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Forum

The State of Bee Monitoring in the United States: A Call to Refocus Away From Bowl Traps and Towards More Effective Methods

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Abstract

Effective monitoring is necessary to provide robust detection of bee declines. In the United States and worldwide, bowl traps have been increasingly used to monitor native bees and purportedly detect declines. However, bowl traps have a suite of flaws that make them poorly equipped to monitor bees. We outline the drawbacks of bowl traps, as well as other passive sampling methods. We emphasize that current methods do not monitor changes in bee abundance. We then propose future approaches to improve bee monitoring efforts, which include improving our understanding of the efficacy and drawbacks of current methods, novel molecular methods, nest censusing, mark-recapture, sampling of focal plant taxa, and detection of range contractions. Overall, we hope to highlight deficiencies of the current state of bee monitoring, with an aim to stimulate research into the efficacy of existing methods and promote novel methods that provide meaningful data that can detect declines without squandering limited resources.

Key words: bowl traps, pan traps, Moericke traps, Apoidea, insect declines

Despite increasing and overwhelming evidence of declines in multiple native bee species (Colla and Packer 2008, Grixti et al. 2009, Cameron et al. 2011, Burkle et al. 2013, Scheper et al. 2014, Koh et al. 2016, Arbetman et al. 2017) there is still not an effective monitoring scheme for the approximately 4,000 species of native, wild bees in the United States. Broadly, monitoring requires collecting data on the abundance and/or occurrence of species to determine whether they are declining in abundance over time or whether they are experiencing range contractions. Monitoring can also include detecting changes in ecological interactions, particularly between bees and the plants that depend on them for pollination.

For wild bees, three data collection methods are commonly employed in monitoring studies: bowl traps, netting, and nonlethal observations. Increasingly, passive sampling, and bowl traps in particular, have been promoted as a way to detect changes in bee abundance and species occurrence (LeBuhn et al. 2013, Gezon et al. 2015, Tang et al. 2015, Droege et al. 2016, Le Féon et al. 2016, LeBuhn et al. 2016a, LeBuhn et al. 2016b, Prado et al. 2017, O'Connor et al. 2019) (but see Tepedino et al. 2015 and response by Lebuhn et al. 2015). Bowl traps (also called bee bowls, pan traps, or Moericke traps) are simple colored bowls or cups that are filled with soapy water; the bright colors attract bees and many other insects that presumably mistake the bowls for flowers. The soap breaks down the surface tension so that the bees fly in and drown. The bowl traps are typically deployed in sets of three bowls made up of a yellow, blue, and white bowl. These arrays are left out for a period of time, typically a day, and then collected. Two alternatives to bowl traps, netting and nonlethal observations, consist of an observer collecting data on individual bees for a timed period, often along transects or in a defined area. During netting, an observer uses either a butterfly net to collect individual bees as they forage or a sweep net to collect bees off of vegetation. During nonlethal observations, an observer may simply observe foraging bees and identify them to species, morphospecies or genus; or an observer may use a butterfly net to catch and temporarily hold bees so they can be identified.

These three methods—bowl traps, netting, and nonlethal observations—have several drawbacks that limit their effectiveness for monitoring bees. Netting and nonlethal observations are labor intensive and can be influenced by the experience of the observer (Westphal et al. 2008). Bowl traps are attractive to scientists because they are cheap, simple to use, easily-repeatable, and reduce the bias of individual researchers (Cane et al. 2000, Westphal et al. 2008). All three methods, however, have a suite of additional flaws, including taxonomic biases and unknown effects of the surrounding floral landscape on catch rates. In addition, the relationship between observed and actual abundance of bees is poorly known. Because of these limitations, none of these sampling methods, as commonly employed, provide accurate estimates of bee abundance or population size.

In this Forum, we discuss the drawbacks of common current methods used to monitor wild bees, with a special focus on bowl trapping. We address how common methods are poorly equipped to monitor bees and particularly to detect changes in abundance. Our focus is on bowl trapping because this method is considered one of the primary monitoring methods and has become increasingly used over the past 15 yr despite its known flaws (Fig. 1). We outline future approaches to monitoring bees, focusing on identifying specific research questions that can be answered effectively by common methods, and identifying those that could be answered by less common methods.

The Drawbacks of Bowl Traps

The primary drawback of bowl traps is they collect a heavily filtered version of the bee fauna. It is well-documented that certain species and genera are collected in bowl traps in huge numbers, while other bees are rarely, if ever, caught (Cane et al. 2000, Cane 2001, Roulston et al. 2007, Wilson et al. 2008, Neame et al. 2013). Bowl traps catch an inordinate number of bees in the family Halictidae, with halictids typically making up the majority of specimens collected. For example, in a study looking at bowl trapping effectiveness at nine sites across North America, Halictidae made up between 40.1 and 99.4% of specimens captured (mean = 74.4%, median = 71.4%) (Droege et al. 2010). These results are typical, with bowl trapping catching mostly Halictidae in various studies of different habitats: Illinois prairie (92.9–98.7%, 80.3%; Geroff et al. 2014, Griffin et al. 2017), remnant Palouse prairie (65.9%; Rhoades et al. 2017), Michigan oak savanna (84.9%; Lettow et al. 2018), Canadian fields and restored landfills (52.7%; Onuferko et al. 2018), Brazilian semideciduous forest (96.5%; Gonçalves and Oliveira 2013), and Swiss hay meadows (72.7%; Buri et al. 2014). Some exceptions to this pattern exist, with a lower proportion of Halictidae found in certain situations such as during bloom in apple orchards (34.2%; Schlueter and Stewart 2015) and ecosystems with hyper-diverse bee fauna such as Utah deserts (36.3%; Wilson et al. 2008). However, it

