Plant Ecol (2016) 217:857–868
DOI 10.1007/s11258-016-0608-7

The diverse effects of habitat fragmentation on plant–pollinator interactions

Yian Xiao · Xiaohong Li · Yusong Cao · Ming Dong

Received: 5 May 2015 / Accepted: 28 April 2016 / Published online: 5 May 2016

Abstract Habitat fragmentation affects a wide variety of biological variables including species' abundance and richness (population demography), phenology, male and female reproductive fitness, and it also affects the degree of specialization versus generalization of pollination networks. Evidence is accumulating that suggests that habitat fragmentation can have significant impacts on plant–pollinator interactions. In this article, we review the literature on habitat fragmentation effects on plants, pollinators, and the pollination network. We also discuss pollination network mechanisms that may be affected by habitat fragmentation. Habitat fragmentation isolates populations and affects ecological properties at both population and community levels. Evidence shows that habitat size and connectivity directly or indirectly influence the abundance of both plant and pollinator species. In general, plant and pollinator diversity and population size decrease with the decreasing size and habitat connectivity. Habitat fragmentation of plant communities can shift plant phenological patterns, contract flowering periods and increase the risk of local pollinator extirpation. Fragmentation has the potential to influence pollination dynamics by altering pollinator or plant densities and by altering pollinator behavior. However, evidence for the impact of habitat fragmentation on plant species' flowering phenology is relatively limited, and little is known about the effect of habitat fragmentation on the phenology of pollinators. Habitat fragmentation also leads to reduced reproduction in many species. In contrast, other species showed neutral or positive responses to habitat fragmentation in female reproductive fitness, especially in plants regularly affected by pollen limitation and pollination limitation which lead to plants' experience selection for increased autogamy in isolated habitats. Habitat fragmentation often leads to the extirpation of specialist species and results in an influx of generalists. However, studies have shown that pollinators tend to be more generalized as habitat fragmentation increases. The reason is that habitat fragmentation changes the composition of the flora, and scatters floral resources, so any remaining pollinators may need to behave as generalists in order to survive. However, the knowledge of potential

Communicated by Martin Nunez.

Y. Xiao (✉) · X. Li · Y. Cao
Key Laboratory for Biodiversity Science and Ecological Engineering of Jiangxi, Ji'an 343009, Jiangxi Province, People's Republic of China
e-mail: iyanxiao@163.com

Y. Xiao · X. Li · Y. Cao
School of Life Sciences, Jinggangshan University, Ji'an 343009, Jiangxi Province, People's Republic of China

M. Dong (✉)
Key Laboratory of Hangzhou City for Ecosystem Protection and Restoration, Hangzhou Normal University, Hangzhou 311121, Zhejiang Province, People's Republic of China
e-mail: dongming@hznu.edu.cn

ecological consequences of habitat fragmentation is limited, especially regarding the effects on a long-term scale and at landscape scales. We propose experiments involving long-term monitoring, permanent samples of flowering plants, pollinators, and their interactions at large spatial and temporal scales.

Keywords Habitat fragmentation · Pollination interaction · Biodiversity · Phenology · Reproductive fitness · Specialization and generalization · Asymmetry

Introduction

A growing body of evidence demonstrates that habitat fragmentation (Bailey et al. 2010; Fahrig 2003) is one of the leading factors affecting biodiversity, causing the retraction of ecosystem functions and services (Cagnolo et al. 2009; Gonzalez et al. 2011; Sala et al. 2000; Valladares et al. 2012). Studies have shown that both species' diversities and community compositions of plants and pollinators are negatively impacted by habitat fragmentation (Abramson et al. 2011; Aizen and Feinsinger 1994; Bailey et al. 2010; Fahrig 2003; Watling and Donnelly 2006). As a result, habitat fragmentation is one of the leading causes of species endangerment (Haddad et al. 2015) which is evident through changes in species' abundance and richness (Winfree 2010), changes in pollinator assemblages (Rands and Whitney 2011), pollen limitation (Thompson et al. 2010); and shifts of pollinator guilds (Johnson 2010), which often accompany species' disappearance, result in the extinction of ecological interactions (Valiente-Banuet et al. 2015). As plant species may represent valuable food resources for their pollinators, and the pollinators are helpful for their pollen output and fruiting whether the plants are self-incompatible or self-compatible (Aguilar et al. 2006), the changes in species' abundance and richness of pants and pollinators resulting from habitat fragmentation would change the resource availability of the mutualistic partners, and then may disrupt plant–pollinator interactions.

Studies have shown that biotic interactions, such as plant–pollinator, plant–herbivore, and intraspecific interactions, may have important effects on population dynamics and ecosystem functions (Klein et al. 2007; Lienert and Fischer 2003; Olesen and Jain 1994; Steffan-Dewenter and Westphal 2008). Human-driven habitat fragmentation has been demonstrated to impact plant and pollinator population dynamics (Fahrig 2003; Gilgert and Vaughan 2011; Keeling et al. 1996; Myneni et al. 1997; Tscharntke and Brandl 2004). In the last decade, ecologists have been increasingly interested in studying the habitat fragmentation's impact on diversity and population dynamics of plants and pollinators (Honnay et al. 2005; Martén-Rodríguez et al. 2011; Sabatino et al. 2010; Sletvold et al. 2010; Smith et al. 2009). Plant species and plant–animal interactions respond to fragmentation in diverse ways (Brudvig et al. 2015). Plant–pollinator interactions may be more resistant to negative effects of fragmentation (Ferreira et al. 2013). However, knowledge on the effect of habitat fragmentation on pollination interactions is still scarce (Araújo et al. 2011; Ashworth et al. 2004; Brudvig et al. 2015).

To identify the possible effects of habitat fragmentation on plant–pollinator interactions, we review evidence of altered community composition, pollen limitation, pollination systems in plants, and assemblage and abundance of pollinators as responses to habitat fragmentation. We outline how these changes may impact plant–pollinator interactions, including their effects on plant–pollinator specialization and generalization, and explain the reasons. We also address the potential consequences of these changes for plant–pollinator interactions. Finally, we present and discuss ideas for future relevant research.

How does habitat fragmentation affect plants and pollinators?

Habitat fragmentation isolates populations and affects many ecological properties at the organismal, population, and community levels (Aguilar and Galetto 2004; Rathcke and Jules 1993), including population dynamics (Winfree 2010), pollination systems, and the reproductive success of individual organisms (Fig. 1).

