Rangelands

Society for Range Management
Volume 33 Number 3, June 2011

Pollinators in Rangelands

Society for Range Management

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Special Issue Acknowledgments

The guest editors and authors would like to thank the sponsors of this special issue. The USDA Natural Resources Conservation Service, the Xerces Society for Invertebrate Conservation, the USDA Forest Service Rocky Mountain Research Station, the Great Basin Native Plant Selection and Increase Project, the Great Basin Restoration Initiative, and the Bureau of Land Management provided support for this special issue.

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The BLM vision for the public lands in the Great Basin is to maintain or restore healthy landscapes and sustainable resources that meets the needs of the public that use and enjoy these lands.

An Introduction to the Special Issue on Pollinators

By Amy C. Ganguli and Jason P. Harmon

Pollinators provide crucial ecosystem services to rangelands. However, pollinators are undergoing a number of challenges that threaten these services. Our intent in organizing and editing this special issue of *Rangelands* is to provide those working in rangeland ecosystems information about why pollination is important to rangelands, why rangelands are important to pollinators, and how these relationships are being threatened. Recently pollinators have garnered attention due to high-profile media coverage of honeybee population declines or collapses. This, coupled with increasing awareness of native pollinator decline, has paved the way for improved management resources for pollinator conservation efforts. Furthermore, federal conservation programs and other conservation-based incentive programs aimed at private lands will likely continue to increase their emphasis on maintaining, enhancing, and restoring pollinator habitat and pollinator populations in rangeland ecosystems.

This special issue on pollinators will describe the connections between pollinators and rangelands, including how rangelands enhance pollinators and the services pollinators provide as well as how pollinators benefit the objectives of rangeland managers.

We begin this discussion by presenting a brief overview of how pollination works in rangelands, focusing on how plants grow and reproduce in rangelands and why they bother with bribing animals to help them in this endeavor (Harmon et al.). Benefits of pollination extend well beyond plant reproduction and fitness. In the process of providing pollination services, pollinators are responsible for a host of additional ecosystem services. The importance of pollinators from a wildlife habitat perspective is discussed by Gilgert and Vaughan, along with examples of how rangeland management for pollinators can provide a useful framework for managing wildlife biodiversity. Pollinator diversity is also important in maintaining plant community diversity. Travers et al. highlight the importance of lepidopteran pollinators (moths and butterflies) and discuss how pollinators are important to the maintenance of rare plant species.

In efforts to bring the issues threatening rangeland pollinators and their habitat to light, Cane describes the challenges that pollinators face in the western United States with an emphasis on wild bees. Rangeland management for pollinators is more specifically discussed by Black et al., who provide general considerations to use when looking at common rangeland management practices such as grazing, prescribed burning, mowing, and herbicide use. Although each of these management practices can result in negative consequences for pollinators, they can also be applied in a manner that will benefit pollinators.

Pollinator services are also a large concern for specialty agricultural crops. In our final paper, Chaplin-Kramer et al. illustrate the value of rangeland for supplying pollination services to production agriculture in California.

Papers in this issue have been peer-reviewed. Because of space limitations, we limited the number of citations within each article. Interested readers can access supplemental literature and data authors have referenced at www.srmjournals.org. To read more about pollinators visit "Buzzing the Literature" (Solga) for recent literature.

Acknowledgments

We would like to thank the USDA–Natural Resource Conservation Service, The Xerces Society of Invertebrate Conservation, the USDA–Forest Service, the Great Basin Native Plant Selection and Increase Project, the US Department of Interior–Bureau of Land Management, and the Great Basin Restoration Initiative for sponsoring this special issue of *Rangelands*. In particular, we would like to express gratitude for the insight and contributions of Scott Black, Wendell Gilgert, Nancy Shaw, Mace Vaughn, and Lori Hidinger. We appreciate the reviewers who provided constructive comments that improved the quality of this issue, as well as the contributions of the invited authors.

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An Overview of Pollination in Rangelands: Who, Why, and How

By Jason P. Harmon, Amy C. Ganguli, and Michelle J. Solga

Pollination is one of the most well-known relationships that can occur between two species. Most of us are told at a very early age that bee pollination of flowers is a *mutualism*, and that mutualisms occur when two species "work together for a mutual benefit." This feel-good, iconic image of nature permeates our impression of how this important interaction works, but, in doing so, it distorts the complexity of how and why numerous plant species interact with a diverse array of pollinators.

To understand pollination in rangeland systems, we need to realize that our concept of mutualisms is usually anthropomorphized. That is, we take human ideas of cooperation and self-sacrifice to describe plants and animal pollinators interacting. Although both plants and pollinators do usually benefit, pollination is not a purposefully unselfish or altruistic relationship. It is probably more accurate to think about pollination as a complex ecological negotiation for desired services. Flowering plants want to attract pollinators and "bribe" them into working for the plant. Meanwhile, numerous potential pollinators try to acquire food and other resources from plants however they can. This alternative viewpoint may help us better understand why plants and pollinators bother interacting with each other and how exactly that interaction works.

In this article we present a brief overview of pollination by using examples and species relevant to rangelands. Our primary goal in providing this background information is to display some of the fascinating richness of plant–pollinator interactions. We hope that doing so will prepare and encourage you to read the subsequent articles to learn about the challenges facing pollinators in rangelands and what we can do about them. In this article we first touch on how plants reproduce and why they use animals to help them. Next, we look at the rewards plants provide pollinators. We then briefly survey the diverse assemblage of animal pollinators found in rangeland habitats. We conclude with a discussion about the nature of pollination interactions, including some complicated associations.

Plant Reproduction—Why Do Plants Pay for Service?

How Plants Reproduce and the Benefits of Pollination by Animals

New plants are created in a variety of different ways. Although plants can produce new individuals asexually, sexual reproduction is required for plants to combine genetic information. For this to occur, pollen from the male part of a plant must come in contact with the female part of a plant of the same species.

The question then is how the plant moves that pollen. For many, the solution is to bribe an animal. Approximately three-quarters of all existing flowering plants engage in some level of plant–pollinator interaction.[1] Plant–pollinator interactions have traditionally been underappreciated in rangelands because the dominant species in these ecosystems are typically wind-pollinated (e.g., plants in the Poaceae, Cyperaceae, Chenopodeaceae, Polygonaceae). Other plants do not move pollen much at all, and are instead self-pollinated such that pollen from one flower fertilizes another flower from the same individual plant or the same flower includes both male and female parts. Wind- or self-pollinated plants, including most grasses (Fig. 1), occur in large populations and typically transport pollen over relatively short distances. Advantages of this reproductive strategy include the ability to reproduce without relying on pollinators and conservation of energy because fewer resources are invested in attracting pollinators. Disadvantages of this reproduction strategy include reduced genetic diversity through reduced instances of outcrossing when compared to animal-pollinated species. In other words, wind-pollinated plants do not exchange as much genetic material with genetically different individuals, and this can ultimately hurt the plant population. Animal-pollinated plants have the advantage of increasing genetic diversity within a plant population through increasing the genetic diversity of their offspring. This is particularly important in the maintenance of rare and endangered plant species (see Travers et al., this issue). However, if animal

Figure 1. Big bluestem is an example of a common wind-pollinated rangelands plant. Despite not needing animal pollinators for reproduction, the pollen from wind-pollinated plants may sometimes be used by bees and other pollinators.

pollinators are not present plants can have poor reproductive success because they produce fewer seeds when they receive less pollen.[2] This means that the level of pollination, for good or for bad, impacts plant population and community dynamics by altering plant abundance, population viability, and floral traits.[2]

Ecosystem Services Provided by Pollination

Pollinators play a critical role in maintaining ecosystem structure and function by providing the pollination services required for many plant species to reproduce. In addition, animal-pollinated plant species produce food for wildlife in the form of seeds and fruits. Pollinators themselves (e.g., beetles, ants, flies, butterflies, and moths) also provide an important food source for many wildlife species (e.g., sage grouse, black bears, grizzly bears, and a variety of songbird species). Plant species that need pollinators also help create healthy and vibrant habitats for recreational opportunities in rangelands including hiking, birding, and hunting. Pollination-derived ecosystem services are further discussed in Gilgert and Vaughn (this issue). The ecosystem services provided by pollination are far reaching and an important part of the goods and services derived from rangeland ecosystems worldwide.

Resources for Pollinators—What Is in It for the Pollinators?

Pollinators don't help plants out of the goodness of their simple circulatory systems. Pollinators expect to be paid for their work. Here, we discuss the primary forms of payment plants offer to entice, reward, and train pollinators to help with plant reproduction.

Pollen

Some 400 million years ago pollen was used as the first food reward plants offered as "payment" for reproduction-related dispersal.[3] Because pollen is an important part of plant reproduction, plants are already making this nutritive-rich substance and it can be offered as a reward without the plant creating any new, specialized structures that are used just for interacting with pollinators.[4]

Pollen may seem like the most abundant pollinator reward (just ask anyone with pollen allergies), but of all the potential animal pollinators in the world, relatively few can digest pollen.[4] However, it is used by many insects that pollinate rangeland plants.[3] For example, most bees collect it and use it to feed their young. Adult syrphids (flower flies) and some butterflies eat the grains themselves, and other insects such as thrips puncture pollen grains so they can suck up the contents.

Pollen is an extremely nutritious food source that contains protein and "essential" amino acids along with lipids, carbohydrates, minerals, enzymes, oils, and pigments.[3,4] However, just as different plants contain different nutrients for herbivores, pollen from different plants contains different nutrients. For instance, some pollen grains are rich in starch, others in lipids. There may be some relationship between nutritive content and how the plant is pollinated, but there are no simple relationships between a plant species, its pollen, and its pollinators.

Just because some plant species use pollen as a reward does not mean that all plants need or even want pollinators to take their pollen. Insects that can take and use pollen for themselves will do so when it benefits them regardless of the plant's interests. Scientists have traditionally thought that some insects visit wind-pollinated plants to "steal" their pollen without benefitting the plant.[5] Numerous examples show insect pollinators visiting wind-pollinated plants and using their pollen; however, the exact relationship between plant and pollinator is less straightforward. Sometimes insects are clearly swiping pollen with no benefit to the plant. Honeybees, for example, collect pollen from the tassels of maize (corn) without visiting the silks where pollen is needed for germination. In other cases, insect visitation does benefit the plant. Solitary bees (Halictidae) actively collect pollen from a temperate grass species and the combination of bees and wind increase seed set in that grass compared to wind pollination alone. Since some insect pollinators use pollen from grasses and other wind-pollinated plants, traditional rangeland grasses could help insect pollinators and the other plants that do use those pollinators.

Nectar

Nectar is the most common reward for pollinators and it is used by representatives from almost all known pollinator groups.[4] Unlike pollen, nectar is not directly related to plant reproduction, but instead is produced through a complicated physiological process specifically for potential pollinators. Since nectar is produced explicitly for pollinators there is often a tight, coevolutionary relationship between the plant's nectar and the plant's potential pollinators.[4]

Figure 2. Munro's globemallow is a flowering rangelands plant that is pollinated by insects such as bees and is visited by many more insects including ants.

This tight correlation can be seen in the nectar's content. Nectar is predominately sugar in a water-based solution, but the types of sugars, their relative concentration, and the amount of nectar produced can all vary considerably.[3,4] Remember that plants do not want a pollinator to visit one flower, drink its fill, and leave. Successful pollination requires a pollinator to visit multiple flowers of the same plant species. Therefore, the plant must strike a delicate balance. Producing lots of nectar costs the plant energy and resources and may result in too few pollinator visits. However, not producing enough nutritious nectar may keep pollinators from being able to fly or reproduce and cause them to go search for better resources.

Nectar isn't all sugar water. It also contains amino acids, proteins, lipids, organic acids, phenolics, alkaloids, terpenoids, and more. Because of the tight connection between nectar and pollinators, each component probably has some relationship to pollination. Similarly, variation in when nectar is produced and how plants allow access to nectar are usually correlated with potential pollinators.

Despite the strong correlation between nectar and pollinators, some animals obtain nectar without pollinating the plant by performing "floral larceny." "Thieves" such as ants and other small insects take nectar through the normal route without actually pollinating (Fig. 2). "Nectar robbers" obtain nectar by chewing a hole or piercing through flower parts. These holes can be used by later, secondary robbers. Although taking nectar without pollinating can negatively affect the plant, in some cases these robbers alter the behavior of real pollinators in a way that ultimately benefits the robbed plant.[6]

Animals aren't the only ones manipulating the situation to their own advantage. Besides altering nectar nutrients, certain plant species alter pollinator behavior by producing nectar containing mildly toxic or narcotic chemicals.[7] Consuming narcotic nectar can enhance pollination by altering the length of visits and encouraging pollinators to keep visiting that flower type.

Other Resources

Plants can provide additional nutritional resources such as food bodies, floral tissues, oils, and extrafloral nectaries for foraging pollinators or their offspring.[3,4] In addition, plant structures can provide nesting materials or even a home itself. In one very specialized example, yucca moths stay inside *Yucca* plant flowers during the day and then pollinate them during the night. Some insects gain protection from predators by hiding in flowers, and certain predatory insects hunt for prey attracted to flowers. Others use flowers as meeting places; males pollinate while waiting for mates inside the flower. Insects can also use particular flowers as warm resting places. Bowl-shaped flowers can act as parabolic solar furnaces that entice the cold-blooded insect to visit and stay longer while providing the pollinator an energetic benefit.[8]

Animal Pollinators—Honeybees Are Just the Start

Pollination is performed by an extraordinary diversity of animals. On a global scale, 200,000 different animal species may act as pollinators for plants.[9] This includes birds, bats, lizards, mice, and other small mammals. Vertebrates, however, make up less than 1% of species that pollinate. The real players are insects. This is true both worldwide and in rangelands where the following insects are the primary groups of pollinators.

Honeybees

Honeybees are the most visual and iconic pollinator and they make a tremendous contribution to many agricultural crops. These highly social insects collect pollen from many plant species, but they are less efficient than other species in pollinating certain crops and many native plants.[10] In North America, humans keep only one species of honeybee, *Apis mellifera* (though there are many "breeds"), which was originally imported from Europe. Since honeybees can forage for pollen and nectar miles away from their colony, they are often important pollinators at the interface of agricultural systems and rangelands.

Native Bees

Unlike the nonnative honeybee, there are over 4,000 other bee species that are native to the United States. A few of them, such as the alfalfa leafcutting bee, are managed by humans to achieve particular pollination services. Many of the rest naturally play an important role in pollination, especially to native plants. A small number of native bees are social like honeybees, in that multiple individuals share a nest and there is some division of labor or shared resources. However, most are solitary nesters. For these species a single female creates a nest for her offspring and provisions it with the nectar and pollen she collects so that her flightless, grub-like offspring can develop into adults. Some native bees are generalists and visit a large number of plant species whereas others are specialized, using only certain plants. This specialization can help them be extremely effective pollinators of particular plants. For example, honeybees may be supergeneralists that can visit vast numbers of plant species, but they don't always "trip" specialized pollination mechanisms that are required for successful pollination. In lotus and locoweed in the western United States, honeybees often end up robbing nectar rather than helping the plants. Conversely, a native alkali bee can effectively pollinate up to 2,000 of these flowers in a day.[9]

Moths and Butterflies

Butterflies and moths are also common rangeland pollinators. Most adults feed extensively on nectar, with butterflies visiting flowers during the day and moths at night. For example, the California bay checkerspot butterfly is an endangered native species that thrives in range habitats and benefits from a well-managed livestock grazing regime.[11] Monarch butterflies are migratory travelers that trek hundreds of miles on their journeys. They and other nomadic butterflies take up huge amounts of nectar to get the energy for their long flights, and in so doing end up being important pollinators in the southwestern United States and the Midwest's prairies. Closely related moths can also be important rangeland pollinators. *Yucca* plants in the southwestern United States need yucca moths to survive, and spurge hawk moths are crucial pollinators for an endangered prairie orchid (Travers et al., this issue).

Other Pollinators

There are many other insect pollinators in rangelands that receive less attention. Beetles were some of the first pollinators and still pollinate the vast majority of flowers worldwide, including native poppies in rangelands.[12] Beetles often land on flowers and eat through both rewards and flower petals while pollinating. Sometimes called "mess and soil" pollinators, they are known for defecating within the flowers as they eat. In prairies, soldier beetles feed on and pollinate goldenrod flowers.

Other rangelands pollinators include flies such as those in colder climates where other pollinator species may be scarce and syrphids, which pollinate flowers as bee-looking adults and eat herbivorous pests such as aphids as juveniles. Wasps and ants can also pollinate native plants, but unlike the closely related bees, they are relatively inefficient since they tend to have less hair than bees and lack pollen-carrying structures. Other insects such as leafhoppers, walking sticks, and thrips are thought to pollinate various prairie plants.

Pollination—Why is it So Complicated?

We have tried to dispel the myth that pollination is simply honeybees flying from flower to flower, and instead establish that pollination is a multifaceted, complex relationship between an enormous diversity of plants and animals. This leads us to a central question: why is pollination so complicated?

We do not want to give the impression that there is a single, simple answer, but competition is an important driving factor for the complexity in pollination just as it is for the diversity of life. Both plants and pollinators are competing with other similar individuals; plants want pollinators to visit them and not others and a given pollinator wants to be the one to receive rewards.[3] An organism can try to gain a competitive edge by being the absolute best at what it does. For example, it may produce the exact perfect nectar. However, another approach is to specialize.

The idea of specialization in pollination systems is that a plant has some specific set of characteristics that allows it to attract and use a specific group of pollinators, and these pollinators then do a very good job of pollinating that plant species. The traditional view is that pollination tends towards this specialization with pollinators and plants acting as "a lock and key." The *Yucca*–yucca moth system we've mentioned is an example in which a plant is only pollinated by a single pollinator species, which only pollinates that one plant. These examples, however, are merely one end of a continuum. On the other end, some plants are pollinated by hundreds of different animal species that can each pollinate many different plants. Rangeland areas have a mixture of specialist and generalist pollinator systems across this spectrum. Of the hundreds of native bee species in the Great Basin, approximately half are specialists in terms of the family of plants they visit, and the other half visit a broader array of plants.[13] Similarly, in the Great Plains about a third are specialists and two-thirds generalists.

Below we outline a few of the ways plant flowers differ and how that affects their relationship with pollinators. Such differences are important for specialization and interacting with the right pollinators to maximize the benefits for both species.

Flower Structure

Flower shape can vary widely and is often important in pollination.[4] Various flower shapes may exist to allow certain pollinators access while effectively forcing the pollinator to take up or deposit pollen. Certain flower shapes can thus be roughly correlated with their pollinators. For example, shallow flowers are often seen in bee-pollinated systems, whereas narrow nectar tubes are seen in moth- and butterfly-pollinated systems, and beetles pollinate large bowl-like flowers. These shapes may also be used in attracting pollinators.

Flower Advertisements

More commonly, flowers use color and fragrance to advertise their presence to potential pollinators.[4] These advertisements help a flower compete for pollinators and potentially help pollinators learn to visit that type of flower. Advertisements are generally not of value themselves, although rewards such as ultraviolet-fluorescent nectar and yellow pollen may help with advertising. Even though we can simply characterize a flower's color apart from its scent, some pollinators may change their response to a color when they perceive a certain scent, thereby making it hard to disentangle the two.

Groups of pollinators are sometimes assigned "favorite" colors by determining what color flowers they visit most frequently, but some often visit flowers of many different colors. Since insect and human vision systems are different, figuring out these colors can be difficult unless we understand the wavelengths and colors the insects can see, the spectral reflectance of the flower, and whether the flower contrasts with its background.[3,4] That being said, there is evidence that pollinators can use "color" in deciding what flowers to visit and even in ascertaining the flower's quality or age.[3,4]

Humans have long appreciated the various odors emanating from flowers, but the origin of those scents comes from pollinator attraction. Sweeping generalizations about odors are difficult since insects have varied abilities to pick up scents. Plants that bloom at night typically have a heavy and pervasive floral scent to attract moths from long distances.[3] Meanwhile, plants that bloom in the day may use odors to help attract pollinators to land from a close range. As you might have expected by now, some plants use attractants to lure in pollinators without giving them nectar, pollen, or any other reward. There are different types of floral mimics in pollination including ones that mimic female insects to attract males to pollinate and others that take advantage of pollinators that have learned the cues of similar-looking, more abundant flowers that do offer rewards.[4]

Conclusion

The study of pollination has a long, rich history, but in many ways we have still only begun to understand the various facets of this important ecological interaction. This is particularly true for rangelands, wildlands, and native habitats. What is clear is that pollination plays a critical role in the reproduction of many rangeland plants and plant communities, and as such, it is an important ecological service in the rangeland ecosystem. As the following articles in this special issue will illustrate, there are a number of threats to this service, but there are also many opportunities for us as managers, scientists, and policy makers to ensure that pollination continues to contribute to the health and well-being of rangeland habitats.

Acknowledgments

The authors thank the two anonymous reviewers for their helpful comments and Lori Hidinger and the *Rangelands* Editorial Board for their help with this special issue of *Rangelands* and for making this article possible. We also thank The Xerces Society for Invertebrate Conservation, USDA–Natural Resources Conservation Service West National Technical Support Center, and USDA–Forest Service for their financial assistance with this article.

References

1. National Research Council. 2007. Status of pollinators in North America. Washington, DC, USA: National Academic Press. 322 p.
2. Knight, T. M., J. A. Steets, J. C. Vamosi, S. J. Mazer, M. Burd, D. R. Campbell, M. R. Dudash, M. O. Johnston, R. J. Mitchell, and T. L. Ashman. 2005. Pollen limitation of plant reproduction: pattern and process. *Annual Review of Ecology, Evolution, and Systematics* 36:467–497.
3. Kevan, P. G., and H. G. Baker. 1983. Insects as flower visitors and pollinators. *Annual Review of Entomology* 28:407–453.
4. Dafni, A. 1992. Pollination ecology: a practical approach. Oxford, United Kingdom: Oxford University Press. 250 p.
5. Adams, D. E., W. E. Perkins, and J. R. Estes. 1981. Pollination systems in *Paspalum dilatatum* Poir. (Poaceae): an example of insect pollination in a temperate grass. *American Journal of Botany* 68:389–394.
6. Maloof, J. E., and D. W. Inouye. 2000. Are nectar robbers cheaters or mutualists? *Ecology* 81:2651–2661.
7. Jakubska, A., D. Przando, M. Steininger, J. Aniol-Kwiatkowska, and M. Kadej. 2005. Why do pollinators become "sluggish"? Nectar chemical constituents from *Epipactis helleborine* (L.) Crantz (Orchidaceae). *Applied Ecology and Environmental Research* 3:29–38.
8. Norgate, M., S. Boyd-Gerny, V. Simonov, M. G. P. Rosa, T. A. Heard, and A. G. Dyer. 2010. Ambient temperature influences Australian native stingless bee *Trigona carbonaria* preference for warm nectar. *PLoS ONE* 5:e12000.
9. Buchmann, S. L., and G. P. Nabhan. 1996. The forgotten pollinators. Washington, DC, USA: Island Press. 186 p.
10. Kearns, C. A., and D. W. Inouye. 1997. Pollinators, flowering plants, and conservation. *Bioscience* 47:297–307.
11. Weiss, S. B. 1999. Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. *Conservation Biology* 13:1476–1486.
12. Schneider, E. L., and D. M. Nichols. 1984. Floral biology of *Argemone aurantiaca* (Papaveraceae). *Bulletin of the Torrey Botanical Club* 111:1–7.
13. Waser, N. M., L. Chittka, M. V. Price, N. M. Williams, and J. Ollerton. 1996. Generalization in pollination systems and why it matters. *Ecology* 77:1043–1060.

