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ORIGINAL PAPER

# Industrial and post-industrial habitats serve as critical refugia for pioneer species of newly identified arthropod assemblages associated with reed galls

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**Abstract** Gravel-sand river terraces were nearly eliminated from central European landscape by river channelization. Monotypic stands of common reed (*Phragmites australis*) growing on such terraces are often stressed by drought, which makes them vulnerable to *Lipara* spp. (Diptera: Chloropidae) gallmakers. Although *Lipara* are considered ecosystem engineers, only fragmentary information is available on the biology of their parasitoids and inquilines. We analyzed the assemblages of arthropods (Arachnida, Collembola, Dermaptera, Psocoptera, Thysanoptera, Hemiptera, Raphidioptera,

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Neuroptera, Coleoptera, Diptera, Lepidoptera and Hymenoptera) that emerged from 17,791 *Lipara*-induced galls collected in winter from 30 reed beds in the Czech Republic, 15 of which were situated at (post)industrial sites (gravel-sandpits, tailing ponds, limestone quarries, colliery dumps, and reclaimed lignite open-cast mines) and 15 were in near-natural habitats (medieval fishponds, and river and stream floodplains). The Chao-1 estimator indicated 229.3 ± 18.1 species in reed galls at (post)industrial and 218.1 ± 23.6 species at near-natural sites, with the Sørensen index reaching only 0.58. We identified 18 red-listed species and four new species for the Czech Republic (*Gasteruption phragmiticola*, *Echthrodelphax fairchildii*, *Haplogonatopus oratorius* and *Enclisis* sp.), representing mostly obligate (64 %) or facultative (9 %) reed specialists. We propose that *Lipara* gall-associated assemblages undergo a long-term cyclic ecological succession. During first 10 years after reed bed formation, only *Lipara* spp. and several other species occur. During next decades, the reed beds host species-rich assemblages with numerous pioneer species (*Singa nitidula*, *Polemochartus melas*) that critically depend on presence of prior disturbances. Middle-aged reed beds (near medieval fishponds) are prevalently enriched in common species only (*Oulema duftschmidi*, *Dimorphopterus spinolae*). Habitats with the longest historical continuity (river floodplains) host again species-rich assemblages with several rare species that probably require long-term habitat continuity (*Homalura tarsata*, *Hylaeus moricei*). Landscape dynamics is thus critical for the persistence of a full spectrum of reed gall inquilines, with (post)industrials serving as the only refugia for pioneer species ousted from their key nesting habitats at once cyclically disturbed gravel-sand river terraces.

**Keywords** Biodiversity conservation · Community structure · Emergence traps · Hydric restoration · Life-history traits · Post-industrial habitats

## Introduction

Higher land use intensity substantially alters the associations among the diversities of multiple animal and plant taxa (Manning et al. 2015). Although many previous studies have investigated the effects of land use on the abundances of particular species and the biodiversity of individual taxonomic groups, there are still significant gaps in our understanding of the ecological consequences of land use changes (Allan et al. 2014; Weiner et al. 2014). Understanding these associations is particularly important as the use of inappropriate indicators can lead to poor conservation management decisions and planning, and wrong estimates of wider biodiversity. Particularly where taxa are trophically diverse, forming a mix of secondary consumers, herbivores and omnivores, their diversity is expected to be weakly correlated (Scherber et al. 2010; Weiner et al. 2014; Manning et al. 2015).

Monotypic stands of the common reed *Phragmites australis* serve as important habitats for numerous threatened vertebrates and host diverse communities of invertebrates. Reed beds are frequently protected as nature reserves and form large parts of endangered wetlands. However, the common reed is also considered to be invasive, particularly in North America, and it is also able to swiftly colonize newly formed (post)industrial habitats, such as sandpits, gravel-sandpits, claypits, former open-cast mines and ash deposits (Tscharntke 1992; van der Putten 1997; Čurn et al. 2007; Lelong et al. 2009; Heneberg et al. 2014).

Arthropods utilize common reed as a food source (sap suckers, leaf- and pollen-feeding species) or also as a nesting resource and shelter (stem borers, gall makers, and gall inquilines). Tewksbury et al. (2002) reported 160 species of reed-associated arthropods in Europe, but only 23 species of reed-associated arthropods in North America, where *Phragmites australis* subsp. *americanus* is considered native, but subsp. *australis* is considered an alien taxon. Interestingly, Canavan et al. (2014) reported only six species of arthropods in South Africa, where common reed is considered native, and only a few species were recorded in Australia (Wapshere 1990).

In total, over 100 oligophagous reed stem boring species are known (Tscharntke 1992, 1993, 1999), of which 11 damage reed shoot tops (Narchuk and Kanmiya 1996; Tscharntke 1999; Gudkov et al. 2006). These include nine species of *Lipara* flies (four of which, *L. lucens*, *L. rufitarsis*, *L. pullitarsis* and *L. similis*, occur in the Czech Republic, all inducing cigar-like galls on the top of reed shoots) and two species of *Steneotarsonemus* thread-footed mites (*S. phragmitidis* and *S. gibber*, which induce morphologically different type of galls).

The females of *Lipara* spp. deposit their eggs on the surface of the reed shoot, into which the first instar larvae bore and feed upon the newly emerging leaves. Meanwhile, the gall is formed, and the *Lipara* larvae enter the gall only when its formation is completed. Larvae of *L. lucens* and *L. rufitarsis* gnaw from the top through the growing point and continue their life cycle inside, whereas larvae of *L. pullitarsis* never pass through the growing point and can be found between the enwrapped leaves (De Bruyn 1994). Because of that, *L. lucens* and *L. rufitarsis* attack especially reed shoots of less than 4.5 mm in diameter. Such thin reed stems are usually formed in response to abiotic stress, including the deficiency in water or nutrients or severe contamination by heavy metals. The stressed stems contain less silicate and cause less mortality of gall-inducing first instar chloropid larvae (Tscharntke 1989). Newly formed reed beds are colonized relatively slowly. The $\geq$50 % probability of the presence of the two most abundant gall makers, *L. pullitarsis* and *Giraudiella inclusa*, is reached only in habitats older than 3 and 6 years, respectively, and larger than 25 and 100 $m^2$, respectively (Athen and Tscharntke 1999).

The reed galls induced by *Lipara* flies host a diverse spectrum of successors. The *Lipara* larvae serve as hosts to parasitoids, some of which are regulated by the physical properties of the galls. The survival of *L. lucens* is higher by 40 % on thicker shoots, which is mainly attributed to the parasitoid *Stenomalina liparae*, which attacks the host larva inside the reed shoot. The ovipositor of *S. liparae* has a mean length of 1.9 $\pm$ 0.2 mm, and when the walls of the shoot are too thick, the parasitoid simply does not reach the larva of *L. lucens*. In contrast, *Polemochartus liparae*, the second most important parasitoid of *L. lucens*, oviposits on the host while it is still attached to the surface of the reed shoot, thus there are no physical barriers to prevent the infestation (De Bruyn 1994). In addition, many inquilines use the *Lipara*-induced galls as a shelter for nesting or overwintering. Some of them also seem to preferentially select galls with narrowly defined physical properties or according to other habitat features, such as the proximity of food sources. In this regard, the previously reported main food source of the wasp *Pemphredon fabricii*, the aphid *Hyalopterus pruni*, shares a similar distribution pattern with its predator—it occurs abundantly at the edge of reed beds, whereas the central parts of large reed beds are subject to infestation that is lower by over one order of magnitude (Tscharntke 1992). Such difference is attributed to the intraseasonal switch of host plants of *H. pruni*—the reed is utilized during the summer, and then, the aphids migrate to their main host, *Prunus* spp. (Dill 1937). Habitat type in general contributes to the variability of reed-associated arthropod assemblages, with only few species considered insensitive to the habitat type (Tscharntke 1989).

Knowledge of the component community of *Lipara* reed gall parasitoids, predators and inquilines is still fragmentary. Few groups of arthropods have been thoroughly studied. These include parasitoids of *Lipara* spp. (e.g., Giraud 1863; Kasparjan 1981; Dely-Draskovits et al. 1994; Nartshuk 2006), dipteran inquilines (Pokorný and Skuhravý 1981; Tscharntke 1999; Grochowska 2008), and aculeate hymenopteran inquilines (Dely-Draskovits et al. 1994; Westrich 2008; Heneberg et al. 2014). Systematically collected data on *Lipara* reed gall inquilines from other groups of arthropods, such as spiders, beetles and hemipterans, are missing, as are large-scale complex studies on *Lipara* gall inquilines, with the exception of the study by Dely-Draskovits et al. (1994).

In this study, we address the arthropod component communities associated with reed galls induced by *Lipara* spp. in their complexity, focusing particularly on the diversity of gall inquilines, which represent a key component of gall assemblages (Sanver and Hawkins 2000). We use the *Lipara* gall communities as a model system to compare the diversity of arthropods belonging to several trophic levels in habitats with strikingly different land use intensity and history. We show that all of the four central European *Lipara* species can be found equally in well-preserved nature reserves and in newly formed (post)industrial habitats. Therefore, we use this opportunity to identify: (1) species that prefer or are limited to the near-natural habitats present in the nature reserves and other well-preserved areas, such as river floodplains and medieval fishponds, (2) species that had the capability to colonize the newly emerging reed beds in the (post)industrial habitats and are equally present in near-natural and (post)industrial habitats, and (3) species that prefer (post)industrial habitats over the near-natural ones due to better availability of bare ground and adjacent xerothermic microenvironments or other yet unknown reasons.

## Materials and methods

### Study area and sampling sites

The study was carried out at 30 reed bed sites in the Czech Republic (Central Europe, 48°39′–50°59′ N, 12°19′–18°29′ E). Detailed description of sampling sites (Table S1) was provided by Heneberg et al. (2014). Half of selected sampling sites were located to near-natural habitats (15 reed beds, of them 12 near ancient fishponds, and 3 along rivers or streams), representing reed beds spanning 0.2–480 ha and occurring within the altitudinal range 163–452 m a.s.l. It is important to note that despite a continual reed bed presence at the examined sites, the actual extent of most of the reed beds was subject to change in the past, and they were harvested for fuel, animal food, litter, or other purposes, or cultivated in part as meadows or fields. Importantly, the *Lipara* flies occupy prevalently the reed bed ecotones, and thus can easily adjust to gradual changes in the reed bed area. Additional 15 sampling sites were represented by reed beds in (post)industrial habitats. As (post)industrial habitats, we classified any sites formed by mining or quarrying, and water bodies and dumps used for the deposition of ash, slug, waste from metallurgic and chemical industry, waste from uranium processing or spoil from colliery mines. The (post)industrial sites examined in this study thus included gravel-sandpits, tailing ponds, stone quarries, colliery dumps and reclaimed lignite open-cast mines. The reed beds formed there between the years 1922 and 2010, and covered areas 0.2–19 ha within the altitudinal range 157–467 m a.s.l. The sampling sites were chosen to represent the whole spectrum of reed beds present throughout the study area (Fig. 1; Table S2), and to allow an assessment of changes

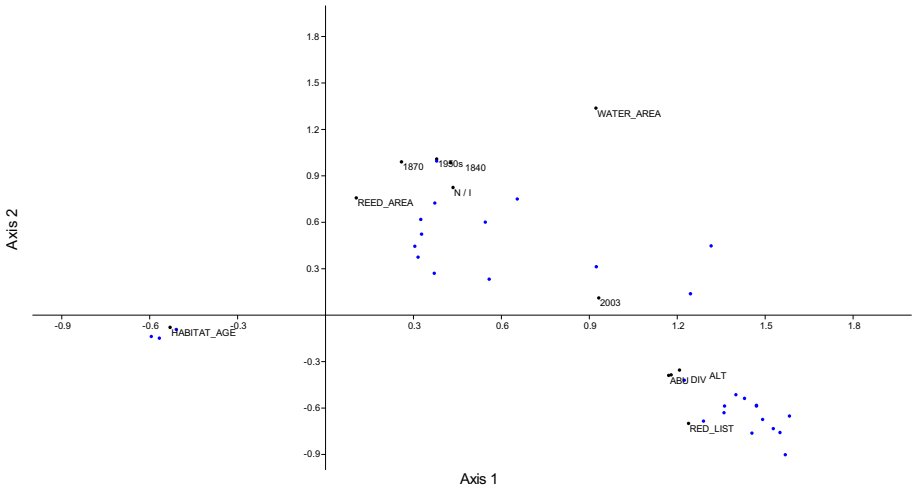


**Fig. 1** Correspondence analysis (Benzecri scaling) of the biotic and abiotic variables (*black dots* labeled by *acronyms*) associated with the sampling sites examined in the course of this study (*blue dots*). The resulting factor scores of correspondence analysis are provided in Table S2

associated with the succession of newly emerging reed beds based on a space-for-time substitution paradigm (Pickett 1989).