Abundance and richness of plant and pollinator

Species' responses to habitat fragmentation may be complex and difficult to test and demonstrate (Andrieu et al. 2009; Gonzalez et al. 2011). Empirical studies demonstrate that habitat size and connectivity have

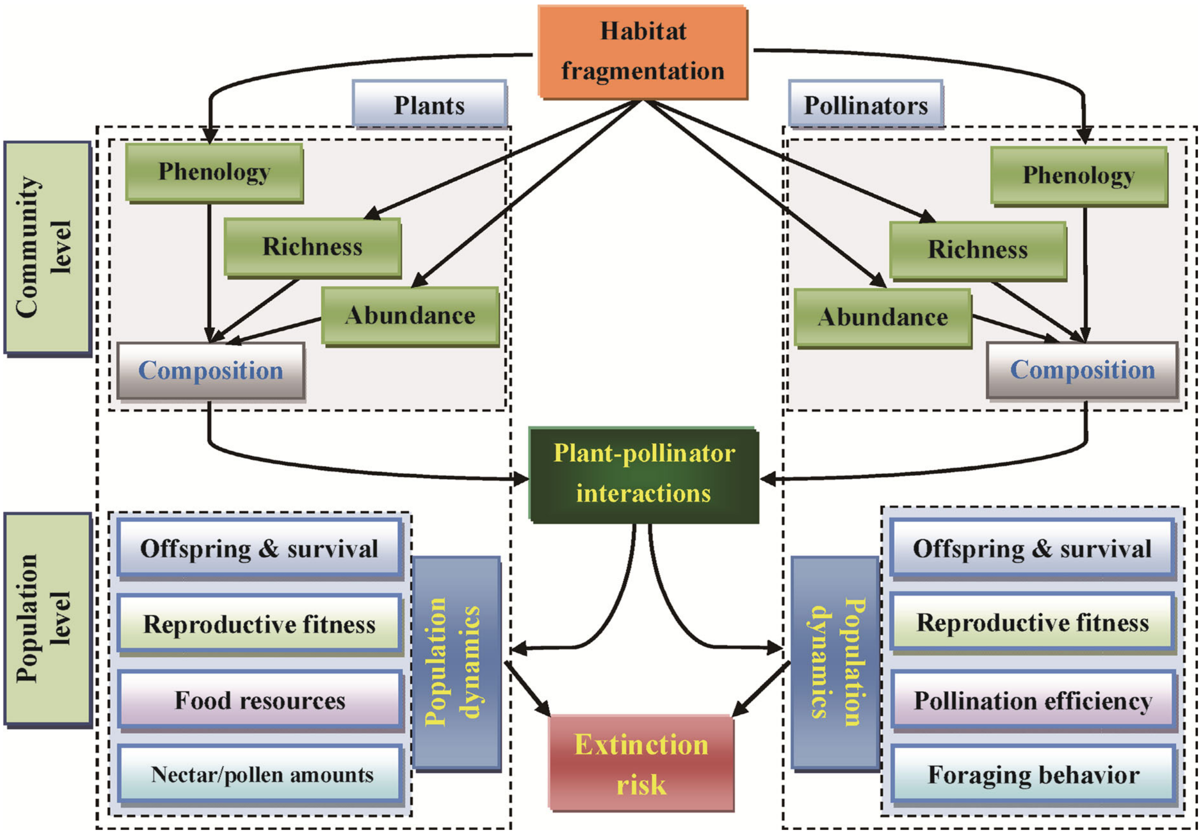

Fig. 1 Illustration of how habitat fragmentation may affect community compositions [including phenology, richness, and abundance of plants (*left*) and pollinators (*right*)] and thereby impact population dynamics. The *lower panels* show key factors affecting demography, plant–pollinator interactions, and the plant and pollinator partners. Adapted from Hegland et al. (2009)

directly or indirectly influenced the abundance of both plant and pollinator species (Aguirre and Dirzo 2008; Fahrig 2003; Tscharntke and Brandl 2004). In general, plant diversity and population size have been shown to decrease with the decreasing habitat size and connectivity (Forchhammer et al. 1998; Menz et al. 2011; Tscharntke and Brandl 2004; Wagenius et al. 2007), although not all species are likely to be equally affected by habitat fragmentation (Cagnolo et al. 2009). For instance, a decrease in habitat size has been shown to have a more pronounced impact on the richness of rare plant species in Manaus (Hoffman and Parsons 1997). Isolation and the edge-to-center ratio (the ratio of the deflection at the edge of the opening to that at the center) of habitats have also been shown to affect abundance and density of *Primula farinose* in north-east Switzerland (Lienert and Fischer 2003).

Habitat fragmentation can have varying degrees of impact on pollinators. In larger habitats adjacent to agricultural areas, pollinators have been shown to have higher species' richness (Jauker et al. 2009), while in smaller habitat areas, insect pollinator diversity has been shown to decrease (Gaston 2000). For example, Bradley et al. (1999) found that species' richness of native pollinators of *Prosopis nigra* (Mimosoideae) and *Cercidium australe* (Caesalpinoideae) declined with the decreasing fragment size, but the frequency of honey bee visits tended to increase in complementary fashion, and the total visit frequency of these species was not affected. However, Huin and Sparks (2000) did not find significant species–area relationships for bees and wasps sampled by pitfall traps and vacuums in 40 urban habitat fragments in California, USA. Species diversity indices, and capture rates of hummingbirds in South Costa Rica, increased asymptotically with patch size (Woodward 1987). Contrarily, species' richness of *Verticordia fimbrilepis* (Myrtaceae) pollinators varied across habitat size. The highest densities were found on linear road-verge populations, and the highest mean visitation rates were detected in the smallest populations (Heard et al. 2007; Yates and Ladd 2005).

To summarize, evidence shows that habitat size and connectivity directly or indirectly influence the abundance of both plant and pollinator species. In general, plant and pollinator diversity and population size decrease with the decreasing size and habitat connectivity.

