Vanbergen, Adam J. 2014. **Landscape alteration and habitat modification: impacts on plant-pollinator systems**.

***Current Opinion in Insect Science (2014) 43 1–6 doi:10.1016/j.cois.2014.09.004***

# Landscape alteration and habitat modification: impacts on plant-pollinator systems

Adam J. Vanbergen[1†]

[1]NERC Centre for Ecology & Hydrology, Bush Estate, Edinburgh EH26 0QB, UK

† Corresponding author: ajv@ceh.ac.uk

**Highlights**

1. Insect pollinators face multiple threats including landscape and habitat alteration.
2. Pollinator traits and network structure govern responses to environmental change
3. Changes in pollinator-mediated connectivity may alter plant mating systems
4. Disrupted mating systems may affect plant persistence and trophic interactions

**Summary**

Insect pollinators provide an important ecosystem service to many crop species and underpin the reproductive assurance of many wild plant species. Multiple, anthropogenic pressures threaten insect pollinators. Land-use change and intensification alters the habitats and landscapes that provide food and nesting resources for pollinators. These impacts vary according to species traits, producing winners and losers, while the intrinsic robustness of plant-pollinator networks may provide stability in pollination function. However, this functional stability might be eroded by multiple, interacting stressors. Anthropogenic changes in pollinator-mediated connectivity will alter plant mating systems (e.g. inbreeding level), with implications for plant fitness and phenotypes governing trophic interactions. The degree to which plant populations can persist despite, or adapt to, pollination deficits remains unclear.

## Introduction

To advance understanding of global change impacts on the natural world requires an increased focus on the changes that occur to the web of biotic interactions that underpin the functions of populations, communities and ecosystems [1, 2]. Many flowering plant species have a facultative or obligate dependence on insect pollination for reproductive success and ultimately population persistence [3]. Furthermore, insect pollination provides an ecosystem service by increasing or stabilizing yields and quality of many fruit, vegetable, oil, seed and nut crops [4, 5], which contribute essential variety and nutrients to human diets [6]. Insect pollinators and the pollination services they deliver face multiple, potentially interacting threats from climate change, pests and pathogens, alien invasive species, and land-use change and intensification [7-9]. Moreover, there is accumulating evidence that pollinator declines, range contractions and community homogenisation have indeed occurred [10-15]. Land-use change and intensification alter the landscape extent and quality of semi-natural habitats that provide the key forage and nesting resources supporting insect pollinators and the pollination service they provide [16-20]. This opinion paper outlines the impact of anthropogenic landscape alteration and habitat modification on pollinators and plant mating systems and the implications for plant population persistence and community dynamics.

## Landscape alteration

Pollinators rely on semi-natural habitat for a diversity of food sources and breeding sites [21, 22]. Land-use change and agricultural intensification has reduced the amount of such semi-natural habitat and simplified landscape structure [23], and is one of many factors [7] linked to historic and continuing losses of wild pollinator biodiversity [10-14, 24]. Forest fragmentation can lead to declines in flower visitation by native pollinator species [25, 26] and the evenness of European wild bee and butterfly communities was decreased by loss of habitat area [27]. A recent analysis revealed that fragmentation of forested landscapes over the long-term resulted in degraded plant-pollinator networks and substantial levels of pollinator extinction [24]. Extensive habitat loss and fragmentation can isolate populations and reduce their persistence by erecting barriers to gene flow, reducing gene diversity and leading to low effective population sizes [28, 29]. Agri-environment interventions targeted at (re)creating pollinator habitats tend to have the greatest positive impact on bee diversity and flower visitation in fields situated in spatially homogenous landscapes dominated by agricultural monocultures and lacking good quality semi-natural habitat [30, 31]. The proportion of semi-natural habitat in the landscape is therefore a strong predictor of pollinator diversity and abundance [20, 25], stable population dynamics [32] and delivery of pollination services to plants [17, 24].

