Loss of parasitoid diversity in China's corn agro-ecosystem over a 30-year time period

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Abstract

Globally, insects are undergoing a rapid decline in abundance and diversity. Despite varying degrees of scientific attention across insect taxa and geographies, these patterns can entail an extinction of ecological interactions and a decay of ecosystem functions. In this study, we compared the spatial distribution, abundance and species composition of *Trichogramma* spp. egg parasitoids (Hymenoptera: Trichogrammatidae) over a 30-year time period in China. During the 1980s and in 2016–2018, egg masses of the Asian corn borer (ACB), *Ostrinia furnacalis*, were systematically sampled in multiple key farming regions. In 2018, five species were identified using morphological and molecular methods, with *Trichogramma ostriniae* representing 90% of the species complex. Since the 1980s, two new species have made their appearance (i.e., *T. brassicae*, *T. bilinggensis*), while nine (out of 12; i.e., 75%) species have disappeared. Across sites, species richness and diversity have declined by a respective 25–86% and 56–100% (except for Heilongjiang province) over this time frame. We hypothesize that this loss of functional diversity is attributed to the progressive intensification of corn cropping systems, involving landscape simplification, pesticide use and the loss of (crop, non-crop) plant diversity. Conversely, no evidence was found that augmentative biological control (as compared to pesticide-based measures) negatively affected the resident parasitoid community in farm settings. Given the drastic reduction in ACB parasitoid richness, agro-ecological measures and diversification strategies should be deployed to restore the ecological resilience of local farming systems. Our work thus carries major implications for food security and helps to muster support for more nature-friendly, pest-resilient farming systems in China and abroad.

Introduction

Over the past decade, several scientific studies have reported a progressive decline of insects in many parts of the globe (Hallmann et al., 2017; Lister and Garcia, 2018; Seibold et al., 2019; Sánchez-Bayo and Wyckhuys, 2019, 2021; Wagner et al., 2021; Cardoso et al., 2020). Multiple context- and taxa-specific drivers have been identified, with land-use change, agrochemical pollution, biological invasions and climate change the most prominent factors (Seibold et al., 2019; Sánchez-Bayo and Wyckhuys, 2019; 2021; Wagner, 2021). As (insect) biodiversity underpins the overall stability and functioning of natural and man-made ecosystems worldwide (Cardinale et al., 2012; Soliveres et al., 2016; Dainese et al., 2019), even subtle insect losses can have major, long-lasting impacts (Janzen, 1971; Kehoe et al., 2021; Crossley et al., 2020). Though extensive cross-taxa studies are missing from Asia, initial surveys show how 18% of local (migratory) insect species experience long-term drops in their population abundance (Guo et al., 2020). Insectivorous dragonflies (Odonata), i.e., taxa that underpin ecosystem services (ES) such as natural biological control, are subject to 14% annual rates of decline (Kadoya et al., 2009; Guo et al., 2020). It remains however to be seen whether this loss in ES-providers is widespread.

Insect-mediated biological control underpins the resilience of agricultural and natural ecosystems and is conservatively valued at $ 4.5–17 billion per year in US alone (Pimentel et al., 1997; Losey and Vaughan, 2006). In China, beneficial insects (i.e., parasitoids, predators) play a key role in regulating populations of the Asian corn borer (ACB), *Ostrinia furnacalis* (Guenée 1854) (Lepidoptera: Crambidae). This widely distributed species is one of the main herbivorous pests of corn (*Zea mays* L.) in Asia Pacific Regions, including China (Nafus and Schreiner, 1991).It annually causes 6–9 million tons yield losses (Zhou et al., 1988; He et al., 2003). Aside from direct (larval feeding) damage to corn stalks and kernels, ACB-induced fungal infection leads to mycotoxin contamination and quality reduction of harvested grains (Song et al., 2009). As corn is China's most important cereal grain crop (cultivated on 41.3 million ha; total yield 260.8 million tons; Anonymous, 2019), ACB attack thus directly relates to the country's food security and rural development. Parasitic wasps of the genus *Trichogramma* are key natural enemies of corn borers in China and across the world (Consoli et al., 2010; Zang et al., 2021). In addition to the action of naturally-occurring *Trichogramma* spp., ACB biological control is provided by augmentative releases of (mass-produced) parasitoids (Wang, 2014; Zhan and Liang, 1999; Zang et al., 2021).

Together with the former USSR, Brazil and Mexico, China is globally renowned for its use of *Trichogramma* spp. in pest control (Van Lenteren et al., 2018), and annually releases millions of *Trichogramma dendrolimi* on roughly 10% of its national corn acreage (Wang et al., 2014; Huang et al., 2020). This practice results in ACB parasitism rates beyond 70% (Feng, 1996) and has been widely adopted in Northeast China since the 1970s (i.e., Heilongjiang, Jilin, Liaoning; Wang et al., 2014). In the remaining areas and throughout Eastern Asia, ACB is primarily managed through recurrent spray applications of synthetic pesticides (e.g., Yang et al., 2021). Meanwhile, China's corn production has been subject to important changes over the past decades. While local corn production is increasingly typified by input-intensive, mechanized farming schemes and mono-cropping (Ely et al., 2016), a fraction of corn growers have adopted more sustainable practices and reduced chemical fertilizer use by 15–18% (Cui et al., 2018). These field-, farm- and landscape-level changes undoubtedly have impacted resident insect populations including biological control agents such as *Trichogramma* spp.

During the 1980s, Zhang et al. (1990) recorded a total of 12 different ACB-associated *Trichogramma* spp. in China's main corn-growing regions. ACB parasitism varied over space and time; certain *Trichogramma* spp. attained higher parasitism levels than others, as equally observed following assisted releases (Tan, 1999; Feng et al., 1999; Wu et al.,2001; Xu et al., 2001; Guo et al., 2005). Though Zhang (1990) did not survey several of today's main corn-growing regions, follow-up parasitoid censuses can help to assess how the resident *Trichogramma* spp. complex has responded to the extensive farming systems changes over the past three decades. It can equally help to evaluate the impact of *T. dendrolimi* augmentative releases (i.e., in Northeast China and Beijing's Miyun district) on the relative abundance and species composition of resident *Trichogramma* spp. Lastly, follow-up surveys equally provide an opportunity to refine integrative taxonomic approaches for the identification of minute parasitic wasps (Schlick-Steiner et al., 2010; Heethoff et al., 2011). Specifically, sole reliance upon morphological features is challenging given the high levels of phenological plasticity among *Trichogramma* spp. and pronounced female-biased sex ratios in field populations (Pinto et al., 1989).

In this study, we report findings of a nationwide ACB parasitoid census that was carried out during 2016–2018 in all of China's main corn-growing regions. The recorded patterns in *Trichogramma* spp. community composition, relative abundance and geographical distribution are then compared with those from the 1980s (i.e., Zhang et al., 1990) and contrasted between areas that did or did not receive *T. dendrolimi* mass-releases. Our study thus provides unprecedented insights into the temporal shifts in (farm-level) insect biodiversity over a 30-year time frame. Our data equally allow further inferences regarding the strength of (insect-mediated) biological control in one of Asia's prime food, feed and fiber crops.

Materials & Methods

Historic parasitoid censuses

Table 1

Sampling sites of Asian corn borer (ACB) egg masses in China. For sampling events during the 1980s and 2016-2018, information is provided on the number of sampling sites and ACB egg masses that were collected in different corn-growing areas. Per sampling event, the number of ACB egg masses is indicated between brackets.

