Indirect Effects of Landscape Spatial Structure and Plant Species Richness on Pollinator Diversity in Ozark Glades

Authors: Grover, Shannon N., Miller, Jesse E. D., and Damschen, Ellen I.

Source: Castanea, 82(1) : 24-31

Published By: Southern Appalachian Botanical Society

URL: https://doi.org/10.2179/16-108

CASTANEA 82(1): 24–31. MARCH

Indirect Effects of Landscape Spatial Structure and Plant Species Richness on Pollinator Diversity in Ozark Glades

Shannon N. Grover,[1]* **Jesse E. D. Miller,**[1,2] **Ellen I. Damschen**[1]
[1]Department of Zoology, University of Wisconsin-Madison, Madison, WI 53706 USA

ABSTRACT Changes in landscape spatial structure—specifically, reductions in habitat area and connectivity—are thought to be a primary cause of pollinator declines across North America. However, the mechanisms by which landscape structure influences pollinator diversity are not well understood. Because flowering plants and pollinators are generally mutualistic, the impact of landscape structure on one can influence the diversity of the other directly or indirectly. Here, we examine the direct and indirect effects of landscape structure on plant and pollinator communities in the naturally patchy, dolomite glade grasslands of the Missouri Ozarks. We quantified landscape spatial structure and the richness of plants and flying invertebrate pollinators in 30 glades. Higher pollinator diversity was not directly related to greater landscape area and connectivity. However, we found evidence for an indirect relationship where better-connected landscapes support higher plant richness, which in turn supports greater pollinator diversity. Our findings highlight the importance of conserving extensive, well-connected natural habitat in order to maintain the plant diversity needed to support diverse pollinator communities.

Key words: Biodiversity, conservation, glade, grassland, indirect effects, multitrophic relationships, Ozarks pollination.

INTRODUCTION North American native pollinators have been declining in recent decades (Buchmann and Nabhan 1996, Potts et al. 2010, Cameron et al. 2011, Burkle et al. 2013, Goulson et al. 2015). This decline potentially impacts not only the persistence of native plant species (Fontaine et al. 2005), but also the crucial agricultural services these insects provide; fruit and vegetable pollination by native insects in the United States alone has been valued at just over 3 billion dollars (Losey and Vaughan 2006). This service depends on the persistence of high-diversity pollinator assemblages, which can better withstand short-term environmental fluctuations as well as long-term stressors such as climate change (Kremen et al. 2007, Bartomeus et al. 2013).

Threats to pollinator diversity include the increased use of pesticides, the spread of exotic species, climate change, and, in particular, habitat loss and fragmentation (Rathcke and Jules 1993, Memmott et al. 2007, Brown and Paxton 2009, Whitehorn et al. 2012, Arbetman et al. 2013, Goulson et al. 2015). Habitat loss and fragmentation are the processes by which habitat patches become smaller and more isolated from each other (Wilcove et al. 1986). These changes in landscape structure can reduce species persistence and community diversity in pollinators as well as in their plant mutualists (MacArthur and Wilson 1967, Rathcke and Jules 1993, Brown and Paxton 2009, Öckinger et al. 2010). Although there is substantial evidence indicating that higher-diversity plant communities support greater pollinator diversity and vice versa (Potts et al. 2003, Fontaine et al. 2005, Ebeling et al. 2008, Blüthgen and Klein 2011), the mechanisms by which changes in landscape structure affect pollinator diversity remain poorly understood. Specifically, it is unclear whether

---

[2]Current address: Department of Environmental Science and Policy, University of California, Davis, CA 95616
*email address: s.vulpinus@gmail.com
Received August 10, 2016; Accepted February 21, 2017;

DOI: 10.2179/16-108

habitat loss reduces pollinator diversity directly, or whether pollinator diversity is more strongly influenced by landscape-induced reductions in plant diversity. Additional insight into this topic might help to better inform management decisions regarding native pollinator conservation.

