• RESEARCH PAPER •

June 2016 Vol.59 No.6: 627–633 doi: 10.1007/s11427-015-4918-0

Landscape changes have greater effects than climate changes on six insect pests in China

Zihua Zhao^{1,2*}, Hardev S Sandhu³, Fang Ouyang¹ & Feng Ge^{1‡}

¹State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China;

²Department of Entomology, College of Plant Protection, China Agricultural University, Beijing 100193, China; ³Everglades Research and Education Center, Institute of Food and Agricultural Sciences, University of Florida, Florida 33430, USA

Received October 1, 2015; accepted December 21, 2015; published online January 29, 2016

In recent years, global changes are the major causes of frequent, widespread outbreaks of pests in mosaic landscapes, which have received substantial attention worldwide. We collected data on global changes (landscape and climate) and economic damage caused by six main insect pests during 1951–2010 in China. Landscape changes had significant effects on all six insect pests. Pest damage increased significantly with increasing arable land area in agricultural landscapes. However, climate changes had no effect on damage caused by pests, except for the rice leaf roller (*Cnaphalocrocis medinalis* Guenee) and armyworm (*Mythinna separate* (Walker)), which caused less damage to crops with increasing mean temperature. Our results indicate that there is slight evidence of possible offset effects of climate changes on the increasing damage from these two agricultural pests. Landscape changes have caused serious outbreaks of several species, which suggests the possibility of the use of landscape design for the control of pest populations through habitat rearrangement. Landscape manipulation may be used as a green method to achieve sustainable pest management with minimal use of insecticides and herbicides.

biological control, cropland expansion, global warming, mosaic landscape, pest damage

Citation: Zhao, Z., Sandhu, H., Ouyang, F., and Ge, F. (2016). Landscape changes have greater effects than climate changes on six insect pests in China. Sci China Life Sci 59, 627–633. doi: 10.1007/s11427-015-4918-0

INTRODUCTIN

Global changes, including landscape change and climate change, have become an important topic in ecology, especially with regard to biodiversity loss and pest outbreaks in agro-ecosystems during recent decades (Batary et al., 2011). These global changes are expected to disturb biotic interactions (such as pest-natural enemy interaction) and reduce ecosystem services (such as biocontrol service) (Bianchi et al., 2006; Zhao et al., 2015a). Recent studies suggest that climate change (global warming, drought, and floods) has altered pest damage, causing rapid changes in phenology, species ranges, life history, and interspecific relationship (Bianchi et al., 2006; Buntgen et al., 2009). Increased crop production in agro-ecosystems has modified agricultural landscapes greatly since the 1950s in several ways, including cropland expansion and the destruction of natural habitats (e.g., grasslands and woodlands) (Cobbold et al., 2012). These changes have also led to high landscape simplification, which is particularly important in agro-ecosystems. The current tendency of crop rotation and improved varieties generates rapid change and evolution in mosaic landscapes (Dangles et al., 2008; Eilers and Klein, 2009). In addition, these landscape changes may be the major drivers of increased pest damage and biodiversity loss in recent decades (Esper et al., 2007; Heller and Zavaleta, 2009).

^{*}Corresponding author (email: zhzhao@cau.edu.cn)

Corresponding author (email: gef@ioz.ac.cn)

[©] The Author(s) 2016. This article is published with open access at link.springer.com

Previous studies have found that oscillations in pest damage from year to year are related to landscape changes in relatively dynamic periods (Holland et al., 2012; Holzschuh et al., 2010; Huang et al., 2013).

In recent years, landscape patterns and climate changes have caused rapid changes in plant resources, which have led to greater fluctuations in pest damage and species diversity (Jonsson et al., 2012; Katsanis et al., 2013). In China, many conventional crop areas (e.g., wheat) have decreased, causing a great transformation in crop arrangement and composition (Kausrud et al., 2012). At the same time, the loss and degradation of natural habitats have accelerated in agricultural landscapes, causing high landscape simplification in agroecosystems (Landis et al., 2000; Koh, 2007). These changes are accompanied by frequent outbreaks of pest population, which have caused serious economic losses worldwide (Macfadyen et al., 2011; Marini et al., 2012).

Climate changes may also affect pest damage. However, many studies on the relationship between landscape changes and pest damage have examined a relatively short temporal scale or have not explicitly included "time" as a variable for analysis in the mosaic cycles of agricultural landscapes (Meehan et al., 2011; Miyashita et al., 2012). Landscape and climate are important aspects of global change that may affect interspecific relationships and insect communities (Montoya and Raffaelli, 2010). However, the simultaneous effects of both landscape changes and climate changes on pest damage have not been reported previously (O'Rourke et al., 2011).

