

Research

Crop Diversity and Land Simplification Effects on Pest Damage in Northern China

Jie Sheng,^{1,*} Feng Gao,^{2,*} Mbhele Andile,² Leyun Wang,² Hardev S. Sandhu,³ Fang Ouyang,⁴ and Zi-Hua Zhao^{2,5}

¹Department of Applied Mathematics, College of Science, China Agricultural University, Beijing 100083, China (shengjie@cau.edu.cn), ²Department of Entomology, College of Plant Protection, China Agricultural University, Beijing 100193, China (zbx2@cau.edu.cn; andilecau@gmail.com; qingzxf@126.com; zhzhao@cau.edu.cn), ³Everglades Research and Education Center, Institute of Food and Agricultural Sciences, University of Florida, Belle Glade, FL (hsandhu@ufl.edu), ⁴State Key Laboratory of Integrated Management of Pest Insects and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing, China (ouyangf@ioz.ac.cn), and ⁵Corresponding author, e-mail: zhzhao@cau.edu.cn

*These authors contributed equally to this research.

Received 5 June 2016; Accepted 19 July 2016

Abstract

Agricultural intensification has brought obvious increases in the extent and intensity of agricultural activities, which simultaneously led to rapid changes in landscape patterns. However, the relationship between agricultural intensification and pest damage was poorly known at the landscape scale, especially in China. We conducted an analysis to examine the relationship between agricultural intensification and pest damage of six pest species by using statistical data from 1987 to 2012 in China. Results showed that high crop diversity could significantly suppress damage of oligophagous pests such as cereal aphids, rice stem borers, and corn borers while having no effects on polyphagous pests such as cotton bollworms and armyworms except for cotton aphids. Landscape simplification has no significant effects on pest damage except cotton bollworms, and there was no interaction between crop diversity and landscape simplification. Moreover, the relationship between crop diversity and crop yields per hectare was significantly negative. The canonical correspondence analysis ordination diagram showed that pest species responded to the crop species differently. These results suggest that crop diversity have potential for sustainable pest management with complete prevention of pest damage on crops, and it is environment friendly.

Key words: crop diversity, biocontrol, cropland expansion, resource concentration hypothesis

Throughout a century ago there were noticeable increases in the extent and intensity of agricultural activities, which simultaneously led to rapid changes in landscape arrangements and cropland expansion (Meehan et al. 2011, Zhao et al. 2013). Over recent years substantial attention has been dedicated to the effects of agricultural intensification on pest damage in ecologically based pest management (Landis et al. 2000, Bianchi et al. 2006, Tschardt et al. 2012b), nonetheless the decreasing crop diversity was assumed to have negative effect on ecological functions resulting in biodiversity loss and disturbance of interspecific relationships (Holzschuh et al. 2010). Furthermore, landscape simplification associated with landscape pattern changes in another topical characteristic in agroecosystems has been a topical issue and an interesting subject in habitat management aiming for ecologically based pest control for many decades (Tschardt et al. 2012a, Zhao et al. 2014). In several field experiments, it has been proven that the diversified crops in a heterogeneous landscape

could suppress the pest population (Meehan et al. 2011, Werling et al. 2011).

Landscape heterogeneity could improve biocontrol service due to high percentage of seminatural habitats which could provide ample food resources and refuges for natural enemies in landscapes with complex structure (Bianchi et al. 2006, Eilers and Klein 2009, Gardiner et al. 2009). As an important component of diversity, negative effects of crop diversity on pest damage have been certified at small spatial scales (Nakahira et al. 2012). Pest populations may be suppressed by high crop diversity yet enhance biocontrol services (Gardiner et al. 2009, Géneau et al. 2012). Diversified agroecosystems have been designed by several researchers to suppress pest populations at field scales which supports the hypothesis that high crop diversity can enhance biocontrol of agricultural pests (Schmidt-Entling and Dobeli 2009).

