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EDITORIAL

# The landscape ecology of pollination

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It is now widely acknowledged that declines in pollinators and pollination are occurring worldwide, and such declines are likely to be problematic for crop production and maintenance of biodiversity. A leading hypothesis is that these declines are partly a function of processes occurring at larger, landscape scales. This hypothesis has stimulated the synthesis of often disparate fields in ecology: landscape, community, behavioral, and pollination ecology. There is therefore a tremendous opportunity for landscape ecologists to apply theory and tools from our discipline to inform these future conservation and restoration efforts. For instance, issues of scale, landscape composition and configuration, and functional connectivity all have at their core fundamental ideas and approaches from landscape ecology. The goal of this special section of *Landscape Ecology* is therefore to further motivate landscape ecologists to pursue both fundamental and applied aspects of landscape-pollination ecology. We have assembled seven leading-edge example manuscripts from a burgeoning field that merges landscape and pollination ecology. The articles in this special section reflect some consistent themes in landscape ecology – for instance the importance of scale, landscape heterogeneity, matrix effects, as well as the independent effects of habitat loss and fragmentation. It is remarkable how consideration of these themes has only recently begun to creep into the pollination ecology and conservation literature. We conclude by presenting future research directions which we think will be fruitful in the field of landscape pollination ecology.

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## About this special issue

Over 85% of wild flowering plants depend to some extent on pollination (Ollerton et al. 2011), and up to $577 billion worth of annual global food production relies on direct contributions by pollinators (IPBES 2016). However, it is now widely acknowledged that declines in pollinators and pollination are occurring worldwide (Dirzo et al. 2014), with potentially disastrous consequences for food production (Winfree et al. 2018) and native biodiversity (IPBES 2016). The health of pollinator populations is particularly important because so many other elements of biodiversity depend on plants for their survival.

A leading hypothesis, with substantial empirical support, is that pollinator and pollination declines are at least partly a function of processes occurring at larger, landscape scales (Potts et al. 2010). This hypothesis has stimulated the synthesis of often disparate fields in ecology: landscape (Turner 1989), community (Ricklefs 1987), behavioral (Lima and Zollner 1996) and pollination ecology (Müller 1883). Indeed, over the past two decades, research testing the effects of landscape attributes on pollination dynamics has increased dramatically (Hadley and Betts 2012).

Despite examples of habitat-mediated pollinator declines (Winfree et al. 2011) there is some cause for optimism. Driven by a recent global report on the state of pollinators by the Intergovernmental Panel on Biodiversity and Ecosystem Services (IPBES 2016), 16 national governments have now signed on to a 'Coalition of the Willing' to reduce impacts to pollinators and pollination services (Coalition of the Willing 2019). Top priority will be given to encouraging land conservation, and land-use planning that contributes to pollinator habitat, pollinator movement, and therefore contributions to crop yield. For instance, a 2015 Presidential Memorandum called for the restoration of $>7$ million acres of pollinator habitat in the United States. This underscores the tremendous opportunity for landscape ecologists to apply theory and tools from our discipline to inform these future conservation and restoration efforts. Where should pollinator habitat be prioritized? What landcover types, and at which spatial scale(s) should such habitats be conserved? To what degree does landscape configuration influence the viability of pollinator populations and the success of pollination services? What factors influence pollinator movement? These are all questions that have at their core fundamental approaches from landscape ecology, but at the time of writing, only 26 papers had been published in the journal *Landscape Ecology* with the term "pollination" in the title, abstract or keywords (according to a Web of Science Search, April 30, 2019). The goal of this special section of *Landscape Ecology* is therefore to further motivate landscape ecologists to pursue both fundamental and applied aspects of landscape-pollination ecology.

In this special section, we have assembled leading-edge examples of a burgeoning field that merges landscape and pollination ecology. First, Harrison et al. (2019), address a critical problem in community ecology and conservation—that rare species, by the very nature of being rare, are difficult to analyze statistically. This is all the more vexing because it is often rare species that are more specialized, and sensitive to environmental change (Julliard et al. 2004; Casey et al. 2015; but see Williams et al. 2005). Harrison et al. (2019) sampled cover types within 3-km diameter landscapes that were dominated by agriculture, forests, or urban area. Importantly, the richness and abundance of rare bees was substantially greater in less human-modified landscapes; these landscape context effects occurred even though local-scale habitats were held constant via research design. To our knowledge, this is the first evidence from North America that landscape context influences rare pollinator species as a group.

