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Assessing the efficacy of bee promoting measures (Hymenoptera, Apiformes) along an urban-rural gradient

Beurteilung der Wirksamkeit von bienenfördernden Maßnahmen
(Hymenoptera, Apiformes) entlang eines Stadt-Land-Gradienten

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Abstract

Cities are emerging as refugia for pollinators, among which bees play a pivotal role for maintaining ecosystem functioning in agricultural and urban settings. While measures to promote bees have been investigated predominantly in the agricultural or rural context, a wide knowledge gap persists with regard to the effectiveness of such measures within urban landscapes. In order to guide research addressing this lack of knowledge, the aim of this perspective paper is to give an overview of the recent research activities based on the published peer-reviewed literature. While research on flower seed mixtures in general focuses on nutritional aspects, studies on plantings of perennial herbs are relatively limited to few plant taxa. Implementation of comparable case studies investigating the effects of tree plantings on bee populations is hampered by a lack of methodological standardization. The conservation value of providing nesting sites in cities needs to be further investigated, in particular concerning ground-nesting bee species. While several case studies indicate a nutritional supporting function of green roofs for urban bee populations, findings with regard to vertical isolation remain equivocal. Various factors driving bee diversity and population structure in the urban context at the local and landscape scale have been identified, the reported relevant landscape scale being represented by radii between 500 and 1000 m in most cases. Future study designs reflecting a continuous and complete gradient of urbanization will be helpful in comparing results on bee promoting measures in agricultural

landscapes (which are numerous) to urban settings (which are still encountered much less frequently). Studies looking into the genetic structure of bee populations with regard to urbanization so far represent only a tiny fraction of bee diversity, and the further development of molecular methods could yield novel tools for assessing the success of bee promoting measures in terms of habitat connectivity in the near future.

Key words: bees, Hymenoptera, conservation, measure, urban, rural, gradient

Zusammenfassung

Die Bedeutung von Städten als Refugien für Bestäuberinsekten zeichnet sich zunehmend ab. Bienen spielen eine wichtige Rolle in der Stabilisierung von Ökosystemen, sowohl im ruralen als auch im urbanen Kontext. Während bienenfördernde Maßnahmen vor allem im landwirtschaftlichen bzw. ruralen Kontext untersucht wurden, besteht eine große Wissenslücke in Bezug auf die Effektivität solcher Maßnahmen in urbanen Landschaften. Ziel dieses Übersichtsartikels ist es, einen Überblick über jüngere Forschungsaktivitäten basierend auf der im Peer-Review-Verfahren publizierten Literatur zu geben, um Empfehlungen für zukünftige Forschungsprojekte zum Schließen dieser Wissenslücke abzuleiten. Während Studien zu Saatgutmischungen hauptsächlich auf Ernährungsaspekte abzielen, sind Studien zu Staudenpflanzungen auf vergleichsweise wenige Pflanzen-

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taxa beschränkt. Die Durchführung vergleichbarer Studien zu Effekten von Baumpflanzungen auf Bienenpopulationen wird durch eine geringgradige Methodenstandardisierung erschwert. Der Naturschutzwert künstlicher Niststrukturen in Städten bedarf weiterer Erforschung, insbesondere im Hinblick auf bodennistende Bienenarten. Während mehrere Fallstudien auf eine Ernährungsfunktion von Gründächern für urbane Bienenpopulationen hindeuten, sind die Ergebnisse bezüglich der vertikalen Isolation von Gründächern nicht eindeutig. Zahlreiche Faktoren wurden identifiziert, die die Diversität und Populationsstruktur im urbanen Raum auf lokaler und Landschaftsebene beeinflussen. Der relevante Landschaftsmaßstab wird in den meisten Fällen durch Radien zwischen 500 und 1000 m repräsentiert. Zukünftige Studien, deren Versuchsaufbau einen kontinuierlichen und vollständigen Urbanisierungsgradienten berücksichtigt, werden von Nutzen sein, um die zahlreichen Ergebnisse zu bienenfördernden Maßnahmen in Agrarlandschaften mit den bislang wenigen Ergebnissen in urbanen Landschaften zu vergleichen. Studien, die die genetische Struktur von Bienenpopulationen im Hinblick auf Urbanisierung berücksichtigen, repräsentieren bislang nur einen sehr kleinen Ausschnitt der Bienenvielfalt. Die Weiterentwicklung molekularbiologischer Methoden könnte in naher Zukunft neuartige Werkzeuge zur Bewertung des Erfolgs bienenfördernder Maßnahmen im Hinblick auf die Habitatkonnektivität bereitstellen.