Modern technology in agriculture has significantly modified the crop arrangements and led to landscape simplification, with the aim

to increase crop yield per unit area to meet the increasing requirement of large human population (Pluess et al. 2010, Poveda et al. 2012). High crop diversity with various crops has been assumed to suppress pest damage from oligophagous and polyphagous pests (Steingrover et al. 2010, Rusch et al. 2011). However, cropland expansion and landscape simplification were considered to have positive effects on pest damage due to abundant food and highly agminated resources (Hamback and Englund 2005, Stephens and Myers 2012, Tscharntke et al. 2012b). In Europe, many agro-environment schemes (e.g., fallow cropping) were designed to suppress pest damage and increase crop yields (Kleijn and Sutherland 2003). So far, the suppression of pest damage through crop diversity is always related to the function of seminatural habitats (Bianchi et al. 2006, Eilers and Klein 2009). However, all these studies were conducted on single crop systems at a local scale, while studies involving the effects of multiple crop systems on pest management and yields are unknown (Nyffeler and Sunderland 2003, Zhao et al. 2015a). Although there is evidence that high crop diversity with high percentage of seminatural habitats can suppress pest damage at the local scale, it remains unclear whether the effects of crop diversity and cropland expansion excluding seminatural habitats on pest damage cascades biocontrol services at a broad scale (Tscharntke et al. 2007). Moreover, there were few field experiments conducted to testify the suppression of pest damage by crop diversity excluding noncrop habitats at a large spatial scale (Batary et al. 2012, Zhao et al. 2015b). Therefore, the relationship between agricultural intensification and ecosystem services such as biocontrol services and yields could provide some insights into the functional importance of agricultural sustainability in mosaic landscapes.

Thus, increasing crop diversity is expected to reduce pest damage, while cropland expansion is in contrast (Tscharntke et al. 2012b, Zhao et al. 2012). Even though this prediction is widely recognized its origin remains unclear. Especially at landscape or regional scales, whether crop diversity and cropland expansion can suppress or enhance pest damage needs further examinations (Lu et al. 2012, Tscharntke et al. 2012b). In addition, the role of crop diversity on yield productivity at large spatial scales is unknown (Tscharntke et al. 2012a). In this study, we focused on the effects of agricultural intensification including crop diversity and cropland expansion on damage from six important pests. We also tested the direct and indirect effects of these two factors on crop yields. We proposed two alternative hypotheses for the mechanism behind this pattern: 1) Landscape diversity directly suppresses pest damage through crop rearrangements at regional scales (Hamback and Englund 2005). 2) The negative effects of landscape diversity on pest damage may be neutralized by cropland expansion aiming to increase per unit yields (Tilman et al. 2012).

Materials and Methods

Pest Species and Studied Regions

To explore factors affecting the relationship between agricultural intensification and pest damage, we collected data on both crop composition and pest outbreak area from five farming provinces (Shandong, Henan, Hebei, Shanxi, and Shan'xi) in northern China from 1987 to 2012.

In China, some pests (e.g. cereal aphids, armyworms) are widely distributed and ever since they have been causing great damage to agricultural crops (Wu et al. 2008, Lu et al. 2012). Therefore, three oligophagous pests (cereal aphids, rice stem borers, and corn borers) and three polyphagous pests (cotton aphids, cotton bollworms, and

armyworms) were selected in this experiment. In general, these six pests have caused serious damage to their host plants and many other economically important crops. In recent years, damage of these agricultural pests increased rapidly in several crops in northern China. A large amount of insecticides was applied to control agricultural pests in crop fields every year. However, these pests became more and more rampant in contrast. For example, cereal aphids (*Sitobion avenae* (F.) and *Schizaphis graminum* (Rondani)) are the most important pests in wheat fields (*Triticum aestivum*), and they could also feed on many other crops (*Fagopyrum esculentum*), causing great damage. Cereal aphids almost erupt every year, which are distributed in most regions in China. Rice stem borers (*Chilo suppressalis* (Walker)) and corn borers (*Pyrausta nubilalis* (Hubner)) are the most important pests on rice and corn, respectively, and they also feed on some other crops including wheat. Rice stem borers and corn borers also caused huge economic losses of their hosts. Cotton aphids (*Aphis gossypii* Glover) are important pests in cotton, can also feed on many other crops and cause great damage. Armyworms (*Mythimna separate* (Walker)) and cotton bollworms (*Helicoverpa armigera* Hubner) are reported as dominant pests on several crops including wheat, maize, corn, cotton, and soybean. The economic losses caused by armyworm were up to 600 million dollars in 2012. In addition, some researchers reported that cotton bollworms (*Heliothis armigera* Hubner) were controlled completely due to wide planting of Bt cotton. However, in recent years, cotton bollworms have caused great damage to other alternative various hosts such as corns and wheat. Furthermore, outbreak area of this pest is still increasing due to wide host ranges. In our study the mentioned pests were considered to test if crop diversity can enhance the biocontrol services on agricultural pests.