Three articles in this special section (Jones et al. 2019; Pfeiffer et al. 2019; Miljanic et al. 2018) moved beyond tests of landscape composition, to also examine the effects of landscape configuration on pollinators. This is of critical importance, because if such configuration effects are revealed, it suggests a path toward planning agricultural and natural landscapes to minimize the effect of pollinator habitat loss via changes to landscape pattern (Hadley and Betts 2012). Pfeiffer et al. (2019) tested for the independent effects of landscape configuration on bumble bee colony density and representation. Bumble bees are critical pollinators in the cranberry farming system examined. In this case, both habitat loss and fragmentation appeared to be important to bees; colony density, as measured in genetic mark-recapture analyses, increased as a function of forest in the surrounding landscape—presumably due to the heightened presence of nesting habitat. High proportions of cultivated land had negative effects on bee density—with implications for large-scale, single-tract farming. Further, high meadow interspersion (a landscape configuration variable) positively influenced colony density. This finding is congruent with other recent research indicating that landscape configuration could be particularly important for pollinators (Sabatino et al. 2010; Hadley et al. 2014; Kormann et al. 2016; Hass et al. 2018).

Jones et al. (2019) tested the basic principles of island biogeography (MacArthur and Wilson 1967) but with insect pollinators in a mountain meadow system (meadows were the 'islands'). They document remarkable interannual turnover in pollinator communities (with 688 species observed over the 7-year study), but little of the variation in species richness could be explained by landscape context. Richness increased non-linearly with meadow size, independent of the amount of meadow in the surrounding landscape, but small meadows had unique pollinator communities. This has implications for the restoration of alpine meadows, which are being encroached upon by native forests—due partly to alterations to regional disturbance regimes.

Miljanic et al. (2018) investigated how local management (whether a study site was in a natural forest remnant, pine plantation, clearcut or cornfield) interacted with landscape composition and configuration to shape bee communities. Such cross-scale interactions, if present, are particularly interesting from a conservation point of view, as effectiveness of local biodiversity conservation management would therefore change with landscape structure (Tscharntke et al. 2012). Interestingly, Miljanic et al.'s results suggest that the importance of compositional heterogeneity and configurational complexity to bee communities amplify in importance as local habitat quality declines (due to anthropogenic habitat modification).

Similarly, Proesmans et al. (2019) found that experimental bumblebee colonies fared better in more diverse landscapes. Proesmans et al. used bumblebee colonies to examine the relative impacts of mass flowering crops and semi-natural habitat on experimental colony performance and pollen collection. Contrary to their expectations they discovered the presence of these mass orchards does not necessarily increase colony performance and pollen collection. Higher proportions of orchard actually reduced colony performance and the amount of pollen collected during periods of mass flowering. Instead, colony performance increased with the amount of semi-natural habitat surrounding the colony, indicating that while orchards can serve as foraging habitat for bumblebees during mass-flowering, colonies fare better in more diverse landscapes. However, their study found that during mass flowering periods bumble bees foraged at a different spatial scale than when these resources were absent. Colony performance was linked to land cover uses at much larger scales following completion of mass flowering, suggesting bees were foraging in different habitat types and over longer distances when orchards were no longer in bloom.

Matrix—the intervening area between habitat patches—is well known to influence biodiversity. However, to date, studies testing for matrix effects on pollinators is rare. Kormann et al. (2018) sampled butterflies on small, species-rich grassland fragments and ask whether matrix effects (in this case cropland) can mediate effects of landscape-scale habitat loss. They found evidence for such an interaction; butterfly communities shifted towards species of higher conservation concern (IUCN Red List status) in connected fragments, but this positive effect only occurred in landscapes with little cropland. This has important implications for butterfly conservation and restoration of degraded agricultural landscapes.

Monitoring pollinator communities across entire landscapes is challenging, as sampling effort is often substantially limited by logistical constraints such as funding. Further, to date, little is known about whether the effects of land-cover changes on pollinator communities are context-dependent. Scherber et al. (2019) tested a grid-based method to sample pollinators across entire agricultural landscapes that varied in the proportion of oil-seed rape, a common mass-flowering crop. Using 250 trap locations, distributed across 10 landscapes and sampled over 2 years, they report that restricting sampling to one or a few habitat types only can strongly bias estimates of landscape-wide species richness. While mass-flowering crops have been shown previously to affect pollinator biodiversity (Holzschuh et al. 2016), Scherber et al. (2019) show that the effect of oil-seed rape on pollinator communities varies strongly among land-use types; while high proportions of oil-seed rape decreased bee species richness in semi-natural habitats, there was no effect when sampling in oil-seed rape fields only. The effect of oil-seed rape on pollinators was also highly scale dependent.