Here, we investigate the importance of the direct effects of landscape structure on pollinator diversity relative to indirect effects mediated by landscape-induced changes in plant species richness. We examine (1) the relationship between landscape spatial structure and pollinator diversity in insular grasslands, and (2) the influence of plant species richness on this relationship. Plants and pollinators differ in the distances they are able to disperse (Howe and Smallwood 1982, Cheplick 1998, Osborne et al. 1999, Nathan and Muller-Landau 2000, Gathmann and Tscharntke 2002, Knight et al. 2005, Pasquet et al. 2008), suggesting that the two groups might respond differently to landscape structure (Burkle and Alarcón 2011). We hypothesized that plants, being less mobile than pollinators, would be more sensitive to landscape structure and would affect pollinators via their mutualistic relationship.

METHODS

Study System

Ozark glades are grasslands characterized by shallow, dry soils with outcroppings of dolomite bedrock (Ware 2002). Glades typically occur on ridgetops and south- and west-facing slopes, where intense insolation, in conjunction with harsh soil conditions and frequent, low-intensity fires, create an environment that generally does not support woody plant dominance (Ware 2002, Miller et al. 2015). The result is a landscape of open grassland patches that are typically 1 to 100+ ha in size and surrounded by a woodland matrix (Ladd and Nelson 1982). The harsh, xeric nature of glade environments also makes them poorly suited to anthropogenic uses, and today glades represent a relatively intact system in comparison to most Midwestern grasslands (Nelson 2005). Glades also contain a high number of endemic and rare plant species relative to other Midwestern grasslands (Nelson 2005).

We conducted plant and pollinator surveys in 30 dolomite glades throughout the Ozark highlands of Missouri. Following consultation with land managers, glades were selected if they had <10% woody vegetation cover. We additionally restricted study sites to glades that had been managed with fire at 3- to 6-yr intervals and had experienced only minor grazing historically (see Miller et al. 2015).

Plant and Pollinator Sampling

We conducted 30 plant and pollinator surveys over the course of 5 wk, from 3 June to 9 July, 2014. We established one 50 m by 2 m study plot at each site and identified all plants growing in the plot to species. We used these data to estimate plant species richness. We also recorded the number of individuals in bloom within the plot to account for potential effects of floral abundance on pollinator activity (Totland 1994).

We sampled pollinators during hours of peak activity between 9:00 AM and 5:30 PM, on days with little to no cloud cover, with temperatures exceeding 24°C. Every bee, butterfly, wasp, or hoverfly observed within the plot's boundaries over the course of 10 min (walking 5 m/min down center of plot) was morphotyped visually based on characteristics distinguishable in the field, similar to approaches used in Memmott et al. (1993), Memmott (1999), and Dicks et al. (2002). Because morphological diversity approximates pollinator functional diversity (Fontaine et al. 2005), we used the richness of the observed morphoguilds as a proxy for pollinator diversity in each glade, opting to sacrifice species-level identification to allow broad sampling across the Missouri Ozarks. Although this technique likely resulted in an underestimation of pollinator richness, our methods were consistent across glades, yielding a meaningful comparison of glade pollinator communities.

Analysis

To quantify landscape spatial structure for each glade, we calculated proximity index, an area-weighted measure of landscape connectivity, within a 1-km radius buffer distance from the study site (see Miller et al. 2015). The proximity index is useful because it captures both habitat area and connectivity, which are difficult to tease apart in natural systems (Gustafson and Parker 1992). Values are lower for smaller, more isolated glades, and higher for larger, well-connected glades (Gustafson and Parker 1992).

We began analysis by screening data to examine its distributional properties and by exploring bivariate relationships among variables of interest using Pearson's correlation. We then created a structural equation meta-model (SEM) following methods described by Grace (2006) for hypothesized relationships among landscape spatial structure, pollinator morphoguild richness, and total plant species richness. By accounting for all variables simultaneously, this method allowed us to compare direct relationships between the three variables while also exploring the possible indirect effect of plant richness on pollinator diversity and vice versa. The meta-model included pollinator richness and plant richness as endogenous variables and proximity index as an exogenous variable, with directed paths from proximity index to both pollinator and plant richness and from plant richness to pollinator richness. To test for the possibility of confounding environmental effects on pollinator richness, we incorporated the date of surveying, percent cloud cover, and number of flowers in bloom into the model as additional exogenous variables, with directed paths from each variable to pollinator morphoguild richness. We then repeated this analysis while excluding wind-pollinated graminoid species from our plant richness values to assess the functional relationship between pollinators and the plants that use biotic pollination.