Effects of Crop Diversity on Pest Damage

The data of crop composition and arrangement in China from 1987 to 2011 was extracted from the statistical list in Management Division of Plant Industry, Ministry of Agriculture of China (<http://www.zzys.moa.gov.cn/>). In each province, crop arrangements and distribution in agricultural landscape were investigated every year, and were classified into 13 main crops (wheat, rice, corn, soybean, potatoes, millet, cotton, oilseeds, hemp, sugar, tobacco, vegetable, and fruit) by unified standard classification. These 13 main crops were satiated in our study according to classification standard, which account for above 99% percentage of the total crop area. The rare crops, which were out of statistics range of standard classification, are not included due to their insignificant contributions to landscape patterns. At the same time, all noncrop habitats including grasslands, woodlands, roads, wetlands, and other habitats were not considered either. We only focused on the effects of crop diversity and cropland expansion on pest damage. Crop arrangements and distribution were derived from human activities and did not interfere with other factors. In every province, changes in crop species between years made no significant differences. Crop diversity was calculated based on area of different crops in each province (Shannon–Wiener indices).

Survey of Pests in China

Data of pest outbreak area and associated pest damage were supplied by National Agricultural Technology Extension and Service Center, the Ministry of Agriculture of China, during 1987–2012. Commercial crop fields at 1,738 locations in main farming provinces of China were surveyed for these pests (cereal aphids, rice stem borers, corn borers, cotton aphids, armyworms, and cotton

bollworms). We did not use pest population as damage indices, but the rate of outbreak area above economic threshold to the total arable area was used according to our previous researches. These pests have aggregated distribution and have great variation in population density in agricultural landscapes. So outbreak area of pests above economic threshold was transformed to rate of outbreak area to the total arable area, which may be a suitable index to conduct analysis with crop diversity at the landscape scale.

These six agricultural pests were surveyed in each province in China, using the same sampling schedule as for investigation. There were 24,463 agricultural and technical staff members involved in these field investigations. On each plant, upper, middle, and lower leaves were examined for pest occurrence. At the same time, all insecticide applications were also recorded.

Statistical Analysis

Shannon–Wiener index was used to calculate crop diversity because this index determines the shift of both crop species richness and abundance. In every province, the annual crop diversity was calculated from 1987 to 2012. Landscape simplification caused by cropland expansion was indicated by the percentage of arable land within the agricultural landscape, which was computed irrespective of crop types or patch connectivity as our previous research (Zhao et al. 2015a). Many other factors including climate changes and chemical application may also affect pest population in time series. In order to eliminate the disturbance effects caused by climate changes in different years, data standardization (min–max normalization) was used to neutralize these effects nationwide such as global warming.

Time for space substitution method was used to analyze the relationship between crop diversity and pest damage, aiming to increase the sample size. This method was derived from space for time substitution, which was mainly applied in evolution of plant communities (Travis and Hester 2005, Hui 2011). We considered only the effects of crop diversity and landscape simplification on pest damage at spatial scales. All pest damage data (outbreak area above the economics threshold) of each province in a year was first converted into percentage of total arable land. Then these percentages of pest occurrence were min–max normalized before being analyzed with crop diversity to avoid interannual variation in every year. The pest damage of six species was calculated accordingly during 1987–2012.

Simple linear regression analysis was used to assess the relationship between agricultural intensification (crop diversity, landscape simplification, and their interactions) and pest damage on the data set gathered from 1987 to 2012. Effects of agricultural intensification on pest damage were analyzed using logistic regression. To identify these relationships, univariate regression analysis was conducted to test all variables. Crop diversity or landscape simplification that had a significant effect on pest damage at landscape scales and crop diversity were subsequently analyzed by regression analysis. The procedure enabled a stepwise model selection by addition and elimination of variables. The best subset of variables was determined on the basis of the Mallows' Cp criterion.

To further evaluate the effects of agricultural intensification on pest damage, the crop yields per hectare in every administrative unit was calculated to analyze their relationship with crop diversity and landscape simplification. Similarly, min–max normalization was applied to transform the crop yields. Then linear regression analysis was used to assess the relationship between crop diversity and yields per hectare on the data set gathered from 1987 to 2012. At the same time, canonical correspondence analysis (CCA, CANOCO 4.5) was

used to determine the influence of crops on different pest species. We used area under each crop as an environmental variable. At the same time, outbreak area above economics threshold of each pest species was used as a dependent variable.