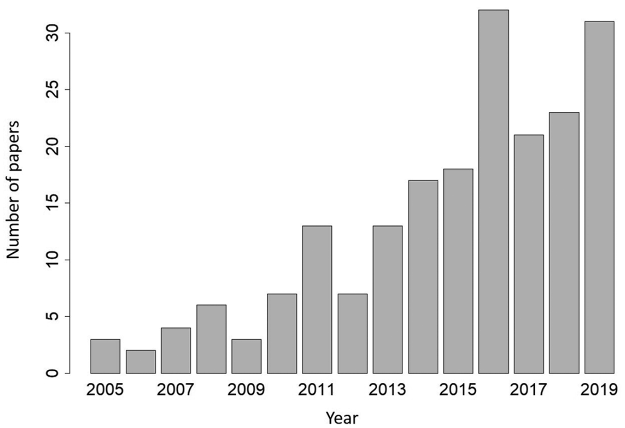

Figure 1. We report the number of records per year yielded by a Web of Science search on the terms 'bowl trap*' OR 'bee bowl*' OR 'pan trap*' OR 'Moericke trap*'. We included only papers that reported original data on wild bees.

is clear that the majority of studies that employ bowl traps catch an overwhelming number of Halictidae.

For the most part, halictids are social and generalist foragers that are common in anthropogenically disturbed habitats (Eickwort 1988), making them inappropriate targets to fulfill the conservation-oriented goals of monitoring efforts. Indeed, Halictidae, and the subgenus *Lasioglossum* (*Dialictus*) in particular, are often considered 'weed bees' (Eickwort 1986) and the late *Dialictus* expert George Eickwort considered vacant lots, trash dumps, and gas station parking lots the ideal places to collect them (Wcislo et al. 1994). The majority of Halictidae caught in bowl traps are either common, abundant, and relatively 'easy' to identify (e.g., *Agapostemon*, *Augochlorella*, *Halictus*) or they are *Dialictus*, a 'morphologically monotonous' 'nightmare taxon' whose species are extremely difficult to identify (Michener 1974, 2007; Gibbs 2018). For the *Dialictus* in particular, there are only a handful of people in North America who can reliably identify them. In fact, *Dialictus* in the western United States have never been revised and it is common to see studies that do not identify *Dialictus* to species or identify them to morphospecies in whole or part (e.g., Kuhlman and Burrows 2017, Ballare et al. 2019, Galbraith et al. 2019). Given the limited resources of bee monitoring efforts, are Halictidae really the bees that we should be focusing on? Particularly in the face of the lack of support for natural history collections (Kemp 2015, ESA 2017) and the limited and declining number of bee taxonomists (Hopkins and Freckleton 2002, Silveira et al. 2002, Batley and Hogendoorn 2009, Eardley et al. 2009, Packer et al. 2009, Kuhlmann 2015), we need to avoid overwhelming limited resources with a flood of specimens that take up space, take up the time of experts, and do not effectively contribute to monitoring efforts.

Bowl traps have several other drawbacks in addition to their taxonomic bias. First, bowl traps do not provide reliable estimates of the abundance of populations since it is not clear what proportion of a population of bees are collected by bowl traps or how this proportion varies by bee species and sex (Cane et al. 2000, Toler et al. 2005, Richards et al. 2010, Wood et al. 2015). As a result, year-to-year data collected from bowl traps provide almost no information about whether bee populations are going up or down. Second, it is not clear whether bowl traps catch more bees when there are no flowers (bees searching for flowers to visit find only bowl traps and visit those instead) or if bowl traps catch more bees when there are many flowers (flowers draw in more bees to the area which then die in the bowl traps) (Cane et al. 2000, Mayer and Kuhlmann 2004, Roulston et al. 2007, Baum and Wallen 2011, Wood et al. 2015). Third, it is also not clear how bowl trap catch is influenced by factors such as the proximity to nest sites or the age and experience of bees (Toler et al. 2005). Finally, because bowl traps are a relatively recent invention and were not used by historic collectors, comparing bowl trap captures to historic net-collected specimens can potentially bias monitoring data.

What Not to Do (or Avoiding Bottlenecks)

Some researchers address the deficiencies of bowl traps by performing an 'all of the above' approach, conducting even more sampling with multiple methods—bowl traps, netting, vane traps, and malaise traps. For example, some view vane traps as the next iteration of new and improved passive sampling methods, but these suffer from many of the same biases as bowl traps, including taxonomic biases in catch rate (Stephen and Rao 2007, Geroff et al. 2014, Joshi et al. 2015, Rhoades et al. 2017) and an uncertain relationship with floral cover (e.g., Joshi et al. 2015). In addition, there are suggestions that vane traps may completely wipe out local populations of some species and should be used with caution (Gibbs et al. 2017). Further, collecting vast numbers of specimens using an 'all of the above' approach causes bottlenecks when these specimens need to be processed, identified, stored, and their data made accessible. Space in particular is a major bottleneck for labs and museums (Schilthuizen et al. 2015). This appears to be a relatively universal problem, and some researchers even explicitly recommend stripping old bee specimens off pins in order to reuse them and save on space (Droege 2015). Combining bowl traps with other passive sampling methods such as vane and malaise traps does not overcome the limitations of bowl traps discussed above.