Differences in eco-evolutionary traits (e.g. mobility, feeding adaptations etc) govern the response of pollinator species to habitat loss or landscape simplification. Overall, wild bee and hoverfly species that are more specialised, nest above ground or have limited dispersal abilities are most vulnerable to habitat loss and degradation [10, 24, 33-35]. For example, Western European bumblebee species in decline tend to be those with late season phenology and possessing specialised long-tongued mouthparts adapted to forage on plants typical of unimproved flower-rich grasslands (e.g. Fabaceae) or legume crops, both habitats that declined in extent in this region during the late twentieth century [36, 37]. Nesting habit is a strong predictor of bee species sensitivity to the loss of semi-natural habitats because of the concomitant loss of particular nesting resources (e.g. stems of perennial grasses, herbs and shrubs or dead wood cavities) [33]. Sociality is another trait affecting vulnerability to landscape alteration. Social bees are central location foragers tied to the colony location, consequently they are more sensitive to the distance to forage resource patches in the surrounding landscape [20, 38] than non-social insects with free-living progeny, such as Diptera [38, 39]. Even within social bee taxa, species-specific differences in mobility and dispersal range will govern responses to habitat loss and/or fragmentation. For instance, relatively common bumblebee species (e.g. *B. pascuorum, B. lapidarius*) in Britain may be somewhat buffered against landscape alteration due to their ability to forage and disperse over greater distances [40] than declining congeners [28, 29]. Such dispersal by highly mobile, generalist species between habitat fragments may ameliorate the effects of landscape fragmentation on pollinator community evenness [27]. Landscape alterations therefore are expected to filter species according to eco-evolutionary traits with knock-on effects for ecological function. Creating and maintaining locally diverse, fine-grained and well-connected habitat structure across the landscape will aid the stability of wild pollinator populations and diversity.

**Habitat modification**

Aside from landscape alteration, anthropogenic perturbation (e.g. pollution, land-use change) and modification (e.g. land management) of habitat structure can alter pollinator communities and pollination processes. Conversion of semi-natural habitat to an agricultural or silvicultural land-use is a prime driver of change to plant-pollinator biodiversity and interactions. Incorporation of semi-natural habitat into livestock farming systems is one example common worldwide. Livestock grazing through consumption of plant biomass, trampling and excreta can modify plant phenological development, reproductive strategies and community structure [39, 41, 42]. Such plant community changes can subsequently affect pollinator abundance or diversity [42] and plant-pollinator interactions [39, 43, 44]. Cattle introduced to Patagonian forests altered the structure of plant-pollinator networks by reducing the frequency of dominant interactions, mainly composed of abundant generalist plant or pollinator species that interacted with many rarer species in the network [43]. Whereas, moderate cattle grazing of birch (*Betula spp*.) habitat in Scotland increased the connectance, via elevated floral species richness, but decreased the nestedness of pollinator visitation networks [39]. Intensive cattle grazing of steppe vegetation, in contrast, eroded plant diversity concentrating pollinator flower visitation onto the remaining few grazing-tolerant ruderal plants [44]. In sum, habitat engineering by grazing livestock has the potential to alter pollinator community structure [39, 43, 44], but the precise outcome likely depends on the habitat type, the land management intensity and the pool of taxa and traits in the community [33, 34].

**Multiple, interacting drivers**

Insect pollinators face multiple, potentially interacting threats [7-9], yet our understanding of how other global changes combine with landscape and habitat alteration to impact on pollinators is relatively poor**.** Decreased genetic diversity of bumblebee populations isolated by habitat fragmentation may increase their vulnerability to parasites that are implicated as a driver of bee declines in America [15, 45]. Pollinator species living at the edge of their climatic limits have more variable population sizes [46] and thus may be more vulnerable to the individual and combined effects of habitat loss/fragmentation and climate change [12, 14]. Climate changes are shifting the thermal limits of pollinator (e.g. butterflies) species distributions, but colonisation rates may be restricted by limited availability of semi-natural habitat in intensively farmed landscapes [12]. Moreover, climate change may disrupt phenological synchrony between plants and pollinators leading to gaps or curtailment in floral resource availability [47, 48] which, exacerbated by deteriorating floral resources in intensively managed landscapes [36, 37], may lead to nutritional deficits for pollinators. Thus there is the potential risk that pollinator populations and species may be extirpated by the additive or synergistic effects of multiple anthropogenic threats.