Agricultural landscapes and climate conditions have evolved rapidly due to anthropogenic disturbance (Otieno et al., 2011). However, the response of insect pests to landscape changes and climate changes in this dynamic process and over long periods have not received much attention (Perrin and Phillips, 1978). The effects of pest damage on crop production in agro-ecosystems varied in different years due to landscape or climate changes, but the reasons for this are largely unknown (Pfannenstiel et al., 2012; Pluess et al., 2010). We selected six important insect pests to analyze how their damage was affected by global changes over time. We also conducted a large-scale spatial analysis, including landscape changes and climate changes.

We expected that landscape changes and climate changes would be related to pest damage, based on the hypothesis that crop simplification and global warming would affect biological control agents (Zhao et al., 2015b; Poveda et al., 2012). Based on the resource concentration hypothesis and habitat management, it was hypothesized that (i) landscape change and climate change would have a great effect on pest damage, and pest damage would increase with increasing landscape simplification and global warming, and (ii) landscape change would be the key driving factor and would have a greater influence on pest damage than climate change due to the polydirectional temperature fluctuations during the past 60 years in China (Figure 1).

RESULTS

During the past 60 years, damage from all six pests, the rice leaf roller (Cnaphalocrocis medinalis Guenee), cereal aphid (Sitobion avenae (Fabricius)), corn borer (Pyrausta nubilalis (Hubern)), rice planthopper (Nilaparvata lugens (Stdl)), cotton bollworm (Helicoverpa armigera Hubner), and armyworm (Mythimna separata (Walker)), increased consistently. Multiple linear regression models indicated a significant increase in damage from all six pests with the expansion of arable land area. The rice leaf roller showed the most sensitive response to arable land area. Furthermore, the slope of the regression between the rice leaf roller and arable land area was 35.79 (F_{1.59}=44.20, P=0.001). However, climate warming had almost no significant effect on pest damage, except that the rice leaf roller and armyworm might have been enhanced slightly by global warming. Relationships between climate change (increase in mean temperature) and pest damage (rice leaf roller and armyworm) were significantly negative (Table 1). In addition, the regression slopes between the damages by these two pests and climate warming were small, only -1.01 for the rice leaf roller ($F_{1,59}$ =2.66, P=0.01) and -0.45 for the armyworm $(F_{1.59}=3.40, P=0.001)$. Climate changes had marginally negative effects on damage by the rice planthopper. The interactions of LC and CC with pest damage were not significant for any pest.

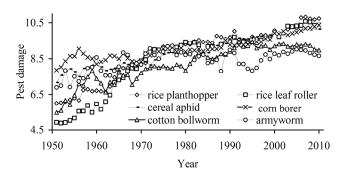


Figure 1 Trends in pest damage during 1950 to 2010.

Table 1The relationship between global changes and damage by sixpests as described by a linear regression model $(REG)^{a)}$

Species	Landscape change	Climate change	Landscape change×Climate change	
rice planthopper	28.94***	-0.63 ^{ms}	5.31 ^{ns}	
rice leaf roller	35.79***	-1.01^{*}	6.01 ^{ns}	
cereal aphid	17.59***	-0.04^{ns}	0.84 ^{ns}	
corn borer	11.88^{***}	0.14 ^{ns}	1.29 ^{ns}	
cotton bollworm	20.86***	-0.34 ^{ns}	2.66 ^{ns}	
armyworm	11.82***	-0.45**	2.17 ^{ns}	

a) ***: *P*<0.001; **: *P*<0.01; *: *P*<0.05; ms: marginally-significant (0.05<*P*<0.1); ns: non-significant.

In the generalized linear model (GLM), relationships between the arable land area and pest damage were significantly positive for all six pests. With an increase in cropland, pest damage increased significantly (rice planthopper: $F_{2,58}$ =62.07, P=0.001; rice leaf roller: $F_{2,58}$ =44.20, P=0.001; cereal aphid: $F_{2,58}$ =60.42, P=0.001; corn borer: $F_{2,58}$ =28.54, P=0.001; cotton bollworm: $F_{2,58}$ =81.48, P= 0.001; armyworm: $F_{2,58}$ =20.74, P=0.001) (Figure 2). However, climate change (global warming) had no significant effects on pest damage except from the rice leaf roller and armyworm (rice planthopper: $F_{2,58}$ =-3.95, P=0.052; rice leaf roller: $F_{2,58}$ =-7.07, P=0.010; cereal aphid: $F_{2,58}$ =-0.073, P=0.795; corn borer: $F_{2,58}$ =-1.43, P=0.237; cotton bollworm: $F_{2,58}$ =-2.092, P=0.147; armyworm: $F_{2,58}$ =-10.59, P=0.002; Figure 2). In contrast to landscape effects, relationships between climate change and pest damage were negative.