Stichwörter: Bienen, Hymenoptera, Schutzmaßnahmen, urban, rural, Gradient

Introduction

Cities emerge as refugia for pollinator diversity (TOMMASI et al., 2004; BALDOCK et al., 2015; SIROHI et al., 2015; HALL et al., 2017; SAMUELSON et al., 2018; but see CARDOSO und GONÇALVES, 2018, RAZO-LEÓN et al., 2018; COLLADO et al., 2019; FITCH et al., 2019b; HARRISON et al., 2019). Among pollinators, bees play a pivotal role and are therefore considered a keystone species group. Maintaining bee diversity is important for ecosystem functioning, not only in agricultural landscapes, but also in urban settings. Conservation of wild bee diversity in urbanized landscapes supports pollination services (MATTESON und LANGELLOTTO, 2009; LOWENSTEIN et al., 2015), which are positively related to urbanization at the landscape scale (THEODOROU et al., 2016). While measures to promote bees have been investigated predominantly in the agricultural or rural context, a wide knowledge gap persists with regard to the effectiveness of such measures within urban landscapes. This is likely to be a consequence of feasibility: better opportunities to replicate study sites within rural compared to urban landscapes (lower costs, larger pool of suitable sampling sites) have probably restricted experimental case studies to agricultural settings (e.g. BYRNE und DELBARCO-TRILLO, 2019), while case studies in cities or along an urbanization gradient have

been conducted as natural experiments lacking experimental habitat manipulation, e.g. using allotment/community gardens (MATTESON et al., 2008; AHRNÉ et al., 2009; VAIDYA et al., 2018), parks (McFREDERICK und LEBUHN, 2006; ZAJDEL et al., 2019), public green spaces and botanical gardens (BANASZAK-CIBICKA und ŽMIHORSKI, 2012; BANASZAK-CIBICKA et al., 2018a; BANASZAK-CIBICKA et al., 2018b), churchyards and cemeteries (BATES et al., 2011), urban agricultural sites (BENNETT und LOVELL, 2019), greenroofs (TONIETTO et al., 2011; HOFMANN und RENNER, 2018; FOURNIER et al., 2020), ornamental flowerbeds (GUNNARSSON und FEDERSEL, 2014), vacant lots and urban farms (SIVAKOFF et al., 2018), golf courses (THRELFALL et al., 2015) and wastelands (TWERD und BANASZAK-CIBICKA, 2019); but see BLACKMORE und GOULSON (2014), POTTER et al. (2019) and Fig. 1 for examples involving experimental manipulation. All types of vegetated urban habitat have a potential of improvement, in the sense of promoting bee populations and diversity, through adapted management or conversion. Bee promoting measures may benefit other pollinator and non-pollinator taxa and, depending on the measure, increase floral diversity within cities. While the social sciences and urban planning play an important role in assessing conservation measures, including bee promoting measures, within cities (e.g. VAN HEEZIK et al., 2012; BELLAMY et al., 2017; BURR et al., 2018; TURO und GARDINER, 2019), more ecological research is needed to guide urban planners in incorporating the needs of bees into their spatially explicit decision taking processes.

Bees need foraging and nesting habitats. They utilize ecological requisites by commuting between different partial habitats, which have to be situated within the commuting flight ranges (i.e. the distances of flights for nest-provisioning and not dispersal distances). Since landscape friction is an important factor underlying the accessibility of food resources for bees and wasps (JOHANSSON et al., 2018), connectivity between habitat patches has to be taken into account especially with regard to urban areas, where habitats tend to be highly fragmented. Habitat corridors can ameliorate potential negative effects of urban environments on pollinator communities (SENAPATHI et al., 2017). As cities gain importance as conservation areas for bee populations, the importance of connectivity between rural and urban populations increases for the maintenance of pollination services in agricultural crops. Acknowledging this agro-economic perspective, the creation of corridors between cities and the surrounding area has been put on the political agenda in Germany (BUNDESMINISTERIUM FÜR UMWELT, NATURSCHUTZ, BAU UND REAKTORSICHERHEIT, 2017).

The aim of this perspective paper is to give an overview of the recent research activities with regard to bee promoting measures in the urban context and to guide research on this topic in the near future towards successful study designs that help clarify so far unresolved issues. Focusing on temperate climates, we deliberately disregarded studies from the tropics.

Case study: Model project „Bee City of Braunschweig“

In 2018, the City of Braunschweig Department of Urban Greenery and Sports successfully applied for considerable funding regarding enhancement of urban biodiversity and climate mitigation from the German Federal Government and the German federal state of Lower Saxony. Together with funding from the city-owned resources, funding totals almost 6 million Euro.

