

## Effects of environmental stressors on bees in the southwestern United States

### **Introduction**

Bees are dominant pollinators of wild and commercial plants in terrestrial ecosystems; an estimated 75% of leading global food crops and 88% of flowering plants depend on animal pollination, predominantly from bees (Klein et al. 2007, Ollerton et al. 2011). Because of their keystone role as pollinators, there is great concern about the impact of environmental change on bee communities. Both wild and managed bee populations have sustained considerable declines in recent decades (Biesmeijer et al. 2006, Potts et al. 2010, Cameron et al. 2011). Bees are threatened by many factors including floral resource scarcity (Roulston and Goodell 2011), pathogen infection (Goulson et al. 2015), habitat loss (Potts et al. 2010), and pesticide exposure (Rundlöf et al. 2015), and they can be exposed to risks across landscapes as they forage widely for pollen and nectar. Understanding the factors driving plant-pollinator dynamics is important for both conservation and agriculture (Kearns et al. 1998).

There are over 4,500 different bee species in North America, and the southwestern United States is a biodiversity hotspot for both bees and plants. There have been 68 bee genera recorded in southern Arizona alone, with over 1,000 species estimated in the area (Terry Griswold, SWRS Bee Genera List). The southwestern United States' wide diversity of ecological habitats supports these plant-pollinator communities. Notably, Grand Canyon National Park hosts five major ecosystems spanning the elevation gradient, from riparian and desert scrub habitats at low elevations to the Pinyon-Juniper woodlands, Ponderosa Pine forest, and mixed conifer forests at higher elevations (US Geological Survey n.d.). These elevational gradients, along with variation in precipitation, create unique habitats for a diversity of bees and plants to live (Huenneke et al. 2015). However, bees in the southwestern United States face considerable challenges today and projected in the future.

In this paper, I will review the effects of environmental stressors on bees in the southwestern United States, focusing on specific threats to bee health and population persistence.

### **The role of resources in bee biology and health**

Understanding the effects of environmental stressors on bees requires knowledge about bees' fundamental resource and habitat requirements and how they may modulate responses to environmental stressors. The two resources most critical to bee survival and reproduction are food and nesting resources.

#### *Food resources*

Bees eat pollen and nectar from flowers, and these resources comprise their primary food source as both larvae and adults (Michener 2000). Floral resources are a major driver of bee abundance and diversity (Roulston and Goodell 2011). The quality, quantity, and distribution of floral resources are primary drivers of bees' reproductive success, community structure, abundance, and richness (Potts et al. 2003, Williams and Kremen 2007). One example of this is a study that

looked at a solitary bee specialist, *Andrena hattorfiana*, and its host plant, *Knautia arvensis*. The authors found that the population of the bee correlated strongly with the population size of the host plant (Larsson and Franzén 2007). Bees vary widely in their resource needs, just as plants vary in the availability of their resources. Larsson and Franzén (2007), for example, calculated that each *A. hattorfiana* offspring was provisioned with the floral resources of two entire *K. arvensis* plants for complete development. In contrast, a specialist bee from the southwestern United States, *Calliopsis pugionis*, could provision over 1,500 offspring with the floral resources of one *Encelia farinosa* plant (Danforth 1990).

In the absence of abundant and diverse floral resources, poor nutrition and food stress may cause reduced fecundity, longevity, larval development, immunocompetence, and stress resistance (Haydak 1970, Brown et al. 2000, Hoover et al. 2006, Brodschneider and Crailsheim 2010, Alaux et al. 2010, Huang 2012, Pasquale et al. 2013). In addition to the base availability of these critical food resources, bees have specific nutritional needs that may not be met by a single species. Plants vary in pollen quality, ranging from 2-60% protein and 1-20% lipids by mass (Roulston and Cane 2000). Protein content may benefit larval development and affect foraging strategy (Brodschneider and Crailsheim 2010, Vaudo et al. 2016).