## Sampling

At each sampling site, 300–1000 reed galls were collected between 12 January and 16 March 2013 as described by Heneberg et al. (2014). Briefly, the deformed reed shoots were cut right under the gall, and protruding leaves were also cut out in order to fit collected galls into rearing bags. At each site, the galls induced by *Lipara* spp. were selected randomly, regardless of their position, size or age, reflecting their variation at each sampling site. Arthropods were allowed to rear when exposed to a daylight cycle, at a temperature between 15 and 23 °C for 3–4 months. The rearing bags were sprayed with water several times a week. Plastic bottles with conservation fluid (ethanol or propylene glycol mixed with water and detergent) were installed proximal to the light source; most of the arthropods were captured into the bottles provided. The total number of reed galls sampled reached 17,791, out of which 8820 (49.6 %) were obtained from near-natural habitats, and 8971 (50.4 %) were collected from (post)industrial habitats.

The sampling was performed by Petr Heneberg, Petr Bogusch and Alena Astapenková. Obtained specimens were identified to species by Petr Baňař (Heteroptera), Petr Bogusch (Hymenoptera: Aculeata, selected other taxa), Kamil Holý (Hymenoptera: Parasitica), Petr Janšta (Hymenoptera: Parasitica), Štěpán Kubík (Diptera), Jan Macek (Hymenoptera: Symphyta, Parasitica, Dryinidae), Igor Malenovský (Auchenorrhyncha, Sternorrhyncha), Miroslav Mikát (Coleoptera, Lepidoptera), and Milan Řezáč (Araneae). Albert Damaška, Alois Hamet, Tomáš Kopecký and Jan Pelikán revised selected specimens of Coleoptera; Pavel Tyrner revised selected specimens of Chrysidoidea. The findings of aculeate hymenopterans (except Dryinidae) obtained from this set of reed galls were analyzed previously (Heneberg et al. 2014).

### Statistical analyses

All arthropods obtained in course of the rearing experiments were analyzed. To estimate their species richness, Chao-1 estimator, corrected for unseen species, was calculated (Colwell and Coddington 1994). To compare species composition of the analyzed datasets, Sørensen similarity index was calculated. Both indices were calculated in EstimateS 9.1.0. We also calculated basic diversity indices for each of the datasets; these included the total number of species found, the total number of individuals found, dominance (=1 - Simpson index), 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). Linear and Spearman correlation coefficients and their significance were calculated when indicated. $\chi^2$ test was used to assess the differences in sex ratios and between the particular habitat types. To analyze the contribution of multiple variables, we applied a correspondence analysis. The resulting factor scores are disclosed in supplementary materials (Tables S2, S3, S4, S5, S6, S7, S8). The correspondence analysis took in account species-specific abundance and the following characteristics of each respective sampling site: altitude [m a.s.l.] (ALT), binary criterion of a presence/absence of near-natural habitat (N_/_I), reed bed area [ha] (REED_AREA), water surface area [ha] (WATER_AREA), habitat age [years] (HABITAT_AGE), relative extent of reed bed in year 2003 [%] (2003) and in 1950s [%] (1950s), relative extent of the water surface area [ha] in 1870s [%] (1870) and in 1840s [%] (1840), number of species reared from reed galls (DIV), number of red-listed species reared from reed galls (RED_LIST), abundance defined as a number of individuals reared per 100 reed galls (ABU). The descriptors of sampling sites were listed in detail in our previous publication (Heneberg et al. 2014). Particularly, the data on the presence of reed beds in the past were retrieved from aerial photographs available from the 1950s onwards, publicly available from http://www.mapy.cz (cited as 28 November 2013) and http://kontaminace.cenia.cz (cited as 28 November 2013). When considering the changes since industrial revolution, the maps created in course of military surveys in nineteenth century were used [Third Military survey initiated by Franz Joseph I. of Austria in 1876–1880, available from http://kontaminace.cenia.cz (cited as 28 November 2013), and Second Military survey initiated by Franz I. of Austria in 1836–1852, available from http://www.mapy.cz (cited as 28 November 2013)]. We used these maps to identify the position and extent of water bodies as they were superimposed over the current maps and orthophotomaps. In the figures, the species names were abbreviated to first three letters from their genus and species names (e.g., *Ischnodemus sabuleti* to Isc_sab). The conservation value of analyzed species was assessed according to the most recent versions of national red lists of spiders (Řezáč et al. 2015) and other arthropods (Farkač et al. 2005). The species included in the Czech Red List were termed as "red-listed" throughout the text, and include all species known as critically endangered (CR), endangered (EN), vulnerable (VU) or least concern [LC—this category refers to those species labeled as "near threatened" (NT) in most other Red Lists but not in that published by Řezáč et al. (2015)]; the other species were termed ecologically sustainable (ES). Together with the red-listed species, we analyzed also newly emerging (NE) species, which were identified in the Czech Republic only recently. The information on habitat specialization were retrieved from Nickel et al. (2002), Kocarek et al. (2005), Macek et al. (2010), Wachmann et al. (2004, 2006, 2007, 2008) and Nentwig et al. (2015). We used the

$\chi^2$ test with Bonferroni correction according to MacDonald and Gardner (2000) to assess the species-specific differences in the species-specific abundance across the study habitats and in sex ratios; in addition, we used uncorrected $\chi^2$ test to test the differences in total abundance between the two habitat types. All the above calculations were performed in PAST 2.14 (Hammer et al. 2001). Data are shown as mean ± SD unless stated otherwise.

## Results

### Global view on the reed gall universe

We sampled 17,791 reed galls, from which we reared 12,062 arthropod individuals. From the reared arthropods, 6031 individuals emerged from the galls collected at (post)industrial sites (67.2 individuals per 100 galls collected), and an identical amount of 6031 individuals emerged from galls collected at near-natural sites (68.4 individuals per 100 galls collected). Thus, the abundance of arthropods in reed galls at (post)industrial sites was nearly identical to that at the near-natural sites ($\chi^2 = 0.9$, $d_f = 1$, $p > 0.05$).

In total, we recorded 236 species of invertebrates emerging from *Lipara* reed galls, which included 14 species of aculeate hymenopteran inquilines (on which we focused earlier, cf. Heneberg et al. 2014), and 222 species of other invertebrates—Arachnida, Collembola and, particularly, numerous insects of the orders Dermaptera, Psocoptera, Thysanoptera, Hemiptera, Raphidioptera, Neuroptera, Coleoptera, Diptera, Lepidoptera, and Hymenoptera: Symphyta, Parasitica and Aculeata: Dryinidae. Arthropods that are not named explicitly in the above list were absent in the specimens that emerged from the collected reed galls. We attempted to identify all specimens to species, with the exception of few groups (adult Cecidomyidae, and insect larvae in general), which led to the identification of 143 species and another 94 morphospecies of arthropods. The Chao-1 species richness estimator (corrected for unseen species in the samples) indicated a species richness of 229.3 ± 18.1 species in reed galls at (post)industrial sites, and 218.1 ± 23.6 species in reed galls at near-natural sites. Despite the estimated species richness was similar to each other, Shannon diversity *t*-test suggested that the differences in diversity between the (post)industrial and near-natural sites are significant ($p < 0.001$ by bootstrapping; $t = 4.01$, $d_f = 11{,}940$), suggesting that the differences exist at the level of particular orders or lower taxonomical units. Both habitat types hosted diverse assemblages with low dominance, with significantly lower dominance identified at near-natural sites (0.098 and 0.089, respectively; $p = 0.002$ by either bootstrapping or permutation). Supporting the above, the levels of Brillouin (3.14 and 3.02, respectively) and Berger–Parker dominance indices (0.208 and 0.196, respectively) were low at both habitat types. The Margalef's species richness index (20.45 vs. 17.69; $p = 0.04$ and 0.01) and Fisher's alpha (34.66 vs. 29.02; $p = 0.03$ and 0.13) were significantly higher at post-industrial sites, suggesting that despite such habitats are less stabilized, they attract more diverse species spectrum of reed gall inquilines. Importantly, the species composition of the examined component communities overlapped only to a limited extent, with the Sørensen similarity index being equal to just 0.58. The correspondence analysis (Fig. 1) showed that the habitat age is a major environmental factor for *Lipara* gall communities as it was highly correlated with the first ordination axis which explained 63.8 % of variance in the species data. The second ordination axis was largely correlated with the habitat (reed bed) size and explained 18.8 % of variance in the species data.

We identified 18 red-listed species and four species that were new for the Czech Republic (*Gasteruption phragmiticola*, *Echthrodelphax fairchildii*, *Haplogonatopus oratorius* and *Enclisis* sp.), consisting mostly of obligate (64 %) or facultative (9 %) reed specialists. Only a few red-listed species (*Clubiona germanica*, *C. subtilis*, *Gibbaranea omoeda*,[1] *Homalura tarsata* and *Hylaeus moricei*) were confined to sites with a long-term presence of reed, whereas most of the others were found at (post)industrial habitats encompassing relatively small areas, which formed only recently[2] (Fig. 2a; Table S3).

## Araneae

We collected 1254 specimens of 32 morphospecies of spiders, 19 of which were identified to species. Nine (47 %) of these species were included on the national Red List (Řezáč et al. 2015), including one species that was considered CR (*Clubiona juvenis*, found at three (post)industrial and two near-natural sites), one EN (*Mendoza canestrinii*), three VU and four LC species. Nine species (47 %) were considered reed bed specialists.

The observed species richness and abundance were nearly identical at the (post)industrial and near-natural sites. A total of 618 individuals of 24 morphospecies emerged from the galls collected at postindustrial sites (6.9 individuals per 100 galls collected), and 636 individuals of 26 morphospecies emerged from the galls collected at near-natural sites (7.2 individuals per 100 galls collected). The Chao-1 estimated species richness was lower at the (post)industrial ($23.7 \pm 1.1$ species) when compared to near-natural sites ($30.6 \pm 5.3$ species). The component communities were similar to each other (Sørensen similarity index 0.71). The differences of the conservation interest consisted of a higher abundance of *Clubiona juvenis* (CR) at (post)industrial sites [19 individuals at 3 (post)industrial sites vs. 3 individuals at 2 near-natural sites] and in the absence of *Mendoza canestrinii* (EN) at (post)industrial sites (0/0 vs. 6/2). The dominant species included *Clubiona phragmitis* (208/9 vs. 79/11), *Singa nitidula*[3] (44/11 vs. 17/6) and *Synageles venator* (51/11 vs. 14/4), which were all more abundant at the (post)industrial sites (Tables 1, S4; Fig. 2b). Of note was the absence of males in *Clubiona subtilis* (Fig. 3).