A major part of this amount will be used for measures to promote the urban bee diversity. About 10 ha of species-rich meadows and 3.3 ha of perennial flower strips, species-rich mixed shrub plantings and extensive ruderal corridors will be created throughout the entire city. Moreover, 7000 m² of roof greening and 7500 m² of facade greening will be implemented. Six orchard meadows totalling 1.8 ha and 15 ha of short rotation plantations for biomass energy production will be created within city boundaries. 500 willow trees (*Salix* spp.) and 650 trees from other genera will be planted throughout the city.

The Institute for Bee Protection, Julius Kühn Institute, took the opportunity to utilize the comprehensive development of bee promoting measures by the city for addressing application-oriented research questions answering which is pivotal to guide successful implementation of such measures by urban planners. These questions regard, inter alia, the influence of local and landscape context on success of implemented measures and the exchange among bee populations along network corridors within the city as well as between the city and the surrounding agricultural landscapes. A further focus is set on adapted strategies targeting at the support of underrepresented bee taxa as well as ecological bee guilds dependent on specific habitat characteristics. After designing implementation measures according to the current state of knowledge, measures will be monitored over multiple years to evaluate their effectiveness for promoting urban bee populations and enhancing bee diversity. The findings are to be processed so that they can be transferred to other cities and municipalities.

An initial monitoring of the state and distribution of the bee diversity in the City of Braunschweig was started in 2019, covering more than 50 study sites spread over the entire city. Seeding of a standardized perennial seed mixture, developed by the Institute of Bee Protection primarily to suit the needs of bees (Table 1), and planting of bee-attractive herbs are planned to take place in 2020. The Institut für Bee Protection is continuously partnering up with various stakeholders in the region and at the national level in order to increase the pool of study sites, including areas in the agricultural landscapes surrounding the city, and to support the exchange of relevant information.

Fallbeispiel: Forschungsmodellprojekt „Bienenstadt Braunschweig“

Im Jahr 2018 bewarb sich das Amt für Stadtgrün und Sport der Stadt Braunschweig erfolgreich um beträchtliche Fördermittel des Bundes und des Landes Niedersachsen für die Erhöhung der städtischen Biodiversität und den Klimaschutz. Zusammen mit den Eigenmitteln der Stadt beläuft sich die Förderung auf fast 6 Millionen Euro.

Ein Großteil dieses Betrags wird für Maßnahmen zur Förderung der städtischen Bienenvielfalt verwendet. In der gesamten Stadt werden etwa 10 ha artenreiche Wiesen und 3,3 ha mehrjährige Blühflächen, artenreiche Staudenmischpflanzungen und ausgedehnte Ruderalkorridore angelegt. Darüber hinaus werden 7000 m² Dachbegrünung und 7500 m² Fassadenbegrünung realisiert. Innerhalb der Stadtgrenzen werden sechs Streuobstwiesen von insgesamt 1,8 ha und 15 ha Kurzumtriebsplantagen zur Energiegewinnung aus Biomasse angelegt. In der ganzen Stadt werden 500 Kopfweiden (*Salix* spp.) und 650 Bäume anderer Gattungen gepflanzt.

Das Institut für Bienenschutz, Julius Kühn-Institut, ergriff die Gelegenheit, umfassende bienenfördernde Maßnahmen in der Stadt für die Beantwortung anwendungsorientierter Forschungsfragen zu entwickeln, die für die erfolgreiche Umsetzung solcher Maßnahmen durch Stadtplaner von zentraler Bedeutung sind.

Diese Fragen betreffen u.a. den Einfluss des lokalen und landschaftlichen Kontextes auf den Erfolg der umgesetzten Maßnahmen und den Austausch zwischen den Bienenpopulationen entlang der Vernetzungskorridore innerhalb der Stadt sowie zwischen der Stadt und den umliegenden Agrarlandschaften. Ein weiterer Schwerpunkt liegt auf angepassten Strategien zur Förderung unterrepräsentierter Bientaxa sowie Bienengilden in Abhängigkeit von spezifischen Habitateigenschaften. Im Anschluss an die Konzeption von Umsetzungsmaßnahmen nach dem aktuellen Wissensstand werden die Maßnahmen über mehrere Jahre hinweg überwacht, um ihre Wirksamkeit zur Förderung städtischer Bienenpopulationen und zur Verbesserung der Bienenvielfalt zu bewerten. Die Erkenntnisse sollen so aufbereitet werden, dass sie auf andere Städte und Gemeinden übertragen werden können.