In many cases, a more targeted approach is a better option than attempting to perform whole-system sampling. For example, although netting has its own limitations, specifically observer bias and the same lack of understanding of the relationship between catch rates and floral abundance, netting is often better than passive sampling because it allows specific taxa to be targeted. This approach allows researchers to address specific monitoring goals, gain valuable ecological data on floral relationships, and importantly, reduce the number of specimens collected. Although netting requires greater initial effort, it can help alleviate the downstream bottlenecks and associated costs from processing, identifying, databasing, and storage. For example, this is the approach taken in a recent study by Strange and Tripodi (2019), where they identified taxa of interest (in this case, bumble bees) and conducted targeted sampling designed to perform a rapid initial assessment of species. Several additional methods exist that also offer better options for bee monitoring; we discuss these further in the next section.

Future Approaches

Moving forward, researchers should focus on a two-pronged approach: first, we need a better understanding of existing methods, with a particular focus on their taxonomic biases and relationship to actual bee abundance. Second, we need to use methods that allow for more targeted collection of data that inform specific monitoring goals such as detecting changes in abundance, species occurrence and species interactions.

One of the primary weaknesses of current trapping methods (bowls, netting, and observation) is that the relationship between capture rate and the actual abundance of bees is unknown and unexplored, and it is currently impossible to infer actual abundance from capture rates. Many studies compare the efficacy of different trap types (e.g., bowl traps vs. netting vs. vane traps vs. malaise traps), generally with a focus on which method captures the most diversity (e.g., Geroff et al. 2014, Prado et al. 2017, Rhoades et al. 2017, O'Connor et al. 2019). However, there have been almost no studies that explore the relationship between sampling method and *actual pollinator abundance*. Evaluating trap effectiveness has been done in other disciplines, such as in studies evaluating the effectiveness of light traps for capturing moths. In these studies, trap effectiveness was measured using capture rates of marked moths, thus allowing a comparison of trapping effectiveness to actual abundance (Baker and Sadovy 1978, Beck and Linsenmair 2006, Truxa and Fiedler 2012, Merckx and Slade 2014). Similar studies are needed in bees in order to make inferences about the actual abundance of bees based on capture rates in both bowl traps and other methods.

We are aware of two studies in bees that compare actual pollinator abundance to other commonly used methods. Larsson and Franzen (2008) measured the efficacy of survey walks compared to mark-recapture abundance estimates and found that each walk observed 5.5–23.4% of the population of the solitary bee *Andrena hattorfiana* (Fabricius). Wood et al. (2015) quantified pollinator abundance using microsatellite analysis to estimate number of bumble bee colonies of two species and compared that estimate to capture rates by bowl traps. They reported no correlation between abundance of bees recorded via these different methods, indicating that bowl traps do not accurately reflect true bee abundance. In general, novel methods using microsatellites offer exciting opportunities to monitor the effective population size of social bees. These species have long been recognized as difficult to monitor because the number of workers in the environment does not necessarily correlate with the true number of active colonies (Herrmann et al. 2007). Microsatellite-based methods have been successfully used to estimate the effective population size of various bumble bee species, with the added benefit that they allow for nonlethal sampling (reviewed in Woodard et al. 2015). These methods also allow for the estimation of nest density and monitoring of effective populations over time (Goulson et al. 2010, Wood et al. 2015). While these methods have so far only been used on bumble bees, they could be expanded to other social species, such as social Halictidae. Indeed, these methods could also be used in combination with traditional lethal collection methods in order to produce estimates of colony abundance.

Marking and mark-recapture studies to estimate the size of bee populations are largely restricted to discrete populations of solitary ground nesting bees (Linsley and MacSwain 1959, Tepedino 1981, Bischoff 2003, Larsson and Franzén 2008, Franzén and Nilsson 2013). These methods have been used to successfully monitor populations and understand long-term population trends (Franzén and Nilsson 2013). Other studies have censused active nests and used measurements of subsets to estimate the total number of nesting individuals (Minckley et al. 1994, Cane 2008, Hanson and Ascher 2018). However, these methods are limited to species that maintain persistent nesting aggregations for long periods, whereas other species move nesting areas in subsequent years despite nesting in huge aggregations (e.g., a population of 423,000 female *Centris caesalpiniae* Cockerell; Rozen and Buchmann 1990). Nest counting and detection methods have also been used to quantify the number of bumble bee colonies in the landscape (Harder 1986, Lye et al. 2012, Iles et al. 2019) and these methods could be expanded to monitor populations over time.

