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RESEARCH PAPER

Protected areas do not outperform urban wastelands in supporting insect pollinators and pollination in central Germany

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ABSTRACT

The Natura 2000 network is central to Europe's conservation efforts to address biodiversity decline, with ongoing plans to expand protected areas and restore habitats across the European Union. However, due to the relative scarcity of biodiversity assessments within Natura 2000 sites, our understanding of how effective these areas are at protecting biodiversity and how they can be improved remains limited. At the same time, urban green spaces and associated disturbed, unmanaged vacant areas, also known as urban wastelands, have gained attention as potential conservation targets due to their high insect species richness. Here, we assess and compare the biodiversity of pollinators within Natura 2000 reserves and urban wastelands to evaluate their relative value for biodiversity protection and pollination services. To achieve this, we compared pollinator communities, their flower-visitation patterns and pollination services using potted experimental plants in flower-rich Natura 2000 sites and paired non-protected, unmanaged, yet similarly flower-rich urban wastelands. While the total biomass and overall abundance of insects did not differ between the two habitat types, wild bee abundance and richness were higher in urban wastelands, whereas pollinator communities were more heterogeneous among Natura 2000 sites. Though insect flower-visitation network metrics were similar across both habitats, seed set of experimental plants was higher in urban wastelands compared to Natura 2000 sites, indicating lower pollination services in the nature reserves. Our findings suggest that while Natura 2000 areas contained unique biodiversity compared to urban wastelands, the current status of protected areas in Germany is inadequate to conserve biodiversity hotspots for bees, including endangered species and the pollination services they provide. We highlight the potential for urban areas to support biodiversity conservation as well as the need to develop targeted strategies for bee conservation in Natura 2000 areas.

Introduction

Declining populations of organism groups worldwide have spurred the setting of conservation goals, with the establishment of protected areas (PAs) being a key tool for mitigating the global decline in biodiversity (Margules & Pressey, 2000). In Europe, the most significant effort in terms of PAs is the creation of Natura 2000 sites (Evans, 2012), which represent the largest coordinated network of PAs in the world, covering approximately 18% of the land surface of the European Union (EU) (European Commission, 2022). However, existing conservation measures have proven insufficient to halt biodiversity loss across the continent (European Commission, 2020). In response, the EU has introduced a new biodiversity strategy aimed at increasing protected land to 30% by 2030 and has enacted a nature restoration law to restore at least 20% of degraded ecosystems, including Natura 2000 areas (European Commission, 2020, 2023; Moldoveanu et al., 2024). However, to effectively halt biodiversity loss, it is crucial to evaluate why biodiversity conservation efforts sometimes fail, despite an increasing

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number of initiatives for its protection (Stoll-Kleemann, 2010).

Insects, which constitute more than 80% of animal biodiversity, are undeniably overlooked in conservation efforts (Cardoso et al., 2011; Chowdhury et al., 2023b). At the same time, insects are frequently reported to suffer from severe declines in biomass, abundance and species richness (Hallmann et al., 2017; Seibold et al., 2019; van Klink et al., 2020; Wagner, 2020), including of formerly abundant species (van Klink et al., 2024). Climate change, land use intensification including the use of pesticides, habitat loss, degradation and fragmentation have all been identified as the main drivers of insect decline (Wagner et al., 2021). Among their many ecological roles, insects are a crucial component of terrestrial biodiversity and are important for the economy, food security and human well-being through the pollination they undertake (Klein et al., 2007; Ollerton et al., 2011; Rodger et al., 2021). Yet, one of the most alarming biodiversity trends is the decline in insect pollinators (Brown & Paxton, 2009; Vanbergen & the Insect Polinators Initiative, 2013).

Currently few PAs are specifically designated for insect conservation (Chowdhury et al., 2023b). Nonetheless, non-targeted insects can benefit from the protection status of PAs through the “umbrella effect”, where conservation efforts focused on specific habitats or species can promote the protection of wider biodiversity (Morán-López et al., 2020). For instance, insect diversity could benefit from PAs by maintaining areas with higher net productivity. However, despite increasing awareness of the need to design PAs to support insect diversity (Samways et al., 2020), we lack studies evaluating whether current PAs support a sufficient range of biodiversity, particularly threatened species (Chowdhury et al., 2023a). Furthermore, research is needed on plant-pollinator interactions within PAs to reveal the ecological specialisation and resource use of plant and insect pollinator communities, as well as assess pollination service provision from these areas.

The evidence regarding the effectiveness of PAs in supporting insect biodiversity is mixed (Chowdhury et al., 2023a). In a recent review, Chowdhury et al. (2023a) reported that only 4 out of 44 studies comparing insect richness inside versus outside PAs found higher species richness within the PAs. Indeed, several studies have indicated that certain insect groups, such as butterflies and beetles, do not sufficiently benefit from PAs (D’Amen et al., 2013; Harry et al., 2019; Hernández-Manrique et al., 2012; Rada et al., 2019; Tzirkalli et al., 2019). In a recent study, Cooke et al. (2023) found that while PAs in Great Britain do harbour higher richness of insects compared to non-protected areas, they also lose biodiversity at the same rate as the surrounding landscape (for SW German, see also Frenzel et al., 2024). Moreover, Hallmann et al. (2017) reported a greater than 75% decline in total insect biomass over 27 years within PAs, including in Natura 2000 sites, indicating that PAs may not effectively mitigate the loss of insects.

Another concern with PAs in mitigating biodiversity loss is that they cover an insufficiently small proportion of the biodiversity currently under threat (D’Amen et al., 2013). For example, while protection status can benefit insect communities already present in nature reserves, Chowdhury et al. (2023b) estimated that three-quarters of global insect biodiversity remains insufficiently covered by PAs. In the EU, assessments are still lacking for most insect groups to determine whether current PAs sufficiently cover large proportions of threatened insect species that persist across the broader landscape. As the EU plans to expand its PAs by 2030 (European Commission, 2020), an open question remains as to whether these new designations will more effectively cover insect biodiversity and how these areas can be used to mitigate insect decline (Chowdhury et al., 2023a, 2023b).

To evaluate the effectiveness of current PAs in supporting insect biodiversity, it is important to consider not only changes in biodiversity within PAs upon their designation but also to compare the performance of PAs with non-protected habitats. Such assessments can be achieved by comparing PAs to areas with similar habitat structure, which helps determine whether PAs contain higher net biodiversity (IPBES, 2019) and thereby contribute to protecting biodiversity across the broader landscape. Such comparisons provide valuable insights into the performance of current PAs and may highlight the need to integrate new habitat types into biodiversity conservation strategies. For example, in the context of protecting pollinators, particularly bees, urban green land-uses have been repeatedly suggested as potentially high-value areas (Baldock, 2020; Hall et al., 2017; Theodorou, Radzevičiūtė, et al., 2020; Wenzel et al., 2019), yet they are rarely included in conservation plans. The relatively good performance of these urban areas is often attributed to land-use types that are difficult to use for species protection on a larger scale, such as allotments or private gardens, since their management relies on multiple stakeholders with different motivations (Baldock, 2020). On the contrary, urban green spaces such as vacant lots, remnant vegetation fragments and urban meadows (aka urban wastelands) are generally flower-rich, easier to manage and can provide essential habitat structures for specific groups of pollinators (e.g. foraging resources and building material for nesting) (Machon, 2021; Twerd & Banaszak-Cibicka, 2019). However, urban wastelands remain relatively understudied and their conservation value for pollinators is largely unknown (Di Pietro & Robert, 2021; Moldoveanu et al., 2024). Therefore, we argue that comparing PAs with urban wastelands would provide insights into how well PAs support pollinator biodiversity and reveal how urban areas could offer complementary biodiversity protection for pollinators, potentially by expanding PA designations into cities.

