Ecological Engineering 93 (2016) 187–198

Contents lists available at ScienceDirect

Ecological Engineering

journal homepage: www.elsevier.com/locate/ecoleng

Off-road motorcycle circuits support long-term persistence of bees and wasps (Hymenoptera: Aculeata) of open landscape at newly formed refugia within otherwise afforested temperate landscape

Petr Heneberg[a,*], Petr Bogusch[b], Milan Řezáč[c]

[a] Charles University in Prague, Third Faculty of Medicine, Prague, Czech Republic
[b] University of Hradec Králové, Faculty of Science, Hradec Králové, Czech Republic
[c] Crop Research Institute, Biodiversity Lab, Drnovská 507, CZ-161 06 Prague, Czech Republic

ARTICLE INFO

Article history:
Received 19 November 2015
Received in revised form 11 March 2016
Accepted 10 May 2016
Available online 24 May 2016

Keywords:
Aggregates quarrying
Biodiversity conservation
Enduro
Habitat conservation
Landscape restoration
Post-industrial sites

ABSTRACT

Newly formed refugia for open landscape species within otherwise afforested temperate landscape suffer from a lack of sustainability. Here, we test the hypothesis proposing off-road motorcycling as a long-term stressor, which could be responsible for the long-term sustainability of afforested habitat patches, particularly those formed in (post-)industrial areas, such as sandpits, claypits, quarries and ash and slug tailing ponds. To test this hypothesis, we analyzed assemblages of bees and wasps (Hymenoptera: Aculeata) within 19 off-road motorcycle circuits distributed across the Czech Republic, representing circuits subject to high- and low-intensity use, as well as recently closed circuits. Off-road motorcycle circuits were associated with specific assemblages of bees and wasps, many of which were of conservation interest. Open landscape species, in particular, as well as those requiring the presence of solitary, sun-exposed trees, thrived under such conditions. Formation of off-road motorcycle circuits, particularly those with low intensity traffic, should be considered an appropriate tool supporting the biodiversity in the highly cultivated landscape of Central Europe, as they host highly diverse assemblages of specialist pollinators and other hymenopterans. Aculeata were sensitive to both the presence and intensity of off-road traffic. The species richness and abundance of red-listed Aculeata were associated with the presence of a fine-grained substrate, low-intensity off-road traffic and high diversity of E_2 plant species and E_1 red-listed plant species. In contrast, the overall abundance of Aculeata was not sensitive to any of these factors. There were no aculeate families specifically associated with closed off-road motorcycle circuits. Off-road motorcycle circuits should be considered to be an appropriate form of reclamation of closed quarries, sandpits and claypits, considering that off-road motorcycles can potentially be used as a management tool to block the afforestation of habitats formed at post-industrial sites.

1. Introduction

Recent trends in biodiversity conservation include the integration of managed human uses in the conservation of threatened biodiversity (Soule, 2013). The importance of human activities for the sustainability of biodiversity in cultural landscape became particularly evident with the abandonment of numerous historical agrotechnical approaches during the course of the 20th and 21st centuries. Many human activities are now recognized as tools that support or even allow the presence of a significant part of threatened species, particularly in regions with long-term impacts of human agricultural activities. In Central Europe, local hotspots of biodiversity are particularly associated with open landscape and wetlands. Historical approaches contributing to the presence of species-rich open landscape included traditional methods of mowing and grazing (Konvicka et al., 2008), mosaic management (Slamova et al., 2013), and traditional woodland management techniques, such as coppicing or woodland pasturing (Spitzer et al., 2008; Košulič et al., 2016). With the abandonment of these techniques, replacement (post-)industrial habitats, such as quarries (Tropek et al., 2010), sandpits (Heneberg et al., 2013) and fly ash deposits (Heneberg et al., 2014; Tropek et al., 2015) began to serve as key refuges for some of the biodiversity found within open landscape. The overall contribution of man-made habitats to bio-

---

[*] Corresponding author at: Charles University in Prague, Third Faculty of Medicine, Ruská 87, CZ-100 00 Prague, Czech Republic.
E-mail address: petr.heneberg@lf3.cuni.cz (P. Heneberg).

http://dx.doi.org/10.1016/j.ecoleng.2016.05.026
0925-8574/

diversity conservation is poorly understood (Siebert and Belsky, 2014), and some of these habitat types have never been examined.

Among human activities with poorly understood impacts on biodiversity is vehicle traffic. Some effects of traffic are well understood, including the detrimental effects of the collisions of vertebrates with cars and trains, which are estimated to cause over one hundred million deaths annually (Seiler and Helldin, 2006). However, linear infrastructure is also associated with positive effects, hosting numerous arthropods, e.g., in road and railway dykes and verges (Moroń et al., 2014). Off-road traffic is stigmatized due to its detrimental effects on the stability of sand dunes in (semi-)desert areas, and is considered to be a causative agent of a decrease of both vertebrates (Berry, 1980) and invertebrates (Griswold, 1996; Kurczewski, 2000; Wilson et al., 2009) that are associated with undisturbed dunes and savanna, including some aculeate hymenopteran species. However, during the 2000s, disturbances introduced by vehicles and explosions in military training areas were shown to be beneficial for disturbance-dependent arthropods by several independent research groups (Mazucco, 2001; Carvell, 2002; Buchholz and Hartmann, 2008; Graham et al., 2008; Warren and Büttner, 2008; Graham et al., 2009; Nilsson and Alves-dos-Santos, 2009; Exeler et al., 2010; Cizek et al., 2013). The effects of such disturbances were particularly important in the otherwise afforested landscape of Central Europe, where militaries unintentionally maintained forest-free patches. In the 1990s, numerous military training ranges were closed in the Czech Republic and other post-communist countries. Aculeate hymenoptera and other arthropods flourished at such closed sites, but after several years, their abundance and diversity decreased sharply with the decreasing availability of bare soil and with the initiation of forest succession unless disturbances were re-introduced as a part of conservation management (P. Heneberg & P. Bogusch, pers. obs.). Due to resource partitioning in food or nesting requirements, the low heterogeneity of microhabitats within intensively cultivated landscapes can have drastic effects on the species diversity of hymenopterans (LaSalle and Gauld, 1993). Reproduction of aculeate hymenopterans requires species-specific nest sites, specific materials for nest construction, nectar and pollen or prey to maintain the activities of adults and to provision larval food (Westrich, 1996). The paucity of aculeate hymenopterans in agricultural landscapes is often due to a lack of suitable nest sites. Their populations can be enhanced by placing suitable trap nests in the habitat (Tscharntke et al., 1998); nest sites are probably more often a limiting factor than food sources, such as flowers or arthropods (Gathmann and Tscharntke, 2002).

Interestingly, there are no systematic studies on the impact of off-road vehicles on the biodiversity of arthropods in landscapes other than deserts or semi-deserts. However, several species-specific studies have suggested that off-road tracks and their vicinity may attract certain aculeate hymenopteran species. As with any disturbed site, these may include alien species, such as *Solenopsis invicta* in the U.S. (Tschinkel and King, 2013), but more commonly by the native species that are rarely encountered in the surrounding landscape, such as *Bembix rostrata* in the Czech Republic (Heneberg & Bogusch, unpubl.), *Lasioglossum majus* in Italy (Boesi et al., 2009), or *Cerceris mimica* in Colorado (Evans, 2000). Some authors noticed that, such as in the case of *Tachysphex pechumani*, a moderate intensity of disturbances by off-road vehicles is responsible for the formation of the *T. pechumani* habitat (Kurczewski, 2008), but the disturbance itself might have detrimental effects when applied within a particular microhabitat at the time of nesting of the species (Kurczewski, 2008; Moan and Tramer, 2008).

In this study, we aim to investigate, whether there are any species that managed to survive in close proximity to off-road motorcycle circuits subject to regular, high-intensity use, circuits subject to irregular, low-intensity use, and recently closed circuits or whether there are any species that even use such sites as refugia within the otherwise intensively cultivated cultural landscape. Importantly, many off-road motorcycle circuits are formed at post-mining sites, which were previously shown to host highly diverse assemblages of specialist pollinators and other arthropods (Heneberg et al., 2013, Heneberg and Řezáč, 2014). It is unclear whether off-road motorcycle circuits suppress the biodiversity associated with such sites (as implied by previous research on the effects of off-road vehicles in sand dunes) or whether they instead allow long-term sustainability of open habitats at post-mining sites. Aculeate hymenopterans are considered to be keystone components of post-mining ecosystems and also of the surrounding cultural landscape, where the abundance and diversity of hymenopterans is declining for various reasons, with direct consequences for plant pollination (Wilson et al., 2009; Garibaldi et al., 2013). Despite evidence showing that (post-)mining sites host diverse hymenopteran fauna, we still do not know what management measures are both necessary and sufficient to prevent the progression of succession towards deciduous woods or shrubby grasslands (Řehounková and Prach, 2008) once mining has ceased. We thus provide evidence allowing for a decision to be made regarding whether the formation of off-road motorcycle circuits should be considered to be an appropriate form of reclamation of closed quarries, sandpits and claypits, considering that off-road motorcycles can potentially be used as a management tool, which is blocking afforestation of the steppe-like habitats formed at post-industrial sites.