For additional readings on pollination and pollinators, see the on-line supplemental material at http://dx.doi.org/10.2111/RANGELANDS-D-11-00008.s1.

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On-line Supplemental Material

Additional Readings

An overview of pollination in rangelands: who, why, and how

by Jason P. Harmon, Amy C. Ganguli, and Michelle J. Solga

BARTH, F. G. 1991. Insects and Flowers: The Biology of a Partnership. Princeton, New Jersey, Princeton University Press. 408 p.

BOGDAN, A.V. 1962. Grass pollination by bees in Kenya. *Proceedings of the Linnean Society London*. 173:57-60.

CHITTKA, L. and J.D. THOMSON. 2001. Cognitive ecology of pollination: animal behavior and floral evolution. Cambridge, Cambridge University Press. 344 p.

COSTELLO, D. 1969. The Prairie World. Minneapolis, MN, University of Minnesota Press. 244 p.

DELAPLANE, K.S. and D.F. MAYER. 2000. Crop pollination by bees. Cambridge, CABI. 344 p.

DUDAREVA, N. and E. PICHERSKY. 2006. Biology of floral scent. Boca Raton, FL, CRC Press. 155 p.

IMMELMAN, K. and C. EARDLEY. 2000. Gathering of grass pollen by solitary bees (Halictidae, *Lipotriches*) in South Africa. *Zoosystematics and Evolution*. 76:263-268.

INOUYE, D.W. 1980. The terminology of floral larceny. *Ecology*. 61:1251-1253.

JOHNSON, S.D. and K.E. STEINER. 2000. Generalization versus specialization in plant pollination systems. *Trends in Ecology & Evolution*. 15:140-143.

KESSLER, D., K. GASE, and I.T. BALDWIN. 2008. Field experiments with transformed plants reveal the sense of floral scents. *Science* 321:1200-1202.

NICHOLSON, S.W. and R.W. THORNBURG. 2007. Nectar chemistry. *In:* Nicholson, S. W., M. Nepi, & E. Pacini [eds.] Nectaries and Nectar. Dordrecht, The Netherlands, Springer. p. 215-264.

PROCTOR, M., P. YEO and A. LACK. 1996. The natural history of pollination. Portland, OR, Timber Press, Inc. 479 p.

ROULSTON, T.H.. J. H. Cane, and S. L. BUCHMANN. 2000. What governs protein content of pollen: Pollinator preferences, pollen-pistil interactions, or phylogeny? *Ecological Monographs.* 70: 617-643.

SMITH, F.G. 1957. Bee botany in East Africa. *East African Agricultural Journal*. 23:119-126.

WASER, N.M. and J. OLLERTON. 2006. Plant-pollinator interactions from specialization to generalization. Chicago, IL, The University of Chicago Press. 488 p.

Rangeland Management for Pollinators

By Scott Hoffman Black, Matthew Shepherd, and Mace Vaughan

Pollinator conservation and rangelands don't seem like obvious bedfellows. In this era of sustainability, the connection between pollinator conservation and row crops or pollinator conservation and orchards is obvious. But pollinator conservation and rangelands?

The reality is that pollinators are a key component of a healthy rangeland ecosystem. As Kevan stated, pollination is "central to all human beings, livestock, and wildlife."[1] Pollinators are essential for rangeland food production, help with nutrient cycling, and are prey for many birds. In essence, they hold a central position in wildlife food webs. For example, many migratory songbirds require a diet of berries, fruits, and seeds from insect-pollinated plants and pollinator larvae are an important component of the diet of many young birds. Belfrage et al. demonstrated that butterfly diversity was a good predictor of bird abundance and diversity, apparently due to a shared requirement for a complex plant community.[2] Pollinators perform such a range of ecological services in natural ecosystems that they are clearly a keystone group in nearly all terrestrial ecosystems and are necessary for plant reproduction and in forming the basis of an energy-rich food web.[3]

The relationship between pollinators and rangeland goes both ways. Pollinators are important for rangelands but rangelands are important for pollinators because they can provide habitat. Pollinators in North America include hummingbirds and bats, but insects—mainly bees, butterflies, moths, wasps, flies, and beetles—make up the vast majority of pollinators. Of these, bees are considered the most important pollinators in temperate North America. There are approximately 4,000 species of native bees in North America, many of which will thrive in the varied conditions offered by rangelands. Shrubland and scrub habitat, in particular, can be very valuable habitat. Surveys of pollinators in different California plant communities show that the chaparral community has the largest diversity of bees per unit area of any ecosystem type.

Bee habitat requires two basic components: flowers on which to forage and nest sites. Many pollinators are adapted to forage on particular plants, so a diverse community of pollinators requires a diverse array of flowers. This can be easily provided by native grassland comprising a variety of grasses and forbs. Most native bees are solitary-nesting. Around 70% of bee species nest in the ground, excavating shallow tunnels in patches of bare soil, with most of the remaining 30% nesting in cavities in old trees or plant stems. Bumble bees require a small cavity such as an abandoned rodent hole. Ground-nesting bees (both solitary bees and bumble bees) are likely the most important pollinators in grasslands, but flies, beetles, and butterflies will also be prevalent.

Rangeland pollinators have benefits that go beyond the boundaries of the range. The role that adjacent natural habitat (including grassland, shrubland, and other rangeland types) plays in providing crop pollination services is increasingly well understood: The value of crop pollination by native, wild bees in the United States is estimated at $3 billion. Proximity to natural or seminatural nonagricultural land is often an important predictor of pollinator diversity in cropland.

There is evidence of declines in both managed and wild pollinators. Causes of declines are difficult to pinpoint, but loss of habitat due to increasing urbanization, expansion of intensive agriculture, invasive plant species, and the widespread use of pesticides all negatively impact pollinator populations, as do disease and parasites affecting the pollinators themselves. Protection of habitat is one way in which rangelands can be of great significance in protecting and conserving pollinators. Natural habitat is integral to maintaining a long-term population of native pollinators in agricultural landscapes. However, it is important that management of rangelands and other nonarable lands takes into account native pollinators.

Rangeland Management for Pollinators: General Considerations

Most of the habitat management techniques considered in this article—grazing, prescribed burns, mowing, and herbicide applications—can be used to benefit pollinators. Each can also have damaging, at times severe, impacts on pollinators if they are not used carefully. (The fifth technique discussed here is insecticide applications.) There's no single management plan that can provide ideal habitat for all pollinator taxa, but there are some general considerations that apply to all situations.

In using any of these techniques, it is important to leave some areas of the site untreated. Mowing or burning the entire habitat, for example, could severely impact pollinators and leave them with little chance to recolonize treated habitat. Historically, landscapes contained sufficient areas where vegetation was in various stages of succession to support populations of pollinators with differing habitat needs. However, now that habitat is typically reduced to fragments in agricultural or otherwise intensively managed landscapes, consideration of the heterogeneous vegetation mosaic required by pollinator communities is needed to ensure healthy populations. As such, it is generally better to treat separate parts of the site in a multiyear cycle, retaining refugia from which pollinators can spread.

Grazing

Grazing in natural areas and rangelands is a common practice throughout the United States. Livestock grazing alters the structure, diversity, and growth habits of the vegetation community, which in turn can affect the associated insect community. Grazing can harm pollinator habitat through destruction of potential nest sites, destruction of existing nests and contents, direct trampling of adult bees, and removal of food resources.[4] Studies of how livestock grazing affects bees also suggest that increased intensity of livestock grazing negatively affects their species richness.[4,5] Grazing during periods when floral resources are already scarce (e.g., midsummer) may result in insufficient forage available for pollinators such as bumble bees, which, in some areas, forage into late September.[5] For example, Hatfield and LeBuhn found that uncontrolled sheep grazing in mountain meadows in the Sierra Nevada removed enough flowering plants to eliminate bumble bees from some study sites.[6] Likewise, grazing during spring when butterfly larvae are active on host plants can result in larval mortality or remove important vegetation (host plants or shelter) and nectar resources.[7]

In Arizona, Debano conducted one of the few studies that focused explicitly on the impacts of domestic livestock grazing on invertebrate communities in a region that historically had not been grazed.[8] The results clearly show that invertebrate species richness, abundance, and diversity were all greater in ungrazed sites. Debano suggested that since insects in the Southwest had not evolved in the presence of buffalo or other large ungulates, adaptations to grazing pressure had not developed, making them more susceptible to the presence of cattle.[8]

Grazing is not necessarily harmful. Many parts of the world have experienced grazing pressure from both domesticated and wild animals for millennia and the indigenous flora and fauna are adapted to grazing. Even in areas where grazing is not historically found, light levels of rotational grazing can have positive effects on maintaining an open, herbaceous-dominated plant community that is capable of supporting a wide diversity of pollinators.[7]

Grazing does need to be carefully planned and implemented to be effective. A Swiss study found that although grazing was an effective management tool for limiting succession, (i.e., slowing the conversion of open grassland to shrubland or woodland) responses to grazing varied greatly among butterfly species.[9] The authors suggest that any management regime be attentive to historical and species-specific characteristics of the species at the site, and that a diversity of management techniques be used on a regional scale in order to preserve the greatest diversity of insect pollinator habitat.

Grazing can be a valuable tool for limiting shrub and tree succession, providing structural diversity, encouraging the growth of nectar-rich plants, and creating potential nesting habitat. However, grazing is usually only beneficial at low to moderate levels and when the site is grazed for a short period followed by ample recovery time—and when it has been planned to suit the local site conditions.

Grazing: Key Points

- Grazing can destroy nest sites and remove forage plants.
- Grazing can greatly alter the structure, diversity, and growth habits of the vegetation community.
- Grazing can be used to maintain open, forb-dominated plant communities that support a diversity of pollinator insects, but only if the correct combination of timing and intensity of stocking rate are found.
- At severely overgrazed sites, livestock should be excluded for long enough to allow the vegetation community to regain a diversity and abundance of forbs.
- Keep grazing periods short, with recovery periods for the habitat relatively long.
- Generally grazing that is of low intensity and short duration in the fall (when there is less competition for floral resources with pollinators) is best.

Mowing

Mowing is often used in place of grazing where site access and topography permit equipment access or where livestock would be inappropriate, such as urban sites and roadsides. Like grazing, mowing can alter grassland succession and species composition by suppressing growth of woody vegetation. Mowing can have a significant impact on insects through direct mortality, particularly for egg and larval stages that cannot avoid the mower. Mowing also creates a sward of uniform height and may destroy topographical features such as grass tussocks when care is not taken to avoid these features or the mower height is too low.[10] Such features provide structural diversity to the habitat and offer potential nesting sites for pollinator insects such as bumble bees. In addition to direct mortality and structural changes, mowing can result in a sudden removal of almost all floral resources for foraging pollinators; therefore it should not be conducted when flowers are in bloom.

Mowing: Key Points

- Mowing has significant impacts on the habitat quality.
- Mowing will create uniform vegetation height and remove flowering resources.
- Mowing can be used to control shrubs and trees to maintain open conditions.
- No more than a third of habitat should be mown in one year.
- Road edges may be an important resource for pollinators. Mowing management could be adapted to the maximum benefit of pollinators.

Prescribed Burns

Fire has played an important role in many native ecosystems, and controlled burns are an increasingly common management tool. Effects of fire management on arthropod communities are highly variable. If used appropriately, fire benefits many insect communities through the restoration and maintenance of suitable habitat. Other studies have found a negative or mixed response of invertebrates to fire.[11]

In Midwestern US prairie systems, fire as a management tool is based on the supposition that prairie species are adapted to wildfires, and thus can cope with regular burns.[11,12] This is dependent, however, on there being adequate unburned areas that can provide sources of colonizers into the burned habitat. In habitat fragments where populations are more isolated, prescribed burning can have much more deleterious effects on the population due to a lack of colonizing capacity. For example, Harper et al. found that overall arthropod species richness decreased in burned prairie sites, as did the abundance of all but one of the species measured.[11] Their results suggest that burning a small habitat fragment in its entirety could risk extirpating some species because of limited recolonization from adjacent habitat. Rare butterflies can also be negatively impacted by prescribed burning. Swengel found that fire had consistent negative effects on prairie-specialist butterfly species, and that these effects persisted for 3 to 5 years postburning.[12] In a recent study of the Mardon skipper, the butterfly was virtually eliminated from the burned portion of the habitat.[13] After 2 years the butterfly population in the burned portion of the site had still not recovered.

Fire can have serious impacts on population levels and unless there are adequate refuges from the fire or adjacent habitat, recolonization of a burned site may not be feasible. Timing of burns is also critical and should not be carried out when target pollinators are in a critical foraging stage. Habitat patches should not be burned completely, but rather a mosaic of burned and unburned areas is ideal.

Prescribed Burns: Key Points

- Fire has played an important role in maintaining many native ecosystems.
- Bee populations are significantly lower in years following a burn.
- It can take years for insect communities to recover from a burn.
- Impacts of burning can be reduced if areas of habitat are left unburned.
- Fires should not burn more than one-third of habitat in any given year.
- A program of rotational burning where small sections are burnt every few years will ensure adequate colonization potential for pollinators.
- As a fire moves through an area it may leave small patches unburned. These skips should be left intact as potential microrefuges.
- Care must be taken to avoid actions that could degrade habitat and kill individual pollinators as a result of heavy equipment use or people trampling meadows.

Herbicide Applications

Herbicides can kill plants that pollinators depend on, thus reducing the amount of foraging and egg-laying resources available.[7,14,15] Just as pollinators can influence the vegetation community, changes in vegetation can have an impact on pollinators. A pollinator community requires consistent sources of nectar, pollen, and nesting material during those times adults are active. The broadcast application of a nonselective herbicide can indiscriminately reduce floral resources, host plants, or nesting habitat.[7] Such a reduction in resources can cause a decline in pollinator reproductive success and/or survival rates.

Moreby and Southway found that invertebrate abundance (notably species of Diptera [flies] and Heteroptera [true bugs]) was consistently higher in unsprayed plots than in plots that received a single autumn application of herbicides.[16] Taylor et al. showed that herbicide applications in field margins reduced the number of arthropods (including Lepidoptera [moth and butterfly] larvae) that were food sources for pheasant and partridge chicks.[17]

Other studies have addressed herbicide use and its effects on pollinators in general. In a review suggesting that pollinators are useful bioindicators, Kevan reported that herbicides reduced the abundance of Asteraceae and Lamiaceae flowers in France, contributing to a decline in bumble bee populations.[1] Kevan also found that herbicide applications have reduced the reproductive success of blueberry pollinators by limiting alternative food sources that can sustain the insects when the blueberries are not in bloom.[1] Kearns et al. state “herbicide use affects pollinators by reducing the availability of nectar plants. In some circumstances, herbicides appear to have a greater effect than insecticides on wild bee populations … Some of these bee populations show massive declines due to the lack of suitable nesting sites and alternative food plants.”[3] In contrast, Russell et al. found that the use of selective herbicide when combined with mechanical removal of shrubs and small trees was an effective method of maintaining power line corridors as effective pollinator habitat.[18] In this study, however, nonselective broadcast herbicides were prohibited as they suppressed important nectar resources.

Herbicides: Key Points

- Herbicides kill plants on which pollinators depend for foraging or egg laying.
- Some herbicides can be lethal to bees by direct application or exposure during foraging.
- During vegetation management, treat only the minimum area necessary for the control of weeds. Take care to minimize overspray to habitat around the weeds.

Insecticide Applications

In rangelands and forested areas, insect pests are targeted with a variety of pesticides and can have a significant negative impact on pollinators.[1,19]

One of the most robust case studies of the effects of insecticides on pollinators details how the use of fenitrothion to control spruce budworm in Canadian forests devastated native bee populations. As summarized by Kevan, the reduction of native pollinators due to fenitrothion caused a series of effects to ripple through the ecosystem.[1] Similar effects were discussed by Alston and Tepedino for the application of broad-spectrum insecticides in rangelands to control grasshoppers.[19] The insecticides used, due to their high toxicity, are not permitted on blooming crops being visited by bees, yet they were allowed to be sprayed on rangelands while native pollinators were foraging on wildflowers. The grasshopper spraying campaigns (generally from mid-April to late May) coincide with the flowering period of several endemic rangeland plants that grow among the grasses, a number of which are listed as endangered or threatened. This time period also overlaps the period of emergence and active foraging of many native bee species.[3] The usage of broadband insecticides in wild areas may potentially result in a number of ecosystem shifts due to pollinator limitation. These include "changes in future vegetation patterns via plant competition, reduction in seed banks, and influences on the animals dependent upon plants for food."[19]

The reports of die-offs of native bees are few and far between. Although there are reports of native pollinator die-offs in nonlaboratory conditions, many such poisonings in the wild are assumed to go unreported because the bees are unmanaged and do not gather in large aggregations. Low fecundity rates mean it can take many years for a native pollinator population to recover from a large reduction. Lethal effects on honeybees are often the primary focus of regulatory procedures for assessing the safety of a new insecticide for pollinators despite the enormous diversity of bees, butterflies, and other pollinating insects that may have a wide variation in their response to the same insecticide. As a result, a pesticide that has been deemed safe for honeybees when used according to the bee label may not be safe for native bees or other pollinators.

Insecticides: Key Points

- Insecticides can be lethal to bees or have sublethal effects such as reducing foraging efficiency or reproductive success.
- A pesticide that has been deemed safe for honeybees may not be safe for native bees, even when applied according to label requirements.
- Insecticides not allowed on blooming crops due to high toxicity may be allowed on rangeland while pollinators forage.
- Insecticide impacts are most severe within the agricultural matrix although spraying for mosquitoes, grasshoppers, or other insects may impact pollinators in a wide range of landscapes.

Conclusion

Pollinators are vitally important for functioning ecosystems worldwide. Managers of rangeland systems can play an important part in pollinator conservation. Pollinator conservation will not require a wholesale shift in how managers work in these landscapes but may require changes to timing, intensity, and scale. If managers start to think about all of the components of these ecosystems—even the ones that are not always easy to see—pollinators and all of the flowering plants that depend on them will benefit.

References

1. Kevan, P. G. 1999. Pollinators as bioindicators of the state of the environment: species, activity and diversity. *Agriculture Ecosystems & Environment* 74:373–393.
2. Belfrage, K., J. Bjorklund, and L. Salomonsson. 2005. The effects of farm size and organic farming on diversity of birds, pollinators, and plants in a Swedish landscape. *Ambio* 34:582–588.
3. Kearns, C. A., D. A. Inouye, and N. M. Waser. 1998. Endangered mutualisms: the conservation of plant–pollinator interactions. *Annual Review of Ecology & Systematics* 29:83–113.
4. Sugden, E. A. 1985. Pollinators of *Astragalus monoensis* Barneby (Fabaceae): new host records; potential impact of sheep grazing. *Great Basin Naturalist* 45: 299–312.
5. Carvell, C. 2002. Habitat use and conservation of bumblebees (*Bombus* spp.) under different grassland management regimes. *Biological Conservation* 103:33–49.
6. Hatfield, R. G., and G. Lebuhn. 2007. Patch and landscape factors shape community assemblage of bumble bees, *Bombus* spp. (Hymenoptera: Apidae), in montane meadows. *Biological Conservation* 139:150–158.
7. Smallidge, P. J., and D. J. Leopold. 1997. Vegetation management for the maintenance and conservation of butterfly habitats in temperate human-dominated habitats. *Landscape and Urban Planning* 38:259–280.
8. Debano, S. J. 2006. Effects of livestock grazing on above ground insect communities in semi-arid grasslands of southeastern Arizona. *Biodiversity and Conservation* 15:2547–2564.
9. Wettstein, W., and B. Schmid. 1999. Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. *Journal of Applied Ecology* 36:363–373.
10. Morris, M. G. 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. *Biological Conservation.* 95:121–226.
11. Harper, M. G., C. H. Dietrich, R. L. Larimore, and P. A. Tessene. 2000. Effects of prescribed fire on prairie

arthropods: an enclosure study. *Natural Areas Journal* 20: 325–335.

12. Swengel, A. B. 2001. A literature review of insect responses to fire, compared to other conservation managements of open habitat. *Biodiversity and Conservation* 10:1141–1169.
13. Black, S. H. and C. Mazzacano. 2010. Mardon skipper Coon Mountain burn site occupancy study and surveys of low divide road sites. Report to the U.S. Forest Service, Oregon Zoo, and U.S. Fish and Wildlife Service. Portland, OR, USA: Xerces Society. 21 p.
14. Vaughan, M. and S. H. Black. 2006. Pesticide considerations for native bees. *In:* Agroforestry AF Note 35. Lincoln, NE, USA: USDA National Agroforestry Center. 4 p.
15. Kremen, C., N. M. Williams, and R. W. Thorp. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America* 99:16812–16816.
16. Moreby, S. J., and S. E. Southway. 1999. Influence of autumn applied herbicides on summer and autumn food available to birds in winter wheat fields in southern England. *Agriculture Ecosystems & Environment* 72:285–297.
17. Taylor, R. L., B. D. Maxwell, and R. J. Boik. 2006. Indirect effects of herbicides on bird food resources and beneficial arthropods. *Agriculture Ecosystems & Environment* 116:157–296.
18. Russell, K. N., H. Ikerd, and S. Droege. 2005. The potential conservation value of unmowed powerline strips for native bees. *Biological Conservation* 124:133–148.
19. Alston, D. G., and V. J. Tepedino. 2000. Direct and indirect effects of insecticides on native bees. *In:* G. L. Cuningham and M. W. Sampson [Technical Coordinators]. Grasshopper integrated pest management user handbook. Washington, DC, USA: USDA Animal and Plant Health Inspection Services. Technical Bulletin 1809. 4 p.

