) species, consisting of 26 H and 17 NE (Fig. 6A, fig. S1, and table S1). For each H, interspecies interactions were either negative (i.e., NE prevent H buildup) or positive (i.e., NE numerically respond to H buildup; Fig. 6A and table S1). Across all (124) bitrophic couplets, only NE progressively declined in abundance over time at rates of 0.65% per annum ($F_{1,16}$ = 13.39, P = 0.002; Fig. 6B). Also, food web connectance declined over time at rates of 1.12% per annum ($F_{1,16}$ = 9.81, P = 0.006; Fig. 6C). Within a given couplet, H abundance (H_n) in a given year was negatively affected by H and NE abundance during the preceding year (i.e., H_{n-1}, NE_{n-1}; table S3).

For four prevalent H, different interannual dynamics were recorded that are potentially reflective of distinct inter- and intraspecific ecological forces, e.g., parasitism and predation. For *Helicoverpa armigera*, 11 associated NE were identified that declined in summed abundance at a rate of 0.28% per annum

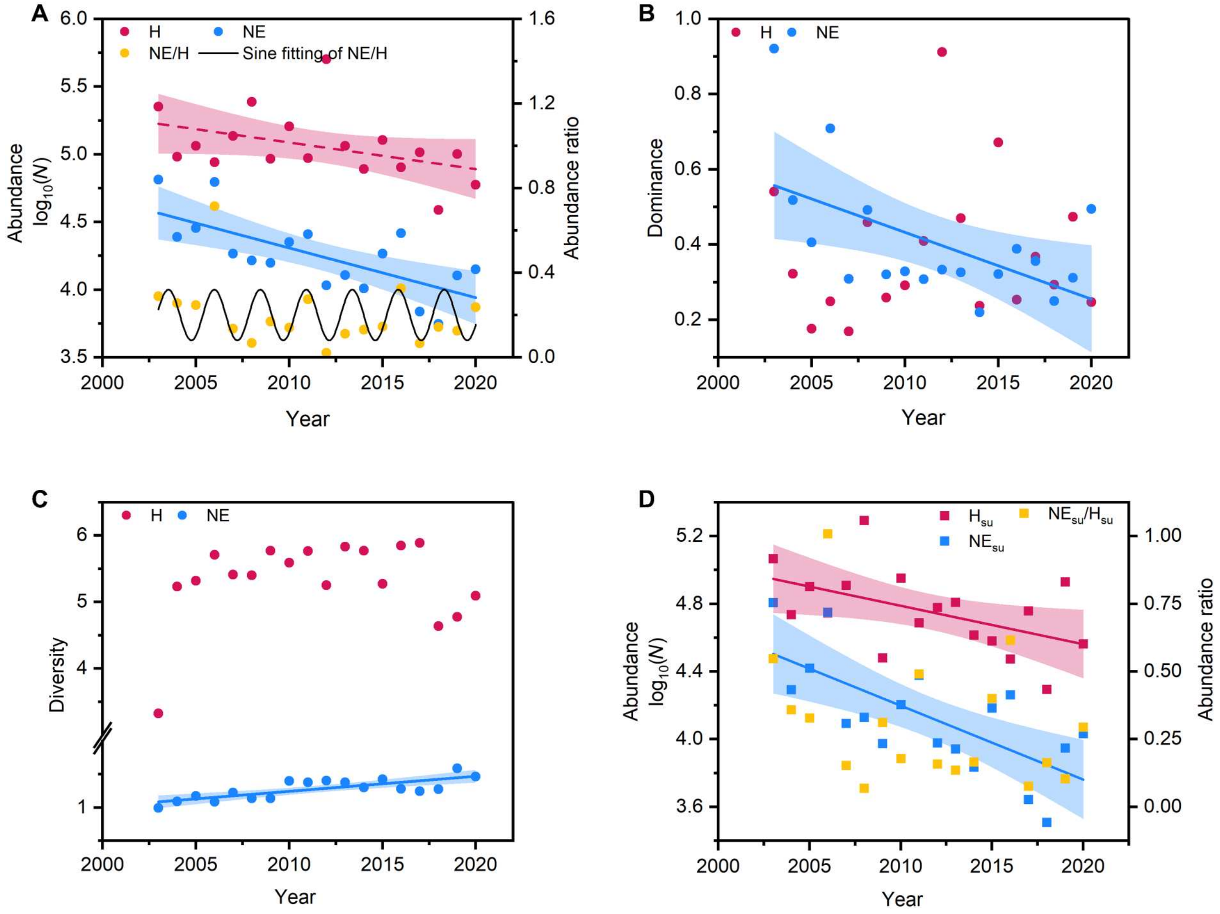

Fig. 2. Year-by-year variation in abundance and community-level indices for H and NE guilds over 2003–2020. H (red dots) and NE (blue dots) comprise a respective total of 80 and 18 species, and their abundance was assessed using high-altitude searchlight trapping on BH (table S1). Panels show temporal trends for different variables: (**A**) Annual abundance of H and NE and the associated NE/H abundance ratio (yellow dots). A sine curve {$y = 0.2 + 0.12*\sin[2.55\ (x - 83.33)]$, $R^2 = 0.293$} was fitted to the abundance ratio. (**B**) H and NE dominance. (**C**) H and NE diversity. (**D**) Summer abundance of H and NE and the associated NE/H abundance ratio. Solid or dashed regression lines with 95% CI (shaded area) either indicate significant ($P < 0.05$) or marginally significant ($0.05 < P < 0.1$) trends based on linear regression models that include abundance [H: $F_{1,16} = 3.61$, $P = 0.08$; NE: $F_{1,16} = 15.66$, $P = 0.001$; (A); H$_{su}$: $F_{1,16} = 3.61$, $P = 0.08$; NE$_{su}$: $F_{1,16} = 15.66$, $P = 0.001$; (D)], dominance [NE: $F_{1,16} = 6.75$, $P = 0.02$; (B)], and diversity [$F_{1,16} = 24.28$, $P < 0.001$; (C)] as the dependent variable, respectively.