2. Material and methods

2.1. Study area and sampling sites

The study was carried out at 19 off-road motorcycle circuits distributed across the Czech Republic (48°39′–50°59′N, 12°19′–18°29′E; Fig. 1). Off-road motorcycle circuits were examined at altitudes 200–470 m above sea level (mean 351 ± 81 m above sea level) and were distributed based on the space-for-time substitution paradigm proposed by Pickett (1989). Three groups of sampling sites were analyzed, representing various intensities of off-road motorcycle circuit use: circuits subject to regular, high-intensity use; circuits subject to irregular, low-intensity use; and recently closed circuits. Regular, high-intensity use circuits ($n = 6$) were defined as those subject to an estimated daily use by >10 individuals per week during the peak season. This category included all circuits subject to the fee for use. Low-intensity use circuits ($n = 9$) were defined as those subject to an estimated daily use of 1–10 individuals per week during the peak season, which typically included free or illegal circuits. Recently closed circuits ($n = 4$) were defined as those previously subjected to regular use, but that have been closed to any off-road traffic for 1–5 years prior the onset of this study.[1]

---

[1] The intensity of the off-road motorcycle circuit use was directly related not only to the traffic intensity itself but also to the associated environmental variables and did not represent a continuum. Circuits subject to regular, high-intensity use were characterized by intensively maintained tracks, grass cut alongside the tracks, frequent presence of large numbers of fans and thus with trampling, and with repeated remodeling of the terrain surrounding the tracks. Circuits subject to irregular, low-intensity use were characterized by unmaintained tracks with their surroundings also lacking any management other than random passages of motorcycles throughout the surrounding terrain. There was a negligible presence of fans, and thus there was no trampling, and the terrain surrounding the tracks was not remodeled at any time or only once at the time of track formation. Recently closed circuits possessed mixed characteristics of the above, but were not subject to any maintenance or other human activities for 1–5 years prior to the study onset, except for the following: one of the recently closed circuits was subject to a grass burn just before the

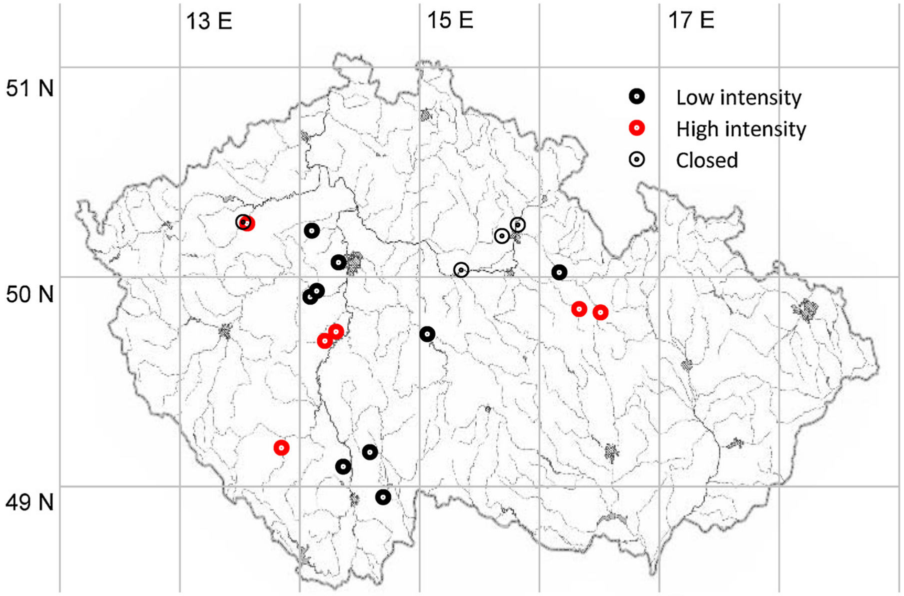

Fig. 1. Location of study sites in the Czech Republic. Black dots represent the circuits subject to regular, high-intensity use. Red dots (grey in the printed version) represent the circuits subject to irregular, low-intensity use. Open dots represent the recently closed circuits.

2.2. Sampling

We used Moericke traps to compare the spectrum of species present at the three types of habitats. Moericke traps have been successfully used for the collection of bees and wasps in a wide range of habitats, cf. Cruz-Sánchez et al. (2011), Vrdoljak and Samways (2012) and Heneberg and Bogusch (2014). Traps were made from round-shaped 570 ml polypropylene containers, 120 mm in upper diameter and 80 mm deep (Obal Centrum, Sezemice, Czech Republic), filled to the upper quarter with water, salt and a mixture of ionic and anionic detergents (Jar, Procter and Gamble, Rakovník, Czech Republic). At each sampling site, we used traps of two colors: white (RAL 9010) and yellow (RAL 1021), and exposed them in pairs or in a line transect with a total of 10 white and 10 yellow traps per sampling site. Collected specimens were stored in 96% ethanol until pinning for identification. Moericke traps were exposed for several days in each of the following three periods: 29 March–21 April 2014, 2 June–27 June 2014, and 4 July–23 August 2014. The sampling periods for each sampling site as well as the number of traps exposed are given in Table **S1**. In total, insects were collected from traps exposed for 5631 trap-days, which were equally distributed throughout the sampling periods (1801, 2020 and 1810 trap-days, respectively). Vandalism and other causes decreased the total number of trap-days by only 4.56% from the expected total (5900 trap-days). White traps were successfully exposed for 2824 days (50.15% of total), and yellow traps were exposed for 2807 days (49.85%). The number of trap-days per single sampling site ranged between 220 and 380, reflecting weather conditions. At each off-road motorcycle circuit, we installed the traps in a close proximity (0–5 m) to the off-road tracks.

Data on the altitude and orientation of the examined sampling sites were obtained from maps and aerial photographs available at <http://www.mapy.cz> (accessed 1-03-2016). Slope angles of macrorelief were measured using an optical reading clinometer to the nearest 0.5°. Soil penetration resistance and soil shear strength resistance were measured as described by Srba and Heneberg (2012). The dry sieve method was used to analyze soil texture as described by Heneberg (2001) using sieves with mesh sizes of 0.072, 0.125, 2.00 and 4.00 mm. Phytocenologic relevés were recorded in 25 m^2 areas, colocalizing with the examined transects, and were performed on 14-July and 18-August-2014. The vegetation cover was quantified using standardized ranks (Braun-Blanquet, 1932; Podani, 2006). Botanical nomenclature is according to Kubát (2002). In total 41 relevés were recorded, one to four per off-road motorcycle circuit, depending on the perceived heterogeneity of the plant assemblages at the sites where the Moericke traps were exposed.

2.3. Data analyses

Habitat specializations and nesting strategies were assessed according to Macek et al. (2010). The red-list status of aculeate hymenopterans was assessed according to Farkač et al. (2005). The species included in the Czech red-list are termed as "red-listed" throughout the text, and include all species known as regionally extinct (RE), critically endangered (CR), endangered (EN) or vulnerable (VU). Together with the red-listed species, we analyzed also the newly emerging (NE) species, which were identified in the Czech Republic only recently. Moericke traps have been successfully used previously for the collection of bees and wasps in a wide range of habitats of Central Europe. We thus were able to compare the data obtained at off-road motorcycle circuits with those obtained previously at the sand dune near Veská (Bogusch, 2008), in sandpits and gravel-sandpits (Heneberg et al., 2013), at ash and slug deposits of power plants (Tropek et al., 2015) and at sandstone rocks covered by early successional stages of burned pine forest and surrounding intact pine forest plantations (Bogusch et al., 2015).

Red-list status of vascular plants was assessed according to Grulich (2012). Vascular plant species included in the Czech red list were termed as "red-listed" throughout the text, and consisted of four categories of species: endangered (C2), vulnerable (C3), near-threatened (C4a) and data deficient species (C4b) according to Grulich (2012).

We analyzed all members of Hymenoptera: Aculeata (except Formicidae) obtained in course of the study. We estimated the species richness using the Chao-1 estimator, corrected for unseen

---

study started, and in another circuit, spruce trees were planted just at the terrain left in the exact shape that was found at the end of its use by off-road motorcycles.

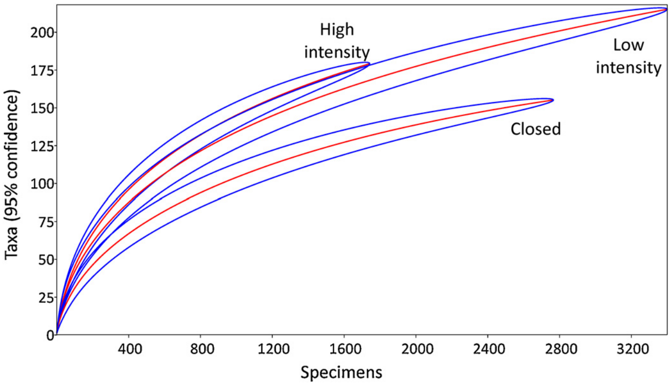

Fig. 2. Expected cumulative number of bee and wasp species at the off-road motorcycle circuits as defined by rarefaction curves and associated Chao-1 estimators. Data were analyzed separately for three intensities of the circuit use: circuits subject to regular, high-intensity use, circuits subject to irregular, low-intensity use, and recently closed circuits.

species. We compared the species richness of the analyzed datasets using Sørensen similarity index. We also calculated rarefaction curves and basic diversity indices for each of the datasets as described (Heneberg and Řezáč, 2014); these included the total number of species found, the total number of individuals found, dominance, Brillouin's index (particularly useful for the partially skewed datasets obtained from Moericke traps, which may be selective for species with certain behavioral habits), Margalef's species richness index, equitability, Fisher's alpha and Berger-Parker dominance index. To compare the diversities, we employed Shannon *t*-test with bias correction term (Poole, 1974). We used the Chi-squared test with Bonferroni correction according to MacDonald and Gardner (2000) to assess the species-specific differences in the abundance across the study habitats. To analyze the contribution of environmental variables, we applied a canonical correspondence analysis. The correspondence analysis took in account 29 environmental variables characterizing each respective sampling site, and species richness and abundance of Aculeata, species richness and abundance of red-listed Aculeata, and species richness of individual Aculeata families found. The calculations were performed in EstimateS 9.1.0 and PAST v. 2.14. Data are shown as mean ± SD unless stated otherwise.

3. Results

3.1. Diversity of bees and wasps at off-road motorcycle circuits

We collected a total of 7912 individuals from 302 species of bees and wasps (Hymenoptera: Aculeata) from 14 families. The highest diversity was found in Crabronidae (50 species), Apidae (45 species), Halictidae (44 species), Andrenidae (36 species), Megachilidae and Pompilidae (31 species each), and Chrysididae, Colletidae and Vespidae (18 species each). The Chao-1 species richness estimator (corrected for unsampled species) indicated a species richness of 388 ± 25 bee and wasp species at the off-road motorcycle circuits that were examined.