**Stability and collapse of pollinator communities**

Filtering and loss of species due to anthropogenic modification of landscapes and habitats may change community structure to the point where pollination function is lost [16, 24]. Simulation modelling of plant-pollinator networks has revealed that if species losses continue to the point that the most generalised species - i.e. those most connected to other species via direct or indirect species interactions in the network - are eliminated, then a sudden cascade of secondary extinctions could arise [49, 50]. However, the most highly linked and common pollinators may be the least sensitive to extinction [35, 51] and networks of plant-pollinator interactions appear relatively robust to species loss because of the stability derived from network topology (e.g. nestedness), the presence of very abundant and connected species, species redundancy and behavioural flexibility [50-53]. For example, adaptive foraging by generalist species may confer network stability, while ‘rewiring’ of the network by remaining species adopting extirpated species niches may compensate for species loss [52, 53]. However, greater specialisation of plant-pollinator interactions or networks increases vulnerability to perturbation and extinction [10, 24, 33, 35]; this might have implications in temperate regions where plant-pollinator networks tend to be more specialised [54]. Finally, recent theoretical and empirical modelling work suggests that if environmental stresses reach a certain level, then individual bee colonies/populations and even inherently robust pollinator community networks could collapse [50, 55]. As pollinators face multiple anthropogenic threats [7, 8], a potential risk is that this multiplicity of stresses may increase the probability of such sudden population or community collapse, although there have been few experimental tests of this to date [38, 56].

**Consequences for plant diversity, fitness and multitrophic interactions**

Insect pollination is a vital ecosystem process supporting plant diversity, with an estimated 87% of flowering plant species globally [3] reliant on animal (mostly insect) pollination for mating and reproductive success [57]. Some studies in northern Europe have linked pollinator and plant decline, with facultative or obligate dependence on insect pollination partly explaining observed declines in wild plant species richness or occurrence [10, 36, 58]. It should be noted, however, that another analysis revealed plant species declines occurred irrespective of the level of plant dependence on pollinators [11], suggesting another common driver (e.g. nitrogen pollution).

Outcrossing plant species often carry high loads of potentially deleterious recessive alleles [57]. Hence modification of plant mating systems by environmental changes (Fig.1) has the potential to elevate the risk of inbreeding depression, affecting plant fitness negatively and potentially driving population evolutionary change [57, 59, 60]. Anthropogenic modification of landscape or habitat structure will drive changes in the densities or dispersion of conspecific plants that change pollinator-mediated connectivity within a plant population (Fig.1) [61]. This can lead to altered pollen flow impacting on the ability of plant individuals to achieve outcrossed mating and avoid biparental inbreeding (i.e. mating among close relatives) and can increase self-fertilisation rates [57].

Large areas of contiguous forest are required for minimum viable population sizes of insect-pollinated tree species [62] and trees isolated by fragmentation can experience altered patterns of visitation by native pollinator species [25, 63]. This can potentially lead to disrupted mating systems, altered phenotypes and reduced plant fitness (Fig.1) [59, 60], although the level of this impact is likely to be dictated by the extent of the habitat fragmentation and the pool of pollinator species and traits in the locale [63]. For example, reduced visitation by native pollinators to forest trees isolated by fragmentation was partly compensated by increased visitation of highly mobile introduced honey bees, leading to some reproductive assurance [64, 65]. Plant reproductive success has also been assured by linear features (e.g. hedgerows) facilitating bee-mediated connectivity of plants in fragmented landscapes [66].

Similarly, habitat modification by land management (e.g. grazing livestock) may directly (e.g. trampling, consumption) or indirectly (e.g. altered pollinator foraging in disturbed community) affect pollen deposition and seed set by changing the densities and dispersion of conspecific plants [67]. It has also recently been shown that grazing management of woodland was associated with increases in the outcrossing rate and the number of different pollen donors in a focal understory plant species, partly reflecting the increased connectivity of insect visitation networks, driven by the greater floral resources in the grazed habitat [39].

Increased self-fertilisation of facultatively outcrossing plants can lead to loss of heterozygosity and increased selection of deleterious alleles, which can reduce plant fitness [57, 59]. Consequently, environmental perturbation that lowers insect-mediated pollen flow can affect the plant phenotype, such as floral traits or volatile emissions, and hence its interspecific interactions across the wider food web [60, 68, 69] (Fig.1). Recent work using experimentally inbred plant lines has shown that inbreeding depressed gene expression in pathways (e.g. jasmonic acid, ethylene) that regulate the induction of defensive compounds and organic volatiles [70]. This altered trophic interactions with inbred plants emitting more constitutive volatiles, which attracted greater numbers of herbivores, but fewer herbivore-induced volatiles leading to reduced natural enemy recruitment [68]. Whether the anthropogenic impacts on pollinator communities, plant mating systems and floral phenotypes [39, 59, 60, 62] lead to similar alteration of multi-trophic interactions has yet to be tested (Fig.1).

