Bee demise and bee rise: From honey bee colony losses to finding measures for advancing entire bee communities

Bienenschwund und Bienenaufschwung: Von Honigbienen-Kolonieverlusten zur Förderung von gesamten Bienengemeinschaften

Doctoral thesis for a doctoral degree
at the Graduate School of Life Sciences,
Julius-Maximilians-Universität Würzburg,
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Hannover

Würzburg 2018

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Summary

My dissertation comprises three studies: (1) an assessment of honey bee colony losses in the USA between 2014 and 2015, (2) an exploration of the potential of reclaimed sand mines as bee habitat, and (3) an evaluation of native and non-native pollinator friendly plants in regard to their attraction to bees. While the first study focuses on honey bees, the latter two studies primarily take wild bees or entire bee communities in focus.

The study on honey bee colony losses was conducted within the framework of the Bee Informed Partnership (BIP, beeinformed.org) and aligns with the annual colony loss surveys which have been conducted in the USA since the winter of 2006/2007. It was the fourth year for which summer and annual losses were calculated in addition to winter losses. Among participants, backyard beekeepers were the largest group (n = 5690), although sideline (n = 169) and commercial (n = 78) beekeepers managed the majority (91.7 %) of the 414 267 surveyed colonies. Overall, 15.1 % of the estimated 2.74 million managed colonies in the USA were included in the study. Total honey bee colony losses (based on the entirety of included colonies) were higher in summer (25.3 %) than in winter (22.3 %) and amounted to 40.6 % for the entire 2014/2015 beekeeping year. Average colony losses per beekeeper or operation were higher in winter (43.7 %) than in summer (14.7 %) and amounted to 49 % for the entire 2014/2015 beekeeping year. Due to the dominance of backyard beekeepers among participants, average losses per operation (or unweighted loss) stronger reflected this smaller type of beekeeper. Backyard beekeepers mainly named colony management issues (e.g., starvation, weak colony in the fall) as causes for mortality, while sideline and commercial beekeepers stronger emphasized parasites or factors outside their control (e.g., varroa, nosema, queen failure).

The second study took place at reclaimed sand mines. Sand mines represent anthropogenically impacted habitats found worldwide, which bear potential for bee conservation. Although floral resources can be limited at these habitats, vegetation free patches of open sandy soils and embankments may offer good nesting possibilities for sand restricted and other bees. We compared bee communities as found in three reclaimed sand mines and at adjacent roadside meadows in Maryland, USA, over two years. Both sand mines and roadsides hosted diverse bee communities with 111 and 88 bee species, respectively. Bee abundances as well as richness and Shannon diversity of bee species were higher in sand mines than at roadsides and negatively correlated with the percentage of vegetational ground cover. Species composition also differed significantly between habitats. Sand mines hosted a higher proportion of ground nesters, more uncommon and more ‘sand loving' bees similar to natural sandy areas of Maryland. Despite the destruction of the original pre-mining habitat, sand mines thus appear to represent a unique habitat for wild bees, particularly when natural vegetation and open sand spots are encouraged. Considering habitat loss, the lack of natural disturbance regimes, and ongoing declines of wild bees, sand mines could add promising opportunities for bee conservation which has hitherto mainly focused on agricultural and urban habitats.

The third study was an experimental field study on pollinator friendly plants. Bees rely on the pollen and nectar of plants as their food source. Therefore, pollinator friendly plantings are often used for habitat enhancements in bee conservation. Non-native pollinator friendly plants may aid in bee conservation efforts, but have not been tested and compared with native pollinator friendly plants in a common garden experiment. In this study, we seeded mixes of 20 native and 20 non-native pollinator friendly plants in two separate plots at three sites in Maryland, USA. For two years, we recorded flower visitors to the plants throughout the blooming period and additionally sampled bees with pan traps. A total of 3744 bees (120 species) were sampled in the study. Of these, 1708 bees (72 species) were hand netted directly from flowers for comparisons between native and non-native plants. Depending on the season, bee abundance and species richness was either similar or lower (early season and for richness also late season) at native plots compared to non-native plots. Additionally, the overall bee community composition differed significantly between native and non-native plots. Furthermore, native plants were associated with more specialized plant-bee visitation networks compared to non-native plants. In general, visitation networks were more specialized in the early season than the later seasons. Four species (*Bombus impatiens*, *Halictus poeyi/ligatus*, *Lasioglossum pilosum*, and *Xylocopa virginica*) out of the five most abundant bee species (also including *Apis mellifera*) foraged more specialized on native than non-native plants. Our study showed that non-native plants were well accepted by a diverse bee community and had a similar to higher attraction for bees compared to native plants. However, we also demonstrated alterations in foraging behavior, bee community assemblage, and visitation networks. As long as used with caution, non-native plants can be a useful addition to native pollinator friendly plantings. This study gives a first example of a direct comparison between native and non-native pollinator friendly plants.

Zusammenfassung

Meine Dissertation umfasst drei Studien: (1) eine Erfassung von Honigbienen-Kolonieverlusten in den USA zwischen 2014 und 2015, (2) die Erforschung des Potenzials renaturierter Sandminen als Habitat für Bienen und (3) eine Evaluierung nativer sowie standortfremder bestäuberfreundlicher Pflanzen hinsichtlich ihrer Attraktivität für Bienen. Während die erste Studie Honigbienen im Fokus hat, verschiebt sich der Fokus der zwei weiteren Studien hin zu Wildbienen bzw. gesamten Bienengemeinschaften.

Die Studie zu Honigbienenkolonieverlusten wurde im Rahmen des Bee Informed Partnerships (BIP, beeinformed.org) durchgeführt und reiht sich ein in die seit dem Winter 2006/2007 jährlich durchgeführten Untersuchungen in den USA. Es ist das vierte Jahr in dem Sommer- und Jahresverluste zusätzlich zu den Winterverlusten kalkuliert wurden. Unter den Teilnehmern bildete die Gruppe der Hobby-Imker den größten Anteil (n = 5690), obwohl nebenberufliche (n = 169) und kommerzielle (n = 78) Imker den Großteil (91,7 %) der 414 267 begutachteten Bienenvölkern bzw. Kolonien hielten. Insgesamt enthielt die Studie 15,1 % der auf 2,74 Mio. geschätzten Gesamtzahl an gehaltenen Bienenvölkern in den USA. Die Gesamtverluste an Honigbienenvölkern (basierend auf der Gesamtheit der erfassten Völker) waren im Sommer mit 25,3 % höher als im Winter mit 22,3 % und bezifferten sich auf 40,6 % für das gesamte Imkerjahr in 2014/2015. Durchschnittliche Kolonieverluste pro Imkerbetrieb waren höher im Winter (43,7 %) als im Sommer (14,7 %) und betrugen 49 % für das gesamte Imkerjahr in 2014/2015. Aufgrund der hohen Anzahl an Hobby-Imkern unter den Teilnehmern reflektieren die durchschnittlichen Kolonieverluste pro Imkerbetrieb (oder ungewichtete Verluste) v.a. die Situation dieser kleineren Imkerbetriebe. Hobby-Imker nannten als Gründe für die Honigbienenmortalität hauptsächlich Probleme des Koloniemanagements (z.B. Verhungerung, schwache Völker im Herbst), während nebenberufliche und kommerzielle Imker stärker Faktoren betonten, die außerhalb ihrer Kontrolle lagen (z.B. Varroamilben, Nosemasporen, Versagen der Königin).

Die zweite Studie fand in renaturierten Sandminen statt. Sandminen sind weltweit zu findende anthropogen veränderte Landschaften, die ein Potenzial für Bienenschutz haben. Obwohl florale Ressourcen in diesen Habitaten limitiert sein können, könnten die vegetationsfreien Flecken auf offenen Sandböden und Böschungen gute Nistplätze für auf Sand spezialisierte und andere Bienen bieten. Wir haben Bienengemeinschaften aus drei renaturierten Sandminen sowie jeweils nahe gelegenen bepflanzten Straßenrändern in Maryland, USA verglichen. Sowohl die Sandminen als auch die Straßenränder enthielten vielfältige Bienengemeinschaften mit 111 (Sandminen) und 88 (Straßenränder) Bienenarten.

Bienenabundanz, Artenreichtum und Shannon Diversität waren höher in den Sandminen als an den Straßenrändern und korrelierten negativ mit dem Anteil an vorhandener Bodenvegetation. Darüber hinaus unterschied sich die Artzusammensetzung signifikant zwischen den beiden Habitattypen. Sandminen enthielten einen größeren Anteil an Bodennistern, mehr seltene Arten und mehr sandliebende Arten, ähnlich natürlicher sandiger Gebiete in Maryland. Trotz der Zerstörung des ursprünglichen prä-Minen Habitats, scheinen Sandminen daher ein einzigartiges Bienenhabitat für Wildbienen darzustellen, besonders wenn die natürliche Besiedlung von Vegetation und offene Sandflächen gefördert werden. Im Hinblick auf Habitatverluste, auf das Fehlen von natürlichen Landschaftsstörungen und auf den weiterschreitenden Rückgang an Wildbienen, könnten Sandminen eine vielversprechende Möglichkeit für Bienenschutz darstellen, der sich bisher stark auf landwirtschaftliche und urbane Habitate konzentrierte.

Bei der dritten Studie handelt es sich um eine experimentelle Feldstudie zu bestäuberfreundlichen Pflanzen. Bienen sind auf Pollen und Nektar von Pflanzen als Nahrungsquelle angewiesen. Aus diesem Grund werden bestäuberfreundliche Pflanzen oft für Habitatverbesserungen im Rahmen von Bienenschutzmaßnahmen gepflanzt. Standortfremde bestäuberfreundliche Pflanzen können dabei die Bienenschutzmaßnahmen unterstützen, wurden aber bisher nicht in einem *Common Garden* Experiment zusammen mit nativen bestäuberfreundlichen Pflanzen getestet bzw. verglichen. In dieser Studie haben wir Saatgutmischungen mit jeweils 20 nativen und 20 standortfremden Pflanzen in zwei separaten Plots in drei Gebieten in Maryland, USA ausgesät. Zwei Jahre lang protokollierten wir über die gesamten Blühzeiträume hinweg Pflanzenbesucher und sammelten Bienen mit Farbschalen. Insgesamt erfassten wir 3744 Bienen (120 Arten), von denen 1708 Individuen (72 Arten) per Hand direkt von den Blüten gesammelt wurden für die Vergleiche zwischen nativen und standortfremden Pflanzen. Abhängig von der Saison waren Bienenabundanz und Artenreichtum entweder ähnlich oder niedriger (frühe Saison und für Artenreichtum auch späte Saison) in nativen Plots verglichen mit den standortfremden Plots. Zusätzlich unterschied sich die Zusammensetzung der Bienengemeinschaft signifikant zwischen nativen und standortfremnden Pflanzen. Darüber hinaus waren die Bienen-Pflanzen-Besuchs-Netzwerke nativer Pflanzen spezialisierter als die Besuchs-Netzwerke standortfremder Pflanzen. Im Allgemeinen waren die Besuchs-Netzwerke in der frühen Saison spezialisierter als in der späten Saison. Vier Arten (*Bombus impatiens*, *Halictus poeyi/ligatus*, *Lasioglossum pilosum*, und *Xylocopa virginica*) der fünf am häufigsten vorkommenden Arten (zusätzlich auch *Apis mellifera*) fouragierten spezialisierter auf nativen Pflanzen als auf standortfremden Pflanzen. Unsere Studie zeigte, dass standortfremde Pflanzen weitläufig von einer artenreichen Bienengemeinschaft angenommen wurden und

eine ähnliche bis höhere Attraktivität für Bienen aufwiesen verglichen mit nativen Pflanzen. Allerdings demonstrierten wir auch Änderungen im Fouragierverhalten, in der Zusammensetzung der Bienengemeinschaft und in den Besuchs-Netzwerken. Insgesamt kann ein vorsichtiger Einsatz standortfremder Pflanzen eine sinnvolle Ergänzung zu nativen bestäuberfreundlichen Anpflanzungen sein. Diese Studie stellt ein erstes Beispiel eines direkten Vergleichs von nativen und standortfremden bestäuberfreundlichen Anpflanzungen dar.

Introduction: The relevance of honey bees and wild bees

The importance of pollinators is tremendous. They maintain the functioning of important ecosystem services by ensuring the survival of the majority of wild plants and the production of 70 % of our food crops by pollination (Ashman et al. 2004; Klein et al. 2007; Ollerton et al. 2011; Ricketts et al. 2008). The economic value of pollination services provided by insects is estimated to approximately $153 billion annually (Gallai et al. 2009). While pollinators are diverse, bees form the most important group. Wild bee species and honey bees both contribute substantially to pollination (Garibaldi et al. 2013). Therefore, recent declines in wild bees and the unsustainable loss rates of managed bees are raising concerns worldwide (Potts et al. 2010a).

Honey bees, *Apis mellifera*, have been domesticated by humans for honey production and crop pollination and are kept worldwide by hobby beekeepers and commercial beekeepers (Southwick and Southwick 1992). Due to their generalist foraging behavior they serve as a versatile pollinator for a tremendous amount of crop plants and have become the most important managed pollinator in agriculture globally (Aizen et al. 2009; Calderone 2012). Especially with intensification of agriculture, managing the availability of pollinators has become increasingly important. Many large-scale crop productions, such as almonds or apples, heavily rely on this species for pollination (Calderone 2012). Due to the high economic relevance of honey bees as pollinators, it is vital to track changes in the global honey bee stock and identify reasons for honey bee mortality (Potts et al. 2010b). In my dissertation, I have assessed annual colony losses of managed honey bees in the US for 2014/2015 within the framework of the Bee Informed Partnership (BIP, beeinformed.org).

In the US, honey bee colony losses have been documented since 2006/2007 which was a winter of particularly high honey bee losses in large parts attributed to the then newly described phenomenon of colony collapse disorder (CCD) (Oldroyd 2007; Stokstad 2007; vanEngelsdorp et al. 2009; vanEngelsdorp et al. 2007). The phenomenon received a considerable amount of media attention and overall raised awareness for honey bee health and protection (Barrionuevo 2007; Sahba 2007; Wells 2007). It highlighted the need for objective assessment of honey bee mortality. Fluctuating honey bee colony losses were also observed in other parts of the world where similar honey bee colony monitoring was started over the past two decades. On the national level, Germany was one of the first countries that introduced a honey bee monitoring program. The federal project DeBiMo (Deutsches BienenMonitoring) was established in 2004 in Germany (DeBiMo 2019; Genersch et al. 2010). Many other countries have developed their own programs in the meantime (Centre for

Ecology & Hydrology 2019; Hendrikx et al. 2009; Porrini et al. 2016). On the international level, programs such as the “European epidemiological surveillance programme on honeybee colony mortality” (EPILOBEE) or the project “Prevention of honey bee COlony LOSSes” (COLOSS) were developed evaluating honey bee losses in Europe and beyond (Brodschneider et al. 2018; Laurent et al. 2016; van der Zee et al. 2014; van der Zee et al. 2012).

Honey bees are managed pollinators and are bred by humans. Therefore, losses can be compensated to a certain extent by reproducing honey bee colonies. However, the high honey bee colony loss rates have confronted beekeepers and the agricultural industry with difficult and costly challenges in recent years (Burgett et al. 2010; Ellis et al. 2010; Traynor 2013; vanEngelsdorp and Meixner 2010). Reasons for high mortality rates of honey bee colonies are e.g., parasites, diseases, pesticides, and changes in floral resource availability (Alaux et al. 2010; Doublet et al. 2015; Goulson et al. 2015; Le Conte et al. 2010; Steinhauer et al. 2018). The difficulties with maintaining the global honey bee stock needed for pollinating our crops arise with a simultaneous increase of acreage of pollinator dependent crops, aggravating the threat of pollination shortages (Aizen and Harder 2009). These conditions emphasize the inherent risk of strongly focusing on a single species for pollination in agricultural productions (Winfree 2008).

Honey bees often are the pollinator of choice, because they are effective pollinators for many crops, easily manageable, and transportable. However, there are examples of other bee species managed for crop pollination. Bumble bees can be domesticated and pollinate a large number of crops such as blueberries, almonds or apples (Drummond 2012; Javorek et al. 2002; Mader et al. 2010; Thomson and Goodell 2001). Also solitary bees such as leafcutter bees are manageable and efficient pollinators of e.g., alfalfa, canola or cranberries and mason bees of e.g., apples, almonds or cherries (Bosch and Kemp 2002; Gruber et al. 2011; Mader et al. 2010; Pitts-Singer and Cane 2011). Hence, we have additional managed pollinators which can help to reduce the risk of pollination shortfalls. The overall advantage of managed and commercialized pollinators is the possibility to transport them directly to the crop at the exact time point needed. However, there are also some drawbacks of pollinator management that apply to honey bees and other managed bee species. The large-scale breeding of bees increases the likelihood of disease outbreaks (Bosch and Kemp 2002; Gisder and Genersch 2016). Due to the extensive transportation of the bees, these diseases easily spread throughout bee populations (Bosch and Kemp 2002; Gisder and Genersch 2016; McMahon et al. 2015). Unfortunately, they are not confined to managed bees, but can also be transmitted to wild bee populations (Furst et al. 2014; Gisder and Genersch 2016;

McMahon et al. 2015). Therefore, the commercial use of managed bees remains a risky business with negative consequences for wild life despite the convenience for crop pollination.

Fortunately, we additionally have a multitude of wild bee species which also pollinate our crops. In many cases, wild bees perform equal or even better pollination services compared to managed pollinators (Garibaldi et al. 2013; Isaacs and Kirk 2010; Kremen et al. 2002; Slaa et al. 2006). In fact, it is often rather the diversity of pollinators than their abundance contributing to high crop yields (Garibaldi et al. 2013; Hoehn et al. 2008; Klein et al. 2003; Kremen et al. 2002). Hence, the best way to secure pollination services is to find measures that maintain abundant and diverse bee communities. Moreover, Kleijn et al. (2015) point out that the mere quantification of economic value of pollination services by certain wild bees should not be the only argument for their conservation. They caution that we do not entirely understand the complexity with which biodiversity per se contributes to the delivery of ecosystem services and which additionally justifies and requires the protection of all wild bee species. For these reasons, the observed declines of wild bee populations are particularly alarming and require conservation actions (Potts et al. 2010a).

The need for bee conservation has also been recognized by society and governments in the meantime. Important milestones for bee conservation were, for example, the International Pollinator Initiative-Plan of Action by the Conference of the Parties (COP) to the Convention on Biological Diversity, the EU Pollinators Initiative, and the development of various national strategies worldwide for pollinator protection such as e.g., the National Strategy to Promote Pollinator Health by the US White House (Byrne and Fitzpatrick 2009; European Commission 2018; Pollinator Health Task Force 2015; Underwood et al. 2017). However, despite the willingness to promote bees, there is a gap between theory and action (Christmann and Aw-Hassan 2012; Garibaldi et al. 2014; Inouye et al. 2017). Part of the reason for this gap is the ongoing and incomplete process of finding appropriate practices for bee promotion (Garibaldi et al. 2014; Inouye et al. 2017). Habitat requirements of bees are not conclusively understood (Winfree 2010). For instance, the proximity to natural or semi-natural habitats is often positively correlated with wild bee abundance and diversity, but not all studies show this trend clearly and uncertainties remain regarding the factors determining the positive correlation (Cane et al. 2006; Holzschuh et al. 2007; Kearns and Oliveras 2009; Kennedy et al. 2013; Kratschmer et al. 2018; Kremen et al. 2004; Le Féon et al. 2010). Floral diversity is seen as one of the key factors, but again studies do not show a consistent relationship between floral diversity and bee diversity or bee abundance: increases in floral diversity are in some cases associated with increased bee abundances (Batáry et al. 2010; Ebeling et al.

2008; Sakagami and Fukuda 1973) and in other cases with decreased bee abundance (Banaszak 1996; Fortel et al. 2014; Neame et al. 2012). In this context, the exact floral composition and the presence of non-native plants can, for example, play a role for the assemblage of bee communities (Bartomeus et al. 2008; Morandin and Kremen 2013; Pardee and Philpott 2014; Wu et al. 2018). Therefore, a more detailed view on the links between floral resources and wild bees is necessary to effectively protect bees. Lastly, enhancement of wild bees has strongly focused on agricultural habitats, while other habitats received very little attention in research (Winfree 2010). Cusser and Goodell (2013) and Russell et al. (2005) have shown how reclaimed coal mines or powerline strips host diverse bee communities. Many more habitats might offer favorable conditions for wild bees or could be improved for bees. These options need to be explored considering the ongoing declines of wild bee populations.

In summary, it is important to maintain healthy honey bee and diverse and abundant wild bee populations in order to secure pollination services. Therefore, I addressed these issues in my dissertation. I commenced my work with a documentation of honey bee mortality in the US as one step towards maintaining healthy honey bee populations. I have further expanded my dissertation on the topic of finding measures which promote entire bee communities. My research aimed at gaining insights into habitat requirements of wild bees to improve their protection. I have assessed the habitats of reclaimed sand mines and roadsides regarding their suitability for wild bees and have evaluated the attraction of native and non-native pollinator friendly plants for wild bees in a field experiment. More detailed introductions to these parts of my dissertation follow the section on honey bee colony losses in the USA.

Honey bee colony losses in the USA

This chapter has been published as

Seitz, N., Traynor, K.S., Steinhauer, N., Rennich, K., Wilson, M.E., Ellis, J.D., Rose, R., Tarpy, D.R., Sagili, R.R., Caron, D.M., Delaplane, K.S., Rangel, J., Lee, K., Baylis, K., Wilkes, J.T., Skinner, J.A., Pettis, J.S., vanEngelsdorp, D., 2015. A national survey of managed honey bee 2014–2015 annual colony losses in the USA. Journal of Apicultural Research 54, 292-304.

Summary

Declines in pollinators and high mortality rates of honey bee colonies are a major concern, both in the USA and globally. Long-term data on summer, winter, and annual colony losses improve our understanding of forces shaping the viability of the pollination industry. Since the mass die-offs of colonies in the winter of 2006 - 2007, generally termed “Colony Collapse Disorder” (CCD), annual colony loss surveys have been conducted in the USA. These surveys gauge colony losses among beekeepers of all operation sizes, recruited to participate via regional beekeeping organizations, phone calls and postal mail. In the last 3 years, these surveys include summer and annual losses in addition to winter losses. Winter losses in this most recent survey include 5,937 valid participants (5,690 backyard, 169 sideline, and 78 commercial beekeepers), collectively managing 414,267 colonies on 1 October 2014 and constituting 15.1 % of the estimated 2.74 million managed colonies in the USA. Annual losses are typically higher than either winter or summer losses, as they calculate losses over the entire year. Total reported losses were 25.3 % [95 % CI 24.7 - 25.9 %] over the summer, 22.3 % [95 % CI 21.9 - 22.8 %] over the winter, and 40.6 % [95 % CI 40.0 - 41.2 %] for the entire 2014 - 2015 beekeeping year. Average losses were 14.7 % [95 % CI 14.0 - 15.3 %] over the summer, 43.7 % [95 % CI 42.8 - 44.6 %] over the winter, and 49.0 % [95 % CI 48.1 - 50.0 %] over the entire year. While total winter losses were lower in 2014-2015 than in previous years, summer losses remained high, resulting in total annual colony losses of more than 40 % during the survey period. It was the first year that total losses were higher in the summer than in the winter, explained in large part by commercial beekeepers reporting losses of 26.2 % of their managed colonies during summer compared to 20.5 % during winter. Self-identified causes of overwintering mortality differed by operation size, with smaller backyard beekeepers generally indicating colony management issues (e.g., starvation, weak colony in the fall), in contrast to commercial beekeepers who typically emphasize parasites or factors outside their control (e.g., varroa, nosema, queen failure). More than two-thirds of all beekeepers (67.3 %) had higher colony losses than they deemed acceptable.

Introduction

Honey bee (*Apis mellifera*) colony losses remain at levels substantially higher than rates which beekeepers identify as acceptable, raising concerns about possible future crop pollination shortfalls (Calderone 2012). In the USA and elsewhere, beekeepers are having difficulty keeping pace with the demand for managed colonies with increasing acreage of pollinator-dependent crops and demand for the insects that service them (Aizen and Harder 2009). Multiple interacting factors drive honey bee colony mortality including parasitization and virus transmission by the ectoparasitic mite, *Varroa destructor*, other parasites and disease, poor nutrition due to changing land use patterns and decreased forage availability, large-scale replacement of nectar and pollen rich nitrogen fixing legumes with synthetic fertilizers, and sublethal impacts of pesticides (Alaux et al. 2010; Doublet et al. 2015; Goulson et al. 2015; Le Conte et al. 2010). Managed honey bee colony numbers have declined steadily in the USA from a high of 5.1 million colonies in 1947 to a low of 2.39 million colonies in 2006 (vanEngelsdorp and Meixner 2010). The large colony losses and the vast media attention given to “Colony Collapse Disorder” (CCD), a condition that emerged in 2006-2007 (Williams et al. 2010a) , has driven a surge in backyard beekeepers, while commercial beekeepers have built in buffers for higher losses, increasing their numbers of managed colonies to meet the requirements of their pollination contracts (vanEngelsdorp and Meixner 2010). Despite widespread high winter losses, the number of managed colonies paradoxically rose 14.6 %, from 2.39 million in 2006 (USDA-NASS 2007) to 2.74 million in 2014 (USDA-NASS 2015) reversing the long-term decline in the USA. Mitigating high annual colony losses through increased splitting of surviving stock or purchasing replacement colonies adds considerably to operation costs. Such costs are observed both in management time and lost revenue from decreased honey production, and because fewer full-strength pollination units may be available at times of high colony demand. Increased honey prices (USDA-NASS 2015) and pollination rental fees (Burgett et al. 2010; Traynor 2013) have helped offset the expense of increasing colony numbers. Whether this constant rebuilding of lost colonies is sustainable over the long-term remains to be seen, especially in light of ever increasing agricultural acreage dependent on pollination (Aizen and Harder 2009).

Trends in available pollination units and seasonal colony losses have proven to be vital when appraising the long-term sustainability of agriculture in the USA. Comparable multi-year records enhance our understanding of the variability in colony losses and may help identify risk factors or risk combinations that otherwise escape casual observation. Surveys conducted in the USA since the winter of 2006 - 2007 allowed beekeepers to self-report numbers of living colonies at specific times of the year. The surveys tracked colony increases and decreases within an operation, the level of acceptable winter losses, whether colonies were moved across states lines, if the operation participated in almond pollination, and the beekeeper-perceived main cause of colony losses. Data from previous surveys have shown that total winter colony losses fluctuated between a high of 36 % in 2007 - 2008 and a low of 22 % in 2011 - 2012. Summer and annual losses were first added to the survey for the 2012 - 2013 beekeeping year, with total summer losses reported to be 25 % in 2012 - 2013 and 20 % in 2013 - 2014. Total annual losses were reported to be 45.0 % and 34.1 % in 2012 - 13 and 2013 - 14 respectively (Lee et al. 2015; Spleen et al. 2013; Steinhauer et al. 2014; vanEngelsdorp et al. 2012; vanEngelsdorp et al. 2008; vanEngelsdorp et al. 2010; vanEngelsdorp et al. 2011; vanEngelsdorp et al. 2007). While winter colony losses have decreased in recent years, the self-described rate of acceptable losses has increased from a low of 13.2 % in the 2010 - 2011 survey (vanEngelsdorp et al. 2012) to 19.1 % last year (Lee et al. 2015), suggesting that beekeepers are adjusting their expectations to buffer against higher rates of colony losses. The present study reports the results from the latest colony mortality survey conducted by the Bee Informed Partnership (BIP, beeinformed.org) in the USA. It covers colony increases and mortality from 1 April 2014 to 1 April 2015, with subdivisions for summer and winter losses.

As in prior surveys, we divided survey respondents into the categories of backyard, sideline, and commercial beekeepers. Respondents typically vary widely in their management choices, including their use of synthetic varroa control. Commercial beekeepers tend to earn their primary income through pollination fees, often migrating colonies across large distances, participating in almond pollination, and maintaining colonies in dense conditions that facilitate disease and parasite transmission (Seeley and Smith 2015). In contrast, backyard beekeepers are frequently stationary, managing fewer colonies and dedicating more time and financial input per unit, but managing hives less intensively. Sideliners fall in between these extremes, earning only part of their income from honey production, pollination, or both. Surveyed beekeepers were also categorized by state, as this can help account for climatic and regional differences in colony management practices and losses (see methods for details). Beekeepers were also asked to report the primary cause of colony losses, as this provides insight into regional management issues beekeepers face and what they perceive as the greatest threat to colony health.

Materials and Methods

Survey

To estimate colony losses in the beekeeping industry from 2014 to 2015 in the USA, we utilized the Internet platform SelectSurvey.com. Beekeepers were invited to participate via e-mail through distribution lists maintained by two national beekeeping organizations (American Beekeeping Federation and American Honey Producer's Association), a beekeeping supply company (Brushy Mountain Bee Farm), two honey bee brokers, two beekeeping journals (American Bee Journal and Bee Culture), and two subscription listservs (Catch the Buzz and ABFAlert). An e-mail request to participate in the survey was also sent to approximately 12,500 beekeepers that signed up to participate via beeinformed.org, responded to a previous BIP survey and indicated their willingness to participate in future surveys, or participated in the USDA Animal Plant Health Inspection Service National Honey Bee Disease Survey and provided their e-mail address. All survey requests asked beekeepers to forward the survey to other beekeepers, resulting in a snowballing distribution of the document. Additionally, requests to distribute the survey information were sent to the Apiary Inspectors of America, state extension apiculturists, industry leaders, and to a number of regional beekeeping clubs, including the Eastern Apicultural Society (eastern US), Heartland Apicultural Society (central US), and the Western Apicultural Society (western US).

Commercial beekeepers, while fewer in number than backyard beekeepers, manage the majority of colonies in the USA and have previously been the hardest subset to reach. Thus to increase participation of commercial beekeepers, we conducted surveys over the phone ($n \approx 20$) or mailed paper surveys ($n \approx 1{,}200$) either through BIP personnel or through state apiarists. As our methods for soliciting responses depended on other organizations and requests to pass on the invitation, we were unable to calculate the total number of beekeepers contacted and so cannot calculate the response rate. Due to solicitation methods, the survey was not randomly conducted, which could lead to biased results (van der Zee et al. 2013). The survey was open online for responses from 1 April through 30 April 2015. Paper surveys were mailed in the third week of March 2015, and completed surveys returned by 29 May were included in our analysis.

The survey consisted of two parts: the "loss survey" and the optional "management survey." After completion of the loss survey, beekeepers were given the option to continue to the management survey. Only the responses to the loss survey are addressed in this study. The loss survey questions and the corresponding definition for valid responses to each question are given in the supplementary material **Appendix, Table A1**.

The 2014–2015 survey included the same core questions as the previous years' winter, summer, and annual loss surveys (Lee et al. 2015; Spleen et al. 2013; Steinhauer et al. 2014). As in the previous surveys in the USA, winter, summer, and annual periods are defined as fixed time periods: summer = 1 April 2014 to 1 October 2014, winter = 1 October 2014 to 1 April 2015, and annual = 1 April 2014 to 1 April 2015 (Lee et al. 2015; Spleen et al. 2013; Steinhauer et al. 2014; vanEngelsdorp et al. 2012; vanEngelsdorp et al. 2008; vanEngelsdorp et al. 2010; vanEngelsdorp et al. 2011; vanEngelsdorp et al. 2007). Since last year's survey (Lee et al. 2015), we also accounted for colony increases and decreases during the fixed time periods.

The loss data were edited to remove invalid responses. Duplicate entries were removed, as were entries from respondents outside the USA and those with insufficient answers to calculate a valid winter or summer loss, including illogical responses such as negative colony numbers. The questionnaire included multiple choice questions with an open entry "other" category, where responses were sorted to either keep the entry as "other" if the cause of death written was effectively different from the listed categories or revised to one of the preexisting categories where appropriate.