## Synthesis and future research in landscape pollination ecology

Together, the articles in this special issue reflect some consistent themes in landscape ecology—for instance the importance of scale, landscape heterogeneity, matrix effects, as well as the independent effects of landscape context and configuration. However, it is remarkable how consideration of these themes has only recently begun to creep into the pollination ecology and conservation literature. The slow update of landscape ecological approaches and theory in pollination ecology may be at least partly due to the challenges of measuring and then modeling interactions between multiple trophic levels at broad scales.

Of course much more needs to be accomplished to test for the generality of these papers' findings in other regions and systems. We propose several topics in landscape pollination ecology that may be particularly fruitful both in terms of understanding the basic ecology of pollination and pollinators, but also for conservation of pollinators and the services they provide.

First, it will be important to uncover the potential mechanisms behind observed effects of landscape configuration on pollinators and pollination. In the past, most pollinators—due to their small sizes—have been challenging to track. However, new technology in the form of micro-radio-telemetry (Hadley and Betts 2009; Hagen et al. 2011; Woodgate et al. 2016) and genetic mark-recapture (López-Uribe et al. 2019) may shed light on daily movement and dispersal behavior of pollinators, as well as their functional connectivity; this will contribute to understanding why particular landscape configurations may help, or hinder pollinator populations. It will be particularly important to initiate studies focused on the spatial scale of effects (Jackson and Fahrig 2015)—both of landscape structure on pollinator populations, but also the influence of pollinator communities on pollination success. For instance, recent work has shown that naturally disturbed early seral forest systems can be particularly important for pollinator populations (Galbraith et al. 2019); but do the benefits of such disturbances to pollinators influence crop production at broader scales than might be expected from quantifying dispersal and movement of individuals? In other words, at what scales might source-sink dynamics occur in pollinator populations?

A second track for research, that might be particularly important for pollinators, will be to test how other stressors could interact with landscape structure to affect populations and movement. Recent work has shown that Neonicotinoid pesticides alter bee behavior (Crall et al. 2018) in ways that are likely detrimental to their fitness. Might such pesticides make colonies more vulnerable to anthropogenic changes to landscape configuration? Climate is another potential interacting factor of crucial importance. Given that many pollinators are ectotherms, how can we expect populations to respond to rising temperatures, and how might such climatic changes be mediated by either extensive or intensive human land-use? Although studies examining the synergistic effects of climate and land-use are becoming increasingly common (Northrup et al. 2019; Powers and Jetz 2019). To our knowledge, none have examined the potential for synergistic effects on pollination.

Third, it will be of great importance to tie the effects of landscape change on pollinators to putative changes in crop production at a variety of scales. We encourage researchers, where possible, to examine not only population-level impacts of land-use change on pollinators, but also to test for whether such changes are meaningful from an ecosystem services perspective.

Fourth, pollinators and pollination is often best conceptualized as a network of interactions rather than simple one-to-one relationships (Bascompte et al. 2006). However, to date very few studies have considered how the structure of such networks is influenced by landscape structure. Given that some pollinators may exhibit limited movement in the matrix (Volpe et al. 2014), one hypothesis worthy of testing is that high landscape connectivity might facilitate greater network connectance—which could in turn facilitate resistance to anthropogenic change (Kaiser-Bunbery et al. 2017).

Finally, as studies on pollinators and pollination in relation to landscape structure emerge and become more common, it will be critical to test for generalities across systems in such responses. Impressive scientific gains have repeatedly been made by those who amass multiple datasets with common protocols across geographic regions (Borer et al. 2014; Pfeifer et al. 2017). Nearly a decade ago, we made the prediction that pollination networks by nature of their structure, may be more vulnerable to fragmentation per se than individual populations of organisms (Hadley and Betts 2012). But the opposite result—resilience—is also plausible (Bascompte et al. 2006). An impressive literature is emerging that tests for independent effects of habitat loss and fragmentation on pollinators and pollination. As this literature accumulates, it will be fascinating, and of crucial importance to managers and policy makers, to test such hypotheses.