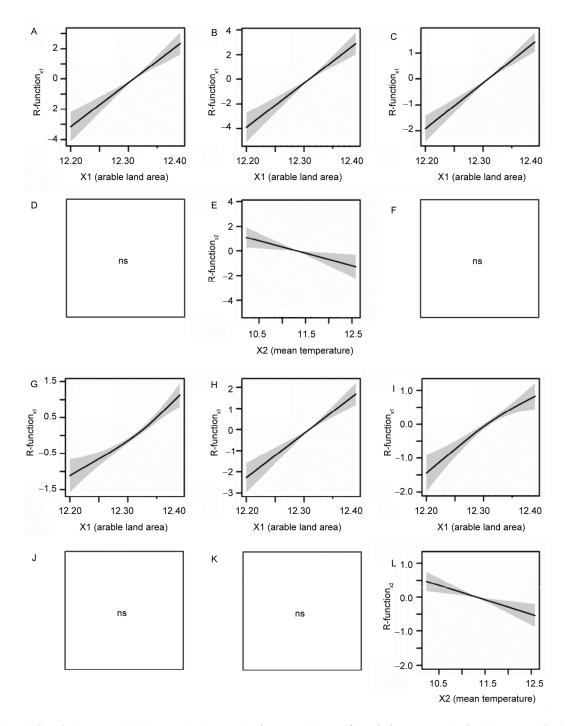


Figure 2 The relationship between global changes (landscape and climate) and damage from six insect pests described by a generalized linear model (GLM). A and D, Rice planthopper. B and E, Rice leaf roller. C and F, Cereal aphid. G and J, Corn borer. H and K, Cotton bollworm. I and L, Armyworm. ns: no significant effects.

Damage from the rice leaf roller and armyworm decreased with increasing mean temperature. The rice leaf roller and armyworm were significantly affected by both landscape and climate changes. However, the other four species were only affected by landscape changes (Figure 2).

The different crop types varied in their influences on different agricultural insect pests. Among oligophagous pests, the expansion of rice and corn had large effects on the damage from the rice planthopper and rice leaf roller, but no effect was found for other non-host crops (wheat and cotton). Additionally, the expansion of corn had significant effects on the cereal aphid and corn borer (Table 2). Among polyphagous pests, the damage caused by the cotton bollworm increased significantly with increasing area of corn and wheat in China. The armyworm was also facilitated by the expansion of two crops (corn and rice) (Table 2).

The RDA diagram showed that the six pest species responded to the landscape changes and climate changes differently (the cumulative percentage variations of species data in the first four axes were, in order, 49.4%, 50.9%, 51.1%, and 51.2% (Figure 3). Specifically, the effects of landscape changes on all six pests were greater than the effects of climate. According to the RDA, landscape changes were best correlated to cereal aphid, followed by cornborer, rice planthopper, cotton bollworm, rice stem roller, and armyworm. Climate changes were weakly correlated to damage by corn borer and wheat aphid, and there was almost no correlation with the other four pests (Figure 3).

DISCUSSION

Previous studies have considered the proportions of arable land and non-crop habitats as appropriate metrics for studying the interactions between pests and landscape changes. In this study, landscape changes affected the damage from all six pests, which indicated that cropland expansion might be one of the main causes of the frequent pest outbreaks in recent times. Cropland expansion and removal of natural habitats were two key aspects in landscape changes. These landscape changes are caused by human activities, and have transformed many agricultural landscapes into expansive monocultures (landscape simplification) with little natural habitat (Schmidt-Entling and Dobeli, 2009). Our results

Table 2 Effects of crop area on damage from six insect pests in China

Species	Corn	Wheat	Rice	Cotton
Rice planthopper	0.9047^{***}	0.1703 ^{ns}	0.2250^{ms}	0.0106 ^{ns}
Rice leaf roller	0.8685^{***}	0.1764^{ns}	0.2968^{*}	-0.0305^{ns}
Cereal aphid	0.9423***	0.1151 ^{ns}	-0.0022^{ns}	-0.0345^{ns}
Corn borer	0.9573^{***}	-0.0601^{ns}	-0.0470^{ns}	-0.0034^{ns}
Cotton bollworm	0.8665^{***}	0.2366^{ms}	0.1800 ^{ns}	0.0508 ^{ns}
Armyworm	0.6004^{***}	0.0696^{ns}	0.4093**	-0.0739^{ns}

a) ***: P<0.001; **: P<0.01; *: P<0.05; ms: marginally significant (0.05<P<0.1); ns: non-significant.