After the initial validation, three subsets of data based on the three time periods were created for analysis: valid for winter loss, valid for summer loss, and valid for annual loss. These subsets were necessary because not all respondents answered the entire set of loss questions. To be valid for a given time period, beekeepers needed to start that time period with at least one colony.

Each beekeeper's set of managed colonies will be referred to as that beekeeper's "operation." To compare different operation sizes, beekeepers were classified into three groups as in previous surveys based on the number of living colonies managed in their operations on 1 October 2014: "backyard beekeepers" managed 50 or fewer colonies, "sideline beekeepers" managed between 51 and 500 colonies, and "commercial beekeepers" managed more than 500 colonies.

Statistics

Total and average colony losses for summer, winter, and annually were calculated for all operations based on vanEngelsdorp et al. (2013) using R code developed and presented in Steinhauer et al. (2014). First, the percentage of operational losses for each respondent was calculated by dividing the number of colonies the beekeeper lost by the number of colonies at risk during that time period (**Appendix, Table A1**, questions 2 - 5, 5 - 8, and 2 - 8, respectively). Total loss results were then calculated by dividing the total number of colonies lost by the total number of colonies at risk in that respective time period, and multiplying that value by 100. Average losses were calculated by summing all the operational losses for that time period, then dividing that by the number of respondents for that same time period. The 95 % confidence intervals (95 % CIs) for the total losses were calculated using a generalized linear model (quasibinomial distribution) (R Development Core Team, 2015). The 95 % CI for average losses were calculated using the Wald formula (see vanEngelsdorp et al., 2013 for details).

Total loss, or weighted loss, calculations counted each individual colony equally, without regard to operation size. This means that beekeepers managing more colonies exerted a greater influence on the total loss results than those managing fewer colonies. Additionally, we computed average loss (or unweighted loss) calculations, where each beekeeper's operational loss was used to calculate the average loss across all operations. Total loss calculations thus reflected commercial operations as they manage significantly more colonies compared to backyard and sideliner operations, while average loss calculations were more representative of backyard beekeepers. Total loss allowed more informative comparisons of loss across seasons and among states, while average loss was more informative for comparing categories of respondents.

We used the Kruskal-Wallis rank sum test to check operational colony losses for significant differences between several factors including operation types (backyard, sideline, commercial), migrating vs. stationary beekeeping, almond pollinating vs. non-almond pollinating, acceptable vs. higher than acceptable losses, and between the various causes of death. In case of significance, the Kruskal-Wallis test was followed by the Mann-Whitney U test (also known as Wilcoxon Rank Sum test) for a pairwise check of significance using a Bonferroni correction when multiple comparisons were conducted. Operation type based differences regarding the likelihood for higher than acceptable losses and for the causes of colony death were detected using the Chi-squared test. All statistical tests were two tailed with a level of significance of $\alpha = 0.05$. All statistical analyses were performed in R (R Development Core Team, 2015).

When reporting colony losses by state, we followed the USDA-NASS method of counting colonies of multistate beekeepers repetitively in each state in which the beekeeper reported having colonies (USDA-NASS 2015). Multistate beekeepers can be migratory or stationary. For states with five or fewer respondents, we do not report the losses, in order to guarantee the anonymity of the participants.

Results

Average and total losses

The survey resulted in 7,570 responses. We removed duplicate (n = 456) and non-U.S. beekeepers (n = 356), and an additional 625 responses because they had invalid data entries. Thus, the final analytical data set comprised 6,133 beekeepers. The valid subsets for summer contained 4,971 responses, for winter 5,937, and 4,775 for annual.

The total loss of colonies for 2014 to 2015 over the summer was 25.3 % [95 % CI 24.7 - 25.9 %], over winter 22.3 % [95 % CI 21.9 - 22.8 %], and annually 40.6 % [95 % CI 40.0 - 41.2 %], see **Appendix, Fig. A1** for a breakdown by operation type. The average losses per operation in summer amounted to 14.7 % [95 % CI 14.0 - 15.3 %], in winter 43.7 % [95 % CI 42.8 - 44.6 %], and annually to 49.0 % [95 % CI 48.1 - 50.0 %] (**Table 1**).

The valid respondents for winter losses managed 414,267 colonies on 1 October 2014, representing approximately 15.1 % of the 2.74 million honey producing colonies nationwide (USDA-NASS 2015). Backyard beekeepers predominated (n = 5,690), but managed only 8.3 % of colonies reported. The 169 sideliners managed 5.6 % of colonies, while 78 commercial beekeepers managed the remaining 86.1 % of the colonies (**Table 2**). Over the winter, 25.7 % of all respondents (n = 1,525) reported they lost zero colonies. When asked to compare their winter losses to the previous year, 34.7 % of beekeepers (n = 2,059) indicated they suffered higher winter losses this year, 26.3 % (n= 1,559) experienced fewer losses, and 22.2 % (n= 1,317) reported similar losses. The remainder either did not respond to the question, or did not know if their losses differed between years, or did not keep bees in the previous year.

Losses by operation type

The majority of beekeeping operations in the USA are small-scale backyard beekeepers and accordingly they make up the majority of valid respondents to our survey for all three seasons. Due to the relatively small operation size of these backyard beekeepers, they proportionally accounted for the fewest number of managed colonies (**Table 2**), while the majority of colonies were maintained by commercial beekeepers. During the winter backyard beekeepers maintained on average 6.1 ± 0.1 colonies, sideliners maintained 136.2 ± 7.8 and commercial beekeepers 4,572.7 ± 867.1 (**Table 3**) with similar means for summer and annual time periods.

Colony losses during both summer and winter were significantly different depending on operation type (summer: Kruskal-Wallis $\chi^2 = 51.879$, Mann Whitney p-values < 0.01; winter:

Kruskal-Wallis $\chi^2 = 29.979$, Mann Whitney p-values < 0.05). During the summer, commercial beekeepers suffered the highest colony losses, approximately 50 % higher average losses than backyard beekeepers (**Fig. 1**). This trend was reversed in the winter, when operational colony losses were twice as high in backyard beekeepers compared to commercial beekeepers. Sideliner losses fell in-between the two other groups during both seasons.

Average colony losses did not differ significantly for commercial or sideline beekeepers who pollinated almonds in California compared to beekeepers who did not (**Table 4**). Migratory and stationary beekeepers also experienced similar colony losses compared to each other (**Table 5**). Most commercial beekeepers moved their colonies into almond orchards and migrated between states, while the majority of sideliners were stationary beekeepers.

Table 1. Total and average colony losses per season. Sample size (n) is the number of beekeepers having provided valid responses. Interim changes include the numbers of increases (+) by splits or purchases and decreases (-) through selling or giving away during a time period. Increases and decreases are taken into account in the calculation of colonies at risk.

Season	**n**	**No. of colonies**					**Total loss (%) [95 % CI]**	**Average loss (%) [95 % CI]**
		1 April 14	**Interim changes**	**1 Oct. 14**	**Interim changes**	**1 April 15**		
Summer	4,971	370,063	+ 204,535 - 26,143	409,700	-	-	25.3 [24.7 - 25.9]	14.7 [14.0 - 15.3]
Winter	5,937	-	-	414,267	+ 65,880 - 9,191	365,770	22.3 [21.9 - 22.8]	43.7 [42.8 - 44.6]
Annual	4,775	337,633	+ 196,741 - 23,517	380,616	+ 64,525 - 9,064	336,386	40.6 [40.0 - 41.2]	49.0 [48.1 - 50.0]

Table 2. Total and average colony losses by operation type. Sample size (n) is the number of beekeepers having provided valid responses.

Season	**Operation type**	**n**	**No. of colonies (start)**	**% of colonies (start)**	**Total loss (%) [95 % CI]**	**Average loss (%) [95 % CI]**
Summer	Backyard	4,751	22,096	6	15.9 [15.3 - 16.5]	14.6 [13.9 - 15.2]
	Sideline	140	16,043	4.3	21.3 [17.8 - 25.1]	14.7 [11.5 - 17.9]
	Commercial	80	331,924	89.7	26.2 [21.6 - 31.1]	21.6 [17.3 - 25.9]
Winter	Backyard	5,690	34,569	8.3	41.2 [40.4 - 42.0]	44.3 [43.4 - 45.3]
	Sideline	169	23,024	5.6	30.9 [27.2 - 34.7]	31.8 [28.0 - 35.5]
	Commercial	78	35,6674	86.1	20.1 [16.9 - 22.9]	22.9 [18.8 - 27.0]
Annual	Backyard	4,566	21,106	6.3	48.5 [47.6 - 49.3]	49.5 [48.5 - 50.5]
	Sideline	136	15,643	4.6	43.3 [38.8 - 47.8]	39.1 [34.8 - 43.4]
	Commercial	73	300,884	89.1	39.9 [35.0 - 44.9]	37.3 [32.4 - 42.1]

Table 3. Colony numbers (mean, median and mode) by operation type for the winter season.

Operation type	n	mean	s.err.	median	mode
Backyard	5,690	6.1	0.1	3	2
Sideline	169	136.2	7.8	99	52
Commercial	78	4,572.7	867.1	2,800	2,000

Table 4. Average colony loss of almond pollinating vs. non-almond pollinating operations. Sample size (n) is the number of beekeepers having provided valid responses.

Operation type	Pollinated almonds	n	Average winter loss (%) [95 % CI]	Kruskal Wallis rank sum test		
				chi²	df	p-value
Commercial	No	13	32.0 [18.4 - 45.6]	1.9177	1	0.1661
	Yes	60	21.6 [17.3 - 26.0]			
Sideline	No	136	33.0 [28.7 - 37.3]	0.2885	1	0.5912
	Yes	18	26.9 [18.9 - 34.9]			

Table 5. Average colony loss of migratory vs. stationary operations. Sample size (n) is the number of beekeepers having provided valid responses.

Operation type	Migrated hives	n	Average winter loss (%) [95 % CI]	Kruskal Wallis rank sum test		
				chi²	df	p-value
Commercial	No	15	21.2 [11.6 - 30.8]	0.3778	1	0.5388
	Yes	58	24.1 [19.2 - 29.0]			
Sideline	No	120	32.1 [27.8 - 36.4]	< 0.001	1	0.9930
	Yes	34	33.1 [24.0 - 42.3]			

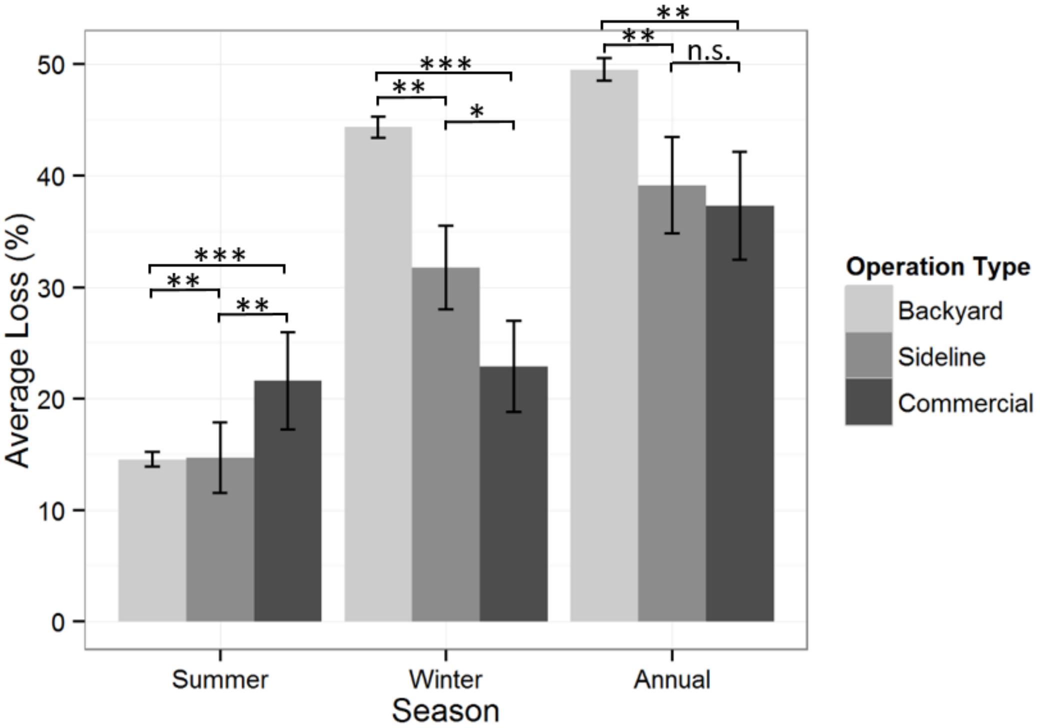


Fig. 1. Operational differences in average colony loss by season. Bars represent 95 % CI. '*' p < 0.05, '**' p < 0.01, '***' p < 0.001, n.s.: not significant.

State losses

Valid responses for each state ranged between a low of 2 (Alaska) and a high of 860 (Pennsylvania) (**Appendix, Table A2**). Pennsylvania and Virginia had the highest number of respondents, two states with very active honey bee inspection programs, state beekeeping programs, and grant initiatives to support new beekeepers. A map that gives an overview of respondents by state in winter is included in the supplementary material (**Appendix, Fig. A2**).

Total losses varied greatly by state throughout all seasons. In summer, total losses ranged from 2.8 % (Rhode Island) to 57.0 % (Oklahoma). In addition to Oklahoma, Pennsylvania, New York, Maine, Wisconsin, and Florida experienced comparably high losses during the summer (**Fig. 2**). In winter, total losses ranged from 5.2 % (Nevada) to 56.2 % (West Virginia). States from the Northeast, Maryland, West Virginia, Arizona, and New Mexico had the highest total losses in winter (**Fig. 3**). Annually, the total losses ranged from 13.9 % (Hawaii) to 63.4 % (Oklahoma) (**Appendix, Fig. A3**).

The average losses per operation also varied greatly by state and ranged from 7.0 % (Arizona) to 29.2 % (Wyoming) in summer, 8.8 % (Hawaii) to 59.5 % (Minnesota) in winter, and 21.2 % (Hawaii) to 64.8 % (Nevada) annually (**Appendix, Figs. A4-A6**).

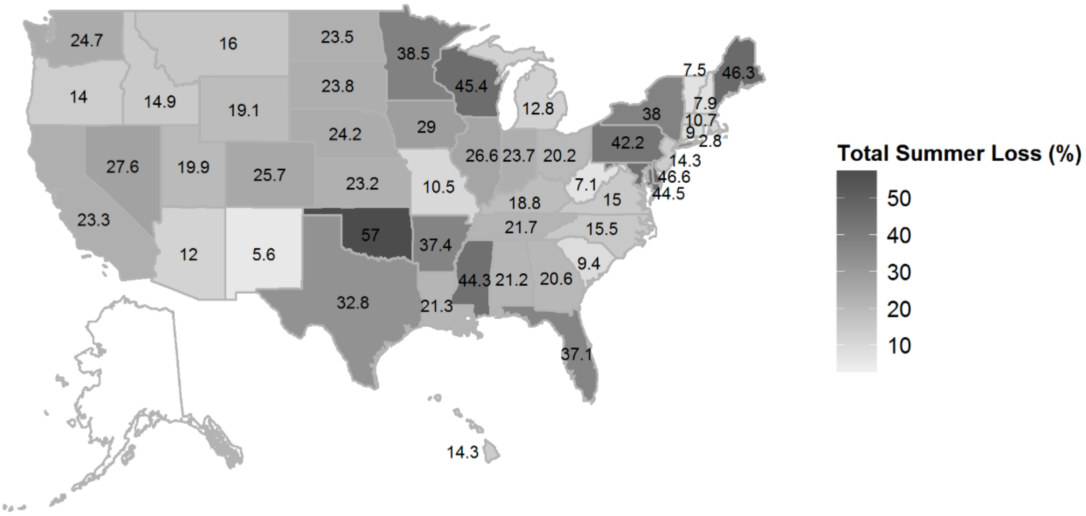


Fig. 2. Total colony loss in summer by state.

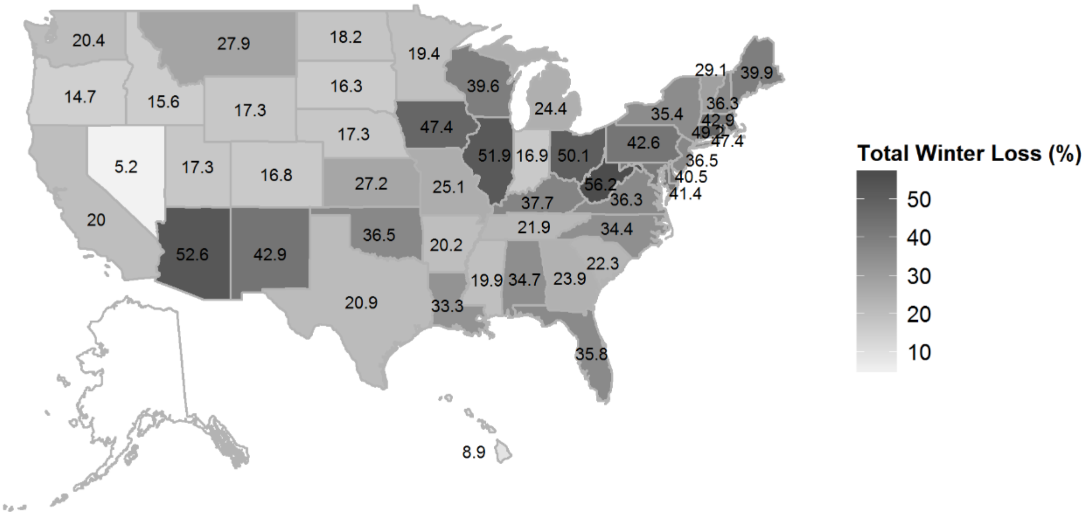


Fig. 3. Total colony loss in winter by state.

Acceptable winter losses

Participants of the survey indicated a loss up to 18.7 % on average as acceptable over winter (n = 5,937). Using this value as our threshold, 67.3 % of beekeepers had higher than acceptable losses. The average loss of beekeepers with acceptable loss levels was 2.6 % [95 % CI: 2.4 - 2.8 %], significantly lower than the average losses of 63.7 % [95 % CI: 62.8 - 64.5 %] experienced by beekeepers above acceptable loss levels (Kruskal-Wallis χ^2 = 4,023.2, p-value < 0.001). Furthermore, the likelihood of having acceptable or higher losses differed significantly by operation type (Chi-squared test: χ^2 = 10.225, p-value = 0.0060). Backyard beekeepers were 30 % more likely than commercial beekeepers to have higher than acceptable losses.

Commercial beekeepers reported a lower percentage as an acceptable loss than backyard or sideline beekeepers. On average, they indicated 14.0 % [95 % CI: 12.4 - 15.6 %] as acceptable, compared to 18.7 % [95 % CI: 18.3 - 19.2 %] of backyard and 19.1 % [95 % CI: 17.1 - 21.2 %] of sideline beekeepers.

Regardless of operation size, beekeepers who experienced high losses also indicated a higher rate of colony losses as acceptable compared to beekeepers with lower losses. Beekeepers who lost less than the 18.7 % loss rate also reported a lower value for acceptable losses, reporting on average acceptable loss rates of only 15.0 %. In contrast beekeepers who lost more colonies than the acceptable rate, typically reported an average of 20.5 % colony losses as acceptable.

Self-reported causes of winter loss

Of the 5,937 beekeepers in our winter subset, 4,224 suffered losses and indicated at least one cause for colony death. The three most frequently named reasons were starvation (n = 1,552), poor winter conditions (n = 1,514), and weak colonies in the fall (n = 1,451). Due to the large proportion of backyard beekeepers participating in the survey, these responses strongly reflect the perceived causes of winter loss for backyard beekeepers. When segregated by operation type, the most commonly reported causes of winter loss differed (**Fig. 4**). Commercial beekeepers reported varroa mites and queen failure as the most common reasons for colony death. Ten of twelve listed possible causes differed significantly by operation type (**Table 6**). CCD, nosema, varroa mites and queen failure were more likely to be reported by commercial beekeepers than by backyard beekeepers (causes indicated from highest to lowest risk ratio). Backyard beekeepers reported small hive beetles, poor winter, starvation, and “do not know” with a greater likelihood than commercial beekeepers (causes indicated from highest to lowest risk ratio). Only the responses in the categories “disaster” and “other” did not differ significantly by operation type. Beekeepers of any operation type that reported losing colonies to poor winter conditions, pesticides, CCD, or “do not know” reported losing more bees than those who did not report those causes (Kruskal-Wallis χ^2 = 143.660, 6.995, 25.996, 72.018, respectively, p-values < 0.01). Beekeepers who reported losing colonies to queen failure, varroa, nosema, or weak conditions in fall had fewer losses compared to beekeepers who did not report those causes (Kruskal-Wallis χ^2 = 101.330, 10.037, 5.554, 5.977, respectively, p-values < 0.05).

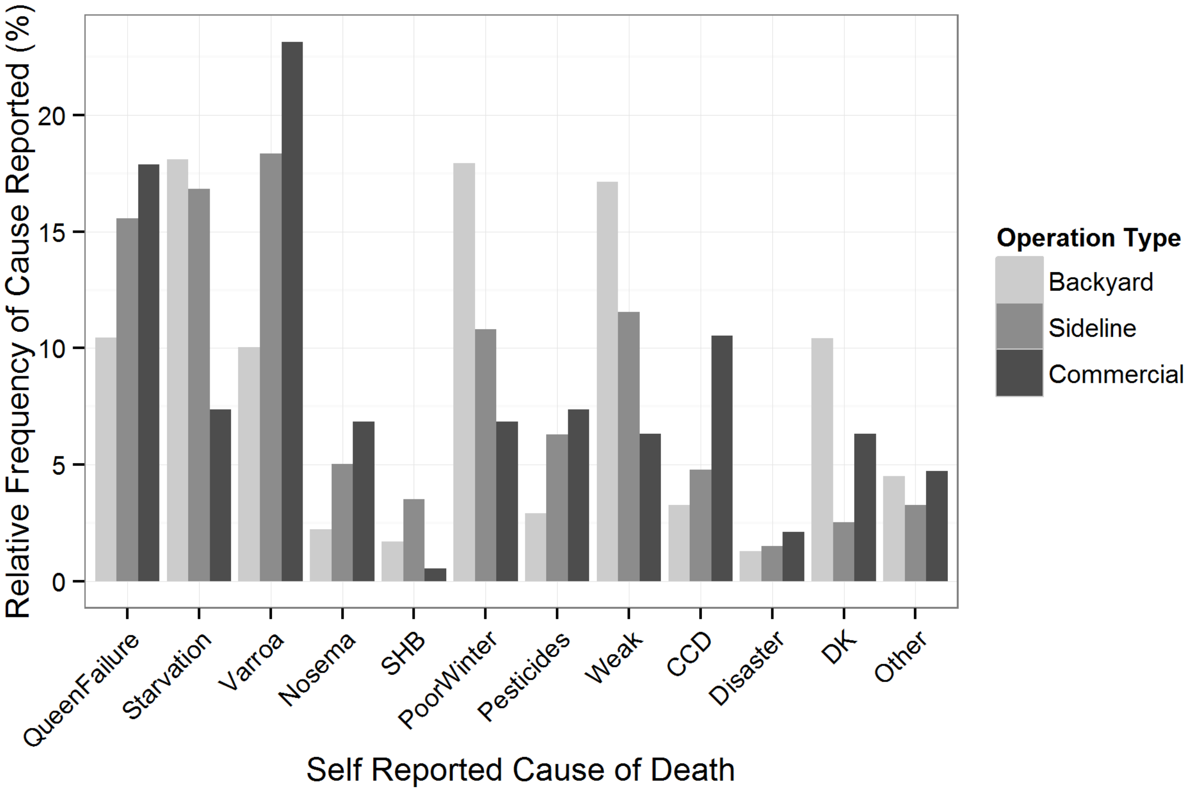


Fig. 4. Self reported causes of winter loss by operation type in relative frequency. SHB: small hive beetle; CCD: colony collapse disorder; DK: do not know

One common symptom of CCD is that no dead bees are found in dead colonies. An additional question in the survey asks respondents if their colonies experienced the symptom of no dead bees found in dead colonies. Of the 4,224 valid respondents for this question, 1,336 beekeepers (31.6 %) reported this symptom. They indicated having lost a total of 38,115 colonies with this symptom, which would represent 36.2 % of the 105,186 colonies lost over the winter last year by all respondents. Operations with this symptom did not have higher losses than operations without the occurrence of the symptom (Kruskal-Wallis χ^2 = 0.564, p-value = 0.4527). Commercial beekeepers were 160 % more likely than backyard beekeepers to report the symptom of no dead bees in the hive (Chi-squared test: χ^2 = 111.18, p-value < 0.001).

Table 6. Causes of death with associated total and average winter losses and operation type differences. SHB: small hive beetle; CCD: colony collapse disorder; DK: do not know. Sample size (n) is the number of beekeepers having provided valid responses. Risk ratios indicate the likelihood of commercial beekeepers to report a cause compared to backyard beekeepers. Risk ratios are only indicated when operation type differences are significant, p-value < 0.05.

Cause of death	**n**	**n (backyard)**	**n (sideline)**	**n (commercial)**	**Average loss [95 % CI]**	**Chi-squared test for operation type differences**			**Risk ratio commercial vs. backyard**
						chi²	**df**	**p-value**	
Queen failure	945	849	62	34	50.2 [48.3 - 52.1]	72.489	2	< 0.001	2.5
Starvation	1,552	1,471	67	14	57.7 [56.2 - 59.2]	12.416	2	0.0020	0.6
Varroa	933	816	73	44	56.1 [54.2 - 58.0]	154.290	2	< 0.001	3.3
Nosema	214	181	20	13	53.9 [50.0 - 57.8]	56.046	2	< 0.001	4.4
SHB	153	138	14	1	61.0 [56.3 - 65.7]	16.551	2	0.0003	0.4
Poor winter	1,514	1,458	43	13	66.3 [64.9 - 67.8]	9.723	2	0.0077	0.6
Pesticides	274	235	25	14	63.9 [60.4 - 67.4]	55.006	2	< 0.001	3.7
Weak	1,451	1,393	46	12	57.3 [55.7 - 58.8]	7.858	2	0.0197	0.5
CCD	305	266	19	20	67.5 [64.3 - 70.6]	63.600	2	< 0.001	4.6
Disaster	115	105	6	4	63.7 [57.9 - 69.4]	4.198	2	0.1226	-
DK	868	846	10	12	66.8 [64.8 - 68.8]	17.168	2	< 0.001	0.9
Other	387	365	13	9	60.0 [57.0 - 63.0]	1.741	2	0.4187	-

Discussion

In this ninth annual survey of winter colony losses in the US (Lee et al. 2015; Spleen et al. 2013; Steinhauer et al. 2014; vanEngelsdorp et al. 2012; vanEngelsdorp et al. 2008; vanEngelsdorp et al. 2010; vanEngelsdorp et al. 2011; vanEngelsdorp et al. 2007), and third reported survey of summer and annual losses, we report similar total and average winter losses as experienced last year (Lee et al. 2015). However, total summer losses were almost 30 % higher than last year, and so for the first time total summer losses exceeded total winter losses. The acceptable loss rate of 18.7 % remained high compared to earlier survey years, suggesting that beekeepers are adjusting their expectations downward when it comes to acceptable colony survival rates. Unfortunately, total summer losses alone exceeded the rate of acceptable loss reported by beekeepers.

Total and average losses

At 22.3 %, this year’s total winter loss is the second lowest rate experienced during the last nine years. In stark contrast, the average winter loss at 43.7 % is among the highest winter mortalities beekeepers have sustained since the survey began. A similar pattern occurred last year, suggesting that commercial beekeepers who manage the majority of colonies in the USA have reined in their winter mortality, thus causing a dip in total winter losses. Backyard beekeepers continue to lose a large proportion of their hives during the winter, elevating the average winter losses, given that this measurement ranks all beekeeping operation types equally.

The winter and annual loss rates experienced by beekeepers in the USA fall toward the upper spectrum of worldwide colony loss rates. Other studies investigating colony losses between 2009 and 2013 in Europe, Canada, China, Turkey, and South Africa reported winter losses between a low of 9.3% among small scale beekeepers (Slovakia 2012/2013) and a high of 46.2 % (South Africa 2010/2011) (Clermont et al. 2014; Pirk et al. 2014; van der Zee et al. 2014). The average winter losses reported by several European countries for 2012 to 2014 ranged between a low of 3.5 % (Lithuania 2013/2014) and a high of 33.6 % (Belgium 2012/2013) (Laurent et al. 2015). The pan-European epidemiological study on honey bee colony losses (EPILOBEE) looked at colony losses in 16 EU countries from 2012-2014, finding that winter mortality decreased in the majority of countries in 2013-2014 compared to the previous year. Annual colony mortality decreased in 8 of the 16 countries and remained unchanged in the remainder (Laurent et al. 2015); however the EPILOBEE study extrapolated results from limited surveying and are not beekeeper self-reported colony losses as reported here. Caution should be used in comparing across studies, due to differences in methodology, sample sizes and proportions of operation types within the evaluated sample. Colony losses for the winter of 2014 - 2015 have so far only been published for the USA and so it is currently unknown how they compare to loss rates experienced elsewhere.

We added summer losses into the loss reports three years ago after two years of piloting it in the survey. Beekeepers lost a quarter of all managed hives during the summer season, a total summer loss rate 30 % higher than last year, yet similar to the rate reported two years ago. This is the first year where total summer losses exceed total winter losses, an unexpected finding that highlights the importance of monitoring colony losses throughout the year. Traditionally, winter losses were believed to be higher than summer losses, as weak colonies have trouble surviving the winter nectar dearth and long-term confinement. Summer, in contrast, is the time of year when colonies typically thrive, expanding on abundant nectar and pollen sources. Our results highlight how colony losses have shifted, especially among commercial beekeepers, who lost 30 % more hives during the summer season compared to winter (26.2 % vs. 20.1 %). In contrast, the average summer loss rate of 14.7 % highlights that backyard beekeepers typically fare much better during the summer than the winter. The difference in summer losses may be due to increased pesticide exposure risk during pollination events for commercial beekeepers or increased disease and viral transmission when commercial colonies are transported or placed in large holding yards, but causes for increased summer losses need further investigation.

The EPILOBEE study conducted during 2013 and 2014 is the only other study that included summer losses (Laurent et al. 2015). Reported summer loss rates were low, ranging from 0.1 % in Lithuania to 11.1 % in France. However, this study only calculated average losses and not total losses. Average loss calculations in our survey reflect the situation of backyard beekeepers, who continue to lose the majority of their colonies during winter and suffer moderate losses during summer. Even so, average summer losses at 14.7 % in the USA are substantially higher than European summer losses, which were below 6 % for all EU countries except Belgium (9.1 %) and France (11.1 %).

Due to the increase in total summer losses, the annual total losses rose to 40.6 % from last year’s low of 34.1 %, but were still lower than the 45.2 % experienced in 2012 – 2013 (Lee et al. 2015; Steinhauer et al. 2014). In contrast, average annual losses at 49.0 % were almost identical to the last two years (49.4 % and 51.5 % respectively), indicating that on average beekeepers lose almost 50 % of their managed hives during the year. Since the majority of respondents are backyard beekeepers, these small scale hobby farmers lose half of their livestock annually. With replacement colonies costing $90 - $175, it is not surprising that many drop out of beekeeping after 1 - 2 years.

Survey respondents vary from year to year, although many participate annually. We ask beekeepers how their winter losses compare to the previous year. Although the average winter losses that we calculated were very similar between the two years, the most common response was that beekeepers experienced higher losses this year (34.7 %), while about one quarter (26.3 %) reported lower losses and just over one fifth (22.2 %) indicated similar losses.