## References


Bascompte J, Jordano P, Oleson JM (2006) Asymetric coevolutionary networks facilitate biodiversity maintenance. Science 5772:431–433

Borer ET, Seabloom EW, Gruner DS, Harpole WS, Hillebrand H, Lind EM, Adler PB, Alberti J, Anderson TM, Bakker JD, Biederman L, Blumenthal D, Brown CS, Brudvig LA, Buckley YM, Cadotte M, Chu C, Cleland EE, Crawley MJ, Daleo P, Damschen EI, Davies KF, DeCrappeo NM, Du G, Firn J, Hautier Y, Heckman RW, Hector A, HilleRisLambers J, Iribarne O, Klein JA, Knops JMH, La Pierre KJ, Leakey ADB, Li W, MacDougall AS, McCulley RL, Melbourne BA, Mitchell CE, Moore JL, Mortensen B, O'Halloran LR, Orrock JL, Pascual J, Prober SM, Pyke DA, Risch AC, Schuetz M, Smith MD, Stevens CJ, Sullivan LL, Williams RJ, Wragg PD, Wright JP, Yang LH (2014) Herbivores and nutrients control grassland plant diversity via light limitation. Nature 508:517

Casey LM, Rebelo H, Rotheray E, Goulson D (2015) Evidence for habitat and climatic specializations driving the long-term distribution trends of UK and Irish bumblebees. Divers Distrib 21:864–875

Coalition of the Willing (2019) Promote Pollinators, The Coalition of the Willing on Pollinators. https://promotepollinators.org/coalition-of-the-willing/

Crall JD, Switzer CM, Oppenheimer RL, Ford Versypt AN, Dey B, Brown A, Eyster M, Guérin C, Pierce NE, Combes SA, de Bivort BL (2018) Neonicotinoid exposure disrupts bumblebee nest behavior, social networks, and thermoregulation. Science 362:683–686

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B (2014) Defaunation in the Anthropocene. Science 345:401–406

Galbraith SM, Cane JH, Moldenke AR, Rivers JW (2019) Wild bee diversity increases with local fire severity in a fire-prone landscape. Ecosphere 10:e02668

Hadley AS, Betts MG (2009) Tropical deforestation alters hummingbird movement patterns. Biol Lett 5:207–210

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

Hadley AS, Frey SJK, Robinson WD, Kress WJ, Betts MG (2014) Tropical forest fragmentation limits pollination of a keystone understory herb. Ecology 95:2202–2212

Hagen M, Wikelski M, Kissling WD (2011) Space use of bumblebees (*Bombus* spp.) revealed by radio-tracking. PLoS ONE 6:e19997

Harrison T, Gibbs J, Winfree R (2019) Anthropogenic landscapes support fewer rare bee species. Landscape Ecol. https://doi.org/10.1007/s10980-017-0592-x

Hass AL, Kormann UG, Tscharntke T, Clough Y, Baillod AB, Sirami C, Fahrig L, Martin J-L, Baudry J, Bertrand C, Bosch J, Brotons L, Burel F, Georges R, Giralt D, Marcos-García MÁ, Ricarte A, Siriwardena G, Batáry P (2018) Landscape configurational heterogeneity by small-scale agriculture, not crop diversity, maintains pollinators and plant reproduction in western Europe. Proc Roy Soc B 285:20172242

Holzschuh A, Dainese M, González-Varo JP et al (2016) Mass-flowering crops dilute pollinator abundance in agricultural landscapes across Europe. Ecol Lett 19:1228–1236

IPBES (2016) Summary for policymakers of the assessment report of the intergovernmental science-policy platform on biodiversity and ecosystem services on pollinators, pollination and food production. In: Potts SG, Imperatriz-Fonseca VL, Ngo HT, Biesmeijer JC, Breeze TD, Dicks LV, Garibaldi LA, Hill R, Settele J, Vanbergen AJ, Aizen MA, Cunningham SA, Eardley C, Freitas BM, Gallai N, Kevan PG, Kovács-Hostyánszki A, Kwapong PK, Li J, Li X, Martins DJ, Nates-Parra G, Pettis JS, Rader R, Viana BF (eds) Secretariat of the intergovernmental science-policy platform on biodiversity and ecosystem services. IPBES, Bonn

Jackson HB, Fahrig L (2015) Are ecologists conducting research at the optimal scale? Glob Ecol Biogeogr 24:52–63

Jones JA, Hutchinson R, Moldenke A, Pfeiffer V, Helderop E, Thomas E, Griffin J, Reinholtz A (2019) Landscape patterns and diversity of meadow plants and flower-visitors in a mountain landscape. Landscape Ecol. https://doi.org/10.1007/s10980-018-0740-y

Julliard R, Jiguet F, Couvet D (2004) Common birds facing global changes: what makes a species at risk? Glob Change Biol 10:148–154

Kaiser-Bunbury CN, Mougal J, Whittington AE, Valentin T, Gabriel R, Olesen JM, Blüthgen N (2017) Ecosystem restoration strengthens pollination network resilience and function. Nature 542:223–227