Phenology

Fragmentation of plant communities increases the proportion of edges, leading to changes in microclimate including changes in light, temperature, and luminosity conditions, which can lead to shifts in plant phenological patterns (Camargo et al. 2011). Habitat fragmentation may contract flowering periods and increase the risk of local pollinator extirpation (Hagen et al. 2012). Evidence for the impact of habitat fragmentation on plant species' flowering phenology is relatively limited. Ison and Wagenius (2014) found that *Echinacea angustifolia* (Asteraceae) plants that were closest to the habitat center have significantly longer flowering periods than plants located at or near the habitat edge. Fragmentation significantly delayed the date of onset of flowering and the peak flowering date of *E. angustifolia* (Asteraceae) and also increased the duration of flowering in western Minnesota (Ison and Wagenius 2014). Reproductive phenology inversely correlated with habitat fragment size in *Syagrus romanzoffiana* (Palmae) (Freire et al. 2013; Genini et al. 2009). Flowering duration of *S. romanzoffiana* was longer in small forest fragments than in large fragments (Freire et al. 2013). Herrerías-Diego et al. (2006) found that the tropical tree, *Ceiba aesculifolia* (Bombacaceae), displayed an earlier date of flowering onset, and an earlier date of peak flowering in undisturbed habitat compared to disturbed habitat. Flower morphology has been found to vary between fragmented and unfragmented habitats. Individuals of *Crepis sancta* (L.) Bornm. (Asteraceae) have more numerous, but smaller capitula, in urban fragments than those in large continuous habitat in southern France (Andrieu et al. 2009). Studies have shown that isolated trees of the tropical tree species, *Pachira quinata* (Bombacaceae), tended to produce more flowers than trees from continuous populations, although their flowering durations and the mean peak flowering dates were similar (Fuchs et al. 2003). However, in New South Wales, Australia, *Senna artemisioides* (Fabaceae) produced more flowers in linear strips than individuals in reserves, although this was not a statistically significant effect, suggesting that the fragmentation did not substantially affect flower production (Cunningham 2000b).

Theoretically, we expect that habitat fragmentation has an impact on the phenology of plants. Pollinators can be affected by habitat fragmentation either directly through changes in their population structure and distribution or indirectly, due to population variations in the local composition and/or distribution of plants (Cagnolo et al. 2009; Potts et al. 2006). Such changes in composition and distribution may alter phenology of nectar and/or pollen resources, impacting the assemblage of pollinators and influencing their behavior and flight patterns (Fahrig 2003; Gaston 2000). Evidence suggests that fragmentation has the potential to influence pollination dynamics by altering pollinator or plant densities and by altering pollinator behavior (Hadley and Betts 2012). Pollinators have been found to be influenced by both patch size and distance between patches, visiting large patches more frequently than small patches. Variations in flower number and plant phenology may impact pollinators, because food availability is one of the most important factors influencing activities of many pollinator species (Hegland et al. 2009). Unfortunately, little is known about the effect of habitat fragmentation on the phenology of pollinators.

Although habitat fragmentation may result in phenological shifts of both plants and their pollinators, the responses would vary in degree to the changing environmental factors, which may result in the change of the phenological match between plants and pollinators. In addition, the phenological mismatch between them may result in flower resource shortage, efficient pollen resource reduction obtained by pollinators, and thus decreases in the pollinator population scale. Also, due to the lack of proper pollinators, plants pollinate unsuccessfully, and the individuals from sexual reproduction decrease sharply, which would result in the decline of plant population.

In summary, habitat fragmentation can shift plant phenological patterns, shorten flowering periods, and affect pollinators directly or indirectly. However, little is known about the effect of habitat fragmentation on the phenology of pollinators, as well as plants.

Plant male and female reproductive fitness

Studies have assessed the potential impacts of habitat fragmentation on reproductive fitness and have revealed diverse responses depending on the species studied (Aguilar and Galetto 2004; Brennan et al. 2009; Neiman et al. 2009). Many species experienced reduced reproduction (Aguilar et al. 2006; Cooley and Willis 2009; Cunningham 2000a; Fenster et al. 2009; Neiman et al. 2009; Wagenius et al. 2007), whereas other species showed neutral (Murcia 1996) or positive changes in female reproductive fitness in response to habitat fragmentation (Cunningham 2000a). Animal pollinated plants, in particular, can be influenced by habitat fragmentation directly or indirectly (Muir and Moyle 2009; Scoville et al. 2009; Streisfeld and Rausher 2009). Moreover, small populations have shown increased interplant variability in reproductive variables (Jacquemyn et al. 2002; Oostermeijer et al. 1998). Thus, the degree of variability of plant reproductive traits leads to uncertainty with regard to successful reproduction in reduced plant populations (Aguilar and Galetto 2004; Oostermeijer et al. 1998).

The reduction in plant population size is likely to affect total reproductive output (Aguilar and Galetto 2004; Jacquemyn et al. 2002; Riba et al. 2009). Habitat fragmentation impacts the mating patterns of *P. quinata*, reducing the number of outcross sires represented in the progeny of isolated trees (Fuchs et al. 2003). However, habitat fragmentation does not negatively affect the reproductive fitness of *C. aesculifolia*, because the highly mobile bat pollinators maintain reproductive connectivity between trees in both continuous and fragmented habitats (Herrerías-Diego et al. 2006). In the long-term, resource-limitations and changes in plant–pollinator interactions are possible mechanisms of substantial decreases in the quantity and quality of seeds produced (Ashworth et al. 2004; Diez et al. 2013; Fenster et al. 2009; Gaston 2000).

Pollen production or pollen probability of being delivered to a female part of the flower refers to the male fitness. In general, habitat fragmentation results in the decrease of plant population size (Menz et al. 2011; Tscharntke and Brandl 2004; Wagenius et al. 2007) and shifts in plant phenological patterns (Camargo et al. 2011), and hence, the pollen resource would decrease. Due to the combination of the negative effects on the assemblage of pollinators and their behavior (Fahrig 2003; Gaston 2000; Wilcock and Neiland 2002), which will lead to the limited quantity or quality of pollen availability on stigmas, the male fitness would decrease.

Pollen limitation and pollination limitation (insufficient pollen transfer by vectors (Moody-Weis and Heywood 2001)) are important effects of habitat fragmentation on plant female reproductive fitness due to the loss of pollinators and/or reduction in pollinator activities (Moody-Weis and Heywood 2001). Both the quantity and quality of pollen received by stigmas can affect seed output (Pender et al. 2014). In animal-pollinated plants, reductions in pollinator activity and spatial restrictions on their foraging result in decreased numbers of ovules fertilized and decreased seed set, either because of declines in the quantity of received pollen grains on stigmas (Feinsinger et al. 1991) or because of increases in the relative amount of low-quality pollen (Waser and Price 1991).

Isolated habitats may select for increased autogamy in plants (Johnston and Schoen 1996; Olesen and Jain 1994). Self-pollination may decrease a plant's sensitivity to pollinator deficit in terms of seed set, but not necessarily for inbreeding depression (Schemske et al. 2009). When habitat fragmentation occurs, both self-compatible (SC) and self-incompatible (SI) plants experience pollen limitation, although SI plants experience more acute pollen limitation (Wagenius et al. 2007). In *Cestrum parqui*, a self-incompatible, pollination-specialist plant species, habitat fragmentation strongly and negatively affected the amount of pollen grains on stigmas and decreased the seed set (Aguilar and Galetto 2004).