Losses by operation type

Commercial and backyard beekeepers differ drastically in scale and in their management practices. The majority of commercial beekeepers migrate their colonies multiple times each year, transporting colonies large distances. Pollination environments potentially expose bees to increased pesticide pressure (Krupke et al. 2012; Pettis et al. 2013) and vast nutritional monocultures that may impact stress resistance (Huang 2012). Despite rigorous pollination schedules, winter mortality for commercial beekeepers is half the rate of backyard beekeepers. This lower rate of winter losses may be due to the southern migration of commercial beekeepers who avoid the northern temperate climate so they can prepare colonies for California almond pollination in February. The lower rate may also be influenced by different management practices. Summer losses in contrast were 50 % higher this year for commercial compared to backyard beekeepers, similar to what beekeepers experienced in the 2012 - 2013 survey. Despite the elevated summer losses, commercial beekeepers suffered significantly lower annual losses compared to backyard beekeepers. European studies have shown similar trends, with lower losses in larger beekeeping operations (van der Zee et al. 2014; van der Zee et al. 2012). Additionally, the international results segregated beekeepers into classes similar to our backyard beekeeper and sideliner categories. Commercial operations managing several thousand colonies (see **Table 3** for average commercial operation size) are relatively uncommon outside the USA.

These stark differences in colony losses between commercial and backyard beekeepers highlight the bifurcation of the beekeeping industry in the USA and may illustrate that the two populations face different honey bee health issues and follow different management practices. Backyard beekeepers, for example, seem to treat less for varroa mites. In the current survey, backyard beekeepers indicated that winter colony losses were predominantly due to “weak in fall”, “poor winter conditions”, and “starvation.” A symptom of heavy varroa parasitization is a dwindling colony that has difficulty surviving the winter (Genersch et al.

2010; Le Conte et al. 2010; Yang and Cox-Foster 2007), suggesting that backyard beekeepers could reduce their winter losses through better varroa management and improved winter preparation. Losses of over 20 % during both the summer and winter period indicate that commercial beekeepers face challenges to honey bee health throughout the year and would benefit from identifying and mitigating the causes of summer losses. The causes of the summer losses are beyond the scope of this survey, but require further investigation. Potential factors underlying higher losses include pesticide exposure, disease and viral transmission, and poor queen quality. Extension and research efforts to reduce colony losses should address these two beekeeping populations separately, finding solutions tailored to the unique needs of each. Even though backyard beekeepers have lower summer losses than commercial beekeepers, their average rate of loss in the summer alone is still higher than the 10 % rate of acceptable colony loss described in EPILOBEE (Laurent et al. 2015) and in Germany (Genersch et al. 2010).

Participating in almond pollination or migrating colonies did not impact colony loss rates. It is often postulated that transporting hives negatively impacts colony health through increased stress, but so far only one study in South Africa has shown a negative effect on honey bee colony survival (Pirk et al. 2014). Previous surveys in the USA have shown no impact or reduced colony mortality in migratory compared to stationary beekeeping operations. The lower colony mortality might be explained by decreased varroa infestation rates, as the number of varroa mites per 100 bees is reduced in migratory hives (Traynor et al. in press [Traynor et al. 2016]).

State losses

High winter losses were concentrated in the Northeast and mid-Atlantic region which experienced a mild fall followed by an exceptionally long and cold winter (NOAA National Centers for Environmental Information 2014, 2015). Such weather patterns often result in colonies entering winter with depleted honey stores, as the bees keep flying during the warm yet nectar barren fall. Bees typically start rearing brood in late winter, using up the majority of their honey stores to raise the broodnest temperature. The long, cold, wet spring delayed spring nectar sources, which may explain why the most commonly self-reported cause of death was starvation. Beekeepers in Arizona and New Mexico also reported high winter losses. Both states experienced low rainfall with record warmth, suggesting that bees may have experienced no break in the brood cycle, resulting in elevated varroa mite levels coupled with reduced nectar availability. Summer losses were highest in Oklahoma, a state that experienced a severe drought in May 2014, which may have negatively impacted spring nectar flows, preventing colonies from building-up after the winter.

Regional variations in colony losses are very common worldwide (Laurent et al. 2015; McMenamin and Genersch 2015). EPILOBEE (Laurent et al. 2015) found a tendency toward higher average losses in colder northern countries in Europe, but other studies, like Genersch et al. (2010) or van der Zee et al. (2014) have not displayed clear regional clustering. Caution should be used when interpreting the data from the latter, as beekeepers self-defined the length of their winter, making it difficult to compare loss rates over the same time frame.

Acceptable winter losses

Self-reported acceptable loss rates over the past 9 years have varied from a low of 13.2 % to a high of 19 % last year (Lee et al. 2015; Spleen et al. 2013; Steinhauer et al. 2014; vanEngelsdorp et al. 2012; vanEngelsdorp et al. 2008; vanEngelsdorp et al. 2010; vanEngelsdorp et al. 2011; vanEngelsdorp et al. 2007). Despite this year's relatively high acceptable loss rate of 18.7 %, two-thirds (67.3 %) of beekeepers exceeded this colony mortality rate. The one-third that stayed below the threshold lost on average only 2.6 % of their hives, while the other two-thirds lost 63.7 % of their colonies on average. This wide divergence highlights that colony losses are not equitably distributed across the industry. Beekeepers who experience lower rates of losses also report lower acceptable loss rates, suggesting that prior personal experience of loss rates influences perception of acceptable colony loss rates. This may help explain why commercial beekeepers report a lower tolerance for colony losses, as they typically experience lower rates of colony loss. Beekeepers in the USA report higher rates of colony loss as acceptable compared to their European counterparts, where a maximum loss of 10 - 12% is considered acceptable (Charrière and Neumann 2010; Genersch et al. 2010; Vejsnæs et al. 2010).

Self-reported causes of winter loss

Beekeepers reported which factors had the greatest impact on colony losses over the winter. The most common causes of colony death selected by beekeepers were starvation, poor winter, weak colonies, queen failure, varroa mites, and "do not know". These were commonly selected choices in previous surveys. In contrast to last year's results, pesticides and CCD were reported with less frequency. Commercial beekeepers reported varroa as the most common cause of colony losses, displacing queen failure as the top reason (Lee et al. 2015; Steinhauer et al. 2014). CCD was the third most commonly selected cause among commercial beekeepers, though they reported varroa more than twice as frequently. Pesticides dropped in the ranking, falling along with starvation to fourth place and followed closely by nosema. Commercial beekeepers have shifted their focus to varroa mites as the leading reason for colony losses, which matches the increased attention this parasite has received in scientific publications and the media as one of the major threats to honey bee survival (e.g., Genersch et al., 2010; van der Zee et al., 2015).

It is somewhat surprising that backyard beekeepers have not listed varroa as a leading cause of colony loss, perhaps because their colonies perish predominantly in the winter and they do not associate the dwindling colony strength as a latent response to this parasite. Hidden predominantly inside the brood cells, varroa is not a directly visible lethal factor and backyard beekeepers may have trouble recognizing its impact on colony health. The diverse factors selected by beekeepers for colony mortality align well with the current perspective that colony losses are driven by multifactorial, interacting factors (McMenamin and Genersch 2015).

Conclusion

This study highlights the benefits of surveying colony losses throughout the year, as this year commercial beekeepers lost more colonies during summer than winter. It demonstrates the importance of considering individual operation types separately, underscoring that the two distinct branches of the beekeeping industry face different hurdles. Backyard beekeepers lost almost 50 % of their colonies over the year, and their average winter losses exceeded the annual average losses of commercial beekeepers. As management surveys have revealed, more than half of all US backyard beekeepers do not manage for varroa (Bee Informed Partnership 2015). Ongoing education efforts have emphasized the negative impact of this parasite, but adoption of best management practices remains low. Several key extension efforts, such as regional Sentinel Hive projects that monitor varroa mite infestation levels in beekeeping club apiaries throughout the active beekeeping season, are working to improve backyard beekeeper understanding of varroa impacts on colony health. Commercial beekeepers meanwhile lost 40 % of their managed hives, equally split between the winter and summer months. When monitored throughout the year, it is evident that beekeepers in the USA are still experiencing unacceptably high losses. Other survey efforts may be underestimating their annual colony loss rates when they neglect summer losses, especially in commercial operations that experience summer stress factors such as pesticide exposure and nutritional monocultures. Additional surveys of summer losses in other countries would help place the losses in the USA into a global context and indicate whether high summer losses are unique to the migratory pollination environment of commercial beekeepers in the USA.

Introduction: Promoting wild bees

The main reason for the decline of wild bees is habitat loss, coinciding with changes in plant community compositions and reductions in the availability and diversity of floral resources (Brown and Paxton 2009; Potts et al. 2010a; Roulston & Goodell, 2011). These primarily anthropogenic induced developments lead to a limitation of food resources and nesting sites of wild bees. Therefore, if we want to conserve wild bee populations (both diversity and abundance), we need to make the creation of good habitats that provide resources for wild bees a top priority (Vanbergen et al. 2013).

The potentials of reclaimed sand mines for bee conservation

For successful promotion of wild bees, their habitat requirements need to be well understood. Generally, the most structurally and florally diverse habitats are considered most promising for sustaining wild bee populations (Blaauw and Isaacs 2014; Fründ et al. 2010; Sjödin et al. 2008), because wild bees need sufficient flowering plants to meet their nutritional needs. Nutritional and morphological constraints differ between bee species. A certain floral diversity is therefore essential to sustain species rich bee communities (Nicolson 2011; Tepedino and Stanton 1982; Vaudo et al. 2015). For this reason, many conservation actions have focused on increasing floral resources in landscapes, e.g., through installing flower strips along agricultural fields (Decourtye et al. 2010; Jönsson et al. 2015; Sutter et al. 2017). Another, often ignored, important factor for maintaining abundant and species rich bee communities is the availability of suitable nesting sites (Gathmann and Tscharntke 2002; Michener 2007; Potts and Willmer 1997). In fact, Potts et al. (2005) showed that bee communities differ in their structure depending on the availability of bare ground and nesting cavities in habitats. While the need for nesting sites has been recognized by the scientific community, it has received less attention than floral resource provisioning in research and conservation efforts (Sardiñas and Kremen 2014; Williams et al. 2010b; Winfree 2010).

Here, we explore the potential of reclaimed sand mines, i.e., vegetation-poor habitats with low vegetational cover and low plant diversity, as suitable habitat for bee communities. Sand mining is a common practice worldwide, where sandy soil layers are mechanically extracted to provide raw materials for construction projects. After sand extraction, the mine land can be reclaimed in different ways, e.g., for housing developments, farmland, green spaces or recreational facilities. If the area is designated as a green space, a large barren landscape remains, which is typically capped with some topsoil from the site and seeded with herbaceous plants of quickly establishing competitive species to prevent erosion. In Maryland and in many other jurisdictions, reclamation and seeding of abandoned mines is prescribed by government regulation. The Code of Maryland Regulations (COMAR), Title 26 requires revegetation of the areas, but does not specify the plants to be used. The seed mixes for reclamation often contain few species of mainly non-native plants (Chaney Enterprises, personal communication). Additional native and non-native plants from the surrounding habitats may further recolonize the area (Pietrzykowski 2008). The resulting plant community in the minimally nutritious sandy soil is spotty and vegetational cover is low (Tropek et al. 2010 & personal observation).

Studies documenting the consequences of sand mining on wild life are scarce. Those that do exist focus on the difficulty that plants have to reestablish in abandoned sand mines (Enright and Lamont 1992; Pietrzykowski 2008; Vivian-Smith and Handel 1996). How abandoned sand mines affect faunistic wild life is largely unknown. In fact, our study is the first to examine how these habitats affect communities of wild bees.

We assessed the bee communities in reclaimed sand mines and compared them with the bee communities in roadside meadows adjacent to the sand mines. The scarce vegetation in reclaimed sand mines leaves numerous patches of bare ground, which can be used for nesting or collecting nesting material by bees (Mader et al. 2011; Michener 2007). Vertical soil structures add further nest sites, creating manifold nesting opportunities for bee communities despite low plant diversity (Michener et al. 1958). Likewise, roadsides are regarded as valuable bee habitat as they provide long meadow like corridors and are relatively undisturbed (Heneberg et al. 2017; Hopwood et al. 2015; Hopwood 2008). However, they show less structural diversity than sand mines (personal observation). We therefore hypothesized that sand mines host a more abundant and more species rich bee community than roadside meadows. Furthermore, we expected distinctive community compositions in the two habitats with a stronger dominance of ground nesting and ‘sand loving’ bee species in sand mines than at roadsides.

The value of native and non-native pollinator friendly plants for wild bees

As highly important pollinators bees rely on the pollen and nectar of plants as their main food source (Carvell et al. 2006; Michener 2007; Vaudo et al. 2015). Providing adequate and sufficient floral resources may be a key for securing wild bee populations (Vanbergen and Initiative 2013). To provide such food resources for bees, many seed companies, botanical associations, etc. have compiled so called “pollinator friendly” seed mixes or plant lists. Flowers of these mixes are believed to have high nectar contents and to be visited by many different pollinators, but have mostly not been scientifically analyzed for their attraction to bees (Ratnieks and Garbuzov 2014). As a starting point, Garbuzov and Ratnieks (2014) found greatly fluctuating bee visitation on 32 garden plants in the UK. Hicks et al. (2016) found greatly varying nectar and pollen quantity and quality among 23 tested pollinator friendly plants in the UK, but did not assess bee visitation to the plants. These results highlight the need for a careful selection of pollinator friendly plants and more detailed studies on the attraction and value of plants for bees.

Moreover, many commercially available pollinator friendly plant mixes often include both native and non-native plants (Fowler 2016; Morandin and Kremen 2013). Selecting plants for pollinators based on the quality or quantity of floral rewards rather than their nativity status can certainly have benefits for bees (Garbuzov and Ratnieks 2014; Harrison and Winfree 2015; Nicolson and Thornburg 2007). The use of standard seed mixes for pollinator friendly plantings could also support conservation efforts. However, we should carefully investigate potential effects of non-native plants on bee communities, in order to secure structurally diverse bee communities which ensure the pollination of crops and wild plants (Garibaldi et al. 2013; Klein et al. 2003; Morandin and Winston 2005; Ollerton et al. 2011).

Previous studies have shown that non-native plants can be accepted by native bees (Drossart et al. 2017; Tepedino et al. 2009; Williams et al. 2011). However, results on differences of bee visitation between native vs non-native plants are divergent. While Williams et al. (2011) or Nienhuis et al. (2009) find no differences between native and non-native plants for bee visitation rates, other studies report of higher abundance of bees or also higher species richness associated with non-native plants (Bartomeus et al. 2008; Lopezaraiza-Mikel et al. 2007; Matteson and Langellotto 2010; Vilà et al. 2009). Yet other studies found lower bee abundances associated with non-native plants (Chrobock et al. 2013; Menz et al. 2011; Morandin and Kremen 2013; Moroń et al. 2009; Pardee and Philpott 2014) with sometimes unchanged (Pardee and Philpott 2014), and in other cases lower (Chrobock et al. 2013; Morandin and Kremen 2013) species richness. In summary, the results of the different studies are not showing a consistent effect of non-native plants on bee abundances and bee species richness. Most of the aforementioned studies focused on invasive non-native vegetation and were also not conducted in an experimental set up. An exception was the study by Morandin and Kremen (2013) who planted agricultural hedgerows and included at least in parts explicitly pollinator friendly plants, but native and non-native plants were mixed in the treatments. None of the studies have directly compared seed mixes of non-native vs native plants.

Additional to effects on bee abundance or species richness, tendencies of comparatively less specialized interactions associated with non-native plants have been shown by some studies

(Lopezaraiza-Mikel et al. 2007; Memmott and Waser 2002; Schweiger et al. 2010; Stout and Morales 2009). In other words, non-native plants tend to support rather generalist bees than specialist bees. An increase in generalist bees and a decrease in specialist bees can alter the bee community composition or the structure of the visitation network (Bartomeus et al. 2008; Vanbergen et al. 2018). Therefore, overall bee abundance or species richness might remain unchanged with the introduction of non-native plants while certain bee species could decline or become threatened as a consequence of the altered bee community composition. Additionally, specialists are overall more sensitive to land use change than generalists (Winfree et al. 2011).

General effects of non-native plants and particularly pollinator friendly non-native plants on wild bee communities remain unclear. In this study, we experimentally tested over two years how plant nativity of plots sown with different seed mixes affected the abundance, richness and community structure of bees as well as the specialization of visitation networks and the specialization of individual bee species. As native and non-native plants were both pollinator friendly we expected similar bee abundance and species richness. Furthermore, we expected a more specialized foraging behavior of bees on native plants compared to non-native plants, because of evolutionary derived specialized interactions. Our study is the first to experimentally compare native versus non-native pollinator friendly plant communities planted in plots of the same size in a common garden experiment.

Methods

Study system sand mines and roadsides

This study took place at three reclaimed sand mines (Sandtown, Councell and Riddle) in Maryland, USA (**Figs. 5 & 6**). We selected areas of sand mines, where sand extraction had been terminated more than four years ago, and which had subsequently been seeded with the same five species seed mix (comprising *Dactylis glomerata* L., *Secale cereale* L., *Trifolium* spec., *Lespedeza cuneata* (Dum. Cours.) G. Don and a species of millet grass). All reclaimed mines were owned by Chaney Enterprises. Further, all sites were located in rural landscapes surrounded by agricultural land, smaller settlements, remnant forest fragments, streams and ponds. The size of each location was 1.1 – 2.4 ha. Distances between sand mines were 3 – 85 km (**Fig. 5**).

At each reclaimed sand mine, we sampled bees along 150 m transects passing diagonally through the study area (**Fig. 6**). Coordinates from the center of the transects were 39.035532, -75.745501 (Sandtown); 39.024634, -75.782515 (Councell); 38.869182, -76.670789 (Riddle). Sand mines were not mown throughout the study.
For comparison, we sampled along a second set of transects following the meadows along rural roads adjacent to the reclaimed sand mines (**Fig. 6**). Coordinates from the center of the roadside transects were: 39.029511, -75.755714 (Sandtown); 39.023808, -75.789106 (Councell); 38.871452, -76.673448 (Riddle). The vegetation along roadsides was mowed approximately three times per year.

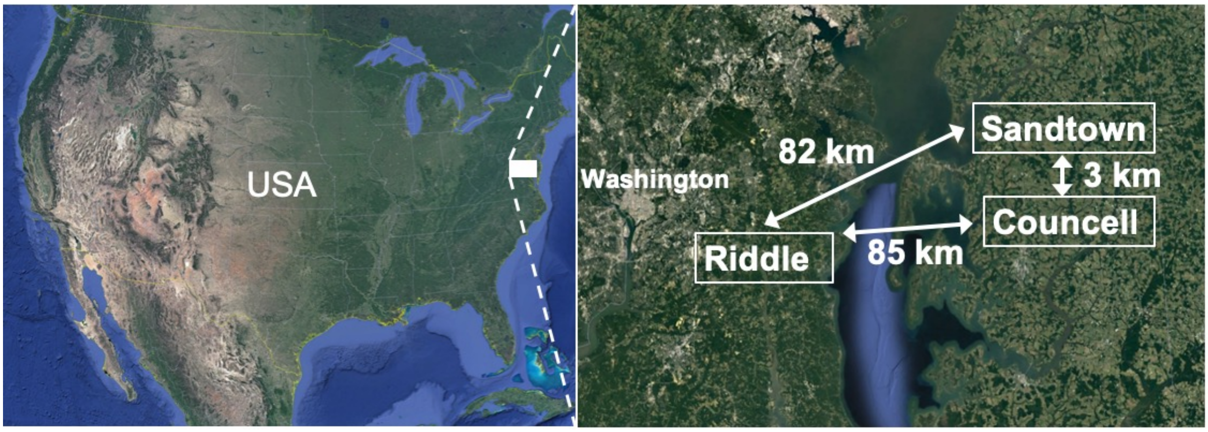


Fig. 5. The three locations (Riddle, Sandtown, and Councell) of this study in Maryland, USA where bee communities were sampled throughout two entire blooming periods (2016 & 2017). Each location comprised an old sand mine and an adjacent roadside. Distances between locations were 3 – 85 km. Map data: Google Earth, US Dept of State Geographer, Image Landsat/Copernicus, Data SIO, NOAA, U.S. Navy, NGA, GEBCO.

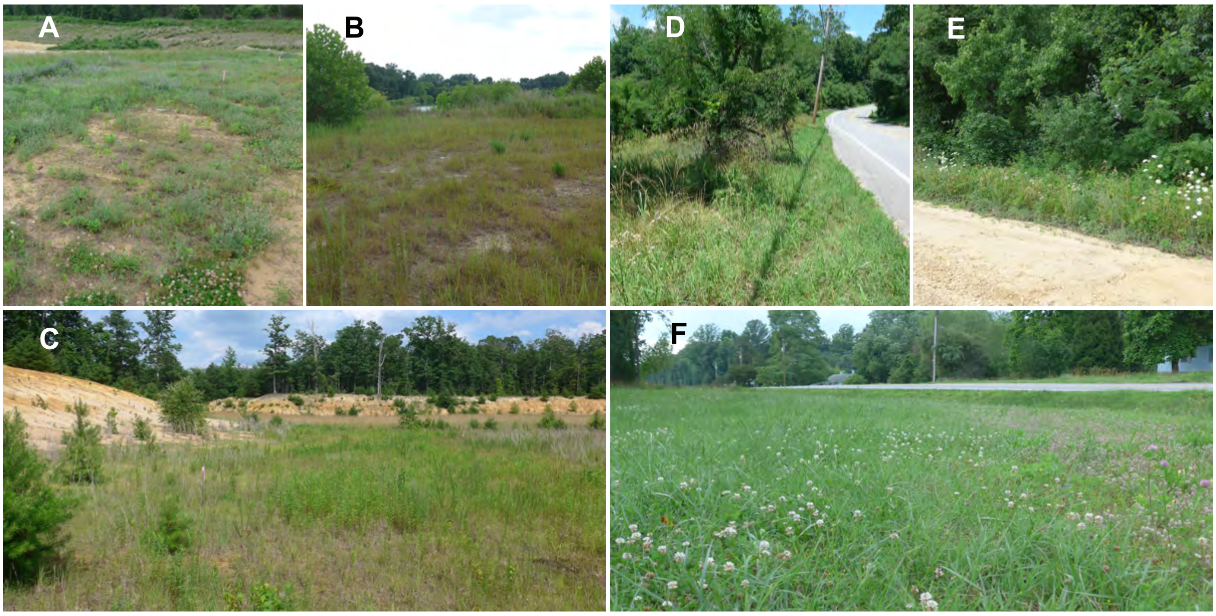


Fig. 6. The study areas in July 2016. Sand mines, on the left (A – C), had mainly herbaceous vegetation with many patches of bare ground and sand cliffs. Roadsides, on the right (D – F), had a more dense herbaceous vegetation with fewer patches of bare ground. Floral diversity and density was usually higher at roadsides. Photographs from the three study locations, i.e., Riddle (A & D), Councell (B & E) and Sandtown (C &F).

Study system farmland with native and non-native pollinator friendly plants

This study took place at the Beltsville research farm of the University of Maryland, USA. The Beltsville facility spans 116 ha in a rural landscape with forest fragments, creeks, and ponds. Crops grown on the arable land include wheat, barley, beans, soybeans, and small plots of vegetables such as squash, cabbage, kale, peppers, cucumbers and tomatoes. The farm is located between the suburbs of the metropolitan area of Washington, DC, and the Patuxent Research Refuge. At the research farm, we established three experimental sites which were 1 – 1.7 km apart from each other (**Fig. 7**). Each site had two plots: one with a native pollinator friendly seed mix and one with a non-native pollinator friendly seed mix (**Figs. 7 & 8**). Plot size was 10 x 10 m and the distance between the two treatment plots was 20 m. Coordinates for the sites are 39.025705, -76.842232 (site A); 39.018170, -76.821249 (site B); and 39.007196, -76.820480 (site C), each measured at the center of each site between native and non-native plots.

Both, the native and non-native seed mixes contained 20 different flower species and two grass species each (**Table 10 & 11** in results). The plants for seed mixes were chosen based on the following criteria: (1) assumed to be pollinator friendly based on existing different lists on pollinator friendly plants (i.e., by The Xerces Society, Pollinator Partnership, USDA, Royal Horticultural Society, Ernst Conservation Seeds, Cusser and Goodell (2013)) ; (2) complimentary flowering periods spanning the whole season of bee activity; (3) an even distribution of flower colors; (4) a mix of different plant families; (5) mostly perennials (12-15 species) with a few annuals/biennials (5-8 species) to facilitate establishment in the first year; (6) adaptation to medium to dry and sandy soil; and (7) availability from seed retailers.

The plots were seeded in April 2016 and reseeded in March 2017. In 2017, *Solidago odora* seeds were not available and were replaced with *Solidago nemoralis* seeds. Throughout both years the plots were continuously hand weeded to remove plant species that were not part of the experiment.

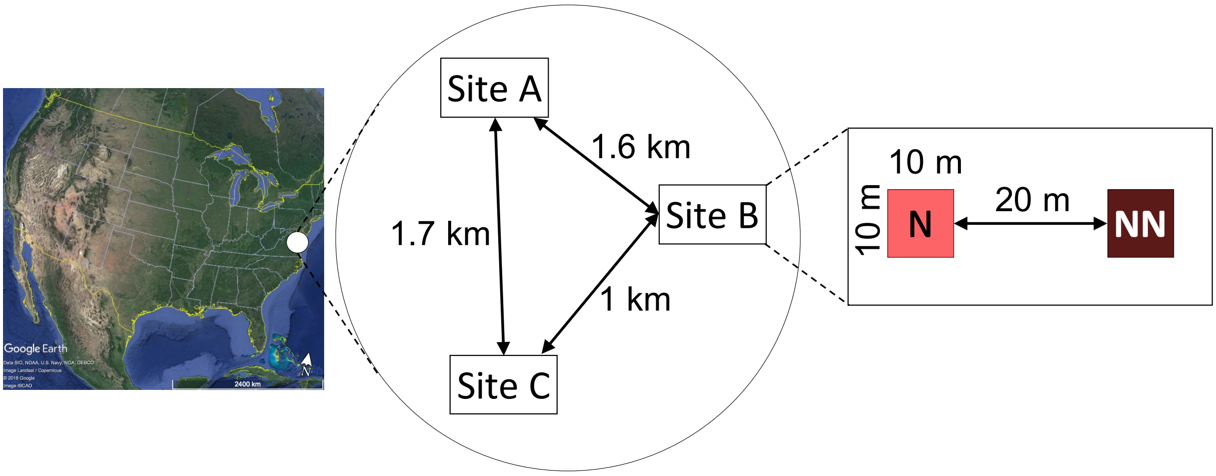


Fig. 7. Overview of the three experimental sites (A, B, C) at the Beltsville research farm. At each site a native plant plot (N) and a non-native plant plot (NN) were established. Map data: Google Earth, US Dept of State Geographer, Image Landsat/Copernicus, Data SIO, NOAA, U.S. Navy, NGA, GEBCO.

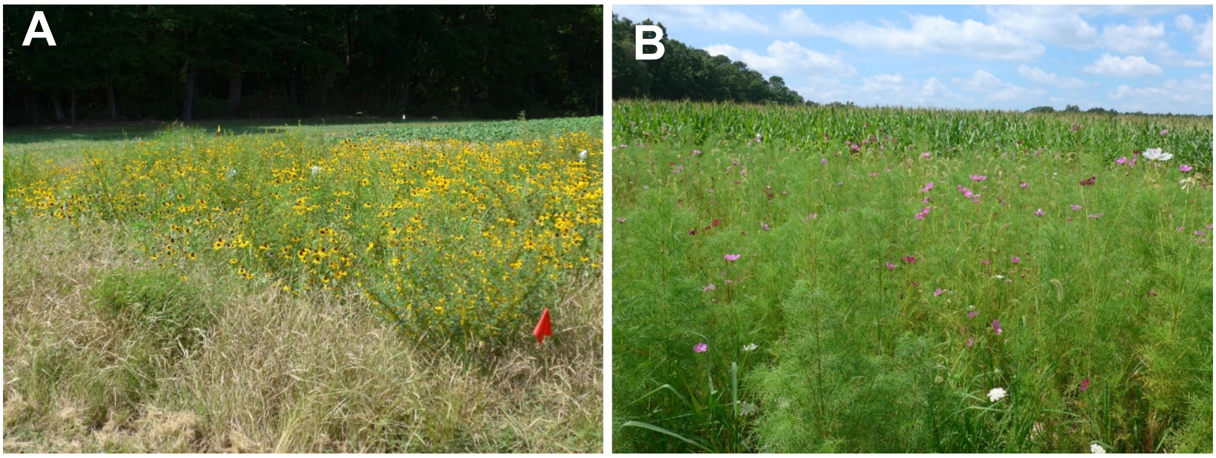


Fig. 8. Examples of experimental plots at site B with (A) native and (B) non-native seed mixes.

Bee sampling at sand mines and roadsides

Sampling was conducted every two to three weeks on rain free and (mostly) sunny days, between April and September of 2016 (10 sampling events) and 2017 (9 sampling events). We sampled bees with pan traps painted either with fluorescent blue, yellow and white, following the guidelines of Droege (2015). The bowls were filled with soapy water and placed along transects for 24 hours. At each 150 m transect, 30 bowls were placed every 5 m in a regular pattern of alternating colors. After 24 hours, we collected bees, drained the soap water with paper nylon-mesh paint strainers (190 micron), and stored them in whirl-pak bags filled with ethanol. Bees were pooled per transect and sampling event, resulting in overall 60 samples (10 per transect) in 2016 and 54 samples (9 per transect) in 2017. In four samples of roadsides, and five samples of sand mines, more than 3 bowls were destroyed by wild animals or tipped over during the sampling event. These samples were excluded from statistical analyses (see chapter Statistics on bee communities at sand mines and roadsides). In the lab, samples were washed, dried, and pinned for identification. Final species determination was done by Sam Droege at the USGS Patuxent Wildlife Research Center. We entered species and sampling information for all bees into the database of www.discoverlife.org which is publicly available online.

In addition, at each study site, we recorded the observed weather (sunny/cloudy) during the sampling time, and obtained current temperature, predicted maximal temperature of the sampling day, and wind speed from www.weather.com. We visually estimated proportion of ground covered by vegetation, measured maximal height of the vegetation to the nearest 10 cm with measuring sticks, counted numbers of different plant species in bloom, recorded floral colors, and visually estimated the percentage of the ground area that was flowering.

Bee sampling at farmland with native and non-native pollinator friendly plants

For this study, bees were sampled by hand netting and with pan traps between April and October in 2016 and 2017. Sampling took place on rain-free and (mostly) sunny days. Each year, hand netting started as soon as the first plants started to bloom (resulting in different starting points for native and non-native plots) and was performed in 30 min random walks through plots. All bees observed to touch reproductive flower parts were captured directly from flowers with a zip lock plastic bag. Nectar or pollen gathering was not assessed. We collected bees into vials filled with ethanol and later transferred them to whirl-paks for storage. All plots were sampled within one day between 9:00 and 18:00 in changing random order. Hand netting was always performed by the same person (N. Seitz). Note that

Cichorium intybus closed its flowers very early in the day, which is why these plants could not be observed when plots were sampled later in the day. We therefore conducted additional sampling of only *Cichorium intybus* in the morning of the next day on two occasions: August 2, 2017, and August 25, 2017. Furthermore, sampling on August 1, 2017 was interrupted by rain and therefore, continued the next day. Over two years, we had 21 hand netting events across sites. In 2016, non-native plots were sampled eight times and native plots five times due to a later onset of flowering. In 2017, non-native plots were sampled 13 times and native plots eleven times at site B and ten times at sites A and C due to a later onset of flowering.

On each day of hand netting, bees were also sampled with pan traps (except for July 15, 2016). Additionally, we sampled bees with pan traps once in April 2016 and once in May 2016 before plants started flowering. We followed guidelines by Droege (2015) for pan trap sampling. We placed twelve pan traps filled with soapy water and in a regular color pattern of fluorescent blue, yellow, and white along plot edges in the morning before the hand netting started and re-collected the traps in the evening after hand netting was finished. When re-collecting traps, we transferred bee specimens into paper nylon-mesh paint strainers (190 micron), drained the soap water and stored samples of each plot in a whirl-pak bag filled with ethanol. We obtained overall nine samples per plot or 54 samples in total, in 2016, and thirteen samples per plot or 78 samples in total, in 2017.