## Heteroptera

We collected 880 specimens of 11 species of true bugs. All specimens were identified to species. No species was included on the national Red List (Farkač et al. 2005); the specimens included the first record of *Dimorphopterus spinolae* in Bohemia.[4] Only four species (36 %), including *D. spinolae*, were considered specialists for Poaceae, including the reed.

[1] *G. omoeda* is considered a species of mountain spruce forests but emerged from reed galls collected in/near an *Alnus glutinosa* forest in the Mesophyticum.

[2] These included, e.g., *Hypsosinga albovittata*, which is a xerothermic species that emerged from reed galls collected at a pine bog and peat meadows with interspersed reed stands in the Mesophyticum.

[3] Some of the dominant spider species were hitherto considered infrequent, with a very limited number of records. For *S. nitidula*, only a single record was known, e.g., for South Bohemia, from where we obtained 21 individuals from five of the seven sampling sites examined in this region.

[4] First record of *Dimorphopterus spinolae* for Bohemia: 1F: Bohdanečský fishpond, Lázně Bohdaneč, PU, 28 January 2013. However, this species is common at numerous sites in Moravia and abroad, where it mainly feeds on *Calamagrostis epigejos* (Wachmann et al. 2007). It causes large-scale damage to reed beds in China, and was even treated with insecticides to suppress its effects (Schaefer and Panizzi 2000).

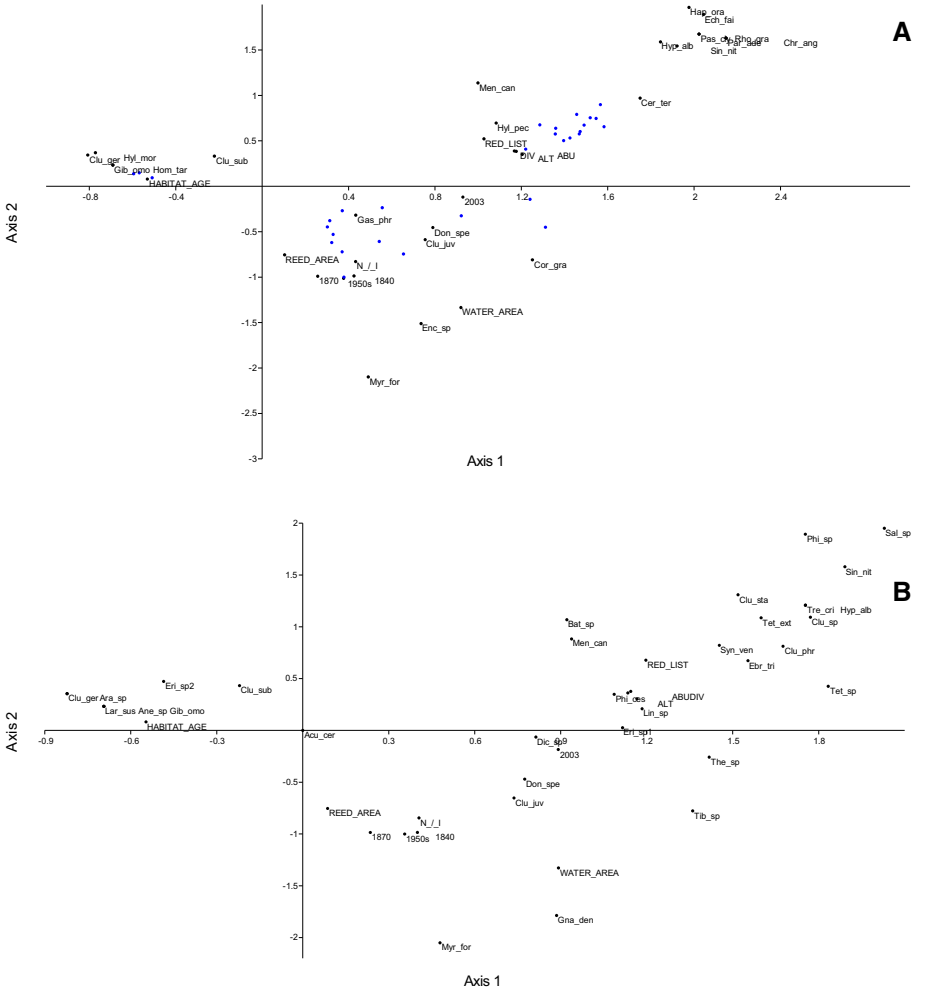


**Fig. 2** Correspondence analysis (Benzecri scaling) of the red-listed species (**a**) and Araneae (**b**) superimposed in the Q mode by biotic and abiotic variables (*black dots* labeled by *acronyms*) and the sampling sites examined in the course of this study (*blue dots*). The particular species are indicated by *black dots* labeled by *acronyms*. The resulting factor scores of correspondence analyses are provided in Tables S3 and S4

The observed species richness, but not the abundance, was nearly identical at the (post)industrial and near-natural sites. The species composition differed except for the species with the highest dominance. A total of 52 individuals of 6 species emerged from the galls collected at postindustrial sites (0.6 individuals per 100 galls collected), and 828 individuals of 8 species emerged from the galls collected at near-natural sites (9.4 individuals per 100 galls collected). The Chao-1 estimated species richness differed between the (post)industrial (6.0 ± 0.2 species) and near-natural sites (13.0 ± 7.1 species). The component communities differed from each other (Sørensen similarity index 0.46). The only dominant species was *Ischnodemus sabuleti* (34/8 vs. 808/9), which was present at

**Table 1** List of spiders (Araneae) reared from the *Lipara*-induced galls collected in January–March 2013 in the Czech Republic

| Species | Acronyms | Red List status | Habitat specialization | Number of individuals | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | (Post)industrial sites | Near-natural sites | $p(\chi^2)$ | F | M |
| *Aculepeira ceropegia* | Acu_cer | ES | | | 1[ab] | | | |
| *Anelosimus* sp. | Ane_sp | | | | 1[ab] | | | |
| *Araniella* sp. | Ara_sp | | | 1 | 2[b] | | | |
| *Bathyphantes* sp. | Bat_sp | | | | 1[ab] | | | |
| *Clubiona germanica* | Clu_ger | VU | | | 1 | | 1 | 0 |
| *Clubiona juvenis* | Clu_juv | CR | R | 19 | 3 | * | 13 | 3 |
| *Clubiona phragmitis* | Clu_phr | ES | R | 208 | 79[b] | *** | 41 | 48 |
| *Clubiona stagnatilis* | Clu_sta | ES | R | 2 | 12[b] | n.s. | 5 | 9 |
| *Clubiona subtilis* | Clu_sub | LC | R | 15 | 3 | n.s. | 18 | 0 |
| *Clubiona* sp. | Clu_sp | | | 229 | 426[b] | *** | | |
| *Dictyna* sp. | Dic_sp | | | 4 | 12 | n.s. | | |
| *Donacochara speciosa* | Don_spe | LC | R | 7 | 2 | | 3 | 1 |
| *Ebrechtella tricuspidata* | Ebr_tri | ES | | 2 | 2 | | | |
| Erigoninae gen. sp. 1 | Eri_sp1 | | | 2 | 17[ab] | * | | |
| Erigoninae gen. sp. 2 | Eri_sp2 | | | | 9[ab] | | | |
| *Gibbaranea omoeda* | Gib_omo | VU | | | 1 | | | |
| *Gnathonarium dentatum* | Gna_den | ES | | 1 | | | 0 | 1 |
| *Hypsosinga albovittata* | Hyp_alb | LC | | | 1[ab] | | | |
| *Larinioides suspicax* | Lar_sus | ES | R | 4 | 2[b] | | 0 | 2 |
| *Linyphia* sp. | Lin_sp | | | 2 | 1[b] | | | |
| *Mendoza canestrinii* | Men_can | EN | fR | | 6 | | 2 | 2 |
| *Myrmarachne formicaria* | Myr_for | VU | fR | 1 | | | | |
| *Philodromus* sp. | Phi_sp | | | 9 | 7[b] | n.s. | | |

**Table 1** continued

| Species | Acronyms | Red List status | Habitat specialization | Number of individuals | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | (Post)industrial sites | Near-natural sites | $p(\chi^2)$ | F | M |
| *Philodromus cespitum* | Phi_ces | ES | | 2 | | | 0 | 2 |
| *Salticus* sp. | Sal_sp | | | 2 | | | | |
| *Singa nitidula* | Sin_nit | LC | R | 44 | 17 | * | 13 | 9 |
| *Synageles venator* | Syn_ven | ES | R | 51 | 14 | *** | 17 | 15 |
| *Tetragnatha extenso* | Tet_ext | ES | R | 2 | | | | |
| *Tetragnatha* sp. | Tet_sp | | | 6 | 6 | n.s. | | |
| *Theridion* sp. | The_sp | | | 2 | 1 | | | |
| *Tibellus* sp. | Tib_sp | | | 1 | | | | |
| *Trematocephalus cristatus* | Tre_cri | ES | | 2 | 9[b] | n.s. | | |

The classification according to the national Red List (Řezáč et al. 2015), obligate (R) and facultative (fR) specialization for reed beds, number of individuals found at post-industrial and near-natural sites, and the ratio of females (F) and males (M) of the adult individuals collected are indicated. The total counts include juvenile individuals (often determined only to the genus level). The number of expected individuals was calculated based on the total number of individuals found and the number of reed galls examined at each habitat type. Species with the total capture rate <10 specimens were excluded from the $\chi^2$ analysis

Significance of observed differences in abundance between (post-)industrial and near-natural sites compared to the expected abundance (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. = not significant) as revealed by the species-specific $\chi^2$ tests with Bonferroni correction at n = 64

[a] Species found at reed beds alongside rivers, but not at other near-natural habitats

[b] Species more abundant at reed beds alongside rivers compared to reed beds near fish ponds

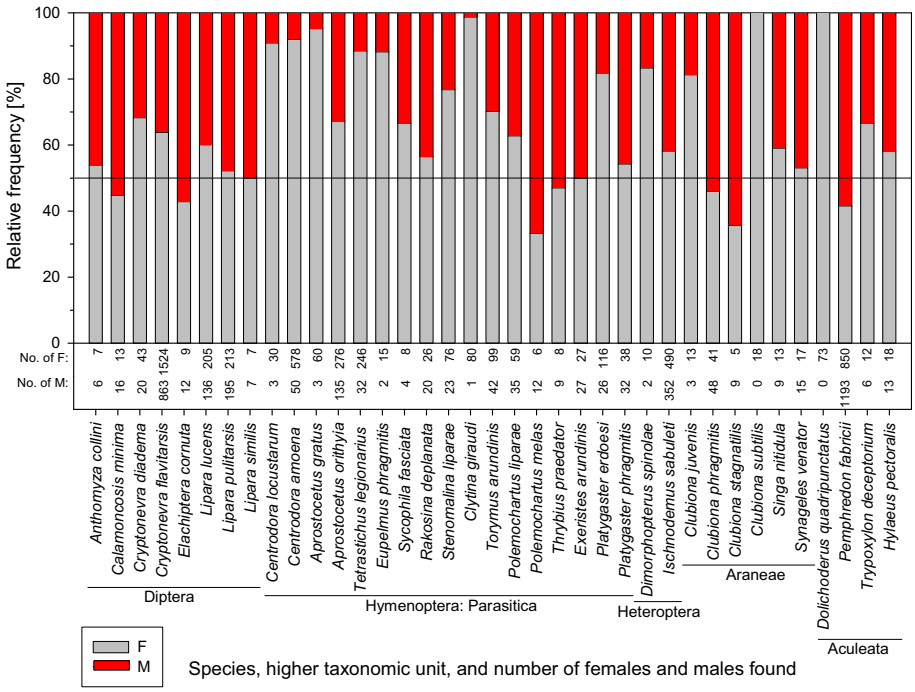


**Fig. 3** Sex ratio in species, of which ≥10 individuals emerged from the *Lipara*-induced reed galls collected during the course of this study. Relative and absolute frequencies of males and females are shown

both types of sites, but much more abundant at the near-natural sites. *Dimorphopterus spinolae* (0/0 vs. 12/2) was present only at near-natural sites (Tables 2, S5; Fig. 4a).