In brief, habitat fragmentation leads to reduced reproduction in many species. In contrast, some other species showed neutral or positive responses to habitat fragmentation in female reproductive fitness, especially in plants which were often affected by pollen limitation and pollination limitation due to their possible selection for increased autogamy in isolated habitats.

How does habitat destruction affect specialization and generalization of plant–pollinator networks?

In symmetric plant–pollinator interaction networks, generalist plants (P_G) are pollinated by many different generalist pollinators (G) (Fig. 2a), while specialist plants (P_S) are pollinated by one or a few taxa of

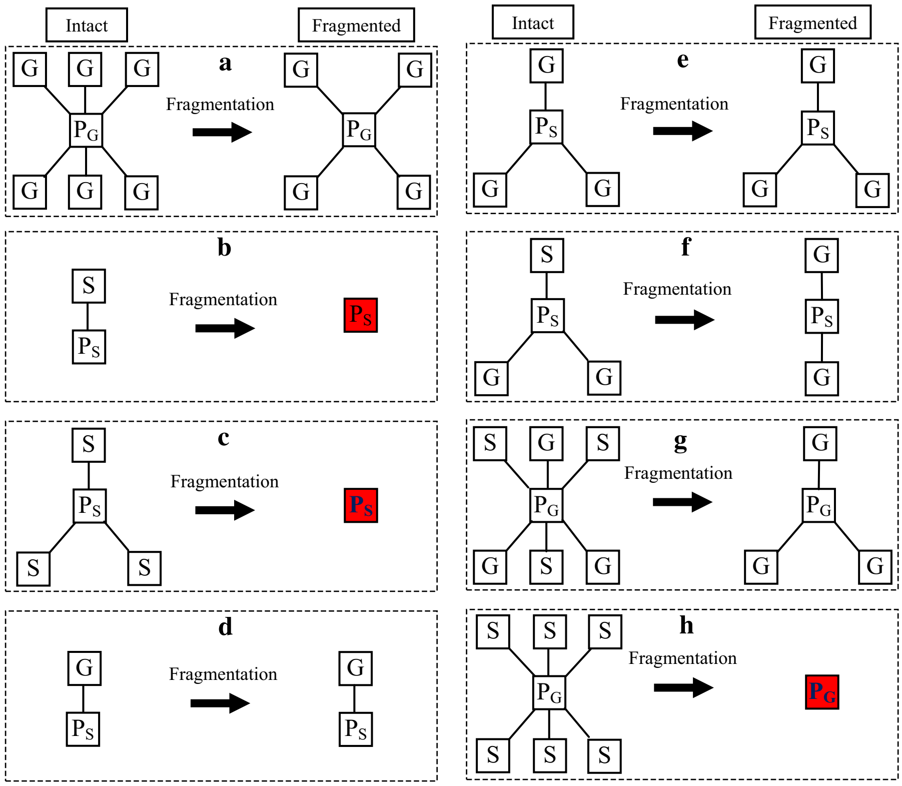

Fig. 2 Schematic representation of effects of habitat fragmentation on specialists and generalists in plant–pollinator interactions. In natural systems, there are four pollinated circumstances. (1) Generalist plants (P_G) are pollinated by many specialist (S) and generalist (G) pollinators, whereas specialist plants (P_S) are pollinated mostly by one or a few generalist pollinators, so that they have similar reproductive susceptibility to habitat fragmentation for specialist and generalist plants. (2) Generalist plants (P_G) are pollinated by many specialist (S) pollinators, whereas specialist plants (P_S) are pollinated by one or a few specialist and a few generalist pollinators; thus, the generalist plants will likely go extinct. (3) Generalist plants (P_G) are pollinated by many generalist (S) pollinators, whereas specialist plants (P_S) are pollinated by one or a few specialist pollinators, and thus, the specialist plants will likely go extinct. (4) Extreme specialist plants (P_S) are pollinated by only generalist pollinators (G), which plants could survive; or by only one specialist pollinators (S), and thus, the specialist plants will likely go extinct. Adapted from Ashworth et al. (2004)

specialist pollinators (S) (Ashworth et al. 2004) (Fig. 2b, c). In asymmetric plant–pollinator interaction networks, specialist plants are pollinated by one or few generalist pollinators, or one specialist pollinators and few generalist pollinators (Fig. 2d, f), while generalist plants are pollinated by a broad range of animals involving not only specialists but also generalists (Abramson et al. 2011; Bascompte et al. 2006; Saavedra et al. 2008; Vázquez and Aizen 2003) (Fig. 2g, h). Plant–pollinator interactions can be disrupted due to changes in availability of mutualistic partners (Hegland et al. 2009). Plant–pollinator interaction networks are strongly dependent upon niche–width demands of both specialists and generalists, including plants and pollinators (Rathcke and Jules 1993; Taki and Kevan 2007). Plants with pollination specialization will be more vulnerable to pollination mutualism disruption resulting from habitat fragmentation, as they cannot compensate for the loss of their few specific mutualist partners with other alternative pollinators (Bond 1994; Fenster and Dudash 2001). Therefore, plants could face risk of extinction under habitat fragmentation due to the loss of most or all of their specialist pollinators. Consequently, it is likely that plant and pollinator communities become more generalized with habitat fragmentation increasing (Fig. 2). However, while studies have shown that pollinators tend to be more generalized as habitat fragmentation increases, this does not seem to be the case for plants (Taki and Kevan 2007; Vázquez and

Simberloff 2002). Many specialist plants persist in fragmented habitat (Aizen et al. 2012) (Fig. 2d, f).

Habitat fragmentation often leads to the extirpation of specialist species and results in an influx of generalists (Matthews et al. 2014). Hence, the ratio of specialist to generalist species is likely to decrease with the increasing habitat area (Matthews et al. 2014) because specialists are at greater risk of extinction due to habitat loss. In plant–pollinator interaction networks, fragmentation can affect not only pollination, but also interactions (Fenster et al. 2004; Olesen and Jain 1994; Schemske et al. 2009). Compared to the historic datasets, Burkle et al. (2013) found that only 24 % of the original plant–pollinator interactions are still intact and only 46 % of forb–bee interactions are intact in fragmented landscapes in Carlinville, Illinois, USA. Their results are likely to indicate that plant–pollinator interaction networks would tend to be become more specialized under habitat fragmentation. In reality, it is not like this, the bees that were specialists, parasites, cavity-nesters, and/or those that participated in weak historic interactions were more likely to be extirpated, that indicates the more generalization of the plant–pollinator interaction under habit fragmentation and loss.