Targeted sampling or re-sampling of pollinators of specific focal plants or plant communities via netting can provide valuable information on pollinators as well as a picture of community-level change over time. Although historic baseline datasets are relatively rare, they provide valuable windows into the past where they do exist (e.g., Robertson 1929, Linsley et al. 1963, Hurd and Linsley 1975, Hurd et al. 1980). Studies that employ this approach have been effective at detecting changes to the bee fauna and the local decline of specific taxa (Frankie et al. 2009, Burkle et al. 2013, Martins et al. 2013, Portman et al. 2018, Cumberland 2019). Sampling of focal plants has the additional advantage of providing ecological data, such as phenological mismatches or changes in interaction strength and frequency between plants and pollinators (Burkle et al. 2013), which can help inform causes and effects of declines (Frankie et al. 2002). In addition, by focusing on a more limited slice of the overall community, we can gain a valuable snapshot of the community without the excessive collection of nontarget bees. These methods can also be expanded to use citizen science or video-recording to allow for sampling that is less resource-intensive and/or nonlethal for sensitive species (Gardener and Daehler 2006, Roy et al. 2016). However, methods targeting focal plants are limited: they are better at detecting changes in species composition rather than changes in abundance. In addition, changes in visitation to one plant could have cascading effects on the visitors to other plants that would be difficult to understand without community-level sampling. However, similar weaknesses exist in passive sampling approaches that do not provide as much ecological data.

Detecting range shifts and contractions is difficult and requires large amounts of high-quality historical data. While there have been a relatively high number of studies documenting local declines and range contractions (e.g., Grixti et al. 2009, Jacobson et al. 2018, Wood et al. 2019), there have been few studies that document large-scale range contractions. This type of study is exemplified by Cameron et al. (2011), who compared current and historical distributions of eight species of North American bumble bees. To make this comparison, they collected almost 18,000 new specimens and acquired over 73,000 historical specimens from 47 institutions; all of these specimens had their identifications confirmed by experts and were databased and georeferenced (Cameron et al. 2011, Koch et al. 2015). In a similar study, Bartomeus et al. (2013) examined 438 species from the eastern United States using over 30,000 historical records from 10 institutions. Each specimen was verified by a taxonomist, and the data captured and standardized. Even with this effort, only 187 of the 438 species had more than 30 independent records and could be used for species-level analysis (Bartomeus et al. 2013). Overall, these types of studies can be robust and effective and should be expanded to additional taxa. However, they require huge amounts of effort and person-hours, and for many rare and uncommon species, there are not enough historical specimens to allow robust detection of range contractions.

Conclusion

Properly monitoring bees requires judicious allocation of limited resources. The current norm is to use passive sampling methods to collect massive numbers of bees with incomplete knowledge of the biases of these methods. In particular, bowl traps are uncritically used to perform whole-system monitoring without a proper appreciation of their limitations. The result is that current monitoring efforts are, for all practical purposes, focused on Halictidae, a group whose small size, social structure, and generalist foraging strategies make them likely to respond positively to human disturbance (Eickwort 1988, Harrison et al. 2018). Overall, bowl traps can be a useful tool for studies that are not focused on monitoring bees. They can also provide valuable data if they are supplemented with other collection methods or if the goal is Halictidae-focused collecting, but they are a poor choice if the goal is to monitor other species of bees or to monitor changes in bee abundance. We contend that bowl traps can be harmful from a monitoring standpoint because they impart a false sense that monitoring is being performed, while at the same time collecting an overwhelming number of Halictidae that then use time, money, and resources that could be better spent on more considered, targeted monitoring methods.

Instead of viewing bowl traps as a go-to method of wild bee monitoring, researchers should work to understand the limitations of current methods and to shift resources towards methods such as mark-recapture, nesting censuses, focal plants, and microsatellites that can detect ecological change and accomplish the monitoring goals of detecting range contractions and changes in true abundance without overwhelming limited resources. Especially as bee researchers face increasing restrictions on passive sampling due to the danger it poses to endangered species such as *Bombus affinis* Cresson (USFWS 2019), it is necessary to develop effective alternative monitoring methods. Finally, though this is not the primary focus of this paper, it is worth noting that the issues outlined here apply more broadly to comparative studies that examine relative differences in bee diversity and abundance. This is a pressing issue that represents a serious potential flaw in much of the bee ecology literature.

References Cited

Arbetman, M. P., G. Gleiser, C. L. Morales, P. Williams, and M. A. Aizen. 2017. Global decline of bumblebees is phylogenetically structured and inversely related to species range size and pathogen incidence. Proc. R. Soc. B Biol. Sci. 284: 20170204.

Baker, R. R., and Y. Sadovy. 1978. Distance and nature of light-trap response of moths. Nature. 279: 818–821.

Ballare, K. M., J. L. Neff, R. Ruppel, and S. Jha. 2019. Multi-scalar drivers of biodiversity: local management mediates wild bee community response to regional urbanization. Ecol. Appl. 29: e01869.

Bartomeus, I., J. S. Ascher, J. Gibbs, B. N. Danforth, D. L. Wagner, S. M. Hedtke, and R. Winfree. 2013. Historical changes in northeastern US bee pollinators related to shared ecological traits. Proc. Natl. Acad. Sci. USA. 110: 4656–4660.

Batley, M., and K. Hogendoorn. 2009. Diversity and conservation status of native Australian bees. Apidologie. 40: 347–354.