RESULTS The observed number of pollinator morphoguilds ranged from 0 to 13 per site, with a median of five morphoguilds. In total, we observed 28 butterfly morphoguilds; six of which were categorized, as large (>100 mm), nine as medium (~75–100 mm), 10 as small (~50–75 mm), and three as extra-small (<50 mm). Common butterflies included members of the genera *Vanessa* [Fabr.], *Phyciodes* Hübner, and *Colias* [Fabr.], and members of the family Hesperiidae.

The remaining 36 morphoguilds included solitary bees, hoverflies, bumblebees, honeybees, and wasps. We categorized 14 of these morphoguilds as large (>20 mm), nine as medium (~10–20 mm), seven as small (~5–10 mm), and six as extra-small body sizes (<5 mm). The bee community included representatives of genera such as *Lasioglossum* Curtis, *Megachile* Latreille, *Xylocopa* Latreille, and *Bombus* Latreille. *Apis mellifera* L. was a dominant species in many glades. *Hemipenthes sinuosa* (Wiedem.) and *Chrysanthrax cypris* Meigen were two of the dominant hover fly species, and wasps in the genus *Polistes* Latreille were common.

Plant species richness ranged from 15 to 53, with a median species richness of 35. The species richness of biotically pollinated plants ranged from 14 to 44, with a median species richness of 30. Warm season grasses such as *Panicum virgatum* L., *Schizachyrium scoparium* Nash, and *Sorghastrum nutans* Nash dominated the plant community. The glade flora also included a diverse assortment of forbs, with a large number of species in the Asteraceae, Fabaceae, and Lamiaceae families.

The relationships between landscape structure and plant richness ($r = 0.36$, $p = 0.04$, $df = 30$), and between plant richness and pollinator morphoguild richness ($r = 0.38$, $p = 0.03$, $df = 31$) were both statistically significant ($p \leq 0.05$). Pollinator morphoguild richness was not significantly correlated with landscape structure ($r = 0.20$, $p = 0.28$, $df = 30$) or floral abundance ($r = 0.03$, $p = 0.85$, $df = 30$). The relationship between the richness of biotically pollinated plants and pollinator morphoguild richness ($r = 0.39$, $p = 0.03$, $df = 31$) was similar to that of total plant species richness. The relationship between landscape structure and biotically pollinated plant richness was not significant, but showed a positive trend ($r = 0.32$, $p = 0.07$, $df = 30$).

Our final SEM (Figure 1) contained significant paths between landscape spatial structure and plant species richness and between plant species richness and pollinator morphoguild richness. The path from proximity index to pollinator richness was not significant and was removed from the final model. Our final model contained an indirect relationship between landscape spatial structure and pollinator morphoguild richness, with plant species richness functioning as an intermediary (Figure 1). The structure of this model did not change when wind-pollinated species were excluded from the plant species richness values (Figure 2), although the relationship between landscape structure and plant species richness became marginally significant ($p = 0.05$ when excluding wind-pollinated species vs. $p = 0.03$ when all plant species were included). Survey date, time, cloud cover, and wind speed were not significantly correlated with plant richness, pollinator richness, or landscape structure, and were not significant when incorporated into the SEM.

DISCUSSION We found positive relationships between landscape structure and plant species richness, and between plant species

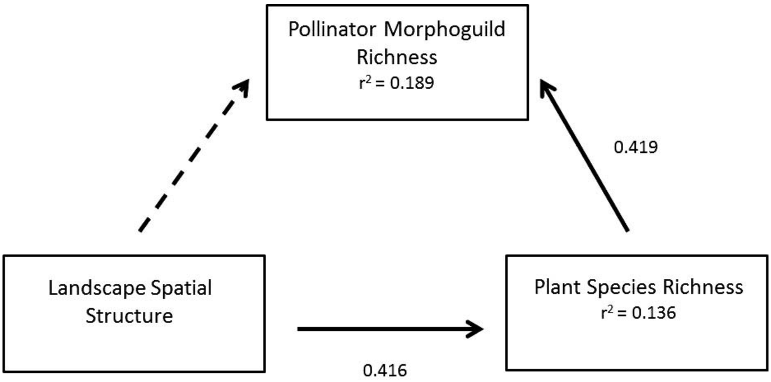

Figure 1. Structural equation model of landscape spatial structure (habitat area and connectivity), plant species richness, and pollinator morphoguild richness. Arrows are labeled with standardized path coefficients and represent directional links between variables. Solid arrows denote significant relationships ($p \leq 0.05$) and dashed arrows denote nonsignificant relationships ($p > 0.05$).