Empirical evidence and theory have shown that specialists can be more sensitive to habitat fragmentation than generalists (Kover et al. 2009) because when facing the absence of a resource or the extinction of a prey, generalists can switch to consume alternative items (Cagnolo et al. 2009). According to "specialization–disturbance" hypothesis, disturbance usually affects specialists negatively, and benefits generalists (Vázquez and Simberloff 2002). Thus generalists are the least likely to suffer extinction in simulations of habitat fragmentation (Fortuna and Bascompte 2006; Gonzalez et al. 2011). Kitahara et al. (2000) found that within lepidopteran communities in central Japan, specialists increased with the decreasing disturbance, while the generalists did not change significantly. Taki and Kevan (2007) found that pollinators but not the plants did tend to be more generalized with the increasing habitat fragmentation although the relationship is not linear in southern Ontario, Canada. Soga and Koike (2013) found that patch isolation only affected specialist species in Tokyo, Japan. The "specialization–asymmetry–disturbance" hypothesis (Vázquez and Simberloff 2002) suggests that changes in abundance to a specialist pollinator would only slightly impact a generalist or specialist plant in asymmetric interactions, but greatly affect specialist plant in symmetric interactions. Evans (2013) found that grazing disturbance affected specialist species more than generalists. However, both of these hypotheses cannot explain why specialists are not more affected by disturbance than generalists in asymmetric plant–pollinator interactions in Nahuel Huapi National Park, Argentina (Vázquez and Simberloff 2002).

In plant–pollinator interaction networks, pollinators seem to be more sensitive and/or quicker to respond to habitat fragmentation than plants (Gaston 2000; Taki and Kevan 2007). Habitat fragmentation is more likely to have an effect on specialist pollinators than on generalist pollinators (Ashworth et al. 2004; Maherali et al. 2009; Taki and Kevan 2007). Because specialist pollinators often exist in small, patchy populations, small fragments are more likely to exclude them, and adverse environmental conditions would likely cause them to perish (Ashworth et al. 2004; Gaston 2000). Furthermore, habitat fragmentation will change the composition of the flora, and may scatter floral resources, so any remaining pollinators which cannot emigrate may need to behave as generalists in order to survive (Ashworth et al. 2004; Wise 2009).

In summary, habitat fragmentation often leads to the extirpation of specialist species and results in an influx of generalists. Moreover, the pollinators tend to be more generalized with the increasing habitat fragmentation. The reason is that habitat fragmentation changes the composition of the flora, and scatters floral resources, so any remaining pollinators may need to behave as generalists in order to survive.

Future research

In the last decade, due to the increasing interest in the habitat fragmentation's impact on plants and pollinators, and their interactions, many related investigations were carried out (Kim et al. 2012; Martén-Rodríguez et al. 2011; Melián and Bascompte 2002; Sabatino et al. 2010; Smith et al. 2009). Empirical studies have shown that fragmentation has large negative direct and indirect influences on species' richness, population's abundance and distribution, and genetic diversity (Fahrig 2003). However, most of these studies have focused on the combined effects of fragmented habitat rather than those of habitat fragmentation per se (Bailey et al. 2010; Fahrig 2003). Thus, future research needs to focus on both of the direct and indirect influences and/or potential effects of habitat fragmentation on pollination interactions. The importance of such indirect effects in causing pollination interaction variation between fragments needs to be tested. Future studies should assess the differences in effects of habitat fragmentation on plants, pollinators, and plant–pollinator interactions (Bailey et al. 2010; Fahrig 2003). In addition, little is known about the patterns of change in most pollinator assemblages (Parmesan 1996). Particularly, we know much less about the potential influences of habitat fragmentation on pollination interactions through latitude and altitude gradients, or among different landscape types, even community types, or biogeographic zones. Furthermore, studies that simultaneously track individuals in multiple sizes or stage classes are exceedingly rare (Smith et al. 2009).

Long-term ecological research programs designed to address the processes in pollination services and pollination interactions are limited (Hegland et al. 2009), although such studies are needed and important to address the ecological questions at the appropriate temporal and spatial scale (Menzel 2006), and to better understand the effects of environmental factors on ecological processes (Schwartz et al. 2006). Most of the prior experiments on the pollination interactions have been conducted in short-term studies which are insufficient to understand processes at the ecosystem level in nature (Menzel 2006; Myneni et al. 1997) and the actual interactions between plants and pollinators (Petanidou et al. 2008). Furthermore, many long-term research and monitoring programs are either ineffective or fail completely owing to poor planning and/or lack of focus (Parmesan and Yohe 2003). Ideally, such experiments should involve long-term monitoring, permanent samples of flowering plants and pollinators, and their interactions (Hegland et al. 2009) at large spatial and temporal scales (Morris 2010), because fragmentation alters the spatial and temporal distributions of floral resources which impact pollinator assemblage (Kremen et al. 2007) (Fig. 1).

For many major taxa and for pollination interactions under habitat loss at the landscape scale, there is a significant lack of relevant life history and ecology data (Bailey et al. 2010; Bommarco et al. 2010; Garibaldi et al. 2011). Although there is now a long history of population-scale and community-scale studies of pollination interactions (Fortuna and Bascompte 2006; Waser et al. 1996), population- and community-scale ecology of pollination interaction studies, however, need a large-scale perspective because local patterns of pollination interaction are impacted by regional settings (Schüepp et al. 2011). Landscape change has been shown to be severely detrimental for the persistence of many species, but studies discerning the relative importance of direct and indirect effects of different landscape change processes are lacking, and long-term studies in this area are particularly scarce (Valdés and García 2011).

Future studies could focus on the long-term processes and patterns of pollination interaction under different types of natural or cultivated landscapes. It is also important to identify what the differences are between pollination interactions in fragmented habitat versus pollination interactions in naturally/existing "patchy" habitats. Several studies have shown that habitat fragmentation has similar effects on specialist and generalist plants, but we have limited knowledge about those effects at the landscape-scale, or how fragmentation affects the asymmetry of pollination interactions.

Conclusions

Habitat fragmentation has clear and important direct and/or indirect effects on abundance, phenology, and reproductive fitness of plants and pollinators, and on pollination interactions. We do not fully understand the relative importance of ecological factors impacting abundance, phenology, and reproductive fitness of plants and pollinators. Nevertheless, the current knowledge of the potential ecological consequences of habitat fragmentation is limited—especially regarding their effects on a long-term scale and at landscape scales. Although the effects of habitat fragmentation on biodiversity and specialization have been documented at community scales, these effects on asymmetry and spatial patterns of plant–pollinator interactions have so far not been addressed thoroughly. Pollination ecologists are faced with huge challenges if they would like to understand these questions clearly in the future (Aizen et al. 2012). In future research, experiments with long-term monitoring, permanent samples of flowering plants and pollinators, and their interactions at large spatial and temporal scales should be pursued. Much work yet needs to be done. We believe that with this needed information, pollination ecologists will have a better understanding of how habitat fragmentation impacts plant–pollinator interactions.