Results

Among oligophagous species, crop diversity had significant negative effects on cereal aphids (Table 1; Fig. 1A). With increases in crop diversity, the damage of cereal aphids decreased. However, landscape simplification had no influence on the damage of cereal aphids. At the same time, we did not find any interactions between crop diversity and landscape simplification. Similar to cereal aphids, the other oligophagous pest species such as rice stem borers and corn borers were also significantly affected by crop diversity (Table 1; Fig. 1B, C). Effects of landscape simplification on these two species were not found. It indicated that high crop diversity could suppress damage of oligophagous pests. However, landscape simplification had no significant effects on oligophagous pests.

Among polyphagous species, only cotton aphids were affected significantly by crop diversity (Table 1; Fig. 1D). The relationship between damage of the other two species (cotton bollworms and armyworms) and crop diversity could not be found (Table 1; Fig. 1E, F). In addition, landscape simplification had no impact on polyphagous species except for cotton worms, which were strongly affected by the interaction of crop diversity and cropland expansion.

Relationship between crop diversity and yields per hectare was negative ($R^2=0.2416$, $F_{1, 875}=35.45$, $P=0.001$), and yields per hectare decreased with increases in crop diversity (Fig. 2A). However, landscape simplification (changes in arable lands) did not affect yields per hectare ($R^2=0.0001$, $F_{1, 875}=0.00$, $P=0.91$, Fig. 2B). In addition, crop diversity and landscape simplification had no interactions on yields per hectare.

Table 1. Effects of crop diversity and landscape simplification on pest damage and their interactions

Variables	T value	P
Cereal aphids		
Crop diversity	4.36	0.0001
Landscape simplification	0.99	0.3248
Crop diversity × landscape simplification	1.00	0.3206
Corn borer		
Crop diversity	11.97	0.0001
Cropland landscape simplification	0.52	0.6050
Crop diversity × landscape simplification	0.60	0.5468
Cotton aphids		
Crop diversity	2.35	0.0201
Landscape simplification	1.72	0.0878
Crop diversity × landscape simplification	1.72	0.0863
Rice stem borer		
Crop diversity	4.29	0.0001
Landscape simplification	0.95	0.3418
Crop diversity × landscape simplification	0.97	0.3316
Cotton ball worm		
Crop diversity	1.91	0.0582
Landscape simplification	1.98	0.0488
Crop diversity × landscape simplification	2.03	0.0436
Armyworm		
Crop diversity	1.23	0.0204
Landscape simplification	0.33	0.7449
Crop diversity × landscape simplification	0.37	0.7141

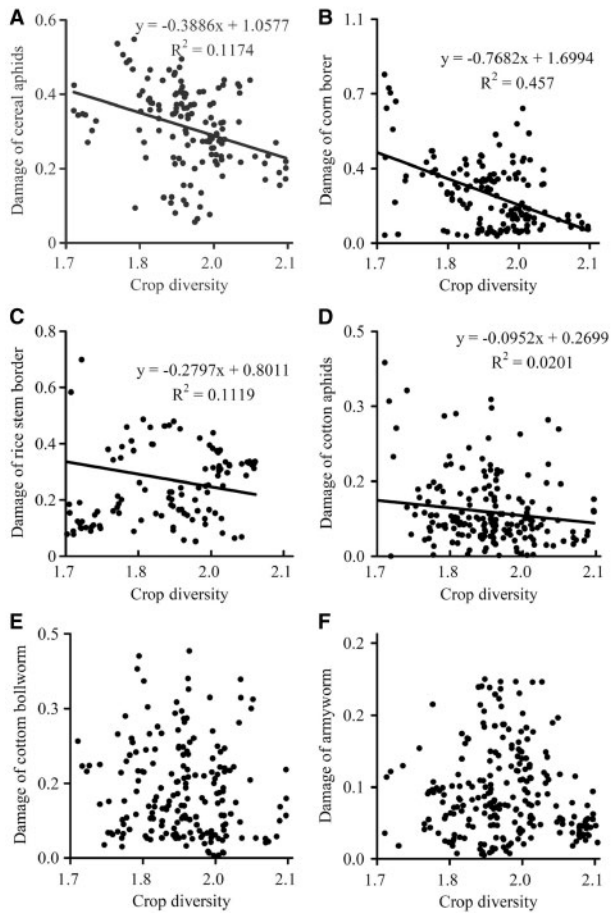


Fig. 1. Effects of crop diversity on pest damage. (A) Cereal aphids, (B) corn borer, (C) rice stem borer, (D) cotton aphids, (E) cotton bollworm, (F) armyworm.