## Conclusions

Pollination is a key ecosystem process that directly and indirectly supports wider biodiversity and ecological function. Recent research initiatives around the world (e.g.www.insectpollinatorsinitiative.net) are advancing our knowledge about the anthropogenic pressures affecting pollinators and pollination [7]. Nonetheless, further research is needed to understand better the threat to this ecosystem service. For example, we need to improve basic understanding of pollinator [meta]population and [meta]community dynamics in anthropogenic landscapes (Fig.1). We should also assess multifactorial impacts (e.g. landscape modification, alien species, disease) on pollinator networks and plant reproduction (Fig.1) and compare species persistence along gradients of habitat degradation. As plants underpin food-webs in most ecosystems, a particular challenge is to investigate the consequences of human-induced changes to pollination for the multitrophic interactions connecting plants and consumers (Fig.1), both above and below ground. Such an integrated approach will further our capacity to predict the resilience of ecosystems to global environmental changes.

Acknowledgments. This paper was partly supported by the UK Insect Pollinators Initiative funded, under the auspices of the Living With Environmental Change partnership, by the Biotechnology and Biological Sciences Research Council, the Natural Environment Research Council, the Department for Environment, Food and Rural Affairs, the Scottish Government, and the Wellcome Trust.

## References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

● of special interest, ●● of outstanding interest.


1. Fortuna, M.A. and J. Bascompte, **Habitat loss and the structure of plant-animal mutualistic networks**. Ecology Letters, 2006. **9**: 278-283.
2. Fontaine, C., P.R. Guimaraes, Jr., S. Kefi, N. Loeuille, J. Memmott, W.H. van der Putten, F.J.F. van Veen, and E. Thebault, **The ecological and evolutionary implications of merging different types of networks**. Ecology Letters, 2011. **14**: 1170-1181.
3. Ollerton, J., R. Winfree, and S. Tarrant, **How many flowering plants are pollinated by animals?** Oikos, 2011. **120**: 321-326.
4. Klein, A.M., B.E. Vaissiere, J.H. Cane, I. Steffan-Dewenter, S.A. Cunningham, C. Kremen, and T. Tscharntke, **Importance of pollinators in changing landscapes for world crops**. Proceedings of the Royal Society B-Biological Sciences, 2007. **274**: 303-313.
5. Garibaldi, L.A., M.A. Aizen, A.M. Klein, S.A. Cunningham, and L.D. Harder, **Global growth and stability of agricultural yield decrease with pollinator dependence**. Proceedings of the National Academy of Sciences of the United States of America, 2011. **108**: 5909-5914.
6. Eilers, E.J., C. Kremen, S.S. Greenleaf, A.K. Garber, and A.M. Klein, **Contribution of pollinator-mediated crops to nutrients in the human food supply**. PLoS ONE, 2011. **6**: e21363.
7. Vanbergen, A.J. and the Insect Pollinators Initiative, **Threats to an ecosystem service: pressures on pollinators**. Frontiers in Ecology and the Environment, 2013. **11**: 251-259.

   ● This review proposes that multiple anthropogenic pressures operating from gene to ecosystem scales are combining to threaten the health, diversity and abundance of wild and managed pollinators.

8. González-Varo, J.P., J.C. Biesmeijer, R. Bommarco, S.G. Potts, O. Schweiger, H.G. Smith, I. Steffan-Dewenter, H. Szentgyörgyi, M. Woyciechowski, and M. Vilà, **Combined effects of global change pressures on animal-mediated pollination**. Trends in Ecology & Evolution, 2013. **28**: 524-534.

9. Potts, S.G., J.C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W.E. Kunin, **Global pollinator declines: trends, impacts and drivers**. Trends in Ecology & Evolution, 2010. **25**: 345-353.

10. Biesmeijer, J.C., S.P.M. Roberts, M. Reemer, R. Ohlemuller, M. Edwards, T. Peeters, A.P. Schaffers, S.G. Potts, R. Kleukers, C.D. Thomas, *et al.*, **Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands**. Science, 2006. **313**: 351-354.