Circuits subject to regular, high-intensity use hosted an estimated 235 ± 19 species of bees and wasps. Circuits subject to irregular, low-intensity use hosted more diverse assemblages, with an estimated 302 ± 27 species of bees and wasps. However, recently closed circuits hosted the least diverse assemblages, with an estimated 190 ± 13 species of bees and wasps (Table 1, Fig. 2). Bee and wasp assemblages at circuits subject to long-term use of any intensity displayed low dominance. The dominance values tripled with the closure of circuits. The closure of the circuit is thus, paradoxically, considered to be a disturbance that is introduced into the already well-established system, which is associated with long-term circuits, and has negative effects on the stability of the associated assemblages. Supporting the above conclusion, the other diversity indices also suggested the deterioration of circuit-associated assemblages following their closure. These included the decrease in the Brillouin index, Margalef's species richness index, Fisher's alpha and equitability, which reflects the changes in the entropy of the analyzed assemblages. The Berger-Parker dominance index increased up to 0.24, suggesting that one quarter of individuals captured at recently closed circuits belonged to a single species only. Despite diversity differences between the closed and active circuits, but not between the circuits of high and low intensity of use, the intensity of use drove the species composition of assemblages associated with the circuits, as the Sørensen similarity index only reached 0.588 when comparing circuits subjected to high and low intensity of use, whereas it reached 0.607-0.618, when comparing these two groups with the recently closed circuits (Table 1).

Of the 302 bee and wasp species identified, we captured 10 or more individuals from 84 species. Of these, 41 (49%) displayed significant differences in their abundance in response to the intensity of use of off-road motorcycle circuits (Table 2). The circuits subject to regular, high-intensity use attracted only common polylectic species of the surrounding landscape, such as *Andrena bicolor*, *A. cineraria* and *A. haemorrhoa*. In contrast, the traffic at such sites was too intense for a characteristic species of trampled paths and dirt roads, *Lasioglossum malachurum*, which abundantly colonized the low-intensity and, particularly, the closed circuits. Additionally, the snail-shell nesting *Osmia bicolor* and its parasite *Chrysura dichroa* were nearly completely absent at circuits subject to high-intensity use. The circuits subject to irregular, low-intensity use were typically associated with *Halictus tumulorum*, *H. simplex*, *H. subauratus*, *Andrena minutula*, *A. strohmella*, *Passaloecus singularis*, *Osmia bicolor*, *Tachysphex obscuripennis*, *Trypoxylon attenuatum*, *Tiphia femorata* and *Bombus lapidarius*, and, similarly to the recently closed circuits, hosted strong populations of *Lasioglossum* spp. The recently closed circuits hosted abundant populations of *Lasioglossum laticeps*, *L. malachurum*, *L. pauxillum*, *L. lucidulum* and *Andrena flavipes*. The majority of captures at recently closed circuits were composed of eusocial species, which formed large aggregations in the burrows dug directly at the surface of disused tracks (Table 2, Fig. 3).

3.2. Species of conservation concern

We found that off-road motorcycle circuits host a highly diverse pattern of rare species, many of which were present in abundant populations at multiple sampling sites. Many of the rare species were considered to be specialists for habitats with bare soil, such as aeolian sand dunes and gravel-sand river terraces, which are nearly absent in the Central European cultural landscape. We found 57 species of bees and wasps classified as regionally extinct, critically endangered, endangered or vulnerable; of those two species were new for Bohemia. Of these red-listed species, 19 species (33%) were present at intensively used circuits and 39 species (68%) were present at occasionally used circuits. Recently closed circuits hosted 21 red-listed species (37%) (Table 3; Fig. 3). Only four red-listed species were captured in all three examined habitats, including *Andrena barbilabris* (VU), *Polistes nimpha* (VU), *Osmia bicolor* (EN) and *Tachysphex obscuripennis* (VU). Importantly, the off-road motorcycle circuits hosted one species that was considered to be regionally extinct (*Nomada femoralis*), and 12 critically endangered species, namely, *Andrena florivaga* (Andrenidae), *Bombus muscorum*, *Ceratina cucurbitina* and *Nomada moeschleri* (all Apidae), *Chrysis chrysostigma*, *Chrysura simplex* and *C. trimaculata* (all Chrysididae), *Hylaeus gracilicornis* (Colletidae), *Halictus*

Table 1
Assessment of the diversity of bees and wasps at the Czech off-road motorcycle circuits, and their distribution according to the intensity of circuit use. Diversity indices are shown; these include the dominance, Fisher's alpha, and equitability, and their comparison using Shannon diversity *t*-test and bootstrapping. List of the species found is provided as Table S5.

Diversity index	Total	High intensity of circuit use	Low intensity of circuit use	Closed circuits	*p* (high vs. low intensity by bootstrapping)	*p* (high intensity vs. closed by bootstrapping)	*p* (low intensity vs. closed by bootstrapping)
Number of species recorded	302	179	215	155	>0.05	>0.05	0.001
Number of individuals captured	7912	1744	3401	2767			
Chao-1 ± SD	388.0 ± 24.9	234.6 ± 18.6	301.7 ± 26.8	189.6 ± 13.4			
Dominance	0.041	0.039	0.041	0.117	>0.05	0.001	0.001
Brillouin	3.89	3.82	3.80	2.98			
Margalef	33.53	23.85	26.32	19.43	>0.05	>0.05	0.001
Equitability	0.69	0.77	0.73	0.61	0.008	0.001	0.001
Fisher's alpha	62.23	50.00	51.01	35.47	>0.05	0.001	0.001
Berger-Parker dominance index	0.10	0.12	0.11	0.24	>0.05	0.001	0.001
Shannon *t*-test (t; d_f; p)					1.37; 3573.4; >0.05	17.81; 4236.9; <0.001	19.03; 5348.2; <0.001
Sørensen similarity index							
High intensity of circuit use			0.588	0.618			
Low intensity of circuit use				0.607			

scabiosae (Halictidae), *Coelioxys alata* (Megachilidae), *Evagetes subglaber* (Pompilidae) and *Stenodynerus chevrieranus* (Vespidae). The recently northwards-expanding rare thermophilic species were particularly characteristic for the examined sampling sites. Of them, *Ceratina cucurbitina* (CR) was recorded for the first time in Bohemia in this study.[2] *Halictus scabiosae* (CR) was recorded for the first time in Bohemia by us (this study[3] and other unpublished data) as well as by J. Straka and H. Kříženecká at multiple postindustrial sites in Bohemia and in urbanized areas of the capital city (Straka et al., 2015) in 2013 and 2014. *Chrysis chrysostigma* (CR)[4] is also considered a NW-spreading species that was found in Slovakia for the first time in the 1950s, in Moravia in 2001 and in Bohemia in 2006 (Bogusch et al., 2007). However, recent records indicate a slow-down or complete stop of *C. chrysostigma* range expansion (P. Bogusch, pers. obs.). Off-road motorcycle circuits also hosted 11 EN and 33 VU species (Fig. 3). Populations of some red-listed species were strong, and the species were captured at multiple circuits. The most frequently captured red-listed species was *Osmia bicolor* (EN, 122 individuals / 9 circuits), followed by *Tachysphex obscuripennis* (VU, 71/8), *Bembecinus tridens* (VU, 24/1), *Episyron rufipes* (VU, 21/1), *Halictus leucaheneus* (VU, 18/6) and *Nomada ferruginata* (VU, 12/3). The red-listed species included those occupying the forest edge ecotone (*Nomada moeschleri*, *Stenodynerus chevrieranus*, *Dipogon subintermedius*, *Osmia uncinata*), forest-steppe landscape (*Evagetes subglaber*, *Euodynerus quadrifasciatus*), steppes (*Andrena florivaga*, *Ceratina cucurbitina*, *Chrysura cuprea*, *C. trimaculata*, *Polistes bischoffi*), open sands (*Bembecinus tridens*, *Dinetus pictus*, *Pompilus cinereus*, *Sphex funerarius*), and trampled paths and dirt roads (*Nomada leucophthalma*), as well as wetland specialists (*Bombus muscorum*). The number of individuals captured did not allow for an assessment of whether the particular red-listed habitat specialists reflected the intensity of use of circuits. Specialists for multiple habitats were found at circuits subject to all of the three analyzed use intensities.

3.3. Habitat specializations and nesting strategies supported by off-road motorcycling

We have shown that off-road motorcycle circuits host diverse assemblages of bees and wasps. When analyzing the conservation potential of off-road motorcycling, we must identify which species benefit from such disturbance. Within the captured specimens, we identified 83 psammophilous species (27.6% of total), including specialists for aeolian sand dunes and gravel-sand river terraces. Another 58 species (19.3%) were considered to be species of other open habitats, typically steppes or forest steppes. The remaining 160 species (53.2%) were considered to be generalists or specialists for other habitat types, e.g., for wetlands, which are frequently present at terrain depressions within off-road motorcycle circuit areas (Fig. 4A). When only considering red-listed species, circuits were associated with 25 red-listed psammophilous species (44%), 13 red-listed species of other open habitats (23%) and 19 red-listed generalists or specialists for other habitats (33%) (Fig. 4B).

Species associated with off-road motorcycle circuits exhibited diverse nested strategies. The most species-rich were the soil burrowers, which were represented by 136 species (45.0% of total), followed by cavity adopters (77 species, 25.5%) and nest parasites (74 species, 24.5%). The less frequent nesting strategies were represented by 10 nest building species (3.3%) and four species that nest in empty snail shells (1.3%) (Fig. 4C). When considering only red-listed species, the spectrum of nesting strategies was similar, and only the share of species that burrow their nests in the soil was decreased. The highest species richness of red-listed species was found in nest parasites, represented by 20 species (35% of total), followed by the species that burrow their nests in the soil (18 species, 32%) and cavity adopters (15 species, 26%). We also identified three red-listed nest-building species (5%) and a single red-listed species that nests in shells (2%) (Fig. 4D).