In this study, we address the knowledge gap regarding how effectively PAs support pollinator biodiversity and the ecosystem services they provide. We do this by comparing insect biodiversity and pollination success between PAs and urban wastelands, both of which lack conservation measures specifically aimed at insect flower visitors. If Natura 2000 areas sufficiently support pollinator biodiversity, they are expected to either maintain relatively high insect biodiversity or if species richness is low, preserve unique insect biodiversity by providing habitat for species of high conservation concern. Conversely, if urban wastelands harbour higher insect pollinator biodiversity or a greater number of threatened species, this would suggest that current PA designations are insufficient for conserving pollinator biodiversity and underscore the potential role of urban areas in conservation efforts.

Beyond assessing pollinator biodiversity, we also examined whether habitat type influences plant-flower visitor interactions. These interactions form networks involving species with varying degrees of ecological specialisation (Bascompte et al., 2003). Specialisation is a key concept in ecology and conservation, serving as a proxy for environmental quality (Devictor et al., 2010; Kaiser-Bunbury & Blüthgen, 2015; Soares et al., 2017). Indeed, increased land-use intensity has been shown to reduce both network- and species-level specialisation (Soares et al., 2017) as well as pollination service provision (Aguilar et al., 2006). By examining insect flower-visitation networks, we gain insights into the specialisation within communities and how flower visitors and plant species make differential use of resources that are directly related to their fitness (Devictor et al., 2010).

Given that certain urban green-land uses are already known for their structural diversity and high-quality habitats for pollinators and pollination service provision (e.g. botanical gardens, private gardens, allotments; Baldock et al., 2015, 2019; Theodorou et al., 2020), our study alternatively focused on urban wastelands (i.e. ruderal habitats such as parking lots and disturbed grass fields in residential areas), where conservation measures have yet to be implemented (Moldoveanu et al., 2024). We used pan-traps and insect-flower visitation transect walks in Natura 2000 sites and urban wastelands explicitly to compare (i) the biomass, abundance and species richness of insect flower visitors and (ii) the composition of flower-visitor communities between the two habitat types. In addition, to assess the value of Natura 2000 areas and urban wastelands in maintaining pollination services, we compared (iii) differences in insect visitation patterns and (iv) seed set of potted experimental plant communities (“pollinometers”) between the two habitat types.

Materials and methods

Study sites

The study was carried out in the federal state of Saxony-Anhalt (Germany) from the 19th of June to the 14th of August 2018. We selected nine flowering plant-rich Natura 2000 sites and nine nearby flowering plant-rich urban wastelands based on Natura 2000 maps, Google Earth v. 7.1.8 and by visiting candidate sites, resulting in a paired design (i.e. nine Natura 2000-urban wasteland pairs; in total, 18 independent sites; Appendix A: Fig. S1) to provide greater statistical power to compare the two habitat types (i.e. we undertook a comparison of a Natura 2000-urban wasteland pair of sites, which we replicated across nine independent pairs of sites; for additional justification of such a design, see Theodorou et al., 2020b). Sites within both habitat types were similar in that they were exclusively dominated by native and natural vegetation consisting of grasses and/or herbaceous plants. To ensure that each site within a Natura 2000-urban wasteland pair was independent, we selected them to be at least 3 km apart (mean of 6.88 km; Appendix A: Fig. S1 and Table S1) (Gathmann & Tscharntke, 2002; Greenleaf et al., 2007). Site pairs were also independent; the minimum distance between two Natura 2000 sites was 7 km and between two urban sites was 5 km (Appendix A: Fig. S1 and Table S1).

We chose Natura 2000 sites that were largely devoid of urban land-uses (Appendix A: Table S2). The selected Natura 2000 sites were in areas dominated by dry semi-natural grassland, steppe, humid and mesophile grassland, forest and arable land (Appendix A: Table S3). For protected habitat types and protected species at these sites, see Appendix A: Tables S4 and S5. The urban sites comprised disturbed habitats, either grass fields in residential areas or ruderal areas close to parking lots (Appendix A: Table S6). At a radius of 600 m, which is within the foraging range of many bee species (Gathmann & Tscharntke, 2002; Greenleaf et al., 2007), Natura 2000 sites had a higher proportion of semi-natural cover (mean = 0.50, SD = 0.22; LMM; χ^2 (1)= 32.15, $p < 0.001$) and agricultural cover (mean = 0.44, SD = 0.21; LMM; $\chi^2(1)=$ 11.28, $p < 0.001$) compared to urban sites (semi-natural, mean = 0.08, SD = 0.05; agricultural, mean = 0.24, SD = 0.16), and urban sites had a higher proportion of urban built-up areas (mean = 0.63, SD = 0.15; LMM; $\chi^2(1)=150$, $p < 0.001$) compared to Natura 2000 sites (mean = 0.02, SD = 0.03). Forest cover did not differ between Natura 2000 sites and urban wastelands ($\text{mean}_N = 0.05$, SD = 0.07; $\text{mean}_U = 0.06$, SD = 0.10; LMM; $\chi^2(1) = 0.23$, $p = 0.63$) (Appendix A: Tables S2 and S7). At each site, we selected a 100 × 50 m area with diverse floral resources, which we used as our Natura 2000 or urban sampling plots. By using these criteria for site selection, we aimed at deploying a paired design to compare sites across multiple, independent locations and sample from sites that appeared a priori to be suitable for insect flower visitors and potentially also for pollination, in localities embedded in a landscape typical of each habitat type in our study region. Additionally, our paired design ensured that each site pair was sampled simultaneously to minimise phenological differences in flowering or insect activity within a pair of sites, thereby enhancing comparability between habitat types. Statistical models therefore necessarily used ‘site pair’ as a random variable when comparing between Natura 2000 and urban wasteland sites (see below: Statistical analysis).

Sampling insects, insect flower visitors, flowering plants and their interactions

Insects were sampled using three sets of blue, yellow and white pan-traps (diameter: 21 cm, height: 2.8 cm) mounted on a stick at vegetation height at each site. Each of the three sets of pan-traps was placed at three locations at each sampling site, 30 m away from each other. Pan-trap locations were stratified toward flower-rich spots and were 2/3 filled with unscented soapy water. Since our approach did not aim at sampling exhaustively the two habitat types, but rather to deploy a standardised sampling methodology to compare between them, we sampled each habitat pair (Natura 2000/urban wastelands) at the same time for three consecutive days. The pan-traps were emptied every day and all insects were stored in 70% ethanol at 4 °C. Pan-trap material was used to estimate insect biomass. All insects were dried at room temperature, separated by insect order and weighed to the nearest of 0.01 g on an electronic scale (S2002; Denver Instrument Bohemia, NY, USA).

While pan-trapping insects, we used insect-flower visitation transect walks to compare insect flower visitor abundance and species richness, as well as the patterns of flower-visitation interactions, between the two habitat types (Natura 2000/urban wastelands). Flower visitors were recorded for two consecutive days by JHM to construct ecological flower-visitation networks using four 30-min transect walks at each site within a 100 × 50 m area, two in the morning (9:00–12:00 am) and two in the afternoon (1:00–4:00 pm). We performed transect walks on sunny days, with a wind speed less than 2.3 m/s and at temperatures above 19 °C (Appendix A: Table S8). Sampling was performed by the same collector at all sites. The use of standardised transects is a common methodology in pollinator studies and, similar to other sampling methodologies, has limitations (Westphal et al., 2008). However, since our study aimed at sampling insect flower visitors using a standardized protocol, transects were appropriate for our objectives.