richness and pollinator morphoguild richness. Landscape structure, however, was not directly correlated with pollinator richness, suggesting that in Ozark glades, plant communities are more sensitive to landscape structure than are pollinator communities. Our results suggest that although landscape structure does not directly influence pollinator diversity, landscape effects on plant species richness can lead to corresponding changes in the pollinator community. This indirect relationship between landscape structure and pollinator diversity highlights the importance of accounting for indirect effects in studies of diversity across trophic levels.

In Ozark glades, higher-diversity plant communities support higher-diversity pollinator communities and vice versa (Potts et al. 2003, Fontaine et al. 2005, Ebeling et al. 2008, Blüthgen and Klein 2011). However, because we were interested in the effects of landscape structure on this mutualism, we designed our structural equation model with a directional path from plant species richness to pollinator morphoguild richness and not the other direction. We reasoned that because landscape structure was not directly correlated with pollinator morphoguild richness, any influence of landscape structure on the plant-pollinator mutualism had to result from

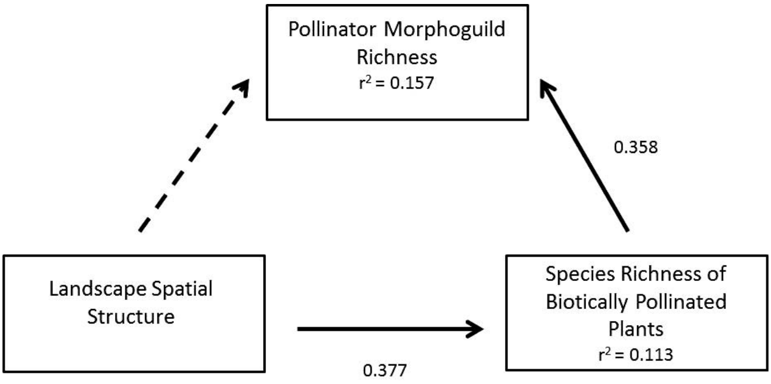

Figure 2. Structural equation model of landscape spatial structure (habitat area and connectivity), the species richness of biotically pollinated plants (excludes wind pollinated graminoid species), and pollinator morphoguild richness. Arrows are labeled with standardized path coefficients and represent directional links between variables. Solid arrows denote significant relationships ($p \leq 0.05$) and dashed arrows denote nonsignificant relationships ($p > 0.05$).

landscape-induced changes in plant species richness.

Pollinator diversity was not correlated with floral abundance. This result supports prior research indicating that floral diversity might be more important than floral abundance in supporting diverse pollinator communities (Steffan-Dewenter and Tscharntke 2001, Potts et al. 2003, Potts et al. 2006). Greater floral diversity might increase the number of available foraging niches via a greater diversity of floral characteristics, thereby facilitating visitation by a higher diversity of pollinators. Potts (2003) found evidence for this pattern, noting that the variety of nectar-foraging resources increases with plant diversity, and that nectar diversity was the best predictor of bee diversity. Junker et al. (2013) reported specialized foraging behavior in response to unique floral traits in every pollinator species observed, demonstrating pollinators' affiliations with particular floral niches. These findings are consistent with the idea that habitats with higher floral diversity support higher numbers of specialist pollinator species with unique foraging niches, as documented by Burkle and Knight (2012), who found greater plant and pollinator richness, as well as a higher proportion of specialist pollinators, in larger Ozark glades.