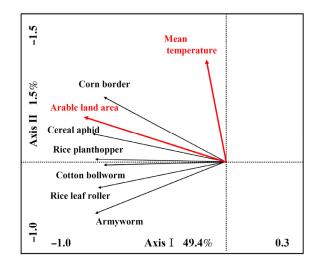


Figure 3 Redundancy analyses (RDA) of the global changes (landscape changes and climate changes) and pest damage.

agree with previous studies (Schmidt et al., 2008; Segoli et al., 2012; Steingrover et al., 2010) in which cropland expansion led to widespread pest outbreaks in agricultural landscapes. However, climate change had a negative effect on the rice leaf roller and armyworm, which was in contrast with cropland expansion. Similarly, locusts (Locusta migratoria manilensis) have also been reported to be negatively affected by global warming (Thies et al., 2011). In addition, climate change did not affect the other four pests in our study. These pests could feed on various hosts and offset the effects of climate changes. The different responses of different species to climate changes have shown that climate change may create new challenges for pest management (Thies et al., 2005). In the present study, we could not conclude that climate change enhanced pest damage. Although this topic has been extensively studied, it is still not possible to reach a universal conclusion. Further studies are required to elucidate this aspect.

Our results revealed that the widespread outbreaks of pests were strongly related to landscape changes. Climate change had little impact on pest damage, except for the rice leaf roller and armyworm. These results can be explained by two arguments. First, spatial scale is an important factor affecting pest damage in agricultural landscapes (Thies et al., 2008) and our analyses were conducted at a relatively large spatial scale (60 years), which might have led to the widespread pest damage caused by landscape changes. Second, there may have only been minor variations in climate in the last 60 years, resulting in a weak relationship between climate change and pest damage that would be hard to observe (Thies et al., 2011). In another study, data from up to 1,000 years were used to analyze these relationships. Some other studies have reported effects of climate changes on pest damage (Tilman et al., 2012; Tscharntke et al., 2007). The identification of landscape changes and climate changes, that may enhance or suppress pest damage can provide valuable information on the relationships between them

(Tscharntke et al., 2012a). The methods to distinguish these factors may be useful for analyzing relationships between global changes and pest damage, and for developing an effective habitat management strategy (Tscharntke et al., 2012b).

Landscape changes have caused frequent outbreaks of several species, which raises the interesting issue whether landscape changes can be used to control pest populations through habitat rearrangement and reorganization. This method is optimal for sustainable pest management, because biological control methods can be explored, which is a necessary step to suppress pest damage through designing mosaic landscapes from a continuous temporal perspective (Vollhardt et al., 2008).

In addition, pest management can be achieved by agricultural landscape design, and modifications can be tested at a landscape scale. Although the above studies opined that pest damage can be reduced by landscape modification, the results are not supported by all studies, especially those in which landscape composition had no effects on biological pest control (Werling and Gratton, 2010).

Landscape changes have three main forms, crop rearrangements, intensification of agriculture, and loss of semi-natural habitats (Werling et al., 2011). Many other factors, including soil type and fertilizer may also affect pest damage, but these were not considered in these studies. Previous studies have indicated that pest population management was positively correlated with the percentage of semi-natural habitats, but negatively correlated with the percentage of arable land in an agricultural landscape.

There is much evidence that biological control services can be achieved through agricultural landscape design and reorganization (White et al., 1995). Some studies have shown that crop arrangements affect pest damage at a local scale (Winqvist et al., 2011; Woltz et al., 2012). However, many other studies have not found any relationship between biological pest control and landscape composition (Zhang et al., 2009). Whether landscape changes can affect pest damage at larger temporal or landscape scales requires further studies (Zhao et al., 2012).