Baum, K. A., and K. E. Wallen. 2011. Potential bias in pan trapping as a function of floral abundance. J. Kansas Entomol. Soc. 84: 155–159.

Beck, J., and K. E. Linsenmair. 2006. Feasibility of light-trapping in community research on moths: attraction radius of light, completeness of samples, nightly flight times and seasonality of Southeast-Asian hawkmoths (Lepidoptera: Sphingidae). J. Res. Lepid. 39: 18–37.

Bischoff, I. 2003. Population dynamics of the solitary digger bee *Andrena vaga* Panzer (Hymenoptera, Andrenidae) studied using mark-recapture and nest counts. Popul. Ecol. 45: 197–204.

Buri, P., J. Y. Humbert, and R. Arlettaz. 2014. Promoting pollinating insects in intensive agricultural matrices: field-scale experimental manipulation of hay-meadow mowing regimes and its effects on bees. Plos One. 9: e85635.

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

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

Cane, J. H. 2001. Habitat fragmentation and native bees a premature verdict? Conserv. Ecol. 5.

Cane, J. H. 2008. A native ground-nesting bee (*Nomia melanderi*) sustainably managed to pollinate alfalfa across an intensively agricultural landscape. Apidologie. 39: 315–323.

Cane, J. H., R. L. Minckley, and L. J. Kervin. 2000. Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: pitfalls of pan-trapping. J. Kansas Entomol. Soc. 73: 225–231.

Colla, S. R., and L. Packer. 2008. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. Biodivers. Conserv. 17: 1379–1391.

Cumberland, C. 2019. Forty years of change in southwestern bee assemblages. Ph.D. dissertation, University of New Mexico, Albuquerque.

Droege, S. 2015. The very handy manual: how to catch and identify bees and manage a collection. USGS Bee Inventory and Monitoring Lab, Patuxent Wildlife Research Center, Beltsville, MD. https://www.usgs.gov/centers/pwrc/science/native-bee-inventory-and-monitoring-lab.

Droege, S., V. J. Tepedino, G. Lebuhn, W. Link, R. L. Minckley, Q. Chen, and C. Conrad. 2010. Spatial patterns of bee captures in North American bowl trapping surveys. Insect Conserv. Divers. 3: 15–23.

Droege, S., J. Engler, E. Sellers, and L. O'Brien. 2016. National protocol framework for the inventory and monitoring of bees. U.S. Fish and Wildlife Service, Fort Collins, Colorado.

Eardley, C. D., M. Gikungu, and M. P. Schwarz. 2009. Bee conservation in Sub-Saharan Africa and Madagascar: diversity, status and threats. Apidologie. 40: 355–366.

Eickwort, G. C. 1986. First steps into eusociality: the sweat bee *Dialictus lineatulus*. Florida Entomol. 69: 742–754.

Eickwort, G. C. 1988. Distribution patterns and biology of West Indian sweat bees (Hymenoptera: Halictidae), pp. 231–253. *In* J. K. Liebherr (ed.), Zoogeography of Caribbean insects. Cornell University Press, Ithaca, NY.

Entomological Society of America (ESA). 2017. Position statement on the importance of entomological collections. Ann. Entomol. Soc. Am. 110: 565–566.

Frankie, G. W., S. B. Vinson, R. W. Thorp, M. A. Rizzardi, and L. E. Newstrom-Lloyd. 2002. Monitoring: an essential tool in bee ecology and conservation, pp. 187–198. *In* P. Kevan and V. L. Imperatriz-Fonseca (eds.), Pollinating bees—The conservation link between agriculture and nature. Ministry of Environment, Brasilia.

Frankie, G. W., M. Rizzardi, S. B. Vinson, and T. L. Griswold. 2009. Decline in bee diversity and abundance from 1972–2004 on a flowering leguminous tree, *Andira inermis* in Costa Rica at the interface of disturbed dry forest and the urban environment. J. Kansas Entomol. Soc. 82: 1–20.

Franzén, M., and S. G. Nilsson. 2013. High population variability and source-sink dynamics in a solitary bee species. Ecology. 94: 1400–1408.

Galbraith, S. M., J. H. Cane, A. R. Moldenke, and J. W. Rivers. 2019. Wild bee diversity increases with local fire severity in a fire-prone landscape. Ecosphere. 10: e02668.

Gardener, M. C., and C. C. Daehler. 2006. Documenting floral visitors to rare Hawaiian plants using automated video recordings. Pacific Conserv. Biol. 12: 189–194.

Geroff, R. K., J. Gibbs, and K. W. McCravy. 2014. Assessing bee (Hymenoptera: Apoidea) diversity of an Illinois restored tallgrass prairie: methodology and conservation considerations. J. Insect Conserv. 18: 951–964.

Gezon, Z. J., E. S. Wyman, J. S. Ascher, D. W. Inouye, and R. E. Irwin. 2015. The effect of repeated, lethal sampling on wild bee abundance and diversity. Methods Ecol. Evol. 6: 1044–1054.

Gibbs, J. 2018. DNA barcoding a nightmare taxon: assessing barcode index numbers and barcode gaps for sweat bees. Genome. 61: 21–31.