The SEM that excluded wind-pollinated plant species had the same overall structure as the original model (Figure 2), however, the r^2 values and standardized path coefficients were slightly lower in the former (Figure 2). This result is unexpected, because excluding nonnectar-providing plant species should help elucidate a functional relationship between pollinators and their resources. Our results suggest that greater plant richness might support higher diversity pollinator communities through an additional mechanism besides nectar-resource provisioning. For example, wind-pollinated species might contribute to pollinator habitat quality by providing non-foraging resources such as nesting sites or materials. Nesting sites and materials are known to be important determinants in pollinator community composition (Potts et al. 2005), although their importance relative to nectar resources has rarely been quantified. There is evidence to suggest that graminoid species in particular can be an important source of nesting resources. Graminoid species often have hollow or pithy stems, ideal nesting habitat for pollinators such as mason bees from the family Megachilidae, which prefer to nest in preexisting structures (Potts et al. 2005). Svensson et al. (2000) also found withered grasses and tussocks to be the favored nesting habitat in a study of eight species of bumblebees.

Plants appeared to be more sensitive than pollinators to landscape spatial structure. One explanation could be that the woodland matrix surrounding glades presents a more hostile environment to plant dispersal than to pollinator dispersal. Grassland plants generally cannot grow in the dense shade of woodlands, and wind-dispersed grassland seeds have been shown to travel poorly through forested areas (Damschen et al. 2014). According to Westrich's (1996) theory of partial habitats, pollinators use multiple habitat types due to diverse resource requirements (such as food, nesting sites, and nesting materials) that cannot be supplied by a single habitat alone. It might be, therefore, that pollinators' increased mobility relative to plants in the woodland matrix is not only due to their increased ability to traverse the landscape (Burkle and Alarcón 2011), but also to their ability to use resources found in this partial habitat. This idea is supported by research documenting pollinators along a wide gradient of canopy cover, with many species performing vital life history functions in the shelter provided by trees (Tscharntke et al. 1998, Grundel et al. 2010).

Although our results lend additional support to the importance of maintaining multiple partial habitats to meet pollinators' diverse resource requirements (Westrich 1996), the relative quantities of each partial habitat are also worth consideration. Our finding that the amount of woodland matrix present in the glade landscape does not directly affect pollinators suggests that the quantity of this partial habitat might have exceeded the threshold required by the pollinator community. Increased plant richness associated with well-connected landscapes appeared to have a positive influence on pollinator diversity; this suggests that resources available in glades might be more limiting to pollinator diversity than resources (such as nesting sites or materials) found in the woodland matrix. Our results, therefore, underscore the importance of maintaining large, well-connected glade habitats to provide pollinator communities with these limiting resources.

Our results indicate that diverse pollinator communities require diverse plant communities and that diverse plant communities require large well-connected habitat areas. However, urban and agricultural landscapes pervade much of North America at present, and the pollinator habitat remaining within these landscapes is highly fragmented. Our observation that pollinator morphoguild richness appears to be primarily limited by plant species richness, not landscape structure, indicates a potential for pollinator conservation within fragmented landscapes, provided that habitat patches are managed to maintain sufficient levels of plant diversity. Kearns and Oliveras (2009) provide one example of how the maintenance of natural habitat in and around an urban landscape can lead to stable pollinator communities over 100 yr, despite drastic land use-changes. However, the feasibility of this strategy at the scale of an agricultural landscape, where much pollinator habitat is currently being lost, remains uncertain. Therefore, our results primarily emphasize the importance of conserving and restoring the large contiguous habitat patches needed to support diverse plant communities, which in turn sustain diverse pollinator communities.

ACKNOWLEDGMENTS We would like to thank the two anonymous referees for their assistance improving the manuscript, as well as the numerous land managers and ecologists who provided advice and assistance with the project. We thank Hannah Gaines Day for providing advice on experimental design, and James Trager and Vera Pfeiffer for assistance with pollinator identification. We are additionally grateful to Justin Thomas for providing expert assistant with plant identification and other aspects of this project. This material is based upon work supported by National Science Foundation (NSF) DEB-0947432 and the NSF Graduate Research Fellowship under Grant No. 2012149884. Any opinion, findings, and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

LITERATURE CITED

Arbetman, M., I. Meeus, C. Morales, M. Aizen, and G. Smagghe. 2013. Alien parasite hitchhikes to Patagonia on invasive bumblebee. Biol. Invas. 15:489–494.