($F_{1,16} = 3.3$, $P = 0.09$; fig. S5, A and B). Abundance of *H. armigera* was negatively affected by H and NE abundance in the previous season (i.e., H_{n-1} and NE_{n-1}; table S3). For *M. separata* (Hübner), seven associated NE were identified, and both H and NE abundance declined over time (fig. S5, C and D). For *M. separata*, H abundance was negatively affected by NE_{n-1} (table S3). Five NE were identified for *Agrotis ipsilon* (Hufnagel; fig. S5E), with abundance of the latter (H) declining over the monitoring period at a rate of 1.02% per annum ($F_{1,16} = 36.21$, $P = 0.00$; fig. S5F). For *A. ipsilon*, NE/H abundance ratio increased over time ($F_{1,16} = 16.02$, $P = 0.001$; fig. S5F), although NE_{n-1}, H_{n-1}, or the Hs-related NEs and their abundance ratio in the previous season (i.e., H_{n-1}, NE_{n-1}, and H_{n-1}/NE_{n-1} ratio) did not affect H *A. ipsilon* abundance (table S3). Last, 8 NE were detected for *Ostrinia nubilalis* (Hübner; fig. S5G), but neither H or NE abundance exhibited notable variation over the 18-year monitoring period (fig. S5H).

DISCUSSION

Insects are integral components of food webs and key integrators of terrestrial, aquatic, and aerial ecosystems (*12*). Through their provision of various ES (e.g., pollination and biological pest control), insects further sustain primary productivity of food, feed, and fiber crops and thereby generate broad societal benefits (*7*, *8*). A progressive loss in insect abundance and diversity, as recently recorded across the globe, may result in a weakening (or extinction) of ecological interactions and decaying ecosystem functions over broad spatial scales (*38*, *39*). Our study presents a data-rich body of evidence on the declining abundance of migratory insect species over nearly two decades in eastern Asia. Overall, annual population abundance of seven (of eight) main NE families declined over time—at rates up to 0.63% per annum ($F_{1,16} = 12.86$, $P = 0.002$; fig. S2, A to H). Within 124 bitrophic couplets, NE equally experienced the steepest losses, i.e., declining at 0.65% per year. In addition to the weakened ecological interactions, several indices (e.g., fluctuating H annual abundance and declining NE dominance) reflect a steady loss of ecological equilibrium. Our work not only

Table 1. Annual and seasonal abundance of NE mediates H abundance over 2003–2020. Three different generalized linear models (GLMs) are built, revealing the underlying determinants of spring time (H_{sn}), fall time (H_{fn}), and annual H abundance (H_n). Explanatory variables include seasonal NE or H abundance in a given year (n) or preceding year (n − 1). *, **, and *** indicate significance at 0.1, 0.05, and 0.01 levels.

Variable	Estimate	Standard error	z value	Pr (>|z|)
$H_{fn} = H_{sn} + NE_{sn} + NE_{sn}/H_{sn}$				
Intercept	1.18×10^{1}	3.97×10^{-1}	29.62	$<2 \times 10^{-16}$***
H_{sn}	-1.33×10^{-4}	8.45×10^{-5}	−1.57	0.12
NE_{sn}	3.05×10^{-4}	2.94×10^{-4}	1.04	0.30
NE_{sn}/H_{sn}	-1.81×10^{0}	1.07×10^{0}	−1.70	0.09*
$H_{sn} = H_{fn-1} + NE_{fn-1} + NE_{fn-1}/H_{fn-1}$				
Intercept	7.47×10^{0}	3.63×10^{-1}	20.56	$<2 \times 10^{-16}$***
H_{fn-1}	-1.45×10^{-6}	1.75×10^{-6}	−0.83	0.41
NE_{fn-1}	1.89×10^{-4}	9.95×10^{-5}	1.90	0.06*
NE_{fn-1}/H_{fn-1}	-7.08×10^{-1}	3.38×10^{0}	−0.21	0.83
$H_{n} = H_{n-1} + NE_{n-1} + NE_{n-1}/H_{n-1}$				
Intercept	4.26×10^{0}	1.64×10^{-1}	25.92	$<2 \times 10^{-16}$***
H_{n-1}	-3.34×10^{-6}	1.33×10^{-6}	−2.52	0.02**
NE_{n-1}	-1.62×10^{-4}	4.78×10^{-5}	−3.40	0.00***
NE_{n-1}/H_{n-1}	9.84×10^{-1}	4.28×10^{-1}	2.30	0.03**

constitutes the first comprehensive, long-term inventory of airborne migratory insects but also offers unprecedented insights into the multidecadal dynamics of diverse insect communities in eastern Asia. Our work thus adds to a rapidly growing body of evidence on the global insect decline, composed of studies that differ in taxonomic coverage, analytical procedures, and sampling methodologies. Our findings signal a marked loss in insect functional diversity, with major consequences for trophic regulatory forces across natural and man-made habitats, (agro)ecological resilience, and food security. Our results underscore an urgent need to conserve NE of pests and to mitigate the core anthropogenic determinants of the insect decline in China and abroad (*40*).