The CCA ordination diagram showed that pest species responded differently to different crops (the cumulative percentage variation of species data in the first four axes was 55.1, 84.3, 92.0, and 96.5%, respectively; Fig. 3). Among oligophagous species, cereal aphids had largest correlation coefficient with wheat crop, followed by vegetables, fruits, and cotton. The other two oligophagous species, corn borers, and rice stem borers were closely correlated to corn and rice, respectively (Fig. 3). Among polyphagous species, cotton aphids were affected greatly by cotton, wheat, and vegetables (Fig. 3). The other two polyphagous species (cotton bollworm and armyworm) had a wide host range, which was affected simultaneously by many crop species (Fig. 3).

Discussion

In the past decades, the tendency to convert diverse crop systems to monoculture crop systems has led to obvious changes in crop arrangement. In our experiments, we found that crop diversity had negative effects on oligophagous pests, but no effects on polyphagous pests except for cotton aphids. It suggests that the decrease in crop diversity in agricultural landscape configuration contributes to an increase in pest damage on crops (Chaplin-Kramer et al. 2011, Gagic et al. 2011). Some researchers found that crop diversity could suppress pest damage at local scales (Jonsson et al. 2012). In our experiments, effects of crop diversity on pest damage varied depending on specific feeding habitats of different species. Crop arrangements

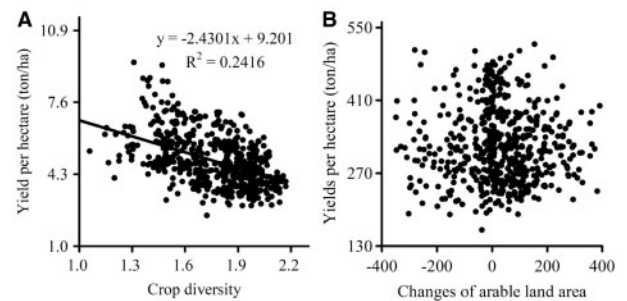


Fig. 2. Effects of crop diversity (A) and changes of arable land area (B) on yield per hectare in China.

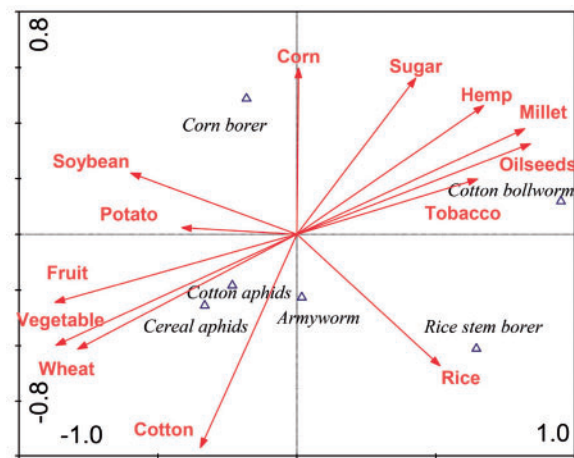


Fig. 3. Canonical correspondence analysis of p@est species and crop species.

have different effects on different pest species because different pests need to shift frequently among their habitats (crops) for food. Therefore, oligophagous and polyphagous pests were affected differently by crop diversity, which is in contrast to the previous reports of the decrease in pest damage with increase in crop diversity.

These differences in these results can be explained in two aspects. On one hand, crop diversity is an important factor affecting pest damage in agroecosystem. However, crop diversity may affect pest population only at a particular spatial scale. At an optimal spatial scale, correlation coefficients between crop diversity and pest population are significant, which couldn't be found at other spatial scales. On the other hand, the possible reason may be the different division of landscape factors, which can classify the same vegetation type into different landscape factors in different field experiments. The different division methods of landscape factors may explain the variable effects of landscape pattern (Zhao et al. 2016). We only considered crop diversity in this experiment, which excluded the effects of seminatural habitats. Therefore, the choice of habitat types may be useful for analyzing the relationship between diversity and pest damage and developing an effective habitat management strategy (Menalled et al. 2003).