Bartomeus, I., M.G. Park, J. Gibbs, B.N. Danforth, A.N. Lakso, and R. Winfree. 2013. Biodiversity ensures plant-pollinator phenological synchrony against climate change. Ecol. Letters 16:1331–1338.

Blüthgen, N. and A.M. Klein. 2011. Functional complementarity and specialisation: the role of biodiversity in plant-pollinator interactions. Basic Appl. Ecol. 12:282–291.

Brown, M.J.F. and R.J. Paxton. 2009. The conservation of bees: a global perspective. Apidologie 40:410–416.

Buchmann, S.L. and G.P. Nabhan. 1996. The forgotten pollinators. Island Press/Shearwater Books, Washington, D.C.

Burkle, L.A. and R. Alarcón. 2011. The future of plant-pollinator diversity: understanding interaction networks across time, space, and global change. Amer. J. Bot. 98:528–538.

Burkle, L.A. and T.M. Knight. 2012. Shifts in pollinator composition and behavior cause slow interaction accumulation with area in plant-pollinator networks. Ecology 93:2329–2335.

Burkle, L.A., J.C. Marlin, and T.M. Knight. 2013. Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. Science 339:1611–1615.

Cameron, S.A., J.D. Lozier, J.P. Strange, J.B. Koch, N. Cordes, L.F. Solter, and T.L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. Proc. Natl. Acad. Sci. U.S.A. 108:662–667.

Cheplick, G.P. 1998. Seed dispersal and seedling establishment in grass populations. p. 84–105. *In:* Cheplick, G.P. (ed.). Population biology of grasses. Cambridge University Press, Cambridge, United Kingdom.

Damschen, E.I., D.V. Baker, G. Bohrer, R. Nathan, J.L. Orrock, J.R. Turner, L.A. Brudvig, N.M. Haddad, D.J. Levey, and J.J. Tewksbury. 2014. How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. Proc. Natl. Acad. Sci. U.S.A. 111: 3484–3489.

Dicks, L., S. Corbet, and R. Pywell. 2002. Compartmentalization in plant-insect flower visitor webs. J. Anim. Ecol. 71:32–43.

Ebeling, A., A.-M. Klein, J. Schumacher, W.W. Weisser, and T. Tscharntke. 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? Oikos 117: 1808–1815.

Fontaine, C., I. Dajoz, J. Meriguet, and M. Loreau. 2005. Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. PLoS Biol. 4:e1.

Gathmann, A. and T. Tscharntke. 2002. Foraging ranges of solitary bees. J. Anim. Ecol. 71:757–764.

Goulson, D., E. Nicholls, C. Botías, and E.L. Rotheray. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 347:1255957.

Grace, J.B. 2006. Structural equation modeling and natural systems. Cambridge University Press, Cambridge, United Kingdom.

Grundel, R., R.P. Jean, K.J. Frohnapple, G.A. Glowacki, P.E. Scott, and N.B. Pavlovic. 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. Ecol. Applic. 20:1678–1692.

Gustafson, E.J. and G.R. Parker. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. Landscape Ecol. 7:101–110.

Howe, H.F. and J. Smallwood. 1982. Ecology of seed dispersal. Annual Rev. Ecol. Syst. 201–228.

Junker, R.R., N. Blüthgen, T. Brehm, J. Binkenstein, J. Paulus, H. Martin Schaefer, and M. Stang. 2013. Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. Funct. Ecol. 27:329–341.

Kearns, C.A. and D.M. Oliveras. 2009. Boulder County bees revisited: a resampling of Boulder Colorado bees a century later. J. Insect Conserv. 13:603–613.

Knight, M.E., A.P. Martin, S. Bishop, J.L. Osborne, R.J. Hale, R.A. Sanderson, and D. Goulson. 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. Molec. Ecol. 14:1811–1820.

Kremen, C., N.M. Williams, M.A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, S.G. Potts, T. Roulston, I. Steffan-Dewenter, D.P. Vázquez, R. Winfree, L. Adams, E.E. Crone, S.S. Greenleaf, T.H. Keitt, A.M. Klein, J. Regetz, T.H. Ricketts. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecol. Letters 10:299–314.

Ladd, D. and P. Nelson. 1982. Ecological synopsis of Missouri glades. p. 1–20. *In:* McGinnes, E.A. (ed.). Proceedings of the cedar glade symposium. Occas. Papers Missouri Acad. Sci. Vol. 7.