Long-term trends in insect biodiversity differ substantially between geographies, ecosystems, and taxonomic groups; however, the fraction of robust, stable, or recovering insect populations is invariably small (*41*, *42*). In line with multiple other studies (*5*, *10*, *34*), our findings underscore how ES providers such as NEs may be exceptionally vulnerable to global environmental change (*43*). Our work shows that key NE such as dragonflies (fig. S2A) are subject to similar rates of decline as monarch butterflies or dung beetles (*34*, *35*). In our study, NE communities also experience progressively lower dominance, an ecological feature that may be more important to ecosystem functioning than individual species traits (*44*) especially in simplified, human-modified settings. Aside from its negative impacts on biological pest control, net NE population declines, shifts in dominance, and altered food web structure may have cascading effects on the integrity and functioning of entire ecosystems (*45*). Although the loss of small-bodied consumers, e.g., insect predators and parasitoids, are thought to carry smaller ecological consequences than that of large-sized vertebrates (*26*), the pace and magnitude of the observed insect NE declines are definitely cause for concern. Strong, sustained drops in NE populations are still likely to cause large cascading impacts on invertebrate H (*46*), but those biologically important effects are not easily discernable (*47*). It is also challenging to anticipate the actual consequences, which may range from an attenuation to unrestricted propagation of H populations, with the former resulting from overexploitation of host plant resources (*48*). Our findings possibly confirm this phenomenon for certain crop-feeding H, where their steady population declines contrast with findings in North America (*42*) and China (*49*). However, while some economically important pests, e.g., *A. ipsilon*, undergo rapid declines (fig. S5E), these trends clearly do not hold for all crop-inhabiting H or pests (*20*). For those H species that undergo strong declines, bottom-up effects on (specialist) NE communities could reinforce the current dynamics and accelerate NE population decline (*27*). Overall, rates of decline for the different trophic guilds and the resulting trophic cascades are likely affected by intrinsic factors, i.e., trophic decoupling and extrinsic factors such as climate variables, resource availability, landscape structure, or habitat quality, e.g., as shaped by anthropogenic stresses (*47*). As compared to primary consumers, higher trophic levels are exceptionally susceptible to climate change, ecosystem simplification, or the ecological disturbances that result from agricultural intensification (*50*). Agrochemical pollution in particular can exert diverse (sub)lethal impacts on NEs (*51*) including prey-mediated effects (*52*), and climate change can impair the ability of parasitoids to track their hosts (*53*). Disentangling the relative contribution of those intrinsic and extrinsic factors is especially important, as this can help to forecast the ultimate ecological outcomes of multiple concurrent anthropogenic stressors and anticipate their eventual rippling effects on human health and societal well-being (*54*).

Flying insects (e.g., ladybeetles, aphids, and lepidopterans) regularly exhibit large seasonal variation in population size and (coupled H-NE) oscillation cycles (*55*), which relate to the demography of individual species, consumer organisms, and the abundance or quality of key trophic resources, e.g., plant hosts or prey items (*56*, *57*). In our study, insect abundance was lowest during spring (i.e., April) and highest in late summer (August), with NE, H, NE/H abundance ratio experiencing oscillation of variable periodicity. These are less pronounced than for single-species dynamics but are reminiscent of the cyclic outbreaks of forest lepidopterans (at 9- to 13-year periodicity) that are regulated by lagged density-dependent processes (*58*) and possibly modulated by other environmental factors (*59*). Similarly, in North American agrolandscapes, aphid H and coccinellid NE populations undergo coupled 2-year oscillations (*55*). Irrespective of these oscillations, marked declines in population size are evident when assessing (interannual) changes at the population peak (i.e., summer H and NE abundance). These are possibly determined by climate-induced phenology shifts (*60*) or agricultural intensification, i.e., insecticide use and agroecosystem simplification (*61*). Also, with insect numbers during fall