3.4. Abiotic variables

All of the examined sampling sites were characterized by relatively high slope angles (15.1 ± 13.2°, range 0.0–44.0°), and with two exceptions were exposed to the south (WSW to ESE). Soil penetration resistance was highly variable (1.20 ± 1.05 kg × cm^{-2}, range 0.01–4.10 kg × cm^{-2}), but soil shear strength resistance was relatively low across all of the examined sites (0.24 ± 0.17 kg × cm^{-2}, range 0.01–0.88 kg × cm^{-2}). Some sampling sites were rich in cobbles and pebbles, whereas the sediments exposed at other sampling sites consisted of loam, silt or loamy soils. Cobbles and pebbles >4.00 mm formed 16.7 ± 17.7% (range 0.0–69.7%) of the analyzed soil specimens. Smaller pebbles of 2.00–4.00 mm formed 14.7 ± 10.3% (range 0.0–37.6%) of the analyzed soil specimens. Most of the material sampled was within the size range 0.125–2.00 mm, which formed 62.9 ± 21.4% (range 13.0–99.0%) of the analyzed soil specimens. Particles of 0.072–0.125 mm were responsible for 3.4 ± 7.7% (range 0.2–44.5%) of the weight of analyzed specimens,

---

[2] 1F 9–14 Jul 2014, Suchomasty, BE, 49.91°N, 14.09°E.

[3] 2F 2–8 Jun 2014, Srbsko, BE, 49.93°N, 14.14°E; 1F, 9–14 Jul 2014, Srbsko, BE, 49.93°N, 14.14°E; 1F 9–14 Jul, Nečín-Strupina, PB, 49.69°N, 14.21°E.

[4] 1F + 1M 8–13 Jun 2014, Záboří nad Labem, KH, 50.03°N, 15.35°E.

Table 2
Species-specific response of bees and wasps to the intensity of use of off-road motorcycle circuits. The examined circuits were split into three categories representing various intensity of use of the circuits. The number of expected individuals was calculated based on the total number of individuals captured and the number of trap-days per each category. Species with the total capture rate <10 specimens were excluded from the analysis. The significance was examined by the species-specific χ^2 tests with Bonferroni correction at n = 84.

Species	Conservation status	Number of specimens	OBSERVED			EXPECTED			$p\ (\chi^2)$	
			High intensity	Low intensity	Closed circuits	High intensity	Low intensity	Closed circuits	Bonferroni correction: $p < 0.05$ equals to $p < 6.0E-4$ at n = 84	Significance of the differences observed (***$p < 0.001$, **$p < 0.01$, *$p < 0.05$, n.s. = not significant)
Lasioglossum laticeps		793	41	89	**663**	253.6	284.5	254.9	1.8E-210	***
Lasioglossum malachurum		655	0	84	**571**	209.5	235.0	210.5	2.7E-201	***
Lasioglossum morio		653	204	**372**	77	208.9	234.2	209.9	1.3E-36	***
Lasioglossum pauxillum		522	57	**232**	**233**	167.0	187.3	167.8	2.8E-24	***
Halictus tumulorum		405	84	**282**	39	129.5	145.3	130.2	5.2E-46	***
Apis mellifera		395	131	**178**	86	126.3	141.7	127.0	1.2E-5	***
Andrena flavipes		351	77	60	**214**	112.3	125.9	112.8	2.5E-30	***
Halictus subauratus		266	14	**223**	29	85.1	95.4	85.5	9.1E-59	***
Andrena minutula		245	64	**136**	45	78.4	87.9	78.8	3.7E-10	***
Andrena bicolor		201	**143**	54	4	64.3	72.1	64.6	5.5E-35	***
Lasioglossum calceatum		171	**76**	**69**	26	54.7	61.3	55.0	4.7E-6	***
Lasioglossum politum		149	0	**99**	50	47.7	53.5	47.9	1.6E-19	***
Passaloecus singularis		138	7	**129**	2	44.1	49.5	44.4	5.1E-44	***
Halictus simplex		136	7	**122**	7	43.5	48.8	43.7	6.3E-38	***
Osmia bicolor	EN	122	3	**80**	39	39.0	43.8	39.2	1.8E-14	***
Andrena gravida		107	27	39	41	34.2	38.4	34.4	2.5E-1	n.s.
Ammophila sabulosa		89	24	26	39	28.5	31.9	28.6	6.2E-2	n.s.
Trypoxylon minus		73	36	22	15	23.3	26.2	23.5	5.0E-3	n.s.
Tachysphex obscuripennis	VU	71	9	**60**	2	22.7	25.5	22.8	8.2E-17	***
Trypoxylon attenuatum		71	2	**66**	3	22.7	25.5	22.8	1.4E-22	***
Lasioglossum leucozonium		68	22	37	9	21.7	24.4	21.9	8.8E-4	n.s.
Andrena nigroaenea		61	25	10	26	19.5	21.9	19.6	6.5E-3	n.s.
Priocnemis perturbator		56	15	29	12	17.9	20.1	18.0	4.0E-2	n.s.
Andrena cineraria		53	**35**	**15**	3	17.0	19.0	17.0	1.4E-7	***
Tiphia femorata		52	8	**42**	2	16.6	18.7	16.7	7.4E-11	***
Bombus pascuorum		51	24	19	8	16.3	18.3	16.4	1.9E-2	n.s.
Andrena haemorrhoa		49	**35**	4	10	15.7	17.6	15.8	1.2E-8	***
Bombus terrestris		45	19	14	12	14.4	16.1	14.5	3.4E-1	n.s.
Hoplitis leucomelana		44	9	**30**	5	14.1	15.8	14.1	3.5E-5	**
Arachnospila anceps		44	8	23	13	14.1	15.8	14.1	4.9E-2	n.s.
Anoplius viaticus		43	19	18	6	13.8	15.4	13.8	3.2E-2	n.s.
Hylaeus annularis		41	5	25	11	13.1	14.7	13.2	1.9E-3	n.s.
Hylaeus confusus		41	11	21	9	13.1	14.7	13.2	1.1E-1	n.s.
Andrena strohmella		40	1	**35**	4	12.8	14.3	12.9	7.3E-11	***
Bombus lapidarius		40	2	**29**	9	12.8	14.3	12.9	3.3E-6	***
Nysson distinguendus		39	4	1	**34**	12.5	14.0	12.5	1.4E-12	***
Lasioglossum sabulosum		38	18	4	16	12.2	13.6	12.2	4.5E-3	n.s.
Lasioglossum punctatissimum		37	**26**	8	3	11.8	13.3	11.9	2.6E-6	***
Diodontus minutus		35	**17**	0	**18**	11.2	12.6	11.3	5.5E-5	**
Tachysphex pompiliformis		34	8	14	12	10.9	12.2	10.9	5.7E-1	n.s.
Andrena fulva		33	13	11	9	10.6	11.8	10.6	6.5E-1	n.s.
Halictus rubicundus		31	**25**	5	1	9.9	11.1	10.0	3.4E-8	***
Lasioglossum lucidulum		29	5	1	**23**	9.3	10.4	9.3	2.3E-7	***
Harpactus elegans		28	2	0	**26**	9.0	10.0	9.0	4.7E-11	***
Lasioglossum lativentre		27	**20**	4	3	8.6	9.7	8.7	1.7E-5	**
Lasioglossum villosulum		27	5	**21**	1	8.6	9.7	8.7	2.1E-5	**
Andrena praecox		25	16	8	1	8.0	9.0	8.0	7.9E-4	n.s.
Hylaeus hyalinatus		25	5	18	2	8.0	9.0	8.0	6.3E-4	n.s.
Bembecinus tridens	VU	24	0	0	**24**	7.7	8.6	7.7	1.0E-11	***
Chrysura dichroa		22	0	**20**	2	7.0	7.9	7.1	4.5E-7	***
Colletes cunicularius		22	2	9	11	7.0	7.9	7.1	5.1E-2	n.s.
Episyron rufipes	VU	21	0	5	**16**	6.7	7.5	6.8	4.0E-5	**
Nomada flavoguttata		19	12	5	2	6.1	6.8	6.1	1.1E-2	n.s.
Oxybelus uniglumis		19	3	**15**	1	6.1	6.8	6.1	4.0E-4	*
Andrena helvola		18	2	0	**16**	5.8	6.5	5.8	1.4E-6	***
Oxybelus trispinosus		18	10	4	4	5.8	6.5	5.8	1.0E-1	n.s.
Halictus leucaheneus	VU	18	6	12	0	5.8	6.5	5.8	5.1E-3	n.s.
Anoplius infuscatus		18	4	7	7	5.8	6.5	5.8	6.6E-1	n.s.
Arachnospila minutula		18	8	7	3	5.8	6.5	5.8	3.2E-1	n.s.
Halictus maculatus		17	7	7	3	5.4	6.1	5.5	4.3E-1	n.s.
Anthidium punctatum		17	1	**15**	1	5.4	6.1	5.5	4.0E-5	**
Osmia rufa		17	**13**	0	4	5.4	6.1	5.5	2.0E-4	*
Hedychrum niemelai		16	2	8	6	5.1	5.7	5.1	2.3E-1	n.s.

Table 2 (*Continued*)

Species	Conservation status	Number of specimens	OBSERVED			EXPECTED			p (χ^2)	
			High intensity	Low intensity	Closed circuits	High intensity	Low intensity	Closed circuits	Bonferroni correction: $p < 0.05$ equals to $p < 6.0E-4$ at n = 84	Significance of the differences observed ($^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, n.s. = not significant)
Cerceris rybyensis		16	0	9	7	5.1	5.7	5.1	2.2E-2	n.s.
Calliadurgus fasciatellus		16	4	10	2	5.1	5.7	5.1	7.0E-2	n.s.
Dolichurus corniculus		14	5	9	0	4.5	5.0	4.5	2.1E-2	n.s.
Megachile centuncularis		14	4	7	3	4.5	5.0	4.5	5.1E-1	n.s.
Andrena nitida		13	7	4	2	4.2	4.7	4.2	2.0E-1	n.s.
Hylaeus brevicornis		13	3	10	0	4.2	4.7	4.2	5.0E-3	n.s.
Auplopus carbonarius		13	2	10	1	4.2	4.7	4.2	8.0E-3	n.s.
Nomada ferruginata	VU	12	0	**12**	0	3.8	4.3	3.9	2.2E-5	**
Chrysis bicolor		12	1	9	2	3.8	4.3	3.9	1.7E-2	n.s.
Nysson spinosus		12	9	0	3	3.8	4.3	3.9	3.3E-3	n.s.
Pemphredon lethifer		12	1	9	2	3.8	4.3	3.9	1.7E-2	n.s.
Nomada signata		11	5	4	2	3.5	3.9	3.5	5.2E-1	n.s.
Dinetus pictus	VU	11	0	0	**11**	3.5	3.9	3.5	9.1E-6	***
Lestica subterranea	VU	11	**11**	0	0	3.5	3.9	3.5	8.3E-6	***
Sphecodes miniatus		11	2	9	0	3.5	3.9	3.5	4.8E-3	n.s.
Bombus sylvarum		10	6	1	3	3.2	3.6	3.2	1.1E-1	n.s.
Nysson maculosus	VU	10	0	7	3	3.2	3.6	3.2	4.0E-2	n.s.
Tachysphex unicolor		10	3	4	3	3.2	3.6	3.2	9.6E-1	n.s.
Sphecodes niger		10	2	8	0	3.2	3.6	3.2	1.1E-2	n.s.
Agenioideus cinctellus		10	4	5	1	3.2	3.6	3.2	3.2E-1	n.s.
Polistes nimpha	VU	10	2	6	2	3.2	3.6	3.2	2.8E-1	n.s.