In our study, the expansion of host crops facilitated pest damage, while non-host crops had no effects on pest damage. Fertilizer input was also an important factor driving pest damage, especially increasing nitrogen fertilizer. The hypothesis that pest damage has a consistently positive correlation with the area of horticulture or agriculture at all spatial scales is supported by our results, which suggest that arable lands are favorable for pest damage. Although entire fields were under conventional management, pest populations in intensively used landscapes cannot be properly controlled by insecticide and herbicide applications. The subsequent re-colonization of pests from surrounding areas is likely to be a rapid process, which may explain the negative effect of intensively used agricultural areas on pest regulation (Zhao et al., 2013a). This study suggests that landscape changes, such as agricultural intensification and degradation

of natural habitats, which are supposed to increase crop yields, simultaneously led to frequent pest outbreaks and resulted in the wider use of insecticides (Zhao et al., 2013b). Landscape manipulation is therefore desirable in terms of biodiversity conservation and recreation, but also to achieve sustainable pest management with minimal use of insecticides and herbicides (Zhao et al., 2013c).

MATERIALS AND METHODS

Study sites

The study site was located in the main agricultural region of China. The region is characterized by a warm temperate continental climate, with a yearly mean temperature of about 8.8°C. In the past 60 years, the agricultural landscape has changed greatly due to agricultural intensification. Almost all crop regions were managed as commercial farms with cropland expansion. In contrast, non-crop habitats (grasslands, pastures, wetlands, and woodlands) managed for biodiversity conservation and sustaining ecosystem services have decreased greatly. At the same time, global warming has accelerated due to human activity. The economic damage caused by agricultural pests has increased greatly under these global changes. Therefore, landscape composition, climate conditions, and pest damage were sampled in all provinces of China to explore the outbreak mechanism of agricultural pests under global changes.

Landscape composition data

Data on all arable land in China were extracted from the statistical list from the Management Division of Plant Industry, Ministry of Agriculture of China (http://www.zzys. moa.gov.cn/) for the period of 1951–2010. Landscape composition was calculated annually at a regional scale throughout China. For analysis examined the total arable land area, including grain crops, wheat, rice, corn, vegetable crop, hemp, sugar, tobacco, fruit and nut crops. Non-crop habitats, including all semi-natural and natural lands (grasslands, forest, wetlands, rangelands, and woodlands), were not considered for this analysis. We defined the landscape change (*LC*) as an index of cropland expansion: $LC = \frac{AREA_{t+1} - AREA_t}{REA_{t+1}}$, where AREA_{t+1} and AREA, were

$$LC = \frac{AREA_{t+1}}{AREA_t}, \text{ where } AREA_{t+1} \text{ and } AREA_t \text{ were}$$

the areas of arable land in consecutive years (t+1 and t). Landscape change (LC) indicated the cropland expansion (arable land area), which was found to be an appropriate method to conduct landscape analysis in a previous research (Ratnadass et al., 2012).

Climate data

Data on temperature, which is an important factor in climate

changes, were extracted from the China Meteorological Data Sharing Service System (http://cdc.cma.gov.cn/home. do) for the period 1951–2010. First, we calculated the yearly mean temperature (YAT) from daily mean temperature (DAT), calculated as: YAT=(DAT₁+DAT₂+DAT₃+·····+ DAT_n)/n. Then, the temperature time series (climate change) was reconstructed from the mean increase in temperature by combining multiple areas. The climate change (*CC*) index was estimated from differences between the yearly mean temperature of consecutive years, for example: $CC=(YAT_{t+1}-YAT_t)/YAT_t$, where YAT_{t+1} and YAT_t are the yearly mean temperatures for years *t*+1 and *t*, respectively.

Pest data

Data on six important pests, the rice leaf roller (*Cnaphalocrocis medinalis* Guenee), cereal aphid (*Sitobion avenae* Fabricius), corn borer (*Pyrausta nubilalis* Hubern), rice planthopper (*Nilaparvata lugens* Stdl), cotton bollworm (*Helicoverpa armigera* Hubner), and armyworm (*Mythimna separata* Walker) were selected for this analysis. The first four species are oligophagous and the last two are polyphagous pests. The biological and ecological characteristics of these six pests have been well-studied previously. However, their outbreak mechanisms were largely unknown. Data on pest damage for 1951–1999 were extracted from the statistical yearbook of plant protection (Chen and Hu, 2003), and the remaining data (2000–2010) were obtained from the Agricultural Technology Extension Service Center, Ministry of Agriculture of China. We defined the pest damage

(*PD*) as an index of crop losses: $PD = \frac{AREA_{outbreak}}{AREA_{total}}$, where

AREA_{outbreak} and AREA_{total} are the area above the economic threshold and the total arable land area, respectively. This index was is also to be an appropriate method to conduct pest analysis in a previous study.