Flower-visitation interactions were defined as an insect touching the reproductive parts of a flower. Upon observing an interaction, we paused the timer and collected both the insect and the flowering plant (if necessary) for identification. The insect was caught with a hand-net, added to a labelled tube containing 70% ethanol and stored at 4 °C for later identification. All insects other than the Anthophila (bees) were identified into six morphogroups: Syrphidae, other Diptera, butterflies, moths, Coleoptera and wasps. Anthophila were identified to species using regional identification keys (Appendix A: Table S9). We collected whole plant samples, including leaves and reproductive structures of the flowering plants, which were identified to species using identification keys (Bäßler et al., 1999; Jäger et al., 2013) (Appendix A: Table S10). Additionally, we used 10 quadrats (1 x 1 m) at each site to estimate the availability of local floral resources. The quadrats were placed using systematic random sampling at a distance of 30 m from each other along three transects. From each quadrat, flowering plant species richness and the number of flower units were calculated as measures of floral resource availability at each site. The definition of a flower unit was assessed based on the ability of a pollinator to visit and touch the reproductive organ of several flowers simultaneously or not. For example, we define a single inflorescence for Asteraceae and Dipsacaceae as a single unit (for specific definitions of flowering units of different taxa and a list of flowering plant species per site, see Appendix A: Tables S11 and S12). We performed the data collection in accordance with the relevant legal guidelines and regulations.

Experimental plant pollination

In addition to estimating and comparing biodiversity and flower-visitation networks between Natura 2000 and urban wastelands, we also measured pollination service provision. To compare pollinator service provision between the two habitat types, we used insect pollinator-dependent self-incompatible plants or “pollinometers” (Theodorou et al., 2016, 2017, 2020b), *Borago officinalis* and *Trifolium pratense*. Both species can be found naturalised or naturally in the study region, both species are mainly visited by bees but differ in their rewards and, based on a previous study, they are visited by a diverse community of insects (Theodorou et al., 2017). Seeds of *B. officinalis* and *T. pratense* were obtained from a supplier of local wildflower seeds i.e seeds were obtained from native or naturalised plants and not from a commercial crop cultivar (Rieger-Hofmann GmbH, Blaufelden, Germany). Plants were germinated and grown in individual pots in an insect-free glasshouse until flowering. Five experimental plants of each species were then placed at each sampling site during the first day and exposed for two additional, consecutive flower-visitor sampling days. All plants had open flower units and were distributed between pairs to achieve a similar number of flowers/inflorescences per site. The plants were randomly placed at 1 m distance from each other near the centre of each sampling site and were part of the transect walks. Due to problems with seed germination, *T. pratense* experimental plants were used in only four of the nine Natura 2000 and urban pairs.

All open flowers/inflorescences of the experimental plants were discretely marked with green coloured wire. The plants were watered daily and flowers/inflorescences that newly opened whilst in situ at a site were marked. At each site, the plants were monitored for at least 20 min in the morning and 20 min in the afternoon to estimate flower visitation rates. At the end of the third day at the site, the plants were brought back to the glasshouse until seed production. Seeds from the initially (prior to placement at a site) marked flowers/inflorescences were counted and used as an estimate of pollination service provision during the two full days of exposure at a field site. Furthermore, at each site we estimated the abundance of potential conspecific pollen donors by counting the number of flower units of co-flowering *T. pratense* and *B. officinalis* plants found in the 10 randomly placed quadrats. No co-flowering naturalised *B. officinalis* plants were observed within the quadrats.

The dependence of *B. officinalis* on insect-mediated pollination was tested in a glasshouse experiment by confining five plants in an insect-free glasshouse chamber throughout their entire flowering period. For *T. pratense*, a different approach was used due to insufficient individual plants to be held separately in the glasshouse. Instead, the dependence of *T. pratense* experimental plants on insect-mediated pollination was evaluated by bagging one open flower/inflorescence of each plant with a fine net (1 mm gauze) throughout the experiment to prevent insect visitation (zero control). Seed set was assessed in the same way as for open flowers on field experimental plants. *Trifolium pratense* experimental plants at field sites produced more seeds (mean = 33, SD = 20) compared with bagged *T. pratense* control flowers that did not produce any seeds (mean = 0, SD = 0). *Borago officinalis* experimental plants at field sites produced more seeds (mean = 1.4, SD = 0.7) compared with the control plants maintained in a glasshouse chamber (mean = 0.3, SD = 0.7; *t*-test, t(21)= 3.26, p = 0.003), demonstrating the dependence of both plant species on insect visitation for high seed set.

Statistical analysis

Comparing insect biodiversity between Natura 2000 and urban wasteland sites

We used linear mixed models (LMMs) and site pair as a random factor to compare insect biomass (derived from pan-traps) in Natura 2000 versus urban wasteland sites. Analyses of biomass were carried out for (i) the entire dataset and (ii) separately for the insect orders Diptera, Coleoptera, Lepidoptera and Hymenoptera. We used generalized linear mixed models (GLMMs) with a negative binomial error structure and site pair as a random factor to compare insect flower visitor abundance (derived from transects), wild bee species richness (derived from transects) and flowering plant abundance and richness (derived from quadrats) in Natura 2000 versus urban sites. Analyses of abundance were carried out for (i) the entire dataset; (ii) separately for the insect orders Diptera, Coleoptera, Lepidoptera and Hymenoptera; separately for Syrphidae (subset of Diptera), wild bee species (all Anthophila excluding honey bees) and (iii) separately for bumble bees and for honey bees. An LMM with site pair as a random factor was also used to compare flowering plant abundance (derived from quadrats) in Natura 2000 versus urban wasteland sites. When comparing insect biomass, flower visitor abundance and bee richness between habitat types, we used flowering plant abundance and flowering plant richness as covariates. Additionally, we included bee abundance as a covariate in the model of bee richness to control for sample size effects. The flowering plant abundance was used as a covariate when comparing flowering plant richness between habitat types.

To test if Natura 2000 sites benefit threatened wild bee species, we classified the bees into two categories based on their conservation status in Germany: (i) conservation concern (endangered/vulnerable/near threatened) and (ii) least concern (Westrich et al., 2011). We counted the number of recorded bee species per category in each habitat type to examine whether threatened bee species were found more frequently in Natura 2000 sites. We used GLMMs with a negative binomial error structure, with conservation category, habitat type and their interaction as fixed factors and pair as a random factor to compare Natura 2000 versus urban sites for each conservation category. Bee abundance was included as a covariate to control for sample size effects. A post-hoc Tukey test was used to compare Natura 2000 versus urban wasteland sites for each bee conservation category using the R package multcomp (Hothorn et al., 2008).

To test for differences in the Natura 2000 and urban wasteland flower visitor and flowering plant (based on quadrats) community composition, we performed a paired permutational multivariate analysis of variance using the *adonis* function, with 1000 permutations, implemented in the R package vegan (Oksanen et al., 2018). We ran separate analyses for all flower visitors and for bees. In the *adonis* analysis, the Bray-Curtis distance matrix of either overall flower visitor composition, bee species or flowering plant species composition was the response variable, with habitat type as a fixed factor. For the flower visitor analyses, flowering plant richness and abundance were used as covariates. The strata (block) argument was set to 'pair' so that randomizations were constrained to occur within each pair and not across all sample sites. We employed non-metric multidimensional scaling (NMDS) to visualize the variation in flower visitor and flowering plant community composition. To evaluate the similarity in bee and flowering plant community composition among the nine sites for each habitat type, we used: (i) the Jaccard similarity index to compare species presence/absence and (ii) the abundance-based Bray-Curtis index. Both indices range from 0 to 1, where 1 indicates identical species composition between sites and 0 indicates no shared species. For each site, we calculated the mean similarity index value over all eight comparisons within the same habitat type and we used LMMs to compare the indexes in Natura 2000 versus urban wasteland sites. Habitat type, flowering plant abundance and the similarity index of flowering plants were used as fixed factors and site pair as a random factor.