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The Value of Pollinators and Pollinator Habitat to Rangelands: Connections Among Pollinators, Insects, Plant Communities, Fish, and Wildlife

By Wendell Gilgert and Mace Vaughan

Recall one of those perfect late spring days you have spent out on the rangelands where you live or work; the wind calm, an azure sky with sparse clouds that provide some relief from the building heat, robust green grass and colorful wildflowers dotting the landscape, and a low background buzz and hum of insects accentuated by the singing of territorial songbirds. It doesn't matter if your recollection is related to shortgrass prairie; pinyon–juniper, sage–steppe, oak, or short-leafed pine savannah; or desert-shrub rangelands, the producers of the buzz and hum you heard are very likely related, essential, and largely ignored denizens of rangeland communities: bees and other native pollinators.

Native pollinating bees are a vital component of the biologically diverse plant and animal community which is critical to healthy, ecologically functional range landscapes. There are more than 20,000 species of bees world-wide. They exist on every continent except Antarctica. Over 4,000 species are known in the United States, most of which are solitary ground-nesting bees. Not only do they provide the essential environmental amenity of pollination, but by providing pollination, they allow for the existence of a host of other environmental services, including the continuation of multiple trophic levels of the food web. Many Lepidoptera (moths and butterflies), wasps, flies, beetles, and other insects also are pollinators, but they are not nearly as efficient as bees in moving pollen from flower to flower.

Managing rangelands to enhance life requisites for native pollinators likely will require adjusting current practices. Because of the lack of recognition of the ecological value of native pollinators it might not be a priority for us to do so. Because ecological services commonly are viewed through an anthropomorphic lens, and where the value assigned depends on the experience and knowledge of the individual, it is important to carefully define the service and what the service provides. Yet, as Aldo Leopold wrote in 1935,[1] we do not often understand the complexity of these services.

> *The long and short of the matter is that all land-use technologies—agriculture, forestry, watersheds, erosion, game and range management—are encountering unexpected and baffling obstacles which show clearly that despite the superficial advances in technique,* we do not yet understand and cannot yet control *the long-term interrelationships of animals, plants, and mother earth* [emphasis added].

For example, from a native bee perspective, prairie dogs provide bare ground for solitary ground-nesting bees,

Rangelands can be managed to supply diverse and abundant flowering plants. Photo by Gary Back.

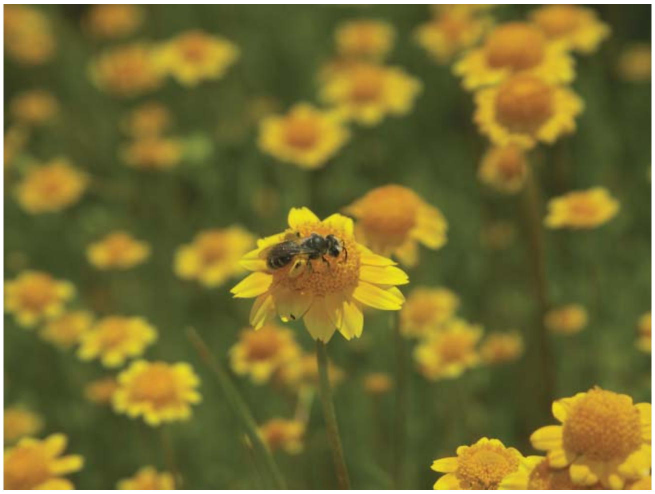
burrows for bumble bee nests, and disturbance to provide early successional habitat to support abundant forbs and legumes, all essential habitat elements. And although prairie dogs also provide soil aeration, reduced soil compaction, and added fertility to the soil from dung, urine, and belowground stored vegetation, it is safe to say that many landowners do not recognize or appreciate the potential pollinator benefits derived from them; rather they see varmints that leave a landscape covered in burrows and often bare of vegetation.

What Is Good Pollinator Habitat?

The most important element of high-quality-pollinator habitat is an abundant and diverse array of flowering plants. These include a wide variety of annual and perennial forbs and legumes, shrubs, vines, and trees that initiate flowering early in the spring and continue late into the fall. Willows (*Salix* spp.) provide some of the earliest flowers in most of North America, a time when ground-nesting miner bees (*Andrena* spp.) and queen bumble bees (*Bombus* spp.) are first emerging. Goldenrod (*Solidago* spp.) and asters continue to flower after the first frosts in autumn and allow new bumble bee queens to store body fat for their winter hibernation. Willows, goldenrod, and all of the flowers that bloom in between, provide the pollen and nectar resources needed by the wide variety of bee species that emerge throughout the growing seasons.

Diverse plant communities provide more than just food to our bees, however. Beetle burrows in trees and shrubs, or the pithy centers of some stems, provide natural nesting sites for about 30% of our native bees. These bees are solitary species that stack their brood cells, one next to the other, inside these tunnels.

The remaining (70%) native bees nest in the ground. These ground-nesting species need to have areas—large or small—of bare soils, usually with full exposure to the sun, into which the females can excavate their nests. In many cases, the surface entrances to these nests look like collections of ant mounds.


A ground-nesting miner bee (genus *Andrena*) collecting pollen and nectar from goldfields (genus *Lasthenia*) at a vernal pool in California's Central Valley (Yolo County). Photo by Mace Vaughan, Xerces Society.

Many bumble bee species also nest under or on the ground, but instead of digging narrow underground tunnels, they utilize existing cavities, such as those left behind by burrowing mammals. Although their nests usually occupy underground burrows, they also take advantage of thick layers of grass or other thatch on the surface where mice or voles construct nests that provide the desired insulation to rear a new generation of offspring.

What Do These Habitat Components Mean for Insect Diversity?

A diversity and abundance of plants that produce nectar and pollen used by insects, combined with a variety of standing or downed dead wood, bare ground, and overgrown vegetation, are the hallmarks of rich heterogeneous pollinator habitat. This habitat should be considered across political and land management boundaries, where pollinator—in this case, native bees—life history requisites are ideally situated within the typical bee flight range. Small bees fly 200 meters or less, but larger species, such as bumble bees, easily can cover more than 2 km in their search for pollen and nectar. When viewed this way, the resources of the sunny meadow take their place alongside those of the stream bank and the forest edge, meeting the diverse needs of pollinators, but also the habitat needs of a wide variety of other insects and invertebrates.

We know that diverse plant communities are important for butterfly and moth (Lepidoptera) diversity.[2] The caterpillars of Lepidoptera species have specific host plant needs. In some cases, a moth or butterfly has a single genus or even species of plant upon which it feeds. Others are much more liberal in their tastes, but in either case, managing for diverse plant communities for native bees will greatly assist in increasing the abundance of Lepidoptera.

Similarly, diverse rangeland plant communities support diverse assemblages of grasshoppers, crickets, and other orthopterans, with the interesting side effect of mitigating or preventing outbreaks. Of the 400 or so grasshopper species in the United States, only about a dozen actually pose a risk of outbreak.[3] These species, and their nonpestiferous cousins, eat a wide variety of plant species, and often are in competition for resources. As a result, diverse plant communities help support a diversity of grasshoppers that compete for limited resources and help prevent outbreaks of economically important species. Likewise, diverse rangeland plant communities provide a consistent supply of floral nectar sources that are utilized by insect predators and parasites that feed upon both nonpest and pest grasshopper species. Some species of blister beetles (Meloidae) and bee flies (Bombyliidae) are grasshopper egg predators, and several species of solitary wasps (Sphecidae) and parasitic flies (e.g., Tachinidae) attack grasshopper nymphs and adults.

Adults of these insects feed on nectar, and this biological control further helps to prevent outbreaks.[4]

What Does Insect Diversity Mean for Fish and Wildlife?

Although native bee pollinators are the main focus of this paper, it is important to recognize the array of invertebrate interactions with fish and wildlife in rangelands. The relationships between heterogeneous plant communities and insects (and other invertebrates) are reflected in a wide variety of other species, from ants to spiders, and have significant implications for fish and wildlife communities. For example, several studies in Japan, New Zealand, North America, and South America have demonstrated that diverse terrestrial plant communities along riparian areas result in the production of abundant insects and spiders that fall or are wind-blown into streams and become critical food resources for fish.[5]

In a recent Rocky Mountain (Wyoming) study, researchers examined trout response to two types of livestock grazing treatments. In one set of treatments, ranchers used high-density, short-duration grazing (HDSD) that closely managed the season of use, the time cattle were allowed to graze in the riparian zone, and the intensity (number) of domestic cattle. The HDSD treatments were compared to season-long continuous grazing where the cattle were turned into large pastures (that included the riparian zones) at the beginning of the season and gathered at the end.

The researchers discovered that the use of high-density, short-duration grazing in the study area riparian zones resulted in an average 2.3-fold increase in the amount of terrestrial invertebrate biomass falling in streams.[6] Willow (*Salix* spp.), red-osier dogwood (*Cornus sericea*), snowberry (*Symphoricarpos albus*), and currant (*Ribes* spp.), as well as Canada goldenrod (*Solidago canadensis*) and yellow sweet clover (*Melilotus officinalis*), all were more prolific in riparian areas managed under the prescriptive grazing utilized by the ranchers in the study area. These plants provide critical pollen and nectar resources required by pollinators. Additional benefits documented in the study were that areas with HDSD grazing areas had three times more aboveground riparian biomass, nearly twice the overhead cover, and more than twice the biomass of trout. Using prescribed grazing management, where livestock herbivory results in the availability of greater aboveground riparian biomass and greater overhanging riparian vegetation cover, can accrue tremendous benefits to pollinators, fish communities and riparian wildlife habitat.

Like the aquatic trout resource, most gallinaceous bird chicks (grouse, quail, and turkey) rely on insects as a source of protein[7] and, overall, 61% of the bird species known to breed in the United States are primarily insectivorous and another 25% are at least partially insectivorous.[8] One study of sage grouse on sage–steppe rangelands found that diverse plant communities were important for diverse Lepidopteran communities, which subsequently were a critical food source for sage grouse chicks.[9] Sage grouse in these forb-rich habitats had significantly higher reproduction and chick survival.[i]

Leaf-cutter bee (genus *Osmia*) visiting wax currant flower (*Ribes cereum*) in eastern Oregon (Lake County). Photo by Mace Vaughan, the Xerces Society.

Similar results have been found in studies looking at the relationship between interseeding forbs into rangeland habitats and the reproduction of Lesser Prairie Chicken (*Tympanuchus pallidicinctus*), Bobwhite Quail (*Colinus virginianus*), Ring-Neck Pheasant (*Phasianus colchicus*), and other gallinaceous game birds. In locations where local populations of these birds are holding steady or experiencing upward population trends, it is apparent that land managers are using practices that maintain vegetation heterogeneity, including early successional vegetation, as a key component of the landscape vegetation mosaic. Management practices, such as fire and grazing, that mimic natural disturbance regimes at an appropriate scale (see article by Black et al., this issue) can be important to implement in order to maintain those diverse landscape conditions. In short, good pollinator habitat is good for game birds. The same is certainly true of songbirds, most of which are insectivorous, and which consume insects found in diverse communities of trees, shrubs, vines, and herbaceous plants.

The connection between pollinators and birds goes beyond their reliance on insectivory. Not only do birds use insects and invertebrates to meet their dietary needs, but they also use seeds that are the result of insect pollination. Once more, plant diversity and abundant forbs have their own direct connections to bird populations. Bee-pollinated fruits and seeds also are the major food source for a wide variety

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[i] Note: The lack of availability of sufficient forbs in the herbaceous understory of sagebrush (*Artemisia* spp.) was identified as one of the threats to the long-term population viability of the Greater Sage Grouse (*Centrocercus urophasianus*) by the United State Fish and Wildlife Service In their 12-Month Findings for Petitions to List the Greater Sage Grouse as Threatened or Endangered in March 2010.

Lesser Prairie Chicken. Photo by Gary Kramer.

Bumble bee (genus ***Bombus***) foraging for pollen and nectar on rabbitbrush (genus ***Chrysothamnus***) in eastern Oregon (Lake County). Photo by Mace Vaughan, the Xerces Society.

of other species, such as goldfinches, titmice, sparrows, and thrushes.

These same fruits and seeds are a critical resource for small and large mammals. Species as varied as voles (*Microtus* spp.) and grizzly bear (*Ursus horribilis*) rely upon seeds and berries. Raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), fox (*Vulpes* spp.), and coyotes (*Canis latrans*), also are known to gorge regularly on berries and seeds that are seasonally abundant.

Although grass production is the primary concern of ranchers producing cattle, the grasses, forbs and shrubs in complex rangeland environments also are the primary nutrition source for communities of large native ungulates. Both grazers and browsers also experience additional dietary benefit if rangelands are managed with increased dicotyledonous floristic resources. For example, 50–75% of mule deer (*Odocoileus hemionus*) diet consists of woody shrubs and forbs, that include bitterbrush (*Purshia tridentata*), mountain mahogany (*Cercocarpus* spp.), rabbitbrushes (*Chysothamnus* spp.), and various species of *Ceanothus*, most of which rely on native bees for pollination. Similarly, pronghorn antelope (*Antilocapra americana*) preferentially select shrubs and forbs, and consume grass for less than 5% of their diet.

Range management that contributes to a heterogeneous landscape is accomplished by judicious and appropriate utilization of such common rangeland conservation practices as range seeding, prescribed burning, brush management, and rangeland mechanical treatment where the integration of a more diverse array of flowering shrubs, forbs and legumes can support diverse fish and wildlife populations that are compatible with cattle and sheep operations, as well as pollinators.

Managing for Pollinators: A Useful Framework for Managing for Wildlife Biodiversity

Because of the multiple connections between pollinator habitat and the diversity of wildlife and plant communities, pollinators provide a very useful framework for managing habitat for biodiversity. Specific recommendations on how to manage large areas of rangeland habitat are given in the article by Black et al. (this issue). However, it is worth emphasizing a handful of core concepts we believe are particularly important.

The overarching objective of good pollinator habitat management and, by extension, high quality fish and wildlife habitat management, is to maintain rangelands with a high level of heterogeneity, which for some rangeland types means a predominance of early successional habitat. Depending on the type of rangeland, this can mean that managed disturbance can be a critically important management consideration. In many rangeland systems, such as grassland prairies, chaparral, and oak savannahs, grazing and fire are essential elements of this disturbance, but must be managed at a scale and intensity that allows forbs and legumes to be abundant, while simultaneously allowing for large areas of rangeland to serve as refugia from intense disturbance.

A contemporary example of landscape heterogeneity as a management goal can be found in the patch-burn grazing systems used at Homestead Ranch in the Flint Hills of Kansas. There, rancher Jane Koger carefully times the scale and intensity of grazing, and burns approximately one-third of each pasture each spring, to reintroduce and mimic historical disturbance on the land. The scale of management is such that large areas of the ranch are not disturbed in any one year, providing refuge areas from which pollinators can recolonize newly disturbed sites. As a result, the ranch supports abundant forbs, pollinators, and other wildlife (J. Koger and M. Weigelt, personal communication, July 2008).

We offer a different example in the Coast Range foothill rangelands adjacent to northern California's Central Valley where the Xerces Society is working with the USDA Natural Resources Conservation Service (NRCS), the local Resource

Conservation District, and a local rancher to replant diverse forbs on his land. The goal of this rangeland project is to create an oasis of pollinator habitat in the midst of a working ranch. This is part of a nationwide effort by the NRCS and the Xerces Society to create pollinator habitats on farms and ranches.

At the Coast Range foothills site, a diverse mix of native forbs and nonnative forage legumes was seeded. The rancher is working to carefully manage grazing on the site to manage yellow star thistle and help the forbs and legumes become well-established. The producer grazed his cattle on the site at a high intensity for a short duration on several occasions. The early outcome is that the grasses are not allowed to dominate the site to the exclusion of forbs and legumes, and invasive yellow star thistle is not allowed to flower; thus it is removed from the site over time. As a result, the forbs are becoming well-established. The producer recognizes that managing for diverse floristic resources is compatible with highly productive ranch management.

Conclusions

In his seminal work "Game Management," naturalist Aldo Leopold identified "the axe, the match, the cow, and the plow," as critical tools for game management.[1] His recognition and endorsement of the use of appropriate management tools to mimic natural disturbance actions have stood the test of time and continue to be cornerstones of wildlife management. Those disturbances serve as the foundation for sustainable rangeland management as well. It is not a coincidence that using disturbance to create heterogeneous landscapes in support of sustainable, healthy rangelands also supports some of the highest quality pollinator habitats.

In the case of pollinators and other invertebrate biodiversity, however, it is important to reconsider the scale of use of the management tools Leopold outlined. Although grazing and fire once occurred at grand scales of thousands, even tens or hundreds of thousands of acres at a time, the patchwork of private lands and high quality habitat (often small remnants) mean that management has to take into account sources of recolonization for pollinators and wildlife alike. The result is that managed disturbance should occur on a third or less of the overall habitat in any one year.

For this kind of management to take hold broadly requires either a commitment on the part of public land managers to target biodiversity (pollinator biodiversity more specifically) as a management goal, or private landowners to see evidence that such practices have long-term benefits in terms of profits or rangeland sustainability.

In the former case, the US Bureau of Land Management (BLM) and the US Forest Service (USFS) increasingly are interested in maintaining biodiversity on the rangelands they manage. Much BLM and USFS attention, for example, over the past year has focused on Greater Sage Grouse (*C. urophasianus*). It is widely recognized, however, that to best support the conservation of this species it is necessary to target management for forb and legume diversity. Similarly, the USFS and the Xerces Society have a growing interest in the conservation of the monarch butterfly. Efforts are underway to map habitat for this species on public lands, and increase the availability of milkweed (*Asclepius* spp.), its larval host plant, and additional nectar sources for adults.

At the same time, private landowners and ranchers are increasingly interested in conservation practices that support wildlife (and pollinators), so long as they are compatible with existing management goals, and technical support is available to support implementation. The NRCS and Xerces Society are working across the country with these landowners and managers to provide financial and technical resources to increase the use of practices that benefit pollinators.

Pollinator conservation, at its core, requires specific attention be paid to plant diversity, both in species composition and structure, a mix of disturbed and undisturbed habitats, and appropriate scale of management. These core management considerations provide a very useful framework for

Diverse spring-flowering native and nonnative forage plants planted for pollinators on rangeland restoration site in the Coast Range foothills of northern California's Central Valley. Plant species in bloom in the late spring include phacelia, lupine, California poppy (*Eschscholzia californica*), and crimson clover. Photo by Claudia Street, Glen County Resource Conservation District.

A monarch (*Danaus plexippus*) caterpillar feeding on milkweed (*Asclepius* sp.). Photo by Mace Vaughan, the Xerces Society.

maintaining habitat that supports not just pollinators, but other invertebrates, fish, and wildlife. As a result, managing rangeland for pollinators provides a useful framework for overall biodiversity conservation, restoration, and management for public and private land managers alike.

References

1. Leopold, A. 1933. Game management. New York, NY, USA: Charles Scribner's Sons. 459 p.
2. Reis, L., D. M. Debinski, and M. L. Weiland. 2002. Conservation value of roadside prairie restoration to butterfly communities. *Conservation Biology* 15(2):401–411.
3. McAdoo, K., L. T. Vermeire, and W. C. Gilgert. 2004. The other grazers. *Rangelands* 26(3):30–37.
4. Branson, D. H., A. Joern, and G. A. Sword. 2006. Sustainable management of insect herbivores in grassland ecosystems: New perspectives in grasshopper control. *BioScience* 56(9):743–755.
5. Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology* 50:201–220.
6. Saunders, W. C., and K. D. Fausch. 2007. Improved grazing management increases terrestrial invertebrate inputs that feed trout in Wyoming rangeland streams. *Transactions of the American Fisheries Society* 136:1216–1230.
7. Liukkonen, A. T. 2001. Nutritional and genetic adaptation of galliform birds: implications for hand-rearing and restocking [PhD dissertation]. Oulu, Finland: University of Oulu. 73 p.
8. Losey, J. E., and D. M. Vaughan. 2006. The economic value of ecological services provided by insects. *BioScience* 569(4):311–323.
9. Gregg, M. A. 2006. Greater sage-grouse reproductive ecology: linkages among habitat resources, maternal nutrition, and chick survival [PhD dissertation]. Corvallis, OR, USA: Oregon State University. 201 p.

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The Hidden Benefits of Pollinator Diversity for the Rangelands of the Great Plains: Western Prairie Fringed Orchids as a Case Study

By Steven E. Travers, Gerald M. Fauske, Kristina Fox, Andrew A. Ross, and Marion O. Harris

The richest and most productive plant communities, including the grasslands typical of the Great Plains, are complex associations of different species dependent on the environment (nutrients and water), as well as ecological connections or relationships with other species. In particular, the mutual benefits of plant–pollinator relationships increase plant reproduction and population growth, increase genetic diversity of individual species, and allow more species to coexist in a plant community, all of which makes a prairie a prairie rather than an admixture of weeds. The diversity of plant species in a grassland is of more than passing interest to rangeland managers because there are clear management benefits to diversity, including increased forage production for livestock and wildlife grazing, improved soil structure, and community resilience to environmental disturbances. Yet, it is easy to overlook the complexity and diversity of pollination relationships of native prairie plants when evaluating long-term management options. Here we argue that the diversity of native grasslands depends on a diversity of pollinators. As a case study, we discuss the complex ecological interactions of pollinators, the Western Prairie Fringed Orchid (*Platanthera praeclara*), and other native prairie species. Our goal is to answer the following questions: How does pollination play a role in the maintenance of rare plant species? How do pollinators other than bees benefit grassland plant communities? And, how do these other pollinators differ from bee pollinators?

How Does Pollination Play a Role in the Maintenance of Rare Plant Species?

The sexual reproduction made possible by pollination increases genetic variation in offspring, with this then allowing for greater evolutionary potential. In plants there are many ways to reproduce. One is "tillering," or asexual reproduction, which produces another individual that is genetically identical to the parent (e.g., ramets produced from stolons or rhizomes). Another is "selfing," where pollen and ovules combine and produce a zygote, but both are from the same plant. Both of these mechanisms of producing a new generation of plants have problems associated with them. The biggest is that asexual reproduction and selfing yield little new genetic variation in the next generation of plants. Breeders of crops and livestock long ago revealed that the potential for new beneficial traits in new varieties depended directly on the amount of genetic variation in the population from which they were selecting. In the same way, genetic variation in future generations of native plants is beneficial because it translates into trait diversity, adaptability, and resilience of populations. Populations with these characteristics have an increased chance of surviving in changing environments.[1]

Outcross pollination is different and has several important benefits. Outcross pollination, where an animal (e.g., insect or bird) or the wind brings pollen from one individual to another, can create brand new combinations of genes in the seeds of the next generation. Pollination can combine genes from different populations adapted to very different local environments and create greater diversity within the gene pools of a species. Another benefit of outcross pollination is the masking or hiding of detrimental traits. Many genetic deficiencies in plants and animals that ultimately can lead to reduced performance or lethality are the product of recessive alleles that cause the most trouble when in the homozygous condition. Selfing and pollination between closely related individuals (inbreeding) increases the occurrence of this homozygous condition where there are two recessive alleles instead of just one. Inbred and excessively selfed plants that have not been outcross-pollinated often are less robust than other plants.