Kormann U, Scherber C, Tscharntke T, Klein N, Larbig M, Valente JJ, Hadley AS, Betts MG (2016) Corridors restore animal-mediated pollination in fragmented tropical forest landscapes. Proc Roy Soc London B 283:e20152347

Kormann U, Scherber C, Tschntke T, Batary P, Rösch V (2019) Connectedness of habitat fragments boosts conservation benefits for butterflies, but only in landscapes with little cropland. Landscape Ecol. https://doi.org/10.1007/s10980-019-00835-6

Lima SL, Zollner PA (1996) Towards a behavioral ecology of ecological landscapes. Trends Ecol Evol 11:131–135

López-Uribe MM, Jha S, Soro A (2019) A trait-based approach to predict population genetic structure in bees. Mol Ecol 28:1919–1929

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton

Miljanic AS, Loy X, Gruenewald DL, Dobbs EK, Gottlieb IGW, Fletcher RJ, Brosi BJ (2018) Bee communities in forestry production landscapes: interactive effects of local-level management and landscape context. Landscape Ecol. https://doi.org/10.1007/s10980-018-0651-y

Müller H (1883) The fertilisation of flowers. Macmillan and Co., London

Northrup JM, Rivers JW, Yang Z, Betts MG (2019) Synergistic effects of climate and land-use change influence broad-scale avian population declines. Glob Change Biol 25:1561–1575

Ollerton J, Winfree R, Tarrant S (2011) How many flowering plants are pollinated by animals? Oikos 120:321–326

Pfeifer M, Lefebvre V, Peres CA, Banks-Leite C, Wearn OR, Marsh CJ, Butchart SHM, Arroyo-Rodriguez V, Barlow J, Cerezo A, Cisneros L, D'Cruze N, Faria D, Hadley A, Harris SM, Klingbeil BT, Kormann U, Lens L, Medina-Rangel GF, Morante-Filho JC, Olivier P, Peters SL, Pidgeon A, Ribeiro DB, Scherber C, Schneider-Maunoury L, Struebig M, Urbina-Cardona N, Watling JI, Willig MR, Wood EM, Ewers RM (2017) Creation of forest edges has a global impact on forest vertebrates. Nature 551:187

Pfeiffer V, Silbernagel J, Guédot C, Zalapa J (2019) Woodland and floral richness boost bumble bee density in cranberry resource pulse landscapes. Landscape Ecol. https://doi.org/10.1007/s10980-019-00810-1

Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, Kunin WE (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345–353

Powers RP, Jetz W (2019) Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. Nat Clim Change 9:323–329

Proesmans W, Smagghe G, Meeus I, Bonte D, Verheyen K (2019) The effect of mass-flowering orchards and semi-natural habitat on bumblebee colony performance. Landscape Ecol. https://doi.org/10.1007/s10980-019-00836-5

Ricklefs RE (1987) Community diversity: relative roles of local and regional processes. Science 235:167–171

Sabatino M, Maceira N, Aizen MA (2010) Direct effects of habitat area on interaction diversity in pollination webs. Ecol Appl 20:1491–1497

Scherber C, Beduschi T, Tscharntke T (2019) Novel approaches to sampling pollinators in whole landscapes: a lesson for landscape-wide biodiversity monitoring. Landscape Ecol. https://doi.org/10.1007/s10980-018-0757-2

Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batary P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Frund J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, Lindenmayer D, Scherber C, Sodhi N, Steffan-Dewenter I, Thies C, van der Putten WH, Westphal C (2012) Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol Rev 87:661–685

Turner MG (1989) Landscape ecology: the effect of pattern on process. Annu Rev Ecol Syst 20:171–197

Volpe NL, Hadley AS, Robinson WD, Betts MG (2014) Functional connectivity experiments reflect routine movement behavior of a tropical hummingbird species. Ecol Appl 24:2122–2131

Williams P (2005) Does specialization explain rarity and decline among British bumblebees? A response to Goulson. Biol Cons 122:33–43

Winfree R, Bartomeus I, Cariveau DP (2011) Native pollinators in anthropogenic habitats. Annu Rev Ecol Evol Syst 42:1–22

Winfree R, Reilly JR, Bartomeus I, Cariveau DP, Williams NM, Gibbs J (2018) Species turnover promotes the importance of bee diversity for crop pollination at regional scales. Science 359:791–793

Woodgate JL, Makinson JC, Lim KS, Reynolds AM, Chittka L (2016) Life-long radar tracking of bumblebees. PLoS ONE 11:e0160333