Region [1]	Province	County		GPS coordinates		Sampling window [2]		Cropping system [3]		Parasited masses
		1980s [4]	2016-2018	1980s	2016-2018	1980s	2016-2018	1980s	2016-2018	1980s
NS	Heilongjiang	Shuangyashan	Qiqihar	Unclear	N47°21'7.86"E123°54'41.17"			SRSW	SRS	Unclear
		Mudanjiang	Harbin	Unclear	N34°37'8.61"E112°26'48.18"			SRSW	SRS	Unclear
	Jilin	Jiamusi	Baicheng	Unclear	N42°15'13.07"E118°52'58.36"			SRS	SCR	Unclear
		Tonghua	Gongzhuling	Unclear	N43°30'8.49" E124°49'0.94"			SRS	SCR	Unclear
	Liaoning	Dandong	Dandong	Unclear	N40°44'6.92" E108°38'48.74"			SRS	SCR	Unclear
		Shenyang	Shenyang	Unclear	N45°37'3.60" E122°49'59.39"			SRS	SCR	Unclear
		Changchun	--	Unclear			--	SRS	SCR	Unclear
	Inner Mongolia	--	Chifeng		N39°59'56.29" E124°20'57.22"			SWC	CS	
		--	Baotou		N43°30'8.49" E124°49'0.94"			SWC	CS	
		--	Bayannur		N41°40'30.64" E123°27'30.98"			WWSC	WWSC	
	Shanxi	--	Xinzhou		N30°50'24.45" E106°06'25.06"			WWSC	WWSC	
	Ningxia	--	Yinchuan		N38°29'9.87" E106°13'39.29"			WWOC	WWSC	
NWI	Xinjiang	--	Bortala		N44°20'59.18" E82°00'28.48"			WWOC	WCC	
		--	Changji		N44°37'58.49"E87°36'02.48"			WWOC	WCC	
		--	Yili		N43°04'07.09"E82°35'14.75"			WWOC	WCC	
		--	Kashi		N38°48'32.67"E77°03'37.15"			WWOC	WCC	
	Gansu	--	Zhangye		N100°56'04.69" E38°99'82.71"			WWOC	WWSC	
HS	Shaanxi	--	Xianyang		N34°19'50.11" E108°42'15.56"			WSC	WWSC	
	Shanxi	Yuncheng	Yuncheng	Unclear	N35°01'37.75" E111°0'4.38"			WSC	WWSC	Unclear
	Beijing	Tongzhou	Fangshan	Unclear	N39°44'48.12" E116°08'12.38"			WSC	WWSC	Unclear
		--	Miyun		N40°22'30.24" E116°50'13.11"			WSC	WWSC	
	Hebei	Baoding	Tangshan	Unclear	N39°37'44.39" E118°10'25.50"			WSC	WWSC	Unclear
		--	Cangzhou		N38°18'13.40" E116°49'59.68"			WSC	WWSC	
		--	Handan		N36°37'31.82" E114°31'59.81"			WSC	WWSC	
	Shandong	--	Jining		N35°24'53.83" E116°34'54.13"			WSC	WWSC	
		--	Liaocheng		N36°27'25.28"E115°58'45.60"			WSC	WWSC	
		Weifang	Weifang	Unclear	N36°42'21.12" E119°09'21.97"			WSC	WWSC	Unclear
		--	Dezhou		N37°40'76.06" E116°59'14.95"			WSC	WWSC	
		--	Laizhou		N37°17'22.86" E120°44'81.99"			WSC	WWSC	
		--	Qufu		N35°57'91.55" 117°.09'68.99"			WSC	WWSC	
	Henan	Xinxiang	Luoyang	Unclear	N34°37'8.61" E112°26'48.18"			WSC	WWSC	Unclear
		--	Luohe		N33°34'58.73" E114°0'39.90"			WSC	WWSC	
		--	Shangqiu		N34°24'55.71" E115°39'1.77"			WSC	WWSC [3]	
	Anhui	Fuyang	Bengbu	Unclear	N32°55'2.35" E117°22'59.21"			WSC	WWSC	Unclear

Region	Province	City	County	Sampling window	GPS coordinates	Cropping pattern (1980s)	Cropping pattern (2016–2018)	Unclear
		–	Suzhou		N33°38'51.88" E116°57'31.08"	WSC	WWSC	
		–	Chuzhou		N32°15'25.21" E118°19'39.24"	WSC	WWSC	
	Jiangsu	Xuzhou	–	Unclear	–	WSC	WWSC	Unclear
		Yancheng	–	Unclear	–	WSC	WWSC	Unclear
SWH	Shaanxi	Hanzhong	Hanzhong	Unclear	N33°04'10.09" E107°01'6.57"	WWSC	WWSC	Unclear
	Hubei	Wuhan	Enshi	Unclear	N30°17'52.09" E109°28'30.31"	WWCR	WWCR	Unclear
	Sichuan	–	Nanchong		N30°50'24.45" E106°06'25.06"	WWCR	WWCR	
		–	Chengdu		N30°56'68.07" E104°19'36.39"	WWCR	WWCR	
	Chongqing	–	Bishan		N29°33'55.90" E106°32'53.82"	WWCR	WWCR	
	Guizhou	Qiannan	Zunyi	Unclear	N28°01'28.19" E106°51'5.07"	WWCR	WWCR	Unclear
		–	Guiyang		N26°36'5.28" E106°42'15.36"	WWCR	WWCR	
	Yunnan	–	Dehong		N24°26'7.70" E98°35'4.70"	SCWC	SCWC	
SH	Anhui	–	Hefei		N31°49'20.30" E117°13'17.39"	WWSC	WWSC	
	Hunan	–	Changsha		N28°13'56.30" E112°56'0.65"	WWSCR	WWSCR	
	Hubei	–	Jingzhou		N30°20'15.52" E112°13'59.72"	WWSCR	WWSCR	
	Zhejiang	Dongyang	Dongyang	Unclear	N29°17'31.78" E120°14'15.30"	WWSCR	WWSCR	Unclear
	Guangxi	–	Guigang		N23°06'52.43" E109°35'41.24"	WWSCV	WWSCV	
	Guangdong	–	Guangzhou		N23°07'54.35" E113°15'34.79"	WWSCV	WWSCV	

1. Region: NS, North Spring Corn Region; NWI, Northwest Inland region; HS, Huang-Huai-Hai Summer Corn Region; SWH, Southwest Hilly Corn Region; SH, South Hilly Corn Region;

2. Sampling window refers to the month of the year (in Roman numerals) during which sampling was conducted. –: indicates absence

3. Cropping pattern: WWSC: winter wheat – summer corn; WWSCR: winter wheat – summer corn/rice; WWSCV: winter wheat – summer corn/vegetables; SCWC: summer corn – winter corn ; SRS: spring corn / rice / soybean; SCR: spring corn / rice ; SRSW: spring corn / rice / spring wheat ; WSC: winter wheat – summer corn / cotton ; WCC: wheat – corn / cotton; SWC: spring wheat – corn; CS: corn – soybean WWOC: winter wheat – other crops.

4. 1980s is based on the paper of Zhang et al. (1990), the same below.

Grey background color of the entire provinces / regions where augmentative releases have been conducted with *T. dendrolimi.*

Data were collated from successive sampling events between 1977 and 1987, carried out by Zhang et al. (1990). More specifically, sampling was carried out in a systematic fashion in 13 corn-growing provinces and municipalities (Table 1) e.g., Heilongjiang, Jilin, Liaoning, Beijing and Zhejiang. ACB egg masses were sampled from different field sites, kept in the laboratory until parasitoid emergence and parasitoids were identified based upon morphological characteristics. For each sampling site, parasitoid species identity and diversity measures were obtained.

Collection of ACB egg masses

There are six main corn-growing regions in China i.e., the North Spring (NS), Huang-Huai-Hai Summer (HS), Southwest Hills (SWH), South Hills (SH), Northwest Inland Irrigation (NWI), and the Qinghai-Tibet Plateau Corn Region. During 2016-2018, ACB egg masses were collected from the first five regions (i.e., NS, HS, SWH, SH, NWI) throughout the *O. furnacalis* oviposition period i.e., mid-July to late October. Egg masses were collected from successive ACB generations i.e., 2nd generation (NS, NWI region), 3rd generation (HS) or 4th to 5th generation (SH, SWH). In total, 49 sampling sites were selected and 20-30 ACB egg masses were collected at min. 5 m distances per site. Only one sampling event was conducted per site, for which GPS coordinates, local cropping patterns and agronomic practices were recorded (Table 1). Upon field collection, ACB egg masses were individualized in sterilized 10 ml micro tubes, covered with a cotton plug and kept at 8°C. Tubes were then transferred to the laboratory and kept at 25°C until the emergence of adult (*Trichogramma* or *Telenomus* spp.) parasitoids. Parasitoids from each single egg mass were considered as an individual population and were maintained at the Institute of Plant Protection,

Chinese Academy of Agricultural Sciences (IPP-CAAS), Beijing, China. Each single population was maintained by allowing the wasps to oviposit in ACB egg masses and by providing 20% honey-water solution as a food source. Dead specimens were kept in sterilized 1.5 ml tube at -20°C until further morphological and molecular analyses.