Flower phenology also plays a role in the availability of food resources for bees. Flowering food resource availability can change dramatically across time and space depending on what plants are flowering, when they flower, and where they are located. In some cases, plant phenology is so responsive to climatic variations that historical records of plant phenology have been used to accurately recall past temperatures (Meier et al. 2007). However, there are many unpredictable habitats where phenology is more erratic. Plant phenology is particularly well studied in desert landscapes of the southwestern United States, where flowering events are often triggered by infrequent rain. A study of flowering plants in the Sonoran Desert found that the flowering time of five of six studied plants was triggered by rain (Meier et al. 2007). The unpredictability of these desert habitats requires that bees be closely matched with their flowering plant hosts so that they will have consistent and available food resources during their reproductive season. Desert bees, just like desert flowers, often have very short activity (or, for the latter, flowering) seasons. Thus, many bees' emergence cues closely match plant flowering cues. For example, solitary specialist bee *Perdita portalis* in the Sonoran Desert emerges during high humidity, which in the desert is triggered by rainfall. By emerging only following rainfall events, bees can better ensure that flowers will be available for foraging (Danforth 1999). *P. portalis* also has a bet-hedging strategy as insurance against potential errors in emergence cues. When conditions are optimal, only about half of all developing larvae pupate, leaving some behind to wait until the next time conditions are right (Danforth 1999).

### *Nesting resources*

Bees use nests to protect their eggs and developing offspring, as well as protect themselves from incidental harm and environmental extremes. There is a huge diversity in nesting habitats and nesting guilds that likely play a large role in their responses to environmental disturbance (Williams et al. 2010). Bees nest above ground and below ground, and they either construct or excavate their own nest structures or use preexisting nest structures (Michener 2000). For example, *Hesperapis rhodocерата* is a solitary bee native to the southwestern United States (most commonly found in southern New Mexico and Arizona); it nests below-ground in loose soils,

and every spring females will excavate their own nests in the soil by digging deep tunnels (Rozen et al. 2016). Bumble bees (*Bombus* spp.; bumble bees in the southwestern United States include *Bombus sonorus* and *Bombus vosnesenskii*) also nest below-ground,\* but they do not excavate their own nests; instead, they use pre-existing cavities, such as rodent burrows, essentially “renting” an existing space (Goulson 2013). (\* Some bumble bees will nest above-ground in pre-existing cavities as well, though this is less common.) Carpenter bees, like *Xylocopa californica* in the southwest, nest above ground. As their common name suggests, carpenter bees excavate their nests by boring tunnels inside wood. On the other hand, many species of mason bee, such as *Osmia lignaria*, also nest above ground, but they use preexisting cavities such as beetle burrows or hollow twigs and plant stems (Bosch and Kemp 2000). Mason bees, although “renters” in pre-existing cavities, use other materials such as mud or leaf material to seal their nests. Many “renters” also use additional materials to complete their nests; for instance, bumble bee renters construct elaborate structures within their nests out of wax (Goulson 2013).

Most bee species nest below ground, but the nesting requirements of bees are diverse and include such materials as mud, leaves, specific soil types, flower petals, sea shells, resin, dead wood, plant and wood fibers, and many sizes of pre-existing cavities (Roulston and Goodell 2011, Danforth et al. 2019, Harmon-Threatt 2020). As with food resources, many bees are adapted to use specific plants for nests. Cane et al. (2006) found that the specialist bee *Hoplitis biscutellae*, which nests above ground inside pre-existing cavities, was more abundant in urban desert landscapes in Arizona than in nearby open desert landscapes with a bigger population of its host pollen plant. The authors speculated that this could have been due to a greater abundance of nesting cavities in the urban desert landscapes (Cane et al. 2006). Nesting strategy has been predicted as one of the most important factors in determining a bee species’ response to environmental disturbance (Williams et al. 2010).

### **Environmental stressors, modulated by bee resource requirements, influence bee health in the southwestern United States**

Environmental change is occurring rapidly worldwide (Tilman et al. 2001). In the southwestern United States and the Grand Canyon, primary challenges to bee population health and persistence include the presence of invasive plants that compete with native flowering resources, exposure to pesticides and other agricultural chemicals, and the increasing intensity of drought that further reduces flowering plant abundance.

#### *Invasive plants*

Invasive species can have sizable impacts on native species abundance, range, and diversity (Parker et al. 1999). In addition to competing for resources, invaders may in some cases fundamentally change the environment, for example, by dramatically changing the soil chemistry so that other plants cannot grow (Vitousek et al. 1987). In the southwestern United States, including the Grand Canyon, one invasive species of particular concern is tamarisk (*Tamarix* spp.), which entered the United States in the 1800s from Europe. Tamarisk is particularly difficult to control because of its deep taproot and propensity to re-sprout following incomplete removal (Hultine et al. 2010).