To evaluate whether differences in bee community structure between Natura 2000 sites and urban wastelands are driven by differences in species' biological traits, we grouped bees according to two life-history traits: nesting behaviour and pollen diet specialisation (Williams et al., 2010). Based on Westrich (2018), bees nesting in e.g. wall substrates, plant material or shells were classified as "above ground nesters" and bee species nesting in soil were classified as "below ground nesters". In addition, based on Westrich (2018), bee species were characterised as oligolectic (i.e. collecting pollen from a single plant family) or polylectic (i.e. collecting pollen from several plant families). However, because pollen preferences in the genus *Hylaeus* were often specified as uncertain in Westrich (2018), we used the assessments by Müller (2023) to determine specialization within this genus. We used GLMMs with a negative binomial error structure, with life-history trait category, habitat type and their interaction as fixed factors and pair as a random factor to compare Natura 2000 versus urban wasteland sites for each life-history trait category. Bee abundance and flowering resource availability were included as covariates in the model to control for sample size effects. A post-hoc Tukey test was used to compare Natura 2000 versus urban wasteland sites for each bee life-history trait category using the R package multcomp (Hothorn et al., 2008).

Comparing flower visitation patterns between Natura 2000 and urban wasteland sites

To evaluate whether habitat type influences plant-flower visitor interactions, we used our flower-visitation data to build bipartite networks for each of the 18 sites. We assessed the sampling completeness of networks within each habitat type following the methodology recommended by Grass et al. (2018). Our results indicate a sampling completeness of 63 ± 19% (mean ± SD) for flower-visitation networks in urban wastelands and 65 ± 20% (mean ± SD) for Natura 2000 networks. Our sampling completeness estimates are consistent with findings from other plant-pollinator network studies: 57% in Devoto et al. (2012) and 50% in Grass et al. (2018). For network analyses, we pooled flower-visitation data from both sampling rounds (morning and afternoon). We used the R package bipartite (Dormann, 2011; Dormann et al., 2009) to calculate common network- and species-level indices to examine variation in flower visitor and flowering plant specialisation/generalisation (i.e. resource use) across Natura 2000 and urban wasteland sites. We calculated H_2', which is a measure of network specialisation and reflects the difference between the number of interactions realised and the expected total number of interactions of a species. H_2' can range from 0 to 1, from extreme specialisation to extreme generalization (Blüthgen et al., 2006). We also calculated flower visitor and flowering plant generality, defined as the mean effective number of interacting partners weighted by their relative abundance (Tylianakis et al., 2007). We further calculated individual level specialisation (d'), which measures how specialised a given flower visitor morphospecies or flowering plant species is with respect to available resources or visitors, respectively, and ranges from 0 for more generalised to 1 for more specialised (Blüthgen et al., 2006). Mean d' was calculated for each flying visitor morphospecies and flowering plant species per network. H_2' and d' are robust against network size, symmetry and sampling effort and thus were not weighted prior to analysis (Blüthgen et al., 2006). We used LMMs to compare network metrics between Natura 2000 and urban wasteland sites. Pair was used as a random factor and local floral richness and abundance were used as covariates.

Comparing pollination service provision between Natura 2000 and urban wasteland sites

We used LMMs, with site pair included as a random factor, to compare the seed set of *B. officinalis* and *T. pratense* between Natura 2000 and urban wasteland sites. Pollination of the experimental plants could be directly affected by the presence of pollinators and indirectly by local flowering plant richness and abundance. Therefore, the abundance and richness of local flowering plants and conspecific pollen donor availability to our experimental plants were used as covariates.

In additional models, we used LMMs to investigate the effects of visitation rates, abundance and richness of bees, local resource availability and network metrics (i.e. H_2', d' and generality) on *B. officinalis* and *T. pratense* seed set. To identify the most important predictors for seed set, we used an automated model selection approach (all subsets) based on the corrected Akaike Information Criterion (AICc) and allowing only up to 3 variables to avoid overfitting, implemented using the R package MuMIn (Barton, 2020). We used a cut-off ΔAICc value of 2 (Burnham & Anderson, 2004) and, if more than one model was retained, we used model averaging (function 'model.avg'; (Barton, 2020)).

All mixed model analyses were performed using the package *lme4* (Bates et al., 2015). We checked each model for multicollinearity using variance inflation factors (VIF) with a cut-off value of 3. VIF was lower than 3 for all predictors, indicating that there were no major effects of collinearity (Zuur et al., 2009). All model (GLMM and LMM) assumptions were checked visually and were found to conform to expectations (e.g. normality of the distribution of residuals, homogeneity of variances, linearity, no outliers). The residuals of all regression models were tested for spatial autocorrelation using Moran's *I* implemented in the R package 'ape' (Paradis & Schliep, 2019). The residuals were not found to be autocorrelated ($p > 0.05$ for all models).

Results

During three days of pan trapping in each site, we collected a total of 199.72 g of insect biomass. Of this, 107.87 g (54%) were Hymenoptera, 62.18 g (31.1%) were Diptera, 19.96 g (10%) were Lepidoptera and 14.70 g (7.4%) were Coleoptera. During four 30-min transect walks at each site, we observed a total of 4287 interactions (N_{Int}), including 115 wild bee species and 101 flowering plant species across all sites. These interactions consisted of 42.5% bee (Anthophila) ($N_{Int} = 1822$), 19.3% Lepidoptera ($N_{Int} = 828$), 15.2% Diptera ($N_{Int} = 653$), 13.7% Coleoptera ($N_{Int} = 587$) and 9.2% wasp ($N_{Int} = 397$) flower visits. Of the bee (Anthophila) visits, most were performed by bumble bees (21.4%, $N_{Int} = 391$) and honey bees (14.6%, $N_{Int} = 266$). Most of the remaining visits were performed by bees of the genera *Halictus* (15.7%, $N_{Int} = 286$), *Lasioglossum* (12.8%, $N_{Int} = 234$) and *Andrena* (12.7%, $N_{Int} = 232$). Most wild bee species sampled were ground nesters (62 out of 115 species, 53.9%; 1273 out of 1556 individuals, 81.81%) and polylectic (77 out of 115 species, 67%; 1249 out of 1556 individuals, 80.3%).

The biomass (derived from pan traps) and abundance (derived from transects) of all insects as well of Lepidoptera and Coleoptera were highly correlated (all insects: Pearson's $r = 0.66$, $df = 16$, $p = 0.002$; Lepidoptera: Pearson's $r = 0.72$, $df = 16$, $p < 0.001$; Coleoptera: Pearson's $r = 0.77$, $df = 16$, $p < 0.001$). In contrast, the biomass (derived from pan traps) and abundance (derived from transects) of Hymenoptera as well of Diptera were not highly correlated (Hymenoptera: Pearson's $r = 0.27$, $df = 16$, $p = 0.27$; Diptera: Pearson's $r = 0.03$, $df = 16$, $p = 0.90$).