The crop arrangement in agricultural landscapes is actually a "mosaic landscape" based on crop diversity at large spatial scales (Werling and Gratton 2010). In addition, this "mosaic landscape" of crop arrangement derived from human activities has important influences on pest damage in agroecosystems (Wu et al. 2008). High crop diversity, which indicates complex "mosaic landscape," is associated with a decline of pest damage and an increase in biocontrol

services (Nakahira et al. 2012). However, in China, the evidence of reduced pest damage with high crop diversity is not based on field's data, but on observations of the preference shown by farmers to grow crops at higher crop diversity to avoid the negative effects of pests and pathogens at local scales (Zhu et al. 2000).

Pest damage is consistently positively correlated with percentage of horticulture or arable land at large spatial scales, suggesting that landscape simplification may be unfavorable for natural enemies, which rely on permanent habitats for at least a part of their life cycle. However, we did not find any relationship between landscape simplification and pest damage except for cotton bollworms. The possible reason may be the wide host range of cotton bollworms, which can provide abundant food resources. The metastatic spread of many pests among different habitats is likely to be a quick process, which may explain the neutral effects of landscape simplification on pest regulation. Intensively used arable lands provide only much food for pests and limited resources for natural enemies, which may offset effects of landscape simplification.

Rearrangement of crop types in modern landscapes is also aimed to enhance yields and may interact with anthropogenic forces that shape functions of ecosystems (Tscharntke et al. 2012b). The crop diversity had a negative effect on yields per hectare, which indicated that high crop diversity was unlucky to the yields. Although landscape simplification may increase total crop yields, per hectare yields were not affected by cropland expansion.

Indirect evidence for these relationships has come from analysis of the effects of agricultural intensification on pest damage and yields. Results from this study provide unique correlative support for these relationships over a wide range of agricultural intensification and pest damage, spanning a globally important agricultural region.

High crop diversity is therefore desirable not only in terms of food requisites, plant patterns, and resource utilization, but also in achieving sustainable agricultural production systems with minimal use of insecticides and herbicides (Zhao et al. 2016). Additionally, crop diversity was supposed to increase crop yields, which is not well supported by our experiments. Moreover, biocontrol functions are relying heavily on landscape patterns that can be facilitated by changing the crop diversity in the agricultural landscape (Winqvist et al. 2011, D'Alberto et al. 2012).

These pests are the most serious pests in several crops throughout China, which outbreak irregularly and caused great economic losses in recent years. This research analyzed the effects of crop diversity and landscape simplification on outbreak area of pests at the landscape scale. The present study focused on quantifying the relationship between crop diversity and outbreak area of pests and identifying the effects of crop diversity on the degree of pests at the landscape scale. Crop diversity is an ecologically based pest management where crop damage can be prevented without any adverse effects on the environment (Macfadyen et al. 2011, Klapwijk et al. 2012).

Acknowledgments

We are grateful to Prof. Dahan He for critical and insightful comments on an initial draft of this manuscript. This project was supported by the National Natural Science of China (31400349).