Some plant species have evolved exclusive relationships with specific pollinators and are incapable of any other means of reproducing. These species go extinct if their pollinator disappears. These kinds of relationships link the biodiversity of a plant community with the biodiversity of overlapping animal communities. On the other hand, communities of plants as a whole benefit synergistically from the mutualistic relationships of their individual species. Pollinators generally benefit from pollinating plants by receiving rewards from the plants, including energy-rich nectar or the pollen itself. In the presence of generalist pollinators, a greater selection of plant species from which to choose can increase visitation to a patch (although more individual plants can increase competition). Multiple plant species in a community all can benefit by the presence of other plants attracting pollinators regionally because this can increase their level of pollinator visitation. By rewarding and attracting pollinators as a group, individual species can receive more pollinator service than each could on its own.

A rich native plant community is a mixture of species that range from common to rare. Rare plants often benefit the most from outcross pollination because they are at greater risk for the genetic problems associated with selfing and inbreeding. First, inbreeding and selfing are more likely in small populations or low-density populations visited by pollinators that move relatively short distances. In rare plants the most likely mates are nearby, and therefore are closely related if they came from the same maternal plant. Small populations also can translate into small gene pools with little genetic diversity. Allee effects refer to the observed pattern that there often is a positive correlation between population density and population growth rate. In plants, this relationship can be related to decreased pollinator visitation to small and low-density patches of individuals. Smaller populations are less likely to attract pollinators due to the relatively small amount of reward provided and because they are simply harder for pollinators to find.[2] Finally, all of these problems linked to reduced genetic diversity are greatly magnified in populations of rare plants. Reduced hardiness and adaptability translate into reduced recruitment, leading to a feedback loop that ends in extinction.[3] When rare plants disappear, plant communities and pollinator communities move towards monoculture and the loss of important ecological services such as improved forage quality and resilience for livestock and wildlife habitat.

A Prairie Ghost

Perhaps the best example of a rare grasslands species that relies on pollinators other than bees is the Western Prairie Fringed Orchid (hereafter WPFO). This fringed orchid is unique in its genus because its range reaches well into the tallgrass prairie habitats typical of the subhumid areas of the Great Plains. Other *Platanthera* species typically are found in more wooded areas in the eastern part of the continent. The flowering stalks of this enigmatic ghost can reach 1 m in height and hold sprays of up to 20 pure white flowers that are each 2 inches across (Fig. 1).

Figure 1. Western Prairie Fringed Orchid (*Platanthera praeclara*) flowering stalk. This species has one of the longest nectar spurs (50 mm) of any North American plant.

The WPFO is a symbol of the vanishing tallgrass prairie. As this type of prairie has been converted to cropland, this orchid has decreased dramatically in abundance. The plants that have been studied the most are found in three metapopulations that are located in the Red River Valley, one in southeastern North Dakota at the Sheyenne National Grassland and the Nature Conservancy's Brown Ranch, the second in northwestern Minnesota on state and Nature Conservancy land, and the third in southern Manitoba at the Manitoba Tall Grass Prairie Reserve. Much less is known about the smaller WPFO populations that occur on public and private lands in Iowa, Missouri, Nebraska, and

Figure 2. Hawkmoth pollinator of fringed orchids and other native prairie plants. Note the finger-like orchid pollinia attached to this moth's head. The biodiversity of grasslands is dependent on non-Apoidea (bee) pollinators such as this.

Kansas. However, preliminary genetic data suggests that small isolated populations share only a few of the same genes as other larger populations and might be diverging evolutionarily (A. A. Ross, unpublished data, 2010). In the United States, the WPFO was listed as a threatened species in 1989 under the Endangered Species Act of 1973. In Canada, it was listed as endangered in 2003 under the federal Species at Risk Act. The WPFO illustrates the importance of diversity for managing populations of rare plant species. Its presence in the Great Plains represents an important contribution to prairie biodiversity.

The orchid is not pollinated by the typical pollinator (i.e., bees). Instead pollinators are hawkmoths of the Family Sphingidae,[4,5] a family of large, mostly crepuscular moths (Fig. 2) capable of flying long distances. Hawkmoths search for nectar sources by integrating sensory information from olfactory and visual systems.[6] The WPFO is highly apparent to these sensory systems because of its large inflorescence and showy white flowers and because of a strong fragrance, which is produced starting at dusk (when hawkmoths begin to fly) and through the night. The reward for visiting the orchid is nectar: on average, each flower of the inflorescence contains 13 µL of nectar. However, because nectar typically only is found in the bottom 18 mm of the 50-mm-long narrow nectar spur, short-tongued pollinators (such as bees) usually cannot access the nectar via the opening of the nectar spur. In contrast, hawkmoth pollinators have a tongue that ranges in length from 28–40 mm. While using the tongue to search flowers for nectar, the moth places its head within the teacup-shaped flower. Here, if the head of the moth has the proper dimensions, the compound eyes contact one or both of the sticky pads (viscidia) that connect to the orchid's pollinia, the paired structures that encase the pollen. When leaving the flower, the moth removes the pollinium, which now takes up a position in front of the moth's head. This is an ideal position for pollinating flowers that are visited subsequently. Such floral visits might be to a flower within the same inflorescence or the flower of a nearby or distant orchid, the latter being possible because hawkmoths fly long distances. Flight occurs during migration and also during the male's search for mates (via tracking of a female-produced sex pheromone) and during the female's search for larval host plants (via orientation to plant visual and chemical cues). The amount of nectar provided by each flower is enormous compared to other prairie flowers and is an important resource for supporting the presence of hawkmoths in the prairie. Nectar is a critical fuel for hawkmoth flight and also provides resources for the female to mature additional eggs.[7]

Unlike some tropical orchids that have a single hawkmoth pollinator, the WPFO appears to recruit whatever hawkmoth species are present in the area. In the Sheyenne National Grassland in southeastern North Dakota, five hawkmoth species have been found carrying WPFO pollinia on their compound eyes and are assumed to be pollinators: Achemon sphinx (*Eumorpha achemon*), wild cherry sphinx (*Sphinx drupiferarum*),[4] spurge hawkmoth (*Hyles euphorbiae*),[8] white-lined sphinx (*H. lineata*), and hermit sphinx (*Lintneria eremitus*).[5] The most obvious case of recruiting any hawkmoth (rather than specializing in recruiting a single species) is the spurge hawkmoth, a European species that was brought to North America 40–50 years ago as a biological control agent for the noxious weed leafy spurge. After its introduction, it was not established in North Dakota until 1998 when numbers of larvae could be found on leafy spurge in western North Dakota. Five years later it was found in southeastern North Dakota (which has plenty of leafy spurge) carrying WPFO pollinia.[8] It is now by far the most abundant of the five hawkmoth species and might be the most important pollinator for this orchid metapopulation. This "rescue" of the orchid was timely because several of its pollinators appear to be rare. For example, the white-lined sphinx (*H. lineata*), is a migrant from the south and rarely shows up in the Sheyenne Grassland (2 of 8 years). The two remaining pollinator species, the hermit sphinx and the wild cherry sphinx, are rare each year, and in some years are not found at all.[5]

Maintaining the orchid's pollinators in the grasslands requires more than just the orchid. Most importantly, each hawkmoth species requires host plants for larvae. The search for host plant is presumably what keeps the female moth flying in a particular area, with visits to orchids then fueling that flight. The host plants of the five hawkmoth pollinators consist of a diverse set of species, ranging from mints to cherry trees. A second requirement for keeping hawkmoths in areas where orchids grow is the presence of plants that provide nectar during the periods before and after orchid flowering. This especially is important for the newly recruited pollinator, the spurge hawkmoth, which appears to have two generations each year. Adults of the first generation start flying in May or early June (before the orchid flowers) and

Table 1. List of plant species flowering coincidentally with Western Prairie Fringed Orchids in western Minnesota. Lepidopteran pollinators have been observed visiting all of these species. Data compiled from Dunnell[9]

Scientific name	Common name
Achillea millefolium	Yarrow
Agoseris glauca	False dandelion
Allium stellatum	Prairie onion
Amorpha canescens	Lead plant
Amorpha fruticosa	False indigo
Anemone canadensis	Canadian anemone
Anemone cylindrica	Candle anemone
Apocynum cannabinum	Indian hemp
Aquilegia canadensis	Red Columbine
Asclepias ovalifolia	Ovalleaf milkweed
Asclepias syriaca	Common milkweed
Calylophus serrulatus	Yellow evening primrose
Campanula rotundifolia	Harebell
Castilleja sessiliflora	Downy paintbrush
Castilleja sulphurea	Yellow painted cup
Cicuta maculata	Water hemlock
Conringia orientalis	Hare's ear mustard
Cypripedium parviflorum	Yellow ladyslipper
Dalea candida	White prairie clover
Dalea purpurea	Purple prairie clover
Delphinium carolinianum	Prairie larkspur
Desmodium canadense	Showy tick-trefoil
Echinacea angustifolia	Purple coneflower
Erigeron philadelphicus	Philadelphia fleabane
Gaillardia aristata	Blanket flower
Galium boreale	Northern bedstraw
Gaura coccinea	Scarlet gaura
Heterotheca villosa	Golden aster
Heuchera richardsonii	Alum root
Liatris aspera	Tall blazing star
Liatris pycnostachya	Prairie blazing star
Lilium philadelphicum	Wood lily
Lobelia spicata	Pale-spike lobelia
Melilotus officinalis	White sweet clover
Monarda fistulosa	Wild bergamot
Oenothera nuttallii	White evening primrose
Oenothera serrulata	Toothed-leaved evening primrose
Onosmodium occidentale	False gromwell
Osmorhiza claytoni	Sweet cicely
Packera plattensis	Prairie groundsel
Panicum virgatum	Switchgrass
Pediomelum esculentum	Large indian breadroot
Penstemon gracilis	Lilac flowered penstemon
Penstemon grandiflorus	Large beardtongue
Pentemon albidus	White penstemon
Physalis virginiana	Ground cherry
Potentilla arguta	Tall cinquefoil
Potentilla pensylvanica	Pennsylvanica cinquefoil
Prunella vulgaris	Self-heal
Psoralea argophylla	Silverleaf scurfpea
Pycnanthemum virginianum	Virginia mountain mint
Ratibida columnifera	Prairie cone flower
Rosa arkansana	Wild prairie rose
Rudbeckia hirta	Black-eyed susan
Symphyotrichum falcatum	White prairie aster
Thalictrum dasycarpum	Tall meadowrue
Thalictrum dioicum	Early meadowrue
Tradescantia occidentalis	Spiderwort
Tragopogon dubius	Goatsbeard
Verbena stricta	Hoary vervain
Vicia americana	Wild vetch
Zigadenus elegans	White camas

continue flying into early July (when the orchid starts flowering). The second generation starts flying in the second half of July into August and pollinates the orchid during the final weeks of flowering. In the years when the white-line sphinx shows up, it also needs nectar plants before and after the orchid flowers.

In turn, these other nectar plants visited by the orchid's pollinators benefit through the outcrossing that is provided. In a study of native prairie plants flowering at the same time and place as WPFO populations in western Minnesota (Table 1), there were 35 species identified that were possible nectar sources and outcrossing beneficiaries from hawkmoth visitation.[9] In the absence of these additional plant species, orchids would be visited less often if the pollinators on which they are so dependent did not have enough to eat and moved on to other places. Rare plants such as the orchid promote diversity of grasslands by supporting pollinators of other plants. They also benefit from a diverse plant community that supports a diverse pollinator community.

A final point is that the orchid provides nectar to other threatened prairie pollinators. A significant proportion of plants (40%) and flowers (10%) are robbed via cuts into the side of the nectar spur (K. Fox, unpublished data, 2008). Fortunately, nectar robbery does not appear to have negative effects for reproduction of the flower or the plant. The robbers appear to be bumblebees, which are important pollinators of other prairie plants, as well as being threatened species of the grasslands. This is an additional ecological service provided by the orchid, and another example of the complex web of relationships that exist between and among prairie plants and prairie insects.

Pollination Services Without Bees

Despite bees receiving the lion's share of attention in regard to pollination of native plants, there are many other insect pollinators that play an arguably more important role in the grasslands of North America. Lepidopteran pollinators (moths and butterflies) are unique in three important ways. First, one species or another is active 24 hours/7 days a week throughout the growing season. Pollinators of other insect orders, including bees and wasps, are virtually all diurnal in their pollinator activities. Within the Lepidoptera, butterflies are diurnal, hawkmoths are mostly crepuscular (active at dusk and dawn), a few are diurnal, some are nocturnal, and a few are matinal (active during pre-dawn). Owlet moths and crambid moths, although mostly nocturnal, also have species active at other times in the 24-hour cycle. Many micro-Lepidoptera are avid diurnal flower visitors as well.

Second, Lepidoptera uniquely transport pollen across a range of distances, including short, intermediate, and very long distances. In general, there is a correlation between body size and distances traveled; micro-Lepidoptera are local, whereas hawkmoths sometimes travel more than a thousand miles. Thus, hawkmoths, whose host plants are native to the Gulf States, might be flitting from flower to flower in the northern Great Plains by the end of the growing season. In contrast, sedge moths or fairy moths only can be local floral visitors. The dispersal abilities of Lepidoptera give plants "options" of local or distant pollination. This means that wide-ranging plants have at their disposal wide-ranging pollinators. Butterflies are known both for their long-distance migrations (monarch) but also for their annual long distance immigrations (painted lady, red admiral). Similarly many common owlet moths move northward with the season (black cutworm, armyworm, corn earworm) and one species (army cutworm) has seasonal migrations from the Great Plains to the Rocky Mountains and back each growing season. The movement of Lepidoptera differs fundamentally from that of bees (which operate locally from a central "base," be it a solitary nest or a communal hive), or flies (which often are seen to work one floral patch), or beetles (which often extensively work the blossoms of a single plant).

Finally, after tallying numbers of species in groups that are predominately floral visitors, we find that there are nearly 4,500 Lepidoptera that are regular floral visitors in North America. By comparison, there are 3,700 Hymenoptera (bees, wasps, ants, etc., that are regular floral visitors [of which 3,500 are bees]), at least 2,000 Coleoptera (beetles), and 1,700 Diptera (flies). This makes the Lepidoptera the largest group of potential pollinator species and shows that the Apoidea (bees) make up only a third of potential plant pollinators (Table 2).

The services these pollinators provide in terms of promoting reproduction and out-crossing in native grasslands is crucial to the maintenance of plant biodiversity. Likewise, these pollinators are dependent on diverse plant (and animal) communities to persist.[10] There are multiple reasons for this interdependence. Excepting most Apoidea (bees), other insect floral visitors usually are dependent on a different host plant (or animal). For example, the asteroid hooded owlet (*Cucullia asteroides*) has aster as its larval host, but adults visit many flowering plants. The hermit sphinx is dependent on mints (Lamiaceae) as a larva, yet has been recorded as a pollinator of the WPFO. Because of the difference between adult feeding behaviors and larval hosts exhibited by non-bee pollinators, a more diverse plant community is required to support these insects. By contrast, although many bees are polylectic (visiting many flowers) or oligolectic (visiting only one type or few types of flowers), non-bee floral visitors are dependent on flowers not only for adult nutrition, but also for larval development. From a flowering plant's "point of view," living in a diverse habitat with many other flowering plant species triples the numbers of available pollinators. A diverse community then supports a diversity of other insect herbivores not involved in pollination services and their itinerant parasites and predators, not to mention a community of scavengers.

The greater diversity of both plants and insects translates into greater complexity of community structure and a greater overlap of functional roles. What does this mean? First, when more than one species performs a particular functional role (pollination of the Western prairie fringed orchid, for example), the loss or temporary population reduction of a particular pollinator species at one locality will not mean the loss of the pollinated plant at that locality or overall. Likewise, a local extinction of one particular plant might not mean the extinction of its pollinator because it will be able to rely on other plants. That means if the plant is reintroduced, its pollinator will still be present and able to pollinate the restored plant. In other words, the loss of one species will not mean the loss of its functional role in the community.

Table 2. North American insect taxa which are predominately floral visitors (data compiled from numerous sources; see Sources for Table 2 at the end of this article)

Order, lower taxa (family, subfamily)	Common name	NA species*
Lepidoptera† (total = 4,472)		
Prodoxidae	Yucca moths	56
Adelidae	Fairy moths	18
Glyphipterygidae	Sedge moths	40
Heliodinidae	Sun moths	20
Ethmidae	Ethmid moths	45
Scythrididae	Scythrid moths	90
Choreutidae	Choreutid moths	46
Sesiidae	Clearwing moths	123
Crambidae: Pyraustinae	Pyraustine snout moths	364
Sphingidae	Hawkmoths	120
Erebidae	Erebid moths	400
Noctuidae (sensu stricto)	Owlet moths	2,350
Papilionoidea	Butterflies	515
Hesperioidea	Skippers	285
Coleoptera (total = 2,007)		
Scarabiidae: Cetonini	Flower chafers	60
Cantharidae	Soldier beetles	370
Cleridae	Clerid beetles	291
Melyridae	Soft-winged flower beetles	520
Phalacridae	Shining flower beetles	28
Meloidae	Blister beetles	410
Anthicidae: Antrhicini	Flower beetles	120
Ceranbycidae: Lepturinae	Flower longhorned beetles	208
Diptera (total = 1,700)		
Bombyliidae	Bee flies	900
Syrphidae	Hover flies	800
Hymenoptera‡ (total = 3,700)		
Apoidea	True bees	3,500
Chrysididae	Chrysidid wasps	200

*Numbers of North American species that have, or likely have floral visiting habits.
†Conservative estimates, the feeding habits of many thousands of microlepidoptera are too incompletely known to characterize by family.
‡Many additional species are incidental flower visitors, but habits are too incompletely known to have separate family listings.

Interestingly, the loss (or gain) of a species (plant or animal) from a diverse community can have long-reaching effects that are not immediately apparent. As an example consider the consequences of the spread of an invasive rangeland plant species. Leafy spurge (*Euphorbia esula*) was introduced into North America. It is an economically important plant in the Sheyenne National Grasslands of southeastern North Dakota because its presence in rangeland reduces the amount of forage available in this multi-use environment; cattle feed on both grasses and forbs, but not leafy spurge. In pastures where spurge is abundant, there is increased grazing pressure on the remaining plant community. One of those native plant groups includes mints, some of which are host plants for the hermit sphinx, which in turn is a pollinator of the WPFO. Another example of introductions with complex consequences includes insects that have been introduced into North America to control leafy spurge. Two of the moths are a leaf tier (*Lobesia euphorbiana* [Freyer]) and the spurge hawkmoth. The larvae of the spurge hawkmonth consumes whole stems of leafy spurge, and the adult moths carry pollinia of the WPFO—an unexpected beneficial outcome. Meanwhile, larvae of *L. euphorbiana* tie the growing tips of leafy spurge. The presence of these moths reduces spurge density and opens areas for cattle grazing. As a consequence, moths increase productivity of a given parcel of rangeland and reduce pressure on the forb community. Increased forb nectar sources, coupled with decreased spurge sources, shifts pollinator activities back to native plants, which also increases rangeland productivity. This in turn, increases survival of pollinators that again drive plant diversity—a positive feedback loop.

Conclusions

A resilient and speciose grassland ecosystem is more than a collection of species. One of the best examples of mutualistic relationships among species, pollination, is a key force in the maintenance and promotion of biodiversity in these ecosystems. Individual plant species and populations reap the benefits of outcrossing and sexual reproduction in the presence of a diversity of pollinators. These benefits translate to higher scales when collections of plant species benefit one another by supporting diverse pollinator communities collectively. In this way there is a positive feedback system where biodiversity begets and supports biodiversity. Moreover, because pollination relationships themselves are diverse from specific to general, the promotion of pollinator species across the taxonomic spectrum from bees to butterflies to beetles is an important part of plant biodiversity and therefore in the best interests of natural resource managers. E.O. Wilson said, "Nature is kept productive and flexible by uncounted thousands of such partnerships."[10] Thus, it behooves everyone interested in the productivity and flexibility of grassland communities to never forget the diversity of these partnerships.

References

1. Westermeier, R., J. Brawn, S. Simpson, T. Esker, R. Jansen, J. Walk, E. Kershner, J. Bouzat, and K. Paige. 1998. Tracking the long-term decline and recovery of an isolated population. *Science* 282:1695–1698.
2. McCarthy, M. 1997. The Allee effect, finding mates and theoretical models. *Ecological Modeling* 103:99–102.
3. Soule, M., and L. S. Mills. 1998. Population genetics—no need to isolate genetics. *Science* 282:1658–1659.
4. Cuthrell, D. L. 1994. Insects associated with the prairie fringed orchids, *Platanthera praeclara* Sheviak & Bowles and *P. leucophaea* (Nuttall) Lindley [MSc. Thesis]. Fargo, ND, USA: North Dakota State University. 76 p.
5. Fox, K. A. 2008. Hawkmoths (Family Sphingidae) associated with the western prairie fringed orchid in southeastern North Dakota [MSc. Thesis]. Fargo, ND, USA: North Dakota State University. 70 p.
6. Raguso, R. A. 2004. Flowers as sensory billboards: progress towards an integrated understanding of floral advertisement. *Current Opinion in Plant Biology* 7:434–440.
7. O'Brien, D. M., D. P. Schrag, and C. Martinez del Rio. 2000. Allocation to reproduction in a hawkmoth: a quantitative analysis using stable carbon isotopes. *Ecology* 81: 2822–2831.
8. Jordan, C. R., G. M. Fauske, M. O. Harris, and D. Lenz. 2006. First record of the spurge hawkmoth as a pollen vector for the western prairie fringed orchid. *Prairie Naturalist* 38:63–66.
9. Dunnell, K. 2010. Plant phenological responses to climate change in the northern Great Plains. [MS. Thesis]. Fargo, ND, USA: North Dakota State University. 78 p.
10. Buchmann, S., and G. Nabhan. 1996. The forgotten pollinators. Washington, DC, USA: Island Press. 292 p.