Molecular identification

For each parasitoid population, genomic DNA was extracted from several specimens using Tris-HCL lytic buffer as per Li (2007). In brief, individual *Trichogramma* sp. or *Telenomus* sp. specimens were crushed in 10 μl of Tris-HCL buffer on parafilm with a sterilized micro-pestle. Next, 25 μl of the homogenate was transferred to a sterilized 200 μl PCR tube and centrifuged. The homogenate was then incubated in a Techne TC-5000 Thermocycler (Techne, Minneapolis, MN) at 65°C for 30 min, and 96°C for 10 min and a final hold at -20°C. Two microliters of DNA was used for the PCR template. The PCR was performed in a total volume of 25 μl using the above thermocycler. For each reaction, we used 2 μl of DNA template, 13 μl mixTaq DNA polymerase, 8 μl DD H_2O, and 1 μl of each forward and reverse primers. To amplify *Trichogramma* spp. COII regions, we used 5'- ATTGGACATCAATGATATTGA-3' (forward) and 5'-CCACCAATTTCTGAACATTGACCA-3' (reverse) primers (Stouthamer et al. 1999). For *Telenomus* spp., the following COI regions were used: 5'—GGTCAACAAATCATAAAGATATTGG—3'(forward) and 5'—TAAACTTCAGGGTGACCAAAAAATCA—3' (reverse). PCR amplification was achieved by initially denaturing DNA at 94 °C for 3 min, followed by 35 amplification cycles (i.e., 30 s at 94 °C, 30 s at 55°C, and 1min at 72 °C), an extension at 72 °C for 8 min and subsequent storage at -20°C. Five microliters of the PCR products were subject to gel electrophoresis on a 1.5% agarose gel that was stained with Ethidium bromide along with a size ladder (Trans 2K® plus DNA Marker100-bp). Following a 25 min electrophoresis run at constant 120 V, DNA bands were visualized under ultraviolet (UV) light and amplification was confirmed based upon the length of the amplification fragment (Fig. 1). Each PCR product was then sequenced in an automatic sequencer (Sangon Biotech, Beijing) to obtain the matching sequences in both directions of DNA strands. The resulting forward and reverse reads were manually aligned and checked for agreement in DNAMAN and DNASTAR (Laser gene v.7). Species were identified by submitting the nucleotide sequences in Gen Bank Database, NCBI using BLAST to search for similarity with nucleotides present in the database. Sequence matches of 99 -100% were used to identify each specimen (or population); confirmed sequences were equally deposited in GenBank.

Morphological identification

Individual parasitoid specimens were slide-mounted following procedures adapted from Noyes (1982). In brief, dried male specimens were incubated in 10% KOH for 24 h at room temperature until body parts became transparent. After pipetting the KOH, each specimen was rinsed three times in distilled water and then washed with ethanol for another three times (70% and 95% concentration; 15-20 min each). Next, dehydrated specimens were soaked in high-quality clove oil overnight, and subsequently transferred onto the glass slide in a drop of clove oil and Canada Balsam (1:1). Specific organs were dissected with a No. 1 needle and properly positioned. After positioning the cover slip on each specimen, slides were air-dried for 3-4 days at room temperature. Pictures were taken using an Olympus SZ61 light microscope (Olympus Corporation, Tokyo, Japan); morphological structures and ratios were defined as per Pinto (1999). For each species, ten individual males were dissected and mounted on glass slides (Fig. 2).

Data processing

For each sampling event and geographical location (i.e., sampling site, province, corn-growing region), we calculated the Shannon-Wiener diversity index (H), based upon the below formula:

$$H = -\sum P_i \ln P_i$$

P_i = proportion of total sample belonging to the ith species

N_i = number of individuals belonging to the ith species

Results

Historic parasitoid censuses

Over 1977-1987, 3166 male *Trichogramma* individuals were identified to species level and 12 congeneric *Trichogramma* spp. were recorded from ACB eggs collected in China's main corn-growing regions (Zhang et al., 1990). Four species were widely distributed: *T. ostriniae* Pang et Chen, *T. dendrolimi* Matsumura, *T. chilonis* Ishii, and *T. evanescens* Westwood. Conversely, eight species were only recorded in some regions: *T. leucaniae* Pang et Chen, *T. poliae* Nagaraja, *T. closterae* Pang et Chen, *T. pintoi* Voegele, *T. ivelae* Pang et Chen, *T. exiguum* Pinto and Platner, *T. forcipiformis* Zhang and Wang, and *T. tielingensis* Zhang and Wang. Overall, the *Trichogramma* spp. community varied greatly between sampling years and locations. While *T. ostriniae* was the dominant species in most corn growing regions, *T. dendrolimi* and *T. chilonis* constituted a respective 97.3% and 88.9% of individuals in Heilongjiang and Guizhou. The community composition exhibited important inter-annual fluctuation. (Zhang et al., 1990). On a province level *Trichogramma* species richness ranged from 2-7 and H indices from 0.12-0.94.

Nationwide survey in 2016-2018

Table 2

Proportional composition of the parasitoid species complex as recorded from ACB egg masses in China. Egg masses were collected during 2016-2018 from key corn-growing regions in China. For each province and corn-growing region, the total number of adult parasitoids and the (proportional) species make-up is indicated. Relative occurrence data are also reported for *Telenomus sp*, which parasitized ACB in Guangxi province.

Region	Province	Total N	Make-up of parasitoid species complex					
			Tere	*Tbi*	*Tde*	*Tch*	*Tbr*	*Tos*
NS	Heilongjiang	52	-	-	0.15		0.04	0.81
	Jilin	65	-	-	0.11	-	-	0.89
	Liaoning	49	-	-	-	-	-	1.00
	Inner Mongolia	82	-	-	-	-	-	1.00
	Shanxi	23	-		-	-	-	1.00
	Ningxia	24	-	-	-	-	-	1.00
NWI	Xinjiang	80	-	-	-	-	1.00	-
	Gansu	70	-	-	-	-	-	1.00
HS	Shaanxi	27	-	-	-	-	-	1.00
	Shanxi	24	-	-	-	-	-	1.00
	Beijing	49	-	-	0.02	0.06	-	0.92
	Hebei	55	-	-	-	-	-	1.00
	Shandong	140	-	-	-	-	-	1.00
	Henan	93	-	-	-	-	-	1.00
	Anhui	63	-	-	-	-	-	1.00
SWI	Hubei	38	-	-	-	0.03	-	0.97
	Sichuan	56	-	-	-	-	-	1.00
	Chongqing	21	-	-	-	-	-	1.00
	Guizhou	61	-	-	-	-	-	1.00
	Yunnan	21	-	-	-	-	-	1.00
	Shaanxi	38	-	-	-	0.05	-	0.95
SH	Anhui	16	-	-	-	-	-	1.00
	Hunan	22	-	0.36	-	0.64	-	-
	Hubei	21	-	-	-	-	-	1.00
	Zhejiang	21	-	-	-	-	-	1.00
	Guangxi	20	0.20	-	-	0.10	-	0.70
	Guangdong	20	-	-	-	-	-	1.00

Species abbreviations: *T. remus* (Tere), *T. bilinggensis* (Tbi), *T. dendrolimi* (Tde), *T. chilonis* (Tch), *T. brassicae* (Tbr), *T. ostriniae* (Tos). Grey background color indicates those provinces / regions where augmentative releases were conducted with *T. dendrolimi*. Total N refers to parasited ACB egg masses from different key corn-growing regions in Provincial level.