Acknowledgments The authors thank Dr. Marc, Helena Puche, and Henry F. Howe for their valuable help and comments on the manuscript. The authors are also grateful to the National Natural Science Foundation of China (No 41561012, 31060069, 31360099), and the Program for New Century Excellent Talents in University of China (No NCET-07-0385) for their support to this study.

References

Abramson G, Soto CAT, Oña L (2011) The role of asymmetric interactions on the effect of habitat destruction in mutualistic networks. PLoS One 6:2235–2239

Aguilar R, Galetto L (2004) Effects of forest fragmentation on male and female reproductive success in *Cestrum parqui* (Solanaceae). Oecologia 138:513–520

Aguilar R, Ashworth L, Galetto L, Aizen MA (2006) Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. Ecol Lett 9:968–980

Aguirre A, Dirzo R (2008) Effects of fragmentation on pollinator abundance and fruit set of an abundant understory palm in a Mexican tropical forest. Biol Conserv 141:375–384

Aizen MA, Feinsinger P (1994) Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. Ecology 75:330–351

Aizen MA, Sabatino M, Tylianakis JM (2012) Specialization and rarity predict nonrandom loss of interactions from mutualist networks. Science 335:1486–1489

Andrieu E, Dornier A, Rouifed S, Schatz B, Cheptou PO (2009) The town Crepis and the country Crepis: How does fragmentation affect a plant–pollinator interaction? Acta Oecol 35:1–7

Araújo MS, Bolnick DI, Layman CA (2011) The ecological causes of individual specialisation. Ecol Lett 14:948–958

Ashworth L, Aguilar R, Galetto L, Aizen MA (2004) Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation? J Ecol 92:717–719

Bailey D, Schmidt-Entling MH, Eberhart P, Herrmann JD, Hofer G, Kormann U, Herzog F (2010) Effects of habitat amount and isolation on biodiversity in fragmented traditional orchards. J Appl Ecol 47:1003–1013

Bascompte J, Jordano P, Olesen JM (2006) Asymmetric coevolutionary networks facilitate biodiversity maintenance. Science 312:431–433

Bommarco R, Biesmeijer JC, Meyer B, Potts SG, Pöyry J, Roberts SPM, Steffan-Dewenter I, Öckinger E (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. Proc R Soc B Biol Sci 277:2075–2082

Bond WJ (1994) Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. Philos Trans R Soc Lond B 344:83–90

Bradley NL, Leopold AC, Ross J, Huffaker W (1999) Phenological changes reflect climate change in Wisconsin. Proc Natl Acad Sci 96:9701–9704

Brennan AC, Bridle JR, Wang AL, Hiscock SJ, Abbott RJ (2009) Adaptation and selection in the *Senecio* (Asteraceae) hybrid zone on Mount Etna, Sicily. New Phytol 183:702–717

Brudvig LA, Damschen EI, Haddad NM, Levey DJ, Tewksbury JJ (2015) The influence of habitat fragmentation on multiple plant-animal interactions and plant reproduction. Ecology 96:2669–2678

Burkle LA, Marlin JC, Knight TM (2013) Plant–pollinator interactions over 120 years: loss of species, co-occurrence, and function. Science 339:1611–1615

Cagnolo L, Valladares G, Salvo A, Cabido M, Zak M (2009) Habitat fragmentation and species loss across three interacting trophic levels: effects of life-history and food-web traits. Conserv Biol 23:1167–1175

Camargo MGG, Souza RM, Reys P, Morellato LP (2011) Effects of environmental conditions associated to the cardinal orientation on the reproductive phenology of the cerrado savanna tree *Xylopia aromatica* (Annonaceae). An Acad Bras Cienc 83:1007–1020

Cooley AM, Willis JH (2009) Genetic divergence causes parallel evolution of flower color in Chilean Mimulus. New Phytol 183:729–739

Cunningham SA (2000a) Depressed pollination in habitat fragments causes low fruit set. Proc R Soc Lond B Biol Sci 267:1149–1152

Cunningham SA (2000b) Effects of habitat fragmentation on the reproductive ecology of four plant species in Mallee Woodland. Conserv Biol 14:758–768

Diez JM, James TY, McMunn M, Ibáñez I (2013) Predicting species-specific responses of fungi to climatic variation using historical records. Glob Change Biol 19:3145–3154

Evans M (2013) Influences of grazing and landscape on bee pollinators and their floral resources in rough fescue prairie. Department of Biological Sciences. University of Calgary

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Feinsinger P, Tiebout HM, Young BE (1991) Do tropical bird-pollinated plants exhibit density-dependent interactions? Field experiments. Ecology 72:1953–1963

Fenster CB, Dudash MR (2001) Spatiotemporal variation in the role of hummingbirds as pollinators of *Silene virginica*. Ecology 82:844–851

Fenster CB, Armbruster WS, Wilson P, Dudash MR, Thomson JD (2004) Pollination syndromes and floral specialization. Annu Rev Ecol Evol Syst 35:375–403

Fenster CB, Armbruster WS, Dudash MR (2009) Specialization of flowers: Is floral orientation an overlooked first step? New Phytol 183:502–506

Ferreira PA, Boscolo D, Viana BF (2013) What do we know about the effects of landscape changes on plant–pollinator interaction networks? Ecol Indic 31:35–40

Forchhammer MC, Post E, Stenseth NC (1998) Breeding phenology and climate. Nature 391:29–30

Fortuna MA, Bascompte J (2006) Habitat loss and the structure of plant-animal mutualistic networks. Ecol Lett 9:281–286

Freire CC, Closel MB, Hasui E, Ramos FN (2013) Reproductive phenology, seed dispersal and seed predation in *Syagrus romanzoffiana* in a highly fragmented landscape. Ann Bot Fenn 50:220–228

Fuchs EJ, Lobo JA, Quesada M (2003) Effects of forest fragmentation and flowering phenology on the reproductive success and mating patterns of the tropical dry forest tree *Pachira quinata*. Conserv Biol 17:149–157