References Cited

- Batary, P., A. Holzschuh, K. M. Orci, F. Samu, and T. Tscharntke. 2012. Responses of plant, insect and spider biodiversity to local and landscape scale management intensity in cereal crops and grasslands. *Agric. Ecosyst. Environ.* 146: 130–136.
- Bianchi, F.J.J.A., C.J.H. Booij, and T. Tscharntke. 2006. Sustainable pest regulation in agricultural landscapes: A review on landscape composition, biodiversity and natural pest control. *Proc. R. Soc. Lond. Ser. B.* 273: 1715–1727.
- Chaplin-Kramer, R., M. E. O'Rourke, E. J. Blitzer, and C. Kremen. 2011. A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol. Lett.* 14: 922–932.
- D'Alberto, C. F., A. A. Hoffmann, and L. J. Thomson. 2012. Limited benefits of non-crop vegetation on spiders in Australian vineyards: regional or crop differences? *Biocontrol* 57: 541–552.
- Eilers, E. J., and A. M. Klein. 2009. Landscape context and management effects on an important insect pest and its natural enemies in almond. *Biol. Control* 51: 388–394.
- Gagic, V., T. Tscharntke, C. F. Dormann, B. Gruber, A. Wilstermann, and C. Thies. 2011. Food web structure and biocontrol in a four-trophic level system across a landscape complexity gradient. *Proc. R. Soc. Lond. Ser. B.* 278: 2946–2953.
- Gardiner, M. M., D. A. Landis, C. Gratton, C. D. DiFonzo, M. O'Neal, J. M. Chacon, M. T. Wayo, N. P. Schmidt, E. E. Mueller, and G. E. Heimpel. 2009. Landscape diversity enhances biological control of an introduced crop pest in the north-central USA. *Ecol. Appl.* 19: 143–154.
- Géneau, C. E., F. L. Wäckers, H. Luka, C. Daniel, and O. Balmer. 2012. Selective flowers to enhance biological control of cabbage pests by parasitoids. *Basic Appl. Ecol.* 13: 85–93.
- Hambäck, P. A., and G. Englund. 2005. Patch area, population density and the scaling of migration rates: The resource concentration hypothesis revisited. *Ecol. Lett.* 8: 1057–1065.
- Holzschuh, A., I. Steffan-Dewenter, and T. Tscharntke. 2010. How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids? *J. Anim. Ecol.* 79: 491–500.
- Hui, C. 2011. Forecasting population trend from the scaling pattern of occupancy. *Ecol. Modell.* 222: 442–446.
- Jonsson, M., H. L. Buckley, B. S. Case, S. D. Wratten, R. J. Hale, and R. K. Didham. 2012. Agricultural intensification drives landscape-context effects on host-parasitoid interactions in agroecosystems. *J. Appl. Ecol.* 49: 706–714.
- Klapwijk, M. J., O. T. Lewis, and O. T. Lewis. 2012. Host-parasitoid dynamics in a fragmented landscape: Holly trees, holly leaf miners and their parasitoids. *Basic Appl. Ecol.* 13: 94–105.
- Kleijn, D., and W. J. Sutherland. 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *J. Appl. Ecol.* 40: 947–969.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45: 175–201.
- Lu, Y., K. Wu, Y. Jiang, Y. Guo, and N. Desneux. 2012. Widespread adoption of Bt cotton and insecticide decrease promotes biocontrol services. *Nature* 487: 362–365.
- Macfadyen, S., P. G. Craze, A. Polaszek, K. van Achterberg, and J. Memmott. 2011. Parasitoid diversity reduces the variability in pest control services across time on farms. *Proc. R. Soc. Lond. Ser. B.* 278: 3387–3394.
- Meehan, T. D., B. P. Werling, D. A. Landis, and C. Gratton. 2011. Agricultural landscape simplification and insecticide use in the Midwestern United States. *Proc. Natl. Acad. Sci. USA.* 108: 11500–11505.
- Menalled, F. D., A. C. Costamagna, P. C. Marino, and D. A. Landis. 2003. Temporal variation in the response of parasitoids to agricultural landscape structure. *Agric. Ecosyst. Environ.* 96: 29–35.
- Nakahira, K., Y. Takada, T. Teramoto, K. Kagoshima, and M. Takagi. 2012. Control of potato aphids by the addition of barley strips in potato fields: a successful example of vegetation management. *Biocontrol Sci. Technol.* 22: 1155–1165.
- Nyffeler, M., and K. D. Sunderland. 2003. Composition, abundance and pest control potential of spider communities in agroecosystems: A comparison of European and US studies. *Agric. Ecosyst. Environ.* 95: 579–612.