Statistical analyses

In order to determine the effects of landscape changes (LC) and climate changes (CC) on pest damage (PD), we first examined the correlation efficient between the occurrence of pest damage and these changes (LC and CC). Multiple linear regressions (REG) and a generalized linear model (GLM) were used to conduct the analysis.

First, in the multivariable linear regression model (REG), we determined the influence of global changes (LC and CC) on PD, with the LC and CC as environmental (independent) variables and PD as the dependent variable (REG procedure, SAS institute Inc., USA, 2006). At the same time, interactions between LC and CC were evaluated in the REG procedure.

Second, in generalized linear model (GLM), we used PD as the dependent variable, and LC and CC as independent variables. We modified the variables and constructed separate models for yearly timescales. Additive effects and sep-

arate interactions of LC and CC were not considered in models due to the absence of a logical relationship. In order to examine the relationship between specific crops and insects pests, we analyzed the effetcs of host crop area on pest damage by using Pearson's correlation and simple linear regression (*lm*). Modeling was performed using the MuMln packages in R statistical computing software.

Redundancy analysis (RDA) was performed to determine the influence of the global changes (*LC* and *CC*) on *PD* (CANOCO 4.5), with *LC* and *CC* as environmental variables and pest damage as the dependent variable.

Compliance and ethics *The author(s) declare that they have no conflict of interest.*

Acknowledgements We are grateful to Prof. Zhihong Li from China Agricultural University and two anonymous reviewers for critical and insightful comments on an initial draft of this manuscript. This work was supported by the National Natural Science of China (31400349, 31572059), the National Key Technology R & D Program (2012BAD19B05) and the State Key Laboratory of Integrated Management of Pest Insects and Rodents (IPM1513).

- Batary, P., Andras, B., Kleijn, D., and Tscharntke, T. (2011). Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. Proc Biol Sci 278, 1894–1902.
- Bianchi, F.J., Booij, C.J., and Tscharntke, T. (2006). Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. Proc Biol Sci 273, 1715–1727.
- Buntgen, U., Frank, D., Liebhold, A., Johnson, D., Carrer, M., Urbinati, C., Grabner, M., Nicolussi, K., Levanic, T., and Esper, J. (2009). Three centuries of insect outbreaks across the European Alps. New Phytol 182, 929–941.
- Cobbold, S.M., and MacMahon, J.A. (2012). Guild mobility affects spider diversity: links between foraging behavior and sensitivity to adjacent vegetation structure. Basic Appl Ecol 13, 597–605.
- Chen, S., and Hu, B. (2003). The Plant Protection of Past Fifty Years in China. Beijing: China Agr Press 50–100.
- Dangles, O., Carpio, C., Barragan, A.R., Zeddam, J.L., Silvain, J.F. (2008). Temperature as a key driver of ecological sorting among invasive pest species in the tropical Andes. Ecol Appl 18, 1795–1809.
- Eilers, E.J., and Klein, A.M. (2009). Landscape context and management effects on an important insect pest and its natural enemies in almond. Biol Control 51, 388–394.
- Esper, J., Buntgen, U., Frank, D.C., Nievergelt, D., and Liebhold, A. (2007). 1200 years of regular outbreaks in alpine insects. Proc Biol Sci 274, 671–679.
- Gagic, V., Hanke, S., Thies, C., Scherber, C., Tomanovic, Z., and Tscharntke, T. (2012). Agricultural intensification and cereal aphid-parasitoid-hyperparasitoid food webs: network complexity, temporal variability and parasitism rates. Oecologia 170, 1099–1109.
- Heller, N.E., and Zavaleta, E.S. (2009). Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol Conserv 142, 14–32.
- Holland, J.M., Oaten, H., Moreby, S., Birkett, T., Simper, J., Southway, S., Smith, B.M. (2012). Agri-environment scheme enhancing ecosystem services: a demonstration of improved biological control in cereal crops. Agr Ecosyst Environ 155, 147–152.
- Huang, Y., Martin, L.M., Isbell, F.I., and Wilsey, B.J. (2013). Is community persistence related to diversity? A test with prairie species in a long-term experiment. Basic Appl Ecol 14, 199–207.
- Jonsson, M., Buckley, H.L., Case, B.S., Wratten, S.D., Hale, R.J., and Didham, R.K. (2012). Agricultural intensification drives land-

scape-context effects on host-parasitoid interactions in agroecosystems. J Appl Ecol 49, 706–714.