Garibaldi LA, Steffan-Dewenter I, Kremen C, Morales JM, Bommarco R, Cunningham SA, Carvalheiro LG, Chacoff NP, Dudenhöffer JH, Greenleaf SS, Holzschuh A, Isaacs R, Krewenka K, Mandelik Y, Mayfield MM, Morandin LA, Potts SG, Ricketts TH, Szentgyörgyi H, Viana BF, Westphal C, Winfree R, Klein AM (2011) Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecol Lett 14:1062–1072

Gaston KJ (2000) Global patterns in biodiversity. Nature 405:220–227

Genini J, Galetti M, Morellato LPC (2009) Fruiting phenology of palms and trees in an Atlantic rainforest land-bridge island. Flora Morphol Distrib Funct Ecol Plants 204:131–145

Gilgert W, Vaughan M (2011) The value of pollinators and pollinator habitat to rangelands: connections among pollinators, insects, plant communities, fish, and wildlife. Rangelands 33:14–19

Gonzalez A, Rayfield B, Lindo Z (2011) The disentangled bank: How loss of habitat fragments and disassembles ecological networks. Am J Bot 98:503–516

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:e1500052

Hadley AS, Betts MG (2012) The effects of landscape fragmentation on pollination dynamics: absence of evidence not evidence of absence. Biol Rev 87:526–544

Hagen M, Kissling WD, Rasmussen C, Carstensen D, Dupont Y, Kaiser-Bunbury C, O'Gorman E, Olesen J, De Aguiar M, Brown L (2012) Biodiversity, species interactions and ecological networks in a fragmented world. Adv Ecol Res 46:89–120

Heard MS, Carvell C, Carreck NL, Rothery P, Osborne JL, Bourke AF (2007) Landscape context not patch size determines bumble-bee density on flower mixtures sown for agri-environment schemes. Biol Lett 3:638–641

Hegland SJ, Nielsen A, Lázaro A, Bjerknes AL, Totland Ø (2009) How does climate warming affect plant–pollinator interactions? Ecol Lett 12:184–195

Herrerías-Diego Y, Quesada M, Stoner KE, Lobo JA (2006) Effects of forest fragmentation on phenological patterns and reproductive success of the tropical dry forest tree *Ceiba aesculifolia*. Conserv Biol 20:1111–1120

Hoffman AA, Parsons PA (1997) Extreme environmental change and evolution. Cambridge Unversity Press, Cambridge

Honnay O, Jacquemyn H, Bossuyt B, Hermy M (2005) Forest fragmentation effects on patch occupancy and population viability of herbaceous plant species. New Phytol 166:723–736

Huin N, Sparks TH (2000) Spring arrival patterns of the cuckoo *Cuculus canorus*, nightingale *Luscinia megarhynchos* and spotted flycatcher *Musciapa striata* in Britain. Bird Study 47:22–31

Ison JL, Wagenius S (2014) Both flowering time and distance to conspecific plants affect reproduction in *Echinacea angustifolia*, a common prairie perennial. J Ecol 102:920–929

Jacquemyn H, Brys R, Hermy M (2002) Patch occupancy, population size and reproductive success of a forest herb (*Primula elatior*) in a fragmented landscape. Oecologia 130:617–625

Jauker F, Diekötter T, Schwarzbach F, Wolters V (2009) Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landsc Ecol 24:547–555

Johnson SD (2010) The pollination niche and its role in the diversification and maintenance of the southern African flora. Philos Trans R Soc Lond B Biol Sci 365:499–516

Johnston MO, Schoen DJ (1996) Correlated evolution of self-fertilization and inbreeding depression: an experimental study of nine populations of *Amsinckia* (Boraginaceae). Evolution 50:1478–1491

Keeling CD, Chin JFS, Whorf TP (1996) Increased activity of northern vegetation inferred from atmospheric CO_2 measurements. Nature 382:146–149

Kim Y, Kimball JS, Zhang K, McDonald KC (2012) Satellite detection of increasing Northern Hemisphere non-frozen seasons from 1979 to 2008: implications for regional vegetation growth. Remote Sens Environ 121:472–487

Kitahara M, Sei K, Fujii K (2000) Patterns in the structure of grassland butterfly communities along a gradient of human disturbance: further analysis based on the generalist/specialist concept. Popul Ecol 42:135–144

Klein AM, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proc R Soc B Biol Sci 274:303–313

Kover PX, Rowntree JK, Scarcelli N, Savriama Y, Eldridge T, Schaal BA (2009) Pleiotropic effects of environment-specific adaptation in *Arabidopsis thaliana*. New Phytol 183:816–825

Kremen C, Williams NM, Aizen MA, Gemmill-Herren B, LeBuhn G, Minckley R, Packer L, Potts SG, Roulston TA, Steffan-Dewenter I, Vázquez DP, Winfree R, Adams L, Crone EE, Greenleaf SS, Keitt TH, Klein AM, Regetz J, Ricketts TH (2007) Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecol Lett 10:299–314

Lienert J, Fischer M (2003) Habitat fragmentation affects the common wetland specialist *Primula farinosa* in north-east Switzerland. J Ecol 91:587–599

Maherali H, Caruso CM, Sherrard ME (2009) The adaptive significance of ontogenetic changes in physiology: a test in *Avena barbata*. New Phytol 183:908–918

Martén-Rodríguez S, Kress WJ, Temeles EJ, Meléndez-Ackerman E (2011) Plant–pollinator interactions and floral convergence in two species of *Heliconia* from the Caribbean Islands. Oecologia 167:1075–1083

Matthews TJ, Cottee-Jones HE, Whittaker RJ (2014) Habitat fragmentation and the species–area relationship: a focus on