The impacts of tamarisk on bee populations in the southwest are manifold. On the one hand, tamarisk competes with native plants and could result in declines in key flowering plants that share the same habitats. For specialist bees (monolectic or oligolectic; bees that have evolved with a particular host plant species or genus), the loss of a host plant could be devastating, because bees have adapted specifically to use the pollens of that plant (Waser and Ollerton 2006). Indeed, the loss of pollen host plants has been identified as one of the primary factors leading to bee population declines in The Netherlands (Scheper et al. 2014). Furthermore, efforts to remove tamarisk, such as mechanical and chemical treatments, can harm bees directly as well as indirectly by inadvertently harming native flowering plant species. On the other hand, generalist (polylectic) bees may in fact be able to use tamarisk as a food resource. A study comparing native bee visitation among invasive plants (including tamarisk) and native plants in Utah found that invasive plant species experienced double the number of bee visits as native plants; however, these bees were almost exclusively generalist bees with a broad diet breadth (Tepedino et al. 2008). The abundance of these invasive plants in some habitats, thus, may benefit bee populations if they are able to use the pollen they provide (Tepedino et al. 2008). However, it should be noted that tamarisk pollen is considered low quality, so it may not be a nutritious choice for bees in the presence of higher quality native flowering plants (Andrada et al. 2004).

### *Pesticides*

Pesticides have also been implicated in bee declines worldwide (Roulston and Goodell 2011, Goulson et al. 2015, Rundlöf et al. 2015). Bees can be exposed to pesticides directly during application, by contacting residues on plants or nest materials, or by consuming contaminated pollen or nectar. Exposure causes mortality and a suite of sublethal effects, such as reduced reproduction (Johnson et al. 2010, Rundlöf et al. 2015), slower larval development (Abbott et al. 2008), impaired foraging behavior (Mommaerts et al. 2010), and impaired learning ability (Stanley et al. 2015). Pesticides are widely applied globally and throughout the southwestern United States and travel through and persist in soil and water. As a result, bees may be exposed to pesticides in any habitat but especially in agroecosystems, where pesticides are used to control agricultural pests, fungal pathogens, and weeds. Bees consume pollen and/or nectar at all life stages, so exposure can occur to larvae and adults (Michener 2000). In Grand Canyon National Park, herbicides are used to control invasive plants such as tamarisk (Belote et al. 2010).

Neonicotinoids are a class of pesticides of particular concern for bees. These compounds are popular and make up nearly a quarter of the total insecticide market worldwide (Jeschke et al. 2011). As systemic pesticides, they are taken up by the plant and permeate all plant tissues, including pollen and nectar, which are the primary food sources for bees. Additionally, they are highly toxic to bees even at very low doses (Blacquière et al. 2012, Rundlöf et al. 2015). In fact, because of their negative impacts on bees, the European Union banned the use of three neonicotinoid insecticides in all field crops following a three-year moratorium to research their effects (Stokstad et al. 2018). However, these pesticides are still used widely in the United States. A study conducted in Colorado measured over a dozen different pesticides in bee samples collected in grasslands and wheat fields, and the most frequently detected pesticide was thiamethoxam, a neonicotinoid (Hladic et al. 2016). Bees that nest below ground in soils, or bees that use soil to construct their nests above ground, could be at additional risk from neonicotinoids because these chemicals persist long-term in soils following application (Sgolastra et al. 2019).

In addition to their direct and sublethal effects, pesticides can increase the susceptibility of bees to other stressors, such as resource limitation and disease (Goulson et al. 2015). For example, the combination of neonicotinoid pesticide exposure and nutritional stress synergistically reduced bee survival in honey bees (Tosi et al. 2017). Infections of a gut parasite spread more in bee colonies exposed to a neonicotinoid pesticide than unexposed colonies (Pettis et al. 2013). These interactive effects of pesticides and other stressors could have a considerable impact on bees in the southwestern United States, where desert ecosystems are predicted to be especially susceptible to projected climate change effects (Archer and Predick 2008).