On all sampling days, we further recorded the weather (sunny/cloudy) and obtained current temperature, predicted maximal temperature and wind speed from www.weather.com. We visually estimated the proportion of ground covered by vegetation and the proportion of floral cover. The estimations were based on the entire plot area (10 x 10 m) and always by the same person (N. Seitz).

Samples from hand netting and pan traps were washed, dried and pinned for identification in the lab. Final species determination was done by Sam Droege at the USGS Patuxent Wildlife Research Center. We made species and sampling information of all bees publicly available at www.discoverlife.org. Note that bee individuals of *Halictus poeyi* and *Halictus ligatus* were indistinguishable and therefore placed in one group (i.e., *Halictus poeyi/ligatus*) as were *Hylaeus affinis* and *Hylaeus modestus*.

Statistics on bee communities at sand mines and roadsides

All statistical analyses were performed with R version R 3.5.1 (R Core Team 2018) in RStudio version 1.1.456 (RStudio Team 2016). Similarities of bee communities in different habitats were analyzed with a permutational multivariate analysis of variance (adonis function in the vegan package) based on a Bray-Curtis distance matrix between abundances of bee species. The number of permutations was set to 100 000 and the distance matrix was calculated with the vegdist function of vegan. We further used non-metrical multi-dimensional scaling (NMDS, function metaMDS, vegan package) for a visual presentation of community differences (**Fig. 10** in results).

We used generalized linear mixed-effect models (GLMM) to analyze the effects of habitat type, the percentage of vegetational ground cover, number of flower species, and maximum temperature of the sampling day on bee abundances and diversity. Our response variables were bee species richness, Shannon diversity, total abundance and abundance of the five most common bee species (*Lasioglossum pilosum*, *Lasioglossum tegulare*, *Lasioglossum coreopsis*, *Halictus poeyi/ligatus*, *Calliopsis andreniformis*). Prior to GLMM modeling, we used a Spearman rank correlation matrix to determine correlations between explanatory variables and between explanatory and response variables (**Table 7**) and only included non-correlating variables in models. All GLMMs included location (each sand mine together with its adjacent roadside were considered one location), and date nested in year as random factors. The response variables were checked for normal distribution with Shapiro tests and graphical assessment of distribution and of residuals. Where necessary, variables were log-transformed (abundance) or square root-transformed (species richness) to meet statistical requirements. For single species abundances, Poisson distributions were used in the models. Only samples with at least 28 (maximum 30) bowls per transect and day were included in the analyses. For models assessing bee abundance, one outlier of 379 individuals was excluded. The remaining samples counted between 0 and 211 individuals.

GLMMs were calculated with the lme4 package; the lmer function was used for normally distributed data and the glmer function for Poisson distributed data. We followed the parsimonious approach, identifying the model with the best fit (i.e., most parsimonious model), and keeping only the explanatory variables of the final (most parsimonious) model. For each response variable, we started with a model that included all explanatory variables followed by stepwise dropping. At each step, models were compared based on Akaike's Information Criterion (AIC) and using REML/ML scores to test whether specific explanatory variables explained a significant proportion of the overall variance by comparing the model with a given explanatory variable to the same model without this variable (anova function of lme4). Rows with NAs were removed for model comparison to obtain data frames of equal lengths. The significance of response variables in the model were assessed with the Anova command of the car package. To assess the variance explained by the final models, we further calculated R^2-values with the delta method using the pseudo-R-squared function of the MuMIn package

Table 7. Spearman rank correlation matrix of all (continuous) explanatory variables. Only non-correlating variables were included in generalized linear mixed-effect models (GLMMs). Asterisks indicate significant correlations (in bold): * p < 0.05, ** p < 0.01, *** p < 0.001. Temperature is included here for completeness, although correlations of temperature with other variables are not assumed to be meaningful.

	Explanatory variables					**Response variables**	
	Percentage of ground cover	Max. height of vegetation	No. of flower species blooming	Percentage of area blooming	Max. temperature	Abundance	Shannon diversity
Explanatory variables							
Max. height of vegetation	0.17						
No. of flower species blooming	0.20	-0.13					
Percentage of area blooming	**0.35*****	-0.01	**0.60*****				
Max. temperature	0.10	**0.53*****	0.10	0.08			
Response variables							
Richness	**-0.36*****	-0.08	**-0.29****	-0.16	-0.09	**0.90*****	**0.87*****
Abundance	**-0.34*****	0.05	**-0.34*****	-0.19	0.03	**0.85*****	
Shannon diversity	-0.20	0.04	**-0.29****	-0.11	-0.06		

Statistics on bee visitation of native vs. non-native pollinator friendly plants at farmland

All statistical analyses were performed with R version R 3.5.1 (R Core Team 2018) in RStudio version 1.1.456 (RStudio Team 2016). Data spanned a period of 4 – 6 months per year corresponding to the entire flowering period of experimental plants. The data set therefore comprised bee and plant species that did not necessarily co-occur due to different phenologies. To restrict network analyses to co-occurring species, we followed the idea by Kantsa et al. (2017) of composing several phenologically matched networks. We differentiated between three partly overlapping seasons, i.e., spring to early summer (April 1 – July 15), mid-summer (June 1 – August 31), and late summer to fall (July 16 – October 3). Each season included data of both sampling years. Mid-summer is overlapping with the early and late season in order to smoothly incorporate the phase of transition from early to late season, capturing the late species of the early season and the early species of the late season. Additionally, it is important to distinguish mid-summer as a season of its own, as studies with limited sampling effort often focus exclusively on this time period.

Species that could only be identified to genus level were only included in networks if no other species of the same genus was present. For the analyses of species specificity (d’, see below), we only included the five most abundant bee species and removed all d’ values that were based on less than three observations per network.

We visualized and analyzed plant-bee visitation networks with the bipartite package (functions plotweb, networklevel & specieslevel) (Dormann et al. 2008). The H2’ index within the function networklevel was used to compare the community level specialization of the different networks (Blüthgen et al. 2006). At the species level, we used the d’ index of the function specieslevel to compare the specializations in plant visitation of single bee species within the larger networks (Blüthgen et al. 2006). Both indices quantify the degree of specialization in a range from 0 (no specialization) to 1 (highest specialization). They are mathematically derived from Shannon entropy and their calculations are not affected by network size or sampling intensity (Blüthgen et al. 2006).

We analyzed differences in bee species richness (per sampling event), abundance (per sampling event), network specificity (H2’; per season) and species specificity (d’; per season) between native and non-native plant plots using generalized linear mixed-effect models (GLMM; lmer function, lme4 package). Data was log transformed (bee species richness and abundance) where necessary in order to obtain normal distribution (as visually assessed with histograms and tested with Shapiro tests). We calculated models for species richness and abundance (per sampling event) for each season and included plant nativity as fixed effect and site and Julian date as random effects. For network and species specificity, we obtained always one H2’ and one d’ (per species) value for each of the 18 networks (each plot type at each site and for each season). Our models for network and species specificity included plant nativity and season as fixed effects and site as random effect. Significance of fixed effects (plant nativity and season) were assessed with the Anova command of the car package. Multiple comparison of means for differences between seasons were analyzed using Tukey post hoc tests (glht function, multcomp package). To finally assess the overall variance explained by models, we calculated R^2-values with the pseudo-R-squared function of the MuMIn package.

To analyze bee species composition, we visualized data using non-metrical multi-dimensional scaling (NMDS, function metaMDS, vegan package) with a Bray-Curtis distance matrix on abundances of the different bee species (**Fig. 13**). Differences in bee species composition between native and non-native plant mixes were then assessed using a permutational multivariate analysis of variance (PERMANOVA, adonis function in the vegan package; 100 000 permutations) also based on Bray-Curtis distances between bee species (vegdist function, vegan package). To avoid pseudo-replication, we only included data of the early and late seasons, but excluded the mid-season for these analyses.

Network analyses as well as statistical analyses on differences of bee abundance, species richness, Shannon diversity, and bee species composition between native and non-native plant plots were based on data from hand netting only. For data of pan trap sampling, we did not distinguish between plant types due to the proximity of native and non-native plots.

Results

Bee communities in sand mines and at roadsides

Over the two year study period, we collected a total of 3900 bees in sand mines and of 1366 bees at roadsides. The numbers of individuals and the numbers of bee species sampled per year were very similar in 2016 and 2017 for each habitat type (**Fig. 9**). Species composition differed between years: While the most commonly sampled bee species were represented in both years in similar abundances, many less commonly sampled bee species only occurred in one sampling year (**Appendix, Table A3, Figs. A7 & A8**). The bee communities in reclaimed sand mines and roadsides differed significantly in their species composition (permutation test based on Bray-Curtis distance matrix: $p = 0.0063$, $R^2 = 0.22$, df = 1, number of permutations = 100 000; **Fig. 10**). Overall, we found 111 bee species in reclaimed sand mines, with 59 species occurring in both years (**Fig. 9 & Appendix, Table A3**). Roadsides hosted a total of 88 bee species, with 47 species overlapping across years (**Fig. 9 & Appendix, Table A3**). Both habitat types showed bee species that were solely confined to this particular habitat (**Appendix, Table A3, Figs. A7 & A8**). We found 38 species only in sand mines, and 15 species only at roadsides. Ten bee species (16 individuals) found in sand mines and six bee species (11 individuals) at roadsides are considered rare or uncommon in Maryland (USA) (**Appendix, Table A3**). Ground nesting bees dominated across habitats, representing 63 % of species at both sand mines and roadsides (**Appendix, Table A4**). The proportion for individuals of ground nesters differed between habitats. At the sand mines, 95 % of individuals were ground nesters, 3 % wood nesters and the remaining either parasites or honey bees (**Appendix, Table A4**). At roadsides, 81 % of individuals were ground nesters, 12 % wood nesters, 5 % parasites of ground nesters and the remaining either parasites of wood nesters or honey bees (**Appendix, Table A4**).

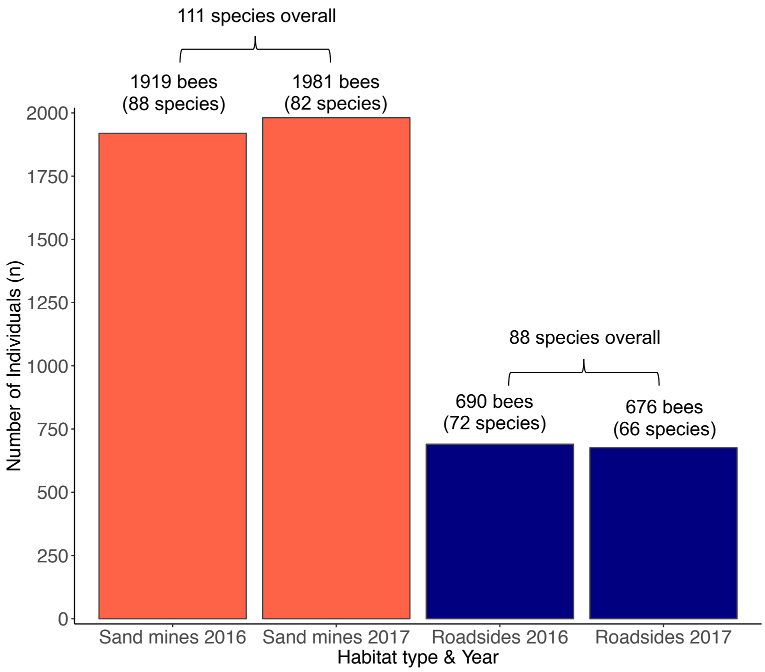


Fig. 9. Total numbers of bee individuals (n) for sand mines (red bars) and roadsides (blue bars) for 2016 and 2017.

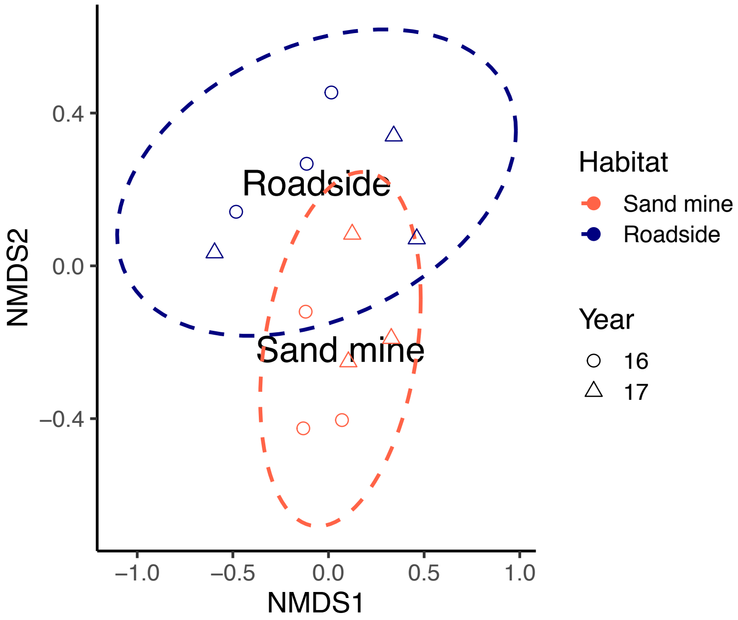


Fig. 10. Differences in bee community composition between sand mines (red symbols) and roadsides (blue symbols) displayed by non-metrical multi-dimensional scaling (NMDS, stress-value = 0.18). Sites are plotted for 2016 (circles) and 2017 (triangles) separately, resulting in two data points per site. Each symbol represents one site in one year (six for sand mines and six for roadsides).

Bee species richness, bee abundance, and Shannon diversity were on average higher in sand mines (mean ± standard deviation (SD), richness: 14 ± 6.5, abundance: 59 ± 56.6, Shannon: 1.6 ± 0.6) than at roadsides (richness: 9 ± 5.2, abundance: 24 ± 24.9, Shannon: 1.3 ± 0.7). Variation in species richness, abundances and Shannon diversity was always best explained by the percentage of vegetational ground cover at each site (**Table 8**). Vegetational ground cover ranged from 65 – 100 % at roadsides and from 25 – 100 % at sand mines and negatively correlated with species richness, abundance and Shannon diversity (**Fig. 11**). When examining the five most abundant species found in the study (*Lasioglossum pilosum*, *Lasioglossum tegulare*, *Lasioglossum coreopsis*, *Halictus poeyi/ligatus*, *Calliopsis andreniformis*), the percentage of vegetational ground cover, and habitat type significantly affected each species' abundance (**Table 9 & Fig. 12**). All *Lasioglossum* species were more abundant in sand mines, while the *Halictus* and *Calliopsis* species were more abundant at roadsides (**Appendix, Table A3**). Furthermore, the number of blooming flower species was negatively correlated with the abundance of *L. coreopsis* and positively with *C. andreniformis*, while the abundance of *L. pilosum* increased with increasing temperature (**Table 9 & Fig. 12**).

Table 8. Results (*chi*^{2}- and *p*-value, degrees of freedom (df) as well as marginal and conditional R^2-values) of the most parsimonious generalized linear mixed effect models (GLMMs) for bee species richness, abundance and Shannon diversity, all with vegetational ground cover as solely remaining explanatory variable. The marginal R^2-value gives the variance explained by the fixed effects, the conditional R^2-value the variance explained by the entire model, including both fixed and random effects.

Response variable	***chi*^{2}**	**df**	***p***	**marginal R^2**	**conditional R^2**
Species richness	47.52	1	< 0.001***	0.25	0.76
Abundance	44.25	1	< 0.001***	0.25	0.74
Shannon diversity	23.45	1	< 0.001***	0.11	0.78

Table 9. Results (*chi*^{2}- and *p*-value, degrees of freedom (df) as well as marginal and conditional R^2-values) of the most parsimonious generalized linear mixed effect models (GLMMs) for the bee species *Lasioglossum pilosum*, *Lasioglossum tegulare*, Lasioglossum *coreopsis*, *Halictus poeyi/ligatus*, and *Calliopsis andreniformis*. Asterisks indicate significant effects: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Results for explanatory variables (habitat type, vegetational ground cover, number (no.) of flower species blooming, and maximal temperature) are only shown if the variable was part of the most parsimonious model. The marginal R^2-value gives the variance explained by the fixed effects, the conditional R^2-value the variance explained by the entire model, including both fixed and random effects.

	Habitat type			**Vegetational ground cover**			**No. of flower species blooming**			**Maximal temperature**				
	***chi*^{2}**	**df**	***p***	***chi*^{2}**	**df**	***p***	***chi*^{2}**	**df**	***p***	***chi*^{2}**	**df**	***p***	**marginal R^2**	**conditional R^2**
Response variable														
L. pilosum	247.25	1	< 0.001***	9.84	1	0.0017 **	-	-	-	10.04	1	0.0015 **	0.48	0.98
L. tegulare	5.86	1	0.0155*	46.40	1	< 0.001***	-	-	-	-	-	-	0.24	0.88
L. coreopsis	40.74	1	< 0.001***	4.11	1	0.0425*	4.56	1	0.0327*	-	-	-	0.60	0.93
H. poeyi/ligatus	47.63	1	< 0.001***	25.20	1	< 0.001***	-	-	-	-	-	-	0.22	0.81
C. andreniformis	17.24	1	< 0.001***	27.44	1	< 0.001***	6.89	1	0.008649 **	-	-	-	0.09	0.93

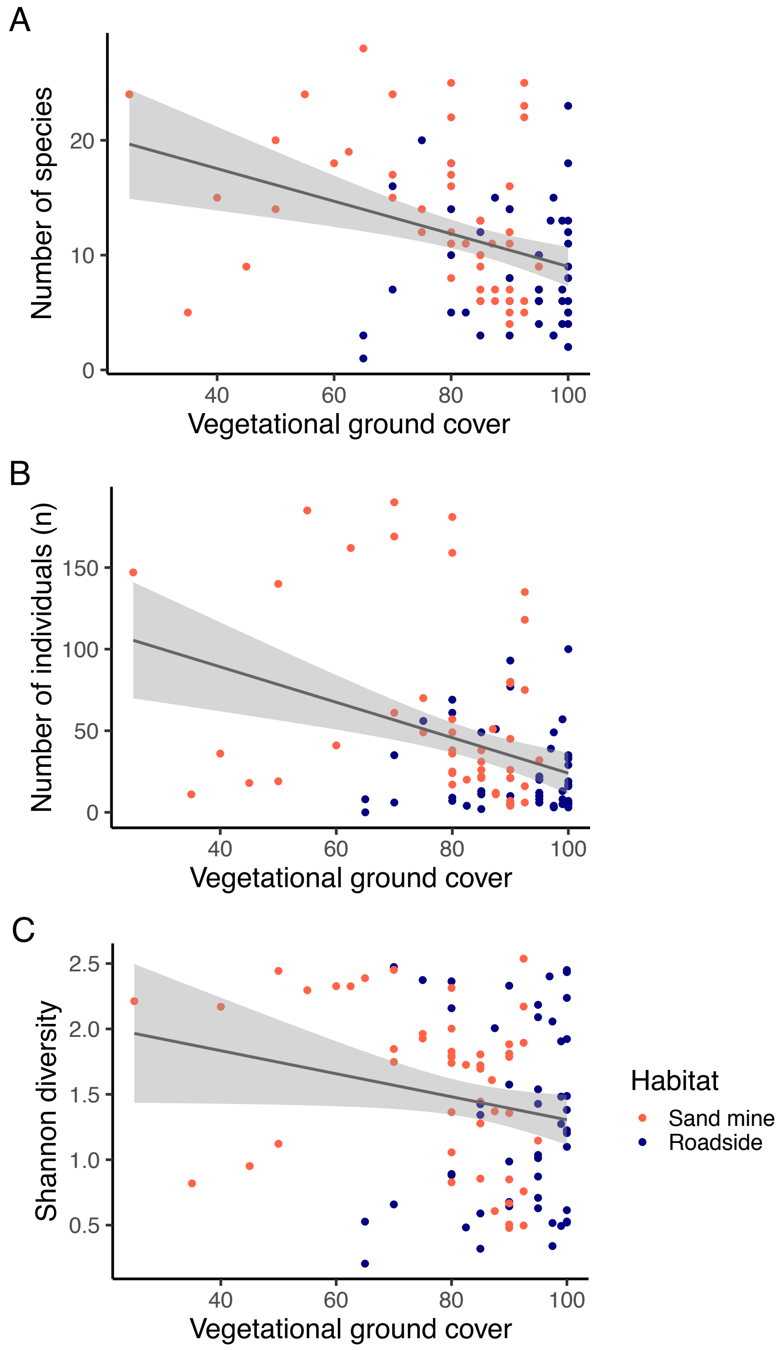


Fig. 11. Correlations between ground cover and (A) species richness, (B) abundance, and (C) Shannon diversity. Data of sand mines is shown in red and of roadsides in blue.

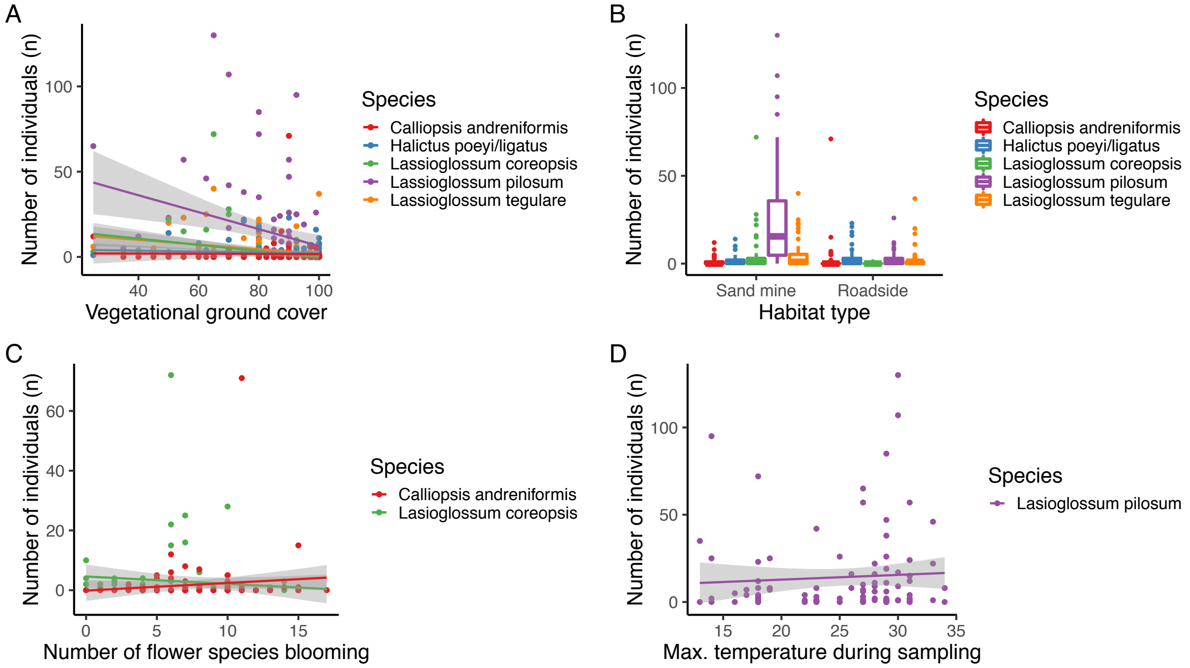


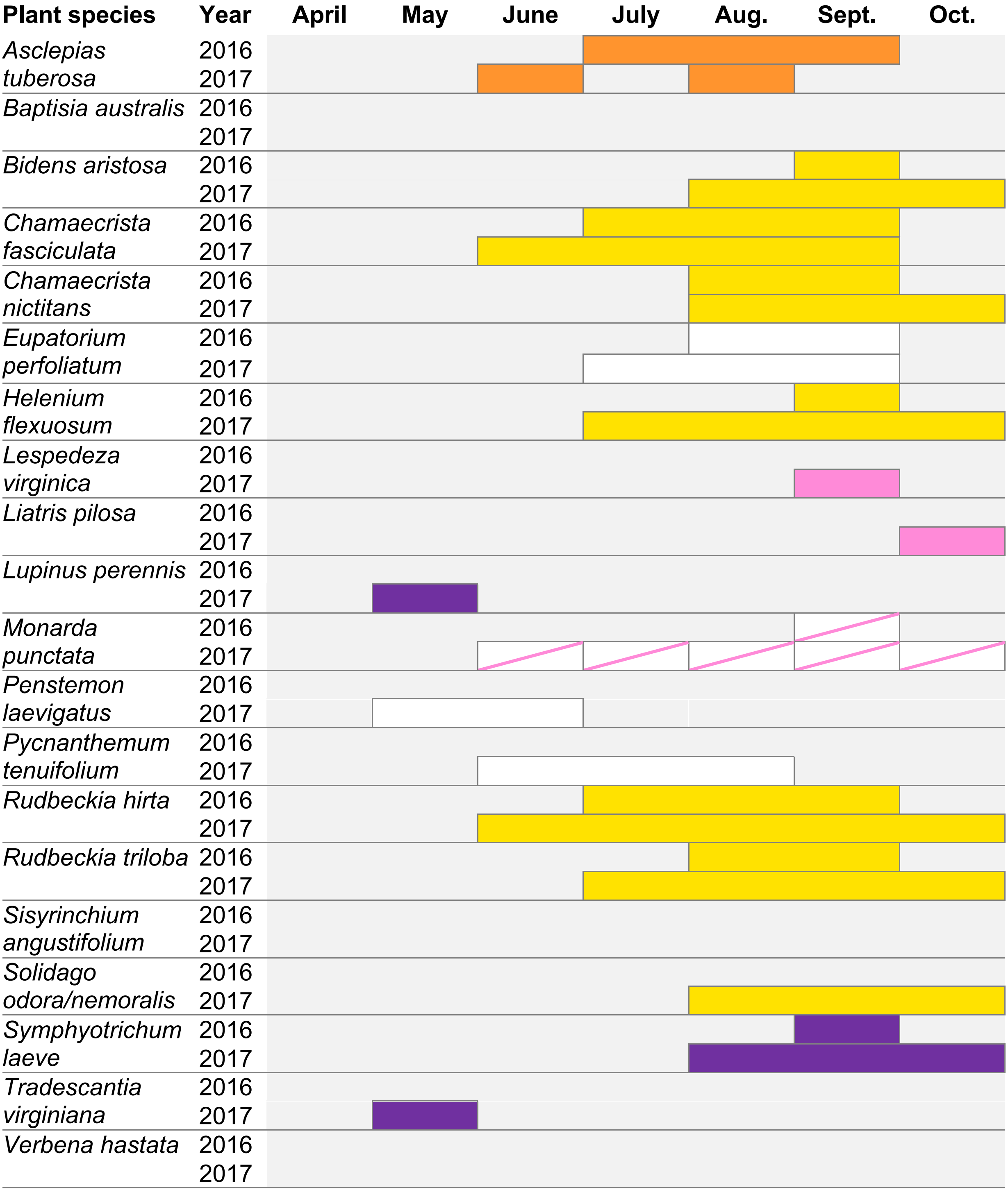
Fig. 12. Abundances as number of individuals (n) of the five most common species in relation to (A) vegetational ground cover, (B) habitat type, (C) number of blooming flower species, and (D) maximal (max.) temperature of the sampling day. Only species for which the variable had a significant explanatory effect were included in each plot.

Bee visitation on native vs. non-native pollinator friendly plants at farmland

Over the two year study period, 17 out of the 20 initially seeded plants came to flower in native plant plots, and 18 in non-native plant plots (**Table 10 & 11**). Non-native plants started flowering earlier than native plants in both years (**Table 10 & 11**). In 2016, the first plants started flowering in June in non-native plant plots and five weeks later in native plant plots (**Table 10 & 11**). In 2017, the onset of flowering was overall two months earlier (**Table 10 & 11**). Non-native plants started flowering in April and native plants in May, again about five weeks later (**Table 10 & 11**). Many plant species had not only an earlier flowering start, but also an overall longer flowering period in the second year. Some plant species did not receive any recorded bee visits, i.e., *Lespedeza virginica*, *Liatris pilosa*, and *Lupinus perennis* in native plots, and *Leucanthemum maximum*, and *Salvia officinalis* in non-native plots. Although floral abundance per species was not precisely quantified, these plant species seemed to be present in particularly low numbers.

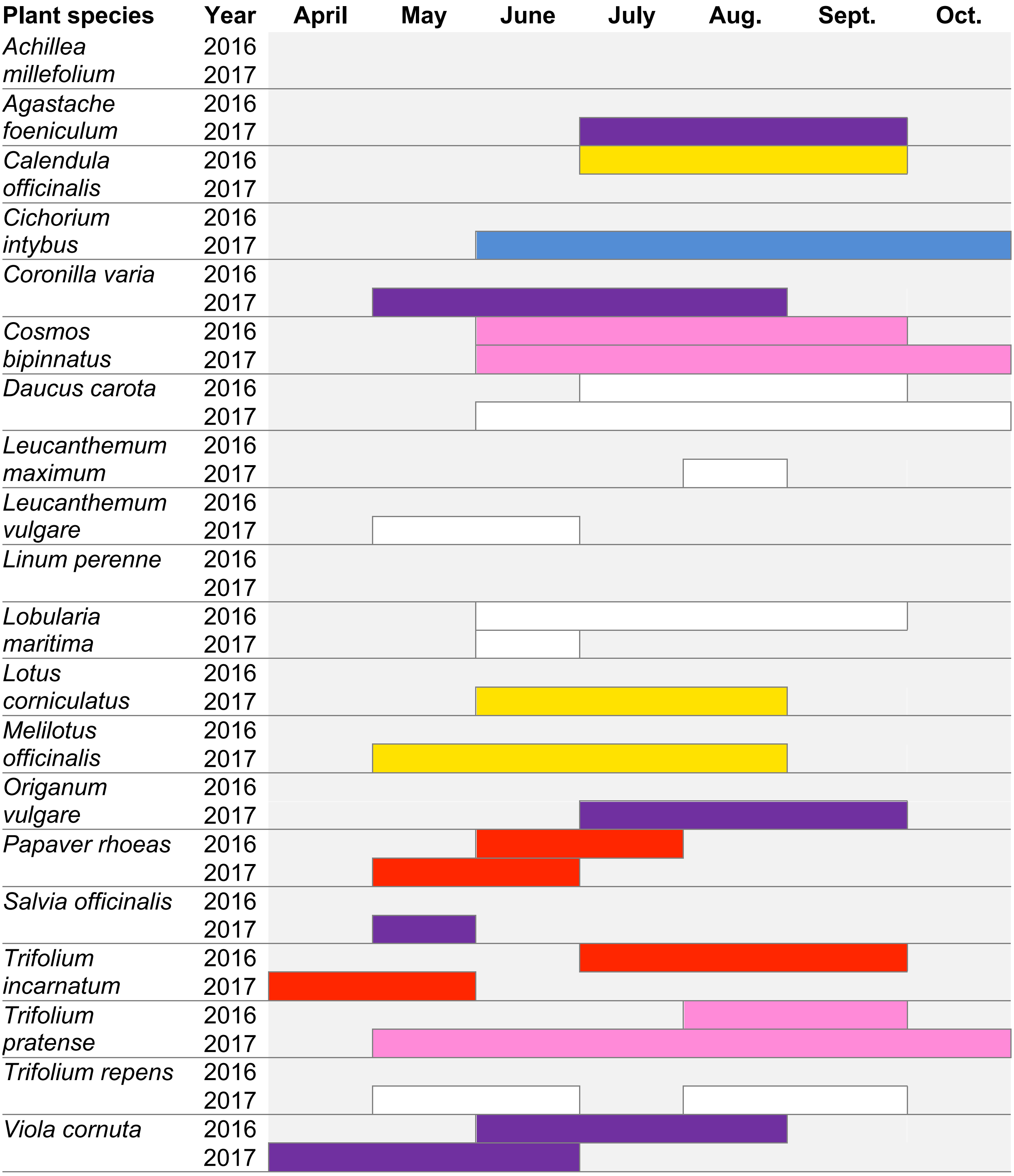
A total of 3744 bees and 120 species were recorded in this study. With pan traps, overall 2036 bees were sampled, including 30 different genera and 107 different species, which represented 89 % of bee species of this study (see **Appendix, Table A5** for complete species list). With hand netting, overall 1708 bees were sampled, including 25 different genera and 72 different species, which represented 60 % of the bee species of this study (**Appendix, Table A5)**. Some bee species were only detected with either one sampling method: of the total of 120 bee species, 48 species (40 %) were confined to pan traps and 13 species (11 %) to hand netting; 59 species (49 %) were sampled with both sampling techniques.