11. Carvalheiro, L.G., W.E. Kunin, P. Keil, J. Aguirre-Gutiérrez, W.N. Ellis, R. Fox, Q. Groom, S. Hennekens, W. Van Landuyt, D. Maes, *et al.*, **Species richness declines and biotic homogenisation have slowed down for NW-European pollinators and plants**. Ecology Letters, 2013. **16**: 870-878.

    ●● Using perhaps the best available wild pollinator and plant occurrence data, this paper revealed how the species richness of different pollinator and plant groups changed at multiple spatial scales in Great Britain, the Netherlands and Belgium between 1950s and 2009.

12. Warren, M.S., J.K. Hill, J.A. Thomas, J. Asher, R. Fox, B. Huntley, D.B. Roy, M.G. Telfer, S. Jeffcoate, P. Harding, *et al.*, **Rapid responses of British butterflies to opposing forces of climate and habitat change**. Nature, 2001. **414**: 65-69.

13. Bommarco, R., O. Lundin, H.G. Smith, and M. Rundlöf, **Drastic historic shifts in bumble-bee community composition in Sweden**. Proceedings of the Royal Society B: Biological Sciences, 2011. **279**: 309-315.

14. Forister, M.L., A.C. McCall, N.J. Sanders, J.A. Fordyce, J.H. Thorne, J. O'Brien, D.P. Waetjen, and A.M. Shapiro, **Compounded effects of climate change and habitat alteration shift patterns of butterfly diversity**. Proceedings of the National Academy of Sciences of the United States of America, 2010. **107**: 2088-2092.

15. Cameron, S.A., J.D. Lozier, J.P. Strange, J.B. Koch, N. Cordes, L.F. Solter, and T.L. Griswold, **Patterns of widespread decline in North American bumble bees**. Proceedings of the National Academy of Sciences of the United States of America, 2011. **108**: 662–667.

16. Garibaldi, L.A., I. Steffan-Dewenter, C. Kremen, J.M. Morales, R. Bommarco, S. Cunningham , L. Carvalheiro, N. Chacoff, J.H. Dudenhöffer, S. Greenleaf, *et al.*, **Stability of pollination services decreases with isolation from natural areas despite honey bee visits** Ecology Letters, 2011. **14**: 1062–1072.

17. Klein, A.-M., C. Brittain, S.D. Hendrix, R. Thorp, N. Williams, and C. Kremen, **Wild pollination services to California almond rely on semi-natural habitat**. Journal of Applied Ecology, 2012. **49**: 723-732.

18. Hoehn, P., T. Tscharntke, J.M. Tylianakis, and I. Steffan-Dewenter, **Functional group diversity of bee pollinators increases crop yield**. Proceedings of the Royal Society B-Biological Sciences, 2008. **275**: 2283-2291.

19. Brittain, C., N. Williams, C. Kremen, and A.-M. Klein, **Synergistic effects of non-Apis bees and honey bees for pollination services**. Proceedings of the Royal Society B: Biological Sciences, 2013. **280**.

20. Kennedy, C.M., E. Lonsdorf, M.C. Neel, N.M. Williams, T.H. Ricketts, R. Winfree, R. Bommarco, C. Brittain, A.L. Burley, D. Cariveau, *et al.*, **A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems**. Ecology Letters, 2013. **16**: 584-599.

● A global meta-analysis showing that species richness and visitation rate/abundance of wild bees visiting 23 crop species is enhanced by the amount of high quality habitat in the landscape together with structurally diverse fields and organic management.

21. Goulson, D., G.C. Lye, and B. Darvill, **Decline and conservation of bumble bees**. Annual Review of Entomology, 2008. **53**: 191-208.
22. Winfree, R., R. Aguilar, D.P. Vazquez, G. LeBuhn, and M.A. Aizen, **A meta-analysis of bees' responses to anthropogenic disturbance**. Ecology, 2009. **90**: 2068-2076.
23. Robinson, R.A. and W.J. Sutherland, **Post-war changes in arable farming and biodiversity in Great Britain**. Journal of Applied Ecology, 2002. **39**: 157-176.
24. Burkle, L.A., J.C. Marlin, and T.M. Knight, **Plant-pollinator interactions over 120 years: loss of Species, co-occurrence, and function**. Science, 2013. **339**: 1611-1615.