### *Drought*

In the absence of precipitation, drought conditions lead to water shortages over time. Current climate change projections suggest that droughts will be more extreme in the future (Trenberth et al. 2014). Predictive models from the Intergovernmental Panel on Climate Change (IPCC) indicate a future with more severe droughts and an overall drier climate than current and historic conditions, especially in the southwestern United States and the Colorado River basin (Cayan et al. 2010). Northern California experienced the driest February on record this year (2020), following an unusually dry January (Pierre-Louis and Popovich 2020). Similar trends have also occurred across other western states including Nevada, Washington, and Oregon (Pierre-Louis and Popovich 2020).

Water resources are critical for growing plants, and water has been identified as likely the most important selective force for plants in dry habitats (Niklas 1997). In southern California shrublands, plant cover and species richness were significantly correlated with precipitation along the coast and inland (Keeley et al. 2005). Flowering and overall growth of California sagebrush (*Artemisia californica*, a foundational species along the western California coast) were also predicted by precipitation. Because flowering plants provide fundamental resources to bees, diminished floral resources due to drought could negatively affect bee populations. Indeed, plant and animal communities have been shown to change dramatically, and quickly, following severe drought in the Sonoran Desert (Turner 1990). In California, drought conditions led to reduced floral availability which in turn was correlated with a decline in bumble bee abundance (Thomson 2016). Thomson (2016) also found that the reduced floral diversity and availability due to lack of precipitation resulted in increased competition between bumble bees and non-native honey bees, which put further stress on bumble bees during drought conditions. Bumble bees have been experiencing range contractions worldwide, notably in North America and Europe, shrinking especially along their southern distributions (Kerr et al. 2015). Adapted to cooler climates, bumble bees may be especially susceptible to climate change, particularly the effects of climate change on their food plant availability (Fitzpatrick et al. 2007, Kerr et al. 2015). However, it appears that the effects of drought are a bigger stressor for bees in less naturally arid regions. A study on bee activity during drought in the Chihuahuan Desert suggests that bees can remain in diapause for years while waiting for rain and thus may be relatively robust to extended drought in desert habitats (Minckley et al. 2013).

### **Conclusion**

Environmental stressors in the southwestern United States affect native bee populations by reducing survival, fecundity, and/or access to critical resources. Invasive plants, such as

tamarisk, compete with required flowering plant resources. Pesticides used in agriculture and for invasive plant control harm bees directly as well as causing sublethal effects that limit bees' survival, fecundity, and stress resistance. Drought also limits flowering plant availability.

In a changing world, it is critical to consider the effects of multiple stressors on bee health in order to conserve and protect their ecological and economic role as pollinators of crops and wild plants. Additional changes to the southwestern United States, such as the potential introduction of honey bees into natural areas (which compete with native bees for resources), the erosion of the Colorado River shoreline (which could reduce area for plant growth), and land-use change from natural areas to agriculture, should be studied further to better understand their interactions and effects on these critical pollinators.