Table 3

Intensity of use of off-road motorcycle circuits drives the species richness and abundance of red-listed bee and wasp species. Number of species, number of individuals, and the number of individuals relative to 1000 trap-days are shown. Number of regionally extinct (RE), critically endangered (CR), endangered (EN), vulnerable (VU), and least concern (LC) species are shown. The examined circuits were split into three categories representing various intensity of use of the circuits. The significance was examined by the species-specific χ^2 tests with Bonferroni correction at n = 5.

Conservation status	Total	Number of species			Total number of individuals	Number of individuals normalized to 1000 trap-days			p (χ^2)	
		High intensity	Low intensity	Closed circuits		High intensity	Low intensity	Closed circuits	Bonferroni correction: $p < 0.05$ equals to $p < 1.0E-02$ at n = 5	Significance of the differences observed ($^{***}p < 0.001$, $^{**}p < 0.01$, $^{*}p < 0.05$, n.s. = not significant)
RE	1	0	1	0	1	0.0	0.5	0.0	N/A	N/A
CR	12	5	6	2	26	2.8	8.9	1.7	1.6E-3	**
EN	11	2	9	5	152	2.2	47.5	28.7	1.6E-16	***
VU	33	12	23	14	235	21.7	63.9	37.0	7.3E-10	***
LC	245	160	176	134	7498	941.7	1562.9	1461.3	5.8E-68	***

whereas silt and clay formed 2.4 ± 3.6% (0.04–17.5%) of the analyzed specimens (Table S2).

All of the sampling sites were located above bedrock of Phanerozoic origin. Ten sites (53%) were located on sediments of Cenozoic origin, five (26%) were of Mesozoic origin, and the bedrock at four sites (21%) was of Paleozoic origin. The sites of Cenozoic origin consisted of unconsolidated sediments, whereas all of the older sediments were subject to previous lithification. Two sites with bedrock of Paleozoic origin consisted of igneous rock; the other sites were located on sediments. The Cenozoic sediments consisted of various types of sands, including aeolian sand (one site), alluvial sand deposits (three sites), gravelsand (one site), sandy gravel (one site), sandy soil (two sites), loessic soil (one site), or ash and slug deposit (one site). Mesozoic sediments consisted of claystone (one site), marlite (two sites), and sandstone (two sites). Paleosoic bedrock consisted of claystone, limestone (one site each), and granodioritic regolith (two sites) (Table S3).

3.5. *Phytocenologic relevés*

Phytocenologic relevés performed within areas of off-road motorcycle circuits were characterized by their mostly low E_3 cover (8.2 ± 22.9%; range 0–80%), but highly variable cover of shrubs, herbs and nonvascular plants, with the E_2 cover reaching 31.0 ± 24.8% (range 0–80%), E_1 cover reaching 61.1 ± 28.5% (range 5–100%), and E_0 cover reaching 8.1 ± 16.9% (range 0–80%). The E_3 species diversity reached 0.3 ± 1.0 species (range 0–5 species) per examined relevé, with no red-listed species The E_2 species diversity reached 2.0 ± 1.4 species (range 0–6 species) per examined relevé, with only a single red-listed E_2 species found at a single examined relevé (*Sorbus aria*, C2b, near Suchomasty, BE). The E_1 species diversity reached 20.5 ± 11.0 species (range 2–42 species) per examined relevé, with 0.7 ± 0.8 red-listed E_1 species (range 0–3 species) per examined relevé. Within all of the examined relevés, we identified, in total, 11 E_3 species; 28 E_2 species, of which one (3.6%) was red-listed; and 251 E_1 species, of which 16

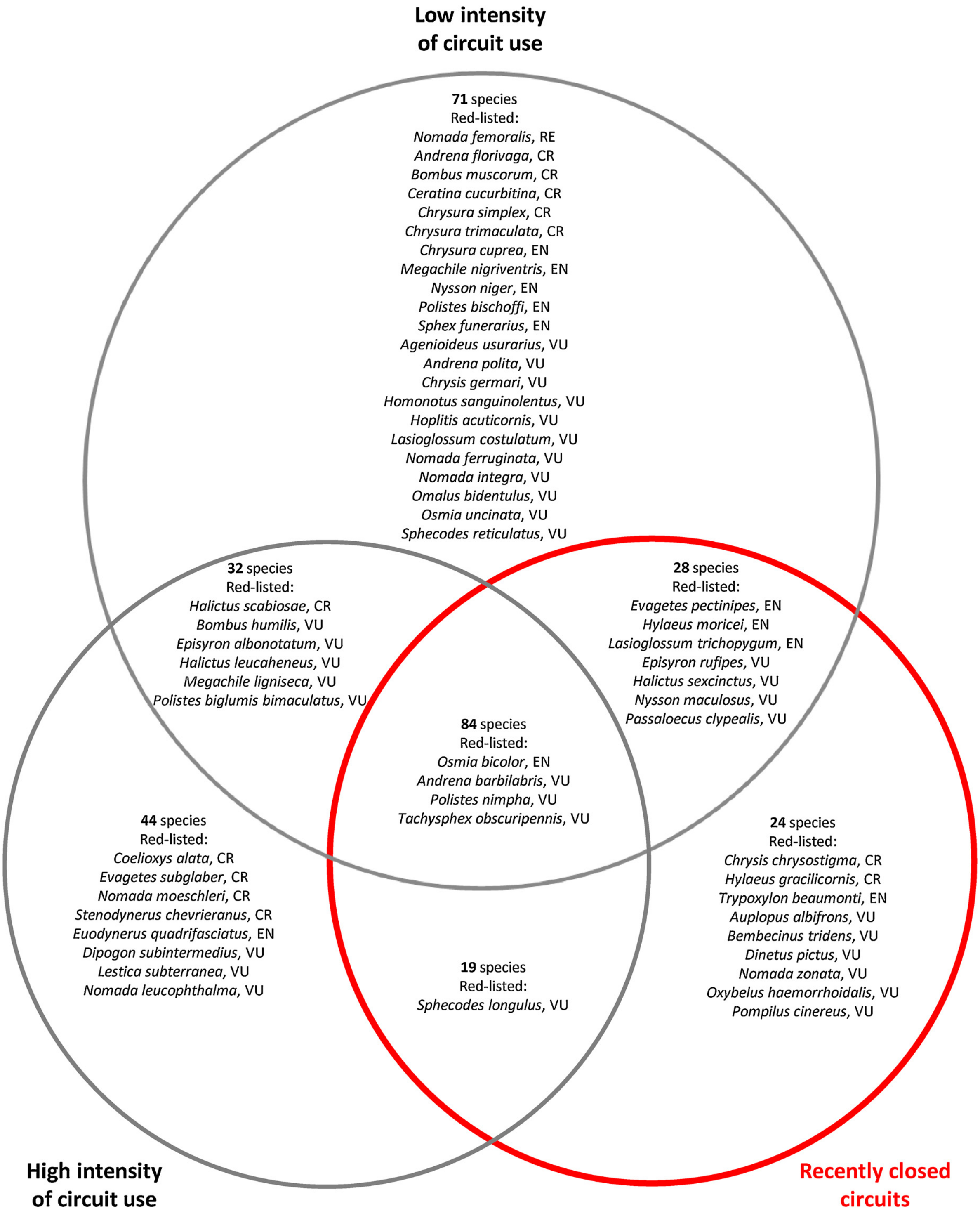

Fig. 3. Venn diagram of the clustering of bee-and wasp species at the off-road motorcycle circuits subject to different intensity of their use. The sampling sites were classified according to three intensities of the circuit use were: circuits subject to regular, high-intensity use, circuits subject to irregular, low-intensity use, and recently closed circuits. In the figure, we show the total number of species found only in one habitat type or shared by multiple habitats, and a complete list of red-listed species found in each of the habitat types.

(6.4%) were red-listed. Among the red-listed species, two were considered endangered (C2b species *Sorbus aria* and *Plantago arenaria*), five were considered vulnerable (C3 species *Cirsium eriophorum*, *Filago arvensis*, *Melampyrum arvense*, *Reseda luteola*, and *Vulpia myuros*), eight were considered nearly threatened (C4a species *Centaurium erythraea*, *Cirsium acaulon*, *Corynephorus canescens*, *Crepis foetida*, *Melica transsilvanica*, *Petrorhagia prolifera*, *Verbascum densiflorum*, and *Viola mirabilis*) and two species were data deficient (C4b species *Alchemilla* cf. *propinqua*, and *Lathyrus nissolia*). Most of the red-listed species were found in only few individuals. Their cover reached only up to 1% of the examined quadrants, and were not found in more than one off-road motorcycle circuit. Exceptions consisted of *Filago arvensis* (3 relevés, 2× r, 1× +), *Centaurium erythraea* (2 relevés, 2× r), *Petrorhagia prolifera* (3 relevés, 1× 1, 2×