    ● An interesting analysis combining historic data with re-survey data to reveal temporal shifts in pollinator network structure due to bee losses, spatial or temporal mismatch in interactions and declining pollination service to a focal wild plant species.
25. Aizen, M.A. and P. Feinsinger, **Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine chaco serrano** Ecological Applications, 1994. **4**: 378-392.
26. Schüepp, C., F. Herzog, and M.H. Entling, **Disentangling multiple drivers of pollination in a landscape-scale experiment**. Proceedings of the Royal Society B: Biological Sciences, 2014. **281**.

    ● This study highlighted the importance of direct effects of heterospecific flower densities in modifying reproductive success of a tree species via competition for pollinator visits.
27. Marini, L., E. Öckinger, K.-O. Bergman, B. Jauker, J. Krauss, M. Kuussaari, J. Pöyry, H.G. Smith, I. Steffan-Dewenter, and R. Bommarco, **Contrasting effects of habitat area and connectivity on evenness of pollinator communities**. Ecography, 2013. **37**, 544-551

28. Ellis, J.S., M.E. Knight, B. Darvill, and D. Goulson, **Extremely low effective population sizes, genetic structuring and reduced genetic diversity in a threatened bumblebee species, Bombus sylvarum (Hymenoptera : Apidae)**. Molecular Ecology, 2006. **15**: 4375-4386.

29. Darvill, B., J.S. Ellis, G.C. Lye, and D. Goulson, **Population structure and inbreeding in a rare and declining bumblebee, Bombus muscorum (Hymenoptera : Apidae)**. Molecular Ecology, 2006. **15**: 601-611.

30. Scheper, J., A. Holzschuh, M. Kuussaari, S.G. Potts, M. Rundlöf, H.G. Smith, and D. Kleijn, **Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis**. Ecology Letters, 2013. **16**: 912-920.

31. Carvell, C., J.L. Osborne, A.F.G. Bourke, S.N. Freeman, R.F. Pywell, and M.S. Heard, **Bumble bee species' responses to a targeted conservation measure depend on landscape context and habitat quality**. Ecological Applications, 2011. **21**: 1760-1771.

32. Oliver, T., D.B. Roy, J.K. Hill, T. Brereton, and C.D. Thomas, **Heterogeneous landscapes promote population stability**. Ecology Letters, 2010. **13**: 473-484.

33. Williams, N.M., E.E. Crone, T.H. Roulston, R.L. Minckley, L. Packer, and S.G. Potts, **Ecological and life-history traits predict bee species responses to environmental disturbances**. Biological Conservation, 2010. **143**: 2280-2291.

34. Bommarco, R., J.C. Biesmeijer, B. Meyer, S.G. Potts, J. Poyry, S.P.M. Roberts, I. Steffan-Dewenter, and E. Ockinger, **Dispersal capacity and diet breadth modify the response of wild bees to habitat loss**. Proceedings of the Royal Society B-Biological Sciences, 2010. **277**: 2075-2082.

35. Aizen, M.A., M. Sabatino, and J.M. Tylianakis, **Specialization and rarity predict nonrandom loss of interactions from mutualist networks**. Science, 2012. **335**: 1486-1489.

36. Carvell, C., D.B. Roy, S.M. Smart, R.F. Pywell, C.D. Preston, and D. Goulson, **Declines in forage availability for bumblebees at a national scale**. Biological Conservation, 2006. **132**: 481-489.

37. Kleijn, D. and I. Raemakers, **A retrospective analysis of pollen host plant use by stable and declining bumble bee species**. Ecology, 2008. **89**: 1811-1823.

38. Parsche, S., J. Frund, and T. Tscharntke, **Experimental environmental change and mutualistic vs. antagonistic plant flower-visitor interactions**. Perspectives in Plant Ecology Evolution and Systematics, 2011. **13**: 27-35.

39. Vanbergen, A.J., B.A. Woodcock, A. Gray, F. Grant, A. Telford, P. Lambdon, D.S. Chapman, R.F. Pywell, M.S. Heard, and S. Cavers, **Grazing alters insect visitation networks and plant mating systems**. Functional Ecology, 2014. **28**: 178-189.