Six species of egg parasitoids were identified i.e., *T. ostriniae* (GenBank accession number MT975337), *T. dendrolimi* (MT975339), *T. chilonis* (MT975340), *T. brassicae* (MT975338), *T. bilinggensis* (MT975341) and *Telenomus sp.* (MW419148). From the 11 samples collected in NS, 15 separate parasitoid populations were obtained with *T. ostriniae* accounting for 92.9% of all individuals (Table 2). In NWI, *T. brassicae* and *T. ostriniae* emerged from field-collected egg masses; the former species was solely recorded from this region. In HS, only *T. ostriniae* was recovered from most sites except for those in Beijing − where the species comprised 91.7-92.0 % of the entire complex. In SWH, 99.5% of emerged parasitoids were *T. ostriniae* while the remaining share were *T. chilonis*. Lastly, in SH, *T. ostriniae* accounted for 66.3% all individuals while a further three species were recorded.

Long-term shifts in occurrence and abundance

Table 3

Occurrence and geographical distribution of 14 different *Trichogramma* species, as determined by (country-wide) sampling events during the 1980s and 2016-2018. Patterns are based on Zhang et al. (1990a) and on nationwide parasitoid censuses carried out over 2016-2018. Distribution patterns describe species-specific coverage of the (5) main corn-growing regions.

Species	Occurrence		Geographical distribution	
	1980s	2016-2018	1980s	2016-2018
T. ostriniae	P$	P	Nationwide	Nationwide
T. dendrolimi	P	P	Nationwide	Heilongjiang, Jilin, Liaoning, Beijing
T. chilonis	P	P	Nationwide	Nationwide*
T. evanescens	P	-	Nationwide	-
T. leucaniae	P	-	Hubei, Liaoning	-
T. poliae	P	-	Liaoning	-
T. closterae	P	-	Liaoning	-
T. pintoi	P	-	Liaoning	-
T. ivelae	P	-	Liaoning	-
T. exiguum	P	-	Liaoning	-
T. forcipiformis	P	-	Liaoning	-
T. tielingensis	P	-	Liaoning	-
T. brassicae	-	P	-	Xinjiang, Heilongjiang
T. bilinggensis	-	P	-	Hunan

$ P indicates presence within a given year, - indicates absence

* Except for the North Spring (NS) region

Over a 30-year time frame, *Trichogramma* spp. community structure and geographic distribution changed considerably (Table 3). While *T. ostriniae* continues to be the most widely distributed species, other parasitoids experienced a more restricted distribution (*T. dendrolimi*) or were entirely absent from 2018 censuses (e.g., *T. evanescens*, *T. leucaniae*). On a province-level, *Trichogramma* species richness declined from 2-7 during the 1980s to 1-3 over 2016-2018. While richness values remained unchanged in Heilongjiang province, they dropped by 25.0-85.7% in the remaining 7 provinces. Province-level changes in species richness were paralleled by shifts in the overall species composition, e.g., with *T. ostriniae* and *T. dendrolimi* switching in their relative abundance in Heilongjiang province (Fig. 3).

On a province level, *Trichogramma* species diversity ranged from 0.12-0.94 and 0.00 - 0.58 during 1977-1987 and 2016-2018, respectively. Compared to the 1980s, overall *Trichogramma* species diversity declined by 56.2-100% except for Heilongjiang province, where it increased by 314.3 %. In the three northeastern provinces where *T. dendrolimi* mass-releases were conducted, species richness ranged from 1-3 (as compared to 1-2 for provinces where no augmentative releases were done). The respective H indices ranged from 0-0.58 to 0-0.09 during 2018.

Discussion

Across the globe, insects are experiencing a precipitous decline (Sánchez-Bayo and Wyckhuys, 2019; Wagner et al., 2021; Cardoso et al., 2020), which could result in a critical loss of ecosystem integrity and functioning. Drawing upon historic census data, extensive field surveys across China's main corn-growing regions and integrative taxonomy approaches, we unveil temporal changes in the egg parasitoid community associated with ACB. Out of the 12 different *Trichogramma* spp. that were identified during the 1980s, only three were recovered over 2016-2018 (while two new species were found in certain areas). In addition to the declines in parasitoid richness and diversity, several *Trichogramma* spp. also exhibited a more restricted geographical distribution. We discuss the underlying drivers of this loss of functional diversity in China's corn agro-ecosystems and the eventual implications for ecological resilience, agricultural sustainability and food security.

Table 4

Comparison of Trichogramma species richness and diversity in 8 key corn-growing regions of China during the 1980s and 2016-2018. Total sample size (i.e., emerged adults) is indicated for each geographical area and sampling period. Data are exclusively shown for provinces that were surveyed during both time periods.

Province	Species richness			Species diversity		
	1980s	2016-2018	Change	1980s	2016-2018	Change
Heilongjiang	3	3	-	0.14	0.58	314.3% á
Jilin	4	2	-50.0%	0.80	0.35	-56.2%
Liaoning	7	1	-85.7%	0.94	0.00	-100.0%
Beijing	4	3	-25.0%	0.76	0.32	-57.9%
Hubei	4	2	-50.0%	0.27	0.09	-66.7%
Shandong	3	1	-66.7%	0.38	0.00	-100.0%
Anhui	2	1	-50.0%	0.12	0.00	-100.0%
Zhejiang	4	1	-75.0%	0.82	0.00	-100.0%

* Total number of emerged parasitoids during the 1980s and 2016-2018. Grey background color indicates those provinces / regions where augmentative releases were conducted with *T. dendrolimi*.

In several sites (e.g., the Northeast Spring Corn Region), the number of ACB parasitoid species was reduced by 50% or more since the 1980s (Zhang, 1990). In Liaoning, parasitoid richness even declined by 87.5% over this time frame (Table 4). This could be ascribed to inaccuracies in earlier (morphology-based) identification, which are common for minute parasitic wasps such as *Trichogramma* ssp. Also, parasitoid community composition can vary considerably throughout the cropping season, with *T. dendrolimi* and *T. ostriniae* being the main parasitoids of a respective 1st vs. 2nd generation ACB in the 1980s (Zhang, 1990). Furthermore, temporal changes in (landscape-level) crop diversity or farming methods can lead to losses in parasitoid diversity (Laliberté and Tylianakis, 2010; Jonsson et al., 2012). For example, the planting area of corn and soybean in Northeast China increased by a respective 160% and 47% over the study period. Meanwhile, in the Huang-Huai-Hai Summer Corn Region, corn acreage increased by 94% increase. Conversely, soybean acreage increased by 116% in Heilongjiang province, where the number of *Trichogramma* spp. remained unchanged. Lastly, the overuse of synthetic pesticides on China's farmland is undoubtedly one of the key drivers of biodiversity loss in agricultural settings and beyond (Wu et al., 2018; Tang et al., 2021). While pesticide-based crop protection can lead to short-term declines in pest pressure (but see Janssen and van Rijn, 2021), these effects are likely outweighed by a steady decay of ecosystem functionalities and ecological resilience.