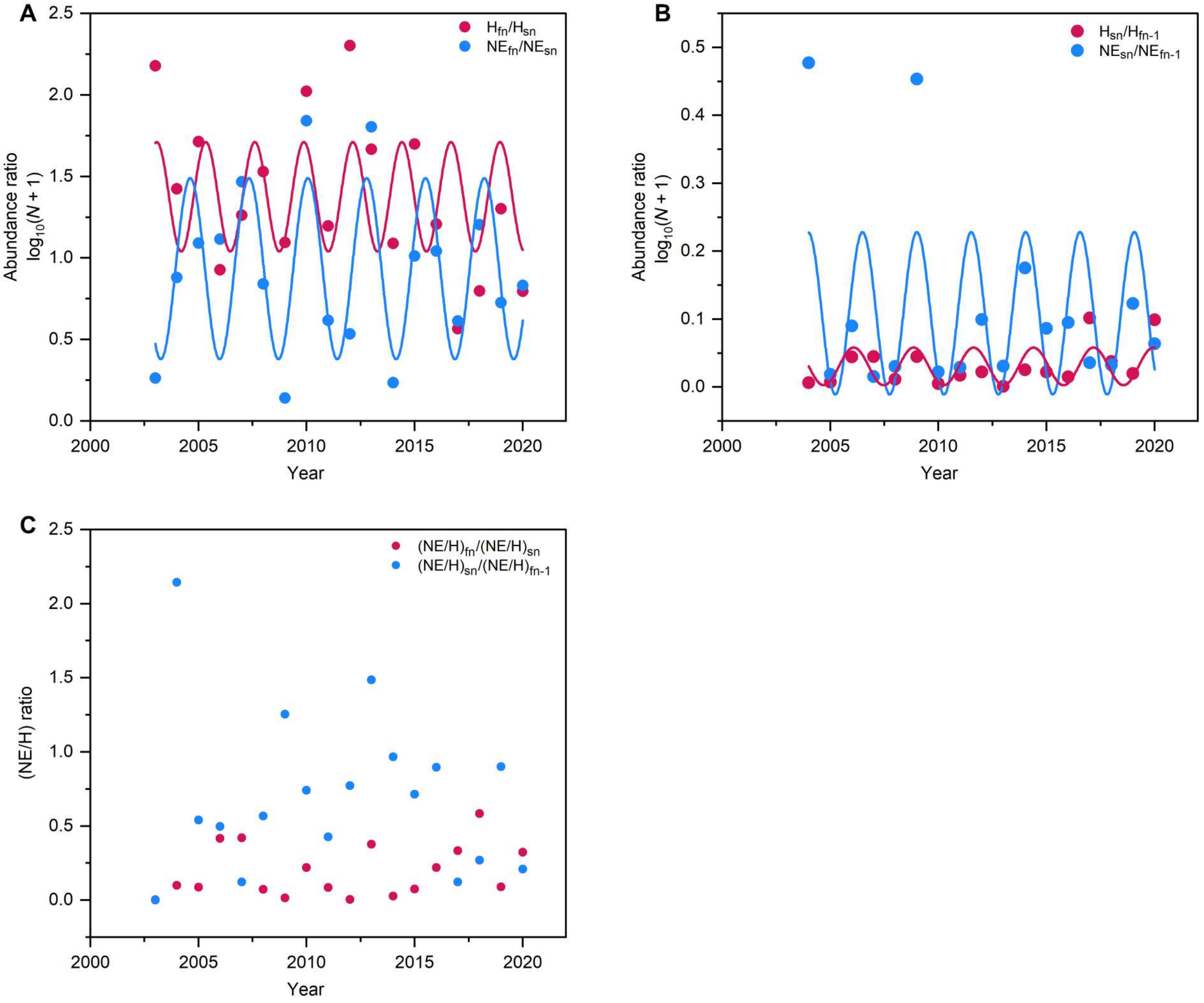

Fig. 3. Interannual and seasonal variation in (absolute or relative) H and NE abundance. (**A**) Annual oscillation and variation in seasonal abundance ratio in spring and fall of H and NE abundance {H_{fn}/H_{sn}: $y = 1.38 + 0.34\sin[2.77(x + 16.71)]$, $R^2 = 0.27$; NE_{fn}/NE_{sn}: $y = 0.93 + 0.55\sin[2.31(x + 115.73)]$, $R^2 = 0.66$}. (**B**) Interannual oscillation and variation in seasonal abundance ratio in spring and fall of NE/H abundance ratio {H_{sn}/H_{fn-1}: $y = 0.03 + 0.03\sin[2.26(x - 44.87)]$, $R^2 = 0.46$; $y = 0.11 + 0.12\sin[2.49(x + 71.65)]$, $R^2 = 0.41$}. (**C**) Interannual and intra-annual variation in the NE/H ratio between spring and fall.

superseding those of spring (*62*), the central role of summer reproduction and overwinter survival becomes evident. A fine-resolution assessment of seasonal dynamics of one or few insect species can help to identify key biotic and/or abiotic determinants of population dynamics and guide conservation measures. Future work is also warranted to ascertain whether insecticide use in summer crops inflict disproportionate mortality on particular H and NE species or to clarify the relative contribution of land-use change and habitat simplification.

Spatiotemporal shifts in NE abundance and diversity can exert strong impacts on the delivery of resulting ES, i.e., biological control (*36*, *63*). The lowered food web connectance in our 124 biotrophic couplets can negatively affect food web robustness and compromise ecosystem stability in the face of biodiversity decline (*64*, *65*). However, as food web robustness is mediated by multiple factors (*66*), an in-depth assessment is required of the relative feeding habits, ecological requirements, and trophic linkages of individual insect species. This work can be geared toward conservation of particular endangered species, e.g., the dragonflies *Pantala flavescens* Fabricius or key ES providers such as the 18 NE species that were described in our study. We quantitatively demonstrate how these NE either prevent or numerically respond to H buildup between and within years. Their joint outcome (i.e., biological control) results from additive or synergistic effects of individual species and may involve seasonally variable consumptive and nonconsumptive interactions (*67*, *68*). As the construction of our trophic couplets was solely based on literature reviews (and did not involve in-field observation or experimentation), we likely failed to discern important interactions that contribute to biological control. This, however, could prove a fruitful avenue for future research and ideally also involves other organisms that act at the interface of aerial and terrestrial ecosystems such as insectivorous birds or bats (*69*).

Many of the phenomena that we recorded using insect radar and light traps can be altered through targeted and scientifically informed action at different organizational scales (*40*, *70*). Some dynamics that are mediated by meteorological variables and continent-wide air calculation patterns (*71*), however, may require