In regards to flowering plants, the most visited plant species in Natura 2000 sites were *Centaurea jacea* ($N_{Int} = 220$), followed by *Scabiosa ochroleuca* ($N_{Int} = 178$), *Falcaria vulgaris* ($N_{Int} = 157$), *Daucus carota* ($N_{Int} = 141$) and *Erygnium campestre* ($N_{Int} = 113$). The most visited plant species in urban wastelands were *Daucus carota* ($N_{Int} = 359$), followed by *Picris hieracioides* ($N_{Int} = 226$), *Echium vulgare* ($N_{Int} = 188$), *Carduus acanthoides* ($N_{Int} = 162$) and *Medicago sativa* ($N_{Int} = 126$). Flowering plant species richness derived from quadrats did not differ between Natura 2000 (mean = 11, SD = 2) and urban wastelands (mean = 13, SD = 3; LMM, $\chi^2(1) = 1.38$, $p = 0.24$), but flower abundance derived from quadrats was lower in Natura 2000 (mean = 32, SD = 16) compared to urban wastelands (mean = 109, SD = 68; LMM, $\chi^2(1) = 10.92$, $p < 0.001$).

Insect biomass and insect flower visitor biodiversity

We found no significant difference in the overall insect biomass as well as in the biomass of each insect order between Natura 2000 and urban wastelands (Table 1 and Appendix A: Fig. S2). Similarly, we found no difference in the overall abundance of insect flower visitors between Natura 2000 and urban wastelands (Table 1 and Fig. 1a). However, abundance patterns varied between insect orders. The abundance of Diptera flower visitors, a subset of all insect visitors, did not differ between Natura 2000 and urban wastelands (Table 1 and Fig. 1b) and, within the Diptera, neither did the abundance of hoverflies (Syrphidae) (Table 1 and Fig. 1c). In contrast, the abundance of Lepidoptera was higher in Natura 2000 sites compared to urban wastelands (Table 1 and Fig. 1d). The abundance of Coleoptera flower visitors did not differ between Natura 2000 and urban wastelands (Table 1 and Fig. 1e). However, the abundance of Hymenoptera was lower in Natura 2000 compared to urban wastelands (Table 1 and Fig. 1f). Among Hymenoptera, the abundance of wild bees and bumble bees, as well as the number of wild bee species, was lower in Natura 2000 compared to urban wastelands (Table 1, Fig. 1g, h and i). In contrast, honey bee abundance did not differ between Natura 2000 and urban wastelands (Table 1 and Appendix A: Fig. S3).

Wild bee species richness was positively related to flowering plant

Table 1

Results of the linear mixed models and generalised linear mixed models to investigate the differences in insect biomass (derived from pan-traps), flower visitor abundance (derived from transects) and wild bee richness (derived from transects) between Natura 2000 and urban wastelands. Statistically significant results are indicated in bold.

	Mean ± SD		Habitat type effect	
Response variable	Natura 2000	Urban wastelands	$\chi^2(1)$	p-value
Insect biomass (derived from pan-traps)				
All taxonomic groups	12.65 ± 7.98	9.53 ± 6.37	0.26	0.60
Diptera	4.11 ± 3.68	2.80 ± 1.29	0.58	0.44
Lepidoptera	1.25 ± 0.99	0.41 ± 0.41	2.79	0.09
Coleoptera	0.57 ± 0.58	1.06 ± 1.84	0.00	0.99
Hymenoptera	6.72 ± 5.36	5.26 ± 3.90	0.94	0.33
Flower visitor abundance (derived from transects)				
All taxonomic groups	235.55 ± 43.27	240.77 ± 89.02	0.92	0.33
Diptera	36.66 ± 25.08	35.88 ± 19.30	0.02	0.86
Syrphidae	10.77 ± 11.08	15.77 ± 16.44	3.19	0.07
Lepidoptera	72.11 ± 59.03	19.88 ± 13.54	6.98	**0.008**
Coleoptera	33.11 ± 27.48	32.11 ± 29.63	0.52	0.47
Hymenoptera	93.66 ± 47.29	152.44 ± 58.10	4.64	**0.031**
wild bees	57.66 ± 34.66	115.11 ± 56.07	7.76	**0.005**
bumble bees	11.55 ± 22.82	31.88 ± 38.14	59.22	**< 0.001**
honey bees	14.77 ± 18.50	14.77 ± 16.70	0.25	0.61
Flower visitor richness (derived from transects)				
wild bees	19.55 ± 7.07	27.11 ± 7.45	3.53	**0.049**

Note: When comparing insect biomass, flower visitor abundance and bee richness between habitat types, flowering plant abundance and richness were included as covariates. Additionally, bee abundance was included as a covariate in the model of bee richness.

species richness (GLMM; $\chi^2(1)$= 5.02, p = 0.025) but not to flower abundance (GLMM; $\chi^2(1)$= 0.28, p = 0.612). Wild bee species abundance was not related to flowering plant species richness (GLMM; $\chi^2(1)$= 0.83, p = 0.361) or flower abundance (GLMM; $\chi^2(1)$= 0.40, p = 0.528).

We found no difference between Natura 2000 and urban wasteland sites in the number of recorded bee species of conservation concern (GLMM; Tukey post hoc test; z = 0.49, p = 0.627; Fig. 2). However, the number of least concern wild bee species was lower in Natura 2000 sites compared to urban wastelands (GLMM; Tukey post hoc test; z = 2.49, p = 0.013; Fig. 2). The number of below ground nesting bee species did not differ between Natura 2000 (mean = 14 ± 4 SD) and urban wastelands (mean = 17, SD = 5; GLMM; Tukey post hoc test; z = 1.70, p = 0.09; Appendix A: Fig. S4). In addition, the number of polylectic bee species did not differ between Natura 2000 (mean = 16, SD = 5) versus urban wastelands (mean = 19, SD = 5; GLMM; Tukey post hoc test; z = 0.63, p = 0.10; Appendix A: Fig. S4). However, the number of above ground nesting bee species was significantly lower in Natura 2000 (mean = 4, SD = 3) than in urban wastelands (mean = 8, SD = 3; GLMM; Tukey post hoc test; z = 3.02, p = 0.002; Appendix A: Fig. S4). Also, the number of oligolectic bee species was lower in Natura 2000 (mean = 2, SD=1) than in urban wastelands (mean = 5, SD = 2; GLMM; Tukey post hoc test; z = 3.76, p < 0.001; Appendix A: Fig. S4).

Insect flower visitor and plant community composition

The community composition of overall insect flower visitors and of bees differed between Natura 2000 and urban wastelands (*adonis*; overall flower visitors: F (1,16) = 3.06, p = 0.002; bee flower visitors: F (1,16) = 2.53, p = 0.002; Appendix A: Fig. S5). Differences in the abundance of bumble bee and solitary bee species as well as the abundance of Lepidoptera drove the differences in community composition between habitat types (Appendix A: Fig. S6). The bee communities among Natura 2000 sites were more heterogeneous than those among urban wastelands. The mean Jaccard similarity index was lower in Natura 2000 (mean = 0.22, SD = 0.02) than in urban wastelands (mean = 0.27, SD = 0.03; LMM; $\chi^2(1)$ = 6.28, p = 0.01) and the mean Bray-Curtis similarity index was significantly lower for Natura 2000 (mean = 0.21, SD = 0.10) compared to urban wastelands (mean = 0.33, SD = 0.10; LMM; $\chi^2(1)$ = 29.17, p < 0.001). The heterogeneity in flowering plant community composition was not a good predictor of the heterogeneity in bee community composition (LMM; Jaccard, $\chi^2(1)$ = 0.66, p = 0.41; Bray-Curtis, $\chi^2(1)$ = 2.95, p = 0.08).