Gibbs, J., N. K. Joshi, J. K. Wilson, N. L. Rothwell, K. Powers, M. Haas, L. Gut, D. J. Biddinger, and R. Isaacs. 2017. does passive sampling accurately reflect the bee (Apoidea: Anthophila) communities pollinating apple and sour cherry orchards? Environ. Entomol. 46: 579–588.

Gonçalves, R. B., and P. S. Oliveira. 2013. Preliminary results of bowl trapping bees (Hymenoptera, Apoidea) in a southern Brazil forest fragment. J. Insect Biodivers. 1: 1–9.

Goulson, D., O. Lepais, S. O'Connor, J. L. Osborne, R. A. Sanderson, J. Cussans, L. Goffe, and B. Darvill. 2010. Effects of land use at a landscape scale on bumblebee nest density and survival. J. Appl. Ecol. 47: 1207–1215.

Griffin, S. R., B. Bruninga-Socolar, M. A. Kerr, J. Gibbs, and R. Winfree. 2017. Wild bee community change over a 26-year chronosequence of restored tallgrass prairie. Restor. Ecol. 25: 650–660.

Grixti, J. C., L. T. Wong, S. A. Cameron, and C. Favret. 2009. Decline of bumble bees (*Bombus*) in the North American Midwest. Biol. Conserv. 142: 75–84.

Hanson, T., and J. S. Ascher. 2018. An unusually large nesting aggregation of the digger bee *Anthophora bomboides* Kirby, 1838 (Hymenoptera: Apidae) in the San Juan Islands, Washington State. Pan-Pac. Entomol. 94: 4–16.

Harder, L. D. 1986. Influences on the density and dispersion of bumble bee nests (Hymenoptera: Apidae). Ecography. 9: 99–103.

Harrison, T., J. Gibbs, and R. Winfree. 2018. Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits. Glob. Chang. Biol. 24: 287–296.

Herrmann, F., C. Westphal, R. F. Moritz, and I. Steffan-Dewenter. 2007. Genetic diversity and mass resources promote colony size and forager densities of a social bee (*Bombus pascuorum*) in agricultural landscapes. Mol. Ecol. 16: 1167–1178.

Hopkins, G. W., and R. P. Freckleton. 2002. Declines in the numbers of amateur and professional taxonomists: implications for conservation. Anim. Conserv. 5: 245–249.

Hurd, P. D., Jr. and E. G. Linsley. 1975. The principal *Larrea* bees of the southwestern United States (Hymenoptera: Apoidea). Smithson. Contrib. Zool. 193: 1–74.

Hurd, P. D., W. E. LaBerge, and E. G. Linsley. 1980. Principal sunflower bees of North America with emphasis on the southwestern United States (Hymenoptera, Apoidea). Smithson. Contrib. Zool. 1–158.

Iles, D. T., G. Pugesek, N. Z. Kerr, N. N. Dorian, and E. E. Crone. 2019. Accounting for imperfect detection in species with sessile life cycle stages: a case study of bumble bee nests. J. Insect Conserv. 23: 945–955.

Jacobson, M. M., E. M. Tucker, M. E. Mathiasson, and S. M. Rehan. 2018. Decline of bumble bees in northeastern North America, with special focus on *Bombus terricola*. Biol. Conserv. 217: 437–445.

Joshi, N. K., T. Leslie, E. G. Rajotte, M. A. Kammerer, M. Otieno, and D. J. Biddinger. 2015. Comparative trapping efficiency to characterize bee abundance, diversity, and community composition in apple orchards. Ann. Entomol. Soc. Am. 108: 785–799.

Kemp, C. 2015. Museums: the endangered dead. Nature. 518: 292–294.

Koch, J. B., J. Lozier, J. P. Strange, H. Ikerd, T. Griswold, N. Cordes, L. Solter, I. Stewart, and S. A. Cameron. 2015. USBombus, a database of contemporary survey data for North American bumble bees (Hymenoptera, Apidae, *Bombus*) distributed in the United States. Biodivers. Data J. 3: e6833.

Koh, I., E. V. Lonsdorf, N. M. Williams, C. Brittain, R. Isaacs, J. Gibbs, and T. H. Ricketts. 2016. Modeling the status, trends, and impacts of wild bee abundance in the United States. Proc. Natl Acad. Sci. USA. 113: 140–145.

Kuhlmann, M. 2015. Expertise in decline. Nature. 521: S58.

Kuhlman, M., and S. Burrows. 2017. Checklist of bees (Apoidea) from a private conservation property in west-central Montana. Biodivers. Data J. 5: e11506.

Larsson, M., and M. Franzén. 2008. Estimating the population size of specialised solitary bees. Ecol. Entomol. 33: 232–238.

LeBuhn, G., S. Droege, E. F. Connor, B. Gemmill-Herren, S. G. Potts, R. L. Minckley, T. Griswold, R. Jean, E. Kula, D. W. Roubik, et al. 2013. Detecting insect pollinator declines on regional and global scales. Conserv. Biol. 27: 113–120.

Lebuhn, G., S. Droege, E. F. Connor, B. Gemmill-Herren, S. G. Potts, R. L. Minckley, R. P. Jean, E. Kula, D. W. Roubik, K. W. Wright, et al. 2015. Evidence-based conservation: reply to Tepedino *et al*. Conserv. Biol. 29: 283–285.