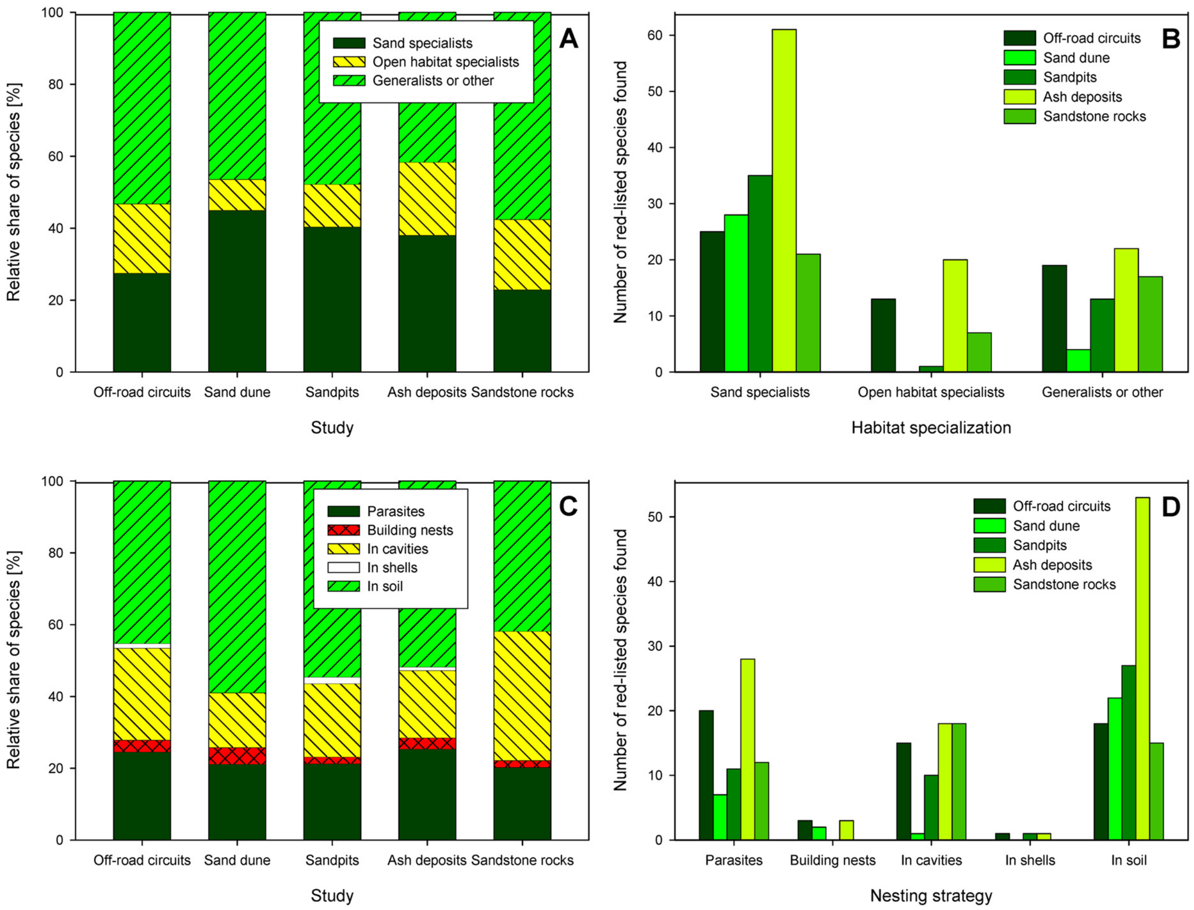

Fig. 4. Habitat requirements (A and B) and nesting strategies (C and D) of bees and wasps found at the Czech off-road motorcycle circuits as compared with previous studies conducted in open habitats within the identical geographical region. We compared here the data obtained in this study (off-road circuits), at the sand dune near Veská (sand dune) (Bogusch, 2008), in sandpits and gravelsandpits (sandpits) (Heneberg et al., 2013), at ash and slug deposits of power plants (ash deposits) (Tropek et al., 2015) and at sandstone rocks covered by early successional stages of burned pine forest and surrounding intact pine forest plantations (sandstone rocks) (Bogusch et al., 2015). (A) Relative share of species of bees and wasps specialized for sandy habitats (sand specialists), other opened habitats (open habitat specialists) and generalists and specialists for other habitat types (generalists or other) found in course of each of the five studies. (B) Number of red-listed species and species new for the Czech Republic specialized for the three above-indicated habitat types and found in course of this study (off-road circuits) or the four comparative studies. (C) Relative share of major nesting strategies of bees and waps found in course of this study (off-road circuits) or the four comparative studies. The nesting strategies were categorized as follows: nesting in soil (including species nesting facultatively in both, soil and cavities), in shells, in cavities (including crevices, old galls, etc.), building nests and parasitic species. (D) Number of red-listed species and species new for the Czech Republic specialized for the five above-indicated nesting strategies and found in course of this study (off-road circuits) or the four comparative studies.

+), *Crepis foetida* (4 relevés, 3× r, 1× +), and *Cirsium acaulon* (1 relevé, 1× 1). The examined off-road motorcycle circuits were not associated with any specific type of E_3 or E_2 vegetation; the most frequently found E_3 species were represented by *Pinus sylvestris* and *Tilia cordata* (2 relevés each). The most frequently found E_2 species were represented by *Pinus sylvestris* (10 relevés), *Populus tremula* and *Betula pendula* (both at 7 relevés), *Sambucus nigra*, *Salix caprea*, *Rosa canina* and *Robinia pseudacacia* (6 relevés each), *Swida sanguinea* (4 relevés) and *Prunus insititia* (3 relevés). However, we found numerous E_1 species shared across multiple sampling sites. These included *Calamagrostis epigejos* (25 relevés, dominant at many of them), *Hypericum perforatum* (24 relevés), *Dactylis glomerata* (23 relevés), *Arrhenatherum elatius* (18 relevés, dominant at many of them), *Artemisia vulgaris* (18 relevés), *Plantago lanceolata* (15 relevés), *Daucus carota* (14 relevés), *Cirsium arvense*, *Urtica dioica* and *Poa compressa* (13 relevés each), and *Agrostis capillaris*, *Festuca rupicola* and *Lotus corniculatus* (12 relevés each). The following species reached >50% cover: *Arrhenatherum elatius* (3 relevés), *Betula pendula*, *Pinus sylvestris*, *Robinia pseudacacia* (2 relevés each), and *Acer campestre*, *Agrostis capillaris*, *Calamagrostis epigejos*, *Cytisus scoparius* and *Populus tremula* (1 relevé each). Detailed data obtained from the relevés are available in Table S4.

Canonical correspondence analysis (Fig. 5) showed that the species richness of red-listed plant species and slope of the terrain were highly correlated with the first ordination axis which explained 54.4% of the variance in the species data. The second ordination axis was highly correlated with the intensity of off-road traffic and explained 22.0% of the variance in the species data, suggesting that the intensity of traffic is a major environmental factor driving the species composition and abundance of Aculeata associated with off-road motorcycle circuits. Note that the red-listed Aculeata abundance and red-listed Aculeata species richness were positively correlated with the presence of a fine-grained substrate, low-intensity off-road traffic and high diversity of E_2 plant species and E_1 red-listed plant species. In contrast, the overall abundance of Aculeata was not sensitive to any of these factors. The species richness of particular Aculeata families responded differently to the environmental factors monitored, but there was no Aculeata family, which would be associated only with closed off-road motorcycle circuits.

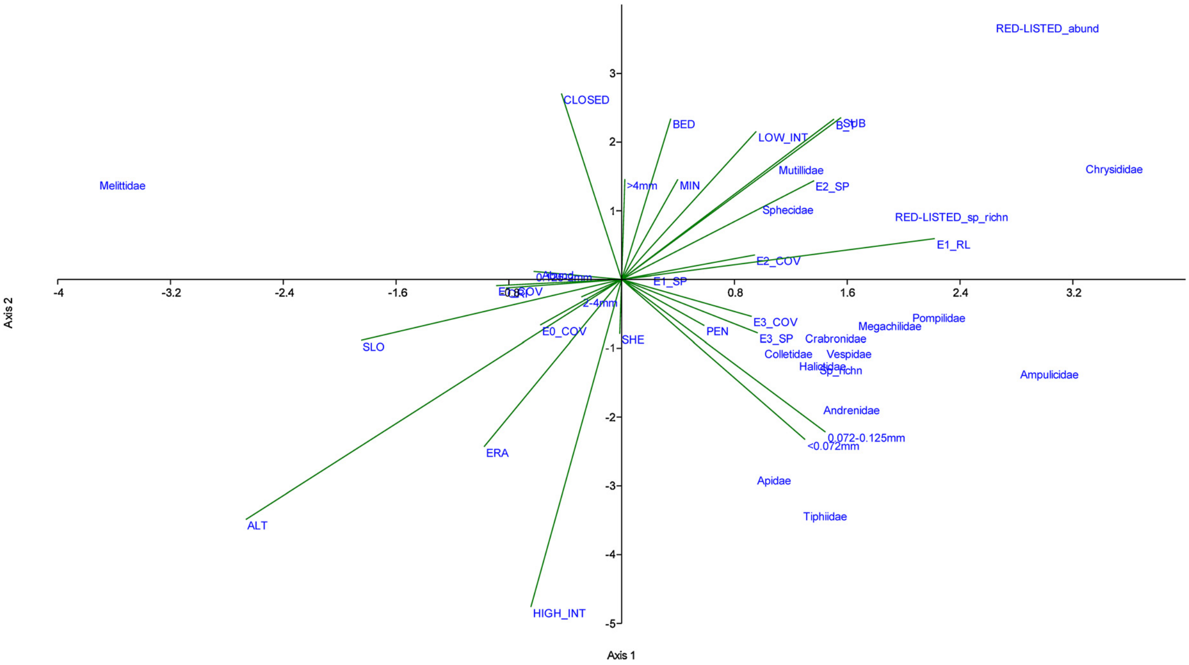

Fig. 5. Results of the canonical correspondence analysis involving biotic and abiotic variables characteristic for each analyzed off-road motorcycle circuit, and the species richness and abundance of Aculeata, of red-listed Aculeata, and species richness of individual Aculeata families found. Acronyms are explained in Table **S6**.