In several sites (e.g., Beijing, Jinan, Shandong), *T. dendrolimi* has been released against *O. furnacalis* for extended periods of time (Yu et al., 1982; Feng et al., 1996, 1999). Our findings do not show that these augmentative releases negatively affected the ACB egg parasitoid community in corn fields. As compared to experiences in Switzerland with *T. brassicae* (Kuske et al., 2003; Babendreier et al., 2003), laboratory-reared *T. dendrolimi* possibly do not readily establish in local corn fields where *T. ostriniae* remains the dominant species. This could relate to differences in competitive advantage (Liu, 2019), host range and host acceptance behavior of both species, with *T. ostriniae* preferably ovipositing in small host eggs (e.g., *Corcyra cephalonica*, *Sitotroga cerealella*), as compared to *T. dendrolimi* which accepts larger eggs such as those from *Antheraea pernyi*. Aside from its clear advantages for laboratory-based mass-rearing (Wang et al., 2014), the preference of *T. dendrolimi* for large-size hosts may also lower its risks for negative environmental impacts in agricultural ecosystems. As comparatively few *T. dendrolimi* were recorded in the field samples, this could also mirror the species' preference for temporally-stable habitats such as natural areas, fruit orchards or forest plots (Oztemiz, 2007; Wang et al., 2014). The latter species is known to parasitize multiple forest-dwelling lepidopterans e.g., *Pandemis heparana*, *Gastropacha populifolia*, *Dictyoploca japonica*, *Dendrolimus punctatus*, *Cerura menciana* (Zhang et al., 1979). Hence, further censuses in non-agricultural settings are essential to ascertain whether inundative releases of *T. dendrolimi* do not negatively impact on resident (non-pest) biota e.g., species belonging to the Saturniidae. Evidently, any future ecological impact assessment of *T. dendrolimi* augmentative biological control needs to be conducted at an ecologically relevant spatial scale and encompass both agricultural and natural habitats.

Changes in host community composition can also bring about shifts in parasitoid species identity and incidence. In areas such as the Northwest Inland Irrigated Corn Region, corn crops are either colonized by *O. furnacalis* or by the European corn borer *Ostrinia nubilalis* (Wang et al, 2017). Both species only co-occur in Yili district of Western Xinjiang, where *O. furnacalis* has been gradually displacing *O. nubilalis* in local cropping systems (Yang et al., 2008, 2011; Wang et al., 2017). In areas where *O. nubilalis* is endemic (e.g., Iran, Turkey), *T. brassicae* is the primary species of *Trichogramma* sp. (Poorjavad et al., 2012; Koca et al., 2018). This can explain why all samples from Xinjiang only yielded *T. brassicae*, while other species (e.g., *T. pintoi*) occur at background abundance levels (Wu et al., 2008). Lastly, *T. dendrolimi* and *T. chilonis* were not recorded in our recent censuses in Xinjiang, although both species are locally used for augmentation biological control (Xu et al., 2001). This might indicate how both species cannot compete with the locally dominant *T. brassicae* and fail to persist in the harsh and ecologically fragile settings of northwestern China. Overall, temporal shifts in host and parasitoid community make-up carry implications for crop protection, and habitat management schemes will need to be attuned to the prevailing biological control agents and local (a-)biotic conditions (Gurr et al., 2017; Perović et al., 2018). Biological and applied ecological studies are thus essential to ensure that (biodiversity-based) management strategies are well-suited to local farming contexts. Similarly, much can be learned from inundative biological control efforts with *T. brassicae* in areas where *O. nubalilis* is endemic (Burgio and Maini, 1995; Hawlitzky, 1994; Suverkropp, 1994; 1997;).

In the 1980s, four *Trichogramma* species, *T. ostriniae*, *T. dendrolimi*, *T. chilonis* and *T. evanescens*, were widely distributed in various areas of China (Zhang et al., 1990). These patterns contrast markedly with those in 2018 (Table 3, 4), where only few areas harbored three species and where one single species (*T. ostriniae*) made up the bulk of the egg parasitoid community in several areas (e.g., Southwest Hilly Corn Region). The above compares to the markedly higher abundance of *T. chilonis* on ACB egg masses during the 1980s (Zhang et al., 1990). Meanwhile, two new *Trichogramma* spp. are recorded from ACB egg masses (i.e., *T. brassicae*, *T. bilinggensis*) and *Telenomus remus* is equally reported from Guangxi province. In some locations, these new species (i.e., *T.*

bilinggensis) represent 36% of the ACB egg parasitoid community. Work is urgently needed to examine the biology, ecology and biological control potential of these new species. On the other hand, *T. remus is a well-studied parasitoid* of many lepidopteran species that provides effective control of the newly-invasive fall armyworm, *Spodoptera frugiperda* (Kenis et al., 2019; Liao et al., 2019; Jiang et al., 2019; Paolo et al., 2020). An in-depth characterization of the emergence of these new species and overall species turnover within the *O. furnacalis* parasitoid community may prove worthwhile e.g., in view of climate-driven range expansion of target pests (Zeng et al., 2020). As such, ecological studies in corn agro-ecosystems within (sub-)tropical settings can help to anticipate community shifts (and associated changes in ecosystem services) under climate change scenarios.

As a follow-up to earlier censuses during the 1980s (Zhang et al., 1990), our survey for ACB egg parasitoids covered a broad range of agro-ecological contexts and farming systems in China. Despite eventual shortcomings in the survey methodology, we report stark drops in *Trichogramma* species richness and diversity in local corn agro-ecosystems. Out of the 12 species that were recorded in the 1980s, only three were recovered during 2016-2018 (i.e., *T. ostriniae*, *T. dendrolimi and T. chilonis*) while two new species have made their appearance. This 75% loss in species richness can be ascribed to faulty identification and major changes in China's agriculture e.g., shifting cultivation patterns, (chemical) intensification and a progressive loss of (crop, non-crop) diversity. Pesticide-centered crop protection likely exerts net negative impacts on resident biota. In the meantime, more extensive follow-up assessments are needed to clarify ecological impacts of inundative biological control with *T. dendrolimi* e.g., in perennial (natural) habitats. Overall, the precipitous decline in functional biodiversity as recorded in our study can lead to an agro-ecological imbalance, with potentially grave impacts for food security and societal wellbeing (Burra et al., 2021). Hence, agro-ecological and biodiversity-based measures are to be prioritized to intensify China's corn production systems in a way that benefits farmers, society at large and the environment. Biological control (e.g., inundative releases of laboratory-reared *Trichogramma* spp.) is to be a cornerstone of those ecological intensification strategies, needs to be underpinned by robust science and guided by full-fledged ecological risk assessments.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this

article.

References

1. Anonymous, 2019. China Agriculture Yearbook. China Agriculture Press, Beijing.

2. Babendreier, D., Schoch, D., Kuske, S., Dorn, S., Bigler, F., 2003. Non-target habitat exploitation by *Trichogramma brassicae* (Hym. Trichogrammatidae): what are the risks for endemic butterflies?. Agri. Forest Entomol. 5(3),199-208. https://doi.org/10.1046/j.1461-9563.2003.00180.x.

3. Burgio G, Maini S. 1995. Control of European corn borer in sweet corn by *Trichogramma brassicae* Bezd. (Hym. Trichogrammatidae). J. Appl. Entomol. 119(1-5),83-87. https://doi.org/10.1111/j.1439-0418.1995.tb01248.x.

4. Burra, D. D., Pretty, J., Neuenschwander, P., Liu, Z., Zhu, Z. R., Wyckhuys, K.A.G., 2021. Human health outcomes of a restored ecological balance in African agro-landscapes. Sci. Total Environ. 775, 145872. https://doi.org/10.1016/j.scitotenv.2021.145872.

5. Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., et al., 2012. Biodiversity loss and its impact on humanity. Nature, 486(7401), 59-67. https://doi.org/10.1038/nature11148.

6. Cardoso, P., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., et al., 2020. Scientists' warning to humanity on insect extinctions. Biol. Conserv. 242, p.108426. https://doi.org/10.1016/j.biocon.2020.108426.

7. Consoli, F. L., Parra, J., Zucchi, R. A.(Eds.), 2010. Egg Parasitoids in Agroecosystems with Emphasis on *Trichogramma* 9. Springer Science & Business Media. https://doi.org/10.1007/978-1-4020-9110-0.

8. Crossley, M.S., Meier, A.R., Baldwin, E.M., Berry, L.L., Crenshaw, L.C., Hartman, G.L., et al., 2020. No net insect abundance and diversity declines across US Long Term Ecological Research sites. Nat. Ecol. Evol. 4(10), 1368-1376. http://dx.doi.org/10.1038/s41559-020-1269-4.