- Katsanis, A., Babendreier, D., Nentwig, W., and Kenis, M. (2013). Intraguild predation between the invasive ladybird Harmonia axyridis and non-target European coccinellid species. Biocontrol 58, 73–83.
- Kausrud, K., Okland, B., Skarpaas, O., Gregoire, J.C., Erbilgin, N., and Stenseth, N.C. (2012). Population dynamics in changing environments: the case of an eruptive forest pest species. Biol Rev 87, 34–51.
- Koh, L.P. (2007). Impacts of land use change on South-east Asian forest butterflies: a review. J Appl Ecol 44, 703–713.
- Landis, D.A., Wratten, S.D., and Gurr, G.M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. Annu Rev Entomol 45, 175–201.
- Macfadyen, S., Gibson, R.H., Symondson, W.O.C., and Memmott, J. (2011). Landscape structure influences modularity patterns in farm food webs: consequences for pest control. Ecol Appl 21, 516–524.
- Marini, L., Ayres, M.P., Battisti, A., and Faccoli, M. (2012). Climate affects severity and altitudinal distribution of outbreaks in an eruptive bark beetle. Climatic Change 115, 327–341.
- Meehan, T.D., Werling, B.P., Landis, D.A., and Gratton, C. (2011). Agricultural landscape simplification and insecticide use in the Midwestern United States. Proc Natl Acad Sci USA 108, 11500–11505.
- Miyashita, T., Chishiki, Y., and Takagi, S.R. (2012). Landscape heterogeneity at multiple spatial scales enhances spider species richness in an agricultural landscape. Popul Ecol 54, 573–581.
- Montoya, J.M., and Raffaelli, D. (2010). Climate change, biotic interactions and ecosystem services. Philos T R Soc B 365, 2013–2018.
- O'Rourke, M.E., Rienzo-Stack, K., and Power, A.G. (2011). A multi-scale, landscape approach to predicting insect populations in agroecosystems. Ecol Appl 21, 1782–1791.
- Otieno, M., Woodcock, B.A., Wilby, A., Vogiatzakis, I.N., Mauchline, A.L., Gikungu, M.W., and Potts, S.G. (2011). Local management and landscape drivers of pollination and biological control services in a Kenyan agro-ecosystem. Biol Conserv 144, 2424–2431.
- Perrin, R.M., and Phillips, M.L. (1978). Some effects of mixed cropping on the population-dynamics of insect pests. Entomol Exp Appl 24, 585–593.
- Pfannenstiel, R.S., Mackey, B.E., and Unruh, T.R. (2012). Leafroller parasitism across an orchard landscape in central Washington and effect of neighboring rose habitats on parasitism. Biol Control 62, 152–161.
- Pluess, T., Opatovsky, I., Gavish-Regev, E., Lubin, Y., and Schmidt-Entling, M.H. (2010). Non-crop habitats in the landscape enhance spider diversity in wheat fields of a desert agroecosystem. Agr Ecosyst Environ 137, 68–74.
- Poveda, K., Martinez, E., Kersch-Becker, M.F., Bonilla, M.A., and Tscharntke, T. (2012). Landscape simplification and altitude affect biodiversity, herbivory and Andean potato yield. J Appl Ecol 49, 513–522.
- Ratnadass, A., Fernandes, P., Avelino, J., and Habib, R. (2012). Plant species diversity for sustainable management of crop pests and diseases in agroecosystems: a review. Agron Sustain Dev 32, 273–303.
- Schmidt-Entling, M.H., and Dobeli, J. (2009). Sown wildflower areas to enhance spiders in arable fields. Agr Ecosyst Environ 133, 19–22.
- Schmidt, M.H., Thies, C., Nentwig, W., and Tscharntke, T. (2008). Contrasting responses of arable spiders to the landscape matrix at different spatial scales. J Biogeogr 35, 157–166.
- Segoli, M., and Rosenheim, J.A. (2012). Should increasing the field size of monocultural crops be expected to exacerbate pest damage? Agr Ecosyst Environ 150, 38–44.
- Simpson, S.J., Clissold, F.J., Lihoreau, M., Ponton, F., Wilder, S.M., and Raubenheimer, D. (2015). Recent advances in the integrative nutrition of arthropods. Ann Rev Entomol 60, 293–311
- Steingrover, E.G., Geertsema, W., and van Wingerden, W.K.R.E. (2010). Designing agricultural landscapes for natural pest control: a transdisciplinary approach in the Hoeksche Waard (The Netherlands). Landscape Ecol 25, 825–838.
- Thies, C., Haenke, S., Scherber, C., Bengtsson, J., Bommarco, R., Clement, L.W., Ceryngier, P., Dennis, C., Emmerson, M., Gagic, V., Hawro, V., Liira, J., Weisser, W.W., Winqvist, C., and Tscharntke, T. (2011).