4. Discussion

In this study, we refuted the paradigm that off-road activities are principally detrimental to biodiversity. This paradigm was largely based on studies performed in arid landscapes (Berry, 1980; Griswold, 1996; Kurczewski, 2000; Wilson et al., 2009), where off-road traffic decreases the availability of bare but intact soil and disturbs slowly growing xerothermophilous plants. In contrast, repeated disturbances are necessary in temperate regions to maintain an open landscape and to prevent afforestation or colonization by fast-growing species in once disturbed but abandoned eutrophized habitats. Whereas natural disturbances are becoming increasingly rare events in intensively cultivated temperate landscapes, human activities often provide disturbed habitats. However, these disturbances are not cyclic, but are, instead, limited both in space and time (Kahn et al., 2001; Laurence, 2006; Prach and Hobbs, 2008). We thus attempted to identify activities that may contribute to the sustainability of open landcapes in post-industrial areas of otherwise afforested landscapes in temperate regions.

Based on our personal experience, we knew that open landscapes are maintained for decades at post-industrial sites subject to off-road motorcycling of any intensity. When we proposed to form such off-road motorcycle circuit as an alternative to the formation of a shooting range, as requested by a landlord, as a method of reclamation of a disused sandpit located within a protected landscape area, we realized that there was no available evidence supporting our hypothesis that regular disturbances (such as moderate off-road motorcycling) should better support the sustainability of the sandpit-associated biodiversity than any other form of management unless the site of interest is well drained and thus capable of maintaining steppe-like formations without provisioning any additional disturbances (which is usually true only for steep slopes under the weather conditions of the Czech Republic). We found that verges of off-road motorcycle circuits hosted numerous disturbance-dependent red-listed plant species (the only exceptions consisted of *Sorbus aria*, the shrub of xerothermic relic rocky habitats, and *Viola mirabilis*, the herb of well established oak woodlands). Whereas all such red-listed species found require regular disturbances that create spots with bare soil, most are not specialized for any extremes regarding the sand and clay content in the soil, these included: *Melampyrum arvense, Reseda luteola, Centaurium erythraea, Crepis foetida, Melica transsilvanica, Verbascum densiflorum, Petrorhagia prolifera, Lathyrus nissolia*. The more narrowly specialized species were represented by heavy marl soil specialists *Cirsium eriophorum* and *C. acaulon*, and by psammophilous species *Plantago arenaria, Filago arvensis, Vulpia myuros* and *Corynephorus canescens*.

We show here that off-road motorcycle circuits host diverse assemblages of bees and wasps, which managed to survive in close proximity to off-road motorcycling tracks with any intensity of off-road traffic (Table 1, Fig. 1). We have even shown that bees and wasps use such sites as refugia in the otherwise intensively cultivated cultural landscape. Interestingly, in agreement with the critics of off-road vehicles, we found that the share of species nesting in the soil is lower in the proximity of off-road motorcycle tracks (this study) than at other comparable post-industrial habitats, such as sandpits and ash deposits (Fig. 4C). This might be attributed to the excessive stress imposed on such species by the traffic itself. Alternatively, it might be caused by the fact that a large portion of our research was conducted on circuits formed on clay, as clay does not support species assemblages of bees and wasps as rich as sand or gravel-sand does. This is supported by the limited number of sand specialists found in the course of this study compared to those found at sand dunes or in sandpits and ash deposits (Fig. 4A). In contrast, the habitats affected by off-road motorcycling hosted very high shares of other open habitat specialists (19% of the species captured), which is a similar value to that found at ash deposits and in burned forest at the sandstone bedrock and is twice as high as that in sandpits and sand dunes (Fig. 4A). This difference is even more prominent when focusing on red-listed species. We found 13 red-listed species specializing in other open habitats, whereas sand dunes did not host a single one and sandpits hosted only one such species (Fig. 4B). Similarly, off-road motorcycle tracks were superior to sandpits when considering the species richness of species building nests or cavity adopters (Fig. 4C). The long-term stability of habitats maintained by off-road motorcycling allowed the formation of complex assemblages with a high share of red-listed nest parasites (Fig. 4D). Clearly, the key benefits of off-road motorcycling circuits consist of the maintenance of forest edges and forest-steppe landscape alongside tracks.

Considering the intensity of use, bee and wasp biodiversity was supported best by low-intensity motorcycling, which ensured that the open habitat was maintained for a long period of time, but did not greatly affect the surrounding terrain. In contrast, high-intensity motorcycling also supported the presence of species of conservation interest, but only at sites that were not mowed or trampled. However, even at such circuits, there were areas within the circuit surroundings that were used less or not at all by audience, and where vegetation was allowed to develop. At circuits undergoing high-intensity use, most of the captured species of conservation interest were bound to the forest edge ecotone or required the presence of sun-exposed solitary trees. At recently closed circuits, the tracks themselves were swiftly occupied by abundant colonies of soil burrowing species. However, the presence of such colonies is temporary and the assemblages associated with recently closed circuits were unstable and deteriorated, probably in response to the circuitsí closure (Table 1, Table 3).

We obtained our data using Moericke traps. Thus, we need to be aware of the limitations of the method – the species spectrum captured is far from complete as some species are not attracted to these traps, as shown by us previously for, e.g., *Pemphredon fabricii* (Heneberg et al., 2014). In this study, we used a combination of white and yellow traps, each of which provided somewhat different species- and sex-specific counts (Figs. S1 and S2). Some species were captured in white traps only, such as *Oxybelus uniglumis*, *O. trispinosus* and *Nomada signata*, or nearly exclusively in yellow traps, such as *Nysson maculosus*, *Passaloecus singularis*, *Calliadurgus fasciatellus* and *Hylaeus confusus* (Fig. S1). Similarly, there were species, in which one sex preferred a different color than the other sex, such as in *Lasioglossum sabulosum* (Fig. S2). This supports previous observations by us and other authors regarding the differential color preferences of hymenopterans (Toler et al., 2005; Gollan et al., 2011; Buri et al., 2014; Heneberg and Bogusch, 2014). As this study did not aim to provide a complete list of species using the study sites, but rather to provide the first ever evidence on the presence or absence of hymenopterans of conservation interest at off-road motorcycle circuits, potential omission of a part of the species spectrum present does not obstruct the interpretation of the results in the context of evidence-based conservation.

In conclusion, we have shown that off-road motorcycle circuits are associated with specific assemblages of bees and wasps, many of which are of conservation interest. Open-landscape species, and those requiring the presence of solitary, sun-exposed trees, particularly thrive under such conditions. Forest-steppe and solitary trees were once a common part of the Central European landscape, but with the change in the landscape management during the 20th century, they became rare elements of the current cultural landscapes. Clay and sand mining provides open landscape, but such activities do not ensure its sustainability for at least several decades. Here, we have shown that off-road motorcycle circuits are capable of maintaining such features and are accepted by specialized species of bees and wasps. Thus, the formation of off-road motorcycle circuits (particularly those with low intensity traffic) should be considered to be an appropriate tool supporting the biodiversity in the highly cultivated landscape of Central Europe, as they host highly diverse assemblages of specialist pollinators and other arthropods. Off-road motorcycle circuits should be considered to be an appropriate form of reclamation of closed quarries, sandpits and claypits, reflecting that off-road motorcycles can potentially be used as a management tool to block afforestation of habitats formed at post-industrial sites.

Acknowledgements

The study was supported by the projects PRVOUK P31/2012 from the Charles University in Prague, MZe RO0415 from the Ministry of Agriculture of the Czech Republic, and Specifický výzkum 2101/2015 from University of Hradec Králové. We thank the landlords and off-road motorcycle circuit operators for allowing access to the study sites and/or providing data on history of the particular sampling sites, and the nature conservation authorities for allowing the access to the protected areas.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2016.05.026.

References

Řehounková, K., Prach, K., 2008. Spontaneous vegetation succession in gravel-sand pits: a potential for restoration. Restor. Ecol. 16, 305–312.

Berry, K.H., 1980. A review of the effects of off-road vehicles on birds and other vertebrates. In: DeGraaf, R.M., Tilghman, N.G., Intermountain Forest and Range Experiment Station, Rocky Mountain Forest and Range Experiment Station, United States Forest Service (Eds.), Workshop Proceedings: Management of Western Forests and Grasslands for Nongame Birds. 11-14 Feb 1980, Salt Lake City. Intermountain Forest and Range Experiment Station, Rocky Mountain Forest, Range Experiment Station & Intermountain Region, Ogden, pp. 451–467.

Boesi, R., Polidori, C., Andrietti, F., 2009. Biology of *Lasioglossum* (*L.*) *majus* (Hymenoptera Halictidae), a largely solitary sweat bee with behavioural adaptations to communality. J. Ethol. 27, 361–367.

Bogusch, P., Straka, J., Kment, P. (Eds.), 2007. Annotated checklist of the Aculeata (Hymenoptera) of the Czech Republic and Slovakia. Acta Entomol. Mus. Nat. Pragae, Suppl. (11), 1–300.

Bogusch, P., Blažej, L., Trýzna, M., Heneberg, P., 2015. Forgotten role of fires in Central European forests: critical importance of early post-fire successional stages for bees and wasps (Hymenoptera: Aculeata). Eur. J. Forest Res. 134, 153–166.

Bogusch, P., 2008. Výsledky inventarizačního průzkumu žahadlových blanokřídlých (Hymenoptera: Chrysidoidea, Vespoidea, Apoidea) navrhované PP Vesecký kopec a návrh změn managementových aktivit. Pardubický kraj, Pardubice.

Braun-Blanquet, J., 1932. Plant Sociology: The Study of Plant Communities. McGraw-Hill Book Company, New York.

Buchholz, S., Hartmann, V., 2008. Spider fauna of semi-dry grasslands on a military training base in Northwest Germany. Arachnol. Mitt. 35, 51–60 (Münster).

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

Carvell, C., 2002. Habitat use and conservation of bumblebees (*Bombus* spp:) under different grassland management regimes. Biol. Conserv. 103, 33–49.

Cizek, O., Vrba, P., Benes, J., Hrazsky, Z., Koptik, J., Kucera, T., Marhoul, P., Zamecnik, J., Konvicka, M., 2013. Conservation potential of abandoned military areas matches that of established reserves: plants and butterflies in the Czech Republic. PLoS ONE 8, e53124.

Cruz-Sánchez, M.A., Asís, J.D., Gayubo, S.F., Tormos, J., González, J.A., 2011. The effects of wildfire on Spheciformes wasp community structure: the importance of local habitat conditions. J. Insect Conserv. 15, 487–503.