    ●● This study showed how land management increased floral resources in a semi-natural habitat to alter pollinator network topology and increase mean outcrossing rates and pollen donor diversity for a focal plant species. This is among the first attempts to link the cascading effects of environmental changes to modified network structure and plant mating.

40. Carvell, C., W.C. Jordan, A.F.G. Bourke, R. Pickles, J.W. Redhead, and M.S. Heard, **Molecular and spatial analyses reveal links between colony-specific foraging distance and landscape-level resource availability in two bumblebee species**. Oikos, 2012. **121** 734-742.

41. Grant, S.A., L. Torvell, T.G. Common, E.M. Sim, and J.L. Small, **Controlled grazing studies on *Molinia* grassland: effects of different seasonal patterns and levels of defoliation on *Molinia* growth and responses of swards to controlled grazing by cattle**. Journal of Applied Ecology, 1996. **33**: 1267-1280.

42. Vulliamy, B., S.G. Potts, and P.G. Willmer, **The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape**. Oikos, 2006. **114**: 529-543.

43. Vazquez, D.P. and D. Simberloff, **Changes in interaction biodiversity induced by an introduced ungulate**. Ecology Letters, 2003. **6**: 1077-1083.

44. Yoshihara, Y., B. Chimeddorj, B. Buuueibaatar, B. Lhaquasuren, and S. Takatsuki, **Effects of livestock grazing on pollination on a steppe in eastern Mongolia**. Biological Conservation, 2008. **141**: 2376-2386.

45. Whitehorn, P.R., M.C. Tinsley, M.J.F. Brown, B. Darvill, and D. Goulson, **Genetic diversity, parasite prevalence and immunity in wild bumblebees**. Proceedings of the Royal Society B-Biological Sciences 2010. **278**: 1195-1202.

46. Oliver, T.H., D.B. Roy, T. Brereton, and J.A. Thomas, **Reduced variability in range-edge butterfly populations over three decades of climate warming**. Global Change Biology, 2012. **18**: 1531-1539.

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

48. Memmott, J., C. Carvell, R.F. Pywell, and P.G. Craze, **The potential impact of global warming on the efficacy of field margins sown for the conservation of bumble-bees**. Philosophical Transactions of the Royal Society B-Biological Sciences, 2010. **365**: 2071-2079.

49. Kaiser-Bunbury, C.N., S. Muff, J. Memmott, C.B. Muller, and A. Caflisch, **The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour**. Ecology Letters, 2010. **13**: 442-452.

50. Jelle Lever, J., E.H. van Nes, M. Scheffer, and J. Bascompte, **The sudden collapse of pollinator communities**. Ecology Letters, 2014. **17**, 350-359.

●●A theoretical paper using simulations to show how certain properties which create stability in mutualistic networks can fail once a critical level of environmental stress is reached. Experimental tests of multifactorial pressures on pollinator networks are urgently needed to corroborate this theoretical insight.

51. Winfree, R., N.M. Williams, J. Dushoff, and C. Kremen, **Species Abundance, Not Diet Breadth, Drives the Persistence of the Most Linked Pollinators as Plant-Pollinator Networks Disassemble**. American Naturalist, 2014. **183**: 600-611.

●● An excellent analysis revealing that as pollinator species are lost with intensifying land-use the most abundant species, and hence most linked to other species in the network , tend to persist.

52. Valdovinos, F.S., P. Moisset de Espanés, J.D. Flores, and R. Ramos-Jiliberto, **Adaptive foraging allows the maintenance of biodiversity of pollination networks**. Oikos, 2013. **122**: 907-917.

53. Ramos-Jiliberto, R., F.S. Valdovinos, P. Moisset de Espanés, and J.D. Flores, **Topological plasticity increases robustness of mutualistic networks**. Journal of Animal Ecology, 2012. **81**: 896-904.

54. Schleuning, M., J. Fründ, A.-M. Klein, S. Abrahamczyk, R. Alarcón, M. Albrecht, Georg K.S. Andersson, S. Bazarian, K. Böhning-Gaese, R. Bommarco, *et al.*, **Specialization of mutualistic interaction networks decreases toward tropical latitudes**. Current biology, 2012. **22**: 1925-1931.

55. Bryden, J., R.J. Gill, R.A.A. Mitton, N.E. Raine, and V.A.A. Jansen, **Chronic sublethal stress causes bee colony failure**. Ecology Letters, 2013. **16**: 1463-1469.