## Literature Cited

- Abbott, V. A., J. L. Nadeau, H. A. Higo, and M. L. Winston. 2008. Lethal and sublethal effects of imidacloprid on *Osmia lignaria* and clothianidin on *Megachile rotundata* (Hymenoptera: Megachilidae). *Journal of Economic Entomology* 101:784–796.
- Alaux, C., Ducloz François, Crauser Didier, and Le Conte Yves. 2010. Diet effects on honeybee immunocompetence. *Biology Letters* 6:562–565.
- Andrada, A., A. Valle, P. Paoloni, and L. Gallez. 2004. Pollen and Nectar Sources used by Honeybee Colonies pollinating Sunflower (*Helianthus annuus*) in the Colorado River Valley, Argentina. *Bol. Soc. Argent. Bot.* 39:75–82.
- Archer, S. R., and K. I. Predick. 2008. Climate Change and Ecosystems of the Southwestern United States. *Rangelands* 30:23–28.
- Belote, R. T., L. J. Makarick, M. J. C. Kearsley, and C. L. Lauver. 2010. Tamarisk Removal in Grand Canyon National Park: Changing the Native–Non-native Relationship as a Restoration Goal. *Ecological Restoration* 28:449–459.
- Biesmeijer, J. C., S. P. M. Roberts, M. Reemer, R. Ohlemuller, M. Edwards, T. Peeters, A. P. Schaffers, S. G. Potts, R. Kleukers, C. D. Thomas, J. Settele, and W. E. Kunin. 2006. Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science* 313:347–351.
- Blacquièrè, T., G. Smaghe, C. A. M. van Gestel, and V. Mommaerts. 2012. Neonicotinoids in bees: a review on concentrations, side-effects and risk assessment. *Ecotoxicology* 21:973–992.
- Bosch, J., and W. P. Kemp. 2000. Development and Emergence of the Orchard Pollinator *Osmia lignaria* (Hymenoptera: Megachilidae). *Environmental Entomology* 29:8–13.
- Bowers, J. E., and M. A. Dimmitt. 1994. Flowering Phenology of Six Woody Plants in the Northern Sonoran Desert. *Bulletin of the Torrey Botanical Club* 121:215–229.
- Brodschneider, R., and K. Crailsheim. 2010. Nutrition and health in honey bees. *Apidologie* 41:278–294.
- Brown, M., R. Loosli, and P. Schmid-Hempel. 2000. Condition-Dependent Expression of Virulence in a Trypanosome Infecting Bumblebees. *Oikos* 91:421–427.
- Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. *PNAS*:1–6.

- Cane, J. H., R. L. Minckley, L. J. Kervin, T. H. Roulston, and N. M. Williams. 2006. Complex Responses Within A Desert Bee Guild To Urban Habitat Fragmentation. *Ecological Applications* 16:632–644.
- Cayan, D. R., T. Das, D. W. Pierce, T. P. Barnett, M. Tyree, and A. Gershunov. 2010. Future dryness in the southwest US and the hydrology of the early 21st century drought. *Proceedings of the National Academy of Sciences* 107:21271–21276.
- Danforth, B. N. 1990. Provisioning behavior and the estimation of investment ratios in a solitary bee, *Calliopsis (Hypomacrotera) persimilis* (Cockerell) (Hymenoptera: Andrenidae). *Behavioral Ecology and Sociobiology* 27:159–168.
- Danforth, B. N. 1999. Emergence dynamics and bet hedging in a desert bee, *Perdita portalis*. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 266:1985–1994.
- Danforth, B. N., R. L. Minckley, J. L. Neff, and F. Fawcett. 2019. *The Solitary Bees: Biology, Evolution, Conservation*. Princeton University Press.
- Fitzpatrick, Ú., T. E. Murray, R. J. Paxton, J. Breen, D. Cotton, V. Santorum, and M. J. F. Brown. 2007. Rarity and decline in bumblebees – A test of causes and correlates in the Irish fauna. *Biological Conservation* 136:185–194.
- Goulson, D. 2013. *Goulson-Bumblebees-Behaviour\_Ecology\_and\_Conservation*:1–330.
- Goulson, D., E. Nicholls, C. Botias, and E. L. Rotheray. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347:1255957.
- Harmon-Threatt, A. 2020. Influence of Nesting Characteristics on Health of Wild Bee Communities. *Annual Review of Entomology* 65:39–56.
- Haydak, M. H. 1970. Honey Bee Nutrition. *Annual Review of Entomology* 15:143–156.
- Hladic, M., M. Vandever, and K. Smalling. 2016. Exposure of native bees foraging in an agricultural landscape to current-use pesticides. *Science of The Total Environment* 542:469–477.
- Hoover, S. E. R., H. A. Higo, and M. L. Winston. 2006. Worker honey bee ovary development: seasonal variation and the influence of larval and adult nutrition. *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* 176:55–63.
- Huang, Z. 2012. Pollen nutrition affects honey bee stress resistance. *Terrestrial Arthropod Reviews* 5:175–189.
- Huenneke, L. F., C. van Riper, and K. A. Hays-Gilpin. 2015. *The Colorado Plateau VI: Science and Management at the Landscape Scale*. University of Arizona Press.
- Hultine, K. R., J. Belnap, C. van Riper, J. R. Ehleringer, P. E. Dennison, M. E. Lee, P. L. Nagler, K. A. Snyder, S. M. Uselman, and J. B. West. 2010. Tamarisk biocontrol in the western United States: ecological and societal implications. *Frontiers in Ecology and the Environment* 8:467–474.
- Inouye, D. W. 2008. Effects of Climate Change on Phenology, Frost Damage, and Floral Abundance of Montane Wildflowers. *Ecology* 89:353–362.
- Jeschke, P., R. Nauen, M. Schindler, and A. Elbert. 2011. Overview of the Status and Global Strategy for Neonicotinoids. *Journal of Agricultural and Food Chemistry* 59:2897–2908.
- Johnson, R. M., M. D. Ellis, C. A. Mullin, and M. Frazier. 2010. Pesticides and honey bee toxicity – USA. *Apidologie* 41:312–331.
- Kearns, C. A., D. W. Inouye, and N. M. Waser. 1998. ENDANGERED MUTUALISMS: The Conservation of Plant-Pollinator Interactions. *Annual Review of Ecology and Systematics* 29:83–112.