Evans, H.E., 2000. Observations on the biology of *Cerceris mimica* Cresson (Hymenoptera: Sphecidae: Philanthinae). J. Kansas Entomol. Soc. 73, 220–224.

Exeler, N., Kratochwil, A., Hochkirch, A., 2010. Does recent habitat fragmentation affect the population genetics of a heathland specialist, *Andrena fuscipes* (Hymenoptera: Andrenidae)? Conserv. Genet. 11, 1679–1687.

Farkač, J., Král, D., Škorpík, M., 2005. Red List of Threatened Species in the Czech Republic: Invertebrates. AOPK ČR, Prague.

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M., 2013.

Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339, 1608–1611.

Gathmann, A., Tscharntke, T., 2002. Foraging ranges of solitary bees. J. Anim. Ecol. 71, 757–764.

Gollan, J.R., Ashcroft, M.B., Batley, M., 2011. Comparison of yellow and white pan traps in surveys of bee fauna in New South Wales, Australia (Hymenoptera: Apoidea: Anthophila). Aust. J. Entomol. 50, 174–178.

Graham, J.H., Krzysik, A.J., Kovacic, D.A., Duda, J.J., Freeman, D.C., Emlen, J.M., Zak, J.C., Long, W.R., Wallace, M.P., Chamberlin-Graham, C., Nutter, J.P., Balbach, H.E., 2008. Ant community composition across a gradient of disturbed military landscapes at Fort Benning, Georgia. Southeast. Nat. 7, 429–448.

Graham, J.H., Krzysik, A.J., Kovacic, D.A., Duda, J.J., Freeman, D.C., Emlen, J.M., Zak, J.C., Long, W.R., Wallace, M.P., Chamberlin-Graham, C., Nutter, J.P., Balbach, H.E., 2009. Species richness, equitability, and abundance of ants in disturbed landscapes. Ecol. Indic. 9, 866–877.

Griswold, T.L., 1996. A new *Microbembex* endemic to the Algodones Dunes, California (Hymenoptera: Sphecidae). Pan Pac. Entomol. 72, 142–144.

Grulich, V., 2012. Red List of vascular plants of the Czech Republic: 3rd edition. Preslia 84, 631–645.

Heneberg, P., Řezáč, M., 2014. Dry sandpits and gravel-sandpits serve as key refuges for endangered epigeic spiders (Araneae) and harvestmen (Opiliones) of Central European steppes aeolian sands. Ecol. Eng. 73, 659–670.

Heneberg, P., Bogusch, P., 2014. To enrich or not to enrich? Are there any benefits of using multiple colors of pan traps when sampling aculeate Hymenoptera? J. Insect Conserv. 18, 1123–1136.

Heneberg, P., Bogusch, P., Řehounek, J., 2013. Sandpits provide critical refuge for bees and wasps (Hymenoptera: Apocrita). J. Insect Conserv. 17, 473–490.

Heneberg, P., Bogusch, P., Astapenková, A., 2014. Reed galls serve as an underestimated but critically important resource for an assemblage of aculeate hymenopterans. Biol. Conserv. 172, 146–154.

Heneberg, P., 2001. Size of sand grains as a significant factor affecting the nesting of bank swallows (*Riparia riparia*). Biologia 56, 205–210.

Kahn, J.R., Franceschi, D., Curi, A., Vale, E., 2001. Economic and financial aspects of mine closure. Nat. Resour. Forum 25, 265–274.

Košulič, O., Michalko, R., Hula, V., 2016. Impact of canopy openness on spider communities: implications for conservation management of formerly coppiced oak forests. PLoS ONE 11, e0148585.

Konvicka, M., Benes, J., Cizek, O., Kopecek, F., Konvicka, O., Vitaz, L., 2008. How too much care kills species: grassland reserves, agrienvironmental schemes and extinction of *Colias myrmidone* (Lepidoptera: Pieridae) from its former stronghold. J. Insect Conserv. 12, 519–525.

Kubát, K., 2002. Klíč ke květeně České republiky. Academia Prague.

Kurczewski, F.E., 2000. History of white pine (*Pinus strobus*)/oak (*Quercus* spp.) savanna in southern Ontario, with particular reference to the biogeography and status of the antennawaving wasp, *Tachysphex pechumani* (Hymenoptera: Sphecidae). Can. Field-Nat. 114, 1–20.

Kurczewski, F.E., 2008. I: Geographic distribution and paleobiogeography of *Tachysphex pechumani* (Hymenoptera: Crabronidae). Northeast. Nat. 15 (Monograph 2), 1–32.

LaSalle, J., Gauld, I.D., 1993. Hymenoptera and Biodiversity. Oxford University Press, Oxford.

Laurence, D., 2006. Optimisation of the mine closure process. J. Clean. Prod. 14, 285–298.

MacDonald, P.L., Gardner, R.C., 2000. Type I error rate comparisons of post hoc procedures for I × : J chi-square tables. Educ. Psychol. Meas. 60, 735–754.

Macek, J., Straka, J., Bogusch, P., Dvorak, L., Bezdecka, P., Tyrner, P., 2010. Blanokřídlí České Republiky 1. Žahadloví. Academia Prague.

Mazucco, K., 2001. Untersuchungen zur Stechimmenfauna des Truppenübungsplatzes Großmittel im Steinfeld, Niederösterreich (Hymenoptera: Apoidea, Sphecidae, Pompilidae, Vespoidea, Scoliidae, Chrysididae, Tiphiidae, Mutillidae). Stapfia 77, 189–204.

Moan, E.K., Tramer, E.J., 2008. III: Ecological observations on *Tachysphex pechumani* (Hymenoptera: Crabronidae). Northeast. Nat. 15, 67–76 (Monograph 2).

Moroń, D., Skórka, P., Lenda, M., Rożej-Pabijan, E., Wantuch, M., Kajzer-Bonk, J., Celary, W., Mielczarek, Ł., Tryjanowski, P., 2014. Railway embankments as new habitat for pollinators in an agricultural landscape. PLoS ONE 9, e101297.

Nilsson, L.A., Alves-dos-Santos, I., 2009. The oligolectic solitary bee *Melitta tricincta* Kirby, (Sw. rödtoppebi) in Sweden (Hymenoptera, Apoidea, Melittidae). Entomol. Tidskr. 130, 85–98.

Pickett, S.T.A., 1989. Space for time substitution as an alternative for long studies. In: Likens, E.G. (Ed.), Long-term Studies in Ecology: Approaches and Alternatives. Springer, Berlin, pp. 112–135.

Podani, J., 2006. Braun-Blanquet's legacy and data analysis in vegetation science. J. Veg. Sci. 17, 113–117.

Poole, R.W., 1974. An Introduction to Quantitative Ecology. McGraw-Hill, New York.

Prach, K., Hobbs, R.J., 2008. Spontaneous succession versus technical reclamation in the restoration of disturbed sites. Restor. Ecol. 16, 363–366.

Seiler, A., Helldin, J.O., 2006. Mortality in wildlife due to transportation. In: Davenport, J., Davenport, J.L. (Eds.), The Ecology of Transportation: Managing Mobility for the Environment. Environmental Pollution, vol. 10. Springer, Netherlands, Dordrecht, pp. 165–189.

Siebert, S.F., Belsky, J.M., 2014. Historic livelihoods and land uses as ecological disturbances and their role in enhancing biodiversity: an example from Bhutan. Biol. Conserv. 177, 82–89.

Slamova, I., Klecka, J., Konvicka, M., 2013. Woodland and grassland mosaic from a butterfly perspective: habitat use by *Erebia aethiops* (Lepidoptera: Satyridae). Insect Conserv. Divers. 6, 243–254.

Soule, M., 2013. The new conservation. Conserv. Biol. 27, 895–897.

Spitzer, L., Konvicka, M., Benes, J., Tropek, R., Tuf, I.H., Tufova, J., 2008. Does closure of traditionally managed open woodlands threaten epigeic invertebrates?: Effects of coppicing and high deer densities. Biol. Conserv. 141, 827–837.

Srba, M., Heneberg, P., 2012. Nesting habitat segregation between closely related terricolous sphecid species (Hymenoptera: Spheciformes): Key role of soil physical characteristics. J. Insect Conserv. 16, 557–570.

Straka, J., Bogusch, P., Tyrner, P., Říha, M., Benda, D., Čížek, O., Halada, M., Macháčková, L., Marhoul, P., Tropek, R., 2015. Faunistic records from the Czech Republic? 380. Hymenoptera: Aculeata. Klapalekiana 50, 77–91.

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

Tropek, R., Kadlec, T., Karesova, P., Spitzer, L., Kocarek, P., Malenovsky, I., Banar, P., Tuf, I.H., Hejda, M., Konvicka, M., 2010. Spontaneous succession in limestone quarries as an effective restoration tool for endangered arthropods and plants. J. Appl. Ecol. 47, 139–147.

Tropek, R., Cerna, I., Straka, J., Kocarek, P., Malenovsky, I., Tichanek, F., Sebek, P., 2015. In search for a compromise between biodiversity conservation and human health protection in restoration of fly ash deposits: effect of anti-dust treatments on five groups of arthropods. Environ. Sci. Pollut. Res. Int. (on-line first, 10.1007/s11356-015-4382-1).

Tscharntke, T., Gathmann, A., Steffan-Dewenter, I., 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. J. Appl. Ecol. 35, 708–719.

Tschinkel, W.R., King, J.R., 2013. The role of habitat in the persistence of fire ant populations. PLoS ONE 8, e78580.

Vrdoljak, S.M., Samways, M.J., 2012. Optimising coloured pan traps to survey flower visiting insects. J. Insect Conserv. 16, 345–354.

Warren, S.D., Büttner, R., 2008. Active military training areas as refugia for disturbance-dependent endangered insects. J. Insect Conserv. 12, 671–676.

Westrich, P., 1996. Habitat requirements of central European bees and problems of partial habitats. In: Matheson, A., Buchmann, S.L., OíToole, C., Westrich, P., Williams, I.H. (Eds.), The Conservation of Bees. Academic Press, London, pp. 1–16.

Wilson, J.S., Messinger, O.J., Griswold, T., 2009. Variation between bee communities on a sand dune complex in the Great Basin Desert, North America: implications for sand dune conservation. J. Arid Environ. 73, 666–671.