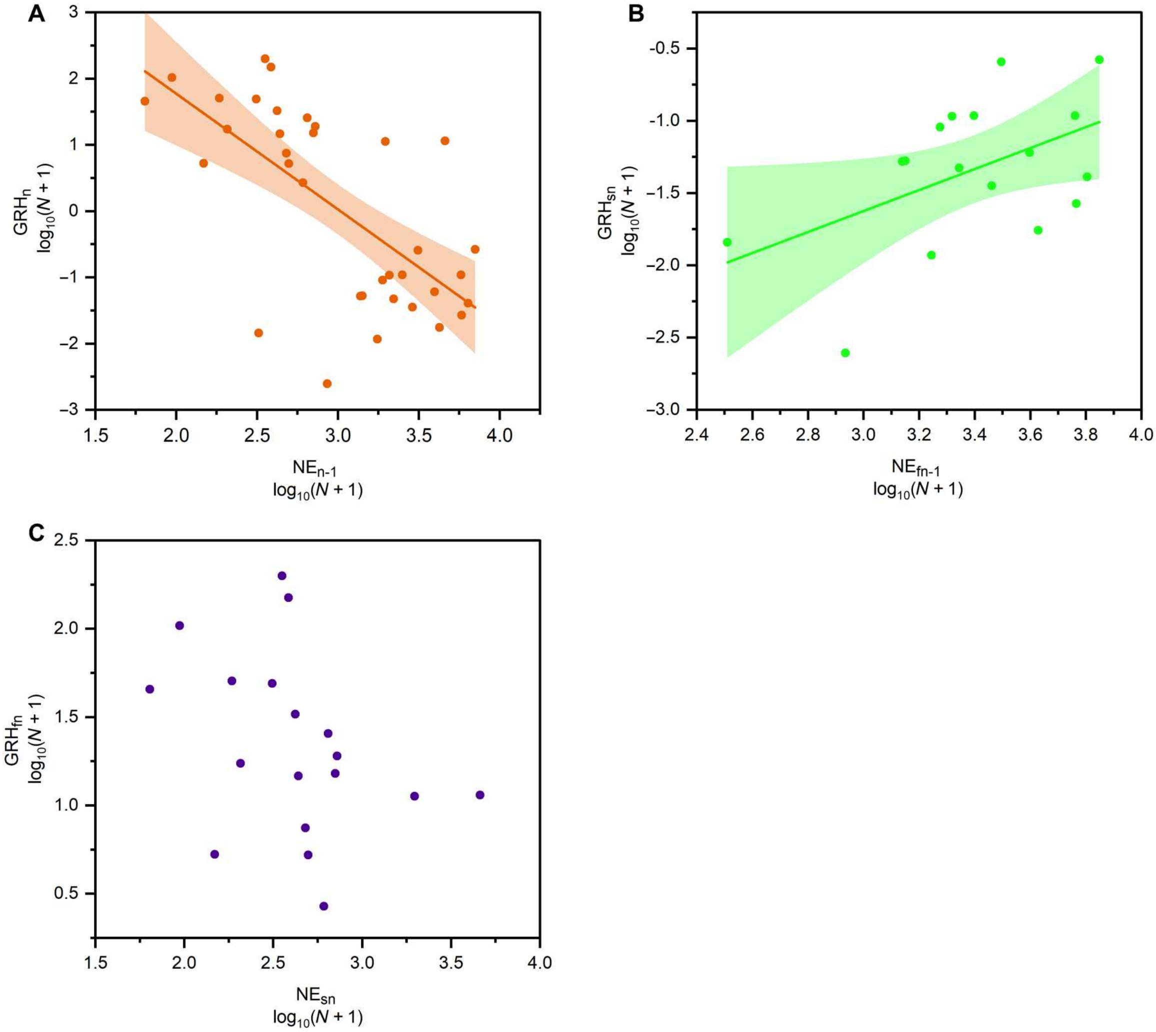

Fig. 4. NE-mediated mitigation of H population buildup across seasons or within a given year. Patterns are drawn using H and NE abundance records, as obtained through light trapping on BH during 2003–2020. (**A**) NE abundance in a previous season (NE$_{n-1}$) negatively relates to the ensuing H population growth in season n (GRH$_n$; $F_{1,33} = 26.51$, $P < 0.001$). Season here only refers to spring and fall. (**B**) NE abundance during fall of year n − 1 (NE$_{fn-1}$) positively relates to spring-time H population growth in the subsequent year (GRH$_{sn}$; $F_{1,15} = 5$, $P = 0.041$). (**C**) Relationship between spring NE abundance (NE$_{sn}$) and fall-time H population growth in the same year (GRH$_{fn}$). Linear regression patterns are highly significant ($P < 0.05$), with the shaded area showing a 95% CI.

sustained action over large spatiotemporal scales. To revert NE population declines and restore ecological equilibria, one can pursue a phasedown of ecologically disruptive activities such as tillage, fertilizer use, insecticide sprays, and prophylactic pesticide applications. Meanwhile, diversification tactics at field, farm, or landscape scales can bolster insect biodiversity and fortify biological control (*72*, *73*). This can also comprise the deployment of insecticidal crop varieties, consciously paired with agroecological measures and put in place on a fraction of the agricultural landscape (*74*, *75*). Mitigation efforts ideally cover natural and man-made ecosystems along the migration route of mobile insect taxa such as noctuid moths (*76*). However, when drawing insect conservation strategies, several elements may be beyond the control of land managers, farmers, or homeowners.

Crop pests provide notable ecosystem disservices, while NEs and pollinators perform ES that underpin the long-term productivity and stability of natural and man-made ecosystems alike (*7*, *8*). In this study, we rely on multiyear radar and light trapping records to delineate the temporal dynamics of 98 migratory insect species in the East Asia monsoon system, highly mobile species that disperse over extensive areas covering key farming regions in the Korean peninsula, China's Northeast Plain, and the North China Plain (*37*). Our analyses unveil how NE populations contract at a rate of 0.85% per year (or 15.24% over 18 years), and multiple (H) species lose their state of ecological equilibrium. Patterns are even more pronounced when accounting for known trophic interactions of 124 H-NE couplets. Our study thus points at a critical decline in (insect) functional diversity and a steady loss in ecological resilience across East Asia. As the first multidecadal insect bio-inventory in eastern Asia, this study illustrates the gravity of the regional (insect) biodiversity crisis. Given the above, active conservation of insect communities is pivotal to ensuring food security, human nutrition, and societal well-being in the face of global environmental change.