56. Hoover, S.E.R., J.J. Ladley, A.A. Shchepetkina, M. Tisch, S.P. Gieseg, and J.M. Tylianakis, **Warming, CO2, and nitrogen deposition interactively affect a plant-pollinator mutualism**. Ecology Letters, 2012. **15**: 227-234.

57. Eckert, C.G., S. Kalisz, M.A. Geber, R. Sargent, E. Elle, P.-O. Cheptou, C. Goodwillie, M.O. Johnston, J.K. Kelly, D.A. Moeller, *et al.*, **Plant mating systems in a changing world**. Trends in Ecology & Evolution, 2010. **25**: 35-43.

58. Weiner, C.N., M. Werner, K.E. Linsenmair, and N. Bluethgen, **Land-use impacts on plant-pollinator networks: interaction strength and specialization predict pollinator declines**. Ecology, 2014. **95**: 466-474.

● A paper showing that land-use intensification induces losses of wildflower diversity that alter the composition of pollinator communities and reduce the abundance of more specialist pollinators.

59. Breed, M.F., M.G. Gardner, K.M. Ottewell, C.M. Navarro, and A.J. Lowe, **Shifts in reproductive assurance strategies and inbreeding costs associated with habitat fragmentation in Central American mahogany**. Ecology Letters, 2012. **15**: 444-452.

60. Brys, R. and H. Jacquemyn, **Effects of human-mediated pollinator impoverishment on floral traits and mating patterns in a short-lived herb: an experimental approach**. Functional Ecology, 2012. **26**: 189-197.

61. Kunin, W.E., **Population size and density effects in pollination: Pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber***. Journal of Ecology, 1997. **85**: 225-234.

62. Dick, C.W., G. Etchelecu, and F. Austerlitz, **Pollen dispersal of tropical trees (Dinizia excelsa: Fabaceae) by native insects and African honeybees in pristine and fragmented Amazonian rainforest**. Molecular Ecology, 2003. **12**: 753-764.

63. Donaldson, J., I. Nanni, C. Zachariades, J. Kemper, and J.D. Thompson, **Effects of habitat fragmentation on pollinator diversity and plant reproductive success in renosterveld shrublands of South Africa**. Conservation Biology, 2002. **16**: 1267-1276.

64. Dick, C.W., **Genetic rescue of remnant tropical trees by an alien pollinator**. Proceedings of the Royal Society of London. Series B: Biological Sciences, 2001. **268**: 2391-2396.

65. Aizen, M.A. and P. Feinsinger, **Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina** Ecology, 1994. **75**: 330-351.

66. Cranmer, L., D. McCollin, and J. Ollerton, **Landscape structure influences pollinator movements and directly affects plant reproductive success**. Oikos, 2011. **121**: 562-568.

67. Vazquez, D.P. and D. Simberloff, **Indirect effects of an introduced ungulate on pollination and plant reproduction**. Ecological Monographs, 2004. **74**: 281-308.

68. Kariyat, R.R., K.E. Mauck, C.M. De Moraes, A.G. Stephenson, and M.C. Mescher, **Inbreeding alters volatile signalling phenotypes and influences tri-trophic interactions in horsenettle (Solanum carolinense L.)**. Ecology Letters, 2012. **15**: 301-309.

●● A study showing that experimentally-induced plant inbreeding led to the altered expression of plant chemical signals, which led to greater and less recruitment of herbivores and natural enemies, respectively. Research is needed to establish if inbreeding arising from pollination deficits in the field will similarly alter plant phenotypes and trophic interactions.

69. Kariyat, R.R., C.M. De Moraes, A.G. Stephenson, and M.C. Mescher, **Inbreeding increases susceptibility to powdery mildew (Oidium neolycopersici) infestation in horsenettle (Solanum carolinense L)**. Plant signaling & behavior, 2012. **7**: 803-6.

70. Kariyat, R.R., J. Mena-Ali, B. Forry, M.C. Mescher, C.M. De Moraes, and A.G. Stephenson, **Inbreeding, herbivory, and the transcriptome of Solanum carolinense**. Entomologia Experimentalis et Applicata, 2012. **144**: 134-144.

440 Figure 1. Global change impacts on pollination and trophic interactions across levels of ecological organisation