## Auchenorrhyncha

We collected 113 specimens of 6 morphospecies of planthoppers and leafhoppers, 3 of which were identified to species. One of them (*Paraliburnia adela*) was included on the national Red List as VU species (Farkač et al. 2005) (1/1 vs. 0/0). The observed species richness was identical at the (post)industrial and near-natural sites despite the abundance was higher at (post)industrial sites, and the species composition differed between the two types of sampling sites. In sum 87 individuals of 4 morphospecies emerged from galls collected at postindustrial sites (1.0 individuals per 100 galls collected), and 26 individuals of 4 morphospecies emerged from galls collected at near-natural sites (0.3 individuals per 100 galls collected). Dominant morphospecies included only the nymphs of reed specialist *Chloriona* sp. (82/7 vs. 14/6) present at both types of sites, but more abundant at the near-natural ones (Table 2).

## Sternorrhyncha

We collected two specimens of two species of jumping plant lice, identified as *Trioza urticae* and *Cacopsylla saliceti/pulchra* (Table 2). Both emerged from galls collected at

**Table 2** List of true bugs (Heteroptera), planthoppers and leafhoppers (Auchenorrhyncha) and jumping plant lice (Sternorrhyncha) reared from the *Lipara*-induced galls collected in January–March 2013 in the Czech Republic

| Species | Acronyms | Red List status | Habitat specialization | Number of individuals | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | (Post)industrial sites | Near-natural sites | $p(\chi^2)$ | F | M |
| **True bugs (Heteroptera)** | | | | | | | | |
| *Anthocoris nemoralis* | Ant_nem | ES | U | | 3[ab] | | 2 | 1 |
| *Dimorphopterus spinolae* | Dim_spi | ES | P | | 12 | * | 10 | 2 |
| *Gastrodes abietum* | Gas_abi | ES | *Picea* | 6 | 1[ab] | | 7 | 0 |
| *Gastrodes grossipes grossipes* | Gas_gro | ES | *Pinus* | 3 | | | 3 | 0 |
| *Ischnodemus sabuleti* | Isc_sab | ES | P | 34 | 808[b] | *** | 490 | 352 |
| *Leptopterna dolabrata* | Lep_dol | ES | P | 1 | | | 1 | 0 |
| *Lygus pratensis* | Lyg_pra | ES | U | 6 | | | 4 | 2 |
| *Orius* (*Orius*) *niger* | Ori_nig | ES | U | 2 | 1[ab] | | 1 | 2 |
| *Notostira erratica* | Not_err | ES | P | | 1[ab] | | 1 | 0 |
| *Orthops* (*Orthops*) *campestris* | Ort_cam | ES | Apiaceae | | 1[ab] | | 1 | 0 |
| *Orthops* (*Orthops*) *kalmii* | Ort_kal | ES | Apiaceae | | 1 | | 1 | 0 |
| **Planthoppers and leafhoppers (Auchenorrhyncha)** | | | | | | | | |
| *Chloriona* sp. | Chl_sp | ES | R | 82 | 14 | *** | | |
| *Idiocerus herrichii* | Idi_her | ES | *Salix* | 3 | 2 | | 1 | 4 |
| Deltocephalinae gen. sp. | Del_sp | ES | P | 1 | | | | |
| *Paraliburnia* cf. *adela* | Par_ade | VU | *Phalaris* | 1 | | | | |
| *Javesella* sp. | Jav_sp | ES | P | | 1[ab] | | | |

**Table 2** continued

| Species | Acronyms | Red List status | Habitat specialization | Number of individuals | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | (Post)industrial sites | Near-natural sites | $p(\chi^2)$ | F | M |
| *Stenocranus major* | Ste_maj | ES | *Phalaris* | | 9[ab] | | 4 | 5 |
| **Jumping plant lice (Sternorrhyncha)** | | | | | | | | |
| *Trioza urticae* | Tri_urt | ES | *Urtica* | 1 | | | 0 | 1 |
| *Cacopsylla saliceti/pulchra* | Cac_sal | ES | *Salix* | 1 | | | 1 | 0 |

The classification according to the national Red List (Farkač et al. 2005), habitat specialization: specialization for reed beds (R), Poaceae including reed (P), ubiquitous and polyphagous species (U) and other host plants, number of individuals found at post-industrial and near-natural sites, and the ratio of females (F) and males (M) of the adult individuals collected are indicated. The number of expected individuals was calculated based on the total number of individuals found and the number of reed galls examined at each habitat type. Species with the total capture rate <10 specimens were excluded from the $\chi^2$ analysis

Significance of observed differences in abundance between (post-)industrial and near-natural sites compared to the expected abundance (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. = not significant) as revealed by the species-specific $\chi^2$ tests with Bonferroni correction at n = 64

[a] Species found at reed beds alongside rivers, but not at other near-natural habitats

[b] Species more abundant at reed beds alongside rivers compared to reed beds near fish ponds

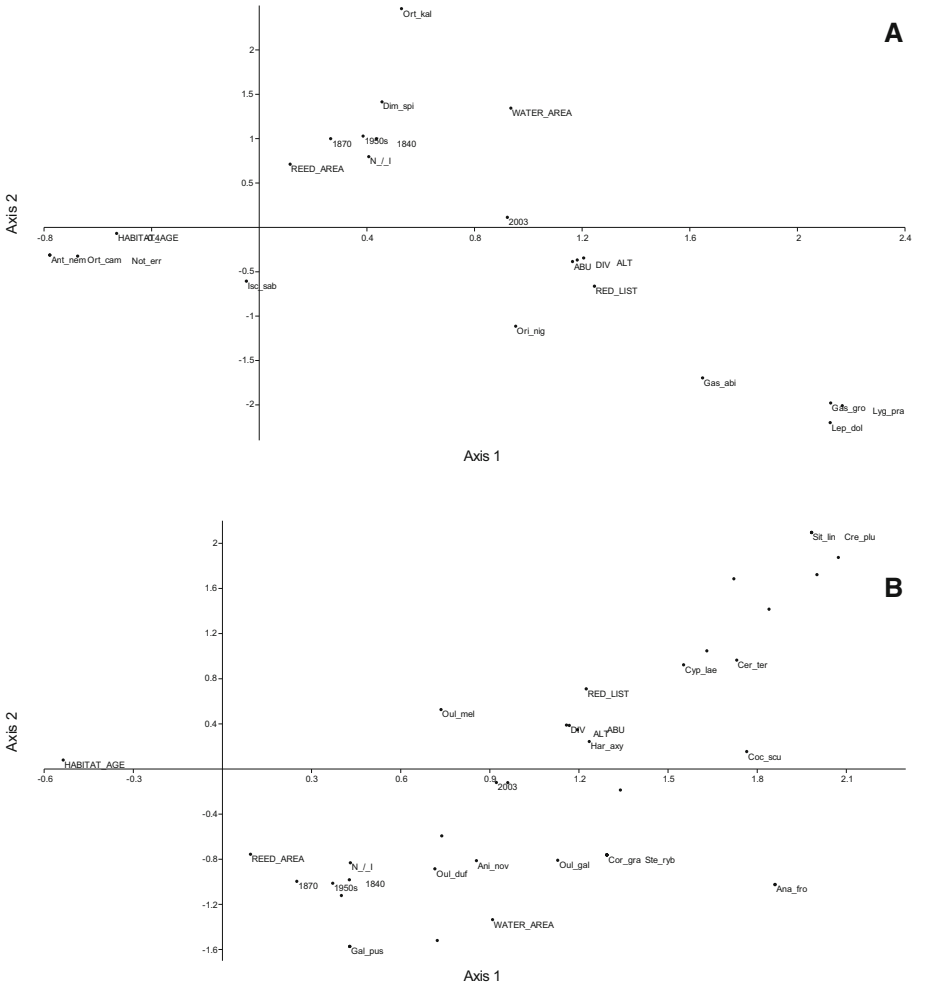


**Fig. 4** Correspondence analysis (Benzecri scaling) of Heteroptera (**a**) and Coleoptera (**b**) superimposed in the Q mode by biotic and abiotic variables (*black dots* labeled by *acronyms*) and the sampling sites examined in the course of this study (*blue dots*). The particular species are indicated by *black dots* labeled by *acronyms*. The resulting factor scores of correspondence analyses are provided in Tables S5 and S6

(post)industrial sites, and are recognized as ES species (Farkač et al. 2005) feeding on *Urtica* spp. and *Salix* spp., respectively.

## Lepidoptera

We collected four specimens of four morphospecies of moths, three of which were identified to species and all of which were recognized as ES species according to the national Red List (Farkač et al. 2005). Two specimens emerged from the galls collected at (post)industrial sites (*Brachmia inornatella* and *Boudinotiana notha*), and two specimens emerged from the galls collected at near-natural sites (*Ethmia quadrillella* and *Eupithecia*

**Table 3** List of beetles (Coleoptera) and moths (Lepidoptera) reared from the *Lipara*-induced galls collected in January–March 2013 in the Czech Republic

| Species | Acronyms | Red List status | Habitat specialization | Number of individuals | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | (Post)industrial sites | Near-natural sites | $p(\chi^2)$ | F | M |
| **Beetles (Coleoptera)** | | | | | | | | |
| *Adalia* (*Adalia*) *bipunctata* | Ada_bip | ES | U | | 1 | | | |
| *Anaspis* (*Anaspis*) *frontalis* | Ana_fro | ES | N | 3 | | | 1 | 2 |
| *Anisosticta novemdecimpunctata* | Ani_nov | ES | fR | 1 | 3 | | | |
| *Anthonomus* (*Furcipus*) *rectirostris* | Ant_rec | ES | N/Rosaceae | 1 | | | | |
| *Attagenus* (*Attagenus*) *pellio* | Att_pel | ES | U | 1 | | | | |
| *Cardiophorus* sp. | Car_sp | | | 1 | | | | |
| *Cerapheles terminatus* | Cer_ter | VU | fR | 4 | 1[ab] | | 2 | 3 |
| *Chaetocnema* sp. | Cha_sp | | | 1 | | | 1 | 0 |
| *Coccidula scutellata* | Coc_scu | ES | fR | 61 | 30 | n.s. | | |
| *Coccinella* (*Coccinella*) *quinquepunctata* | Coc_qui | ES | U | 1 | | | | |
| *Cordicollis gracilis* | Cor_gra | VU | fR | | 2 | | | |
| *Crepidodera plutus* | Cre_plu | ES | N/*Salix* | 2 | | | 0 | 2 |
| *Cyphon laevipennis* | Cyp_lae | ES | R | 28 | 13 | n.s. | | |
| *Dasytes* (*Mesodasytes*) *plumbeus* | Das_plu | ES | N/wood | | 1[ab] | | 0 | 1 |
| *Demetrias* (*Aetophorus*) *imperialis* | Dem_imp | ES | R | | 1[ab] | | | |
| *Demetrias* (*Demetrias*) *monostigma* | Dem_mon | ES | R | 1 | | | | |
| *Galerucella* (*Neogalerucella*) *pusilla* | Gal_pus | ES | N/*Lythrum* | | 2 | | | |
| *Harmonia axyridis* | Har_axy | ES | U | 1 | 1[ab] | | | |
| *Isochnus sequensi* | Iso_seq | ES | N/Salicaceae | | 1 | | | |
| Lathridiidae: Corticariinae gen. sp. | | | | | 1 | | | |