Table 10. Plant list with flowering periods of native plants used in the native plant seed mix. The months of flowering are indicated with colored bars, corresponding to the color of the flowers. In 2016, ten of 20 native plants were flowering. In 2017, 17 native plants were flowering. This seed mix also contained the two grass species *Elymus virginicus* and *Schizachyrium scoparium*.



Plant species	Year	April	May	June	July	Aug.	Sept.	Oct.
Asclepias tuberosa	2016				🟧	🟧	🟧	
	2017			🟧		🟧		
Baptisia australis	2016							
	2017							
Bidens aristosa	2016						🟨	
	2017					🟨	🟨	🟨
Chamaecrista fasciculata	2016				🟨	🟨	🟨	
	2017			🟨	🟨	🟨	🟨	
Chamaecrista nictitans	2016					🟨	🟨	
	2017					🟨	🟨	🟨
Eupatorium perfoliatum	2016					⬜	⬜	
	2017				⬜	⬜	⬜	
Helenium flexuosum	2016						🟨	
	2017				🟨	🟨	🟨	🟨
Lespedeza virginica	2016							
	2017						🩷	
Liatris pilosa	2016							
	2017							🩷
Lupinus perennis	2016							
	2017		🟪					
Monarda punctata	2016						▨	
	2017			▨	▨	▨	▨	▨
Penstemon laevigatus	2016							
	2017		⬜	⬜				
Pycnanthemum tenuifolium	2016							
	2017			⬜	⬜	⬜		
Rudbeckia hirta	2016				🟨	🟨	🟨	
	2017			🟨	🟨	🟨	🟨	🟨
Rudbeckia triloba	2016					🟨	🟨	
	2017				🟨	🟨	🟨	🟨
Sisyrinchium angustifolium	2016							
	2017							
Solidago odora/nemoralis	2016							
	2017					🟨	🟨	🟨
Symphyotrichum laeve	2016						🟪	
	2017					🟪	🟪	🟪
Tradescantia virginiana	2016							
	2017		🟪					
Verbena hastata	2016							
	2017							

Table 11. Plant list with flowering periods of non-native plants used in the non-native plant seed mix. The months of flowering are indicated with colored bars, corresponding to the color of the flowers. In 2016, eight of 20 non-native plants were flowering. In 2017, 17 non-native plants were flowering. This seed mix also contained the two grass species *Dactylis glomeratus* and *Eragrostis curvula*.



Plant species	Year	April	May	June	July	Aug.	Sept.	Oct.
Achillea millefolium	2016							
	2017							
Agastache foeniculum	2016							
	2017				🟪	🟪	🟪	
Calendula officinalis	2016				🟨	🟨	🟨	
	2017							
Cichorium intybus	2016							
	2017			🟦	🟦	🟦	🟦	🟦
Coronilla varia	2016							
	2017		🟪	🟪	🟪	🟪		
Cosmos bipinnatus	2016			🩷	🩷	🩷	🩷	
	2017			🩷	🩷	🩷	🩷	🩷
Daucus carota	2016				⬜	⬜	⬜	
	2017			⬜	⬜	⬜	⬜	⬜
Leucanthemum maximum	2016							
	2017					⬜		
Leucanthemum vulgare	2016							
	2017		⬜	⬜				
Linum perenne	2016							
	2017							
Lobularia maritima	2016			⬜	⬜	⬜	⬜	
	2017			⬜				
Lotus corniculatus	2016							
	2017			🟨	🟨	🟨		
Melilotus officinalis	2016							
	2017		🟨	🟨	🟨	🟨		
Origanum vulgare	2016							
	2017				🟪	🟪	🟪	
Papaver rhoeas	2016			🟥	🟥			
	2017		🟥	🟥				
Salvia officinalis	2016							
	2017		🟪					
Trifolium incarnatum	2016				🟥	🟥	🟥	
	2017	🟥	🟥					
Trifolium pratense	2016					🩷	🩷	
	2017		🩷	🩷	🩷	🩷	🩷	🩷
Trifolium repens	2016							
	2017		⬜	⬜		⬜	⬜	
Viola cornuta	2016			🟪	🟪	🟪		
	2017	🟪	🟪	🟪				

At native plant plots, a total of 719 bees of 20 genera and 49 species (representing 68 % of hand netted species) were caught with hand netting, and a total of 989 bees of 23 genera and 63 species (88 %) at non-native plant plots. Bee community compositions differed between native and non-native plant plots (PERMANOVA: $p = 0.034$, $R^2 = 0.17$, df = 1; **Fig. 13**). Of the 72 hand netted species, 11 species were only found at native and 23 species only at non-native plants. Many bee species, such as *Apis mellifera*, *Halictus poeyi/ligatus*, *Bombus bimaculatus* and *Lasioglossum tegulare*, occurred on both native and non-native plants, but were more abundant on non-native plants (**Appendix, Table A5**). Other bee species, such as *Xylocopa virginica*, *Lasioglossum trigeminum* and *Augochloropsis metallica_metallica,* were more abundant at native plants. Abundances of the most abundant and third most abundant bee species, *Apis mellifera* and *Xylocopa virginica* respectively, differed strongly between native and non-native plots (**Appendix, Table A5**). From a total of 470 *Apis mellifera* bees, 88 visited native and 382 non-native plants (**Appendix, Table A5**). *Xylocopa virginica* showed an opposite visitation pattern: from a total of 470 individuals, 228 visited native plants, and 16 non-native plants. *Apis mellifera* was the only non-native bee species visiting our experimental plants.

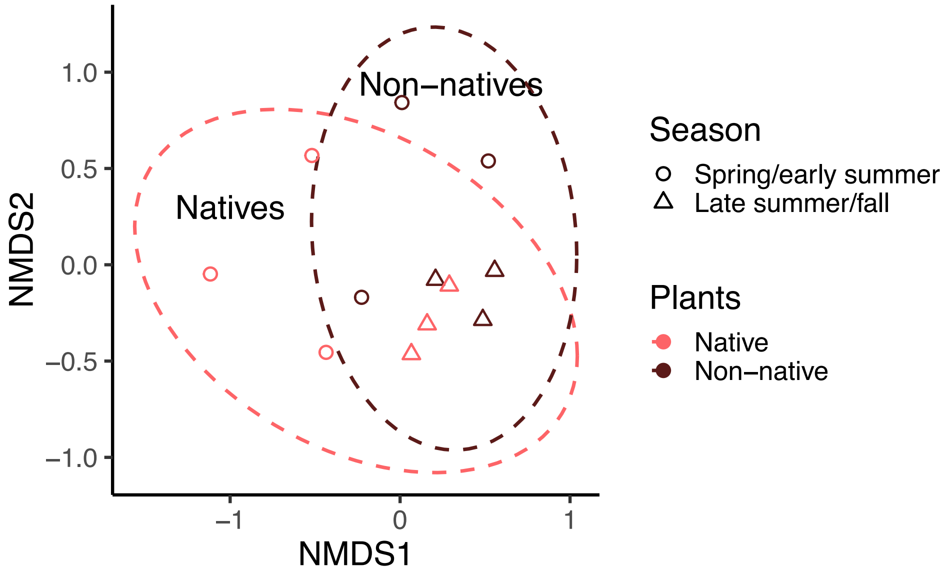


Fig. 13. Differences in bee community composition between native plant plots (pink symbols) and non-native plant plots (dark red symbols) displayed by non-metrical multi-dimensional scaling (NMDS, stress-value = 0.14). Sites are plotted for spring/early summer (circles) and late summer/fall (triangles) separately, resulting in two data points per site. Each symbol represents one site in one season (six for native plant plots and six for non-native plant plots).

Two oligolectic bee species, i.e., *Osmia distincta* and *Melissodes desponsus*, were recorded. *Osmia distincta* is specialized on plants of the genus *Penstemon* (Fowler 2016) and three females of this species were found on *Penstemon laevigatus* plants at native plant plots (**Appendix, Table A5 & Appendix, Figs. A9-A14**). One additional male and female were caught with pan traps (**Appendix, Table A5**). *Melissodes desponsus* typically forages on *Cirsium* plants (Fowler 2016) which were not included in our experiment. Almost all *Melissodes desponsus* recorded were male bees and found exclusively on non-native plants (i.e., on *Cosmos bipinnatus* (7 males, 1 female) and on *Daucus carota* (1 male)) (**Appendix, Table A5 & Appendix, Figs. A9-A14**). An additional female was caught with pan traps. We recorded six additional oligolectic bee species in pan traps which were not recorded visiting any of the experimental plants (host plant genus in brackets): *Andrena erigeniae* (*Claytonia*), *Andrena violae* (*Viola*), *Melissodes denticulata* (*Vernonia*), *Melitoma taurea* (*Ipomoea*), *Peponapis pruinose* (*Cucurbita*), *Ptilothrix bombiformis* (*Hibiscus)* (**Appendix, Table A5**).

Bee abundance and species richness recorded per hand netting event differed between native and non-native plots in some but not all seasons (species richness at native plots was 4.3 ± 3.4, 4.5 ± 3.0, and 4.4 ± 2.6 (mean ± sd) for spring/early summer, summer, and late summer/fall respectively, and at non-native plots 4.7 ± 2.3, 4.7 ± 2.4, and 5.4 ± 2.5; bee abundance was 12.2 ± 12.4, 12 ± 9.0, and 16.9 ± 15.0 at native plots and 20.2 ± 24.9, 16.5 ± 22.2, and 13.9 ± 10.0 at non-native plots for spring/early summer, summer, and late summer/fall respectively; **Fig. 14**). In spring to early summer, both abundance and species richness were significantly lower at native plots than at non-native plots (**Fig. 14**, **Table 12**). Species richness was also significantly lower at native plots in late summer to fall (**Fig. 14**, **Table 12**).

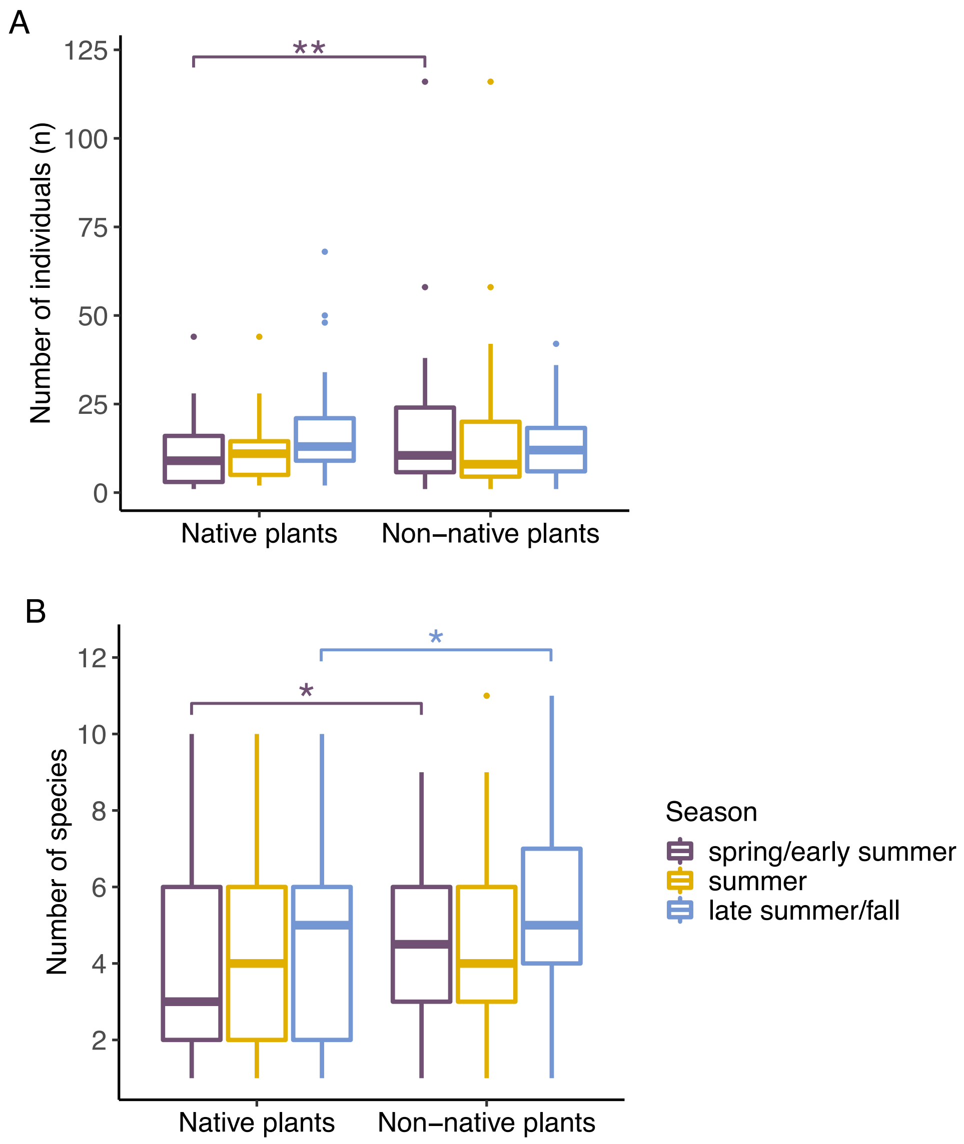


Fig. 14. Bee abundance (A) as number of individuals (n) and bee species richness (B) at native and non-native plots by season (data pooled for both observation years). Statistical differences between native vs non-native plants per season were assessed with GLMMs (**Table 12**) and are indicated here with asterisks when significant: * $p < 0.05$, ** $p < 0.01$. This and the following box plots show the interquartile range (IQR) of data, which extends from the 25th percentile (first quartile; lower edge of box) to the 75th percentile (third quartile; upper edge of box). The line within the box indicates the median. The lower whiskers extend to the smallest observation, but not further than 1.5 * IQR from the 25th percentile. The upper whiskers extend to the largest observation, but not further than 1.5 * IQR from the 75th percentile. Outliers are plotted as individual points.

Table 12. Results (*chi*^{2}- and *p*-value, degrees of freedom (df) as well as marginal and conditional R^2-values) of the linear mixed effect models (GLMM) for bee species richness and abundance in the three different seasons with plot type (native/non-native) as explanatory variable and site and date as random effects. The marginal R^2-value gives the variance explained by the fixed effects, the conditional R^2-value the variance explained by the entire model, including both fixed and random effects. Spring to early summer covered the period from April 1 – July 15; summer June 1 – August 31; and late summer to fall July 16 – October 3.

Response variable	***chi*^{2}**	**df**	***p***	**marginal R^2**	**conditional R^2**
Species richness (spring/early summer)	3.91	1	**< 0.05***	0.07	0.40
Species richness (summer)	1.79	1	0.18	0.02	0.30
Species richness (late summer/fall)	5.59	1	**< 0.05***	0.06	0.33
Abundance (spring/early summer)	7.08	1	**< 0.01****	0.11	0.52
Abundance (summer)	0.36	1	0.55	< 0.01	0.30
Abundance (late summer/fall)	0.16	1	0.69	< 0.01	0.37

The specialization (H2’) of the recorded plant-bee networks also differed between plot types and seasons (**Fig. 15, Table 13**). Native plant plots had more specialized networks than non-native plots and early season networks were more specialized than late season networks (**Table 13**). Generally, early season networks included fewer plant and bee species (**Fig. 15 & Appendix Figs. A9-A14**).

The five most abundant bee species across both native and non-native plant plots were *Apis mellifera*, *Halictus poeyi/ligatus*, *Xylocopa virginica*, *Bombus impatiens*, and *Lasioglossum pilosum*, in order of decreasing abundance (**Appendix, Table A5**). *Xylocopa virginica*, *B. impatiens*, and *L. pilosum* showed a more specialized foraging behavior at native than at non-native plant plots (**Fig. 16 & Table 13**). The honey bee *A. mellifera* changed its foraging specialization over the seasons with its highest specialization early in the year and lowest specialization later in the year (**Fig. 16 & Table 13**). The other species’ specificity remained similar throughout seasons, but *X. virginica*, and *B. impatiens* were absent in the early season (**Fig. 16 & Table 13**).

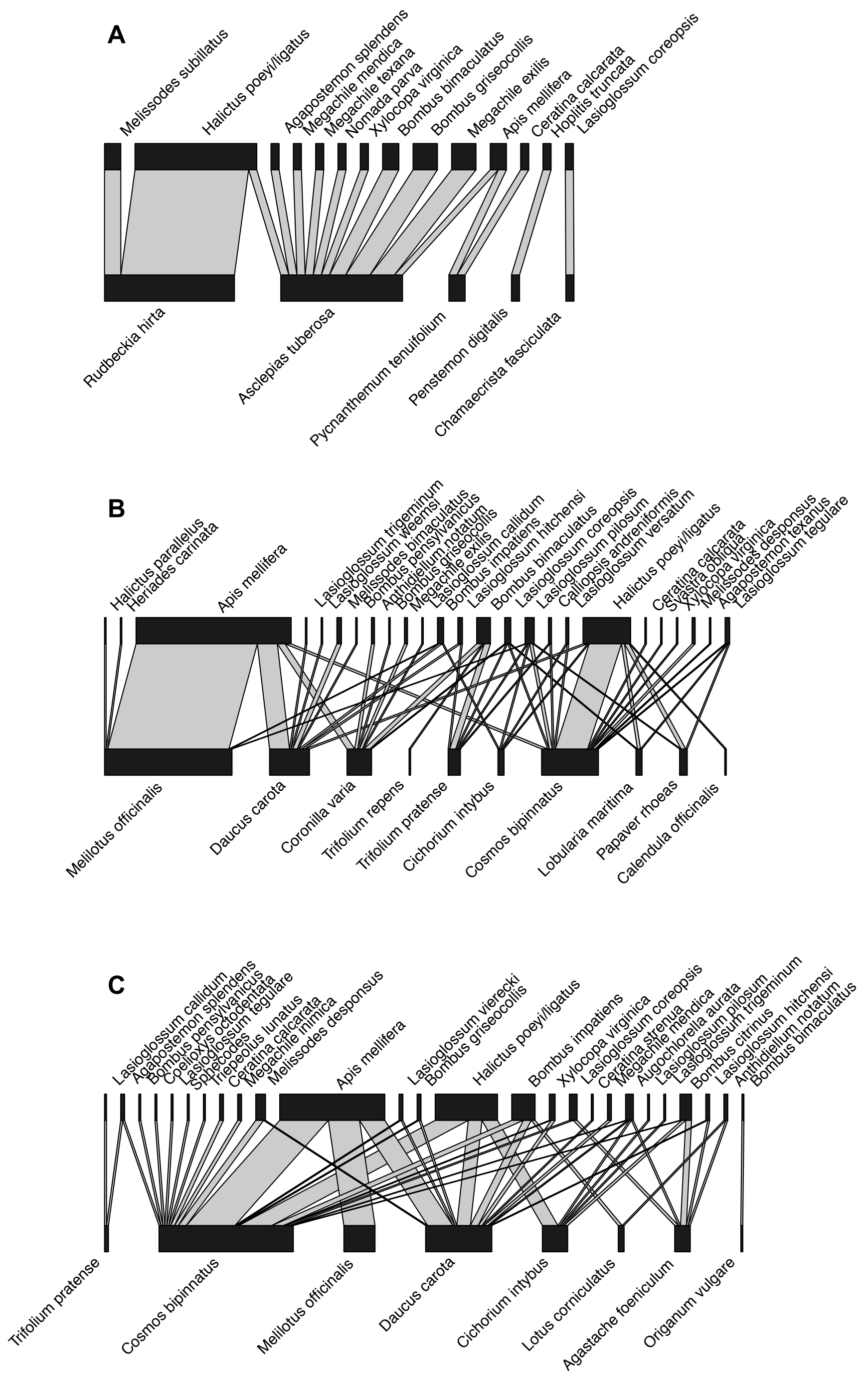


Fig. 15. Plant-bee networks: (A) in spring/early summer for native plants of site C (H2’ = 0.82); (B) in summer for non-native plants of site A (H2’ = 0.57); and (C) in late summer/fall for non-native plants of site B (H2’ = 0.34). The H2’ value gives the degree of network specialization and ranges from 0 (no specialization) to 1 (highest specialization). Bee species are indicated with black bars in the upper network levels. Thickness of bars relates to the bee species’ abundance within the network. Plant species are indicated by black bars in the lower network levels. Here, thickness of bars relates to the number of visits a plant species received. Grey lines between the network levels show bee visitations to plants. Thickness of these connecting lines relates to the frequency of visits. See **Appendix, Figs. A9-A14** for networks of all sites and for all seasons including H2’ values.

Table 13. Results (*chi*^{2}- and *p*-value, degrees of freedom (df) as well as marginal and conditional R^2-values) of the linear mixed effect models (GLMM) for the plant-bee network specialization (H2’) and for individual specialization (d’) of the five most abundant bee species with plant nativity and season as explanatory variables and site as random factor; also shown are results (direction of seasonal difference and *p*-value) of the tukey post hoc test on differences between seasons. Values of d’ and H2’ (by plant type) are indicated as mean ± sd. Individual values of H2’ per network are included in **Fig. 15** and **Appendix, Figs. A9-A14**. Species specialization of *Bombus impatiens* and *Xylocopa virginica* only included data of two seasons: summer and late summer to fall, because these species were not present in sping to early summer. Seasons are abbreviated as follows: early = spring to early summer; mid = summer; and late = late summer to fall. Asterisks indicate significant effects: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. The marginal R^2-value gives the variance explained by the fixed effects, the conditional R^2-value the variance explained by the entire model, including both fixed and random effects.

	Plant nativity			**Season**			**Tukey post hoc for season**			
	***chi*^{2}**	**df**	***p***	***chi*^{2}**	**df**	***p***	**direction**	***p***	**marginal R^2**	**conditional R^2**
H2’ Native: 0.64 ±0.11 Non-native: 0.44 ±0.18	12.19	1	**< 0.001*****	11.03	2	**< 0.01****	early > late	**< 0.01****	0.58	0.58
d' (*Apis mellifera*): 0.74 ±0.21	2.00	1	0.16	35.32	2	**< 0.001*****	early > late mid > late	**< 0.001***** **< 0.001*****	0.56	0.77
d' (*Bombus impatiens*) 0.60 ±0.15	8.30	1	**< 0.01****	1.09	1	0.30			0.29	0.66
d' (*Halictus poeyi/ligatus*) 0.66 ±0.15	1.33	1	0.25	14.19	2	0.12			0.25	0.25
d' (*Lasioglossum pilosum*) 0.53 ±0.13	4.06	1	**< 0.05***	1.49	2	0.48			0.38	0.38
d' (*Xylocopa virginica*) 0.83 ±0.16	33.49	1	**< 0.001*****	0.04	1	0.85			0.81	0.81

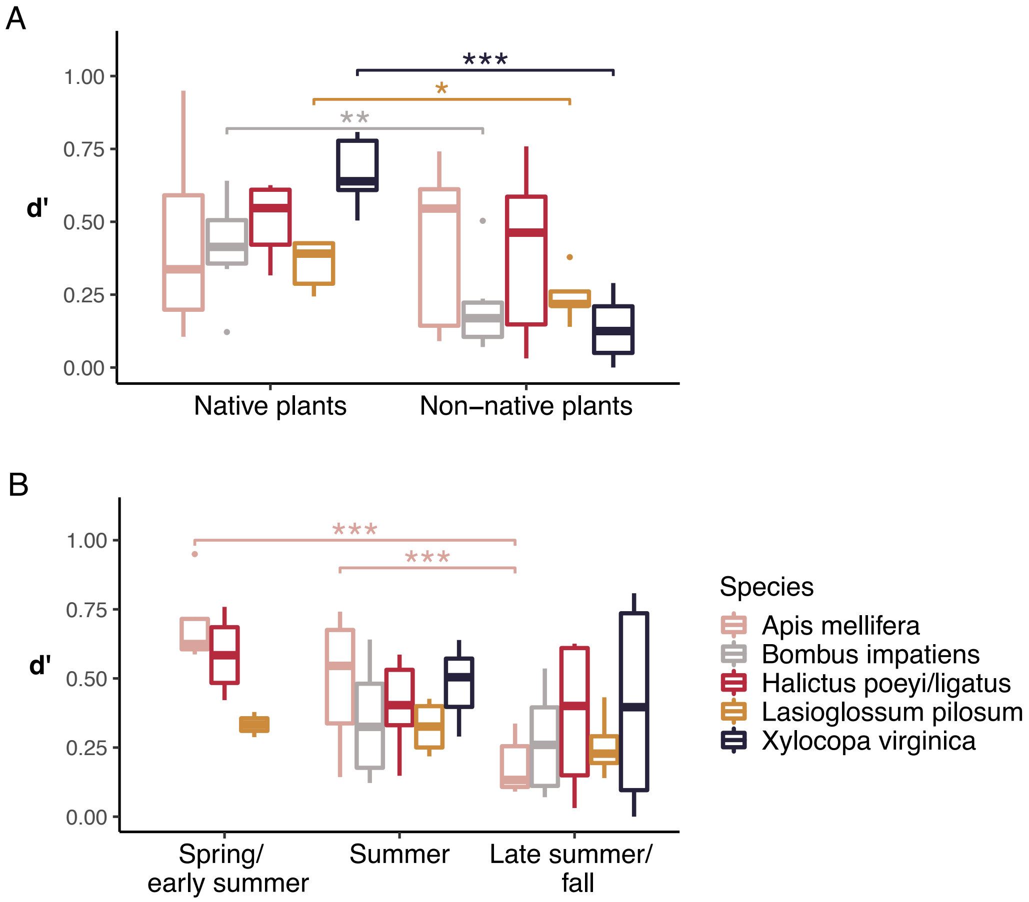


Fig. 16. Species specificity (d') of the five most abundant bee species shown for (A) native and non-native plant plots and for (B) season. The d' index provides information on the degree of specialization of individual species and ranges from 0 (not specialized) to 1 (highly specialized). It is based on interaction links between bee species and plant species, but also takes into account the dominance of each linked plant species in the interaction network. Thus, bee species visiting the most dominant plant species are considered less specialized than bee species visiting plants that are rarely visited by other bee species. Statistical differences between plant types and seasons per bee species were assessed with GLMMs (**Table 13**) and are indicated here with asterisks when significant: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Discussion

The potentials of reclaimed sand mines for bee conservation

We found diverse, albeit differing, bee communities in reclaimed sand mines and along roadsides. The number of bees identified at sand mines and roadsides represent 25 % and 20 % respectively of the total of 430 bee species that have been documented as being resident in the state of Maryland, USA (North American Native Bee Collaborative 2017). As we sampled with pan traps only, and without netting or emergence traps, we can assume that the actual bee communities include even more species across all sites (Grundel et al. 2011; Roulston et al. 2007; Sardiñas and Kremen 2014; Wilson et al. 2008). Thus, both roadsides and sand mines can be regarded as important bee habitats, considering the high number of species found with only one sampling method.

While both reclaimed sand mines and roadsides support diverse bee communities, those communities in reclaimed sand mines were largest and most diverse, confirming our hypothesis. This difference is likely explained by differences in percentage of vegetational ground cover between the two habitats. The percentage of vegetational ground cover generally predicted species richness, bee abundance, and Shannon diversity better than habitat type per se, and was lower in sand mines than at roadsides. This negative correlation between vegetational ground cover and bee presence supports our rationale of increased nesting opportunities. The importance of bare (sandy) soil was further supported by the slightly larger proportion of ground nesters found in the reclaimed sand mines. It seems like many bees used the vegetation free patches for nesting. Notably, we observed numerous nesting holes on flat and vertical soil structures in the sand mines and barely any signs of nesting at the roadsides. Availability of nesting substrates has been shown to influence bee abundances and bee community structures in another study (Potts et al. 2005). Soil texture, slope of the terrain and the availability of vertical soil structures are all considered important factors for nest site selection and thus suitable habitat for bees (Michener et al. 1958; Potts and Willmer 1997; Wuellner 1999). In these regards, sand mines seem to offer favorable conditions enabling abundant and species rich bee communities.

Globally, the majority of bee species are ground nesters whose fitness depends on the availability of patches of bare ground (Cane 1991; Michener 2007; Shepherd 2012). In fact, 70 – 75 % of bees are generally considered ground nesters (Department of Entomology at Cornell University 2018; Shepherd 2012; Westrich 1996; Wilson and Carril 2015), while Sardiñas and Kremen (2014) speculate based on Cane (1991) and Michener (2007) that an even larger proportion of bees are ground nesters. It also needs to be taken into account that nesting behavior is not known for all species. For example, for four species of this study nesting behavior is unknown. Creating or maintaining habitats suitable for ground nesting bees is therefore especially important. Moreover, the proportions of ground nesting individuals in this study were consistently higher across habitats than suggested above. Even roadsides, which are not particularly supportive of ground nesters, hosted more than 80 % of ground nesting bees. This illustrates that estimates of ground vs. wood nesters deserve further attention and possibly reevaluation both locally and globally.

At single species levels, both vegetational ground cover and habitat type significantly influenced bee abundance. The abundance of certain species was also affected by temperature or numbers of blooming flower species, indicating species specific habitat or climatic requirements. Bee activity typically increases with temperature which may be the reason for the higher abundances of *L. pilosum* at higher temperatures (Burrill and Dietz 1981; Heard and Hendrikz 1993; Szabo and Smith 1972). However, the optimal temperature windows for flight and foraging activity differ between species which may explain the lack of an overall effect of temperature on abundances or species richness in our study (Corbet et al. 1993; Kwon and Saeed 2003; Stone et al. 2003).

Floral richness can further affect bee abundances. Although many bee species become more abundant with increased floral diversity (Batáry et al. 2010; Ebeling et al. 2008; Sakagami and Fukuda 1973), other bee species can become less abundant with increased floral species diversity (Banaszak 1996; Fortel et al. 2014; Neame et al. 2012). In our study, abundance of *C. andreniformis* increased, while abundance of *L. coreopsis* decreased with increasing plant species richness. Generally, increased floral diversity results in increased foraging possibilities for bees, but requirements for plant community composition can differ between species as can activity periods. For example, *L. coreopsis* started its flight season earlier in the year than *C. andreniformis* when fewer plants were present. Although plant species diversity was lower in early seasons, the plant community composition was most likely more appropriate for *L. coreopsis* than community compositions later in the season, resulting in a negative relationship between floral diversity and the abundance of this species.

Reclaimed sand mines and roadsides also differed in the composition of their bee communities. Sand mines did not only host more bee species than roadsides, but were also associated with specific bee species. Some of those species were uncommon or rare for Maryland or typical for sandy areas. For example, four species (predominantly or exclusively) recorded at sand mines (i.e., *Agapostemon splendens*, *Lasioglossum vierecki*, *Perdita* *octomaculata* and *Perdita boltoniae*) were described by Droege et al. (2009) to be characteristic for and be regionally restricted to the so called micro-deserts of the Patuxent river, a natural sandy landscape in Maryland. *Agapostemon splendens* and *L. vierecki* were more abundant in sand mines, while the uncommon species *P. octomaculata* and the rare species *P. boltoniae*, both oligolectic bees, were only found once in sand mines. The overlap of the sand mine bee community with the micro-deserts of the Patuxent river further indicates that reclaimed sand mines can offer a bee habitat similar to some natural landscapes.

While the importance of floral resources for bees is well established (Banaszak 1996; Batáry et al. 2010; Baude et al. 2016), our study highlights the importance of nesting sites and resources. In fact, floral resources explained little of the variation in bee abundance or diversity, whereas the percentage of bare ground was a strong predictor for all parameters. We assume that the percentage of bare ground is correlated with nesting site availability, but we did not assess nesting site availability directly. Further research is necessary to verify this assumption and to better understand the relative effects of nesting and floral resources on limiting bee populations.