The community composition of flowering plants (derived from quadrats) differed between Natura 2000 and urban wastelands (*adonis*; F (1,16) = 2.254, p = 0.003′ Appendix A: Fig. S7). The relative abundance of *Daucus carota, Achillea millefolium, Medicago sativa* and *Pastinaca sativa* contributed to the differences in community composition between habitat types. The flowering plant communities among Natura 2000 sites were more heterogeneous than those among urban wastelands; the mean Jaccard similarity index was lower in Natura 2000 (mean = 0.26, SD = 0.06) than in urban wastelands (mean = 0.33, SD = 0.04; LMM; $\chi^2(1)$ = 6.88, p = 0.008) and the mean Bray-Curtis similarity index was significantly lower for Natura 2000 (mean = 0.15, SD = 0.07) compared to urban wastelands (mean = 0.19, SD = 0.07; LMM; $\chi^2(1)$ = 3.95, p = 0.04).

Flower-visitation patterns

There were no significant differences between Natura 2000 and urban wasteland sites in network level specialisation (H_2) (mean_N = 0.41, SD = 0.08, mean_U = 0.43, SD = 0.05; LMM; $\chi^2(1)$ = 0.14, p = 0.70; Appendix A: Fig. S8), flower visitor specialisation (d’) (mean_N = 0.33, SD = 0.07, mean_U = 0.35, SD = 0.04; LMM; χ^2 (1) = 1.92, p = 0.16; Appendix A: Fig. S8), flower visitor generality (mean_N = 4.09, SD = 0.67, mean_U = 3.99, SD = 0.91; LMM; $\chi^2(1)$ = 0.006, p = 0.93; Appendix A: Fig. S8) and plant generality (mean_N = 4.32, SD = 1.57, mean_U = 5.24, SD = 0.81; LMM; $\chi^2(1)$ = 1.18, p = 0.27; Appendix A: Fig. S8). These results suggest similar insect flower-visitor and plant species resource use patterns across habitat types.

Pollination

Borago officinalis plants produced fewer seeds per flower when experimentally exposed to flower visitors in Natura 2000 sites (mean = 1.1, SD = 0.7) compared to urban wastelands (mean = 1.7, SD = 0.5; LMM; $\chi^2(1)$ = 4.48, p = 0.034; Fig. 3a). *Trifolium pratense* plants also produced fewer seeds per inflorescence when experimentally exposed to

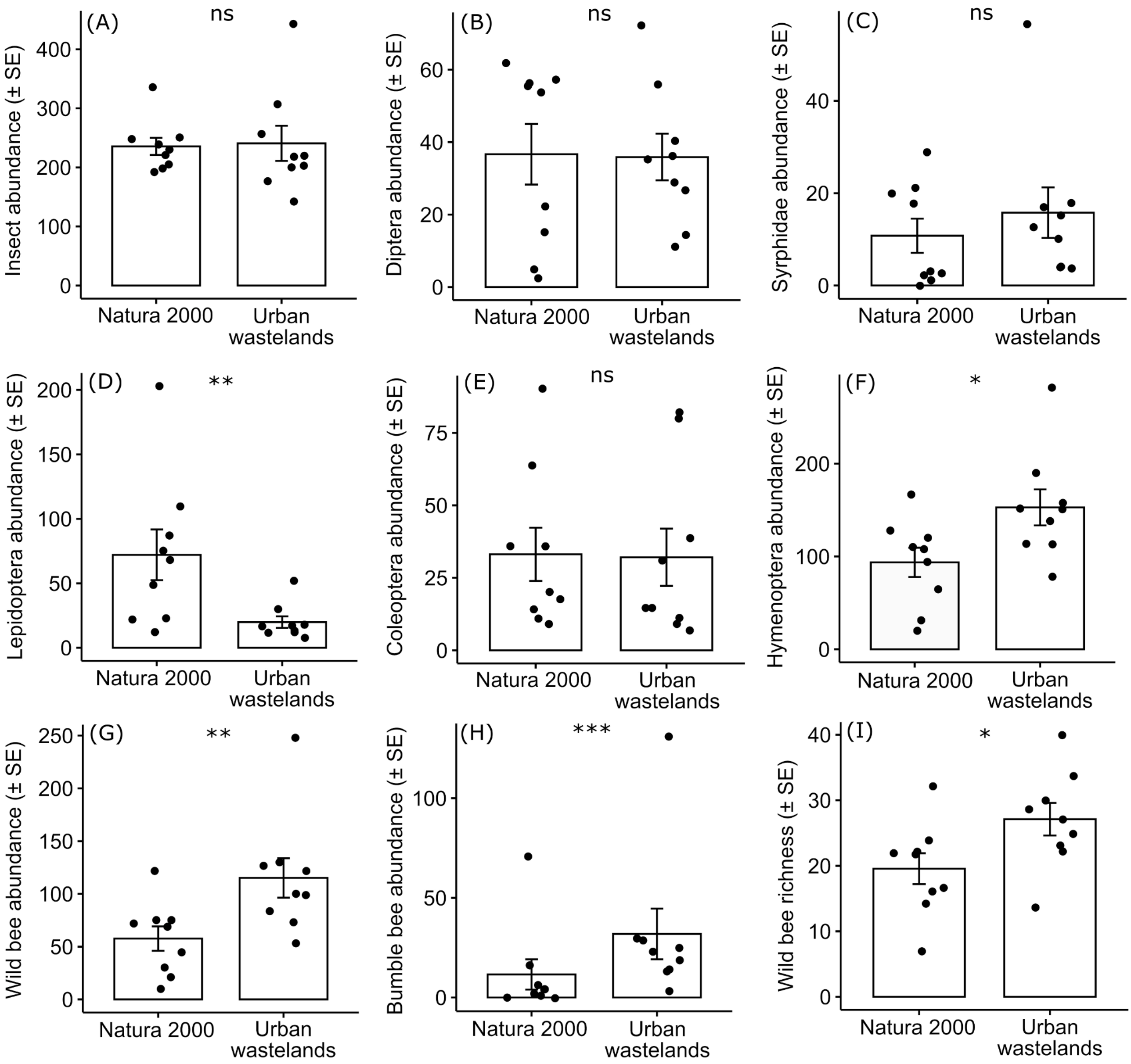

Fig. 1. Abundance and species richness of insect pollinators. Mean (A) overall insect, (B) Diptera, (C) hoverfly (Syrphidae), a subset of Diptera, (D) Lepidoptera, (E) Coleoptera, (F) total Hymenoptera abundance, and (G) wild bee abundance, (H) bumble bee abundance and (I) wild bee species richness (the latter three: subsets of Hymenoptera) derived from transects at N = 9 flower-rich Natura 2000 versus N = 9 paired flower-rich urban wastelands. Data points represent observed data; means ± SE are shown; GLMM: ns, not significant, *, $p < 0.05$; **, $p < 0.01$ and ***, $p < 0.001$.

flower visitors in Natura 2000 sites (mean = 21, SD = 21) compared to urban wasteland sites (mean = 45, SD = 11; LMM; $\chi^2(1) = 10.03$, p = 0.001; Fig. 3b, although note the limited sample size/number of sites). Most *B. officinalis* flower visitors were non-*Bombus* wild bees (N = 154, 59.69%), bumble bees (N = 42, 16.27%) and honey bees (N = 41, 15.89%) whilst the majority of *T. pratense* flower visitors were Lepidoptera (N = 12, 40%), non-*Bombus* wild bees (N = 6, 20%) and bumble bees (N = 5, 16.67%).