**Table 3** continued

| Species | Acronyms | Red List status | Habitat specialization | Number of individuals | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | (Post)industrial sites | Near-natural sites | $p(\chi^2)$ | F | M |
| *Nedyus quadrimaculatus* | Ned_qua | ES | N/*Urtica* | | 1 | | | |
| *Odacantha* (*Odacantha*) *melanura* | Oda_mel | ES | fR | | 1 | | | |
| *Orchestes* (*Alyctus*) *testaceus* | Orc_tes | ES | N/*Alnus* | 1 | | | | |
| *Oulema duftschmidi* | Oul_duf | ES | P | 1 | 4 | n.s. | N/D | 4 |
| *Oulema duftschmidi* / *melanopus* | | ES | P | 27 | 70 | * | 97 | 1 |
| *Oulema gallaeciana* | Oul_gal | ES | P | 1 | 2[b] | | N/D | 3 |
| *Oulema melanopus* | Oul_mel | ES | P | 20 | 27[ab] | | N/D | 47 |
| *Paradromius* (*Manodromius*) *linearis* | Par_lin | ES | fR | 1 | | | | |
| *Paradromius* (*Paradromius*) *longiceps* | Par_lon | ES | R | | 1 | | | |
| Phalacridae gen. sp. | Pha_sp | | | 1 | 2 | | | |
| *Phyllotreta vittula* | Phy_vit | ES | P | | 1 | | 1 | 0 |
| *Pria dulcamarae* | Pri_dul | ES | N/*Solanum* | | 1 | | 1 | 0 |
| *Rhinusa* sp. | Rhi_sp | | | | 1 | | | |
| *Sitona lineatus* | Sit_lin | ES | N/Viciaceae | 1 | | | 0 | 1 |
| *Stephostethus rybinskii* | Ste_ryb | ES | fR | | 1 | | | |
| Coleoptera: larvae | | | | 73 | 158[b] | *** | | |
| **Moths (Lepidoptera)** | | | | | | | | |
| *Ethmia quadrillella* | Eth_qua | ES | N/Boraginaceae | 0 | 1 | | 1 | 0 |
| *Brachmia inornatella* | Bra_ino | ES | R | 1 | 0 | | 0 | 1 |
| *Boudinotiana notha* | Bou_not | ES | N/Salicaceae | 1 | 0 | | 1 | 0 |
| *Eupithecia* sp. | Eup_sp | ES | | 0 | 1[ab] | | 1 | 0 |

**Table 3** continued

| Species | Acronyms | Red List status | Habitat specialization | Number of individuals | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | (Post)industrial sites | Near-natural sites | $p(\chi^2)$ | F | M |
| Lepidoptera-larvae | | | | 14 | 8[b] | n.s. | | |

The classification according to the national Red List (Farkač et al. 2005), habitat specialization: obligate (R) and facultative (fR) specialization for reed beds, Poaceae including reed beds (P), ubiquitous species (U), and species, which occur on other plant species only (N), number of individuals found at post-industrial and near-natural sites, and the ratio of females (F) and males (M) of the adult individuals collected are indicated. The number of expected individuals was calculated based on the total number of individuals found and the number of reed galls examined at each habitat type. Species with the total capture rate <10 specimens were excluded from the $\chi^2$ analysis

Significance of observed differences in abundance between (post-)industrial and near-natural sites compared to the expected abundance (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. = not significant) as revealed by the species-specific $\chi^2$ tests with Bonferroni correction at $n = 64$

[a] Species found at reed beds alongside rivers, but not at other near-natural habitats

[b] Species more abundant at reed beds alongside rivers compared to reed beds near fish ponds

sp.) (Table 3). *Ethmia quadrillella* represents an uncommon species of mesophilous sites and wetlands, developing on roots of Boraginaceae. *Brachmia inornatella* represents a species rare in Central Europe, developing in stems of *Phragmites australis*, and is considered the only reed bed specialist among the Lepidoptera, which emerged from the reed galls during the course of this study.

## Coleoptera

We collected 328 specimens of 34 morphospecies of beetles, of which 29 were identified to species. Only two species were included on the national Red List (Farkač et al. 2005); they were classified as VU (*Cerapheles terminatus*, 4/2 vs. 1/1, and *Cordicollis gracilis*, 0/0 vs. 2/1). In total 15 species (36 %) were considered specialists for Poaceae, including the reed beds, and four species (14 %) were considered ubiquitous saprophages and aphidophages. For 10 species (34 %), there was no prior evidence on their overwintering and/or development in reed galls (*Dasytes plumbeus*, *Pria dulcamarae*, *Anaspis frontalis*, *Galerucella pusilla*, *Crepidodera plutus*, *Anthonomus rectirostris*, *Isochnus sequensi*, *Orchestes testaceus*, *Nedyus quadrimaculatus* and *Sitona lineatus*).

The observed species richness and abundance were nearly identical at the (post)industrial and near-natural sites. The species composition was similar, except that the species found at low frequency were randomly distributed between the (post)industrial and near-natural sites. Nevertheless, all of the dominant species were found at both types of sampling sites. A total of 159 individuals of 20 morphospecies emerged from the galls collected at postindustrial sites (1.8 individuals per 100 galls collected), and 169 individuals of 23 morphospecies emerged from the galls collected at near-natural sites (1.9 individuals per 100 galls collected). Most of the species were captured in low numbers, which caused that the Chao-1 estimated species richness was high in both analyzed habitats but was associated with a high degree of uncertainty, reaching $66.2 \pm 34.4$ species at the (post)industrial sites and $38.5 \pm 11.6$ species at near-natural sites. The component communities differed from each other (Sørensen similarity index 0.43). The dominant species included *Oulema melanopus* (males: 20/8 vs. 27/7),[5] *Coccidula scutellata* (61/6 vs. 30/6) and *Cyphon laevipennis* (28/4 vs. 13/4). All of these species were present at both types of sites, but the latter two species were more abundant at the post-industrial sites (Tables 3, S6; Fig. 4b).

## Hymenoptera: Symphyta

We collected 15 specimens of seven morphospecies of sawflies, six of which were identified to species; all recognized as ES species according to the national Red List (Farkač et al. 2005). Four morphospecies emerged from galls collected at (post)industrial sites (*Pontania brevicornis*, *Ametastegia glabrata*, *Cladius brullei* and *Pontania* sp.), and four emerged from galls collected at near-natural sites (*Euura gemmacinerae*, *Amauronematus viduatus*, *Ametastegia glabrata*, *Brachythops flavens*) (Table 4). All the species represented ubiquitous species, for which common reed did not serve as a host plant, the reed galls were used only to pupate. The only dominant species was *Ametastegia glabrata* (males: 2/1 vs. 5/3).

[5] Males of *O. melanopus* were approximately 10× more abundant than males of *O. duftschmidi*. Females of these two species were 1.9× more abundant than males at both types of sampling sites (27/10 vs. 70/6 of females) but were indistinguishable from each other.

**Table 4** List of Hymenoptera: Parasitica, Symphyta and Aculeata (Dryinidae) reared from the Lipara-induced galls collected in January–March 2013 in the Czech Republic

| Species | Acronyms | Red List status | Habitat specialization | Number of individuals | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | (Post)industrial sites | Near-natural sites | $p(\chi^2)$ | F | M |
| **Parasitica: Ceraphronoidea** | | | | | | | | |
| Ceraphronidae gen. sp. 1 | Cer_sp | | | | 1[ab] | | 2 | 1 |
| Ceraphronidae gen. sp. 2 | | | | 2 | | | | |
| *Dendrocerus serricornis* | Den_ser | ES | U | 1 | | | | |
| **Parasitica: Chalcidoidea** | | | | | | | | |
| *Aphelinus* gen. sp. 1 | | | | 1 | | | 0 | 1 |
| *Aphytis* gen. sp. 1 | | | | 1 | | | 1 | 0 |
| *Centrodora* cf. *acridiphagus* | Cen_acr | ES | N/D | 17 | 42[b] | n.s. | 59 | 0 |
| *Centrodora amoena* | Cen_amo | ES | fR | 325 | 296[b] | n.s. | 578 | 50 |
| *Centrodora locustarum* | Cen_loc | ES | fR | 1 | 32[ab] | *** | 30 | 3 |
| *Centrodora* sp. 1 | | ES | | 3 | | | 2 | 1 |
| *Centrodora* sp. 2 | | ES | | 3 | | | 2 | 1 |
| *Centrodora* sp. 3 | | ES | | | 7[ab] | | 7 | 0 |
| *Boucekiella* sp. 1 | Bou_sp | | | 23 | | *** | 12 | 11 |
| Encyrtidae gen. 1 sp. 1 | | | | 1 | | *** | 1 | 0 |
| Encyrtidae gen. 2 sp. 1 | | | | 3 | | | 2 | 1 |
| Encyrtidae gen. 3 sp. 1 | | | | | 141 | | 92 | 49 |
| Encyrtidae gen. 4 sp. 1 | | | | 1 | | | 0 | 1 |
| Encyrtidae gen. 5 sp. 1 | | | | | 4 | | 2 | 2 |
| Encyrtidae gen. 6 sp. 1 | | | | 1 | | | 0 | 1 |
| *Boucekiella depressa* | Bou_dep | ES | R | | 2 | | 2 | 0 |
| *Aprostocetus gratus* | Apr_gra | ES | R | 18 | 14 | n.s. | 60 | 3 |
| *Aprostocetus orithyia* | Apr_ori | ES | R | 220 | 190[b] | n.s. | 276 | 135 |
| *Aprostocetus* sp. 1 | | | | 7 | 2 | | 7 | 2 |
| Eulophidae gen. 1 sp. 1 | | | | 3 | 15[b] | n.s. | 6 | 12 |