Ein erstes Monitoring des Zustands und der Verteilung der Bienenvielfalt in der Stadt Braunschweig wurde 2019 begonnen, welches mehr als 50 über die gesamte Stadt verteilte Untersuchungsstandorte umfasst. Die Aussaat einer standardisierten mehrjährigen Samenmischung, die vom Institut für Bienenschutz vor allem im Hinblick auf die Bedürfnisse der Bienen entwickelt wurde (Tabelle 1), und die Pflanzung von bienenfreundlichen Stauden sind für 2020 geplant. Das Institut für Bienenschutz sucht fortlaufend die Vernetzung mit weiteren Akteuren in der Region und auf nationaler Ebene, um den Umfang der Untersuchungsflächen, auch in den Agrarlandschaften der Umgebung der Stadt, zu erhöhen und den Austausch relevanter Informationen zu unterstützen.

Fig. 1. The Model project „Bee City of Braunschweig“, a case study involving bee promoting measures along an urban-rural gradient

Bee promoting measures

In addition to the presented bee promoting measures, adapted management of urban green spaces can develop resource poor areas into bee friendly habitats. Simple measures such as mowing less frequently increases the diversity and abundance of bees foraging in suburban lawns (LERMAN et al., 2018).

Flower seed mixtures

Creating foraging habitats for bees by seeding flower mixtures has been demonstrated as an effective way to promote wild bee populations in the agricultural landscape (e.g. HEARD et al., 2007; HAALAND et al., 2011; BLAAUW und ISAACS, 2014; FELTHAM et al., 2015; JÖNSSON et al., 2015; SCHEPER et al., 2015; WILLIAMS et al., 2015; BALZAN et al., 2016). Very often, effectiveness of a seed mixture is assessed from a purely botanical perspective, i.e. in terms of species richness and abundance of flowering species without taking effects on bee populations into consideration (e.g. LANE et al., 2019).

The vast number of seed mixtures is probably one reason for the high number of studies on this topic (at least in the agricultural context). In general, plant selection focuses on nutritional aspects (nectar and pollen supply; Table 1). Nectar and pollen quantity of plant species used in commercial seed mixtures varies widely, the tested perennial mixture producing more nectar and pollen than the tested annual mixture (HICKS et al., 2016). POTTER et al. (2019) used DNA-metabarcoding of pollen sampled by wild bees to assess the extent to which bees forage in wildflower strips sown in an urban environment and to identify key plant species for bee foraging. In an agricultural setting, WARZECHA et al. (2018) identified a fraction of plant species contained within four seed mixtures as key species crucial for the flower visiting bee community. Perennial seed mixtures are to be preferred over annual mixtures, in order to allow for a build up of bee populations over multiple years (but see CARVELL et al., 2006; RUNDLÖF et al., 2018). With regard to collection of leaf material used for nest construction, relevant bee species tend to prefer certain plant species over others (MACIVOR, 2016b). However, compared to floral food resources, this aspect has so far received little attention in the development of seed mixtures and other bee promoting measures. The same is true for potential provision of above-ground nesting sites, in case the vegetation is (at least in part) not manipulated (e.g. mowed) over two winter periods (Fig. 2).

Plantings of perennial herbs

Plantings of perennial herbs are a bee-promoting measure much less studied compared to flower seed mixtures, probably due to the much higher costs involved in the former. Economical feasibility might be a reason why plantings of herbs are rarely encountered in the agricultural context, where the limited half life of set-aside patches potentially reduces the financial investments. On the opposite, green spaces in cities are much more per-

sistent over time, and the exposure in public spaces probably justifies higher financial investments in such plantings, which citizens generally regard as environmental enrichment. Moreover, unlike seed mixtures, planters can be used for floral enrichment in areas with a high coverage of impermeable substrate. Compared to seed mixtures, plantings allow for a more flexible and target-oriented design of vegetation structure and configuration, thus enabling plant designers to better incorporate aesthetic needs and functional aspects within the urban context into the development of the urban green infrastructure. Studies delivering taxonomically detailed data on flower visitation of plant taxa suitable for planting focus on certain taxa, such as *Geranium* spp. (MASIEROWSKA et al., 2018) and *Lobularia maritima* (SIMAO et al., 2018), or aim at potential differences between native and exotic plant species (e.g. MATTESON und LANGELOTTO, 2011; SALISBURY et al., 2015). Even small patches with planted herbs can have a positive effect on bee communities in a city (SIMAO et al., 2018).

Tree plantings

Research on tree species and cultivars suitable for bee foraging is pivotal for urban bee conservation, since city planners, facing increasing problems of draught stress in city trees, and shifting towards novel tree taxa, lack solid data necessary to take bee foraging into account in their decisions. Few studies have investigated the effect of floral resources in trees on bee populations. While floral resources close to the ground (i.e. flower seed mixtures and plantings of herbs) are easily accessible and can be studied using long-established methods, floral resources in trees are much more difficult to access and the respective methodology is much less standardised. Classical approaches such as transect walks and observation plots are not applicable, and various trap types such as pan traps and flight interception traps need further methodological development in order to yield results that are comparable over multiple studies.