9. Cui, Z.L., Zhang, H.Y., Chen, X.P., Zhang, C.C., Ma, W.Q., Huang, C.D., et al., 2018. Pursuing sustainable productivity with millions of smallholder farmers. Nature, 555(7696), 363-366. https://doi.org/10.1038/nature25785.

10. Dainese, M., Martin, E.A., Aizen, M.A., Albrecht, M., Bartomeus, I., Bommarco, R., et al., 2019. A global synthesis reveals biodiversity-mediated benefits for crop production. Sci. Adv. 5(10), p.eaax0121. http://dx.doi.org/ 10.1126/sciadv.aax0121.

11. Ely, A., Geall, S., Song, Y., 2016. Sustainable maize production and consumption in China: practices and politics in transition. J. Clean. Prod. 134, 259-268. https://doi.org/10.1016/j.jclepro.2015.12.001.

12. Feng, J., 1996. The effect and influence factors on the use of *Trichogramma dendrolimi* to control *Ostrinia furnacalis*. Entomol. J. East China. 5, 45-50.

13. Feng, J.G., Tao, X., Zhang, A.S., Yu, Y., Zhang, C.W., Cui, Y.Y., 1999. Studies on using *Trichogramma* spp. reared on artificial host egg to control corn pests. Chin. J. Biol. Contr. 15, 97-99. http://dx.doi.org/10.3969/j.issn.2095-039X.1999.03.001.

14. Guo, J.L., Fu, X.W., Zhao, S.Y., Shen, X.J., Wyckhuys, K.A., Wu, K.M., 2020. Long-term shifts in abundance of (migratory) crop-feeding and beneficial insect species in northeastern Asia. J. Pest Sci. 93(2), 583-594. http://dx.doi.org/10.1007/s10340-019-01191-9.

15. Guo, W.C., He, J., Xu, J.J., Tuerxun., Tan, Y.F., Mao, G., et al., 2005. Studies on harmless control of *Ostrinia furnacalis* in maize field of Xinjiang. J. Maize Sci. 13, 108-110. http://dx.doi.org/ 10.3969/j.issn.1005-0906.2005.01.033.

16. Gurr, G.M., Wratten, S.D., Landis, D.A., You, M., 2017. Habitat management to suppress pest populations: progress and prospects. Ann. Rev. Entomol. 62, 91-109. https://doi.org/10.1146/annurev-ento-031616-035050.

17. Hallmann, C.A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., et al., 2017. More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PloS one, 12(10), p.e0185809. http://dx.doi.org/10.1371/journal.pone.0185809.

18. Hawlitzky, N., Dorville, F.M., Vaillant, J., 1994. Statistical study of *Trichogramma brassicae* efficiency in relation with characteristics of the European corn borer egg masses. Res. Popul. Ecol. 36(1),79-85. https://doi.org/10.1007/BF02515088.

19. He, K.L., Wang, Z.Y., Zhou, D.R., Wen, L.P., Song, Y.Y., Yao, Z.Y., 2003. Evaluation of transgenic Bt corn for resistance to the Asian corn borer (Lepidoptera: Pyralidae). J. Econ. Entomol. 96, 935-940. https://doi.org/10.1093/jee/96.3.935.

20. Heethoff, M., Laumann, M., Weigmann, G., Raspotnig, G., 2011. Integrative taxonomy: combining morphological, molecular and chemical data for species delineation in the parthenogenetic *Trhypochthonius tectorum* complex (Acari, Oribatida, Trhypochthoniidae). Front. Zool. 8(1), 1-10. http://dx.doi.org/10.1186/1742-9994-8-2.

21. Huang, N.X., Jaworski, C., Desneux, N., Zhang, F., Yang, P.Y., Wang, S., 2020. Long-term, large-scale releases of *Trichogramma* promote pesticide decrease in maize in northeastern China. Entomol. Gen. 40(2020).331-335. http://dx.doi.org/10.1127/entomologia/2020/0994.

22. Janssen, A., van Rijn, P. C., 2021. Pesticides do not significantly reduce arthropod pest densities in the presence of natural enemies. Ecol. Lett. 24(9), 2010-2024. https://doi.org/10.1111/ele.13819.

23. Janzen, D.H., 1971. The deflowering of central America. Natural History 83, 49-53.

24. Jiang, Y.Y., Liu, J., Zhu, X.M., 2019. Analysis on the occurrence dynamics and future trend of *Spodoptera frugiperda* invasion in China. Plant Prot. 39, 33-35. http://dx.doi.org/10.3969/j.issn.1672-6820.2019.02.006.

25. Jonsson, M., Buckley, H.L., Case, B.S., Wratten, S.D., Hale, R.J., Didham, R.K., 2012. Agricultural intensification drives landscape-context effects on host–parasitoid interactions in agroecosystems. J. Appl. Ecol. 49(3), 706-714. https://doi.org/10.1111/j.1365-2664.2012.02130.x.

26. Kadoya, T., Suda, S.I., Washitani, I., 2009. Dragonfly crisis in Japan: a likely consequence of recent agricultural habitat degradation. Biol. Conserv. 142(9),1899-1905. https://doi.org/10.1016/j.biocon.2009.02.033.

27. Kehoe, R., Frago, E., Sanders, D., 2021. Cascading extinctions as a hidden driver of insect decline. Ecol. Entomol. 46(4), 743-756. https://doi.org/10.1111/een.12985.

28. Kenis, M., Du Plessis, H., Van den Berg, J., Ba, M.N., Goergen, G., Kwadjo, K.E., et al., 2019. *Telenomus remus*, a candidate parasitoid for the biological control of *Spodoptera frugiperda* in Africa, is already present on the continent. Insects 10(4), 92. https://doi.org/10.3390/insects10040092.

29. Koca, A.S., Mren, M., HalilKütük., 2018. Determination of the genetic variation within the egg parasitoid,*Trichogramma brassicae*, Bezdenko (Hymenoptera: Trichogrammatidae) populations in Düzce Province, Turkey. Uluslararası Tarım ve Yaban Hayatı Bilimleri Dergisi, 4(1).26-32. https://doi.org/10.24180/ijaws.395438.

30. Kuske, S., Widmer, F., Edwards, P.J., Turlings, T.C., Babendreier, D., Bigler, F., 2003. Dispersal and persistence of mass released *Trichogramma brassicae* (Hymenoptera: Trichogrammatidae) in non-target habitats. Biol. Control 27(2), 181-193. http://dx.doi.org/10.1016/S1049-9644(02)00191-3.

31. Laliberté, E., Tylianakis, J.M., 2010. Deforestation homogenizes tropical parasitoid–host networks. Ecology, 91(6), 1740-1747. https://doi.org/10.1890/09-1328.1.

32. Li, Z. X., 2007. Molecular differentiation of the four most commonly occurring *Trichogramma* species in China. Eur. J. Entomol. 104(3),363-367. http://dx.doi.org/10.14411/EJE.2007.054.

33. Liao, Y.L., Yang, B., Xu, M.F., Lin, W., Wang, D.S., Chen, K.W.,et al., 2019. First report of *Telenomus remus* parasitizing *Spodoptera frugiperda* and its field parasitism in southern China. J. Hymenop. Res. 73, 95-102.   http://dx.doi.org/ 10.3897/jhr.73.39136.

34. Lister, B.C., Garcia, A., 2018. Climate-driven declines in arthropod abundance restructure a rainforest food web. Proc. Natl. Acad. Sci. 115(44), 201722477. https://doi.org/10.1073/pnas.1722477115.

35. Liu, G.Q., 2019. Intra egg competition of *Trichogramma* dominant parasitic Asian corn borer (*Ostrinia furnacalis*) based on microsatellite markers, p23-29, Master's Thesis. Jilin Agriculture University, Changchun. http://dx.doi.org/10.27163/d.cnki.gjlnu.2019.000151.

36. Losey, J.E., Vaughan, M., 2006. The economic value of ecological services provided by insects. Bioscience 56(4),311-323. https://doi.org/10.1641/0006-3568(2006)56[311:TEVOES]2.0.CO;2.