**Table 4** continued

| Species | Acronyms | Red List status | Habitat specialization | Number of individuals | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | (Post)industrial sites | Near-natural sites | $p(\chi^2)$ | F | M |
| Eulophinae gen. 2 sp. 1 | | | | 1 | 2 | | 1 | 2 |
| Eulophinae gen. 3 sp. 1 | | | | 1 | | | 1 | 0 |
| *Melittobia* sp. 1 | | | | 33 | 12[ab] | n.s. | 45 | 0 |
| *Melittobia* sp. 2 | | | | 3 | 8[b] | n.s. | 11 | 0 |
| *Pediobius* sp. 1 | | | | 4 | 47[b] | *** | 46 | 7 |
| *Pediobius* sp. 2 | | | | 1 | 1[ab] | | 2 | 0 |
| *Pediobius* sp. 3 | | | | 3 | | | 3 | 0 |
| *Pronotalia* sp. 1 | | | | 27 | 32 | n.s. | 54 | 5 |
| Tetrastichinae gen. 1 sp. 1 | | | | 2 | 4 | | 1 | 5 |
| Tetrastichinae gen. 1 sp. 2 | | | | 3 | 9 | n.s. | 3 | 9 |
| Tetrastichinae gen. 2 sp. 1 | | | | 29 | | *** | 26 | 3 |
| Tetrastichinae gen. 3 sp. 1 | | | | 9 | 8 | n.s. | 16 | 1 |
| Tetrastichinae gen. 4 sp. 1 | | | | | 5[b] | | 4 | 1 |
| Tetrastichinae gen. 5 sp. 1 | | | | 3 | | | 3 | 0 |
| Tetrastichinae gen. 6 sp. 1 | | | | 1 | 6 | | 7 | 0 |
| Tetrastichinae gen. 7 sp. 1 | | | | 6 | 3[b] | | 9 | 0 |
| Tetrastichinae gen. 8 sp. 1 | | | | 1 | | | 1 | 0 |
| *Tetrastichus legionarius* | Tet_leg | ES | R | 172 | 106 | ** | 246 | 32 |
| *Tetrastichus* sp. | | | | 2 | | | 2 | 0 |
| *Eupelmus* (sg. *Macroneura*) sp. | | | | | 1[ab] | | | |
| *Eupelmus phragmitis* | Eup_phr | ES | R | 16 | 1 | * | 15 | 2 |
| *Eurytoma* sp. 1 | | | | 2 | 6[b] | | 4 | 4 |
| *Eurytoma* sp. 2 | | | | 1 | 5 | | 5 | 1 |
| *Eurytoma* sp. 3 | | | | 1 | | | 1 | 0 |

**Table 4** continued

| Species | Acronyms | Red List status | Habitat specialization | Number of individuals | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | (Post)industrial sites | Near-natural sites | $p(\chi^2)$ | F | M |
| *Tetramesa phragmitis* | Tet_phr | ES | R | 4 | 3[b] | | 6 | 1 |
| *Sycophila fasciata* | Syc_fas | ES | R | 9 | 3 | n.s. | 8 | 4 |
| *Anagrus* sp. | | | | 26 | 2[b] | *** | 17 | 10 |
| *Asaphes suspensus* | Asa_sus | ES | U | 3 | | | 0 | 3 |
| *Callitula elongata* | Cal_elo | ES | R | 4 | 2[ab] | | 6 | 0 |
| *Gyrinophagus* sp. 1 | | | | 24 | 11[b] | n.s. | 35 | 0 |
| *Gyrinophagus* sp. 2 | | | | 7 | | | 6 | 1 |
| *Pachyneuron* sp. | | | | 2 | | | 1 | 1 |
| *Rakosina deplanata* | Rak_dep | ES | R | 31 | 15 | n.s. | 26 | 20 |
| *Stenomalina liparae* | Ste_lip | ES | R | 65 | 32[b] | n.s. | 76 | 23 |
| *Clytina giraudi* | Cly_gir | ES | R | 47 | 34[b] | n.s. | 80 | 1 |
| *Torymus arundinis* | Tor_aru | ES | R | 62 | 79[b] | n.s. | 99 | 42 |
| Chalcidoidea gen. sp. | | | | 4 | | | | |
| Platygastroidea / Chalcidoidea gen. sp. | | | | 1 | | | | |
| **Parasitica: Cynipoidea** | | | | | | | | |
| *Alloxysta fulviceps* | All_ful | ES | fR/*Praon* | 2 | | | | |
| *Rhoptromeris* sp. | | | | 1 | 2 | | | |
| **Parasitica: Evanioidea** | | | | | | | | |
| *Gasteruption phragmiticola* | Gas_phr | NE | R | 1 | 2[ab] | | 3 | 0 |
| **Parasitica: Ichneumonoidea** | | | | | | | | |
| Braconidae gen. sp. | | | | 2 | 1 | | 1 | 2 |
| *Polemochartus liparae* | Pol_lip | ES | R | 58 | 36[b] | n.s. | 59 | 35 |
| *Polemochartus melas* | Pol_mel | ES | R | 20 | 2 | n.s. | 6 | 12 |

**Table 4** continued

| Species | Acronyms | Red List status | Habitat specialization | Number of individuals | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | (Post)industrial sites | Near-natural sites | $p(\chi^2)$ | F | M |
| *Diaeretus* sp. | | | | 1 | $3^{ab}$ | | | |
| *Praon* sp. | | | | 2 | | | | |
| *Bracon* sp. | | | | | $3^{ab}$ | | | |
| Ichneumonidae gen. sp. | | | | 23 | | *** | | |
| Cryptinae gen. sp. | | | | 2 | 1 | | 2 | 1 |
| *Gambrus ornatus* | Gam_orn | ES | P | | $3^{b}$ | | 2 | 1 |
| *Hoplocryptus centricolor* | Hop_cen | ES | R | 1 | | | 1 | 0 |
| *Hoplocryptus* sp. | | | | 1 | | | 0 | 1 |
| *Thrybius praedator* | Thr_pra | ES | R | 9 | $8^{b}$ | n.s. | 8 | 9 |
| Ctenopelmatinae gen. sp. | | | | | $1^{ab}$ | | 1 | 0 |
| *Endromopoda detrita* | End_det | ES | P | 4 | $3^{b}$ | | 7 | 0 |
| *Ephialtes* sp. | | | | 2 | | | 1 | 1 |
| *Exeristes arundinis* | Exe_aru | ES | R | 45 | 8 | *** | 27 | 27 |
| Pimplinae gen. sp. | | | | 1 | | | 1 | 0 |
| *Polysphincta rufipes* | Pol_ruf | ES | U | 2 | | | 2 | 1 |
| *Zatypota percontatoria* | Zat_per | ES | U | | 2 | | 1 | 1 |
| *Enclisis* sp. | Enc_sp | NE | | | 1 | | 0 | 1 |
| **Parasitica: Platygastroidea** | | | | | | | | |
| *Inostemma* sp. | | | | 4 | $3^{b}$ | | 4 | 3 |
| *Platygaster erdoesi* | Pla_erd | ES | U/*Cassida* | 33 | $109^{b}$ | *** | 116 | 26 |
| *Platygaster phragmitis* | Pla_phr | ES | R | 38 | $31^{b}$ | n.s. | 38 | 32 |
| *Scelio* sp. 1 | | | | | 1 | | 1 | 0 |
| Scelionidae gen. 1 sp. 1 | | | | 2 | 5 | | 6 | 1 |
| Scelionidae gen. 1 sp. 2 | | | | 2 | | | 0 | 2 |

**Table 4** continued

| Species | Acronyms | Red List status | Habitat specialization | Number of individuals | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | (Post)industrial sites | Near-natural sites | $p(\chi^2)$ | F | M |
| Scelionidae gen. 1 sp. 3 | | | | 11 | 1 | n.s. | 10 | 2 |
| Scelionidae gen. 2 sp. 1 | | | | 2 | | | 2 | 0 |
| Scelionidae gen. 3 sp. 1 | | | | | 4 | | 3 | 1 |
| **Parasitica: Proctotrupoidea** | | | | | | | | |
| *Trichopria nigra* | Tri_nig | ES | U | | 1 | | | |
| **Symphyta** | | | | | | | | |
| *Amauronematus viduatus* | Ama_vid | ES | U | | 1 | | 1 | 0 |
| *Ametastegia glabrata* | Ame_gla | ES | U | 2 | 5[b] | | 4 | 3 |
| *Brachythops flavens* | Bra_fla | ES | U | | 3 | | 2 | 1 |
| *Cladius brullei* | Cla_bru | ES | U | 1 | | | 1 | 0 |
| *Euura gemmacinerae* | Euu_gem | ES | U | | 1[b] | | | |
| *Pontania brevicornis* | Pon_bre | ES | U | 1 | | | | |
| *Pontania* sp. | | | U | 1 | | | 1 | 0 |
| **Aculeata: Chrysidoidea, Dryinidae** | | | | | | | | |
| *Echthrodelphax fairchildii* | Ech_fai | NE | P | 5 | | | | |
| *Gonatopus clavipes* | Gon_cla | ES | P | 1 | | | | |
| *Gonatopus distinctus* | Gon_dis | ES | P | 1 | | | | |
| *Haplogonatopus oratorius* | Hap_ora | NE | P | 1 | | | | |

The classification according to the national Red List (Farkač et al. 2005), habitat specialization: obligate (R) and facultative (fR) specialization for reed beds, Poaceae including reed beds (P), and ubiquitous species (U) or hosted by such specialists, number of individuals found at post-industrial and near-natural sites, and the ratio of females (F) and males (M) of the adult individuals collected are indicated. The number of expected individuals was calculated based on the total number of individuals found and the number of reed galls examined at each habitat type. Species with the total capture rate <10 specimens were excluded from the $\chi^2$ analysis

Significance of observed differences in abundance between (post-)industrial and near-natural sites compared to the expected abundance (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. = not significant) as revealed by the species-specific $\chi^2$ tests with Bonferroni correction at $n = 64$

[a] Species found at reed beds alongside rivers, but not at other near-natural habitats

[b] Species more abundant at reed beds alongside rivers compared to reed beds near fish ponds

### Hymenoptera: Parasitica and Aculeata (Dryinidae)

We collected 2938 specimens of 99 morphospecies of parasitic hymenopterans. Of them, 36 morphospecies were identified to species. The particular superfamilies identified included Ceraphronoidea (3 morphospecies), Chalcidoidea (59 morphospecies), Cynipoidea (2 morphospecies), Evanioidea (a single species), Ichneumonoidea (20 morphospecies), Platygastroidea (9 morphospecies), Proctotrupoidea (a single species) and Chrysidoidea (4 species). The national Red List of parasitic hymenopterans is very short in extent because of uncertainties due to limited or aged information available. No species found were included in the national Red List (Farkač et al. 2005), but at least four were considered rare in the study area (*Eupelmus phragmitis*, *Tetramesa phragmitis*, *Rakosina deplanata* and *Callitula elongata*), and another four species were new for the Czech Republic.[6] Altogether 28 species (67 %) were considered specialists for Poaceae, being frequently strictly confined to the reed beds and reed galls induced by the *Lipara* flies. The remaining 33 % of species were considered ubiquitous. There were no species considered specialists for other habitats.

The observed (but not estimated) species richness and abundance were similar at the (post)industrial and near-natural sites. The species composition differed, except for the species with the highest dominance. A total of 1524 individuals of 84 morphospecies emerged from the galls collected at postindustrial sites (17.0 individuals per 100 galls collected), and 1414 individuals of 61 morphospecies emerged from the galls collected at near-natural sites (16.0 individuals per 100 galls collected). The Chao-1 estimated species richness differed between the (post)industrial (99.9 $\pm$ 9.3 species) and near-natural sites (66.5 $\pm$ 4.5 species). The component communities were relatively similar to each other (Sørensen similarity index 0.60). The dominant species were *Centrodora amoena*[7] (325/14 vs. 296/12), *Aprostocetus orithyia*[8] (220/8 vs. 190/8), *Tetrastichus legionarius* (172/3 vs. 106/9), *Platygaster erdoesi* (33/5 vs. 109/8), *Torymus arundinis* (62/7 vs. 79/8) and an unidentified species of Encyrtidae gen. sp. found at near-natural sites in the Pannonian part of Moravia only (0/0 vs. 141/2). Several unidentified morphospecies, and *Gambrus ornatus* (0/0 vs. 3/3), *Centrodora locustarum* (1/1 vs. 32/2) and *Platygaster erdoesi* (33/5 vs. 109/8) were present prevalently at near-natural sites. Several unidentified morphospecies,

[6] The new species for the Czech Republic included *Gasteruption phragmiticola* (1 ex.: fishpond Baroch, Hrobice, PU, 28 January 2013, 1 ex.: Knovízský stream, Olovnice, ME, 16 February 2013, 1 ex.: disused ash/slag deposit of the lignite power station Triangl, Olešník, CB, 16 March 2013), *Enclisis* sp. (1 ex.: fishpond Proudnice, Žíželice-Hradištko, KO, 25 January 2013), *Haplogonatopus oratorius* (1 ex.: sandpit Dobříň, LT, 2 February 2013) and *Echthrodelphax fairchildii* (1 ex.: sandpit Dobříň, LT, 2 February 2013, 2 ex.: spoil heap Mariánské Radčice, MO, 3 February 2013, 1 ex.: spoil heap Pokrok, Duchcov, TE, 3 February 2013, 1 ex.: gravel-sandpit Vojkovice, ME, 17 February 2013).