total species richness obscures the impact of habitat loss on habitat specialists. Divers Distrib 20:1136–1146
Melián CJ, Bascompte J (2002) Food web structure and habitat loss. Ecol Lett 5:37–46
Menz MHM, Phillips RD, Winfree R, Kremen C, Aizen MA, Johnson SD, Dixon KW (2011) Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. Trends Plant Sci 16:4–12
Menzel A (2006) European phenological response to climate change matches the warming pattern. Glob Change Biol 12:1969–1976
Moody-Weis JM, Heywood JS (2001) Pollination limitation to reproductive success in the Missouri evening primrose, *Oenothera macrocarpa* (Onagraceae). Am J Bot 88:1615–1622
Morris RJ (2010) Anthropogenic impacts on tropical forest biodiversity: a network structure and ecosystem functioning perspective. Philos Trans R Soc B Biol Sci 365:3709–3718
Muir CD, Moyle LC (2009) Antagonistic epistasis for ecophysiological trait differences between *Solanum* species. New Phytol 183:789–802
Murcia CI (1996) Forest fragmentation and the pollination of neotropical plants. In: Schelhas J, Greenberg R (eds) Forest patches in tropical landscapes. Island Press, Washington, pp 19–36
Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. Nature 386:698–702
Neiman M, Olson MS, Tiffin P (2009) Selective histories of poplar protease inhibitors: elevated polymorphism, purifying selection, and positive selection driving divergence of recent duplicates. New Phytol 183:740–750
Olesen JM, Jain SK (1994) Fragmented plant populations and their lost interactions. In: Loeschcke V, Tomiuk J, Jain SK (eds) Servation genetics. Birkhäuser, Basel, pp 417–426
Oostermeijer JGB, Luijten SH, Křenová ZV, Den Nijs HCM (1998) Relationships between population and habitat characteristics and reproduction of the rare *Gentiana pneumonanthe* L. Conserv Biol 12:1042–1053
Parmesan C (1996) Climate and species' range. Nature 382:765–766
Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42
Pender RJ, Morden CW, Paull RE (2014) Investigating the pollination syndrome of the Hawaiian lobeliad genus *Clermontia* (Campanulaceae) using floral nectar traits. Am J Bot 101:201–205
Petanidou T, Kallimanis AS, Tzanopoulos J, Sgardelis SP, Pantis JD (2008) Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. Ecol Lett 11:564–575
Potts SG, Petanidou T, Roberts S, O'Toole C, Hulbert A, Willmer P (2006) Plant–pollinator biodiversity and pollination services in a complex Mediterranean landscape. Biol Conserv 129:519–529
Rands SA, Whitney HM (2011) Field margins, foraging distances and their impacts on nesting pollinator success. PLoS One 6:e25971
Rathcke BJ, Jules ES (1993) Habitat fragmentation and plant–pollinator interactions. Curr Sci India 65:273–277
Riba M, Mayol M, Giles BE, Ronce O, Imbert E, Van Der Velde M, Chauvet S, Ericson L, Bijlsma R, Vosman B, Smulders MJM, Olivieri I (2009) Darwin's wind hypothesis: does it work for plant dispersal in fragmented habitats? New Phytol 183:667–677
Saavedra S, Reed-Tsochas F, Uzzi B (2008) Asymmetric disassembly and robustness in declining networks. Proc Natl Acad Sci 105:16466–16471
Sabatino M, Maceira N, Aizen MA (2010) Direct effects of habitat area on interaction diversity in pollination webs. Ecol Appl 20:1491–1497
Sala OE, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774
Schemske DW, Mittelbach GG, Cornell HV, Sobel JM, Roy K (2009) Is there a latitudinal gradient in the importance of biotic interactions? Annu Rev Ecol Evol Syst 40:245–269
Schüepp C, Herrmann JD, Herzog F, Schmidt-Entling MH (2011) Differential effects of habitat isolation and landscape composition on wasps, bees, and their enemies. Oecologia 165:713–721
Schwartz MD, Ahas R, Aasa A (2006) Onset of spring starting earlier across the Northern Hemisphere. Glob Change Biol 12:343–351
Scoville A, Lee YW, Willis JH, Kelly JK (2009) Contribution of chromosomal polymorphisms to the G-matrix of *Mimulus guttatus*. New Phytol 183:803–815
Sletvold N, Grindeland JM, Jon Å (2010) Pollinator-mediated selection on floral display, spur length and flowering phenology in the deceptive orchid *Dactylorhiza lapponica*. New Phytol 188:385–392
Smith SD, Ané C, Baum DA (2009) Macroevolutionary tests of pollination syndromes: a reply to Fenster et al. Evolution 63:2763–2767
Soga M, Koike S (2013) Patch isolation only matters for specialist butterflies but patch area affects both specialist and generalist species. J For Res JPN 18:270–278
Steffan-Dewenter I, Westphal C (2008) The interplay of pollinator diversity, pollination services and landscape change. J Appl Ecol 45:737–741
Streisfeld MA, Rausher MD (2009) Genetic changes contributing to the parallel evolution of red floral pigmentation among *Ipomoea* species. New Phytol 183:751–763
Taki H, Kevan PG (2007) Does habitat loss affect the communities of plants and insects equally in plant–pollinator interactions? Preliminary findings. Biodivers Conserv 16:3147–3161
Thompson JN, Laine AL, Thompson JF (2010) Retention of mutualism in a geographically diverging interaction. Ecol Lett 13:1368–1377
Tscharntke T, Brandl R (2004) Plant-insect interactions in fragmented landscapes. Annu Rev Entomol 49:405–430
Valdés A, García D (2011) Direct and indirect effects of landscape change on the reproduction of a temperate perennial herb. J Appl Ecol 48:1422–1431
Valiente-Banuet A, Aizen MA, Alcántara JM, Arroyo J, Cocucci A, Galetti M, García MB, García D, Gómez JM,

Jordano P (2015) Beyond species loss: the extinction of ecological interactions in a changing world. Funct Ecol 29:299–307

Valladares G, Cagnolo L, Salvo A (2012) Forest fragmentation leads to food web contraction. Oikos 121:299–305

Vázquez DP, Aizen MA (2003) Null model analyses of specialization in plant–pollinator interactions. Ecology 84:2493–2501

Vázquez DP, Simberloff D (2002) Ecological specialization and susceptibility to disturbance conjectures and refutations. Am Nat 159:606–623

Wagenius S, Lonsdorf E, Neuhauser C (2007) Patch aging and the s-Allee effect: breeding system effects on the demographic response of plants to habitat fragmentation. Am Nat 169:383–397

Waser NM, Price MV (1991) Outcrossing distance effects in *Delphinium nelsonii*: Pollen loads, pollen tubes, and seed set. Ecology 72:171–179

Waser NM, Chittka L, Price MV, Williams NM, Ollerton J (1996) Generalization in pollination systems, and why it matters. Ecology 77:1043–1060

Watling JI, Donnelly MA (2006) Fragments as islands: a synthesis of faunal responses to habitat patchiness. Conserv Biol 20:1016–1025

Wilcock C, Neiland R (2002) Pollination failure in plants: why it happens and when it matters. Trends Plant Sci 7:270–277

Winfree R (2010) The conservation and restoration of wild bees. Ann N Y Acad Sci 1195:169–197

Wise MJ (2009) To duck or not to duck: resistance advantages and disadvantages of the candy-cane stem phenotype in tall goldenrod, *Solidago altissima*. New Phytol 183:900–907

Woodward FI (1987) Climate and plant distribution. Cambridge University Press, Cambridge

Yates CJ, Ladd PG (2005) Relative importance of reproductive biology and establishment ecology for persistence of a rare shrub in a fragmented landscape. Conserv Biol 19:239–249