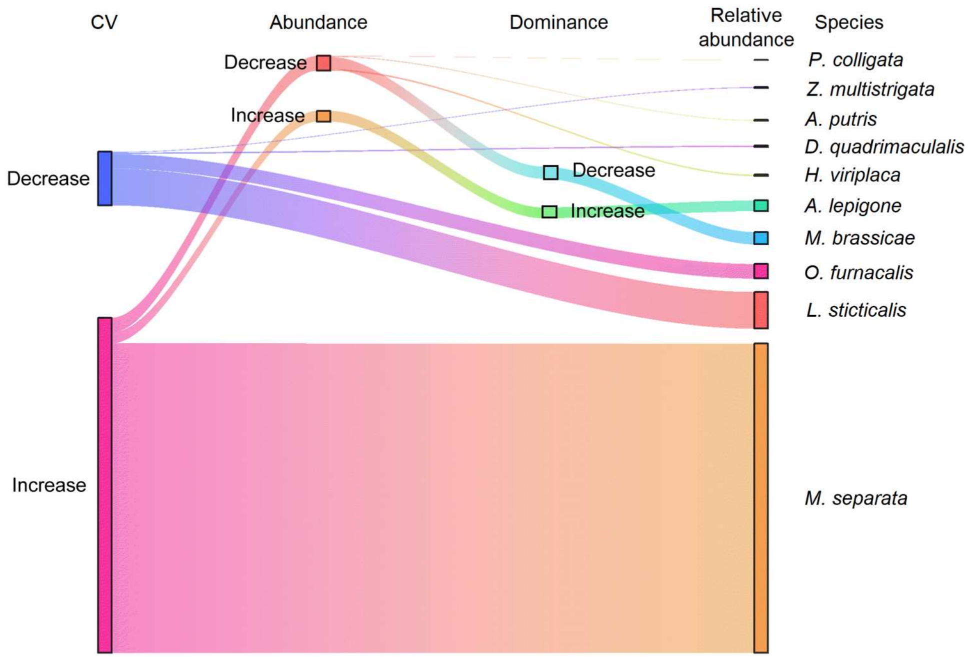

Fig. 5. Temporal trends in the CV for monthly H abundance over 2003–2020 for a subset of species. CV values are annually calculated using monthly abundance records over June to September; long-term CV trends reflect potential gains or losses in ecological equilibrium. Patterns are shown for 10 (of 80) H species that either exhibit statistically significant increases or decreases in CV values over time ($P < 0.1$). The relative magnitude of CV for either group of species is shown by pink or blue bars on the left, while the relative abundance of each species is shown in the colored bars on the right. Species with significant changes in abundance and dominance are equally indicated.

METHODS

Study site and monitoring approach

Research was conducted in BH (38°24′N, 120°55′E): a 2.5-km^2 island within China's Bohai Gulf. During 2003–2020, migratory insects were consistently collected using a vertical searchlight trap (model JLZ1000BT; Shanghai Yaming Lighting Co. Ltd., Shanghai, China) placed 8 m above sea level. Searchlight was operated daily from 6:00 p.m. to 6:00 a.m. between 1 April and 31 October, except during times of extreme weather (e.g., heavy storm, thunder, or lightning) and power shortage. A nylon collection bag (60 net mesh) was attached beneath the trap and trapped insects were collected from this bag every morning. Next, field-caught insects were kept in a −20°C refrigerator for further species-level identification. As no crops are cultivated on BH island, all light-trapped individuals are considered to be migrants that engaged in (high-altitude) flight over at least 40 to 60 km from China's mainland. This was annually corroborated by sweep nettings at variable times and in different habitats across BH.

Insect migration fluxes were equally quantified in real time by a purpose-built scanning entomological radar (SER; Wuxi Haixing Radar Co. Ltd., Wuxi, China), positioned on BH. The SER includes RA-722UA hardware (Anritsu Co. Ltd., Kanagawa Prefecture, Japan), a rain-weather radar antenna (model 711; Wuxi Haixing Radar Co. Ltd., Wuxi, China), an antennal control system, and a feed system. Every day, radar observations were made continuously at eight elevation angles, i.e., 3°, 5°, 8°, 12°, 18°, 28°, 45°, and 58° (*77*). Recordings were made from sunset to sunrise during April to October, except during radar failure or severe weather conditions. During 2003–2017, the SER device was manually operated. From 2018 onward, software was upgraded and the radar was switched to automatic operation mode. However, as radar recordings proved incomplete and did not yield species-level data, they were solely used to document the overall temporal patterns in migratory insect abundance (and not species- or guild-specific trends).

Species identification and data filtering

Trapped insects were hand-sorted and identified up to species level, using methods described by Guo *et al.* (*20*). Aquatic insects (primarily Dytiscidae and Hydrophilidae) were not considered for further analyses. Also, given the difficulties to identify certain field-trapped insects to species level, abundance data for aphids, house flies, and ants were reported at the superfamily (i.e., Aphidoidea, Muscoidae, and Formicidae) level. As abundance level of aphids, Tachinid flies and ants were not systematically collected over the full study period (e.g., only 7 of 18 years for aphids), these three taxa were excluded from subsequent multiyear analyses. These omissions, however, are important given that Tachinidae constitute key parasitoids of various crop pests, while the wingless counterparts of reproductive ants are voracious predators in multiple agroecosystems, e.g., maize. For the assessment of H and NE dynamics, we equally removed unidentified species and "neutral insects" (i.e., mosquitoes) from the database. Last, we only included species with average abundance above 25 individuals per year over the entire 18-year time period. Next, abundance of each single (H or NE) species was computed on a daily, monthly, or annual basis. Over these time frames, overall abundance of the two main feeding guilds (i.e., H and NE) was also determined by summing the respective species-level abundance values.