Our study agrees with previous studies which also found landscapes with early successional stages after disturbance to support diverse bee communities (Klemm 1996; Steffan-Dewenter and Tscharntke 2001). In fact, sand mines which have low quality soil may be particularly good bee habitat, because early successional stages persist for a much longer period than in other habitats (e.g., post fire or grazing). Our results further raise the question whether we should not rather allow spontaneous, natural succession instead of promoting reclamation activities in order to increase recolonization of native and often rare plants and to promote more specialized bee communities (Pietrzykowski 2008; Steffan-Dewenter and Tscharntke 2001). Alternatively, selecting specifically pollinator friendly plants instead of generic plant mixes in the reclamation process of sand mines could additionally promote bee communities.

In conclusion, we demonstrated that sand mines are a valuable bee habitat opening new perspectives for bee conservation. Conserving or creating bee habitats at times when natural landscapes are in decline becomes increasingly important (Carvell et al. 2017; Tonietto and Larkin 2018; Traveset et al. 2018). To date, bee conservation actions have focused on agricultural and urban contexts. Reclaimed sand mines which are relatively cheap to conserve, may offer an additional opportunity for bee conservation activities.

We still do not fully understand how to best create or sustain landscapes to protect bees and other pollinators. Nesting substrates are one of the key elements for promoting wild bees. Future studies should tackle the multitude of factors determining suitable nesting options for different species and how they affect bee community assemblage.

The value of native and non-native pollinator friendly plants for wild bees

Our study showed that a seed mix of non-native pollinator friendly flowers was well accepted by a diverse bee community. Depending on the season, non-native plants attracted either similar or higher numbers of individuals and species compared to native plants. Particularly during the early and late seasons, many bees favored non-native over native plants. Whereas, no differences were found during the middle of summer. For spring and early summer, native plants were still scarce which could have contributed to the lower attraction of these plots. During summer and fall though, the number of flowers was similar and would not explain differences of attraction found in the late season. Possibly non-native plants of those seasons offered higher quantities or qualities of pollen and nectar. Sometimes, another reason for a better fit of non-native plants for bees is seen in more ‘showy’ flowers compared to the less conspicuous native plants (Carvalheiro et al. 2014). However, our study targeted explicitly pollinator friendly plants and neither native nor non-native plants can be regarded more ‘showy’ than the other.

Previous studies on non-native plants have shown effects ranging from lower over similar to higher bee abundance or species richness compared to native plants, but none of these studies strictly focused on pollinator friendly plants, neither did they differentiate between seasons (Bartomeus et al. 2008; Chrobock et al. 2013; Lopezaraiza-Mikel et al. 2007; Matteson and Langellotto 2010; Menz et al. 2011; Morandin and Kremen 2013; Moroń et al. 2009; Nienhuis et al. 2009; Pardee and Philpott 2014; Vilà et al. 2009; Williams et al. 2011). Our study only supports findings of similar and higher attraction of non-native plants for bees. There was overall no evidence for lower attractiveness of non-native plants.

Besides differences in bee abundance and richness, native and not-native plant communities differed in the composition of bees they attracted. For example, honey bees (*Apis mellifera*) were more abundant on non-native plants, while another polylectic but native bee, *Xylocopa virginica*, was more abundant on native plants. This result supports previous findings showing that not all bee species respond equally to non-native plants (Pardee and Philpott 2014; Schweiger et al. 2010). Such species-specific preferences likely have multiple (potentially interacting) reasons, e.g., species-specific nutritional requirements (Leonhardt and Blüthgen 2012; Nicolson 2011; Somme et al. 2015; Vaudo et al. 2016), previous habitat experience (Harmon-Threatt and Kremen 2015; Vaudo et al. 2015), or competition between bee species (Somme et al. 2015; Wilms et al. 1996).

Not only the bee community composition, but also the structure of the plant-bee networks differed between the plant types. As expected, networks associated with native plants were more specialized than networks associated with non-native plants. Native plants share a longer history of interaction with native bees than non-native plants. The longer the time period of interacting partners in a shared environment, the more chances are there for the development of more specialized interactions which could explain the higher degree of specialization in interaction of native plants and bees (Fenster et al. 2004). Accordingly, other studies found that non-native plants are visited particularly by the most generalized insects (Lopezaraiza-Mikel et al. 2007; Memmott and Waser 2002; Schweiger et al. 2010; Stout and Morales 2009).

The disproportional benefit of non-native plants for generalist (or polylectic) bees over specialist (or oligolectic) bees is a common concern regarding the use of non-native plants (Bartomeus et al. 2008; Lopezaraiza-Mikel et al. 2007; Winfree et al. 2011). In our study, we overall recorded only two oligolectic bee species visiting flowers, preventing more robust inferences. However, although oligolectic bees clearly depend on their native host plants for pollen collection, they appear to readily accept non-native plants for nectar collection or as resting areas, as suggested by the occurrence of *Melissodes desponsus* males on non-native plants in our study.

Most bee species at both plant types were generalists. Although generalist bees typically feed on a broad range of floral resources, their foraging patterns can vary with the spectrum of plants available (Somme et al. 2015; Vaudo et al. 2016). Thus, their level of specialization can vary. Interestingly, three out of the five most abundant generalist species in our study showed more specialized foraging when feeding on native plants than when feeding on non-native plants. Although non-native networks often included slightly more plant species than native networks, this difference should not have influenced the degree of specialization as both d’ and H2’ are largely robust against variations of network size, shape and sampling intensity (Blüthgen et al. 2006). One reason for their more specialized foraging behavior on native plants could be overall stronger differences in plant nutritional profiles, where fewer plant species meet the nutritional requirements of bees and are therefore preferred. On the other hand, the foraging on fewer plant species could also mean an exceptionally good fit to the visiting generalist bee species where less additional resources from other plants are needed. Again, evolutionary processes may have played a role, where native bees developed a greater degree of specialization for certain native plant species over time.

Across both plant types, network specialization changed over the seasons. Specialization was highest in the early season and decreased towards the later seasons. Honey bees followed the same pattern at the species level specialization. The higher degree of network specialization coincided with a lower number of plant species in the networks in spring. A comparatively low number of plants in spring compared to other seasons is not uncommon for grasslands (Mallinger et al. 2016). However, as previously mentioned, neither d’ nor H2’ should be affected by the size or shape of the network matrix (Blüthgen et al. 2006). Thus, seasonal variations in network or species specialization cannot be explained by seasonal variations in flower availability. Possibly, nutritional profiles of spring plants differed more strongly than during later seasons accounting for the differences in the degrees of specialization. Kantsa et al. (2017) assessed plant pollinator networks in the Mediterranean and highlighted how network structure and species roles within networks change over the seasons. Therefore, they introduced the approach of multiple phenologically matched networks instead of static networks across the entire flowering period. While they observed an overall lower level of specialization of phenologically matched networks compared to static networks, they did not provide information on network specialization by season. We are lacking other studies on network and species specialization differentiated by season in order to detect of general tendencies.

The flowering periods of the plants changed from one year to the next. In the second field year, many plants started flowering earlier and additionally had prolonged flowering periods. These changes are likely related to the early stage of the small scale meadow establishment. Lee-Mäder et al. (2013) indicate that regular flowering of (perennial) wildflower meadows usually begins in the third year. Nonetheless, flowers were not only generally scarce in spring, but for the first five weeks of the season, exclusively non-native plants were flowering, rendering them valuable resources for the local bee community when native plants were still completely absent. Likewise, Mallinger et al. (2016) pointed out that floral resources in natural grasslands are often scarce in spring and bees rely on additional floral resources, e.g., of nearby woodlands or anthropogenically managed habitats. Woodlands are often not available in direct proximity of pollinator friendly meadows. Therefore, non-native plants can be an easier measure to provide the needed additional resources at this critical time.

Our study suggests that non-native plants can complement native pollinator friendly plantings. A broad range of bees feed on them and they can buffer gaps in native plant flowering, e.g., in early spring. However, non-native plants can apparently alter the composition as well as individual and network specialization of bee communities with unknown consequences for plants and bees. Besides, specialist bees may be more likely to be lost when only non-native plants are planted, suggesting that non-native plants should be used complementary to native pollinator friendly plantings and with caution, e.g., non-invasive plant species should be preferred. Furthermore, our results highlight the importance of analyzing entire flowering periods instead of a focus solely on summer and taking into account phenological matching for network analyses. Moreover, we recommend to conduct more research that experimentally compares native vs. non-native pollinator friendly plant mixes to tailor pollinator friendly plantings to abundant and structurally diverse bee communities. Studies in other regions of the world, at different scales and with other plant species could deepen our knowledge further on the benefits and risks of non-native pollinator friendly plantings in order to globally improve conservation strategies for bees.

General conclusions for bee conservation

Both managed honey bees and the multitude of wild bees are currently facing difficulties in survival (Biesmeijer et al. 2006; Brodschneider et al. 2018; Koh et al. 2016; Ollerton 2017; Potts et al. 2010a; Requier et al. 2018). The honey bee colony losses that we documented between 2014 and 2015 in the US underscore these worldwide observed struggles. There are various reasons for high mortality rates of honey bees and declines of wild bee populations which are partly overlapping. For honey bees, parasites and diseases are at the forefront of problems (Steinhauer et al. 2018; Vanbergen and Initiative 2013). While parasites and diseases have been important causes of honey bee mortality for a long time, their relevance grew further over the past years with e.g., a surge in *Varroa* mite infestations and an escalation of virus prevalence (Genersch 2010; Traynor et al. 2016). This trend may also explain the recent approximation of summer losses with winter losses that we documented along with Lee et al. (2015) and Kulhanek et al. (2017) for the prior and subsequent year, because pests and diseases exert year-round pressures on honey bees. So far, diseases are primarily considered a threat for managed bees (Vanbergen and Initiative 2013). However, the diseases of managed bees are transmitted to wild bees and may cause wild bee population declines with increasing frequency, especially as wild bees, unlike managed bees, do not receive treatments against diseases (Furst et al. 2014; Gisder and Genersch 2016; McMahon et al. 2015). Therefore, honey bee health is of equal importance to wild bees. Further intensification of honey bee keeping may raise disease prevalence for honey bees and consequently for wild bees in the future, but will strongly depend on honey bee management practices and disease control by beekeepers (Gisder and Genersch 2016; Jacques et al. 2017; Traynor et al. 2016).

Sublethal effects of pesticides are a shared threat to all bees, managed, unmanaged, social or solitary. Pesticides can e.g., impair foraging, learning or homing behavior of bees (Blacquière et al. 2012; Henry et al. 2012; Sandrock et al. 2014). They can also weaken immune responses of bees and make them more susceptible to diseases or pest infestations (Dively et al. 2015; Tsvetkov et al. 2017). Furthermore, they can reduce reproduction, overwintering success or overall density of wild bees (Rundlof et al. 2015; Woodcock et al. 2017). Sublethal effects of pesticides are not always straight forward, but their negative effects need to be taken into account for bee conservation (Kerr 2017). In general, bees profit from reducing pesticide applications. Agricultural landscapes with organic or pesticide free farming host a higher diversity of bees than areas of conventional farming (Holzschuh et al. 2008).

For wild bees, habitat loss due to degradation of natural habitats and the linked reductions of floral resources and nesting sites are particularly harmful and are considered the key driver for their decline (Baude et al. 2016; Kennedy et al. 2013; Ollerton 2017; Vanbergen and Initiative 2013; Williams et al. 2010b). Therefore, habitat creation and habitat enhancements should be at the center of conservation efforts for wild bees. The research of my dissertation focused on these measures. I found reclaimed sand mines to be a valuable and previously underestimated bee habitat which can help to compensate for habitat loss. Future studies should explore further options for bee habitats outside the agricultural context in order to extent our opportunities for bee protection. In addition, we can improve anthropogenically impacted environments, such as e.g., reclaimed sand mines, with pollinator friendly plantings. Although pollinator friendly plantings are a common recommendation for bee habitat enhancement, more research is needed on the differential attraction and value of plant species for bees. As one step towards a better understanding of pollinator friendly plantings, my PhD studies indicated that non-native flowers can be useful additions to pollinator friendly plantings, but simultaneously revealed their potential to affect bee foraging patterns and alter plant-bee network structures.

The results of my work in the sand mines and with pollinator friendly plants can help to improve conservation strategies for wild bees. Moreover, we can expect a positive effect from wild bee habitat enhancements for honey bees too due to the link of honey bee health to nutrition (Brodschneider and Crailsheim 2010; Dolezal and Toth 2018). Diverse floral foraging resources increase honey bee fitness (Di Pasquale et al. 2016; Di Pasquale et al. 2013). Furthermore, landscapes with higher proportions of semi-natural areas are associated with decreased honey bee mortality (Kuchling et al. 2018). Therefore, structurally diverse landscapes offering nesting sites and adequate floral resources are not only of great importance for wild bees, but additionally offer crucial benefits for honey bees. Honey bee colony losses and wild bee declines are connected due to shared health threats. Similarly, their promotion is connected and can be achieved in accordance with each other. Ultimately, it is the diversity of bees that is most important to protect which secures the pollination of our crops, but also of our wild flowers, providing us with food and plant biodiversity (Ollerton 2017; Winfree 2010).

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Data Analysis and Interpretation	NSe	NSt	DvE	KT	KR, MW, JE, RR, DT, RS, DC, KD, JR, KL, KB, JW, JS, JP
Manuscript Writing			NSt, KR, MW, JE, RR, DT, RS, DC, KD, JR, KL, KB, JW, JS, JP		
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Writing of Discussion	NSe & KT	DvE			
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Doctoral Researcher's Name	Date	Place	Signature

Primary Supervisor's Name	Date	Place	Signature

Statement for published figures

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Figure	**Author Initials,** Responsibility decreasing from left to right				
1	NSe	NSt			
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4	NSe	NSt			
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Funding

The German Academic Exchange Service (DAAD) awarded me a PhD scholarship for my research stay at the University of Maryland and the University of Würzburg awarded me a SCIENTIA PhD scholarship. Additionally, my research was supported by the Explorers Club through the Exploration Fund Grant/Mamont Scholar program and by a grant of the Universitätsbund Würzburg. Furthermore, Ernst Conservation Seeds sponsored the seed mixes for the study on pollinator friendly plants.

Acknowledgements

The path of this PhD was rocky and I would not have been able to conquer it if I hadn’t had numerous people standing behind me.

I would like to thank my thesis committee, Thomas Schmitt, Alex Keller, and particularly my two advisors, Dennis vanEngelsdorp who invited me to be part of his group when I showed up at his lab with neither a plan nor funding and who enabled me to put my own research ideas into action, and Sara Leonhardt who has accompanied my PhD at every step with much support from nearby and far, who unceasingly believed I was capable of doing a PhD, who came up with solutions when I thought everything was lost, and whose feedback I value as truly constructive.

I am grateful for having had the opportunity to be part of two wonderful work groups in the US and in Germany who have provided very stimulating and pleasant work environments who have helped me to grow, who supported my work and who inspired me. Many thanks to my field assistants, Victor Settles and Lena Amano who traveled with me hundreds of miles and helped me collect bees in sand mines and who carefully washed and pinned countless numbers of bees. I am very thankful to Sam Droege for his contagious enthusiasm about native bees, for lots of advice on bee handling and research development, and for identifying thousands of bees for me. My gratitude further goes to Chaney Enterprises who allowed me to work on their property and kindly accommodated my research at the sand mines. I also greatly appreciate the help I received from Mark Fiely at Ernst Conservation Seeds for assistance in plant selection, plant handling and coordinating the sponsorship of Ernst Conservation Seeds.

I would also like to thank my entire family who’s love, support and caring helped me to get through this time, who got my back even at the most stressful, crazy times and who catch me each time I’m falling. Thank you, Jutta, Martin, Marlene, Oma Lorchen & Sabine Seitz und Mirko, Mattis & Mika Hoffmann!

Furthermore, I am immensely grateful to Carol A. Husain, an amazing psychological counselor, who has offered me professional guidance at the most difficult times of my life, who helped me to find balance, strength, and mindfulness within myself allowing me to be productive.

Lastly, I am lucky to have so many incredible, fabulous, loving human beings around me as my friends: Anna Kaitinnis, Ramune Pansa, Ruth Castillo, Inga Roesler, Theda Dourado, Mareike Rehl, Kathrin Flügel, Julia Hess, Marina Cascaes Cardoso, Silvia Alvarez, Carolina Diller, Eliezer Gurarie, Lindsey Reed, Scott Burdick, Lisa Kuder, Nathalie Steinhauer, Elske Tielens, Fabienne Maihoff, Birte Peters, Julia Maiershofer, Seth Langer, Jessica Reed, Saph McLean, Nina Mast, Gracie Baker & Dani Gilmour. Thank you for inspiring me, motivating me, listening to me in good and bad times, hugging me in hours of desperation, making me lunch or dinner, having coffee with me, going to the field with me despite of detesting any kind of living insect, helping me to produce very pretty, last minute figures for a poster, figuring out R code for me, doing a triathlon with me for distraction from stress, going dancing with me, truly believing in me, and telling me that I was strong when I didn’t feel it. Thank you for accompanying me on this rocky path!

Appendix

Table A1. Survey questions. The allowed entries are included below each question. A required response is indicated by a “*”.

1.	In what state(s) did you keep your colonies in between April 2014 - April 2015?* Multiple choice with multiple selections allowed of all US states, or "Other" category with open entry
2.	How many living colonies did you have last spring on April 1, 2014?* Numeric (integer) open entry
3.	How many colonies, splits, and/or increases did you make / buy between April 1, 2014 and October 1, 2014?* Numeric (integer) open entry
4.	How many colonies, splits, and/or increases did you sell or give away between April 1, 2014 and October 1, 2014?* Numeric (integer) open entry
5.	How many living colonies did you have on October 1, 2014?* Numeric (integer) open entry
6.	How many colonies, splits, and/or increases did you make / buy between October 1, 2014 and April 1, 2015?* Numeric (integer) open entry
7.	How many colonies, splits, and/or increases did you sell / give away between October 1, 2014 and April 1, 2015?* Numeric (integer) open entry
8.	How many total living colonies (overwinter surviving colonies plus purchase or splits) did you have on April 1, 2015?* Numeric (integer) open entry
9.	What was the largest number of living colonies you owned between April 1, 2014 and April 1, 2015? Numeric (integer) open entry
10.	What was the smallest number of living colonies you owned between April 1, 2014 and April 1, 2015? Numeric (integer) open entry
11.	You indicated you had ###### colonies alive on April 1, 2014. How many of those specific colonies were still alive on October 1, 2014? Numeric (integer) open entry
12.	You indicated you had ###### colonies alive on October 1, 2014. How many of those specific colonies were still alive on April 1, 2015? Numeric (integer) open entry
13.	What percentage of loss, over the winter, would you consider acceptable? Percentage with value between 0-100
14.	Was your winter loss this year higher or lower than last year? Single choice entry with the following possible choices: Higher, Lower, Same, Unsure, Did not keep bees last year

15.	What percentage of the colonies that died over the winter (between October 1, 2014 and April 1, 2015) were lost without dead bees in the hive or apiary?	Percentage with value between 0-100
16.	In your opinion, what factors were the most prominent cause (or causes) of colony death in your operation between October 1, 2014 and April 1, 2015?	Multiple choice with multiple selections allowed of the following answers: I did not experience any winter loss, Queen failure, Starvation, Varroa mites, Nosema disease, Small Hive Beetles, Poor wintering conditions, Pesticides, Weak in the fall, Colony Collapse Disorder (CCD), Don't know, Other (open entry)
17.	Did you move any of your colonies last year (between April 1, 2014 and April 1, 2015) at least once across state lines?*	Single choice of Yes or No
18.	In what zip or postal code is your operation based?	Numeric open entry
19.	What percentage of your hives did you send to or move into California almond orchards for pollination in 2014?	Percentage with value between 0-100
20.	Approximately what percentage of your operation moved across state lines at least once between April 1, 2014 and April 1, 2015?	Percentage with value between 0-100
21.	Please indicate in which states you kept bees for the months listed.	Multiple choice, with multiple selections allowed of the following: all states, all months
22.	On December 31, 2014, please list the number of colonies you had in each state.	Numeric entry only, 1 per state

Table A2. Overview of colonies by state for summer, winter & annually. For states with five or fewer respondents, losses are not reported, in order to guarantee the anonymity to the participants.

	Summer Loss				Winter Loss									Annual Loss		
	n (# of operations)	Total # of colonies (04/2014)	Total Loss [95 % CI]	Average Loss [95 % CI]	n (# of operations)	n Backyard	n Sideline	n Commercial	% BK exclusively in state	Total # of colonies (10/2014)	% colonies exclusively in state	Total Loss [95 % CI]	Average Loss [95 % CI]	n (# of operations)	Total Loss [95 % CI]	Average Loss [95 % CI]
US	4,971	370,063	25.3 [24.7 - 25.9]	14.7 [14.0 - 15.3]	5,937	5,690	169	78	N/A	414,267	N/A	22.3 [21.9 - 22.8]	43.7 [42.8 - 44.6]	4,775	40.6 [40.0 - 41.2]	49.0 [48.1 - 50.0]
STATE																
Alabama	29	308	21.2 [12.8 - 31.6]	16.6 [8.9 - 24.3]	31	30	1	0	96.8	354	97.2	34.7 [26.2 - 44]	29.7 [20.7 - 38.7]	28	48 [38.6 - 57.6]	40.6 [30.6 - 50.7]
Alaska	2	-	-	-	2	-	-	-	-	-	-	-	-	2	-	-
Arizona	9	424	12 [8.1 - 16.8]	7 [-2.3 - 16.3]	10	8	1	1	90.0	1,032	36.0	52.6 [43 - 62.1]	34.5 [11.4 - 57.7]	9	58.8 [48.6 - 68.6]	39.2 [12.6 - 65.7]
Arkansas	100	1,935	37.4 [33.4 - 41.5]	16.5 [11.5 - 21.4]	103	99	3	1	94.2	2,072	80.6	20.2 [16.2 - 24.5]	31.2 [24.9 - 37.5]	96	48.3 [45 - 51.6]	36.5 [30.5 - 42.6]
California	199	285,926	23.3 [21 - 25.7]	18.9 [15.6 - 22.1]	208	127	24	57	63.9	320,003	10.8	20 [18 - 22]	27.4 [23.6 - 31.1]	183	38.2 [35.5 - 40.9]	37.7 [33.6 - 41.9]
Colorado	190	44,693	25.7 [25.3 - 26.2]	17.8 [13.8 - 21.8]	214	211	2	1	97.7	63,126	1.6	16.8 [16 - 17.7]	48.1 [42.8 - 53.4]	178	38 [37.4 - 38.6]	52.6 [47.1 - 58.1]
Connecticut	56	334	9 [4.9 - 14.8]	13.8 [8.1 - 19.5]	71	68	3	0	94.4	701	59.5	49.2 [42.4 - 55.9]	55.4 [46.8 - 64]	56	57.3 [49.8 - 64.5]	56.7 [47.8 - 65.5]
District of Columbia	3	-	-	-	5	-	-	-	-	-	-	-	-	3	-	-
Delaware	16	18,291	46.6 [44.3 - 48.8]	17.8 [8.7 - 26.9]	20	17	1	2	70.0	18,426	0.3	40.5 [38.2 - 42.8]	36 [22.4 - 49.5]	16	61 [59.6 - 62.5]	48.1 [33.4 - 62.9]
Florida	100	35,732	37.1 [34 - 40.3]	20.8 [16 - 25.6]	111	89	16	6	87.4	27,403	8.3	35.8 [33.4 - 38.1]	24.8 [19.3 - 30.3]	93	55.3 [52.2 - 58.4]	36.4 [30.4 - 42.3]
Georgia	74	4,347	20.6 [16.7 - 24.9]	16.4 [11.7 - 21]	81	71	8	2	86.4	3,977	40.7	23.9 [19.7 - 28.5]	42 [34.3 - 49.7]	74	34.9 [30.4 - 39.6]	49.3 [41.7 - 57]
Hawaii	30	14,716	14.3 [10.6 - 18.6]	15.4 [7.3 - 23.5]	34	24	6	4	97.1	10,165	99.1	8.9 [4.7 - 14.9]	8.8 [4.2 - 13.5]	28	13.9 [8 - 21.6]	21.2 [13.3 - 29.1]
Idaho	55	84,225	14.9 [11.6 - 18.7]	13.4 [7.7 - 19.1]	62	48	1	13	77.4	74,921	0.3	15.6 [13.2 - 18.2]	30.1 [22.2 - 37.9]	48	27.7 [23 - 32.7]	38 [29.5 - 46.5]

	Summer Loss				Winter Loss									Annual Loss		
	n (# of operations)	Total # of colonies (04/2014)	Total Loss [95 % CI]	Average Loss [95 % CI]	n (# of operations)	n Backyard	n Sideline	n Commercial	% BK exclusively in state	Total # of colonies (10/2014)	% colonies exclusively in state	Total Loss [95 % CI]	Average Loss [95 % CI]	n (# of operations)	Total Loss [95 % CI]	Average Loss [95 % CI]
Illinois	105	756	26.6 [22.9 - 30.5]	16.5 [11.9 - 21.1]	137	136	1	0	97.8	1,133	76.0	51.9 [47 - 56.8]	57.7 [51.4 - 63.9]	102	62.4 [57.3 - 67.3]	60.1 [53.3 - 66.9]
Indiana	97	510	23.7 [18.4 - 29.7]	12.4 [8.2 - 16.6]	138	136	1	1	97.1	3,770	25.2	16.9 [13.4 - 20.7]	43.8 [37.9 - 49.8]	92	48.5 [43.2 - 53.8]	45.5 [39.1 - 51.9]
Iowa	36	569	29 [18.7 - 41]	11.9 [5.5 - 18.2]	47	43	4	0	93.6	947	68.7	47.4 [39 - 55.8]	53.1 [45.2 - 60.9]	36	61.4 [51 - 71.1]	59.2 [51.1 - 67.2]
Kansas	40	907	23.2 [18.9 - 27.9]	11.1 [5.7 - 16.5]	44	42	2	0	97.7	871	85.4	27.2 [20.9 - 34.3]	37.4 [26.9 - 47.9]	39	42.4 [35 - 49.9]	44.9 [33.8 - 56.1]
Kentucky	60	478	18.8 [13.4 - 25]	20.8 [13.7 - 27.9]	70	68	2	0	97.1	674	74.5	37.7 [31.7 - 44]	42 [33.7 - 50.4]	59	47.9 [41.7 - 54.1]	54.4 [46.5 - 62.4]
Louisiana	20	8,920	21.3 [19 - 23.7]	24.9 [11.3 - 38.5]	22	20	1	1	86.4	3,617	12.6	33.3 [30.5 - 36.1]	30.8 [19.6 - 42]	18	44.3 [40.6 - 48]	43.2 [31 - 55.5]
Maine	103	18,582	46.3 [45.2 - 47.4]	10.9 [7.2 - 14.6]	126	122	2	2	96.0	18,910	4.0	39.9 [38.9 - 40.8]	47.8 [41.2 - 54.4]	103	60.5 [59.7 - 61.4]	53.4 [46.9 - 59.8]
Maryland	132	9,767	44.5 [42.8 - 46.2]	15.7 [11.4 - 20.1]	158	153	4	1	93.7	10,577	8.6	41.4 [39.9 - 42.9]	46.6 [41.3 - 51.9]	126	60.9 [59.8 - 62]	52.8 [47.5 - 58.2]
Massachusetts	152	789	10.7 [8.2 - 13.7]	14 [10.6 - 17.4]	195	191	4	0	97.4	1,477	75.9	42.9 [38.2 - 47.7]	51.6 [46.3 - 56.9]	150	46.1 [40.8 - 51.5]	55.9 [50.4 - 61.4]
Michigan	216	8,078	12.8 [11 - 14.8]	15.3 [12.1 - 18.5]	284	274	9	1	98.2	9,594	90.2	24.4 [21.9 - 27.1]	48.7 [44.5 - 53]	210	31.8 [28.6 - 35.1]	53.9 [49.5 - 58.3]
Minnesota	85	76,031	38.5 [33 - 44.1]	20.2 [13.9 - 26.5]	109	96	5	8	85.3	77,361	0.9	19.4 [17.1 - 21.9]	59.5 [52.8 - 66.2]	77	50.6 [45.5 - 55.7]	63.4 [56.6 - 70.1]
Mississippi	13	12,766	44.3 [40.8 - 47.7]	34.9 [21.1 - 48.6]	12	9	1	2	83.3	6,123	5.3	19.9 [12.6 - 28.9]	29.3 [13.2 - 45.3]	11	38.7 [35.1 - 42.3]	45.2 [29.9 - 60.6]
Missouri	96	1,142	10.5 [8.2 - 13.3]	13.8 [9.8 - 17.8]	114	107	7	0	97.4	1,823	96.4	25.1 [20.8 - 29.9]	33 [27.3 - 38.7]	94	34.8 [30.1 - 39.7]	44.9 [39.1 - 50.8]
Montana	27	32,058	16 [11.4 - 21.6]	12.3 [6.1 - 18.5]	31	22	1	8	74.2	30,059	5.0	27.9 [20.3 - 36.4]	39.7 [27.5 - 51.9]	26	40.1 [30.4 - 50.3]	43.1 [30.3 - 56]

	Summer Loss				Winter Loss									Annual Loss		
	n (# of operations)	Total # of colonies (04/2014)	Total Loss [95 % CI]	Average Loss [95 % CI]	n (# of operations)	n Backyard	n Sideline	n Commercial	% BK exclusively in state	Total # of colonies (10/2014)	% colonies exclusively in state	Total Loss [95 % CI]	Average Loss [95 % CI]	n (# of operations)	Total Loss [95 % CI]	Average Loss [95 % CI]
Nebraska	12	52,112	24.2 [21.5 - 26.9]	26.3 [14.4 - 38.2]	15	13	0	2	80.0	72,610	0.1	17.3 [15.7 - 18.9]	52.5 [34.1 - 70.8]	12	37.3 [36 - 38.6]	52.4 [35.3 - 69.5]
Nevada	8	1,463	27.6 [21.1 - 34.7]	24.8 [6.8 - 42.8]	7	5	1	1	71.4	1,146	2.5	5.2 [0.1 - 29.3]	52 [21.1 - 82.8]	7	26.7 [18.1 - 36.7]	64.8 [41.8 - 87.8]
New Hampshire	43	206	7.9 [3.9 - 13.6]	12.9 [5.8 - 19.9]	59	57	2	0	94.9	651	65.9	36.3 [30.7 - 42.1]	50.9 [40.9 - 60.9]	42	39.4 [31.8 - 47.2]	56.6 [45.4 - 67.8]
New Jersey	93	475	14.3 [11.2 - 17.9]	8.7 [5.6 - 11.8]	112	108	4	0	94.6	1,295	80.5	36.5 [32 - 41.1]	37.4 [30.9 - 43.9]	93	48.2 [42.3 - 54.1]	41 [34.2 - 47.9]
New Mexico	21	1,586	5.6 [3.9 - 7.5]	7.7 [0.5 - 14.9]	24	23	0	1	95.8	1,926	6.5	42.9 [39.7 - 46.1]	30.6 [16.3 - 45]	21	46.1 [42.8 - 49.5]	35.1 [20.4 - 49.8]
New York	149	24,610	38 [35.1 - 41]	12.8 [9.3 - 16.4]	182	166	10	6	95.1	26,818	13.6	35.4 [33.8 - 37]	40 [35.1 - 44.9]	146	54.2 [51.6 - 56.8]	45.2 [40 - 50.4]
North Carolina	277	1,938	15.5 [13.1 - 18]	15.9 [13 - 18.7]	301	297	4	0	97.7	2,300	97.3	34.4 [31.3 - 37.7]	35.7 [32 - 39.5]	254	41.6 [38.3 - 45]	43.2 [39.4 - 47.1]
North Dakota	34	175,813	23.5 [18.5 - 29.1]	23.6 [16.1 - 31.1]	34	6	2	26	11.8	199,777	0.0	18.2 [15.1 - 21.6]	25.2 [17.6 - 32.8]	30	37.7 [32.6 - 43]	39 [31.5 - 46.5]
Ohio	275	1,940	20.2 [17.5 - 23.1]	12.4 [9.8 - 15.1]	345	337	8	0	98.0	3,387	86.1	50.1 [46.5 - 53.7]	49.4 [45.4 - 53.5]	270	59.1 [55.1 - 63.1]	51.8 [47.5 - 56.1]
Oklahoma	38	8,026	57 [54.2 - 59.7]	20.4 [12 - 28.8]	40	36	1	3	90.0	5,880	5.4	36.5 [32 - 41.2]	37.9 [27.9 - 48]	36	63.4 [61.3 - 65.5]	44.2 [34 - 54.3]
Oregon	152	38,020	14 [12.2 - 15.9]	12.9 [9.5 - 16.3]	177	169	1	7	94.9	38,036	33.9	14.7 [13.4 - 16]	28.9 [24.1 - 33.6]	142	25.2 [22.7 - 27.8]	36.6 [31.4 - 41.9]
Pennsylvania	693	22,075	42.2 [41.1 - 43.2]	13.2 [11.6 - 14.9]	860	841	17	2	98.3	24,766	24.5	42.6 [41.7 - 43.6]	53.2 [50.7 - 55.6]	674	61.1 [60.3 - 61.9]	58.4 [55.9 - 60.9]
Puerto Rico	0	-	-	-	0	-	-	-	-	-	-	-	-	0	-	-
Rhode Island	22	193	2.8 [0.5 - 7.9]	7.6 [1.6 - 13.6]	26	24	2	0	73.1	397	24.4	47.4 [36.5 - 58.4]	51.1 [35.9 - 66.3]	22	47.9 [36.6 - 59.3]	49.5 [35.3 - 63.8]
South Carolina	74	2,009	9.4 [6.2 - 13.5]	16.9 [11.4 - 22.4]	79	75	3	1	89.9	2,061	27.2	22.3 [18.6 - 26.3]	31.9 [25 - 38.8]	71	26.2 [22.1 - 30.6]	42.3 [35.1 - 49.5]
South Dakota	17	67,434	23.8 [19.1 - 29]	15.8 [6.4 - 25.2]	16	9	0	7	50.0	76,136	0.0	16.3 [12.5 - 20.7]	32.7 [18.1 - 47.2]	15	36.1 [31.6 - 40.8]	37.4 [21.9 - 52.9]