- Keeley, J. E., M. Baer-Keeley, and C. J. Fotheringham. 2005. Alien Plant Dynamics Following Fire in Mediterranean-Climate California Shrublands. *Ecological Applications* 15:2109–2125.
- Kerr, J. T., A. Pindar, P. Galpern, L. Packer, S. G. Potts, S. M. Roberts, P. Rasmont, O. Schweiger, S. R. Colla, L. L. Richardson, D. L. Wagner, L. F. Gall, D. S. Sikes, and A. Pantoja. 2015. Climate change impacts on bumblebees converge across continents. *Science* 349:177–180.
- Klein, A. M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tschardt. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* 274:303–313.
- Larsson, M., and M. Franzén. 2007. Critical resource levels of pollen for the declining bee *Andrena hattorfiana* (Hymenoptera, Andrenidae). *Biological Conservation* 134:405–414.
- Meier, N., T. Rutishauser, C. Pfister, H. Wanner, and J. Luterbacher. 2007. Grape harvest dates as a proxy for Swiss April to August temperature reconstructions back to AD 1480. *Geophysical Research Letters* 34.
- Michener, C. D. 2000. *The Bees of the World*. JHU Press.
- Minckley, R. L., T. H. Roulston, and N. M. Williams. 2013. Resource assurance predicts specialist and generalist bee activity in drought. *Proceedings of the Royal Society B: Biological Sciences* 280:20122703.
- Mommaerts, V., S. Reynders, J. Boulet, L. Besard, G. Sterk, and G. Smagghe. 2010. Risk assessment for side-effects of neonicotinoids against bumblebees with and without impairing foraging behavior. *Ecotoxicology (London, England)* 19:207–215.
- Niklas, K. J. 1997. *The Evolutionary Biology of Plants*. University of Chicago Press.
- Ollerton, J., R. Winfree, and S. Tarrant. 2011. How many flowering plants are pollinated by animals? *Oikos* 120:321–326.
- Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: Toward a Framework for Understanding the Ecological Effects of Invaders. *Biological Invasions* 1:3–19.
- Pasquale, G. D., M. Salignon, Y. L. Conte, L. P. Belzunces, A. Decourtye, A. Kretzschmar, S. Suchail, J.-L. Brunet, and C. Alaux. 2013. Influence of Pollen Nutrition on Honey Bee Health: Do Pollen Quality and Diversity Matter? *PLOS ONE* 8:e72016.
- Pettis, J. S., E. M. Lichtenberg, M. Andree, J. Stitzinger, R. Rose, and D. vanEngelsdorp. 2013. Crop Pollination Exposes Honey Bees to Pesticides Which Alters Their Susceptibility to the Gut Pathogen *Nosema ceranae*. *PLoS ONE* 8:e70182–9.
- Pierre-Louis, K., and N. Popovich. 2020. California Had Its Driest February on Record. Here's How Bad It Was. - *The New York Times*.  
<https://www.nytimes.com/interactive/2020/03/03/climate/dry-california.html>.
- 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.
- Potts, S. G., B. Vulliamy, A. Dafni, G. Neeman, and P. Willmer. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? *Ecology* 84:2628–2642.
- Price, M. V., and N. M. Waser. 1998. Effects of experimental warming on plant reproductive phenology in a subalpine meadow. *Ecology* 79:1261–1271.