37. Nafus, D.M., Schreiner, I., 1991. Review of the biology and control of the Asian corn borer, *Ostrinia furnacalis* (Lep: Pyralidae). Trop Pest Manag. 37, 41–56. https://doi.org/10.1080/09670879109371535.

38. Noyes, J. S., 1982. Collecting and preserving chalcid wasps (Hymenoptera: Chalcidoidea). J. Nat. Hist. 16, 315–334. https://doi.org/10.1080/00222938200770261.

39. Oztemiz, S., 2007. *Trichogramma* species (Hymenoptera: Trichogrammatidae) egg parasitoids of Lepidoptera in the Eastern Mediterranean Region of Turkey. Proc. Entomol. Soc. Wash. 109, 718–720.

40. Paolo, S.M., Cesar R.S., Odair A.F. 2020. Release density, dispersal capacity, and optimal rearing conditions for *Telenomus remus*, an egg parasitoid of *Spodoptera frugiperda*, in maize. Biocontrol. Sci. Techn. 30(10),1040-1059. https://doi.org/10.1080/09583157.2020.1776841.

41. Perović, D. J., Gámez-Virués, S., Landis, D. A., Wäckers, F., Gurr, G. M., Wratten, S. D., et al., 2018. Managing biological control services through multi-trophic trait interactions: review and guidelines for implementation at local and landscape scales. Biol. Rev. 93(1), 306-321. https://doi.org/10.1111/brv.12346.

42. Pimentel, D., Wilson, C., McCullum, C., Huang, R., Dwen, P., Flack, J., et al., 1997. Economic and environmental benefits of biodiversity. BioScience 47(11), .747-757. https://doi.org/10.2307/1313097.

43. Pinto, J.D., 1999. Systematics of the North American species of *Trichogramma* Westwood (Hymenoptera: Trichogrammatidae). Memoirs Entomol Soc Wash. 22 (1998), 1-287.

44. Pinto, J.D., Velten, R.K., Platner, G.R., Oatman, E.R., 1989. Phenotypic plasticity and taxonomic characters in *Trichogramma* (Hymenoptera: Trichogrammatidae). Ann. Entomol. Soc.Am. 83,414−425. https://doi.org/10.1093/aesa/82.4.414.

45. Poorjavad, N., Goldansaz, S. H., Machtelinckx, T., Tirry, L., Stouthamer, R., Leeuwen, T. V., 2012. Iranian *Trichogramma*: ITS-2 DNA characterization and natural *Wolbachia* infection. Biocontrol 57(3), 361-374. https://doi.org/10.1007/s10526-011-9397-z.

46. Sánchez-Bayo, F., Wyckhuys, K.A., 2019. Worldwide decline of the entomofauna: A review of its drivers. Biol. Conserv. 232,8-27. https://doi.org/10.1016/j.biocon.2019.01.020.

47. Sánchez-Bayo, F., Wyckhuys, K.A., 2021. Further evidence for a global decline of the entomofauna. Austral Entomol. 60(1), 9-26. https://doi.org/10.1111/aen.12509.

48. Schlick-Steiner, B.C., Steiner, F.M., Seifert, B., Stauffer, C., Christian, E., Crozier, R.H., 2010. Integrative taxonomy: a multisource approach to exploring biodiversity. Ann. Rev. Entomol. 55, 421-438. https://doi.org/10.1146/annurev-ento-112408-085432.

49. Seibold, S., Gossner, M.M., Simons, N.K., Blüthgen, N., Müller, J., Ambarlı, D., et al., 2019. Arthropod decline in grasslands and forests is associated with landscape-level drivers. Nature, 574(7780), 671-674. https://doi.org/10.1038/s41586-019-1684-3.

50. Soliveres, S., Van Der Plas, F., Manning, P., Prati, D., Gossner, M.M., Renner, S.C., et al., 2016. Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536(7617), 456-459. https://doi.org/10.1038/nature19092.

51. Song, L.Q., Wei, L.M., Wang, Z.Y., He, K.L., Cong, B., 2009. Effect of infestation by the Asian corn borer together with *Fusarium verticillioides* on corn yield loss. Acta Phytophyl. Sin. 36, 487-490. http://dx.doi.org/ 10.3321/j.issn:0577-7518.2009.06.002.

52. Stouthamer, R., Hu, J., Kan, F., Platner, G. R., Pinto, J. D., 1999. The utility of internally transcribed spacer 2 DNA sequences of the nuclear ribosomal gene for distinguishing sibling species of *Trichogramma*. BioControl. 43,421−440. http://dx.doi.org/10.1023/A:1009937108715

53. Suverkropp, B.P., 1994. Landing of *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae) on maize plants. Norwegian J. Agri. Sci. Supplement 16: 243-254.

54. Suverkropp, B.P., 1997. Host-finding behaviour of *Trichogramma brassicae* in maize. 249 p., PhD Thesis, Wageningen University, The Netherlands.

55. Tan, Y.Q., 1999. Present status and prospect in *Trichogramma* application in Heilongjiang Province. Chin. Agri. Sci. Bull. 15, 50-51.

56. Tang, F.H., Lenzen, M., McBratney, A., Maggi, F., 2021. Risk of pesticide pollution at the global scale. Nat. Geosci. 14(4), 206-210. https://doi.org/10.1038/s41561-021-00712-5.

57. van Lenteren, J.C., Bolckmans, K., Köhl, J., Ravensberg, W.J., Urbaneja, A., 2018. Biological control using invertebrates and microorganisms: plenty of new opportunities. BioControl 63(1), 39-59. https://doi.org/10.1007/s10526-017-9801-4.

58. Wagner, D.L., Grames, E.M., Forister, M.L., Berenbaum, M.R., Stopak, D., 2021. Insect decline in the Anthropocene: Death by a thousand cuts. Proc. Natl. Acad.Sci. 118(2).1-10. https://doi.org/10.1073/pnas.2023989118.

59. Wang, Y.Z., Kim, K.S., Guo, W.C., Zhang, Y.Y., Wang, Z.Y., Coates, B.S., 2017. Introgression between divergent corn borer species in a region of sympatry: Implications on the evolution and adaptation of pest arthropods. Mol. Ecol. 26, 6892− 6907. https://doi.org/10.1111/mec.14387

60. Wang, Z.Y., He, K.L., Zhang, F., Lu, X., Babendreier, D., 2014. Mass rearing and release of *Trichogramma* for biological control of insect pests of corn in China. Biol. Contr, 68, 136-144. https://doi.org/10.1016/j.biocontrol.2013.06.015.

61. Wu, J., Guo, W.C., Turxun., He, J., Xu, J.J.,2008. Effects of heat stress on parasitic functional response of *Trichogramma pintoi*. Xinjiang Agri. Sci. (S2), 122-126.

62. Wu, L., He, N.P., Hou, D.W., 2001. Studies on controlling effect of *Trichogramma chilonis* to corn borer. J. Jilin Agri. Sci. 26, 35-37. http://dx.doi.org/ 10.3969/j.issn.1003-8701.2001.06.007.

63. Wu, Y., Xi, X., Tang, X., Luo, D., Gu, B., Lam, S. K., et al., 2018. Policy distortions, farm size, and the overuse of agricultural chemicals in China. Proc. Natl. Acad. Sci.115(27), 7010-7015. https://doi.org/10.1073/pnas.1806645115.

64. Xu, J.J., Guo, W.C., He, J., Tuerxun., 2001. Primary report on control technique of Asian corn borer by using *Trichogramma* in Xinjiang. Xinjiang Agri. Sci. 38, 315-317. http://dx.doi.org/10.3969/j.issn.1001-4330.2001.06.006.

65. Yang, R.S., Wang, Z.Y., He, K.L., Bai, S.X., 2008. Sequence analysis of mtDNA-COII gene and molecular phylogeny of *Ostrinia* spp. from China (Lepidoptera: Crambidae). Acta Entomol. Sin. 51,182−189. 10.16380/j.kcxb.2008.02.005.