	Summer Loss				Winter Loss									Annual Loss		
	n (# of operations)	Total # of colonies (04/2014)	Total Loss [95 % CI]	Average Loss [95 % CI]	n (# of operations)	n Backyard	n Sideline	n Commercial	% BK exclusively in state	Total # of colonies (10/2014)	% colonies exclusively in state	Total Loss [95 % CI]	Average Loss [95 % CI]	n (# of operations)	Total Loss [95 % CI]	Average Loss [95 % CI]
Tennessee	78	1,045	21.7 [16.6 - 27.4]	16.3 [10.3 - 22.4]	82	76	6	0	96.3	1,223	90.2	21.9 [17.2 - 27.2]	39.3 [31.9 - 46.7]	73	36.3 [31.5 - 41.3]	46.3 [38.7 - 53.8]
Texas	152	114,435	32.8 [29.1 - 36.6]	13.6 [10.4 - 16.8]	157	139	3	15	87.3	109,746	2.6	20.9 [19.1 - 22.8]	21.3 [17 - 25.5]	139	46.3 [42.9 - 49.7]	29.6 [24.8 - 34.5]
Utah	45	13,875	19.9 [18.6 - 21.2]	17.7 [10.2 - 25.1]	47	40	3	4	85.1	16,677	1.3	17.3 [15 - 19.8]	43.5 [34.4 - 52.6]	41	33.6 [31.7 - 35.5]	49.5 [40.4 - 58.6]
Vermont	51	361	7.5 [4.8 - 10.9]	9.7 [4.5 - 14.9]	67	63	4	0	94.0	707	58.7	29.1 [24 - 34.6]	32.9 [24.2 - 41.7]	50	34.1 [27.9 - 40.6]	36.3 [26.7 - 45.8]
Virginia	614	2,923	15 [13.5 - 16.7]	15 [13.1 - 16.8]	722	709	13	0	98.8	5,365	98.8	36.3 [34.3 - 38.4]	42.9 [40.2 - 45.6]	590	46.1 [43.7 - 48.4]	48.2 [45.4 - 51]
Washington	131	86,530	24.7 [22.9 - 26.5]	13.2 [9.8 - 16.5]	158	145	3	10	93.0	107,980	1.0	20.4 [18.3 - 22.7]	45.6 [39.8 - 51.4]	128	39.3 [36.7 - 42]	52.2 [46.4 - 58]
West Virginia	50	474	7.1 [4.4 - 10.7]	13.8 [6.4 - 21.2]	54	52	2	0	87.0	829	46.8	56.2 [47.6 - 64.5]	35.1 [26.7 - 43.6]	47	60.9 [51.2 - 69.9]	39.2 [30 - 48.3]
Wisconsin	125	20,945	45.4 [43.9 - 46.9]	19.3 [15.2 - 23.5]	161	147	11	3	94.4	21,404	10.4	39.6 [38.3 - 41]	58.1 [52.4 - 63.7]	124	60.2 [58.8 - 61.5]	62.7 [56.9 - 68.6]
Wyoming	13	12,730	19.1 [16.5 - 21.8]	29.2 [13.1 - 45.4]	12	8	0	4	66.7	14,282	0.2	17.3 [8.8 - 28.8]	41.5 [21.8 - 61.2]	11	32.5 [23.9 - 42.1]	52.9 [36.5 - 69.3]

Table A3. Complete species list of sand mines and roadsides with information on nesting, (regional) conservation status, number of individuals (n) per habitat type (sand mines and roadsides) and year (2016 and 2017). Regional conservation status is based on Fowler (2016).

			Number of individuals (n)						
			Sand mines			**Roadsides**			**Total**
Species	**nesting**	**(regional) conservation status**	**2016**	**2017**	**total**	**2016**	**2017**	**total**	
Agapostemon	ground					1		1	1
Agapostemon sericeus	ground		3	2	5	9	9	18	23
Agapostemon splendens	ground		68	53	121	14	8	22	143
Agapostemon texanus	ground		14	3	17	11	2	13	30
Agapostemon virescens	ground		12	5	17	5		5	22
Andrena alleghaniensis	ground		1		1				1
Andrena arabis	ground	uncommon	1		1				1
Andrena asteris	ground			1	1				1
Andrena asteroides	ground	rare					1	1	1
Andrena barbara	ground		2	1	3		1	1	4
Andrena bisalicis	ground	uncommon	5		5				5
Andrena carlini	ground		5	1	6				6
Andrena commoda	ground		2		2	1		1	3
Andrena confederata	ground	uncommon		1	1				1
Andrena cressonii	ground		6		6	3		3	9
Andrena erigeniae	ground	common	1		1	12	1	13	14
Andrena illini	ground		1	1	2	2		2	4
Andrena imitatrix/ morrisonella	ground		4	3	7				7

			Number of individuals (n)						
			Sand mines			**Roadsides**			**Total**
Species	**nesting**	**(regional) conservation status**	**2016**	**2017**	**total**	**2016**	**2017**	**total**	
Andrena macra	ground		1		1				1
Andrena miserabilis	ground		2		2	3	3	6	8
Andrena nasonii	ground		5	2	7	3	6	9	16
Andrena perplexa	ground		1	3	4		1	1	5
Andrena species	ground					1		1	1
Andrena trachandrena	ground						2	2	2
Andrena vicina	ground			1	1		1	1	2
Andrena violae	ground					1		1	1
Apis mellifera	hive		5	16	21	1	11	12	33
Augochlora pura	wood		6	2	8	4		4	12
Augochlorella aurata	ground		46	29	75	28	17	45	120
Augochlorella near_gratiosa	ground		1		1	3		3	4
Augochloropsis metallica_fulgida	ground			1	1	1		1	2
Augochloropsis metallica_metallica	ground		3	5	8	1		1	9
Bombus bimaculatus	ground		1	1	2				2
Bombus citrinus	parasite [ground]		1		1				1
Bombus fervidus	ground	vulnerable (IUCN)		1	1	2		2	3
Bombus fervidus/ pensylvanicus	ground	vulnerable (IUCN)					1	1	1
Bombus griseocollis	ground		1	1	2				2
Bombus impatiens	ground		2	1	3	1	2	3	6

			Number of individuals (n)						
			Sand mines			Roadsides			Total
Species	**nesting**	**(regional) conservation status**	**2016**	**2017**	**total**	**2016**	**2017**	**total**	
Bombus pensylvanicus	ground	vulnerable (IUCN)		1	1	1	3	4	5
Calliopsis andreniformis	ground		23	66	89	15	98	113	202
Ceratina calcarata	wood		3	1	4	20	12	32	36
Ceratina dupla	wood		12	12	24	18	3	21	45
Ceratina mikmaqi	wood		1	3	4				4
Ceratina species	wood			1	1				1
Ceratina strenua	wood		1		1	42	18	60	61
Coelioxys immaculata	parasite [wood]		1	1	2				2
Coelioxys octodentata	parasite [wood& ground]						1	1	1
Coelioxys sayi	parasite [wood]		3		3				3
Colletes thoracicus	ground		1		1				1
Eucera hamata	ground		3	11	14	1	2	3	17
Eucera rosae	ground			4	4		1	1	5
Halictus confusus	ground		3		3	10	5	15	18
Halictus parallelus	ground			3	3	3		3	6
Halictus poeyi/ligatus	ground		14	62	76	71	99	170	246
Halictus producta	NA						1	1	1
Halictus rubicundus	ground		7		7				7
Heriades carinata	wood		1		1				1
Hoplitis pilosifrons	wood			2	2	4		4	6
Hoplitis producta	wood			1	1				1
Hoplitis spoliata	wood			1	1				1

			Number of individuals (n)						
			Sand mines			Roadsides			Total
Species	**nesting**	**(regional) conservation status**	**2016**	**2017**	**total**	**2016**	**2017**	**total**	
Hoplitis truncata	wood			1	1				1
Hylaeus affinis/ modestus	wood					4		4	4
Hylaeus modestus	wood					4		4	4
Lasioglossum	ground		79	53	132	15	12	27	159
Lasioglossum admirandum	ground		4	1	5				5
Lasioglossum birkmanni	ground					2		2	2
Lasioglossum bruneri	ground		30	49	79	4	4	8	87
Lasioglossum callidum	ground		11	21	32		8	8	40
Lasioglossum coreopsis	ground		70	189	259	4	6	10	269
Lasioglossum coriaceum	ground					5	1	6	6
Lasioglossum cressonii	wood		2	5	7	2	3	5	12
Lasioglossum ephialtum	ground			2	2				2
Lasioglossum floridanum	ground		13	3	16	23	6	29	45
Lasioglossum fuscipenne	ground		1		1	3		3	4
Lasioglossum gotham	ground		1	4	5				5
Lasioglossum hitchensi	ground		50	89	139	12	7	19	158

			Number of individuals (n)						
			Sand mines			**Roadsides**			**Total**
Species	**nesting**	**(regional) conservation status**	**2016**	**2017**	**total**	**2016**	**2017**	**total**	
Lasioglossum illinoense	ground		72	71	143	40	6	46	189
Lasioglossum imitatum	ground		28	92	120	3	5	8	128
Lasioglossum leucocomum	ground		18	13	31	3	3	6	37
Lasioglossum lionotum	parasite [ground]	uncommon		3	3		1	1	4
Lasioglossum lustrans	ground	rare	1		1		1	1	2
Lasioglossum nelumbonis	ground		2		2				2
Lasioglossum nymphaearum	ground/wood			1	1				1
Lasioglossum oblongum	wood		1	2	3	1	2	3	6
Lasioglossum pectorale	ground		15	7	22	25	7	32	54
Lasioglossum pilosum	ground		957	645	1602	75	61	136	1738
Lasioglossum platyparium	parasite [ground]		1	1	2	1		1	3
Lasioglossum smilacinae	ground		4	1	5				5
Lasioglossum subviridatum	wood			4	4				4
Lasioglossum tegulare	ground		109	166	275	62	75	137	412
Lasioglossum trigeminum	ground		20	60	80	3	13	16	96

			Number of individuals (n)						
			Sand mines			**Roadsides**			**Total**
Species	**nesting**	**(regional) conservation status**	**2016**	**2017**	**total**	**2016**	**2017**	**total**	
Lasioglossum versatum	ground		2	13	15	7	8	15	30
Lasioglossum vierecki	ground		7	26	33	8	20	28	61
Lasioglossum weemsi	ground			1	1		1	1	2
Lasioglossum zephyrum	ground		15	11	26				26
Megachile brevis	wood		14	33	47		2	2	49
Megachile mendica	ground		2	4	6				6
Megachile mucida	wood		1		1				1
Megachile pseudobrevis	wood		1		1				1
Megachile rotundata	wood		1	1	2				2
Megachile texana	ground		2		2				2
Melissodes	NA						1	1	1
Melissodes apicata	NA	rare					1	1	1
Melissodes bimaculatus	ground		14	23	37	24	31	55	92
Melissodes comptoides	ground		14	19	33	10	2	12	45
Melissodes desponsa	ground					1	1	2	2
Melissodes trinodis	ground		5	7	12	1	3	4	16
Melitoma taurea	ground	common	2	7	9	3	5	8	17
NA	NA		3		3	2	3	5	8
Nomada articulata	parasite [ground]		1	5	6	5	34	39	45

			Number of individuals (n)						
			Sand mines			**Roadsides**			**Total**
Species	**nesting**	**(regional) conservation status**	**2016**	**2017**	**total**	**2016**	**2017**	**total**	
Nomada australis	parasite [ground]			1	1	1	10	11	12
Nomada bidentate_group	parasite [ground]		3	1	4	2	3	5	9
Nomada denticulata	parasite [ground]		1		1	1		1	2
Nomada imbricata	parasite [ground]			1	1		2	2	3
Nomada luteoloides	parasite [ground]					1		1	1
Nomada maculata	parasite [ground]					5		5	5
Nomada pygmaea	parasite [ground]		2		2		1	1	3
Osmia atriventris	wood					3	2	5	5
Osmia bucephala	wood		1		1	1	1	2	3
Osmia collinsiae	wood		4		4	3		3	7
Osmia distincta	NA	uncommon	1		1				1
Osmia lignaria	wood		1		1	2		2	3
Osmia pumila	wood		6	3	9	13	3	16	25
Osmia taurus	wood					1	1	2	2
Peponapis pruinosa	ground		1	2	3	2	3	5	8
Perdita boltoniae	NA	rare		1	1				1
Perdita octomaculata	ground	uncommon	1		1				1
Ptilothrix bombiformis	ground	common	49	24	73	9	5	14	87
Sphecodes atlantis/cressonii	parasite [ground]			1	1		1	1	2

			Number of individuals (n)						
			Sand mines			**Roadsides**			**Total**
Species	**nesting**	**(regional) conservation status**	**2016**	**2017**	**total**	**2016**	**2017**	**total**	
Sphecodes coronus	parasite [ground]		1	2	3		1	1	4
Sphecodes illinoensis	parasite [ground]			2	2				2
Sphecodes pimpinellae	parasite [ground]					1		1	1
Sphecodes species	parasite [ground]		1		1				1
Svastra obliqua	ground		1	4	5		1	1	6
Triepeolus remigatus	parasite [ground]					1		1	1
Xylocopa virginica	wood			3	3				3

Table A4: Nesting behavior of the bees sampled in both habitats given as proportions of species and individuals. The nesting in hives is confined to honey bees.

	Ground	Ground/wood	Hive	Nesting unknown	Parasite [ground]	Parasite [wood]	Parasite [wood/ground]	Wood
Sand mine								
Species	63.16 %	0.88 %	0.88 %	1.75 %	11.40 %	1.75 %	0 %	20.18 %
Individuals	95.18 %	0.03 %	0.54 %	0.05 %	0.72 %	0.13 %	0 %	3.36 %
Roadside								
Species	63.16 %	0 %	1.05 %	3.16 %	14.74 %	0 %	1.05 %	16.84 %
Individuals	81.19 %	0 %	0.88 %	0.22 %	5.22 %	0 %	0.07 %	12.42 %

Table A5. Complete species list of bees sampled at the farmland with number of individuals (n) per sampling method (pan traps and hand netting) and plant type (native and non-native plants).

	Number of individuals (n)		
Species	**handnetting native plots**	**handnetting non-native plots**	**pan traps**
Agapostemon		1	
Agapostemon sericeus			1
Agapostemon splendens	3	18	29
Agapostemon texanus	3	7	118
Agapostemon virescens	5	5	42
Andrena (Trachandrena)		1	3
Andrena atlantica		2	
Andrena banksi			2
Andrena barbara			3
Andrena carlini			3
Andrena cressonii			1
Andrena erigeniae			1
Andrena imitatrix/morrisonella			1
Andrena macra			2
Andrena miserabilis			4
Andrena nasonii			16
Andrena perplexa		1	6
Andrena vicina			1
Andrena violae			2
Andrena wilkella		13	4
Anthidiellum notatum		4	2
Anthidium manicatum			2
Anthidium oblongatum			1
Apis mellifera	88	382	84
Augochlora pura	2	3	45
Augochlorella aurata	11	15	216

	Number of individuals (n)		
Species	**handnetting native plots**	**handnetting non-native plots**	**pan traps**
Augochloropsis metallica_fulgida	1	2	
Augochloropsis metallica_metallica	6	2	6
Bombus		4	
Bombus bimaculatus	8	22	8
Bombus citrinus	1	10	
Bombus fervidus			3
Bombus fervidus/pensylvanicus		2	6
Bombus griseocollis	3	5	2
Bombus impatiens	31	41	28
Bombus pensylvanicus		3	1
Calliopsis andreniformis	1	2	55
Ceratina		4	3
Ceratina calcarata	15	16	22
Ceratina dupla	1	1	4
Ceratina mikmaqi	1		6
Ceratina strenua	1	2	9
Coelioxys octodentata	1	1	1
Coelioxys sayi		1	
Eucera hamata			13
Halictus confusus	2	1	11
Halictus parallelus		4	1
Halictus poeyi/ligatus	173	254	198
Halictus rubicundus			4
Heriades carinata		1	
Hoplitis pilosifrons			2
Hoplitis producta			2
Hoplitis truncata	2		1
Hylaeus affinis/modestus	1	4	8
Hylaeus modestus		2	1

	Number of individuals (n)		
Species	**handnetting native plots**	**handnetting non-native plots**	**pan traps**
large green bee	6		
Lasioglossum	7	6	40
Lasioglossum abanci			2
Lasioglossum admirandum			7
Lasioglossum bruneri		2	26
Lasioglossum callidum	4	2	18
Lasioglossum coeruleum		1	
Lasioglossum coreopsis	10	11	39
Lasioglossum coriaceum	3		33
Lasioglossum cressonii		1	13
Lasioglossum ephialtum			6
Lasioglossum floridanum			14
Lasioglossum fuscipenne	3	1	1
Lasioglossum gotham			1
Lasioglossum hitchensi	8	7	53
Lasioglossum imitatum	1	1	
Lasioglossum leucocomum			2
Lasioglossum nelumbonis			1
Lasioglossum oblongum	1		5
Lasioglossum pectorale	1	1	3
Lasioglossum pilosum	19	19	232
Lasioglossum subviridatum	1	4	36
Lasioglossum tegulare	4	9	104
Lasioglossum trigeminum	11	2	82
Lasioglossum versatum	5	3	39
Lasioglossum vierecki	2	2	9
Lasioglossum weemsi		2	5
Megachile brevis		1	22
Megachile exilis	3	4	2

	Number of individuals (n)		
Species	**handnetting native plots**	**handnetting non-native plots**	**pan traps**
Megachile gemula			1
Megachile georgica	1		1
Megachile inimica	1	3	1
Megachile mendica	6	8	8
Megachile montivaga			1
Megachile petulans		1	
Megachile texana	1		
Melissodes	1		2
Melissodes bimaculatus		5	72
Melissodes comptoides			8
Melissodes denticulata			3
Melissodes desponsus		9	1
Melissodes subillatus	9		
Melissodes trinodis	2		1
Melitoma taurea			2
NA	3	3	11
Nomada			2
Nomada articulata		8	27
Nomada australis		4	36
Nomada bidentate_group			4
Nomada denticulata			3
Nomada imbricata			1
Nomada luteoloides			1
Nomada maculata			1
Nomada parva	1	1	2
Nomada pygmaea			4
Nomada texana	1		
Nomada vegana		2	
Osmia atriventris		2	8

	Number of individuals (n)		
Species	**handnetting native plots**	**handnetting non-native plots**	**pan traps**
Osmia bucephala			8
Osmia collinsiae			4
Osmia distincta	3		2
Osmia georgica		1	2
Osmia pumila		2	22
Osmia sandhouseae			1
Osmia subfasciata			3
Osmia taurus			1
Peponapis pruinosa			1
Pseudopanurgus near_labrosiformis			4
Ptilothrix bombiformis			1
small dark bee	9	4	
small green bee	2		
Sphecodes		2	1
Stelis louisae	1		1
Svastra obliqua		2	1
Triepeolus lunatus	1	1	2
Triepeolus remigatus			1
Xylocopa virginica	228	16	1

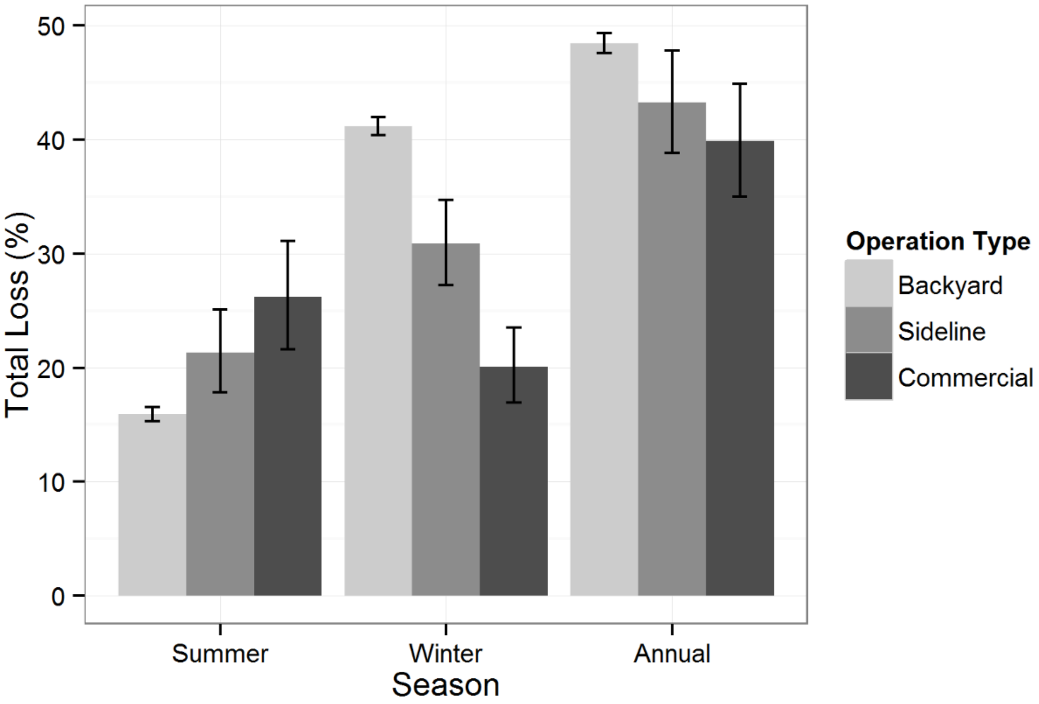

Fig A1. Operational differences in total colony loss by seasons. Bars represent 95 % CI.

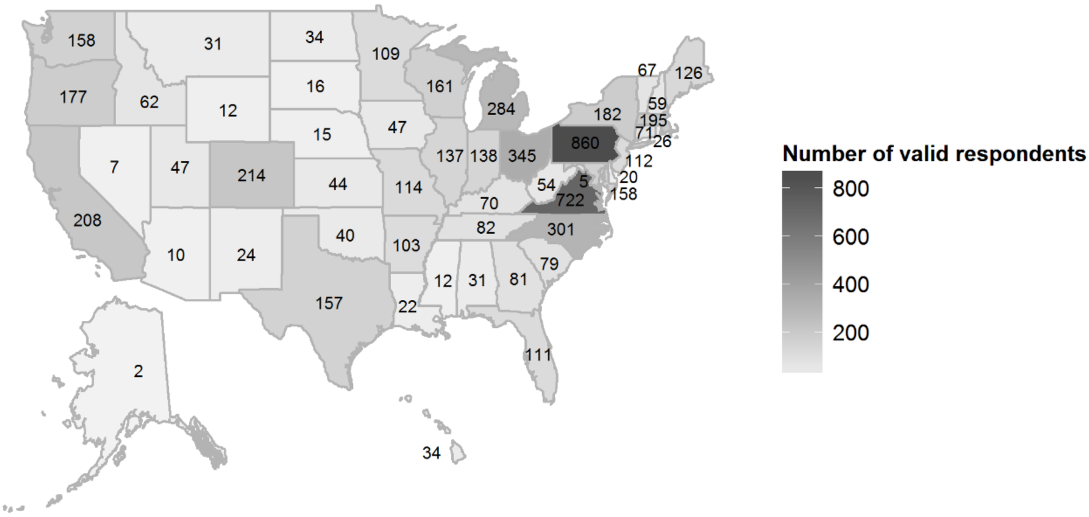

Fig A2. Valid responses by state for winter colony loss.

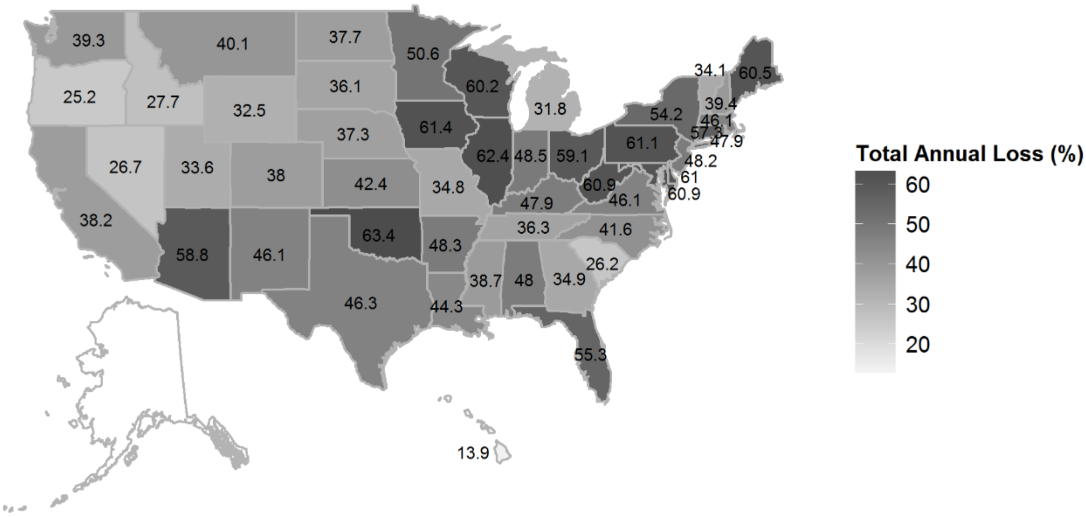

Fig. A3. Total colony loss annually by state.

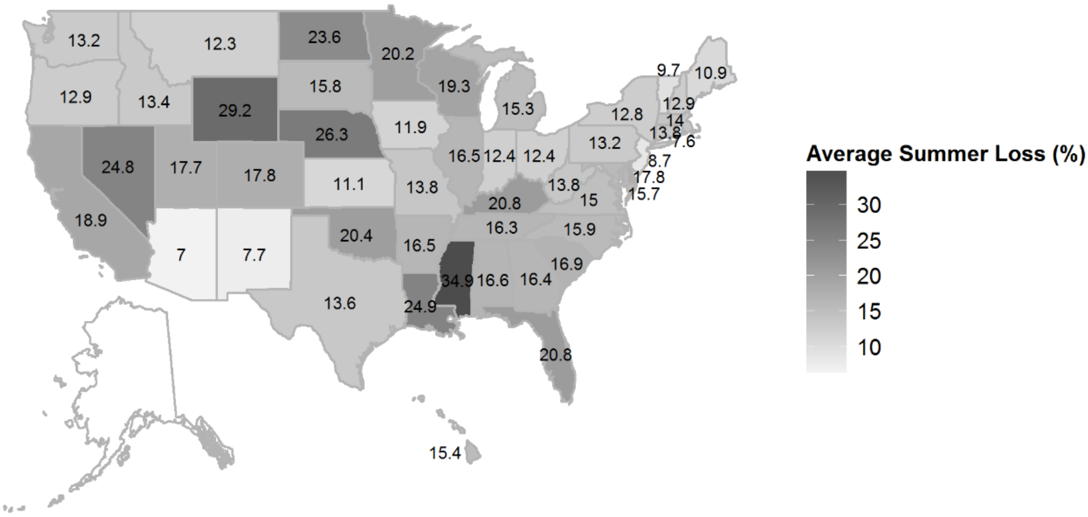

Fig. A4. Average colony loss in summer by state.

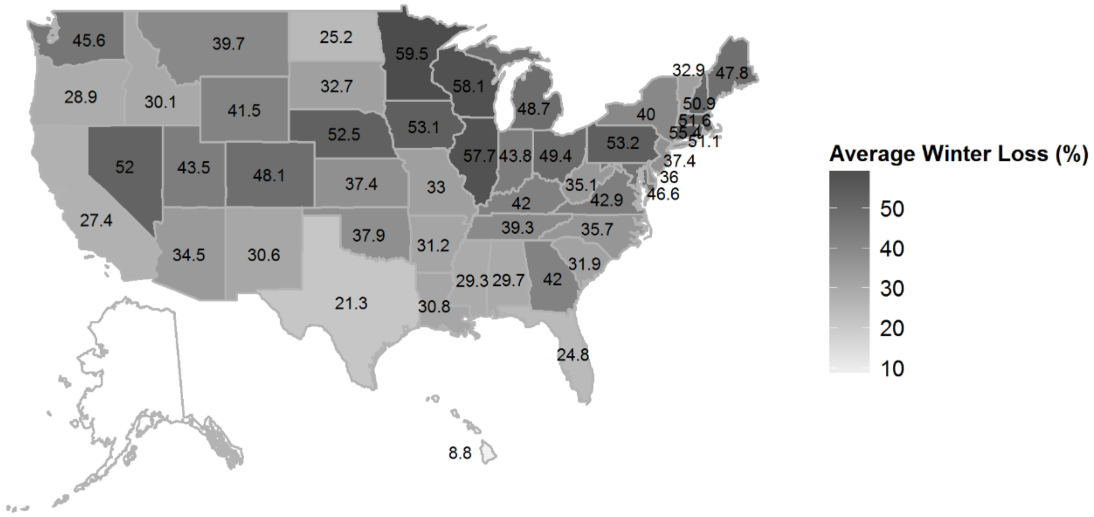

Fig. A5. Average colony loss in winter by state.