The automated model selection approach to explore the potential of multiple factors influencing pollination resulted in one best model for *B. officinalis* seed set and three best models for *T. pratense* seed set (deltaAICc < 2; Appendix A: Table S13). We found a positive relationship between *B. officinalis* seed set and wild be abundance (LMM; z = 4.09, df = 15.98, $p < 0.001$; Fig. 4a; Appendix A: Table S13). We also found a positive relationship between *T. pratense* seed set and bumble bee abundance (LMM; z = 2.77, df = 3.17, p = 0.02; Fig. 4b; Appendix A: Table S13).

Discussion

Protected areas (PAs) are seldom designed specifically for insect conservation, raising concerns about whether the current PA designations adequately support biodiversity (Chowdhury et al., 2023a, 2023b). In this study, we assessed how Natura 2000 reserves perform compared to nearby urban wastelands and vice versa in supporting insect flower visitors and their pollination services during the summer months. Our findings indicate that the two habitat types are similar in terms of insect biomass and flower visitor abundance. However, in the context of bee diversity, Natura 2000 sites exhibited reduced bee species richness, indicating that current PA designations may be insufficient for supporting key pollinator groups. Furthermore, Natura 2000 sites had reduced provision of pollination services in the two experimental plant species. These findings highlight potential shortcomings in current PA designations regarding the conservation of insect groups crucial for pollination services. In the context of expanding PA designations in

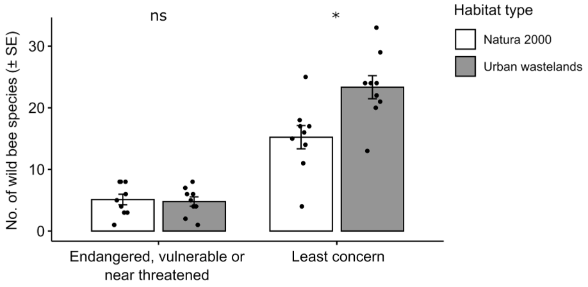

Fig. 2. Conservation listed and least concern wild bee species. A comparison of the number of conservation listed and least concern wild bee species (derived from transects) found at N = 9 flower-rich Natura 2000 versus N = 9 paired flower-rich urban wasteland sites, based on the German national Red List using IUCN criteria (Westrich et al., 2011). Urban wasteland sites are shown in grey and Natura 2000 sites in white. Data points represent observed data; means ± SE are shown. GLMM: ns, not significant; *, $p < 0.05$ (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article).

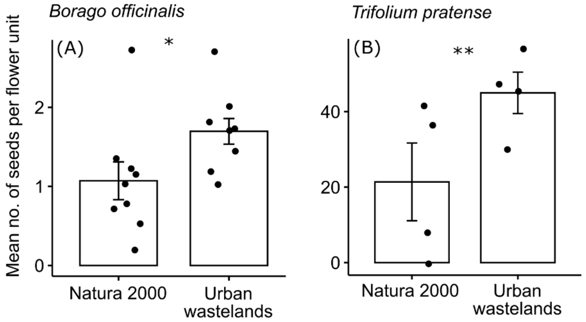

Fig. 3. Pollination service provision. Mean number of seeds per flower unit for (A) *Borago officinalis* experimental plants at N = 9 flower-rich Natura 2000 versus N = 9 paired flower-rich urban wasteland sites and (B) *Trifolium pratense* experimental plants at N = 4 flower-rich Natura 2000 versus N = 4 paired flower-rich urban wasteland sites. Data points represent observed data; means ± SE are shown; LMM: *, $p < 0.05$; **, $p < 0.01$.

Europe (European Commission, 2020), our results further highlight the potential of urban wastelands for biodiversity conservation, particularly in supporting a broader diversity of bee species. Furthermore, our study demonstrates that the success of urban areas in maintaining bee biodiversity is not confined to managed, high-quality habitats. Instead, we propose that carefully selected urban wastelands can also serve as important reservoirs of bee biodiversity, contributing to the mitigation of bee species loss.

Insect biomass, insect flower visitor abundance, richness and community composition

The overall insect biomass, as well as the biomass of each insect order, did not differ between the flower-rich Natura 2000 sites and nearby urban wastelands, suggesting that both habitat types have similar levels of productivity. Similarly, the overall abundance of insect flower visitors did not differ between Natura 2000 and nearby urban wastelands. However, bees, the main Hymenoptera flower visitors, were less abundant and had lower species richness in Natura 2000 sites compared to urban wastelands. In addition, the lower richness of specialist pollen foragers in PAs, which are known to be more vulnerable to extinction (Biesmeijer et al., 2006), suggest that the current Natura 2000 sites provide insufficient protection to bees. Our findings are in line with previous studies, such as Casanelles-Abella et al. (2023), who reported that bee biodiversity hotspots in Switzerland do not align well with protected areas, as well as with Baldock et al. (2015), who found lower bee abundance and richness in nature reserves in the UK compared to nearby urban sites. Additionally, our results are consistent with previous studies showing that urban green land uses can support high levels of bee biodiversity (Saure, 1996; Theodorou et al., 2020a). Overall, our results suggest that the effectiveness of current Natura 2000 PAs in supporting pollinator diversity should be improved, while also highlighting the potential of urban wastelands for pollinator conservation (Baldock, 2020; Di Pietro & Robert, 2021; Gardiner et al., 2013; Moldoveanu et al., 2024; Twerd & Banaszak-Cibicka, 2019).

An open question is why and how urban wastelands (e.g. ruderal habitats, vacant lots and remnant vegetation fragments), generally considered poor-quality habitats for biodiversity, can maintain higher bee diversity and similar numbers of threatened bee species as PAs. Two principal reasons may explain this. First, moderate disturbance within urban environments could increase landscape heterogeneity and the availability of suitable bee habitats, floral and nesting resources. This increased niche diversity can decrease competition and facilitate species coexistence, thus enhancing bee diversity (Faeth et al., 2011; Twerd & Banaszak-Cibicka, 2019). Indeed, the higher richness of bee species in urban sites could reflect the greater availability and continuity of floral resources, as well as the more diverse range of nesting possibilities, such as fence posts, cavities in walls, dead wood and bare soil (Fetridge et al., 2008; Kühn et al., 2004; Neame et al., 2013; Neumann et al., 2024; Twerd & Banaszak-Cibicka, 2019). The higher diversity of above ground nesting bee species in urban sites further highlights the potential for nesting resources to be a limiting factor in supporting bee biodiversity in protected areas. Second, Natura 2000 sites are often embedded within a typically fragmented European landscape, with a high proportion of