Depending on the species, trees and other flowering woody plants can be used for augmenting floral resources for bees in urban and suburban landscapes (MACH und POTTER, 2018). HAUSMANN et al. (2016) found 19% of the Berlin bee fauna foraging on city trees, with higher visitation rates to tree flowers by wild bees in surroundings with a higher proportion of green spaces. For common city-dwelling bees species, trees can be an important pollen source (MACIVOR et al., 2014). SOMME et al. (2016) investigated the suitability of widespread urban trees as resources for pollinating insects by analyzing the amount of nectar production as well as the chemical composition of nectar and pollen. In addition to floral resources, honeydew might be an alternative nutritional resource for wild bees offered by trees, at least for bumblebees (CAMERON et al., 2019). Willows are an important nutritional resource for bees early in the year. In this dioecious species, male trees support a greater abundance of bees, and species assemblages differ among willow pedigrees (TUMMINELLO et al., 2018).

Table 1. The seed mixture used in the project “Bee City of Braunschweig” (Fig. 1). The mixture consists of 47 annual and perennial plants. The table shows the total number of bee species (excluding *Apis mellifera* and *Bombus* spp.) collecting pollen from these plant taxa, as well as the number of oligolectic (collecting pollen from one or a few plant families) and narrow oligolectic bee species (collecting pollen from one or a few plant genera) collecting pollen from these plant species (data obtained from WESTRICH, 2018). Based on these data, more than 200 species could benefit from the plants included in the mixture.

Species	Family	Total number of bee species	Number of narrow oligolectic bee species	Number of oligolectic bee species
<i>Achillea millefolium</i>	Asteraceae	28	–	7
<i>Anthemis arvensis</i>	Asteraceae	6	–	4
<i>Anthemis tinctoria</i>	Asteraceae	7	–	6
<i>Anthriscus sylvestris</i>	Apiaceae	25	–	2
<i>Ballota nigra</i>	Lamiaceae	7	–	2
<i>Barbarea vulgaris</i>	Brassicaceae	13	–	5
<i>Betonica officinalis</i>	Lamiaceae	5	–	3
<i>Campanula rotundifolia</i>	Campanulaceae	28	10	–
<i>Campanula trachelium</i>	Campanulaceae	17	8	–
<i>Cardamine pratensis</i>	Brassicaceae	19	–	2
<i>Centaurea cyanus</i>	Asteraceae	8	–	–
<i>Centaurea jacea</i>	Asteraceae	39	–	7
<i>Centaurea scabiosa</i>	Asteraceae	31	–	7
<i>Cichorium intybus</i>	Asteraceae	38	–	10
<i>Crepis biennis</i>	Asteraceae	20	–	7
<i>Daucus carota</i>	Apiaceae	25	–	4
<i>Echium vulgare</i>	Boraginaceae	38	3	–
<i>Heracleum sphondylium</i>	Apiaceae	31	–	3
<i>Hippocrepis comosa</i>	Fabaceae	16	–	2
<i>Hypericum perforatum</i>	Clusiaceae	16	–	–
<i>Hypochaeris radicata</i>	Asteraceae	33	–	11
<i>Isatis tinctoria</i>	Brassicaceae	18	–	1
<i>Knautia arvensis</i>	Dipsacaceae	13	–	3
<i>Lathyrus pratensis</i>	Fabaceae	10	1	4
<i>Leontodon autumnalis</i>	Asteraceae	29	–	9
<i>Leucanthemum vulgare</i>	Asteraceae	22	–	2
<i>Matricaria recutita</i>	Asteraceae	5	–	1
<i>Medicago lupulina</i>	Fabaceae	1	–	–
<i>Melilotus albus</i>	Fabaceae	23	–	6
<i>Papaver rhoeas</i>	Papaveraceae	10	–	–
<i>Picris hieracioides</i>	Asteraceae	40	–	14
<i>Plantago media</i>	Plantaginaceae	7	–	–
<i>Ranunculus acris</i>	Ranunculaceae	43	1	–
<i>Ranunculus bulbosus</i>	Ranunculaceae	20	1	–
<i>Reseda lutea</i>	Resedaceae	10	1	–
<i>Reseda luteola</i>	Resedaceae	4	1	–
<i>Salvia pratensis</i>	Lamiaceae	20	–	–
<i>Scabiosa columbaria</i>	Dipsacaceae	7	–	3
<i>Sinapis arvensis</i>	Brassicaceae	66	–	6
<i>Stachys sylvatica</i>	Lamiaceae	4	–	1
<i>Tanacetum vulgare</i>	Asteraceae	21	–	7
<i>Teucrium scorodonia</i>	Lamiaceae	5	–	–
<i>Trifolium medium</i>	Fabaceae	3	–	2
<i>Trifolium pratense</i>	Fabaceae	28	–	7
<i>Verbascum lychnitis</i>	Scrophulariaceae	2	–	–
<i>Verbascum nigrum</i>	Scrophulariaceae	1	–	–



Fig. 2. Fall aspect of an uncut wildflower strip in Friedland (Lower Saxony, Germany). Vegetation remaining uncut over two winter periods can provide above-ground nesting opportunities for wild bees suitable for reproduction (Photo: André Krahner).