- Pluess, T., I. Opatovsky, E. Gavish-Regev, Y. Lubin, and M. H. Schmidt-Entling. 2010. Non-crop habitats in the landscape enhance spider diversity in wheat fields of a desert agroecosystem. *Agric. Ecosyst. Environ.* 137: 68–74.
- Poveda, K., E. Martínez, M. F. Kersch-Becker, M. A. Bonilla, and T. Tscharntke. 2012. Landscape simplification and altitude affect biodiversity, herbivory and Andean potato yield. *J. Appl. Ecol.* 49: 513–522.
- Rusch, A., M. Valantin-Morison, J. P. Sarthou, and J. Roger-Estrade. 2011. Multi-scale effects of landscape complexity and crop management on pollen beetle parasitism rate. *Landscape Ecol.* 26: 473–486.
- Schmidt-Entling, M. H., and J. Dobeli. 2009. Sown wildflower areas to enhance spiders in arable fields. *Agric. Ecosyst. Environ.* 133: 19–22.
- Steingrover, E. G., W. Geertsema, and W.K.R.E. van Wingerden. 2010. Designing agricultural landscapes for natural pest control: A transdisciplinary approach in the Hoeksche Waard (The Netherlands). *Landscape Ecol.* 25: 825–838.
- Stephens, A.E.A., and J. H. Myers. 2012. Resource concentration by insects and implications for plant populations. *J. Ecol.* 100: 923–931.
- Tilman, D., P. B. Reich, and F. Isbell. 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proc. Natl. Acad. Sci. USA.* 109: 10394–10397.
- Travis, S. E., and M. W. Hester. 2005. A space-for-time substitution reveals the long-term decline in genotypic diversity of a widespread salt marsh plant, *Spartina alterniflora*, over a span of 1500 years. *J. Ecol.* 93: 417–430.
- Tscharntke, T., R. Bommarco, Y. Clough, T. O. Crist, D. Kleijn, T. A. Rand, J. M. Tylianakis, S. van Nouhuys, and S. Vidal. 2007. Conservation biological control and enemy diversity on a landscape scale. *Biol. Control* 43: 294–309.
- Tscharntke, T., Y. Clough, T. C. Wanger, L. Jackson, I. Motzke, I. Perfecto, J. Vandermeer, and A. Whitbread. 2012a. Global food security, biodiversity conservation and the future of agricultural intensification. *Biol. Conserv.* 151: 53–59.
- Tscharntke, T., J. M. Tylianakis, T. A. Rand, R. K. Didham, L. Fahrig, P. Batary, J. Bengtsson, Y. Clough, T. O. Crist, C. F. Dormann, et al. 2012b. Landscape moderation of biodiversity patterns and processes - eight hypotheses. *Biol. Rev.* 87: 661–685.
- Werling, B. P., and C. Gratton. 2010. Local and broadscale landscape structure differentially impact predation of two potato pests. *Ecol. Appl.* 20: 1114–1125.
- Werling, B. P., T. D. Meehan, B. A. Robertson, C. Gratton, and D. A. Landis. 2011. Biocontrol potential varies with changes in biofuel-crop plant communities and landscape perennality. *Glob. Change Biol. Bioenergy* 3: 347–359.
- Winqvist, C., J. Bengtsson, T. Aavik, F. Berendse, L. W. Clement, S. Eggers, C. Fischer, A. Flohre, F. Geiger, J. Liira, et al. 2011. Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. *J. Appl. Ecol.* 48: 570–579.
- Wu, K. M., Y. H. Lu, H. Q. Feng, Y. Y. Jiang, and J. Z. Zhao. 2008. Suppression of cotton bollworm in multiple crops in China in areas with Bt toxin-containing cotton. *Science* 321: 1676–1678.
- Zhao, Z. H., D. H. He, and C. Hui. 2012. From the inverse density-area relationship to the minimum patch size of a host-parasitoid system. *Ecol. Res.* 27: 303–309.
- Zhao, Z. H., P. J. Shi, X. Y. Men, F. Ouyang, and F. Ge. 2013. Effects of crop species richness on pest-natural enemy systems based on an experimental model system using a microlandscape. *Science China Life Sci.* 56: 818–822.
- Zhao, Z. H., C. Hui, H. Sandhu, F. Ouyang, Z. Dong, and F. Ge. 2014. Responses of cereal aphids and their parasitic wasps to landscape complexity. *J. Econ. Entomol.* 107: 630–637.
- Zhao, Z. H., H. Sandhu, F. Gao, and D. H. He. 2015a. Shifts in natural enemy assemblages resulting from landscape simplification account for biocontrol loss in wheat fields. *Ecol. Res.* 30: 493–498.
- Zhao, Z. H., C. Hui, Z. H. Li, and B. L. Li. 2015b. Habitat heterogeneity stabilizes the spatial and temporal interactions between cereal aphids and parasitic wasps. *Basic Appl. Ecol.* 16: 510–518.
- Zhao, Z. H., R.V.P. Gadi, C. Hui, and B. L. Li. 2016. Approaches and mechanisms for ecologically based pest management across multiple scales. *Agric. Ecosyst. Environ.* 230: 199–209.
- Zhu, Y. Y., H. R. Chen, J. H. Fan, Y. Y. Wang, Y. Li, J. B. Chen, J. X. Fan, S. S. Yang, L. P. Hu, H. Leung, et al. 2000. Genetic diversity and disease control in rice. *Nature* 406: 718–722.