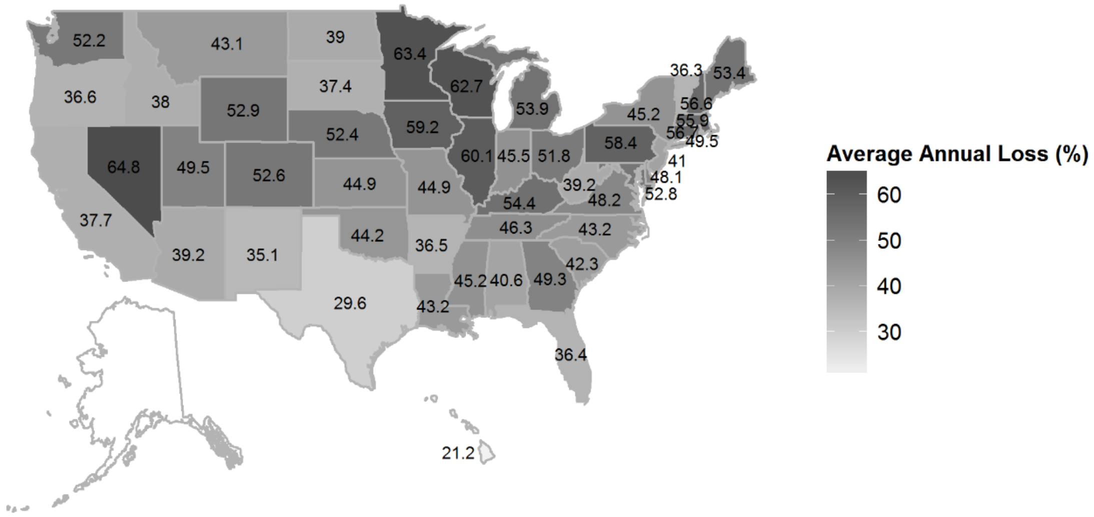

Fig. A6. Average colony loss annually by state.

Fig. A7. Number of individuals per species for sand mines (red) and roadsides (blue) in 2016, ordered by the most common species (top) to the least common species (bottom).

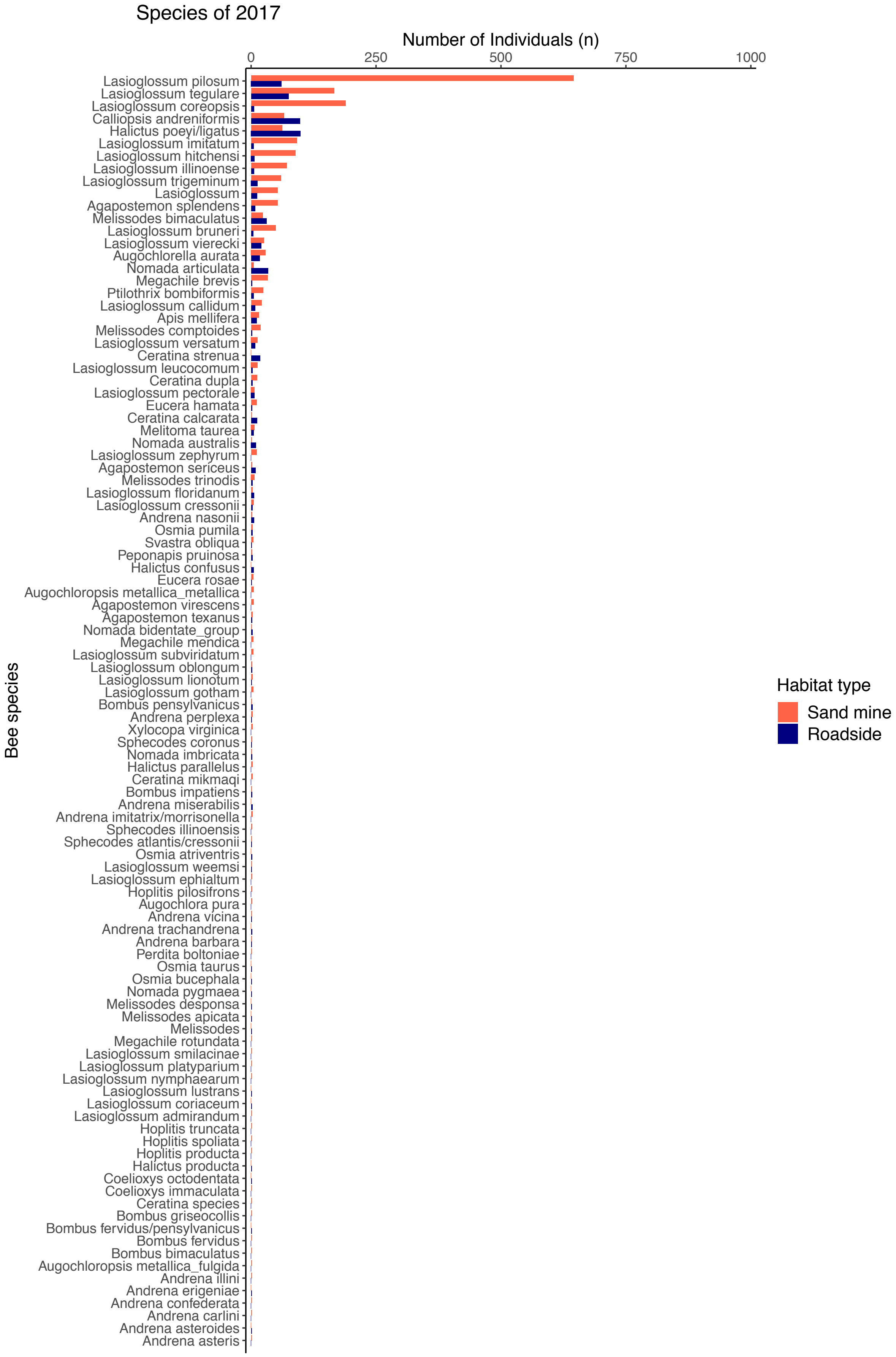

Fig. A8. Number of individuals per species for sand mines (red) and roadsides (blue) in 2017, ordered by the most common species (top) to the least common species (bottom).

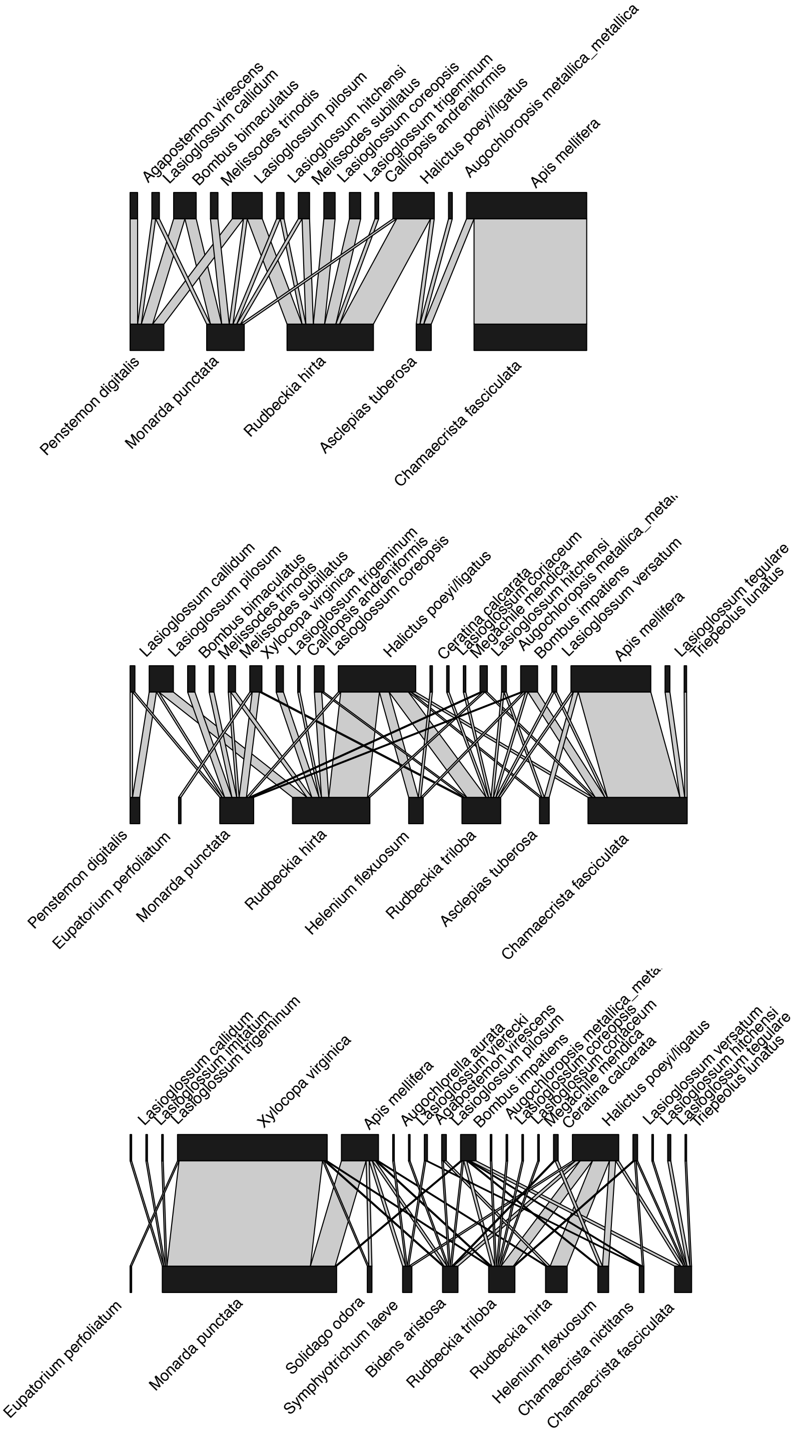

Fig. A9. Plant-bee networks at native plots of site A, (top) in spring/early summer (H2’ = 0.74); (middle) in summer (H2’ = 0.50); and (bottom) in late summer/fall (H2’ = 0.59). The H2’ value gives the degree of network specialization and ranges from 0 (no specialization) to 1 (highest specialization). Bee species are indicated by black bars in the upper network levels. Thickness of bars relates to the bee species’ abundance within the network. Plant species are indicated by black bars in the lower network levels. In the lower network level, thickness of bars relates to the number of visits a plant species received. Grey lines between the network levels show bee visitations to plants. Thickness of these connecting lines relates to the frequency of visits.

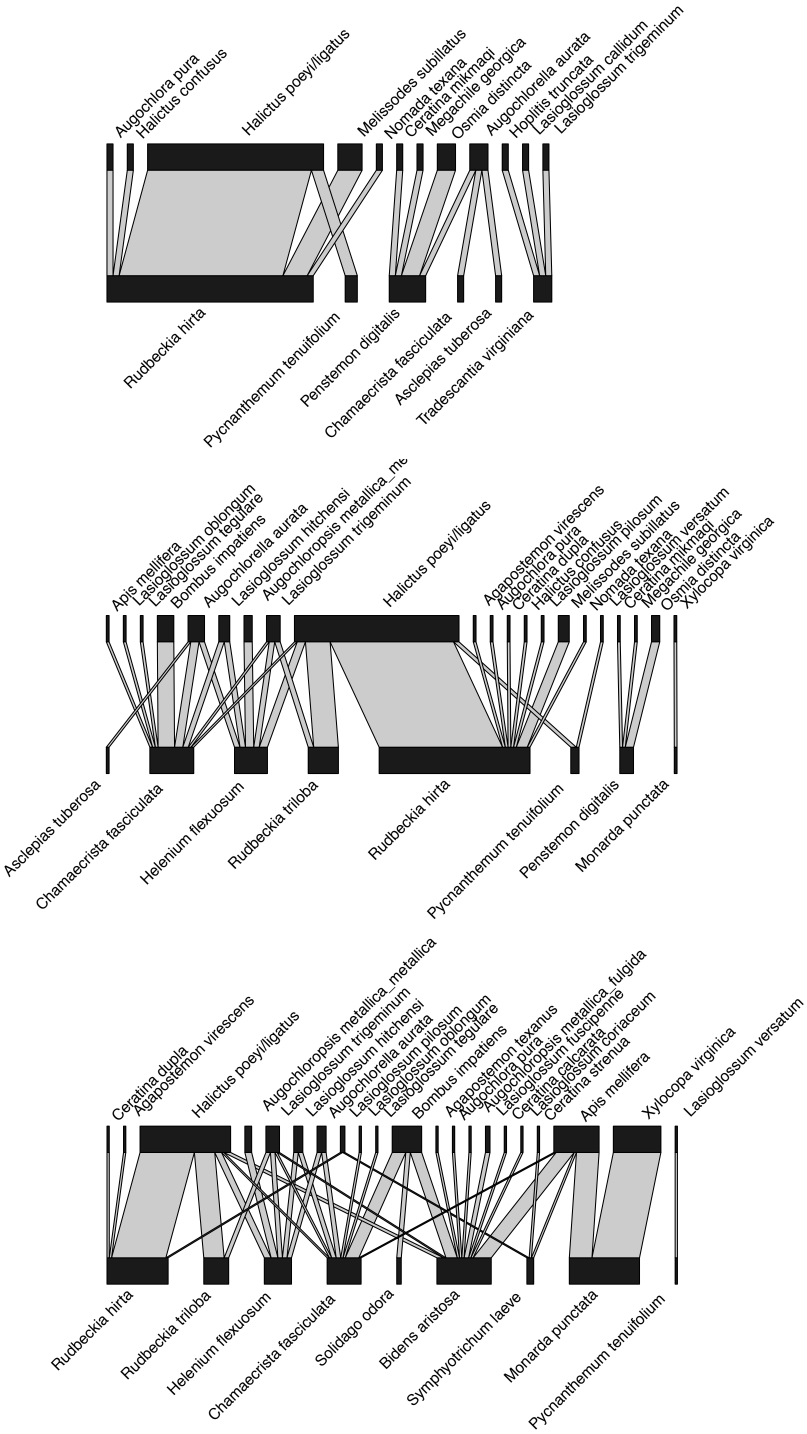

Fig. A10. Plant-bee networks at native plots of site B, (top) in spring/early summer (H2’ = 0.71); (middle) in summer (H2’ = 0.58); and (bottom) in late summer/fall (H2’ = 0.61). The H2’ value gives the degree of network specialization and ranges from 0 (no specialization) to 1 (highest specialization). Bee species are indicated by black bars in the upper network levels. Thickness of bars relates to the bee species’ abundance within the network. Plant species are indicated by black bars in the lower network levels. In the lower network level, thickness of bars relates to the number of visits a plant species received. Grey lines between the network levels show bee visitations to plants. Thickness of these connecting lines relates to the frequency of visits.

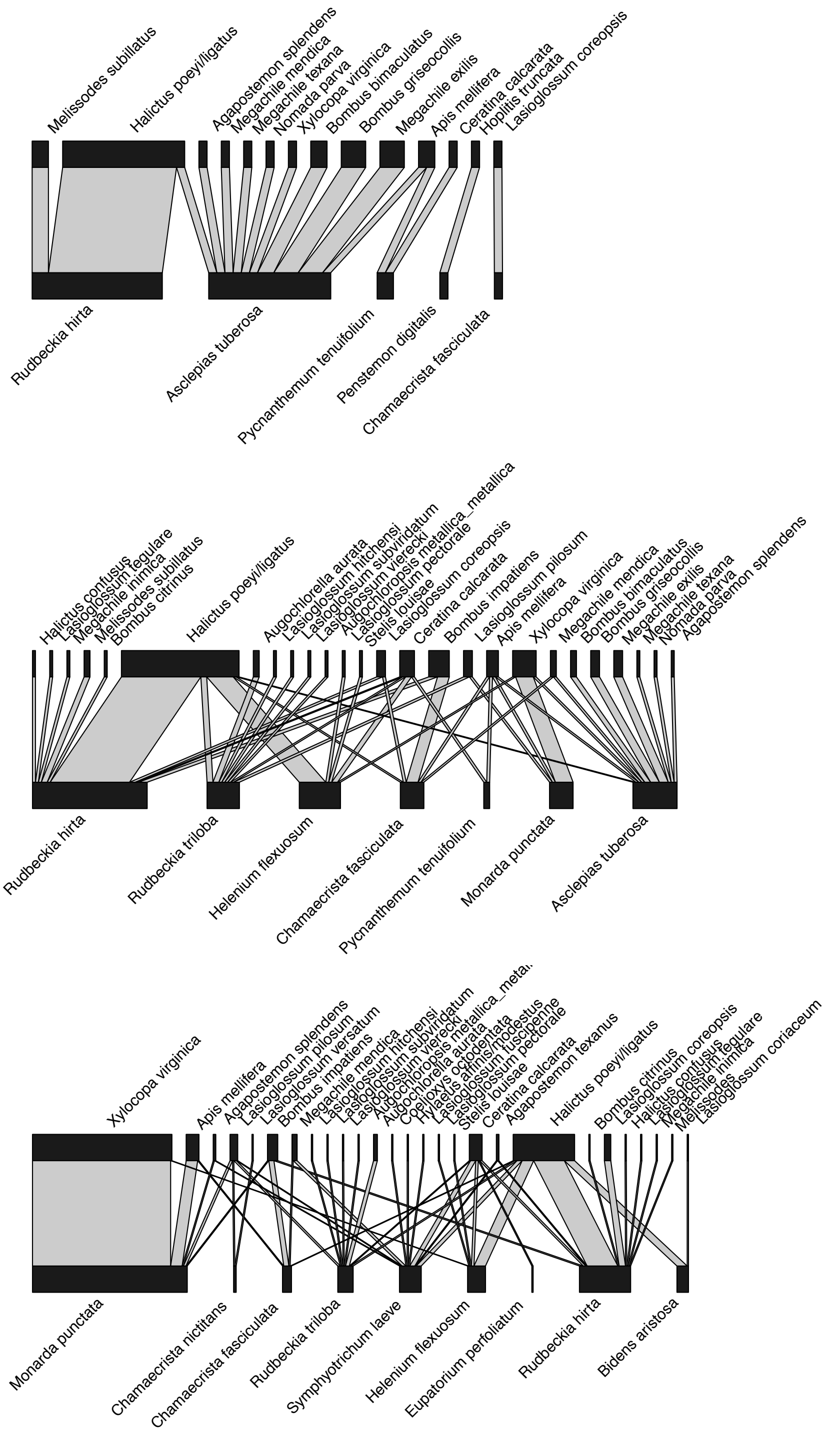

Fig. A11. Plant-bee networks at native plots of site C, (top) in spring/early summer (H2’ = 0.82); (middle) in summer (H2’ = 0.5); and (bottom) in late summer/fall (H2’ = 0.68). The H2’ value gives the degree of network specialization and ranges from 0 (no specialization) to 1 (highest specialization). Bee species are indicated by black bars in the upper network levels. Thickness of bars relates to the bee species’ abundance within the network. Plant species are indicated by black bars in the lower network levels. In the lower network level, thickness of bars relates to the number of visits a plant species received. Grey lines between the network levels show bee visitations to plants. Thickness of these connecting lines relates to the frequency of visits.

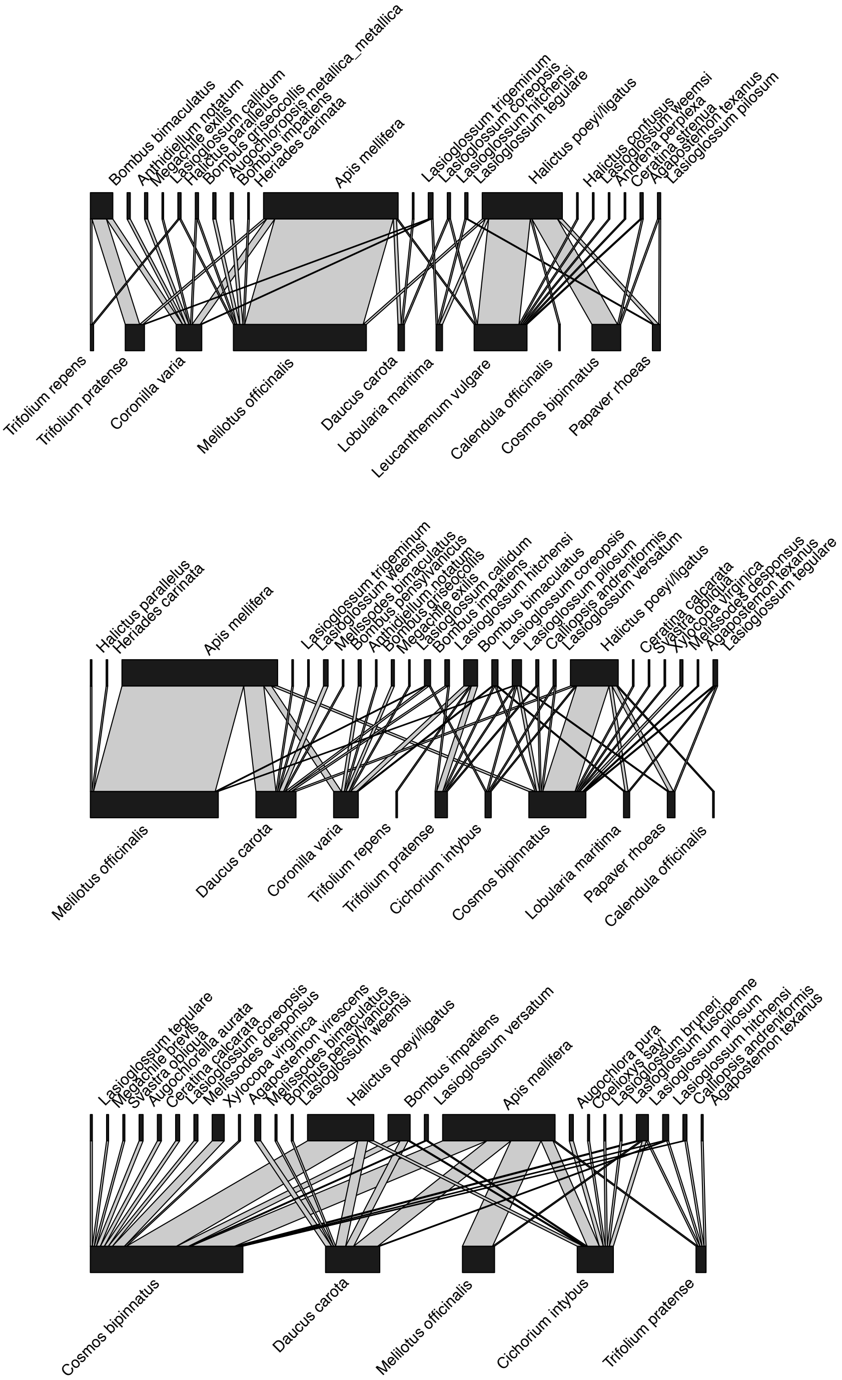

Fig. A12. Plant-bee networks at non-native plots of site A, (top) in spring/early summer (H2' = 0.61); (middle) in summer (H2' = 0.57); and (bottom) in late summer/fall (H2' = 0.27). The H2' value gives the degree of network specialization and ranges from 0 (no specialization) to 1 (highest specialization). Bee species are indicated by black bars in the upper network levels. Thickness of bars relates to the bee species' abundance within the network. Plant species are indicated by black bars in the lower network levels. In the lower network level, thickness of bars relates to the number of visits a plant species received. Grey lines between the network levels show bee visitations to plants. Thickness of these connecting lines relates to the frequency of visits.

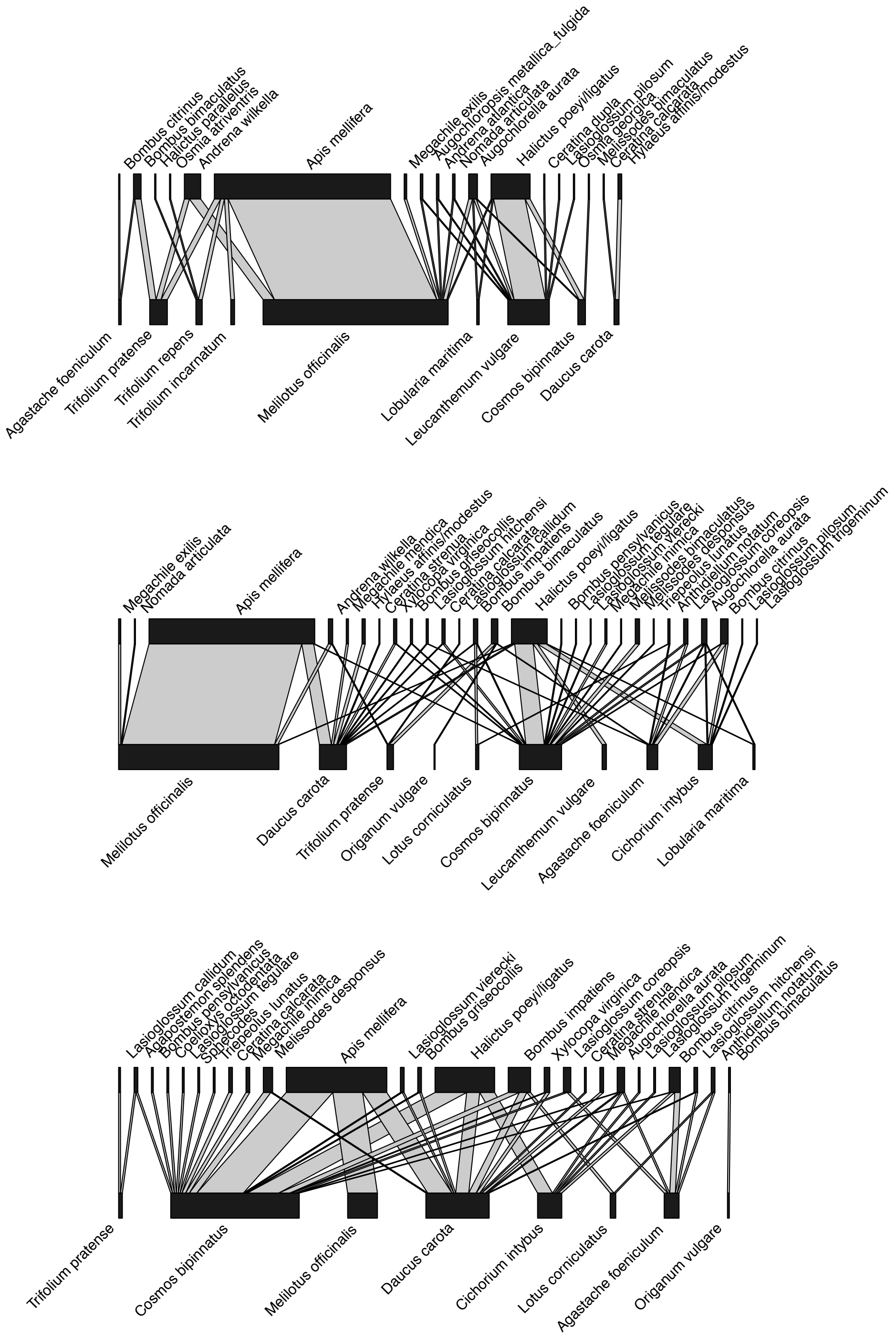

Fig. A13. Plant-bee networks at non-native plots of site B, (top) in spring/early summer (H2’ = 0.59); (middle) in summer (H2’ = 0.64); and (bottom) in late summer/fall (H2’ = 0.34). The H2’ value gives the degree of network specialization and ranges from 0 (no specialization) to 1 (highest specialization). Bee species are indicated by black bars in the upper network levels. Thickness of bars relates to the bee species’ abundance within the network. Plant species are indicated by black bars in the lower network levels. In the lower network level, thickness of bars relates to the number of visits a plant species received. Grey lines between the network levels show bee visitations to plants. Thickness of these connecting lines relates to the frequency of visits.

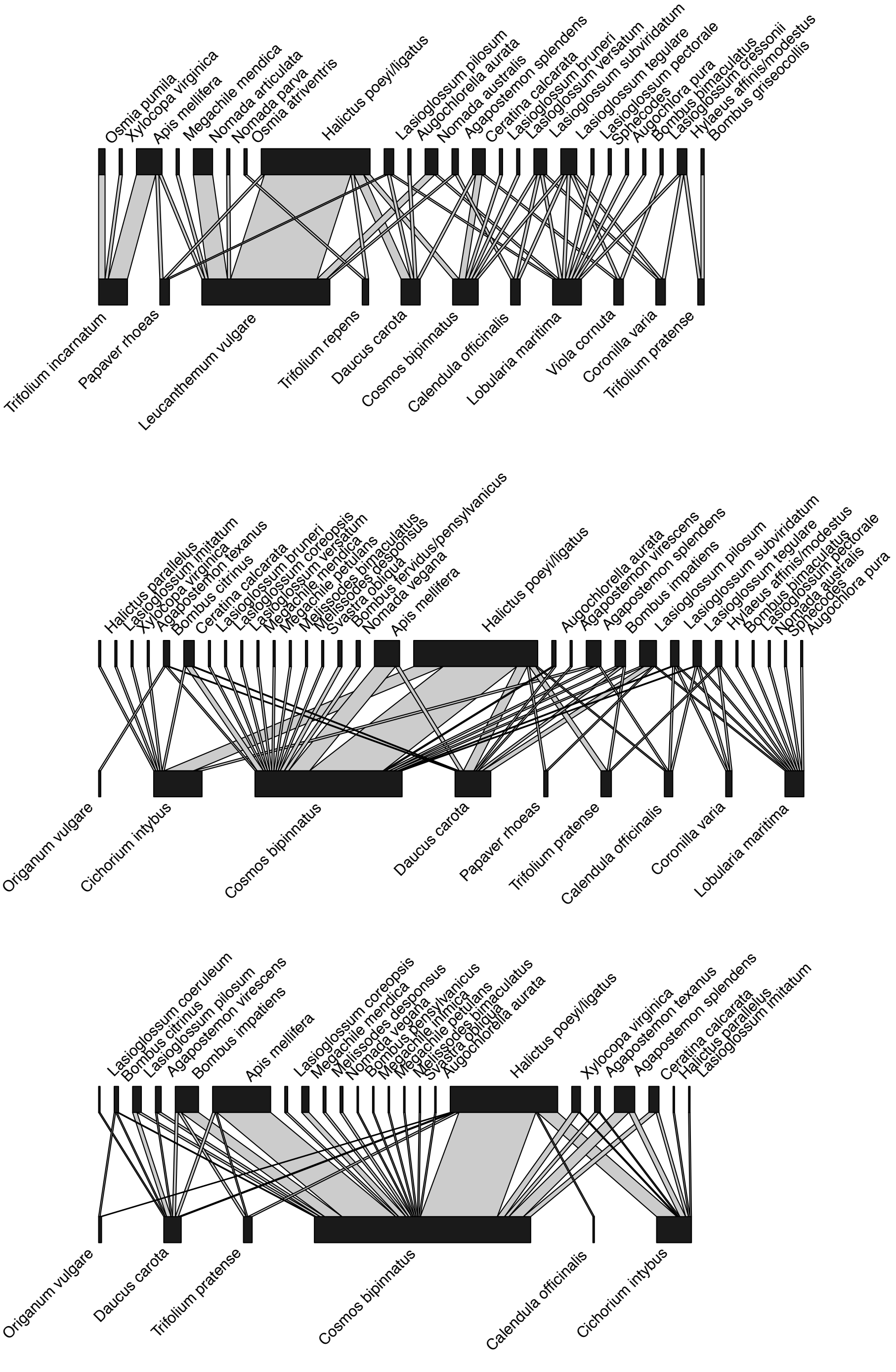

Fig. A14. Plant-bee networks at non-native plots of site C, (top) in spring/early summer (H2’ = 0.51); (middle) in summer (H2’ = 0.28); and (bottom) in late summer/fall (H2’ = 0.18). The H2’ value states network specialization and ranges from 0 (no specialization) to 1 (highest specialization). Bee species are indicated by black bars in the upper network levels. Thickness of bars relates to the bee species’ abundance within the network. Plant species are indicated by black bars in the lower network levels. In the lower network level, thickness of bars relates to the number of visits a plant species received. Grey lines between the network levels show bee visitations to plants. Thickness of these connecting lines relates to the frequency of visits.

Affidavit

I hereby confirm that my thesis entitled “Bee demise and bee rise: From honey bee colony losses to finding measures for advancing entire bee communities” is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

Furthermore, I confirm that this thesis has not yet been submitted as part of another examination process neither in identical nor in similar form.

Place, Date Signature

Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, die Dissertation „Bienenschwund und Bienenaufschwung: Von Honigbienen-Kolonieverlusten zur Förderung von gesamten Bienengemeinschaften“ eigenständig, d.h. insbesondere selbständig und ohne Hilfe eines kommerziellen Promotionsberaters, angefertigt und keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben.

Ich erkläre außerdem, dass die Dissertation weder in gleicher noch in ähnlicher Form bereits in einem anderen Prüfungsverfahren vorgelegen hat.

Ort, Datum Unterschrift