- Roulston, T. H., and J. H. Cane. 2000. Pollen nutritional content and digestibility for animals. *Plant Systematics and Evolution* 222:187–209.
- Roulston, T. H., and K. Goodell. 2011. The Role of Resources and Risks in Regulating Wild Bee Populations. *Annual Review of Entomology* 56:293–312.
- Rozen, J. G., G. I. Stage, and R. R. Snelling. 2016. *Hesperapis rhodocera*: behavioral biology, egg, and larval instars, including behavioral and larval comparisons with *H. larrea* (Hymenoptera, Melittidae, Dasypodainae). (*American Museum novitates*, no. 3856).
- Rundlöf, M., G. K. S. Andersson, R. Bommarco, I. Fries, V. Hederström, L. Herbertsson, O. Jonsson, B. K. Klatt, T. R. Pedersen, J. Yourstone, and H. G. Smith. 2015. Seed coating with a neonicotinoid insecticide negatively affects wild bees. *Nature* 521:77–80.
- Scheper, J., M. Reemer, R. van Kats, W. A. Ozinga, G. T. J. van der Linden, J. H. J. Schaminée, H. Siepel, and D. Kleijn. 2014. Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. *Proceedings of the National Academy of Sciences* 111:17552–17557.
- Sgolastra, F., S. Hinarejos, T. L. Pitts-Singer, N. K. Boyle, T. Joseph, J. Lückmann, N. E. Raine, R. Singh, N. M. Williams, and J. Bosch. 2019. Pesticide Exposure Assessment Paradigm for Solitary Bees. *Environmental Entomology* 48:22–35.
- Stanley, D. A., K. E. Smith, and N. E. Raine. 2015. Bumblebee learning and memory is impaired by chronic exposure to a neonicotinoid pesticide. *Scientific Reports* 5:16508.
- Stokstad, E., 2018, and 2:45 Pm. 2018, April 27. European Union expands ban of three neonicotinoid pesticides. <https://www.sciencemag.org/news/2018/04/european-union-expands-ban-three-neonicotinoid-pesticides>.
- 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.
- Thomson, D. M. 2016. Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. *Ecology Letters* 19:1247–1255.
- Thomson, J. D. 2010. Flowering phenology, fruiting success and progressive deterioration of pollination in an early-flowering geophyte. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:3187–3199.
- Tilman, D., J. Fargione, B. Wolff, C. DAntonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting Agriculturally Driven Global Environmental Change. *Science* 292:281–284.
- Tosi, S., J. C. Nieh, F. Sgolastra, R. Cabbri, and P. Medrzycki. 2017. Neonicotinoid pesticides and nutritional stress synergistically reduce survival in honey bees. *Proc. R. Soc. B* 284:20171711.
- Trenberth, K. E., A. Dai, G. van der Schrier, P. D. Jones, J. Barichivich, K. R. Briffa, and J. Sheffield. 2014. Global warming and changes in drought. *Nature Climate Change* 4:17–22.
- Turner, R. M. 1990. Long-Term Vegetation Change at a Fully Protected Sonoran Desert Site. *Ecology* 71:464–477.
- US Geological Survey. (n.d.). Grand Canyon Ecosystems. <https://www.usgs.gov/science-support/osqi/yes/national-parks/grand-canyon-ecosystems>.
- Vaudo, A. D., H. M. Patch, D. A. Mortensen, J. F. Tooker, and C. M. Grozinger. 2016. Macronutrient ratios in pollen shape bumble bee (*Bombus impatiens*) foraging strategies

- and floral preferences. *Proceedings of the National Academy of Sciences* 113:E4035–E4042.
- Vitousek, P. M., L. R. Walker, L. D. Whiteaker, D. Mueller-Dombois, and P. A. Matson. 1987. Biological Invasion by *Myrica faya* Alters Ecosystem Development in Hawaii. *Science* 238:802–804.
- Waser, N. M., and J. Ollerton. 2006. *Plant-Pollinator Interactions: From Specialization to Generalization*. University of Chicago Press.
- 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.
- Williams, N. M., and C. Kremen. 2007. **Resource Distributions Among Habitats Determine Solitary Bee Offspring Production in a Mosaic Landscape**. *Ecological Applications* 17:910–921.