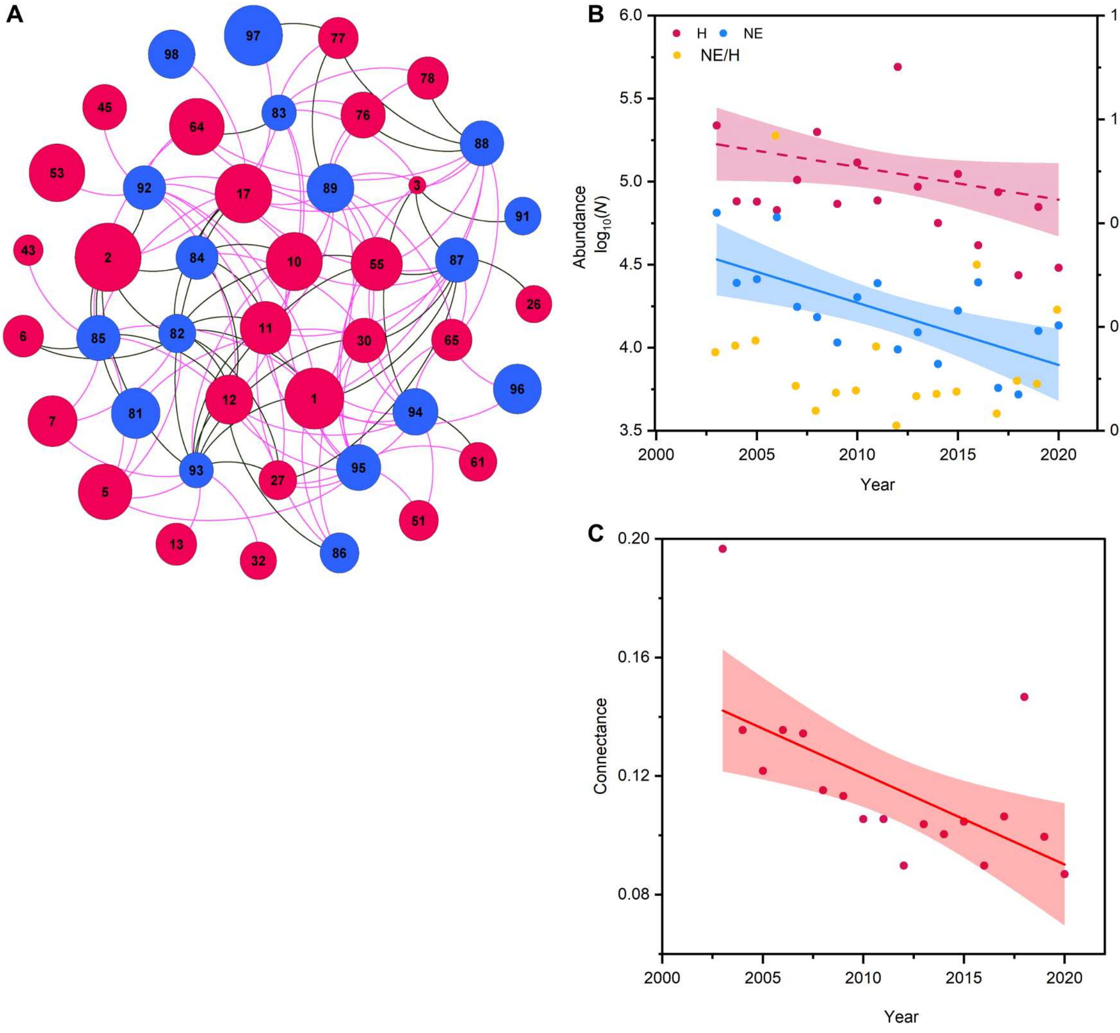

Fig. 6. Multiyear trends in (relative) species abundance and network connectance for a food web composed of 124 bitrophic H × NE couplets. (**A**) Quantitative food web composed of migratory H (red circles) and NE (blue circles), captured with searchlight traps over 2003–2020 on BH. Digits within a given circle indicate species identity (table S1). Circle size reflects the relative annual abundance of each species. Interspecies links comprise positive (magenta), negative (black), or both positive and negative (purple lines) NE × H correlations. (**B**) Temporal shifts in annual abundance of the H and NE species that constitute the 124 couplets and the associated NE/H abundance ratio (H: $F_{1,16} = 4.29$, $P = 0.06$; NE: $F_{1,16} = 13.39$, $P = 0.002$). (**C**) Temporal decline in connectance of the assembled NE × H food web ($F_{1,16} = 9.81$, $P = 0.006$). Solid and dashed lines with a shaded 95% CI indicate statistically significant ($P < 0.05$) or marginally significant ($0.05 < P < 0.1$) trends based on linear regression models.