Sources for Table 2

1. Arnett, R. H. Jr., M. C. Thomas, P. E. Skelley and J. H. Frank. 2002. American Beetles. Volume 2. Polyphaga: Scarabaeoidea through Curculionoidea. Washington, DC, USA: CRC Press.
2. McAllpine, J. F. 1981. Manual of Nearctic Diptera. Volume 1. Monograph 27. Ottawa, Ontario, Canada: Research Branch, Agriculture Canada. 674 p.
3. Michner, C. D. 2007. The Bees of the World. 2nd Edition. Baltimore, MD, USA: Johns Hopkins University Press.
4. Opler, P. A. and G. O. Krizek. 1984. Butterflies east of the Great Plains. Baltimore, MD, USA: Johns Hopkins University Press.
5. Powell, J. A. and P. A. Opler. 2009. Moths of Western North America. Berkeley, CA, USA: University of California Press.
6. Royer, R. A. 2003. Butterflies of North Dakota. Minot, ND, USA: Minot State University Science Monograph 2. 192 p.
7. Tuttle, J. P. 2007. The Hawkmoths of North America. Washington, DC, USA: Wedge Entomological Foundation.

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Meeting Wild Bees' Needs on Western US Rangelands

By James H. Cane

Rangelands are areas that are too arid, or with soils too shallow, to support either forests or cultivated agriculture, but that nonetheless produce enough vegetation for livestock grazing. Some arid rangeland regions, notably those with warm, dry climates in temperate zones (e.g., the warm deserts of the United States and adjacent Mexico, parts of Australia, South Africa, California, and around the Mediterranean) host great diversities of native bees,[1] primarily nonsocial species among which are many floral specialists. Conversely, the world's forested lowland tropics support many more social species of bees, but they have far less bee diversity overall.[1] Bees are generally the most important group of pollinators for every continental flora. To better grasp the relevance of human impacts on rangeland bee faunas, and what we can do about it, some generalizations about bees are presented.

Unfamiliar Bees

There are about 20,000 described species of bees, with possibly another 10,000 yet to be recognized.[1] Bees comprise more species than mammals, reptiles, amphibians, and birds combined. The highly social species, such as the true honeybees (*Apis*) and the stingless bees (*Meliponini*), have perennial colonies with queens and unmated female workers; they are broad floral generalists found most commonly in the humid tropics. Honeybees are most well known, yet they differ greatly from most other bees. Outside of the tropics, most individuals and species of bees are solitary, each female (of the nonparasitic species) having a central nest that she creates and then provisions for her progeny with individual pellets or masses of pollen moistened with nectar or sometimes floral oils. Most species nest underground (Fig. 1). Others nest aboveground in old beetle tunnels in deadwood or pithy or hollow dead twigs or stems (Fig. 2), or they occasionally make freestanding nests against hard surfaces. Many species have a single 3–5-week adult generation each year. This characteristic is especially prevalent in more arid biomes such as rangelands, where seasonal precipitation often results in a distinct season of bloom and bee activity. An annual life cycle favors some species to evolve taxonomic specialization for pollen, termed *oligolecty*, which in turn may allow a greater diversity of species to cohabitate. The necessary coordination of bee emergence with bloom seems particularly common in arid, temperate biomes such as rangelands. In summary, the typical rangeland bee is solitary (not social), nests underground, has one generation annually, and is likely, to some degree, to be a floral specialist for pollen. General reading about the fascinating life histories and ecology of bees can be found in *Bees of the World*,[2] *The Forgotten Pollilnators*,[3] the entry on bees in the *Encyclopedia of Entomology*,[4] or at the USDA-ARS Pollinating Insects Lab's Web site.[i]

I will now review some of the human factors with known or expected implications for native bees, with a focus on western rangelands. Missing from this list are climate warming and climate change. In addition, precipitation is a primary factor controlling plant growth and flowering in these arid landscapes, specifically shifting patterns, frequencies, durations and intensities of droughts, as well as various human water-extraction schemes. The timing and amounts of soil moisture strongly impact the rangeland wildflower communities upon which bees depend. However, we cannot yet predict shifts in rangeland precipitation even 1 year in advance, much less any changes in variability under future climates. I therefore prefer to focus on the damage that we know we have done and continue to do to rangelands and on how to implement practical repairs on those landscapes. Most of my recent experience in rangelands comes from the warm deserts and sage-steppe of the western United States, which undoubtedly colors my perspective when extrapolating essentials to rangelands in other parts of the world.

Invasive Exotics

Rangeland bees are threatened indirectly by those invasive exotic weeds that displace native plant communities. Contrary to some popular notions, bees are not averse to nonnative plants per se. Old World clover and alfalfa crops, for instance, are avidly visited by diverse New World bees,[5] as are several other papilionaceous legumes that are more

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[i] http://www.ars.usda.gov/Services/Services.htm?modecode=54-28-05-00 under "What Are Bees?" at the "Products and Services" tab.

Figure 1. Schematic cross-section illustrating the subterranean nest of the European bee *Meliturga clavicornis*. Depicted are the main tunnel, mother bee, and her larval progeny at different stages of development on their provision masses of pollen moistened with nectar. From a plate in *Die Europaischen Bienen* by H. Friese (1923). Reproduced with permission.

invasive in the US West (e.g., yellow sweet clover [*Melilotus officinalis*][6] and sericea [*Lespedeza cuneata*]). Nonetheless, few of the aggressive exotics infesting rangelands of the American West are useful to native bees. Among the exceptions are saltcedar (*Tamarix pentandra*), which is abundantly visited by diverse nectar-seeking bees and wasps, and several thistles (e.g., bull thistle [*Cirsium vulgare*]), which attract bees that visit native thistles. In California, yellow starthistle (*Centauria solstitialis*) attracts bees too, but mostly exotic species that are also of European origin.[7] Otherwise, the disruptive exotic weeds of North American rangelands are mostly wind- (or self-) pollinated grasses (e.g., cheatgrass [*Bromus tectorum*] and buffelgrass [*Cenchrus ciliaris*]) and forbs (e.g., Russian thistle [*Salsola kali*]). Most of the exotic forbs of the Great Basin with somewhat more showy flowers, such as red storksbill (*Erodium cicutarium*), tumblemustard (*Sisymbrium altissimum*), and white top (*Cardaria draba*), do not seem to attract many native pollinators.

Figure 2. Nest of the solitary bee *Osmia kincaidii* in a twig of sumac (*Rhus trilobata*) split open to reveal the linear series of cocoons. Photo by author.

In contrast with livestock, there is no evidence that bees avoid foraging at these exotics because their rewards are unpalatable or toxic. Their threat to bees is entirely due to their capacity to degrade and displace native forb communities (see *Rangelands* special issue, February 2010) by enhancing fire frequencies[8] or by poisoning soils through allelopathy[9] among other mechanisms. After exotic weeds thickly infest disturbed sites, they can impede natural plant recolonization as well as rehabilitation efforts, thereby impeding the restoration of native bee communities. Notably, the 20+ exotic species of bees in North America have produced little detectable disruption of native bee communities thus far, certainly not on a par with exotic plants.[10] The European honeybee's impact on native bees—mostly through exploitative competition for pollen and nectar—remains debatable and may prove unknowable because they were introduced four centuries ago, long before anyone studied our native bees. In my opinion, it is the precise and targeted elimination of the worst exotic plants—particularly by well-conceived biological control methods—that will eventually benefit native bees the most, if removing the exotic weedy species helps to heal native plant communities.

Pesticides and Rangeland Pollinators

Pollinators in extensive rangelands are unlikely to encounter toxic insecticides. In contrast, insecticide poisoning is a substantial risk for bees venturing into conventional cropland and orchards, as well as too many suburban landscapes. In sprawling rangeland landscapes, insecticide use is rarely economical or warranted, which is fortunate for bees. One exception in the Intermountain West involves treating outbreaks of grasshoppers and Mormon crickets with bran bait laced with carbaryl insecticide. Bees typically do not contact, collect, or ingest such baits, and even if they do, bees and their progeny are reportedly unharmed.[11] Herbicides are more widely used on rangelands, but because they do not kill bees, their impact is manifested through their effect on native wildflower communities. This could be beneficial if an aggressive exotic species is selectively removed, or it could be detrimental if all forbs are removed to promote grass monocultures. In general, bees of rangelands are at little direct risk from pesticide exposure, except where rangelands abut more intensive land uses (e.g., cultivated crops or urban sprawl) and their attendant insecticides.

Fire and Bees

The casual observer gazing at a charred landscape might conclude that fires destroy rangelands. In those parts of the Great Basin and prairie biomes of North America that are without invasive weed problems or altered fire cycles, however, native grasses and forbs generally benefit from infrequent fire[12,13] at the expense of woody plants, such as junipers (*Juniperus*) and sagebrush (*Artemesia*), which die when burned. What then of bees? Obviously, those bee species nesting in twigs and stems (Fig. 2) are swiftly killed by the flames. However, 85% of bee species in the eastern United States nest underground (no estimates are available for other locations).[10] Their ground-nesting habit (Fig. 1) generally leaves them unharmed by rangeland fires because conduction of a fire's surface heat into mineral soils is sharply curtailed with depth.[14] Recent experiments in my lab with heated, damp sand showed that bees of every life stage generally survived temperatures up to 50°C. Such lethal heat from fire penetrates no more than 5–10 cm below the surface in the absence of thick combustible surface duffs,[15] which bees typically avoid for nesting. Jack Neff and I have found that only 9% of 460 bee species with reported nest depths dig such shallow nests. Consequently, most bees should survive the heat of typical rangeland fires (Fig. 3). This prediction is borne out by ongoing postfire bee surveys in the Great Basin by my student, Byron Love. Where native floras were largely intact before burning, native bee faunas as much as 9 km beyond the edges of huge wildfires remain diverse and abundant in the months, years and decades after burning. For these rangeland bee faunas, fire is inconsequential, except for its influences on the wildflower communities upon which bees depend.

Tillage and Sprawl

Irreversible habitat losses do result from urban areas sprawling into rangelands, as does land-use conversion into irrigated farmlands. Where other development (e.g., intense fossil fuel extraction or mining) disrupts rangeland plant communities, their bee faunas undoubtedly suffer, but how much and how permanently is not known. Nearly all of California's Central Valley (55,000 km^2) was transformed by cultivated agriculture, aided by altered hydrology and domination by exotic Eurasian annual grasses. John Muir's description of bloom in the former perennial bunchgrass ecosystems is exuberant: "The Great Central Plain of California, during the months of March, April, and May, was one smooth, continuous bed of honey bloom, so marvelously rich that, in walking from one end of it to the other, a distance of more than 400 miles, your foot would press about a hundred flowers at every step" (p. 338).[16] Muir's enthusiastic hyperbole about bloom intimates that a rich, native bee community must once have existed in California's Central Valley, but no bee biologist was there to collect at that time. Today, that native bee fauna is generally sparse, depauperate, and composed mostly of floral generalists (see Chaplin-Kramer et al., this issue).

Figure 3. Nest entrance and soil tumulus of the bee *Andrena subtilis* in the season following a grass fire in sage-steppe. Photo by author.

Much of the tall- and mid-grass prairies of the central US Great Plains states were plowed to grow annual grain crops that, with few exceptions (e.g., sunflower), do not feed bees. For instance, only 0.1% of Iowa's original prairies remain.[17] In the rural environs of Carlinville in southern Illinois, a rich native bee fauna has persisted largely intact from the early 20th century into the 1970s.[18] Its subsequent fate with regard to further agricultural intensification, including hedgerow removal and stream-course engineering, is unknown.

More recently, center-pivot irrigation has allowed agricultural intensification to expand westward into more arid rangelands; 8 million hectares in the United States are currently irrigated by center-pivot methods, though not all of it in the West. When aquifers run dry or soils become overly salinated from such arid land irrigation, as can often be inevitable, these farmlands are abandoned. Their churned salty soils, boosted nitrogen loads, and abundance of Eurasian weeds do not favor the return of diverse native plant communities (although desirable forbs can be seeded in the corners left by circles). Even in old crested wheatgrass seedings, however, our collections in northwest Utah and adjacent Idaho have revealed a small lingering subset of the common floral generalists.

Subsets of native bee faunas are surprisingly resilient amid urban sprawl all around the world.[19] A similar rangeland example is illustrated by the remarkably rich bee fauna at creosote bushes (*Larrea tridentata*) growing in the alleys and vacant lots of Tucson, Arizona,[20] a city of the Sonoran desert. These encouraging observations do not justify complacency about curbing urban sprawl and tillage of rangelands, but they do provide hope that surprising numbers of native bees are present and ready to respond to rehabilitation efforts that include suitable wildflowers.

Livestock Grazing Past and Present

How resilient are native bee communities following rangeland abuse? The extent, severity, causes and cures for past rangeland degradation by livestock grazing in the American West were laid out in a 1936 report to Congress, "The Western Range." This well-organized, lucid, and detailed

620-page account is accessible on the Web.[ii] Much less familiar is a case of well-documented historical rangeland devastation[21] that geographically coincides with a thoroughly known regional bee fauna.

The setting is the Chihuahuan desert scrub and semi-desert grasslands in southeastern Arizona, centered around the towering Chiricahua Mountains. Before 1870, the region was sparsely populated, first by native peoples and then Spanish settlers. Soon thereafter, cattle and sheep grazing plus hard-rock mining activities and logging exploded onto the landscape.[21] In less than 50 years, millions of acres of native perennial grassland were denuded by overgrazing, resulting in plant communities now dominated by unpalatable native shrubs and exotic annuals. In 1891, more than 100,000 cattle grazed Cochise County alone, matched by as many or more sheep. Two years of drought ensued, killing one-half to three-quarters of the herds. The cycle repeated several times into the mid-20th century. Perennial streams and springs dried up. Vast swaths of the conifer forests of the Chiricahua Mountains were clear-cut to supply timbers for copper mines, lumber for mining towns, and charcoal for silver smelters. These intensive land uses have subsided substantially in recent decades, although the rangelands are still grazed.

Did many native bee species survive this devastation? For the past 50 years, the Southwest Research Station of the American Museum of Natural History has regularly hosted bee taxonomists, ecologists, and their students, resulting in a comprehensive regional collection. More than 500 species of native bees are known to reside in the Chiricahua Mountains and especially its surrounding valleys (John Ascher, personal communication, December 2010), despite the ecological degradation during the previous 150 years. Admittedly, some of the dominant invading native shrubs produce abundant flowers that attract diverse bee faunas (e.g., creosotebush [*Larrea tridentata*] hosts >120 bee species),[22] unlike the wind-pollinated dominant shrubs and grasses of some other rangelands such as the Great Basin. The persistence of diverse native bee faunas on such degraded rangelands bodes well for positive outcomes that can come from rangeland restoration projects that include seeding of bee-pollinated forbs. Progressive management practices for livestock and control of exotic weeds will often be needed if these seedings are to flourish.

An ongoing research study is quantifying the response of native bee communities to recent cessation of grazing and farming in a neighboring warm-desert rangeland. Dr. Robert Minckley's study area is set on a former large ranch in the San Bernardino Valley of northeastern Sonora, Mexico, contiguous with the Chiricahua region mentioned above. Grazing was terminated in 2000, after which native bee and floral community responses were compared in permanent plots of warm desert, scrub grassland, field, and riparian habitats. Control sites had not been grazed since 1979. In all, 24,000 individual bees were sampled the first year, representing 306 native species, one-third of which were represented by a single specimen (substantial rarity is the common experience with bee faunal studies). As expected, nearly all of the bee species were nonsocial, most nested underground, and many were floral specialists. Riparian zones returning to cottonwood forest after grazing were unfavorable to this fauna. Otherwise, cessation of grazing resulted in more abundant native bees in each habitat, but the list of species remained constant by habitat type. Monitoring has continued for a further 8 years, with ongoing analysis. A rich, if sparser, bee fauna persisted despite chronic disturbance by grazing; during the decade following the cessation of grazing, that fauna has multiplied somewhat, but its composition has, so far, remained much the same.

Historically, severe grazing clearly degraded and altered native plant communities worldwide, including the western United States. Recovery is far from certain when, as in the last example, livestock are merely removed. Glen Canyon in Utah is a US National Recreation Area today, but for many decades, beginning in the mid-19th century, it was heavily grazed by sheep and other livestock. Studies of plant macrofossil remains in packrat middens (Fig. 4) revealed the composition of plant communities of this high-desert rangeland's during the past 965 years.[23] Its plant communities endured repeated prehistorical stresses such as severe droughts, but it was the episode of severe livestock grazing that markedly transformed the dominant vegetation, with some palatable forbs and shrub species removed or greatly diminished. Despite elimination of sheep grazing, this plant community remains altered, populated by a more spatially homogenous list of unpalatable though still mostly native plant species, most of which are not used by bees. Native bee communities may need more than mere passive stewardship of wildflower communities following an historical episode of severe grazing disturbance.

Figure 4. Fossil packrat middens contain preserved fragments and seeds of local vegetation. Photo courtesy of Julio Betancourt, USGS Tucson.

[ii] Available at http://books.google.com.

Figure 5. Commercial seed production field for northern sweetvetch (*Hedysarum boreale*), a perennial herbaceous legume of the Rocky Mountains and eastern Great Basin. Photo by author.

Figure 6. Female of the ground-nesting native bee *Eucera frater* foraging at flowers of threadstem milkvetch (*Astragalus filipes*), a host dominated by diverse bees of the genus *Osmia*. Photo by author.

Expanding the Meal Table for Native Bees

Ultimately, restoring native bee communities to rangeland habitats will, in many places, require or benefit from active restoration of their native plant communities. Specifically, large-scale seeding efforts can be coupled with judicious grazing and fire management. Rocky soils, steep slopes, and harsh climates will limit the number of sites or techniques (e.g., seed drilling vs. aerial seeding) where this approach can be practiced with some hope of success. Restoring rangeland bee communities to presettlement diversity and abundance is not a reasonable objective, both because we lack historical samples of those faunas (and so will remain ignorant of any restoration target) and also because humans caused key ecological transformations that seem irreversible (e.g., degraded cryptobiotic crusts). However, current rangeland bee faunas worldwide would undoubtedly benefit from enhanced diversity and abundance of their native floral hosts. Especially for ground-nesting bees, it seems that carrying capacity in a given habitat is constrained by limited pollen and nectar resources rather than inadequate nesting opportunities.[24] This is good news because we are progressing in our abilities and capacity to grow and seed wildflowers, but we are generally unsuccessful in creating soil conditions that bees are certain to adopt for nesting. Such plant community rehabilitation by reseeding is increasingly practical and reliable for a growing list of native forbs attractive to native bees.

In North America, especially for the prairies and sagebrush-steppe habitats, a cadre of bold and skilled commercial seed growers is producing seed of diverse native grasses and forbs (Fig. 5). Farmed wildflower seed is cheaper; production is more plentiful and reliable; and the resulting seed is often of better quality than wild-harvested seed—all market factors necessary for widespread adoption and large-scale application. The Great Basin wildflowers in line for restoration efforts are all widespread, prevalent species. They represent diverse plant families and happen to be both attractive to native bees (Fig. 6) and are in need of bees' pollination services.[25] Just one of the species, basalt milkvetch (*Astragalus filipes*), is unmatched as a host for bees of the genus *Osmia* (which are prevalent in the Great Basin); we have found fully one-third of all *Osmia* species of North America visiting its flowers.[26] In turn, most of the other Great Basin forbs considered for seed production are visited by one or more species of *Osmia*.

The same can be said for many prevalent prairie forbs useful for restoration in the U.S. Great Plains. For instance, purple prairie-clover (*Dalea purpurea*) is in commercial seed production on several hundred acres in five states. It both requires bees for seed set (a critical fact for growers) and is used by 50+ species of native bees for pollen and nectar.[27] A close prairie relative, leadplant (*Amorpha canescens*), retains a rich bee fauna, including a dominant specialist, even among small prairie remnants.[28] This additional evidence indicates that relict bee communities are poised to take advantage of nearby revegetation efforts.

Recent advances in seed growing, harvest, cleaning, storage, dormancy management, and especially mechanical seeding technologies are facilitating successful rehabilitation demonstrations on the large acreages needed to convince land managers of their practicality. Research and field trials funded and coordinated through the Great Basin Native Plant Selection and Increase Project through the USDI-BLM Great Basin Restoration Initiative and the USDA-FS Rocky Mountain Research Station are at the vanguard of such rehabilitation programs.[iii] I am convinced that native wildflower restoration is the key to bee community restoration in many rangeland habitats.

Acknowledgments

I thank Douglas Johnson, Leonard DeBano, and Nancy Shaw for their insights and helpful reviews, Bob Minckley for sharing his exciting research results (now in review), and John Ascher for his expert faunal estimate for the Chiricahua watershed.