Losey, J.E. and M. Vaughan. 2006. The economic value of ecological services provided by insects. Bioscience 56:311–323.

MacArthur, R.H. and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.

Memmott, J. 1999. The structure of a plant-pollinator food web. Ecol. Letters 2:276–280.

Memmott, J., P.G. Craze, N.M. Waser, and M.V. Price. 2007. Global warming and the disruption of plant-pollinator interactions. Ecol. Letters 10:710–717.

Memmott, J. and H.C.J. Godfray. 1993. Parasitoid webs. p. 217–234. *In:* Lasalle, J. and I.D. Gould (eds.). Hymenoptera and biodiversity. CAB International, Wallingford, UK.

Miller, J.E.D., E.I. Damschen, S.P. Harrison, and J.B. Grace. 2015. Landscape structure affects specialists but not generalists in naturally fragmented grasslands. Ecology 96:3323–3331.

Nathan, R. and H.C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends Ecol. Evol. 15:278–285.

Nelson, P. 2005. Terrestrial natural communities of Missouri. Missouri Department of Natural Resources, Jefferson City, Missouri.

Öckinger, E., O. Schweiger, T.O. Crist, D.M. Debinski, J. Krauss, M. Kuussaari, J.D. Petersen, J. Pöyry, J. Settele, K.S. Summerville, and R. Bommarco. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecol. Letters 13:969–979.

Osborne, J.L., S.J. Clark, R.J. Morris, I.H. Williams, J.R. Riley, A.D. Smith, D.R. Reynolds, and A.S. Edwards. 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. J. Appl. Ecol. 36:519–533.

Pasquet, R.S., A. Peltier, M.B. Hufford, E. Oudin, J. Saulnier, L. Paul, J.T. Knudsen, H.R. Herren, and P. Gepts. 2008. Long-distance pollen flow assessment through evaluation of pollinator foraging range suggests transgene escape distances. Proc. Natl. Acad. Sci. U.S.A. 105: 13456–13461.

Potts, S.G., J.C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W.E. Kunin. 2010. Global pollinator declines: trends, impacts and drivers. Trends Ecol. Evol. 25:345–353.

Potts, S.G., T. Petanidou, S. Roberts, C. O'Toole, A. Hulbert, and P. Willmer. 2006. Plant-pollinator biodiversity and pollination services in a complex Mediterranean landscape. Biol. Conserv. 129:519–529.

Potts, S.G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. Willmer. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? Ecology 84:2628–2642.

Potts, S.G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and P. Willmer. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecol. Entomol. 30:78–85.

Rathcke, B.J. and E.S. Jules. 1993. Habitat fragmentation and plant-pollinator interactions. Curr. Sci. 65:273–277.

Steffan-Dewenter, I., and T. Tscharntke. 2001. Succession of bee communities on fallows. Ecography 24:83–93.

Svensson, B., J. Lagerlöf, and B.G. Svensson. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. Agric. Ecosyst. Environ. 77:247–255.

Totland, Ø. 1994. Influence of climate, time of day and season, and flower density on insect flower visitation in alpine Norway. Arctic Alpine Res. 26:66–71.

Tscharntke, T., A. Gathmann, and I. Steffan-Dewenter. 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. J. Appl. Ecol. 35:708–719.

Ware, S. 2002. Rock outcrop plant communities (glades) in the Ozarks: a synthesis. S. W. Naturalist 47:585–597.

Westrich, P. 1996. Habitat requirements of central European bees and the problems of partial habitats. p.1–16. *In:* Matheson, A., S.L. Buchmann, C. O'Toole, P. Westrich, and I.H. Williams (eds.). The conservation of bees. Linnean Society symposium series. Volume 18. Academic Press, London, United Kingdom.

Whitehorn, P.R., S. O'Connor, F.L. Wackers, and D. Goulson. 2012. Neonicotinoid pesticide reduces bumble bee colony growth and queen production. Science 336:351–352.

Wilcove, D.S., C.H. McLellan, and A.P. Dobson. 1986. Habitat fragmentation in the temperate zone. Conserv. Biol. 6:237–256.