Literature-based identification of trophic linkages

To define H-NE trophic couplets and draw more complex quantitative food webs, we gathered literature evidence of feeding interactions between different species. As above, we only considered H and NE species that were caught using searchlight traps and that surpassed abundance thresholds over the 18-year monitoring period. Literature searches were then used to detect (published) evidence of predation or parasitism of a given NE species on a particular insect H. Systemic searches were manually performed by one single person in the following literature databases: China National Knowledge Infrastructure (CNKI), PubMed, and Centre for Agriculture Bioscience International (CABI). All searches ended in March 2022 but covered varying time periods, as defined by the earliest time period of the database. Search results were generated through subject retrieval (fig. S1). First, search strings were composed of the common name of the presumed H or NE species (i.e., presumed H and NE) in Chinese (for CNKI) or by combining its common and scientific name (for PubMed and CABI). When a given query yielded more than 100 records for a particular H-NE couplet, searches were refined by adding "prey, enemy" or "parasitoid, enemy" to the respective search string (in either English or Chinese, depending on the focal database). For each couplet, literature records from different databases were pooled, duplicates were removed, and full-text articles were accessed. Only those studies that simultaneously reported both (presumed H and NE) species and confirmed the exact trophic interaction were used to build bitrophic couplets or H-centered food webs (table S1). Records of intraspecific cannibalism, interspecific intraguild predation, and facultative hyperparasitism were omitted. Next, using the annual abundance of individual (NE and H) species, we constructed food webs in Gephi 0.92 using the Fruchterman-Reingold algorithm.

For four common crop pests, i.e., *H. armigera* (Hübner), *M. separata* (Walker), *A. ipsilon* (Hufnagel), and *O. nubilalis* (Hübner), an in-depth literature screening was done to characterize the associated NE species. For each bitrophic couplet and pest species, daily trap capture records of the constituent H and NE species were used to detect temporal shifts in interspecific interactions.

Species diversity and population-level indices

Insects undertake migratory flight in opposite directions during different times of the year, i.e., northward in spring and southward in fall in the study area (*78*). Meanwhile, summer flight occurs in both directions (*37*). For spring (April to May), fall (September to October), and summer (June to August), we computed abundance of the two main feeding guilds (H and NE) and the NE/H abundance ratio. Next, we determined the interannual variation of these three (season-specific) parameters. We further calculated population diversity using the Margalef Diversity Index: $E = (S-1)/\ln N$, and population dominance using $B = n_{\max}/N$, and food web connectance was calculated following the formula $C = L/S^2$. In the above equations, S represents species number, N depicts total abundance of all species, $n_{\max}$ depicts abundance of the most common species in a given year, and L refers to all the trophic links in food webs. To assess the extent to which NE contribute to H population regulation (or biological control), we related NE abundance to the subsequent H population growth rate over specific time intervals. Per year and season, H population growth rate ($\mathrm{GRH_n}$) was defined as Growth Rate = $(\mathrm{H_n}\text{-}\mathrm{H_{n-1}})/\mathrm{H_{n-1}}$ (*79*), in which $\mathrm{H_n}$ or $\mathrm{H_{n-1}}$ refers to abundance in the study season or previous season. Other indices such as $\mathrm{GRH_{sn}}$ and $\mathrm{GRH_{fn}}$ represent H population growth rate in spring n and fall n, respectively. Interannual stability in the population size of individual species or entire feeding guilds was assessed using CV. More specifically, a progressively increasing CV value indicates a loss of ecological stability and vice versa (*80*, *81*). For species that displayed statistically significant interannual CV variation, temporal trends in abundance and dominance were also determined. Calculation of CV values was restricted to June to September, as monitoring data were most complete over these months—with overall (NE, H) abundance accounting for 95.6% of all trapped individuals throughout the entire 18-year monitoring period.

Statistics

Generalized linear models (GLM) were used to investigate time-lagged relationships between H abundance, NE abundance, and a NE/H abundance ratio. In this regard, three different GLMs were built. First, we examined whether either of the three variables during spring affects H fall abundance during a given year. Second, we assessed whether the three variables during fall relate to H abundance during spring of the subsequent year. Third, we assessed whether the above three variables during one season affect H abundance in the subsequent season across years. For all GLM analyses, we used a negative binomial error distribution for count data (i.e., H and NE abundance) and a normal error distribution for the NE/H abundance ratio. Models were validated using histograms of normalized residuals and plots of residuals against fitted values (*82*).

Mean separation was done using Tukey's Studentized Range Test (HSD) at a 0.05 significance level. Seasonal H and NE abundance or NE/H abundance ratios were compared using Student's *t* test. Next, to assess seasonal effects on H or NE abundance, one-way analysis of variance (ANOVA) was performed using Tukey's Studentized Range Test (HSD) at a 0.05 significance level. Marginal significance of CV data was using Tukey's Studentized Range Test (HSD) at a 0.1 significance level to include more species. Polynomial functions were applied to reveal interannual H-NE correlation, heatmaps of NE/H abundance ratio were obtained by using the Z score [N (0,1)] conversion, and Pearson's correlation was used to test relationships among specific H and NE. Before analysis, all data were examined for normality and heteroscedasticity. Where necessary, abundance data were log-transformed and abundance ratio values were arcsine-transformed or $\log_{10}(x+1)$–transformed. GLMs were calculated in R version 3.5.1 (*83*), and sinusoidal curves and the related time-lag calculation were fitted in OriginPro 9.8.0 software (OriginLab Corporation, Northampton, MA), while the remaining statistical analyses were conducted using SPSS 26.0 Version (IBM Corp, New York, NY).

Supplementary Materials

This PDF file includes:
Figs. S1 to S5
Tables S1 to S3

Other Supplementary Material for this manuscript includes the following:
Data files S1 to S7

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