References

1. Michener, C. D. 2007. The bees of the world. Baltimore, MD, USA: Johns Hopkins University Press. 953 p.
2. O'Toole, C., and A. Raw. 1991. Bees of the World. New York, NY, USA: Facts on File, Inc. 192 p.
3. Buchmann, S. L., and G. P. Nabhan. 1996. The forgotten pollinators. Washington, DC, USA: Island Press. 292 p.
4. Cane, J. H. 2008. Bees (Hymenoptera: Apoidea: Apiformes). *In:* J. L. Capinera [ed.]. Encyclopedia of Entomology. New York, NY, USA: Springer-Verlag Press. p. 419–434.
5. Bohart, G. E. 1957. Pollination of alfalfa and red clover. *Annual Review of Entomology* 2:355–380.
6. Tepedino, V. J., B. A. Bradley, and T. L. Griswold. 2008. Might flowers of invasive plants increase native bee carrying capacity? Intimations from Capitol Reef National Park, Utah. *Natural Areas Journal* 28:44–50.
7. Barthell, J. F., J. M. Randall, R. W. Thorp, and A. M. Wenner. 2001. Promotion of seed set in yellow star-thistle by honey bees: Evidence of an invasive mutualism. *Ecological Applications* 11:1870–1883.
8. Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into Western North America: an ecological chronicle. *Agro-Ecosystems* 7: 145–165.
9. Bais, H. P., R. Vepachedu, S. Gilroy, R. M. Callaway, and J. M. Vivanco. 2003. Allelopathy and exotic plant invasion: From molecules and genes to species interactions. *Science (Washington, D.C.)* 301:1377–1380.
10. Cane, J. H. 2003. Exotic non-social bees (Hymenoptera: Apoidea) in North America: Ecological implications. *In:* K. V. Strickler and J. H. Cane [eds.]. For non-native crops, whence pollinators of the future? Lanham, MD, USA: Thomas Say Publications in Entomology, Entomological Society of America. p. 113–126.
11. Peach, M. L., D. G. Alston, and V. J. Tepedino. 1995. Sublethal effects of carbaryl bran bait on nesting performance, parental investment, and offspring size and sex ratio of the alfalfa leafcutting bee (Hymenoptera, Megachilidae). *Environmental Entomology* 24:34–39.
12. Wrobleski, D. W., and J. B. Kauffman. 2003. Initial effects of prescribed fire on morphology, abundance, and phenology of forbs in big sagebrush communities in southeastern Oregon. *Restoration Ecology* 11:82–90.
13. Seefeldt, S. S., M. Germino, and K. Dicristina. 2007. Prescribed fires in *Artemisia tridentata* ssp. *vaseyana* steppe have minor and transient effects on vegetation cover and composition. *Applied Vegetation Science* 10:249–256.
14. Debano, L. F., D. G. Neary, and P. F. Ffolliott. 1998. Fire's effects on ecosystems. New York, NY, USA: John Wiley and Sons. 333 p.
15. Pyne, S. J., P. L. Andrews, and R. D. Laven. 1996. Introduction to wildland fire. New York, NY, USA: John Wiley and Sons. 769 p.
16. Muir, J. 1894. The Mountains of California. New York, NY, USA: The Century Co. 381 p.
17. Smith, D. D. 1981. Iowa prairie, an endangered ecosystem. *Proceedings of the Iowa Academy of Science* 88:7–10.
18. Marlin, J. C., and W. E. Laberge. 2001. The native bee fauna of Carlinville, Illinois, revisited after 75 years: a case for persistence. *Conservation Ecology* 5:87–89.
19. Cane, J. H. 2005. Bees, pollination, and the challenges of sprawl. *In:* E. Johnson and M. Klemens [eds.]. Nature in fragments: the legacy of sprawl. New York, NY, USA: Columbia University Press. p. 109–124.
20. Cane, J. H., R. Minckley, T. Roulston, L. J. Kervin, and N. M. Williams. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications* 16:632–644.
21. Bahre, C. J. 1991. A legacy of change. Tucson, AZ, USA: University of Arizona Press. 231 p.
22. Minckley, R. L., J. H. Cane, L. Kervin, and T. H. Roulston. 1999. Spatial predictability and resource specialization of bees (Hymenoptera: Apoidea) at a superabundant, widespread resource. *Biological Journal of the Linnean Society, London* 67:119–147.
23. Cole, K. L., N. Henderson, and D. S. Shafer. 1997. Holocene vegetation and historic grazing impacts at Capitol Reef National Park reconstructed using packrat middens. *Great Basin Naturalist* 57:315–326.
24. Roulston, T. H., and K. Goodell. 2010. The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology* 56:293–312.
25. Cane, J. H. 2008. Pollinating bees crucial to farming wildflower seed for U.S. habitat restoration. *In:* R. R. James and T. L. Pitts-Singer [eds.]. Bees in agricultural ecosystems. New York, NY, USA: Oxford University Press. p. 48–64.
26. Watrous, K. W., and J. H. Cane. 2011. Breeding biology of the threadstalk milkvetch, *Astragalus filipes* (Fabaceae), with a review of the genus. *American Midland Naturalist* 165:225–240.
27. Cane, J. H. 2006. An evaluation of pollination mechanisms for purple prairie-clover, *Dalea purpurea* (Fabaceae: Amorpheae). *American Midland Naturalist* 156:193–197.
28. Slagle, M. W. and S. D. Hendrix. 2009. Reproduction of *Amorpha canescens* (Fabaceae) and diversity of its bee community in a fragmented landscape. *Oecologia* 161:813–823.

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[iii] See http://www.fs.fed.us/rm/boise/research/shrub/greatbasin.shtml.

Value of Wildland Habitat for Supplying Pollination Services to Californian Agriculture

By Rebecca Chaplin-Kramer, Karin Tuxen-Bettman, and Claire Kremen

Rangelands can provide an important ecosystem service to adjacent agricultural fields by providing foraging and nesting habitat that supports populations of naturally occurring crop pollinators, chiefly bee species.[1] Rangeland habitats such as grasslands, meadows, savannah, and shrublands support diverse bee communities due to the wide variety of nesting habitats they supply. Such habitats include undisturbed ground, cavities in the ground and trees, and hollow-stemmed grasses and reeds that are suitable for species of ground-nesting, wood- and cavity-nesting, and stem-nesting bees, respectively.[2] Similarly, rangeland habitats often provide a diverse array of flowering forbs, shrubs, and trees that furnish successive blooms, supporting the needs of multiple bee species across their flight seasons.[3] These bee populations and communities are then available to provide crop pollination in adjacent agricultural fields.[4] Our paper outlines a method for quantifying the value of pollination services supplied by wild bee communities based on the area of nearby wildland habitats,[1] chiefly rangelands, to pollinator-dependent crops in California, one of the largest agricultural economies in the world.[5]

The Role of Pollinators in Agricultural Systems

Pollination services are critically important to human health and well-being, due to the large number of crop species (75%) that depend on animal pollinators to produce fruits or seeds (either partially or completely[6]) and the essential nutrients supplied by these crop species (e.g., globally, > 90% of vitamins A and C are derived from pollinator-dependent crops). Approximately 35% of the total biomass of crop production depends on animal pollinators.[6] Worldwide, pollination services, including those provided by managed bees imported to crop fields and those freely provided by wild bees, are valued at €153 billion per year (approximately $216 billion per year), 9.5% of annual global crop value.[7]

Managed Pollinators

Around the world, modern “industrialized” agricultural systems rely extensively on a single, managed, pollinator species, the honeybee (*Apis mellifera*), to provide crop pollination.[8] Large monoculture farms of pollinator-dependent species, such as almond, melon, blueberry, and apple, create a huge demand for pollinators during a short time interval, often overwhelming the capacity of naturally occurring pollinator species to provide these services. At the same time, such farms often have reduced abundances of wild bee species,[1] possibly due to the lack of alternative floral resources other than the mass-flowering crop,[9] and/or the lack of nest sites[10] and frequent use of pesticides.[10,11] Consequently, growers must import managed honeybees during crop bloom,[1] treating pollination as an input much like fertilization, irrigation, or pest control.

Reliance of growers on honeybees for crop pollination increases grower vulnerability to shortages in honeybee supply. In the United States, the number of honeybee colonies has declined steadily since the 1940s;[12] high annual rates of colony loss have also occurred in many regions of North America, Europe, the Middle East, and Asia since approximately 2005,[13] probably due to synergistic effects of viral and parasitic diseases, malnutrition, loss of genetic diversity, and pesticide exposure.[14] The reduced supply of honeybees in the United States has increased the cost of honeybee rentals,[15] as well as the uncertainty and difficulty of obtaining this critical farming input.[12] Growers that receive some pollination services from wild bees thus enjoy an economic advantage.[16]

Wild Pollinators

Wild pollinators are known to supply sufficient pollination services for fruit set and/or seed set for pollinator-dependent crops, under environmental conditions that support diverse and abundant pollinator communities.[1,17,18] Diverse pollinator communities provide greater magnitude and temporal stability of pollination services through various mechanisms, including complementarity of foraging behavior in space and/or time and varied responses of different species to changing environmental conditions.[19] Both diversity and abundance of wild pollinator communities are also known in some circumstances to enhance the pollination efficiency of managed honeybees through alteration of honeybee foraging behavior.[20] Healthy communities of wild bees could provide growers with an "insurance policy" for pollination services against honeybee losses.[18,19]

A quantitative synthesis across a wide variety of crops and biomes showed that crop-visiting wild bees are most abundant and diverse near natural or seminatural habitat, with an exponential decline of diversity and abundance as distance from natural habitat increases.[21] Relevant habitats included meadow, shrubland, savannah woodland, seminatural woodland, and tropical and temperate forests. In addition, specific studies have found a positive relationship between the diversity and abundance of bees and the pollination services provided, as the proportional area of natural habitat increases.[1,17] Natural habitat most likely promotes the diversity and abundance of wild bee pollinators on croplands by providing both nesting sites and alternative floral resources when crops are not blooming.[22]

The Value of Pollination Services Provided by Wild Bees

While the services provided by wild bees are valuable, only a few of the studies measuring values of pollination service have distinguished between the values flowing from wild versus managed bees.[8] For the United States, pollination services provided by wild bees were estimated at $3.07 billion (in 2003 dollars), representing 15.3% of the total pollination service value.[23] This calculation assumes a fixed ratio of wild pollinators to honeybees across all landscapes. In contrast, studies that calculated values based on the observed abundances of wild pollinators obtained much higher values and proportions of pollination services attributable to wild pollinators. For example, in New Jersey and Pennsylvania, wild bees provided 62 ± 5% of the total value of pollination services to watermelon ($9.95 million[16]) due to favorable environmental conditions that promote wild bee abundance in these regions.[18] Even fewer studies have related the value of pollination services to the occurrence of natural habitat as a primary determinant of bee community abundance, diversity, and pollination function. In Indonesia, where the increase in coffee production from animal-mediated pollination is due entirely to wild bees,[24] the increase in the value of coffee production due to the presence of natural habitat was estimated at €46/ha (approximately $26 per acre), and the value of coffee production was projected to decline by 0.3–13.8% as natural habitat cover decreased under differing scenarios of land-use change over a 20-year period.[25] In Canada, Morandin and Winston estimated that canola farmers could return up to 30% of their fields to forb-filled meadows without losing value, since canola yields increased with pollinator abundance and diversity, which was strongly related to the proportional area of meadowlands.[17] While these spatially explicit studies have been limited in scope to one crop, studies with broader scope[23] have not been spatially explicit. This study is the first to integrate spatial information into a large-scale, multicrop database.

Many economic valuation studies on pollination have been conducted without considering the ecology of the system: the reliance of the pollinators on off-farm habitat for floral resources or nesting and overwintering sites or the pollinators' foraging range. In the example that follows, we explore a method of estimating the economic value of wild bee pollination services for Californian agriculture based on the amount and location of natural habitats relative to California's agricultural production areas. We used results from a field study that established the relationship between natural habitat and wild pollination services in California's Central Valley,[1] and we extrapolated this relationship to other crops and agricultural landscapes in California using spatial landcover data to generate both a statewide estimate and a map of this ecosystem service. While such an extrapolation makes a number of assumptions, and while results must be interpreted with caution, it is a first step toward integrating ecological data into a spatial model for economic valuation. We present these results as a case-study of spatially explicit ecological/economic valuation, while recognizing the limitations of the current data and identifying improvements that could be made with the addition of further data.

Case Study: Value of Wild Bee Pollination Services to California Agriculture

We estimated in four steps the value of wild bee pollination in California using ecological data. First, we classified California crops according to their dependence on animal pollinators and multiplied this by commodity economic data to obtain the total value of pollination service (PS_T) for each crop by county.[23] Second, we selected land cover types capable of providing habitat for wild pollinator species, creating a geospatial dataset of pollinator-relevant natural and seminatural habitats. Third, using a pre-established relationship between natural habitat and the proportion of pollination needs met, we generated another geospatial dataset translating pollinator-relevant habitat surrounding cropland to a pollination services index. Finally, we calculated the pollination service value from wild pollinators by multiplying the pollination received (from Step 3) by the total value of pollination to the crops (from Step 1).

Step 1: Calculating PS_T to Crops in California

Klein et al.[6] categorized globally produced crop species into five categories based on the reduction of fruit or seed set in the absence of animal pollinators: "Essential" (> 90% yield reduction without pollinators), "Great" (40–90% reduction), "Modest" (10–40% reduction), "Little" (<10% reduction), and "No increase" (no change without pollinators). We used this information to classify the 130 crops grown in California according to their pollination dependence.

We obtained commodity-value data from the USDA National Agriculture Statistics Service's County Agricultural Commissioner's Data for 2007.[26] Each county reports the acreage, yield, sales price, and value (price × yield) of each crop planted. We multiplied the value of each crop in each county by its amount of pollination dependence to estimate the value of pollination services for each crop in each county (PS_{crop}). Because the Klein et al.[6] data indicated a range of yield reduction in the absence of pollination, we estimated a lower and upper bound for PS_{crop}. These upper and lower bounds for PS_{crop} were each then summed for all crops in a given county to provide a total countywide estimate of the upper- and lower-bound values of pollination services ($PS_{Tcounty}$).

The values for $PS_{Tcounty}$ could also be summed across all counties to give a statewide estimate of PS_T. This value represents the total potential value of pollination to California agriculture if pollination needs are met by any pollinator (wild or managed honeybee stocks), for comparison against the value of pollination services from wild pollinators (PS_W), as described below.

Some crops that were lumped into broader unspecified groups by the USDA (such as "seed–unspecified," "fruit and vinecrop–unspecified," "row crops–unspecified," etc.) could not be classified according to pollinator dependence, and these were omitted from the analysis. These crops represent a value of $973.38 million (3% of the total economic value of nonanimal crops in California). We did not include animal products (worth an additional $13.5 billion per year) or animal-related crops (i.e., pasture, silage, or hay, together worth $2.1 billion per year) in our estimates of agricultural value, although these products may rely on pollinator-dependent forage such as alfalfa.

Step 2: Selecting Pollinator-Relevant Habitat

We used the national LANDFIRE Existing Vegetation Type (EVT) dataset to create our pollinator-relevant natural habitat map. The LANDFIRE EVT data product (30-m resolution) was developed using Landsat imagery (2000–2002), biophysical gradient data, and a classification and regression tree (CART)-based predictive modeling approach to assign NatureServe's Ecological Systems vegetation types[27] to each 30-m pixel.[28]

We inspected the 144 vegetation types of NatureServe's Ecological Systems that fell within 2.4 km of any agricultural land parcel in this dataset, classifying them based on their importance to pollinators (yes = important habitat that would be used by pollinators, no = not important, and maybe = possibly important, see below). We chose a radius distance of 2.4 km because it was the scale determined by Kremen et al.[1] to be most predictive of pollination services in a multiscale spatial analysis of the role of natural habitat in explaining pollinator abundance, diversity, and crop pollination services on farm sites in Yolo County, California. Pollinator-relevance was determined for each vegetation type based on the presence of plant species attractive to pollinators and cover criteria, as described in the NatureServe documentation that accompanies the legend for the LANDFIRE dataset.[29] Plant species that would be used by pollinators for floral resources were identified using lists provided by the Xerces Society,[i] the USDA's Agricultural Research Service,[ii] and relevant plant-pollinator interaction data from California natural habitats,[30] and they are listed in Supplemental Table 1 (see supplemental materials online at http://dx.doi.org/10.2111/ RANGELANDS-D-11-00002.s1).

For shrubland and herbaceous vegetation types, if the vegetation type contained two or more plant species providing floral resources to pollinators, it was included as relevant pollinator habitat ("yes"). For forest and woodland vegetation types, we utilized data on canopy cover from the LANDFIRE Existing Vegetation Cover (EVC) dataset[28] as an additional variable to determine habitat suitability for pollinators. We considered forest and woodland habitats, when listed as containing pollinator-relevant plants, to be unsuitable as pollinator habitat when occurring in dense stands (> 60% canopy closure, defined by LANDFIRE as "closed" or "dense"), because dense forests stands provide relatively few floral resources in their understory and have cooler, darker microclimates less favorable to pollinator activity. We considered such habitats to be suitable when occurring with an open canopy (< 60% canopy closure). When species information was incomplete for a vegetation type, or if only one pollinator-relevant plant species was present, we assigned the vegetation type to a "maybe" category, which we included or excluded to determine the sensitivity of the analysis to uncertainty in pollinator habitat. There were 16 vegetation types in the "maybe" category, accounting for 14,000 km^2 (5,400 square miles), or approximately 3–4% of the entire California area.

The LANDFIRE land cover map was converted from existing vegetation types to a binary grid (relevant pollinator habitat = 1 and irrelevant habitat = 0), using ESRI ArcGIS software.[31] Two maps were generated: a "yes" map that only included habitat in the "yes" category as relevant pollinator habitat, and a "yes/maybe" map that included both the "yes" and "maybe" categories as relevant pollinator habitat. Only natural habitat (which in our definition includes all unmanaged vegetation types, even those containing invasive species) was considered when creating this map of relevant pollinator habitat. We did not consider the role of farmlands or residential areas, even though such habitats also provide habitat for bees,[9,18] because our goal was to quantify the ecosystem service of pollination provided by natural and seminatural habitats.

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[i] Available at: http://www.xerces.org/Pollinator_Insect_Conservation/generalplantsforbees.htm.

[ii] Available at: http://www.ars.usda.gov/Research/docs.htm?docid=12052.

Step 3: Estimating the Pollination Services Index for Wild Pollinators

Using an empirical relationship between natural habitat and the proportion of pollination needs met,[1] we generated another set of maps translating pollinator-relevant habitat surrounding cropland to a pollination services index (PSI). We calculated the proportion of relevant natural habitat within a 2.4-km radius of each agricultural pixel, with a circular moving window, using ESRI ArcGIS software.[31] We then used this proportion in the following equation to determine an index of pollination services provided by wild pollinators.

$$\mathrm{PSI} = 0.001 \times e\,{}^\wedge\!\left[5.3222964 + \left(3.7181972 \times \text{proportion of pollinator habitat}\right)\right]$$

The equation was based on the observed empirical relationship between the proportion of natural habitat and pollen deposition (a measure of pollination services) from wild pollinators on watermelon, at 22 fields situated along a spatial gradient in Yolo County, California, from farms surrounded by natural habitat to isolated farms.[1 (Fig. 4)] Watermelon is a pollinator-dependent crop in the "Essential" category.[6] Each flower requires multiple visits by bees to receive enough pollen (approximately 1,000 grains) to set a fruit.[32] The original empirical relationship modeled pollen deposition,[1] but it was modified here (by multiplying by 0.001) to model the sufficiency of pollination services. In extrapolating to other crops, we reasoned that watermelon serves as a conservative indicator for the sufficiency of pollination services. Because watermelon has relatively high demands both for pollen deposition and number of visits to achieve fruit set, when watermelon receives sufficient services from wild bees, we might expect that other less-demanding crops do also. In addition, watermelon is a good indicator crop because it attracts a large number of bee species across a range of sizes and morphologies, many of which visit other crops.[1,19]

This equation was applied to the entire statewide dataset, first for all relevant habitat ("yes") and then for all relevant and possibly relevant ("yes/maybe") habitat. When the formula produced PSI > 1, we capped the values at 1.0, since pollination services > 100% of pollination needs do not provide additional value.

Step 4: Calculating Value of PS_W

We calculated the value from PS_W for each agricultural pixel *i* by multiplying the PSI received by that pixel by the total value of pollination to the crops in that pixel. To obtain the total value of pollination to crops in a given pixel, we measured the total agricultural area in each county, as designated in the vegetation classes of the LANDFIRE EVT dataset. (The LANDFIRE estimate was used rather than the Agricultural Commissioner's data to maintain consistency with the rest of our spatial analysis; comparison revealed that the two datasets were similar within 5%.) We converted the upper- and lower-bound estimates of $PS_{Tcounty}$ to $PS_{Tcounty}$ per pixel by dividing by the number of pixels of agricultural land in each county. We then multiplied $PS_{Tcounty}$ per pixel by the PSI_i (maximum: 1.0) in that pixel to calculate the value of pollination service provided by wild pollinators from natural habitat at each pixel (PS_{Wi}).

$$\mathrm{PS}_{Wi} = \mathrm{PSI}_i \times \mathrm{PS}_{\mathrm{Tcounty}} \,/\, \text{pixel}$$

This generated four maps of PS_{Wi} (hereafter, scenarios): using upper- and lower-bound estimates of PS_T crossed against relevant habitat for both the "yes" and "yes/maybe" maps of relevant pollinator habitat. We calculated summary statistics for each county and for the State of California based on each of the four scenarios, using zonal statistics in ESRI ArcGIS software[31] to obtain the countywide and statewide values of annual ecosystem service value of wild pollinators to California agriculture.

Case-Study Findings: The Value of Pollination and Pollinators

The total crop value of California agriculture (not including animal products or pasture) is over $29 billion per year (10% of US total value[26]). Broken down into the pollinator-dependent categories defined by Klein et al.,[6] the "Essential" category makes up 1.3% of that total value; "Great" makes up 17.5%; "Modest" makes up 8.7%; "Little" makes up 12.3%; and "No increase" makes up 56.8% (unspecified crops that could not be categorized comprising the remaining 3.3%; Fig. 1, Supplemental Table 2—online at http://dx.doi.org/10.2111/RANGELANDS-D-11-00002.s1). Together, crops in the first four categories (hereafter "pollinator-dependent crops") were worth $11.7 billion in 2007, occupying over 2.5 million acres (37%) of nonpasture agricultural land.

PS_T (managed plus wild pollinators) for the state of California is $2.7–6.3 billion per year based on the lower to upper bounds of dependency values,[6] which comprises 23–54% of the total value of pollinator-dependent crops (Fig. 2). Pollination services to "Essential" crops account for 6.4–13.6% of the PS_T; "Great" crops account for 72.6–76.9%; "Modest" crops account for 9.5–15.8%; and "Little" crops account for 0–5.2%. The counties with the highest PS_T include Fresno, Kern, and Stanislaus (Supplemental Table 3—online at http://dx.doi.org/10.2111/RANGELANDS-D-11-00002.s1), due primarily to the large acreage of crops grown there but also the type of crops. Specifically, Stanislaus ranks seventh in total crop acreage compared to Fresno (ranked first) and Kern (ranked second), but has a larger proportion of "Great" crops (i.e., almonds and stone fruit) compared to other crops. When considering mean $PS_{Tcounty}$ per pixel of agricultural land within each county, the rankings shift substantially. Santa Cruz, San Diego, and Ventura counties enter the top ranks, partially due to the high proportion of "Great" crops (e.g., apple and avocado) grown there. Santa Cruz and Ventura counties also have high ratios of crop

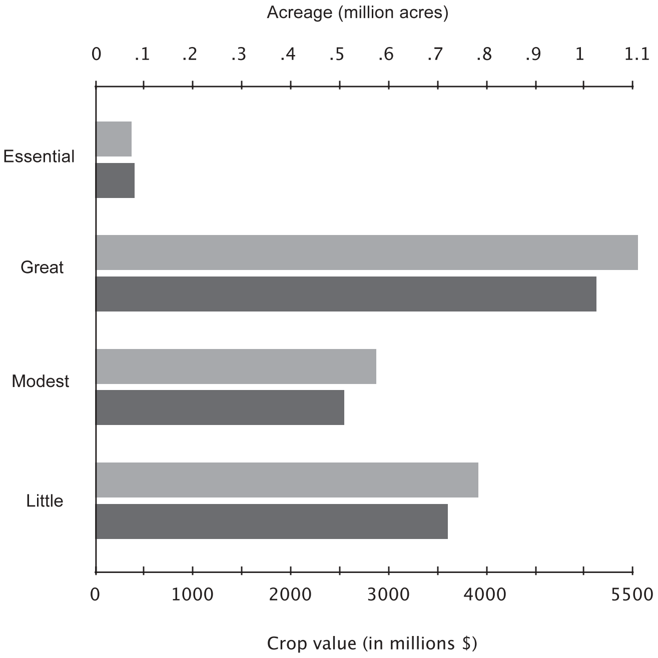

Figure 1. Crop values (darker bars) and harvested acreages (light bars) of pollinator-dependent crops in California, based on the categories defined by Klein et al.[6]

value to acreage (the second and fifth highest in the state, respectively).