LeBuhn, G., E. F. Connor, M. Brand, J. F. Colville, K. Devkota, R. B. Thapa, M. Kasina, R. K. Joshi, K. Aidoo, P. Kwapong, et al. 2016a. Monitoring pollinators around the world, pp. 3–16. *In* B. Gemmill-Herren (ed.), Pollination services to agriculture. Routledge, London and New York.

LeBuhn, G., S. Droege, E. Connor, B. Gemmill-Herren, and N. Azzu. 2016b. Protocol to detect and monitor pollinator communities: Guidance for practitioners. UN: Food and Agriculture Organization, Rome, Italy.

Lettow, M. C., L. A. Brudvig, C. A. Bahlai, J. Gibbs, R. P. Jean, and D. A. Landis. 2018. Bee community responses to a gradient of oak savanna restoration practices. Restor. Ecol. 26: 882–890.

Le Féon, V., M. Henry, L. Guilbaud, C. Coiffait-Gombault, E. Dufrêne, E. Kolodziejczyk, M. Kuhlmann, F. Requier, and B. E. Vaissière. 2016. An expert-assisted citizen science program involving agricultural high schools provides national patterns on bee species assemblages. J. Insect Conserv. 20: 905–918.

Linsley, E. G., and J. W. MacSwain. 1959. Ethology of some *Ranunculus* insects with emphasis on competition for pollen. Univ. Calif. Publ. Entomol. 16: 1–33.

Linsley, E. G., J. W. MacSwain, and P. H. Raven. 1963. Comparative behavior of bees and Onagraceae. I. *Oenothera* bees of the Colorado Desert. Univ. Calif. Publ. Entomol. 33: 1–24.

Lye, G. C., J. L. Osborne, K. J. Park, and D. Goulson. 2012. Using citizen science to monitor *Bombus* populations in the UK: nesting ecology and relative abundance in the urban environment. J. Insect Conserv. 16: 697–707.

Martins, A. C., R. B. Goncalves, and G. A. R. Melo. 2013. Changes in wild bee fauna of a grassland in Brazil reveal negative effects associated with growing urbanization during the last 40 years. Zoologia. 30: 157–176.

Mayer, C., and M. Kuhlmann. 2004. Synchrony of pollinators and plants in the winter rainfall area of South Africa—observations from a drought year. Trans. R. Soc. South Africa. 59: 55–57.

Merckx, T., and E. M. Slade. 2014. Macro-moth families differ in their attraction to light: implications for light-trap monitoring programmes. Insect Conserv. Divers. 7: 453–461.

Michener, C. D. 1974. The social behavior of the bees: a comparative study. Harvard University Press, Cambridge.

Michener, C. D. 2007. The bees of the world, 2nd ed. Johns Hopkins University Press, Baltimore.

Minckley, R. L., W. T. Wcislo, D. Yanega, and S. L. Buchmann. 1994. Behavior and phenology of a specialist bee (*Dieunomia*) and sunflower (*Helianthus*) pollen availability. Ecology. 75: 1406–1419.

Neame, L. A., T. Griswold, and E. Elle. 2013. Pollinator nesting guilds respond differently to urban habitat fragmentation in an oak-savannah ecosystem. Insect Conserv. Divers. 6: 57–66.

O'Connor, R. S., W. E. Kunin, M. P. D. Garratt, S. G. Potts, H. E. Roy, C. Andrews, C. M. Jones, J. M. Peyton, J. Savage, M. C. Harvey, R. K. A. Morris, S. P. M. Roberts, I. Wright, A. J. Vanbergen, and C. Carvell. 2019. Monitoring insect pollinators and flower visitation: the effectiveness and feasibility of different survey methods. Methods Ecol. Evol. 10: 2129–2140.

Onuferko, T. M., D. A. Skandalis, R. León Cordero, and M. H. Richards. 2018. Rapid initial recovery and long-term persistence of a bee community in a former landfill. Insect Conserv. Divers. 11: 88–99.

Packer, L., J. C. Grixti, R. E. Roughley, and R. Hanner. 2009. The status of taxonomy in Canada and the impact of DNA barcoding. Can. J. Zool. 87: 1097–1110.

Portman, Z. M., V. J. Tepedino, A. D. Tripodi, A. L. Szalanski, and S. L. Durham. 2018. Local extinction of a rare plant pollinator in Southern Utah (USA) associated with invasion by Africanized honey bees. Biol. Invasions. 20: 593–606.

Prado, S. G., H. T. Ngo, J. A. Florez, and J. A. Collazo. 2017. Sampling bees in tropical forests and agroecosystems: a review. J. Insect Conserv. 21: 753–770.

Rhoades, P., T. Griswold, L. Waits, N. A. Bosque-Pérez, C. M. Kennedy, and S. D. Eigenbrode. 2017. Sampling technique affects detection of habitat factors influencing wild bee communities. J. Insect Conserv. 21: 703–714.

Richards, M. H., J. L. Vickruck, and S. M. Rehan. 2010. Colony social organisation of *Halictus confusus* in southern Ontario, with comments on sociality in the subgenus *H*. (*Seladonia*). J. Hymenopt. Res. 19: 144–158.