Nesting sites

In addition to nutritional resources, nesting sites (Fig. 3) have to be taken into consideration in urban bee conservation (FORTEL et al., 2016). In cities, bee composition can be biased toward cavity-nesting species, while soil-nesting species may occur less frequently due to soil limitation and/or disturbance (MATTESON et al., 2008). A number of case studies indicate a trend toward fewer ground-nesting bee species in urban habitats (HERNANDEZ et al., 2009). This may be due to extensive sealing of the soil within cities. For cavity-nesting species, an urban matrix can provide better nesting opportunities compared to the surrounding countryside in some situations (CANE et al., 2006). EVERAARS et al. (2011) observed effects of microsite conditions on the occurrence of

Osmia bicornis in an urban context. Distribution and density of suitable nesting sites play an important role in enhancing bee populations and connectivity among them in urban settings (LÓPEZ-URIBE et al., 2015). So-called ‘bee hotels’ (i.e. artificial nesting structures for above-ground nesting species) are successfully applied in the fields of environmental education and public outreach. However, their potential as measures for conserving bee species remains to be further elucidated (MACIVOR and PACKER, 2015).

Green roofs

Green roofs represent a special case of herb plantings and/or seeding in the city, since the plant species pool for this purpose is very limited. Nevertheless, city dwelling



Fig. 3. Urban nesting habitat for ground-nesting bees. Nesting habitat on urban green in Braunschweig (Lower Saxony, Germany; left), with an aggregation of *Andrena vaga* (right, female with *Salix* pollen load) in spring (Photos: André Krahner).

bees use green roofs as forage habitats, e.g. for collection of *Sedum* pollen (MACIVOR et al., 2015), and probably also as nesting sites, to some extent. Due to the microclimate on flat-topped buildings, thermophilic species are probably overrepresented in these habitats, while limited plant species numbers are likely to result in underrepresentation of pollen specialist bees on green roofs (HOFMANN und RENNER, 2018). At the local scale, plant and bee community composition of green roofs are correlated (TONIETTO et al., 2011). Findings with regard to potential vertical isolation, especially for small bee species, remain equivocal (HOFMANN und RENNER, 2018). KRATSCHEMER et al. (2018) observed higher wild bee diversity and abundance on green roofs with fine substrates and increasing forage availability, and conclude that areas with fine and deeper substrates would benefit eusocial and ground nesting bees. Proportion of green space in the surrounding area is positively correlated with overall bee abundance and species richness (TONIETTO et al., 2011) and species richness of cavity nesting bees and wasps (MACIVOR, 2016a), emphasizing the importance of connectivity between green roofs and the surrounding habitat.

Local and landscape factors driving bee diversity and population structure

Urban pollinator communities are influenced by both local and landscape-level factors (BALDOCK, 2020). Local factors such as flower density, number of plant species (BATES et al., 2011; FISCHER et al., 2016) and sun exposure (EVERAARS et al., 2011) can be driving the distribution of bee species. In cities, floral diversity locally increases bee species richness (HENNIG und GHAZOU, 2012; HAMBLIN et al., 2018). Increasing local temperatures reduce bee abundance in cities (HAMBLIN et al., 2018), although higher average temperatures within cities may provide better microclimatic conditions for the mostly thermo- and

xerophilic wild bee species compared to the surrounding rural landscape (Fig. 4). Local land use is an important factor driving bee species richness and abundance (but see DYLEWSKI et al., 2019), and higher bee species richness and abundance was observed on sites with a higher proportion of permeable substrate at the local scale along an urban-rural gradient (CHOATE et al., 2018). The importance of local factors is, however, likely to differ between bee species, depending on the commuting flight ranges and other life history traits. For example, FOSTER et al. (2017) did not find an effect of local land use on bumblebee species richness, and only marginal effects of land use on bumblebee abundance.