The value of PS_W to California agriculture is between \$937 million and \$2.4 billion per year (Table 1). Fresno and Kern remain in the top three counties for PS_W, but they are topped by Tulare for both the high- and low-range estimates (Supplemental Table 3). Tulare also ranks highly on a per pixel basis, for both maximum and minimum values of PS_{Wi} (Fig. 3, Supplemental Table 3), along with Santa Cruz, San Diego, Orange, and Yuba counties. While PS_{Wi} for Santa Cruz and San Diego are likely driven by the crops' pollination dependency and value (as noted above, both of these ranked highly on $PS_{Tcounty}$ per pixel), Tulare and Yuba have high PSI scores and thus high PS_T per pixel due to the abundance of pollinator habitat grown in the vicinity of agricultural areas. Level of pollinator-dependence was a 100-fold greater source of uncertainty than the designation of "pollinator-relevant" habitat (Table 1, around \$1.5 billion for the difference between the upper- and lower-bound pollinator-dependence estimates vs. between \$6 million and \$17 million for the difference between the "yes" and "yes-maybe" cases of pollinator-relevant habitat).

Our calculation for PS_T (managed plus wild bees) was 9–21% of the total value of (nonanimal) crops produced in California, which at the upper range is higher than the global estimate (9.5%[7]), due to the relatively large acreages and high values of pollinator-dependent crops grown in the state. Our goal was to partition this total pollination service value into the values attributable to managed and wild bees; it is the wild bee contribution (PS_w) that constitutes the ecosystem service derived from nature.[8,22] According to our estimate, the proportion of total pollination services provided by wild bees in the state of California was 35–39%, substantially higher than Losey and Vaughan's[23] estimate of 15.3% for the United States, which assumed a constant ratio of wild to managed bees. In contrast, our spatially explicit estimation method utilized the empirically derived log-linear relationship between wild bee pollination services and the surrounding proportion of natural habitat[1] and is both more accurate and directly tied to the landscape composition of natural habitats surrounding agricultural areas.

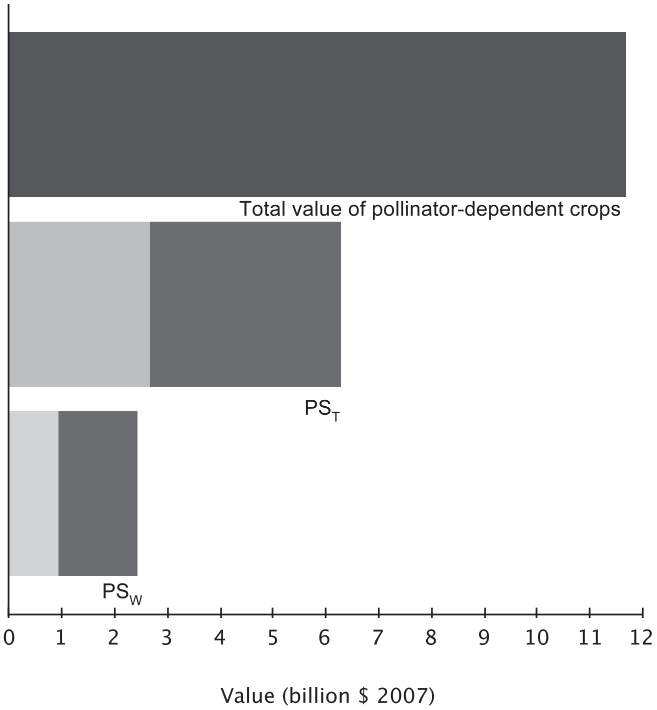

Figure 2. Value of pollinator-dependent crops, value of pollination services (PS_T, wild and managed), and value of pollination services from wild pollinators (PS_W) for California. The light bars show lower-bound estimates and the darker bars show the upper-bound estimates for PS_T and PS_W.

Case-Study Caveats and Limitations

Economic values of pollination services vary by orders of magnitude depending on the calculation method used (proportional production value or replacement cost methods[8]) and whether factors such as price elasticity and variable costs are included.[7,16] Our goal was to incorporate an additional level of ecological realism by utilizing field and landcover

Table 1. The four scenarios for pollination service value from wild pollinators (PS_W), in millions of 2007 dollars

Bound	Dependency estimate	Bee-relevant habitat	PS_W (millions)
Lowest	Lower	Yes	\$937.30
Mid–low	Lower	Yes–maybe	\$943.74
Mid–high	Upper	Yes	\$2,410.79
Highest	Upper	Yes–maybe	\$2,427.15

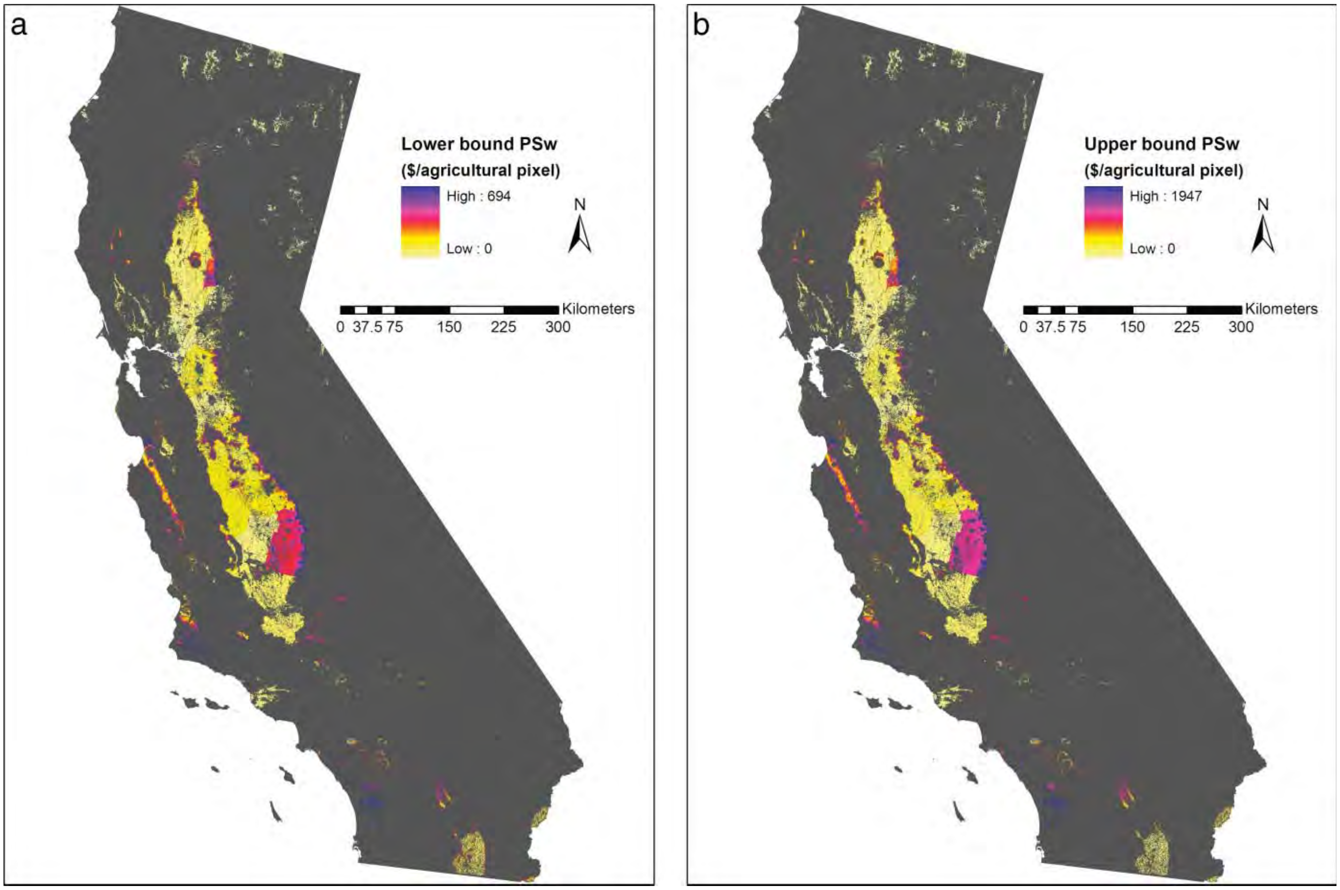

Figure 3. Map of pollination service value provided by wild pollinators per pixel (PS_{Wi}) for the (a) lowest (lower-bound dependence estimate with only "yes" pollinator habitat) and (b) highest (upper-bound dependence estimate with "yes" and "yes-maybe" pollinator habitats) scenarios. The main difference between scenarios is not where areas of high value occur, but the magnitude of that value (shown on scales inset at right of map). Values are shown in 2007 dollars per pixel of agricultural land. The large hotspot in the southeastern portion of the map is Tulare County.

data to generate a spatially explicit valuation of pollination services from wild bees. We used a single valuation method, the proportional dependence method,[8,23] that was feasible to apply to our large dataset. However, this method overestimates total values of pollination services because it ignores farmer behavior, which would tend to abate production losses due to absolute loss or increased costs of pollination services.[33] An improvement on the proportional dependence method subtracts the variable costs of production (e.g., harvesting costs) from the total crop value. These costs can vary depending on the level of pollination services and crop yield.[16] We did not attempt to make this correction because obtaining variable cost data for 85 crops over such a large geographic area was not feasible, and because the relative value of wild versus managed pollinators should not change due to the inclusion of variable costs (although relative values would change if managed pollinators are considered the primary pollinators and wild the secondary pollinators compared to vice versa[16]).

While in general, use of the production value method overestimates values of pollination services, sources of uncertainty specific to our study tend to underestimate pollination services. We underestimated total pollination-service value because in some cases the type of crop was unspecified or was not fully specified. If the unspecified crops, whose pollination dependencies cannot be determined, followed a similar distribution to the specific crops, we would have underestimated the total value of pollination in California agriculture by $91.8–216.1 million (3.4% of the lower versus upper estimate, respectively). If sunflower crops were grown exclusively for hybrid seed production, their dependence on pollinators would change from "Modest" to "Essential",[20] increasing the PS_T by $22.3–29.3 million (0.4–1.1%). Finally, we did not consider the value of pollination to meat or dairy production, despite the fact that pollinators are important to forage crops such as alfalfa.

We also likely underestimated the value of wild pollination services for California because our indicator crop, watermelon, requires a greater number of pollinator visits to produce a marketable fruit than many other crops.[32] Thus other crops may be sufficiently pollinated with fewer pollinators and less surrounding natural habitat. While the exact nature of the relationship between natural habitat and wild bee abundance, diversity, and pollination services may change

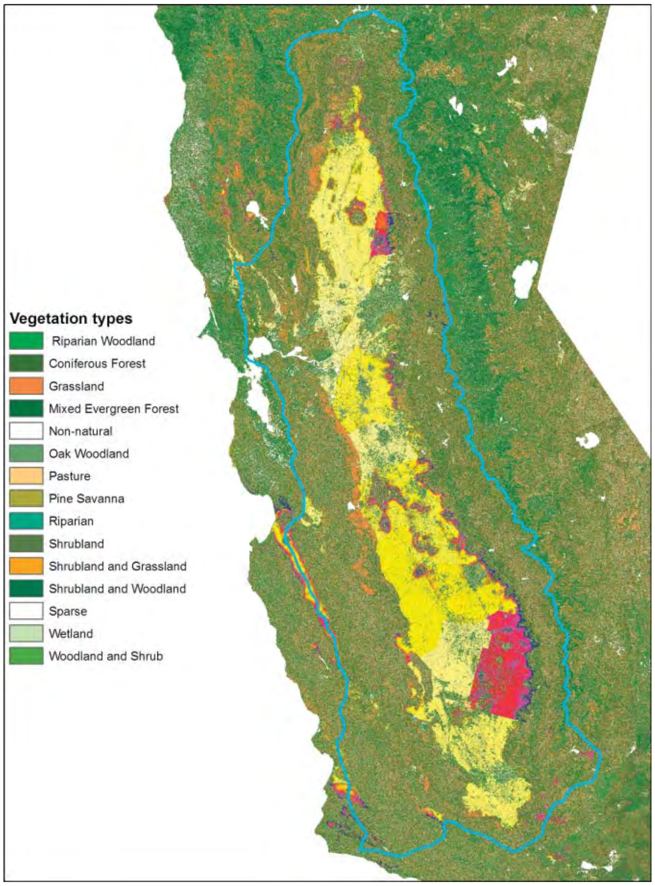

Figure 4. Map of pollination service value provided by wild pollinators (PS_W) overlaid on coarse categories of vegetation types. Grasslands are shown in orange, and they border much of the agricultural area receiving pollination services. Different types of forest are shown in various shades of green. Values of pollination services provided by wild pollinators (PS_{Wi}) are shown as in Figure 3. The blue boundary shows the priority conservation acquisition area for the California Rangeland Conservation Coalition (see http://www.carangeland.org/images/Rangeland_Coalition_Map.pdf for more detail), which encompasses much of the habitat important to providing pollination services to farmland.

from crop to crop, the positive relationship between natural habitat and wild bee pollination services of watermelon is repeated in our studies of almond (C. Kremen, unpublished data, 2009) and other crops (tomato[4] and sunflower[20]) in California and in a worldwide synthesis.[21] As more of these relationships are quantified, they could be incorporated into a more detailed analysis than was possible in this study with current data, but this case study represents a first step toward integrating spatially explicit ecological data into economic valuation.

Another source of error that may underestimate the true value of wildlands to pollination services is that we only considered vegetation types as suitable or potentially suitable pollinator habitat if they provided floral resources, but some habitats poor in floral resources may still provide regions suitable for nesting (e.g., the dense forest vegetation that we excluded) and contribute to pollinator abundance. Other models of pollination services can incorporate the value of nesting habitat separately from its value for floral resources.[34] Since we have not accounted for the nesting value of this vegetation type, we may have underestimated pollinator abundances on nearby farmland. Furthermore, we recognize that different vegetation types will provide greater or lesser value as pollinator habitat depending on the number and type of floral resources they provide. Our analysis simply selects all habitats that may contribute floral resources, without differentiating those that provide many or most of the resources needed to sustain pollinator communities from those providing only a few.

The spatial resolution of the crop data was available only at the county level, which required us to assume homogeneity of crop plantings at the countywide scale (all pixels were ascribed the same "basket" of crop types). At this resolution, hotspots on the pollination services map are typically counties with large areas of crops or small-to-large areas of high-value crops that receive a large amount of benefit from pollination services, either because the crops they grow are highly dependent on animal pollinators or because they are close to habitat that can meet their pollination needs, or both. Farm-level spatial data on crop plantings would improve the accuracy of the spatial model and the resulting countywide and statewide valuations, as well as the resolution of the map for conservation planning, permitting teasing apart areas that receive high benefit from pollination services due to habitat proximity from those growing high proportions of high value crops.

Conclusions and Applications

Much of the natural vegetation promoting the ecosystem service of pollination on farmlands is rangeland (Fig. 4). Rangelands have the potential to provide many ecosystem services simultaneously (e.g., forage, pollination services, carbon sequestration, etc.) and identifying these services and what factors contribute to maintaining them will help guide management practices to optimize ecosystem service provision. Therefore, mapping ecosystem services is essential to improving management in order to visualize areas of overlap and the connection between certain habitats. Furthermore, to the extent that the land providing these pollination services is unprotected, a map of pollination service values such as those provided here may provide important guidance for conservation prioritization of rangeland areas.[35] Despite the limitations of the analysis presented here, it furthers the ecologically grounded and spatially explicit economic valuation of pollination services and provides a methodology upon which future efforts can build. Continuing to integrate ecological, economic, and geospatial data will be necessary for future management of landscapes for the provision of vital ecosystem services such as pollination.

Acknowledgments

The authors wish to thank Carsten Goff and the LANDFIRE EVT, and the Geospatial Innovation Facility at UC Berkeley

for the spatial data and facilities to conduct these analyses. We thank Tiffany Shih and Chieko Plotts for their work on the initial stages of data acquisition.

References

1. Kremen, C., N. M. Williams, R. L. Bugg, J. P. Fay, and R. W. Thorp. 2004. The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecology Letters* 7:1109–1119.
2. 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. *Ecological Entomology* 30:78–85.
3. Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'Eman, and P. G. Willmer. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* 84:2628–2642.
4. Greenleaf, S. S., and C. Kremen. 2006. Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biological Conservation* 133:81–87.
5. Walker, R. A. 2004. The conquest of bread: 150 years of agribusiness in California. New York, NY, USA: The New Press. 382 p.
6. Klein, A. M., B. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of crop pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London Series B-Biological Sciences* 274:303–313.
7. Gallai, N., J. M. Salles, J. Settele, and B. E. Vaissiere. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics* 68:810–821.
8. Allsopp, M. H., W. J. De Lange, and R. Veldtman. 2008. Valuing insect pollination services with cost of replacement. *PLoS ONE* 3. (9): e3128. doi:10.1371/journal.pone.0003128.
9. Holzschuh, A., I. Steffan-Dewenter, and T. Tscharntke. 2008. Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos* 117:354–361.
10. Williams, N. M., E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation* 143:2280–2291.
11. Brittain, C. A., M. Vighi, R. Bommarco, J. Settele, and S. G. Potts. 2010. Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic and Applied Ecology* 11:106–115.
12. National Research Council. 2007. Status of pollinators in North America. Volume xiii. Washington, DC, USA: National Academy Press. 326 p.
13. Neumann, P., and N. L. Carreck. 2010. Honey bee colony losses. *Journal of Apicultural Research* 49:1–6.
14. 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 in Ecology & Evolution* 25:345–353.
15. Sumner, D. A., and H. Boriss. 2006. Bee-economics and the leap in pollination fees. *Giannini Foundation of Agricultural Economics Update* 9:9–11.
16. Winfree, R., and B. J. Gross. 2010. A new method for valuing crop pollination. *In*: B. Gross. Beneficial bees and pesky pesks [dissertation]. Berkeley, CA, USA: University of California. p. 7–25.
17. Morandin, L. A., and M. L. Winston. 2006. Pollinators provide economic incentive to preserve natural land in agroecosystems. *Agriculture Ecosystems & Environment* 116:289–292.
18. Winfree, R., and C. Kremen. 2009. Are ecosystem services stabilized by differences among species? A test using crop pollination. *Proceedings of the Royal Society B-Biological Sciences* 276:229–237.
19. Klein, A. M., C. M. Mueller, P. Hoehn, and C. Kremen. 2009. Understanding the role of species richness for pollination services. *In:* D. Bunker, A. Hector, M. Loreau, C. Perrings, and S. Naeem [eds.]. Biodiversity, ecosystem functioning, and human wellbeing: an ecological and economic perspective. New York, NY, USA: Oxford University Press. p. 195–208.
20. Greenleaf, S. S., and C. Kremen. 2006. Wild bees enhance honey bees' pollination of hybrid sunflower. *Proceedings of the National Academy of Sciences* 103:13890–13895.
21. Ricketts, T. H., J. Regetz, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, A. Bogdanski, B. Gemmill-Herren, S. S. Greenleaf, A. M. Klein, M. M. Mayfield, L. A. Morandin, A. Ochieng, and B. F. Viana. 2008. Landscape effects on crop pollination services: are there general patterns? *Ecology Letters* 11:499–515.
22. 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. Vazquez, R. Winfree, L. Adams, E. E. Crone, S. S. Greenleaf, T. H. Keitt, A. M. Klein, J. Regetz, and T. H. Ricketts. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* 10:299–314.
23. Losey, J. E., and M. Vaughan. 2006. The economic value of ecological services provided by insects. *BioScience* 56:311–323.
24. Klein, A. M., I. Steffan-Dewenter, and T. Tscharntke. 2003. Bee pollination and fruit set of Coffea arabica and C-canephora (Rubiaceae). *American Journal of Botany* 90:153–157.
25. Priess, J. A., M. Mimler, A. M. Klein, S. Schwarze, T. Tscharntke, and I. Steffan-Dewenter. 2007. Linking deforestation scenarios to pollination services and economic returns in coffee agroforestry systems. *Ecological Applications* 17:407–417.
26. USDA. 2007. Census of agriculture. Table 1. Historical highlights: 2007 and earlier census years. Available at: http://www.agcensus.usda.gov/Publications/2007/Full_Report/ Volume_1,_Chapter_1_US/index.asp. Accessed 16 September 2010. See also http://www.nass.usda.gov/Statistics_by_State/ California/Publications/AgComm/.
27. Comer, P., D. Faber-Langendoen, R. Evans, S. Gawler, C. Josse, G. Kittel, S. Menard, M. Pyne, M. Reid, K. Schulz, K. Snow, J. Teague. 2003. Ecological systems of the United States: a working classification of U.S. terrestrial systems. Arlington, VA, USA: NatureServe. 75 p.
28. U.S. Department of Interior, Geological Survey. 2006. The national map LANDFIRE national existing vegetation type layer. (Last updated September 2006.) Available at: http://gisdata.usgs.net/website/landfire/. Accessed 3 January 2010.
29. NatureServe. 2007. International ecological classification standard: terrestrial ecological systems of the United States. Natural heritage central databases. Arlington, VA, USA: NatureServe.

30. Williams, N. M., D. Cariveau, R. Winfree, and C. Kremen. 2010. Bees in disturbed habitats use, but do not prefer, alien plants. *Basic and Applied Ecology* doi:10.1016/j.baae.2010.11.008.
31. [ESRI] Environmental Systems Resource Institute [computer program]. 2009. ArcGIS 9.2. Redlands, CA, USA: ESRI.
32. Stanghellini, M. S., J. T. Ambrose, and J. R. Schultheis. 1997. The effects of honey bee and bumble bee pollination on fruit set and abortion of cucumber and watermelon. *American Bee Journal* 137:386–391.
33. Muth, M. K., and W. N. Thurman. 1995. Why support the price of honey. *Choices 2nd quarter*: 19–23.
34. Lonsdorf, E., C. Kremen, T. Ricketts, R. Winfree, N. Williams, and S. Greenleaf. 2009. Modelling pollination services across agricultural landscapes. *Annals of Botany* 103: 1589–1600.
35. Cameron, D. 2007. Biological prioritization of rangelands: approach and methods. California Rangeland Conservation Coalition. The Nature Conservancy. Available at: http://www.carangeland.org/images/Approach_and_Methods.pdf. Accessed 14 December 2010.

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Value of Wildland Habitat for Supplying Pollination Services to Californian Agriculture

by Rebecca Chaplin-Kramer, Karin Tuxen-Bettman and Claire Kremen

Supplemental Table 1. Plants utilized by wild pollinators, adapted from USDA's Agricultural Research Service ("Plants attractive to native bees") and the Xerces Society ("General plants for bees").