Robertson, C. 1929. Flowers and insects lists of visitors of four hundred and fifty-three flowers. Science Press Printing Company, Lancaster, PA.

Roulston, T. H., S. A. Smith, and A. L. Brewster. 2007. A comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera: Apiformes) fauna. J. Kansas Entomol. Soc. 80: 179–181.

Roy, H. E., E. Baxter, A. Saunders, and M. J. O. Pocock. 2016. Focal plant observations as a standardised method for pollinator monitoring: opportunities and limitations for mass participation citizen science. PLoS One. 11: 1–14.

Rozen, J. G., and S. L. Buchmann. 1990. Nesting biology and immature stages of the bees *Centris caesalpiniae*, *C. pallida*, and the cleptoparasite *Ericrocis lata* (Hymenoptera: Apoidea: Anthophoridae). Am. Museum Novit. 2985: 1–30.

Scheper, J., M. Reemer, R. van Kats, W. A. Ozinga, G. T. van der Linden, J. H. 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. Proc. Natl Acad. Sci. USA. 111: 17552–17557.

Schilthuizen, M., C. S. Vairappan, E. M. Slade, D. J. Mann, and J. A. Miller. 2015. Specimens as primary data: museums and 'open science'. Trends Ecol. Evol. 30: 237–238.

Schlueter, M. A., and N. G. Stewart. 2015. Native bee (Hymenoptera: Apoidea) abundance and diversity in North Georgia apple orchards throughout the 2010 growing season (March to October). Southeast. Nat. 14: 721–739.

Silveira, F. A., C. Pinheiro-Machado, I. Alves-dos-Santos, A. M. P. Kleinert, and V. L. Imperatriz-Fonseca. 2002. Taxomomic constraints for the conservation and sustainable use of wild pollinators—The Brazilian wild bees, pp. 41–50. *In* P. G. Kevan, and V. L. Imperatriz-Fonseca (eds.), Pollinating bees—the conservation link between agriculture and bature. Ministry of Environment, Brasilia.

Stephen, W. P., and S. Rao. 2007. Sampling native bees in proximity to a highly competitive food resource (Hymenoptera: Apiformes). J. Kansas Entomol. Soc. 80: 369–376.

Strange, J. P., and A. D. Tripodi. 2019. Characterizing bumble bee (Bombus) communities in the United States and assessing a conservation monitoring method. Ecol. Evol. 9: 1061–1069.

Tang, M., C. J. Hardman, Y. Ji, G. Meng, S. Liu, M. Tan, S. Yang, E. D. Moss, J. Wang, C. Yang, C. Bruce, T. Nevard, S. G. Potts, X. Zhou, and D. W. Yu. 2015. High-throughput monitoring of wild bee diversity and abundance via mitogenomics. Methods Ecol. Evol. 6: 1034–1043.

Tepedino, V. J. 1981. The pollination efficiency of the squash bee (*Peponapis pruinosa*) and the honey bee (*Apis mellifera*) on summer squash (*Cucurbita pepo*). J. Kansas Entomol. Soc. 54: 359–377.

Tepedino, V. J., S. Durham, S. A. Cameron, and K. Goodell. 2015. Documenting bee decline or squandering scarce resources. Conserv. Biol. 29: 280–282.

Toler, T. R., E. W. Evans, and V. J. Tepedino. 2005. Pan-trapping for bees (Hymenoptera: Apiformes) in Utah's west desert: the importance of color diversity. Pan-Pac. Entomol. 81: 103–113.

Truxa, C., and K. Fiedler. 2012. Attraction to light-from how far do moths (Lepidoptera) return to weak artificial sources of light? Eur. J. Entomol. 109: 77–84.

U.S Fish and Wildlife Service (USFWS). 2019. Survey protocols for the rusty patched bumble bee (*Bombus affinis*). Version 2.2. USFWS, Bloomington, MN.

Wcislo, W. T., B. N. Danforth, and U. G. Mueller. 1994. George Campbell Eickwort (1949–1994). Insectes Soc. 41: 461–463.

Westphal, C., R. Bommarco, G. Carré, E. Lamborn, N. Morison, T. Petanidou, S. G. Potts, S. P. M. Roberts, H. Szentgyörgyi, T. Tscheulin, et al. 2008. Measuring bee diversity in different European habitats and biogeographical regions. Ecol. Monogr. 78: 653–671.

Wilson, J. S., T. Griswold, and O. J. Messinger. 2008. Sampling bee communities (Hymenoptera: Apiformes) in a desert landscape: are pan traps sufficient? J. Kansas Entomol. Soc. 81: 288–300.

Wood, T. J., J. M. Holland, and D. Goulson. 2015. A comparison of techniques for assessing farmland bumblebee populations. Oecologia. 177: 1093–1102.

Wood, T. J., J. Gibbs, K. K. Graham, and R. Isaacs. 2019. Narrow pollen diets are associated with declining Midwestern bumble bee species. Ecology. 100: e02697.

Woodard, S. H., J. D. Lozier, D. Goulson, P. H. Williams, J. P. Strange, and S. Jha. 2015. Molecular tools and bumble bees: revealing hidden details of ecology and evolution in a model system. Mol. Ecol. 24: 2916–2936.