In addition to local factors, bee populations are influenced by landscape factors such as habitat configuration and connectivity, since bees generally use different partial habitats within the landscape. Therefore, mapping of land use within a study area on the landscape scale can help explain the distribution pattern of bee populations, in addition to local factors such as on-site floral richness and nesting opportunities. While classical mapping of landscape features on the ground is time consuming and resource intensive, landscape classification based on remote-sensing data is a feasible option to take landscape effects into consideration. These data are available for rural and urban landscapes at the same resolution, and can be further refined by additional data, e.g. higher-resolution data gathered for administrative purposes. SAMUELSON und LEADBEATER (2018) propose a landscape classification protocol targeted at ecological research on pollinators, providing a case study along an urban-rural gradient.

The EU CORINE Land Cover inventory (EUROPEAN UNION, COPERNICUS LAND MONITORING SERVICE, 2020a) offers a uniform classification of the most important types of ground cover. Some of these types are relevant for the distribution of bee populations, such as natural grasslands, forests, urban green spaces and surface water bodies. It is also possible to calculate the proportion of



Fig. 4. Xerotherm urban habitat. Sun exposed nesting habitat in Berlin-Dahlem (Germany; left), with multiple nest entrances of a halictid bee species (right) in spring (Photos: André Krahnert).

impervious substrate in a landscape from land use classification (FORTEL et al., 2014). More directly, the proportion of impervious substrate can be used as a proxy for urbanization. Following this approach, FITCH et al. (2019a) linked changes in the observed sex ratio in bee communities to urbanization, and SCHOCHET et al. (2016) found species specific effects of urbanization on the occurrence of different bumblebee species. Data on coverage of impervious substrate (Fig. 5) are readily available from the EU Copernicus program (EUROPEAN UNION, COPERNICUS LAND MONITORING SERVICE, 2020b).

In heterogeneous urban landscapes, land use exerts direct and indirect effects on floral resources and the flower-visiting insect fauna dominated by bees (MATTESON et al., 2013). Based on previous studies in urban settings, the most relevant landscape scale for bees is a radius of about 500–1000 m (but see PARDEE und PHILPOTT, 2014). FORTEL et al. (2014) found a significant effect of impervious substrate on bee abundance and species richness at radii of 500 and 1000 m, but not at a radius of 2000 m. A 500 m radius has been chosen as the relevant landscape scale for the analysis of plant-pollinator networks (GESLIN et al., 2013), effects of wildflower plantings on bee species richness and abundance in different agricultural landscapes (BATARY et al., 2010; GRASS et al., 2016), and the bee fauna visiting flowering lawn weeds along an urban-rural gradient (LARSON et al., 2014). Significantly negative effects of percent agricultural cover in the surrounding landscape on bee species richness and phylogenetic diversity were observed at a 750 m radius (GRAB et al., 2019). In an urban landscape, LOWENSTEIN et al. (2014) identified the smallest tested radius of 100 m as

the relevant scale with regard to the influence of land cover and sociometric variables, such as solar radiation, impervious substrate, tree canopy cover and population density, on bee abundance, species richness and community composition. However, in this study system there was a high degree of similarity in correlations between response and predictor variables over the analyzed radii from 100–1500 m (LOWENSTEIN et al., 2014), rendering it impossible to identify the most relevant landscape scale from these results. Correlations between bee genus richness and landscape diversity peaked a radius of 1000 m (THEODOROU et al., 2017).

The molecular tools to analyse genetic exchange within population such as microsatellites are under ongoing development (e.g. MOHRA et al., 2000; NEUMANN und SEIDELMANN, 2006; ČERNÁ und STRAKA, 2012). Population structure has been investigated in several bee species (DARVILL et al., 2006; EXELER et al., 2008; ČERNÁ et al., 2013), also in an urban context (LÓPEZ-URIBE et al., 2015). Using genome-wide SNPs, THEODOROU et al. (2018) found little evidence of population structure in *Bombus lapidarius* associated with urbanization.

Differing sensitivity to microclimatic characteristics of urban habitats (BURDINE und MCCLUNEY, 2019) and land use change (CARIVEAU und WINFREE, 2015) might change the suitability for particular bee species to persist in the cities in the longer term. The evolutionary adaptations of bees to the urban environment have been studied with regard to wing morphology (BEASLEY et al., 2019), while MACIVOR und MOORE (2013) found indications for ecologically adaptive traits with regard to the use of plastics for nest construction in an urban environment.