Genus	Common Name
Abelia	abelia
Acacia	acacia
Acer	maple
Achillea	yarrow
Aconitum	monkshood
Agastache	hyssop
Ajuga	carpet bugle
Althea	hollyhock
Allium	allium
Amelanchier	serviceberry
Anchusa	wild forget-me-not
Anethum	dill
Aquilegia	columbine
Arctostaphylos	manzanita
Argemone	prickly poppy
Armeria	sea thrift
Aster	aster
Astragalus	locoweed
Baileya	desert marigold
Baptisia	false indigo
Berberis	barberry
Borago	borage
Brassica	mustard
Calamintha	calamint
Callirhoe	wine cups, poppy mallow
Calluna	heather
Camissonia	camissonia
Campanula	bell flower
Caragena	Siberian peashrub
Carpobrotus	ice plant
Carthamnus	safflower
Caryopteris	blue mist spirea
Cassia	senna
Ceanothus	buckbrush
Centaurea	bachelor's button, corn flower
Cerastium	snow-in-summer
Cercidium	palo verde
Cercis	redbud
Cercocarpus	mountain mahogany
Chaenomeles	flowering quince
Chilopsis	desert willow
Chrysanthemum	chrysanthemum
Chrysothamnus	rabbit brush, chamisa
Citrullus	watermelon
Citrus	grapefruit, orange, lemon
Coronilla	crownvetch
Cucurbita	squash, gourd, pumpkin
Clarkia	clarkia
Cosmos	cosmos
Coriandrum	coriander
Coreopsis	coreopsis
Cuphea	false heather
Cydonia	fruiting quince
Cynara	artichoke, cardoon
Cynoglossum	comfrey
Daucus	carrot
Delphinium	larkspur
Digitalis	foxglove
Echinacea	cone flower
Echium	pride of Madeira
Erigeron	fleabane
Eriodictyon	yerba santa
Eriogonum	wild buckwheat
Eryngium	eryngo, button-celery
Erysimum	wallflower
Eupatorium	joe pye weed
Euphorbia	spurge
Ferocactus	barrel cactus
Foeniculum	fennel
Fragaria	strawberry
Fremontodendron	flannelbush
Gaillardia	blanket flower
Gaura	gaura
Gentiana	blue gentian
Geraea	desert sunflower
Geum	avens
Gilia	gilia
Glycyrrhiza	licorice
Grindelia	gumweed
Hackelia	wild formet-me-not
Hedeoma	sweetscent, mock pennyroyal
Hedysarum	sweet vetch, french honeysuckle
Helenium	sneezeweed
Helianthella	sunflower
Helianthus	sunflower
Heliotropium	heliotrope
Hibiscus	rose-of-sharon, hollyhock
Hieracium	hawkweed
Holodiscus	cliff spirea, mountainspray
Hymenopappus	false cosmos
Hymenoxys	alpine sunflower
Hyptis	desert lavendar
Ilex	holly
Iliamna	mountain hollyhock
Kallstroemia	Arizona poppy
Keckiella	bush penstemon
Lamium	dead nettles
Larrea	creosote bush
Lathyrus	everlasting pea
Lavendula	lavendar
Layia	tidytips
Lespedeza	bush clover
Lesquerella	bladderpod
Liatris	blazing star
Limnanthes	meadowfoam, fried egg flower
Linanthus	mountain phlox
Linaria	toadflax
Linum	flax

Genus	Common Name
Lotus	birdsfoot trefoil, lotus
Lycium	wolfberry
Mahonia	mahonia
Malus	apple
Malva	mallow
Medicago	alfalfa, medic
Melilotus	sweet clover
Mentha	mint
Mentzelia	blazing star
Mertensia	bluebells
Mimulus	monkey flower
Monarda	bee balm
Myoporum	myoporum
Nemophila	blue eyes
Nepeta	catmint
Ocimum	basil
Oenothera	evening primrose
Opuntia	pear cactus
Origanum	oregano
Oxydendrum	sourwood
Oxytropis	locoweed
Parkinsonia	Mexican palo verde
Pedicularis	lousewort
Penstemon	penstemon
Perovskia	Russian sage, filigran
Petalostemon	prairie clover
Phacelia	bluebells, scorpionweed
Phyllodoce	mountain-heath
Physalis	groundcherry
Physocarpus	ninebark
Physostegia	obedient plant
Pieris	fetterbush
Platystemon	creamcups
Polemonium	Jacob's ladder
Pontederia	pickerelweed
Prosopis	mesquite
Prunella	henbit
Prunus	cherry, plum
Psorothamnus	dalea
Purshia	cliff rose
Pycnanthemum	mountain mint
Raphanus	mustard
Ratibida	Mexican hat
Rhamnus	buckthorn
Rhus	sumac
Ribes	currant
Robinia	black locust
Romneya	Matilija poppy
Rosa	rugosa-type and wild roses
Rosmarinus	rosemary
Rubus	raspberry, blackberry, brambles
Rudbeckia	black-eyed susan
Salix	willow
Salvia	salvia

Genus	Common Name
Sambucus	elderberry
Scabiosa	pincushion flower
Sedum	sedum, stonecrop
Senecio	senecio
Sidalcea	checkermallow
Silybum	milk thistle
Solanum	nightshade
Solidago	goldenrod
Sphaeralcea	globemallow
Spiraea	spiraea
Stachys	lamb's ear
Stanleya	prince's plume
Sympytum	comfrey
Talinum	flame flower
Tanacetum	tansy
Tecoma	yellow trumpet bush
Teucrium	germander
Thermopsis	false lupine, golden pea
Thymus	thyme
Tilia	basswood
Tithonia	Mexican sunflower
Trichostema	bluecurls
Trifolium	clover
Vaccinium	blueberry, cranberry
Valeriana	valerian
Verbena	verbena
Verbesina	golden crownbeard
Veronica	speedwell, veronica
Viburnum	arrowood, snowball bush
Vicia	vetch
Viguiera	showy golden-eye
Viola	violets
Wyethia	mules ear
Zinnia	zinnia

Supplemental Table 2. Crop value (in millions of dollars, 2007) and harvested acreage for the four categories of pollinator-dependent crops grown in California.

	Crop	Value (million $)	Acreage
ESSENTIAL	melons, cantaloupe	168.37	35,404
Total Value (million $):	melons, watermelon	76.80	11,310
402.38	melons, honeydew	56.26	12,226
Total Acreage:	kiwifruit	44.75	3,747
74,388	squash	31.37	5,727
	pumpkins	15.54	4,649
	quince	6.97	340
	tomatillo	1.84	411
	seed clover	0.28	513
	macadamia nuts	0.19	61
GREAT	almonds	2,799.51	713,790
Total Value (million $):	peaches	539.51	75,553
5,127.01	plums	387.88	106,342
Total Acreage:	cherries	326.15	29,925
1,109,788	nectarines	271.09	35,108
	avocados	268.93	64,521
	raspberries	165.06	3,489
	apples	107.63	15,999
	pears	76.89	13,244
	blueberries	51.90	2,331
	apricots	45.25	11,275
	seed alfalfa	35.15	31,031
	bushberries	20.31	756
	cucumbers	15.88	3,698
	plumcots	14.76	2,645
	blackberries	1.05	63
	boysenberries	0.07	18
MODEST	strawberries	1,624.16	36,057
Total Value (million $):	cotton	801.53	470,661
2,545.24	pomegranates	43.16	12,514
Total Acreage:	sunflower seed	36.64	44,235
575,359	figs	23.01	9,709
	eggplant	14.91	1,572
	okra	0.75	223
	guavas	0.62	154
	chestnuts	0.29	62
	beans, fava	0.17	172
LITTLE	tomatoes	1,357.97	360,476
Total Value (million $):	oranges	1,103.53	189,774
3,608.49	lemons	435.12	44,534
Total Acreage:	peppers, bell	226.35	20,446
783,271	tangerines & mandarins	121.30	15,741
	beans (snap, lima, kidney, pink, blackeye)	107.61	75,203
	citrus, unspecified	84.73	5,968
	grapefruit	65.97	11,628
	dates	48.62	5,988
	safflower	22.24	47,934
	persimmons	15.94	2,380
	peppers, chili	11.92	1,715
	tangelos	4.73	828
	kumquats	1.19	224
	limes	0.98	351
	peanuts	0.29	81

Supplemental Table 3. Total pollination service value (PS_T) and pollination service value from wild pollinators (PS_W) by county. $PS_{T/px}$ is the value of PS_T per pixel, which is the same for all pixels in a county. Lowest PS_{Wi} is the minimum value for a pixel in the lowest scenario (Figure 3a); highest PS_{Wi} is the maximum value for a pixel in the highest scenario (Figure 3b).

County	Lower PS_T	Upper PS_T	Lower $PS_{T/px}$	Upper $PS_{T/px}$	Lowest PS_W	Highest PS_W	Lowest PS_{Wi}	Highest PS_{Wi}
Butte	73,393,400	156,714,460	64.03	136.72	22,526,000	48,602,100	19.65	42.40
Calaveras	12,240	27,234	0.53	1.18	12,223	27,197	0.53	1.18
Colusa	51,576,000	120,278,210	36.20	84.42	14,320,500	34,882,900	10.05	24.48
Contra Costa	2,075,930	5,226,560	9.90	24.91	724,807	1,831,390	3.45	8.73
El Dorado	4,227,200	9,405,520	112.01	249.21	4,137,610	9,206,190	109.63	243.93
Fresno	607,324,100	1,306,516,510	111.96	240.86	145,532,992	313,429,000	26.83	57.78
Glenn	56,617,800	127,692,870	53.58	120.83	15,542,800	35,768,500	14.71	33.85
Imperial	234,056,300	85,577,340	61.11	81.53	24,212,700	32,700,900	23.07	31.15
Kern	75,658,000	574,756,430	33.47	150.05	60,911,300	149,928,000	15.90	39.14
Kings	5,590,160	214,018,900	96.42	94.69	17,075,800	48,340,100	7.56	21.39
Lake	94,640	12,438,106	0.43	214.53	3,911,640	8,703,400	67.47	150.11
Lassen	616,800	210,574	7.85	0.96	63,037	182,447	0.29	0.83
Los Angeles	107,398,700	1,876,220	79.25	23.88	518,287	1,576,570	6.60	20.06
Madera	7,338,960	244,654,770	76.96	180.53	36,687,100	83,830,700	27.07	61.86
Mendocino	172,423,100	16,329,186	86.39	171.23	5,224,980	11,625,600	54.79	121.91
Merced	72,353,200	391,655,770	78.26	196.23	59,495,700	137,576,000	29.81	68.93
Monterey	4,443,500	263,679,850	136.73	285.19	38,572,500	141,784,000	41.72	153.35
Orange	681,150	16,639,147	2.34	512.01	2,423,150	9,073,760	74.56	279.21
Placer	38,148,630	1,807,639	76.64	6.21	510,609	1,367,740	1.75	4.70
Riverside	12,583,700	89,104,529	15.18	179.02	22,666,300	52,949,100	45.54	106.38
Sacramento	3,276,000	27,566,000	18.63	33.25	5,029,850	11,082,200	6.07	13.37
San Benito	2,114,440	10,908,180	16.52	62.04	1,801,550	6,002,200	10.25	34.14
San Bernardino	60,428,130	4,679,389	256.35	36.57	1,609,680	3,562,320	12.58	27.84
San Diego	199,431,600	150,957,992	84.86	640.40	54,584,800	136,360,000	231.56	578.48
San Joaquin	8,837,100	429,943,560	32.08	182.95	52,609,100	113,922,000	22.39	48.48
San Luis Obispo	1,072,900	29,915,140	29.40	108.61	6,461,410	21,886,300	23.46	79.46
San Mateo	43,922,030	1,580,020	103.41	43.30	891,943	1,393,930	24.44	38.20
Santa Barbara	4,731,830	147,253,854	43.60	346.68	31,446,200	105,430,000	74.03	248.21
Santa Clara	56,985,200	11,893,517	694.33	109.58	3,235,110	8,147,570	29.81	75.07
Santa Cruz	4,860,800	159,778,850	6.78	1946.81	36,803,900	105,968,000	448.43	1291.16
Solano	2,856,840	14,631,638	11.73	20.39	1,702,420	5,139,790	2.37	7.16
Sonoma	246,367,100	6,356,469	187.63	26.11	2,060,520	4,587,870	8.46	18.84
Stanislaus	84,373,340	548,533,250	0.00	417.75	9,964,200	21,115,700	7.59	16.08
Sutter	20,263,040	68,739,100	50.98	52.41	18,192,900	41,092,300	13.87	31.33
Tehama	186,404,500	45,085,264	68.36	113.42	16,405,800	39,790,500	41.27	100.10
Tulare	86,991,900	446,886,030	225.14	163.88	170,175,008	569,046,000	62.41	208.68
Ventura	18,165,020	289,533,010	12.30	749.34	3,156,320	8,646,340	8.17	22.38
Yolo	13,550,300	49,760,812	31.16	33.69	14,111,100	28,094,200	9.55	19.02
Yuba	2,667,468,180	26,806,080	836.85	61.65	31,983,600	72,497,400	73.56	166.74

By Michelle Solga

Buzzing the Literature

This section is an invited contribution that reviews new publications available about pollinators. Copies of these publications can be obtained by contacting the respective publishers or senior authors (addresses shown in parentheses).

Pollinator Decline

Reconstruction of historical pollination rates reveals linked declines of pollinators and plants. A. Pauw and J. A. Hawkins. 2011. *Oikos* 120:344–349. (Dept of Botany and Zoology, Stellenbosch Univ, Private Bag X1, Matieland, 7602, South Africa.) Recent declines in pollinators have been associated with the concern over loss of pollination services, although specific evidence of pollination loss has been difficult to come by. In this research, a new method was devised to analyze present and historical plant-pollinator relationships using the oil-collecting bee *Rediviva peringueyi* and the oil-secreting orchid *Pterygodium catholicum* as study species. When historical pollination rates were compared to present rates, a decline in the pollination and abundance of this orchid was found.

Global pollinator declines: trends, impacts and drivers. S. G. Potts, J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. *Trends in Ecology and Evolution* 25:345–353. (Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, Univ of Reading, Reading RG6 6AR, UK.) A review highlighting the declining trend in pollinators, the potential causes of their decline, and the potential impact of pollinator decline on ecosystem services.

Bee Conservation

Translating research into action; bumblebee conservation as a case study. D. Goulson, P. Rayner, B. Dawson, and B. Darvill. 2011. *Journal of Applied Ecology* 48:3–8. (Bumblebee Conservation Trust, Univ of Stirling, Stirling FK9 4LA, UK.) Evidence of bumblebee declines in Europe, Asia, and North America warrant an increase in conservation efforts for this pollinator. In order for bumblebee conservation efforts to be successful, existing knowledge derived from research needs to be communicated to governmental policy makers, as well as land managers that implement on-the-ground conservation practices.

Forage use and niche partitioning by non-native bumblebees in New Zealand: implications for the conservation of their populations of origin. G. C. Lye, J. C. Kaden, K. J. Park, and D. Goulson. 2010. *Journal of Insect Conservation* 14:607–615. (School of Biological and Environmental Sciences, Univ of Stirling, Stirling, FK9 4LA, UK.) Four bumblebee species native to Britain were introduced into New Zealand starting in 1885, providing an opportunity to study these species from a conservation standpoint. Of these four species, one is extinct, two are declining, and one is considered common in Britain. In New Zealand these four species have an overlap in forage use, thought to be caused by the scarcity of diverse forage resources in the area. In Britain declining abundance of the preferred forage resources of these bumblebees is offered as a potential cause for their decline.

The plight of the bees. M. Spivak, E. Mader, M. Vaughn, and N. H. Euliss, Jr. 2011. *Environmental Science and Technology* 45:34–38. (University of Minnesota, St. Paul, MN 55108, USA.) This review presents the contemporary causes for native and honey bee decline and potential solutions for mitigating this decline.

The montane bee fauna of north central Washington, USA, with floral associations. J. S. Wilson, L. E. Wilson, L. D. Loftis, and T. Griswold. 2010. *Western North American Naturalist* 70:198–207. (Dept of Biology, Utah State Univ, 5305 Old Main Hill, Logan, UT 84322-5305, USA.) The mountainous areas of north central Washington include habitats that range from shrub steppe to high-elevation alpine meadows, which are home to diverse assemblages of native bees and forbs.

The conservation and restoration of wild bees. R. Winfree. 2010. *Annals of the New York Academy of Sciences Year in Ecology and Conservation Biology 2010,* 1195:169–197. (Dept of Entomology, Rutgers Univ, New Brunswick, NJ 08901, USA.) This review discusses the economical and ecological contributions made by native bees, potential causes of native bee decline, and the importance of bee conservation.

Habitat

Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. R. Grundel, R. P. Jean, K. J. Frohnapple, G. A. Glowacki, P. E. Scott, and N. B. Pavlovic. 2010. *Ecological Applications* 20:1678–1692. (US Geological Survey, Great Lakes Science Center, 1100 North Mineral Springs Road, Porter, IN 46304, USA.) Native bee communities responded positively to environmental factors such as plant diversity, resources for nesting, and fire history and negatively to forest canopy cover.

Bee communities (Hymenoptera: Apoidea) of small Iowa hill prairies are as diverse and rich as those of large prairie preserves. S. D. Hendrix, K. S. Kwaiser, and S. B. Heard. 2010. *Biodiversity and Conservation* 19:1699–1709. (Dept of Biological Sciences, Univ of Iowa, 134 Biology Building, Iowa City, IA 52242-1324, USA.) Small hill prairie remnants in northeast Iowa can provide floral resources for native bees; however, their visitation may be influenced by surrounding landscape features such as agricultural row crops and open water.

How many flowering plants are pollinated by animals? J. Ollerton, R. Winfree, and S. Tarrant. 2011. *Oikos* 120: 321–326. (School of Science and Technology, Univ of Northampton, Avenue Campus, Northampton, NN2 6JD, UK.) Pollination is important in providing increased genetic diversity to plants, as some plants are unable to reproduce or set their seed without this vital service. This study uses 42 published and unpublished surveys to compile a community-level comprehensive data set of animal pollinated plants.

Reproduction of *Echinacea angustifolia* in fragmented prairie is pollen-limited but not pollinator-limited. S. Wagenius and S. P. Lyon. 2010. *Ecology* 91:733–742. (Div of Plant Biology and Conservation, Chicago Botanic Garden, 1000 Lake Cook Road, Glencoe, IL 60022, USA.) *Echinacea angustifolia*, a native tallgrass prairie forb, is common in small prairie remnants of the Midwest. Pollinator visitation was greater in isolated plants, but reproduction of *E. angustifolia* under these circumstances did not increase.

Environmental Disturbance

The effect of invasive *Lythrum salicaria* pollen deposition on seed set in the native species *Decodon verticillatus*. E. M. DaSilva and R. D. Sargent. 2011. *Botany* 89:141–146. (Dept of Biology, Univ of Ottawa, 30 Marie-Curie Street [160 Gendron Hall], Ottawa, ON K1N 6N5, Canada.) Invasive plants have the potential to compete with native plant species for pollinators ultimately affecting the native plant's fitness. In a glasshouse experiment, native loosestrife *Decodon verticillatus* showed a decrease in seed set when hand pollinated with a mixture of conspecific and heterospecific pollen from the invasive wetland plant *Lythrum salicaria* when compared to pollination with conspecific pollen alone.

Ecological and life-history traits predict bee species responses to environmental disturbances. N. M. Williams, E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. *Biological Conservation* 143:2280–2291. (Dept of Entomology, Univ of California, One Shields Ave, Davis, CA 96616, USA.) A global analysis of 19 studies determined that life history and ecological traits can influence the response of bees to anthropogenic disturbances. These results in turn aid land managers and stakeholders in future land use decisions.

Ecosystem Restoration

Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. M. H. M. Menz, R. D. Phillips, R. Winfree, C. Kremen, M. A. Aizen, S. D. Johnson, and K. W. Dixon. 2011. *Trends in Plant Science* 16:4–12. (Botanic Gardens and Parks Authority, King's Park and Botanic Garden, Fraser Ave, West Perth 6005, Australia.) Plant-pollinator interactions should be considered in restorations of degraded ecosystems. Restoration ecologists and pollination biologists need to work in tandem to ensure a sustainable habitat is provided that will benefit native pollinators.

Management Factors

Impacts of a pesticide on pollinator species richness at different spatial scales. C. A. Brittain, M. Vighi, R. Bommarco, J. Settele, and S. G. Potts. 2010. *Basic and Applied Ecology*

11:106–115. (Centre for Agri-Environmental Research, Univ of Reading, Reading RG6 6AR, UK.) Effects of the insecticide fenitrothion in vine fields in Italy was investigated for its effect on wild pollinators. Cultivated and uncultivated systems were compared, and pollinators were sampled at three spatial scales. Wild bees, as compared to bumblebees or butterflies, showed particular sensitivity to the effects of this insecticide.

Management tradeoffs between focal species and biodiversity: endemic plant conservation and solitary bee extinction. P. M. Severns and A. R. Moldenke. 2010. *Biodiversity and Conservation* 19:3605–3609. (Dept of Botany and Plant Pathology, Oregon State Univ, Corvallis, OR 97331, USA.) Land management choices can have implications to biodiversity of a habitat that are unintended. Management that promoted eradication of one species to promote endemic plant conservation had negative consequences on a rare solitary bee that was dependent on the eradicated floral resource. Management practices should be evaluated for unintended consequences that can have negative impacts on the biodiversity of an area.

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VOLUME 59, NUMBER 3, MAY 2006

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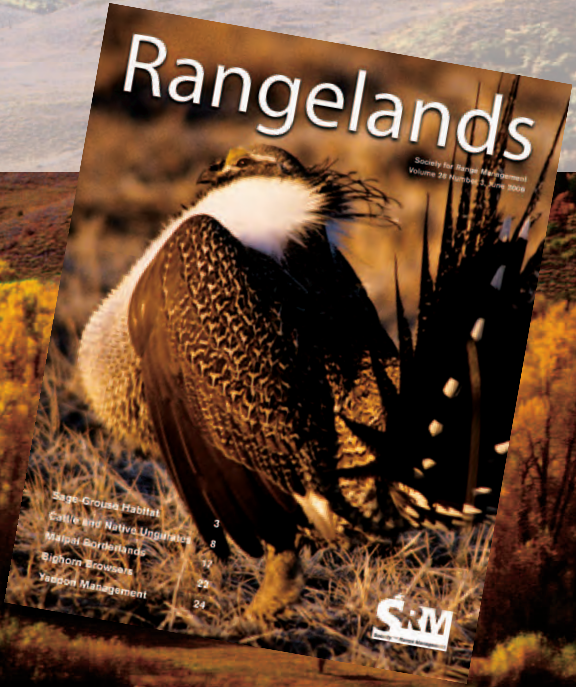

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