[7] Nartshuk (2006) questioned the association of *Centrodora amoena* (Aphelinidae) with their *Lipara* hosts proposed by Fulmek (1968), with Orthoptera serving as the only confirmed hosts. In our material from *Lipara*-induced galls, *Centrodora amoena* was a dominant species (628 individuals emerged), with Orthoptera completely absent in the examined dataset. Therefore, it is likely that the initial observation by Fulmek was correct.

[8] *Aprostocetus orithyia* and *A. gratus* were reported as specialized parasites of *Giraudiella inclusa* by Tscharntke et al. (1991), who also questioned the previous record of *A. orithyia* association with *Lipara lucens* (Graham 1987) and questioned all of the other host records of *A. gratus* (which was never associated with *Lipara* flies or any other dipterans reported in our study). In particular, *A. orithyia* was a dominant species in our dataset (410 individuals emerged). Although our materials contained hundreds of potential cecidomyid hosts, it is important to note that all of this material originated from the microhabitat (galls) that was induced exclusively by *Lipara* flies. Therefore, Graham was probably correct when reporting it from *Lipara* galls, but it remains to be tested whether the *Lipara* spp. themselves can host these two species.

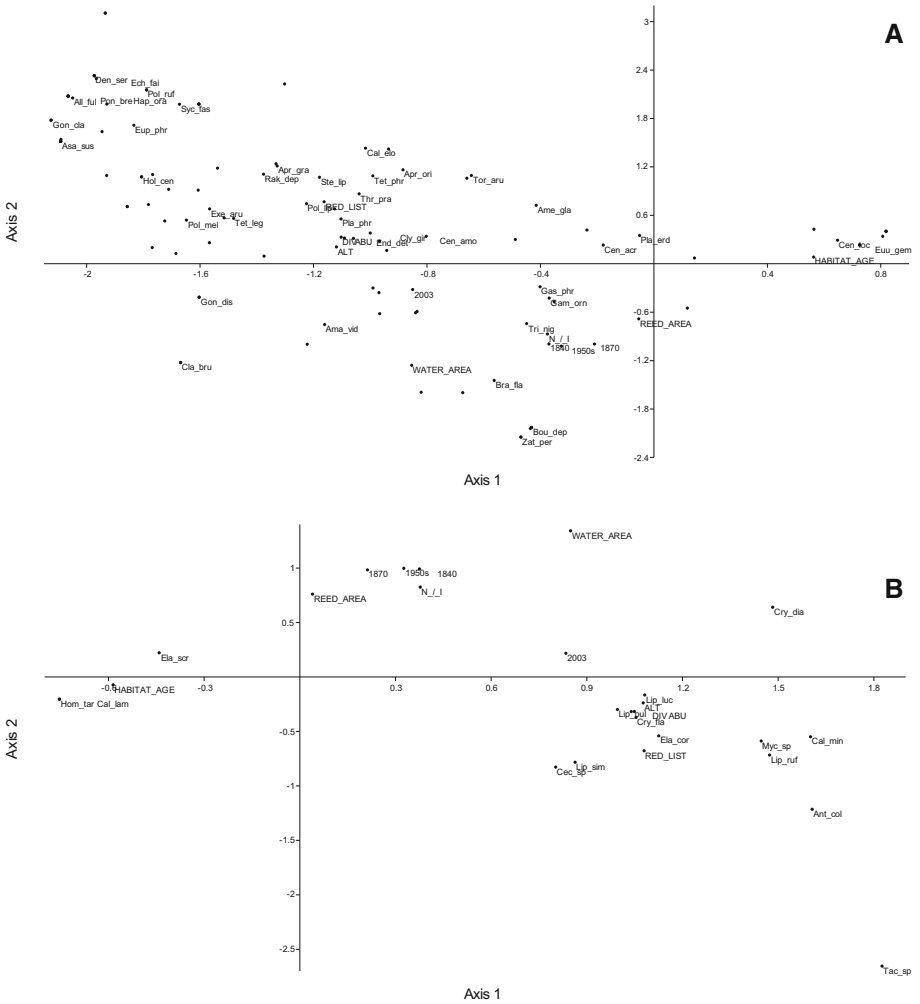


**Fig. 5** Correspondence analysis (Benzecri scaling) of Hymenoptera: Parasitica and Aculeata (Dryinidae) (**a**) and Diptera (**b**) superimposed in the Q mode by biotic and abiotic variables (*black dots* labeled by *acronyms*) and the sampling sites examined in the course of this study (*blue dots*). The particular species are indicated by *black dots* labeled by *acronyms*. The resulting factor scores of correspondence analyses are provided in Tables S7 and S8

and *Eupelmus phragmitis* (16/2 vs. 1/1), *Polemochartus melas* (16/5 vs. 2/2) and *Exeristes arundinis* (45/8 vs. 8/3) were present prevalently at (post)industrial sites (Tables 4, S7; Fig. 5a). Besides *Lipara* spp. and other dipterans, the putative host spectrum of parasitic hymenopterans found included lepidopterans (*Gambrus ornatus*), other hymenopterans (*Holocryptus centricolor*, *Thrybius praedator*, *Endromopoda detrita*), spiders (*Polysphincta rufipes*, *Zatypota percontatoria*), and leafhoppers and planthoppers (*Gonatopus clavipes*, *G. distinctus*). Numerous species were skewed towards females; among them were *Clytina giraudi* (99 %), *Aprostocetus gratus* (95 %), *Centrodora amoena* (92 %), *Centrodora locustarum* (91 %), *Tetrastichus legionarius* (88 %) and *Eupelmus phragmitis* (88 %) (Fig. 3).

## Diptera

We collected 4021 specimens of 15 morphospecies of Diptera. Only the species of Chloropidae (11 species) and Anthomyzidae (1 species) were identified to species. Cecidomyiidae (729 ex.), Mycetophilidae (3 ex.) and Tachinidae (5 ex.) were not identified to species. The national Red List of Chloropidae is very short in extent because of uncertainties due to limited or aged information available. Only a single species, *Homalura tarsata*, was included on the national Red List (Farkač et al. 2005). The dipterans found were represented by reed gall-inducing species of the genus *Lipara* (four species), obligate reed gall specialists (three species: *Calamoncosis minima*, *Cryptonevra diadema* and *Cryptonevra flavitarsis*), two facultative reed gall inquilines (*Anthomyza collini* and *Calamoncosis laminiformis*), two facultative reed herbivores (*Elachiptera cornuta* and *Elachiptera scrobiculata*), and a species associated with reed beds, but without sufficient data to classify its feeding and nesting strategy (*Homalura tarsata*). There were no ubiquitous species, and no species were considered specialists for other habitats.

The observed species richness, abundance and composition were similar at the (post)industrial and near-natural sites. A total of 2055 individuals of 12 morphospecies emerged from the galls collected at postindustrial sites (22.9 individuals per 100 galls collected), and 1966 individuals of 14 morphospecies emerged from the galls collected at near-natural sites (22.3 individuals per 100 galls collected). The Chao-1 estimated species richness was lower at the (post)industrial ($11.0 \pm 0.4$ species) compared to near-natural sites ($17.0 \pm 4.2$ species). The component communities were similar to each other (Sørensen similarity index 0.88). *Cryptonevra flavitarsis* was recognized as a highly dominant species and was the only invertebrate species found at all sampling sites in course of this study (1203/15 vs. 1180/15). Several species were more prevalent at the (post)industrial sites, including *Anthomyza collini* (11/6 vs. 2/1), *Calamoncosis minima* (24/6 vs. 5/1) and *Cryptonevra diadema* (57/8 vs. 6/1).

We non-selectively collected both the 0.5 year-old galls and the older galls when present at the sampling site; therefore we were able to evaluate the species composition of gall-inducing *Lipara* flies. The most common species were *L. pullitarsis* (181/13 vs. 227/15) and *L. lucens* (185/15 vs. 156/14), whereas less common species were *L. similis* (9/4 vs. 5/3, present in Bohemia only) and *L. rufitarsis* (4/2 vs. 1/1, present in both the Moravian and Bohemian thermophyticum) (Tables 5, S8; Fig. 5b). Consistent with the ecological characteristics of *Lipara* flies, *L. rufitarsis* was associated with the most recently emerged reed beds, whereas *L. similis* was associated with well-established habitats, which were usually more eutrophicated and thus allowed the growth of higher and thicker reed stands. We found skewed sex ratios in multiple dipteran species; the populations of *Cryptonevra diadema* and *C. flavitarsis* were both skewed towards the females (68 and 64 %, respectively). Similarly, the reared *Lipara lucens* were slightly skewed towards females (60 %), but the sex ratio of *L. pullitarsis* and *L. similis* was equal (Fig. 3).

## Other taxa and larvae

The emergence traps contained also the following taxa, which originated from the collected reed galls: Pseudoscorpiones: *Chelifer cancroides* (0/0 vs. 1/1), Neuroptera: *Semidalis aleurodiformis* (4/2 vs. 0/0), Raphidioptera: *Raphidia notata* (0/0 vs. 1/1),

**Table 5** List of flies and midges (Diptera) reared from the Lipara-induced galls collected in January–March 2013 in the Czech Republic

| Species | Acronyms | Red List status | Habitat specialization | Number of individuals | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | (Post)industrial sites | Near-natural sites | $p(\chi^2)$ | F | M |
| *Anthomyza collini* | Ant_col | ES | R | 11 | 2 | n.s. | 7 | 6 |
| *Calamoncosis laminiformis* | Cal_lam | ES | P | | 1[ab] | | 0 | 1 |
| *Calamoncosis minima* | Cal_min | ES | R | 24 | 5 | * | 13 | 16 |
| Cecidomyiidae gen. sp. | Cec_sp | | | 360 | 369[b] | n.s. | 484 | 245 |
| *Cryptonevra diadema* | Cry_dia | ES | R | 57 | 6[ab] | *** | 43 | 20 |
| *Cryptonevra flavitarsis* | Cry_fla | ES | R | 1203 | 1180 | n.s. | 1524 | 863 |
| *Elachiptera cornuta* | Ela_cor | ES | P | 14 | 7[b] | n.s. | 9 | 12 |
| *Elachiptera scrobiculata* | Ela_scr | ES | P | | 5[b] | | 2 | 3 |
| *Homalura tarsata* | Hom_tar | EN | R | | 1[ab] | | 1 | 0 |
| *Lipara lucens* | Lip_luc | ES | R | 185 | 156 | n.s. | 205 | 136 |
| *Lipara pullitarsis* | Lip_pul | ES | R | 181 | 227[b] | n.s. | 213 | 195 |
| *Lipara rufitarsis* | Lip_ruf | ES | R | 4 | 1 | | 5 | 5 |
| *Lipara similis* | Lip_sim | ES | R | 9 | 5[b] | n.s. | 7 | 7 |
| Mycetophilidae gen. sp. | | | | 2 | 1 | | 3 | 0 |
| Tachinidae gen. sp. | | | | 5 | | | 5 | 0 |

The classification according to the national Red List (Farkač et al. 2005), habitat specialization: obligate (R) and facultative (fR) specialization for reed beds, Poaceae including reed beds (P), ubiquitous species (U), and species, which occur on other plant species only (N), number of individuals found at post-industrial and near-natural sites, and the ratio of females (F) and males (M) of the adult individuals collected are indicated. The number of expected individuals was calculated based on the total number of individuals found and the number of reed galls examined at each habitat type. Species with the total capture rate <10 specimens were excluded from the $\chi^2$ analysis

Significance of observed differences in abundance between (post-)industrial and near-natural sites compared to the expected abundance (*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, n.s. = not significant) as revealed by the species-specific $\chi^2$ tests with Bonferroni correction at $n = 64$

[a] Species found at reed beds alongside rivers, but not at other near-natural habitats

[b] Species more abundant at reed beds alongside rivers compared to reed beds near fish ponds

Dermaptera: *Forficula auricularia* (0/0 vs. 2/2), Collembola (35/8 vs. 18/5), Thysanoptera (3/2 vs. 1/1), and Psocoptera (0/0 vs. 1/1). Additionally, the emergence traps contained larvae of Coleoptera (73/10 vs. 158/12), Lepidoptera (14/5 vs. 8/3), Diptera (2/2 vs. 9/2) and Hymenoptera (1/1 vs. 0/0).