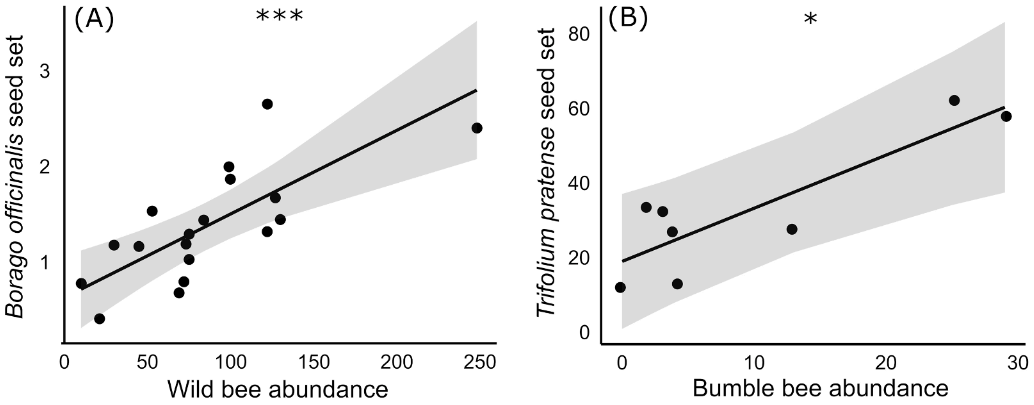

Fig. 4. Biodiversity ecosystem service relationships. Relationships between (A) wild bee abundance (derived from transects) and *Borago officinalis* seed set and (B) bumble bee abundance (derived from transects) and *Trifolium pratense* seed set. Data points represent partial residuals. Plotted lines show the predicted relationship and shaded areas indicate the 95% confidence intervals; LMM: *, $p < 0.05$; ***, $p < 0.001$.

agricultural fields in their surroundings. Agricultural intensification (e.g. pesticide use) in these regions could be the causal driver that negatively impacts pollinator communities in areas adjacent to Natura 2000 sites (Hallmann et al., 2017; Kennedy et al., 2013). A previous study found several types of pesticide in Natura 2000 reserves in Germany (Brühl et al., 2021). These effects are further exacerbated by the small sizes and isolation of PAs (Burkey, 1989). Given the higher bee species richness in urban wastelands, our results emphasise the potential of urban areas in implementing targeted local management practices to support bees and to broaden the utilization of anthropogenic landscapes for nature conservation.

Flower visitation patterns and pollination service provision

The patterns of resource use in flower-visitation networks were broadly similar between the two habitat types. While a previous study reported differences in plant and pollinator specialisation between urban sites and nature reserves in the UK (Baldock et al., 2015), in our study plant-flower visitor network properties were similar between Natura 2000 PAs and urban sites; generalisation and specialisation levels of plants and flower visitors did not differ between habitat types. These findings might be partly due to our study design, which involved simultaneously sampling flower-rich sites in both habitat types with similar levels of flower richness between Natura 2000 and urban wasteland sites. Previous studies have argued that plant species richness is a primary driver of shifts in flower visitor and plant specialisation/generalisation (Baldock et al., 2015; Theodorou et al., 2017). Due to the comparable number of plant species available in both habitat types, flower visitors interact with a similar number of plants species, resulting in a similar degree of specialization. Consequently, plants in both habitats attract a similar number of flower visitors.

We found the seed set of pollinator-dependent plants to be lower in Natura 2000 PAs compared to urban wasteland sites; experimental *B. officinalis* and *T. pratense* plants produced fewer seeds in Natura 2000 PAs compared to nearby urban wastelands. The seed set of pollinator-dependent plants is influenced by flower visitor abundance and flower visitor quality (e.g. pollen deposition, flower visitation constancy) (Willmer, 2011). That overall flower visitor abundance did not differ between the two habitat types in our study emphasises the importance of flower visitor quality for pollination. Our plants were primarily visited by bees, with wild bee and bumble bee (a subset of wild bee) abundance being higher at urban sites and the most important predictors of *B. officinalis* and *T. pratense* seed set, respectively. We argue that the most likely explanation for the reduced seed set in Natura 2000 sites is the lower overall bee abundance, or because of reduced abundance of specific groups, such as bumble bees. Bees, including bumble bees, are important pollinators i.e. they are high quality visitors for pollination that are thought to contribute significantly to the reproduction of the majority of flowering plants and crops (Klein et al., 2007; Ollerton et al., 2011). While we used only two plant species to assess pollination service provision, these species have a large variety of bee families as visitors. However, because these plant species are adapted to bee pollination, interpretation of pollination service provision across entire plant communities should be made with caution.

Based on our results, we suggest that future conservation efforts should consider integrating urban habitats into regional management plans to safeguard pollinators and the valuable ecosystem services they provide. More specifically, our findings highlight that urban green land uses, such as vacant lots, remnant vegetation fragments and urban meadows, can provide valuable habitats for bees and could be easily used for species protection on a larger scale (Baldock, 2020; Di Pietro & Robert, 2021; Twerd & Banaszak-Cibicka, 2019). While we found high bee diversity in areas often regarded as having questionable conservation value such as ruderal areas close to parking lots, carefully selecting urban areas with suitable nesting resources such as cavities, bare ground and nest building materials could further increase the potential of cities for pollinator conservation.

Despite the overall lower species richness of bees in Natura 2000 sites compared to urban wastelands, the heterogeneity of bee communities in PAs underscores their importance for bee biodiversity, indicating that they cannot be replaced by urban wasteland habitats. In addition, in contrast to Hymenoptera, Lepidoptera were more abundant in Natura 2000 sites. This suggests that these sites offer better habitats for butterflies and moths, likely due to the greater availability of host plants for oviposition or larval feeding (Kajzer-Bonk & Nowicki, 2022; Rada et al., 2019) as well as potentially longer historical land-use continuity (Ibbe et al., 2011). We propose that additional management efforts are necessary to improve bee diversity within currently designated PAs. For example, local management practices play a crucial role in species persistence and plant species community structure in semi-natural grasslands (Bonari et al., 2017). For bees, the timing and extent of mowing or grazing practices within PAs may be vital for their survival and persistence (Lerman et al., 2018; Weiner et al., 2011). Although many studies focus on the effects of mowing and grazing intensity on pollinators, the timing of these practices may equally impact which floral resources are available and whether these resources remain available across the season and years (Lerman et al., 2018; Rakosy et al., 2022; Weiner et al., 2011). Specifically, oligolectic bee species, which we found to be rarer in PAs, must track the phenology of few, specific plant species (Anderson et al., 2021) and may be particularly sensitive to irregular management practices, as the removal of their floral resources cannot easily be compensated for by other plant species. Occasional synchronization between mowing or grazing events and the peak flowering of these plant species could severely impact the populations of oligolectic bees in a single year. Therefore, studies focusing on management practices in PAs are urgently needed to provide insights into how to enhance pollinator diversity in Natura 2000 grasslands.

Conclusions

In conclusion, while Natura 2000 areas provide some protection for pollinator communities, the currently designated PAs in our region appear insufficient in supporting both species-rich bee communities and threatened bee species compared to urban wastelands. Given the similar insect biomass and abundance between the two habitat types, Natura 2000 areas do not seem to broadly benefit flower visitors more than urban wastelands. Moreover, the lower diversity of bees in PAs in our study region seems to have negative consequences for the reproduction of bee-pollinated plant species. To provide more comprehensive protection for biodiversity, future conservation actions could benefit from incorporating urban areas into their strategies, and nature restoration initiatives should include insect pollinator conservation in their biodiversity objectives.

CRediT authorship contribution statement

Panagiotis Theodorou: Writing – review & editing, Writing – original draft, Visualization, Supervision, Formal analysis, Data curation, Conceptualization. **Wilhelm H.A. Osterman:** Writing – review & editing, Methodology, Investigation, Conceptualization, Writing – original draft. **Janna H. Mrozek:** Methodology, Investigation, Conceptualization. **Bilyana S. Wild:** Methodology, Investigation, Conceptualization. **Michael Beckmann:** Writing – review & editing, Resources, Conceptualization. **Julia Osterman:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Robert J. Paxton:** Writing – review & editing, Supervision, Resources, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available in Figshare at DOI: https://doi.org/10.6084/m9.figshare.24001695.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2025.02.001.

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