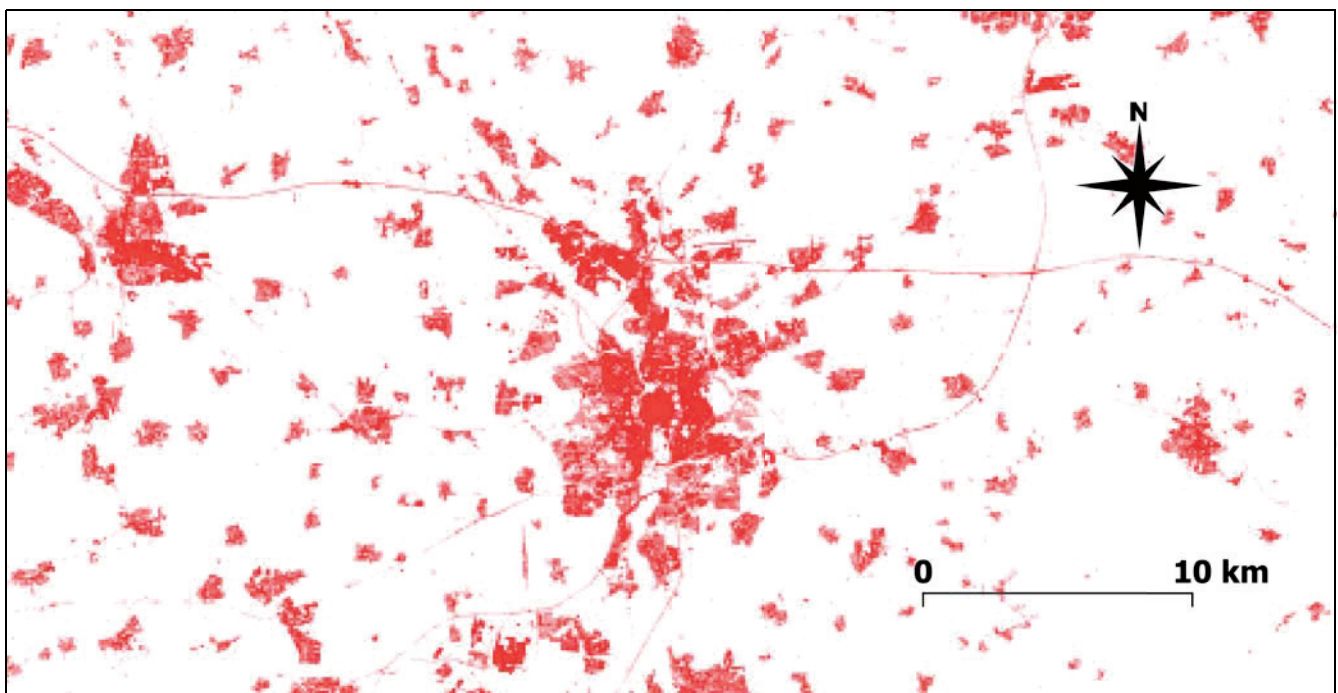


Fig. 5. Coverage of impervious substrate in Braunschweig and surroundings (Lower Saxony, Germany). Increasing coverage of impervious substrate is represented by increasing red colour. Data were obtained from the EU Copernicus program (EUROPEAN UNION, COPERNICUS LAND MONITORING SERVICE, 2020b).

A citizen scientist approach has been suggested as a plausible option for bee monitoring at morphospecies level, depending on volunteer training and engagement (MASON und ARATHI, 2019). However, because bee species identification at species level is notoriously difficult and requires professional training, detailed information on the development of bee populations can only be gathered through a professional long-term monitoring program.

Guidance on near-future research

From the overview of recently published studies, several aspects are suggested that could guide research on bee promoting measures in urban settings towards study designs capable of resolving so far unresolved issues.

First of all, it is suggested that study designs are used which best represent a continuous degree of urbanization along a gradient which stretches from highly urbanized landscapes to landscapes dominated by intensive agriculture. Such studies will be very helpful in comparing results on bee promoting measures in agricultural landscapes (which are rather numerous) to urban settings (which are still encountered much less frequently). In this way, some lessons learned within the agricultural context can potentially be transferred to urban settings, and research on urban bee conservation can focus on the remaining open questions. Studies should stretch over multiple years, allow an estimation of activity density in the sampled habitats, and should incorporate before-after as well as with-without impact design, in order to compensate for annual fluctuations in population size and thus to estimate the impact of a measure on population development.

The relevant landscape scale should be identified for each study system and with regard to the research question, since the available studies indicate some (although relatively small) variation in the relevant scale. Modern GIS and publicly available data based on remote sensing allow an easy incorporation of landscape scale factors into ecological modelling. Methodological standardization needs to be tackled with regard to use of floral resources in trees by bees. Case studies on genetic structure of bee populations with regard to urbanization are still relatively scarce and represent only a tiny fraction of phylogenetic and functional bee diversity. Development of the relevant molecular methods has progressed over the past years, and the results from studies on genetic population structuring are promising with regard to future adaptations of molecular tools for documenting the success of bee promoting measures in terms of habitat connectivity.

Conflicts of interest

The authors declare that they do not have any conflicts of interest.

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