66. Yang, R.S., Wang, Z.Y., He, K.L., Bai, S.X., Jiang, Y.R., 2011.Genetic diversity and phylogeny of the genus *Ostrinia* (Lepidoptera: Crambidae) inhabiting China inferred from mitochondrial *CO I* gene. J. Nanjing Agri. Univ. 34,73−80. http://dx.doi.org/:10.7685/j.issn.1000-2030.2011.05.014.

67. Yang, X.M., Wyckhuys, K.A., Jia, X.P, Nie, F.Y., Wu, K.M., 2021. Fall armyworm invasion heightens pesticide expenditure among Chinese smallholder farmers. J. Environ. Manage. 282,111949. https://doi.org/10.1016/j.jenvman.2021.111949.

68. Yu, S.H., Wang, E.R., Zhang, Y.L., Li, G.Q., Wen, X.F., Hao, X.R.,et al., 1982. Primary study on the control of corn borer by pine Moth-*Trichogramma* Labelled With [32]P. Appl. Atomic Ener. Agri. (2), 31-36.

69. Zang, L.S., Wang, S., Zhang, F., Desneux, N., 2021. Biological control with Trichogramma in China: history, present status, and perspectives. Ann. Rev. Entomol.66, .463-484. http://dx.doi.org/10.1146/annurev-ento-060120-091620.

70. Zeng, J., Liu, Y.Q., Zhang, H.W., Liu, J., Jiang, Y.H., Wyckhuys, K.A., et al., 2020. Global warming modifies long-distance migration of an agricultural insect pest. J. Pest Sci. 93(2), 569-581. https://doi.org/10.1007/s10340-019-01187-5.

71. Zhan, G.X., Liang, G.W., 1999. Research and application of *Trichogramma* in China. Acta Agri. Jiangxi 11, 39-46. http://dx.doi.org/10.19386/j.cnki.jxnyxb.1999.02.009.

72. Zhang, J., Wang, G.H., GE, W.F., Wang, E.J., Chen, X.H., Fang, Y.F., 1979. Investigation of *Trichogramma* Species in Liaoning Province (preliminary report). J. Shenyang Agri. Univ. (01), 75-84 + 59.

73. Zhang, J., Wang, J.L., Cong, B., Yang, C.C., 1990. A faunal study of *Trichogramma* species on *Ostrinia furnacalis* in China. Chin. J. Biol. Contr. 6, 49-53. http://dx.doi.org/10.16409/j.cnki.2095-039x.1990.02.001.

74. Zhou, D.R., Wang, Y.S., Li, W.D., 1988. Studies on the identification of the dominant corn borer species in China. Acta Phytophyl. Sin. 15, 145-152. http://dx.doi: 10.13802 / j.cnki.zwbhxb.1988.03.001.
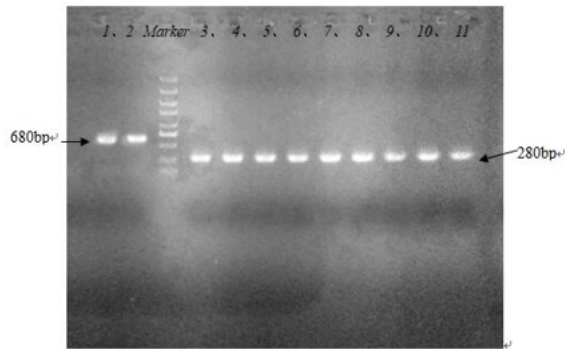
Figures

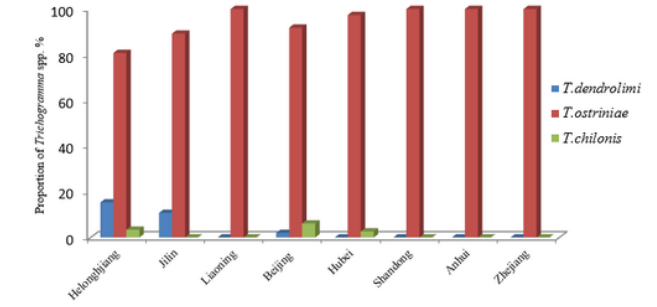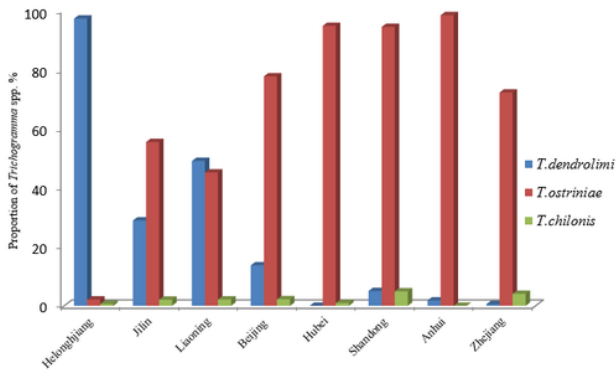### Figure 1

Partial result map of PCR amplification of COI and COII gene sequence,1,2 for *Telenomus remus*, 3,4 for *T. ostriniae*, 5,6 for *T. dendrolimi*, 7,8 for *T. chilonis*, 9,10 for *T. brassicae*, 11 for *T. bilinggensis*.
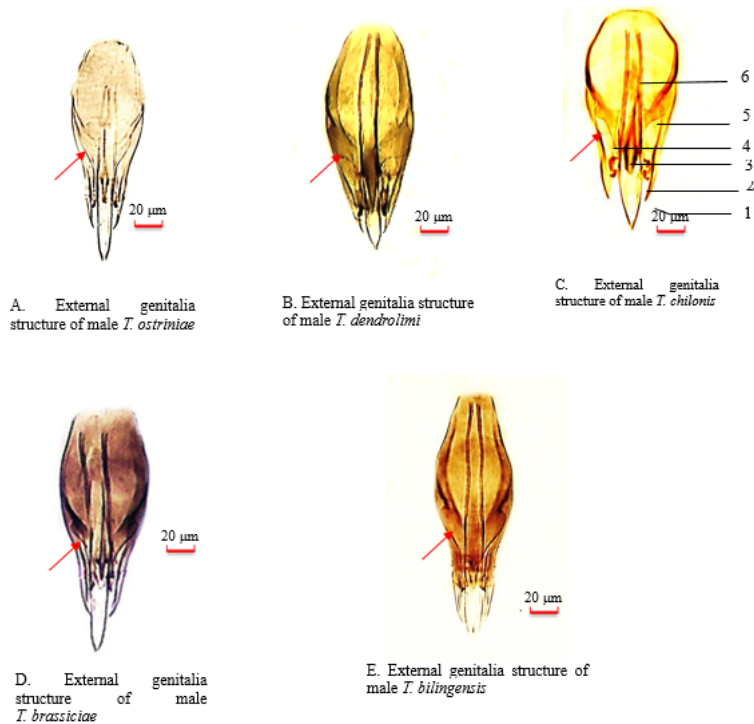
Figure 2

Male genitalia of *Trichogramma* species. 1. Gonoforceps, GF; 2. Chelate structures, CS; 3. Median ventral projection, MVP; 4. Dorsal expansion of gonobase, DEG; 5. Lateral lobes, LL; 6. Central ridge, CR. Red arrows indicate the difference structures of LL.

Panel A. *T. ostriniae*: DEG is highly sclerotized and triangular, and LL is not obvious; B. *T. dendrolimi*: DEG is highly sclerotized and markedly constricted at the base, with broadly rounded LL reaching to the edge; C. *T. chilonis*: Outer margin of the LL curves slightly towards the venter; D. *T. brassiciae*: Outer margin of LL is straight; E. *T. bilingensis*: outer margin of LL is prominent and blunt, larger than that of *T. brassiciae* and *T. chilonis*.

Figure 3

Relative abundance of the three most common *Trichogramma* spp. as recorded during sampling events in the 1980s (panel A) and during 2016-2018 (panel B). Patterns are shown for 8 different corn-growing provinces.