The relationship between agricultural intensification and biological control: experimental tests across Europe. Ecol Appl 21, 2187–2196.

- Thies, C., Roschewitz, I., and Tscharntke, T. (2005). The landscape context of cereal aphid-parasitoid interactions. P Roy Soc B-Biol Sci 272, 203–210.
- Thies, C., Steffan-Dewenter, I., and Tscharntke, T. (2008). Interannual landscape changes influence plant-herbivore-parasitoid interactions. Agr Ecosyst Environ 125, 266–268.
- Tilman, D., Reich, P.B., and Isbell, F. (2012). Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. P Natl Acad Sci USA 109, 10394–10397.
- Tscharntke, T., Bommarco, R., Clough, Y., Crist, T.O., Kleijn, D., Rand, T.A., Tylianakis, J.M., van Nouhuys, S., and Vidal, S. (2007). Conservation biological control and enemy diversity on a landscape scale. Biol Control 43, 294–309.
- Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., and Whitbread, A. (2012a). Global food security, biodiversity conservation and the future of agricultural intensification. Biol Conserv 151, 53–59.
- Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batary, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Frund, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., and Westphal, C. (2012b). Landscape moderation of biodiversity patterns and processes—eight hypotheses. Biol Rev 87, 661–685.
- Werling, B.P., and Gratton, C. (2010). Local and broadscale landscape structure differentially impact predation of two potato pests. Ecol Appl 20, 1114–1125.
- Werling, B.P., Meehan, T.D., Robertson, B.A., Gratton, C., and Landis, D.A. (2011). Biocontrol potential varies with changes in biofuel-crop plant communities and landscape perenniality. Gcb Bioenergy 3, 347–359.
- White, A.J., Wratten, S.D., Berry, N.A., and Weigmann, U. (1995). Habitat Manipulation to Enhance Biological-Control of Brassica Pests by Hover Flies (Diptera, Syrphidae). J Econ Entomol 88, 1171–1176.
- Winqvist, C., Bengtsson, J., Aavik, T., Berendse, F., Clement, L.W., Eggers, S., Fischer, C., Flohre, A., Geiger, F., Liira, J., Part, T., Thies, C., Tscharntke, T., Weisser, W.W., and Bommarco, R. (2011). Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. J Appl Ecol 48, 570–579.
- Woltz, J.M., Isaacs, R., and Landis, D.A. (2012). Landscape structure and habitat management differentially influence insect natural enemies in an agricultural landscape. Agr Ecosyst Environ 152, 40–49.
- Zhang, Z., Cazelles, B., Tian, H., Stige, L.C., Brauning, A., and Stenseth, N.C. (2009). Periodic temperature-associated drought/flood drives locust plagues in China. P Roy Soc B-Biol Sci 276, 823–831.
- Zhao, Z., He, D., and Hui, C. (2012). From the inverse density-area relationship to the minimum patch size of a host-parasitoid system. Ecol Res 27, 303–309.
- Zhao, Z., Hui, C., He, D., and Ge, F. (2013a). Effects of position within wheat field and adjacent habitats on the density and diversity of cereal aphids and their natural enemies. Biocontrol 58, 765–776.
- Zhao, Z., Hui, C., Ouyang, F., Liu, J., Guan, X., He, D., and Ge, F. (2013b). Effects of inter-annual landscape change on interactions between cereal aphids and their natural enemies. Basic Appl Ecol 14, 472–479.
- Zhao, Z., Shi, P., Men, X., Ouyang, F., and Ge, F. (2013c). Effects of crop species richness on pest-natural enemy systems based on an experimental model system using a microlandscape. Sci China Life Sci 56, 758–766.
- Zhao, Z., Ouyang, F., and Ge, F. (2015a) Cropland expansion facilitated the outbreak of cereal aphids during 1951–2010 in China. Sci Bull 60, 1036–1037
- Zhao, Z., Hui, C., He, D., and Li, B. (2015b). Effects of agricultural intensification on ability of natural enemies to control aphids. Sci Rep 5, 8024.
- **Open Access** This article is distributed under the terms of the Creative Commons Attribution License which permits any use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.