## Discussion

The species composition of arthropod assemblages associated with reed galls strongly differed between the near-natural and (post)industrial sites, and both habitats hosted very diverse assemblages of reed gall inquilines. In agreement with Athen and Tscharntke (1999), we revealed the habitat age and size as key drivers of the species composition of site-specific assemblages. However, Athen and Tscharntke used a different time scale, focusing on sewage purification plants aged 2–11 only years and spanning just 10–2500 $m^2$ in size. They found that the diversity of the insect assemblages attacking these newly formed small reed beds increases with the age and size of these habitats. Extending the scale of their variables, we analyzed the (post)industrial habitats of 6–91 years of age, near-natural sites (fishponds) aged up to 599 years and several reed beds in floodplains along the meandering rivers expected to be present onsite since the last glacial period. We also scaled up the variability in the area of examined habitats up to 480 ha for near-natural habitats and up to 19 ha for (post)industrial habitats. We found that the model provided by Athen and Tscharntke (1999) is valid only in early successional stages of limited area. The initial increase in the abundance and, particularly, the species-richness of reed gallers and their parasitoids lasts for only a few years. Later, the species diversity associated with the reed galls becomes stabilized, and, instead, the assemblages seem to undergo a process of succession instead of enrichment (Table 6; Fig. 6). This situation clearly resembles that well known from forests subject to an initial disturbance followed by a long-term ecological succession (cf. Attiwill 1994; Hubbell et al. 1999). Higher microhabitat heterogeneity associated with increased vegetation diversity surrounding, and sometimes interspersing, the newly forming reed bed (Haddad et al. 2001; Hawkins and Porter 2003), and the presence of rare stress-tolerant plants preferred by certain threatened herbivores (Nickel and Hildebrandt 2003; Dennis et al. 2004) may significantly contribute to the diversity of newly formed, disturbed and only patchily colonized sites. However, the availability of the key resource, the common reed, from the very beginning of the establishment of such sites probably causes the absence of any transient increase in the species richness of reed gall-associated arthropods. Thus, the situation does not resemble the previously reported species succession gradients of aculeate hymenopterans, vascular plants and some other taxa at early successional stages of dry post-quarrying and post-mining sites (cf. Heneberg et al. 2013; Prach et al. 2013).

Our data confirmed previous conclusions of other large biodiversity assessments conducted in other habitats, such as grasslands (Allan et al. 2014; Manning et al. 2015), heathlands (Cameron and Leather 2012), mosaic temperate landscapes (Duelli and Obrist 1998; Oertli et al. 2005), or tropical forests (Lawton et al. 1998), showing that the higher land use intensity substantially alters the study environment, affecting differentially the trophically diverse taxa. Importantly, we found that the higher land use is associated with a formation of replacement niches for pioneer species that are only rarely found in the latter stages of reed bed succession. These species occurred previously at active river terraces, which were freshly formed from sand or gravel-sand, but such habitats were nearly completely destroyed in the study region as well as throughout large parts of the industrialized world. Thus, higher land use (in terms of mining, quarrying and associated activities) led to a formation of specific habitats instead of habitat deterioration when focusing on the reed beds. Despite the newly formed reed beds served as important strongholds for pioneer species of invertebrates ousted from the surrounding cultural landscape, they did not host the whole species spectrum associated with *Lipara*-induced

**Table 6** Characteristic features of developmental stages of *Lipara*-induced reed gall-associated assemblages

| Reed bed age (habitat) | Species richness | Red-listed species | Common species |
|---|---|---|---|
| <10 years | Low | None | Only >50 % occupancy of reed beds by *Lipara pullitarsis* at ≥25 $m^2$ and ≥3 years of reed bed age. Increase in parasitism of *L. pullitarsis* by *Stenomalina liparae* from 5 to 35 % during first 10 years following the reedbed formation (see Athen and Tscharntke 1999 for details) |
| 10–100 years (post-industrial areas, gravels and river terraces) | High | *Echthrodelphax fairchildii*, *Passaloecus clypealis*, *Rhopalum gracile* | **Araneae:** *Clubiona phragmitis*, *Clubiona stagnatilis*, *Singa nitidula*, *Tetragnatha extensa*, **Heteroptera:** *Gastrodes abietum*, *Gastrodes grossipes*, *Lygus pratensis*, **Coleoptera:** *Cerapheles terminatus*, *Cyphon laevipennis*, *Coccidula scutellata*, **Hymenoptera:** *Alloxysta fulvices*, *Eupelmus phragmitis*, *Polemochartus melas*, *Polysphincta rufipes*, *Sycophila fasciata*, **Diptera:** *Anthomyza collini*, *Calamoncosis minima*, *Lipara rufitarsis*, *Cryptonevra diadema* |
| 100–700 years (ancient fishponds) | High | None | **Araneae:** *Myrmarachne formicaria*, **Heteroptera:** *Dimorphopterus spinolae*, **Coleoptera:** *Anisosticta novemdecimpunctata*, *Oulema duftschmidi*, **Hymenoptera:** *Ametastegia glabrata*, *Brachythops flavens*, *Gambrus ornatus*, **Diptera:** none |
| >1000 years (meandering river floodplains) | High | *Homalura tarsata*, *Hylaeus moricei* | **Araneae:** *Clubiona germanica*, *Clubiona subtilis*, *Gibbaranea omoeda*, **Heteroptera:** *Ischnodemus sabuleti*, **Coleoptera:** none, **Hymenoptera:** *Centrodora locustarum*, *Platygaster erdoesi*, **Diptera:** *Elachiptera scrobiculata* |
| Species insensitive to habitat age | N/A | *Donachocara speciosa*, *Hylaeus pectoralis* | **Araneae:** none, **Heteroptera:** none, **Coleoptera:** none, **Hymenoptera:** *Aprostocetus orithyia*, *Centrodora amoena*, *Pemphredon fabricii*, *Torymus arundinis*, **Diptera:** *Cryptonevra flavitarsis*, *Lipara lucens*, *Lipara pullitarsis* |

galls. Shared environmental drivers are expected to play a role in positive associations among species within the analyzed assemblages (cf. Wolters et al. 2006; Qian and Ricklefs 2008).

We identified numerous species-specific associations of reed gall-associated arthropods that differed from previously published data. In contrast to the findings by Tscharntke (1999), only some of the phytophagous insects found by us in reed galls were

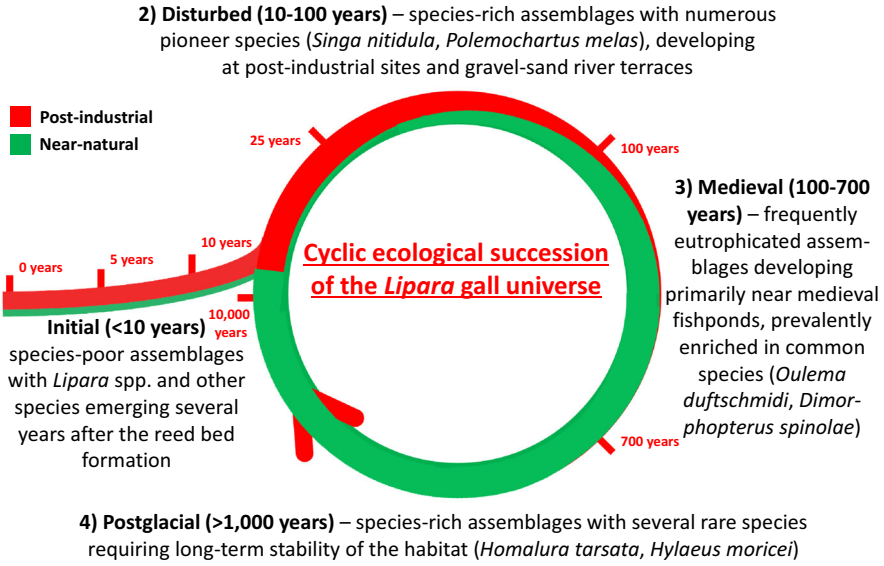


**Fig. 6** Cyclic ecological succession of *Lipara*-induced reed gall-associated assemblages. The initial stages were analyzed in detail by Athen and Tscharntke (1999); the assemblages formed at the latter three stages of reed bed evolution were examined in course of this study. There is only negligible share of early successional reed beds developing spontaneously in intensively cultivated central European landscape, which highlights the importance of (post-)industrial sites as refugia

monophagous on reed; some were facultative common reed herbivores (e.g., *Elachiptera cornuta* and *E. scrobiculata*), and many others used the galls only as a shelter for overwintering but were trophically associated with other plant species (Table 2).

The reed galls served as an important winter niche for spiders collected by reed bed passerines, which typically specialize for *Clubiona juvenis*, *C. phragmitis* and *Singa* spp. (Schmidt et al. 2005). Five *Clubiona* spp., including the CR *C. juvenis*, were particularly abundant in the collected material. When comparing our data to previous studies on reed beds (Fig. 7), we found that the species composition of spider assemblage associated with reed galls collected in winter (this study) differs from those found by employing a broad range of sampling techniques in Czech and French reed beds in spring (Holec 2000; Schmidt et al. 2005), and that it strongly differs even from that obtained by collecting spiders on dead reed stalks in Belgium in winter (Decleer 1988). Only 3 species were found in all 4 of these studies, whereas over 20 spider species were found exclusively in the reed galls during the course of this study (Fig. 7). Schmidt et al. (2005) reported that the dominant reed gall-associated species *C. juvenis* is negatively affected by reed cutting, which may be consistent with frequent overwintering of this species in reed galls, which are typically destroyed by such reed management.

We recorded four species of hymenopteran parasitoids for the first time in the Czech Republic. *Echthrodelphax fairchildii* (Dryinidae) is a semi-solitary ectoparasitoid of Delphacidae planthoppers, originally described from Hawaii, and known from Bangladesh, India, Indonesia, Philippines, Malaysia, Thailand, Vietnam, Japan (Olmi 1984), China (He and Xu 2002) and Romania (Nagy 1967, questioned by Olmi 1984). We found this species at four sampling sites (all in (post)industrial habitats), thus it should be considered a

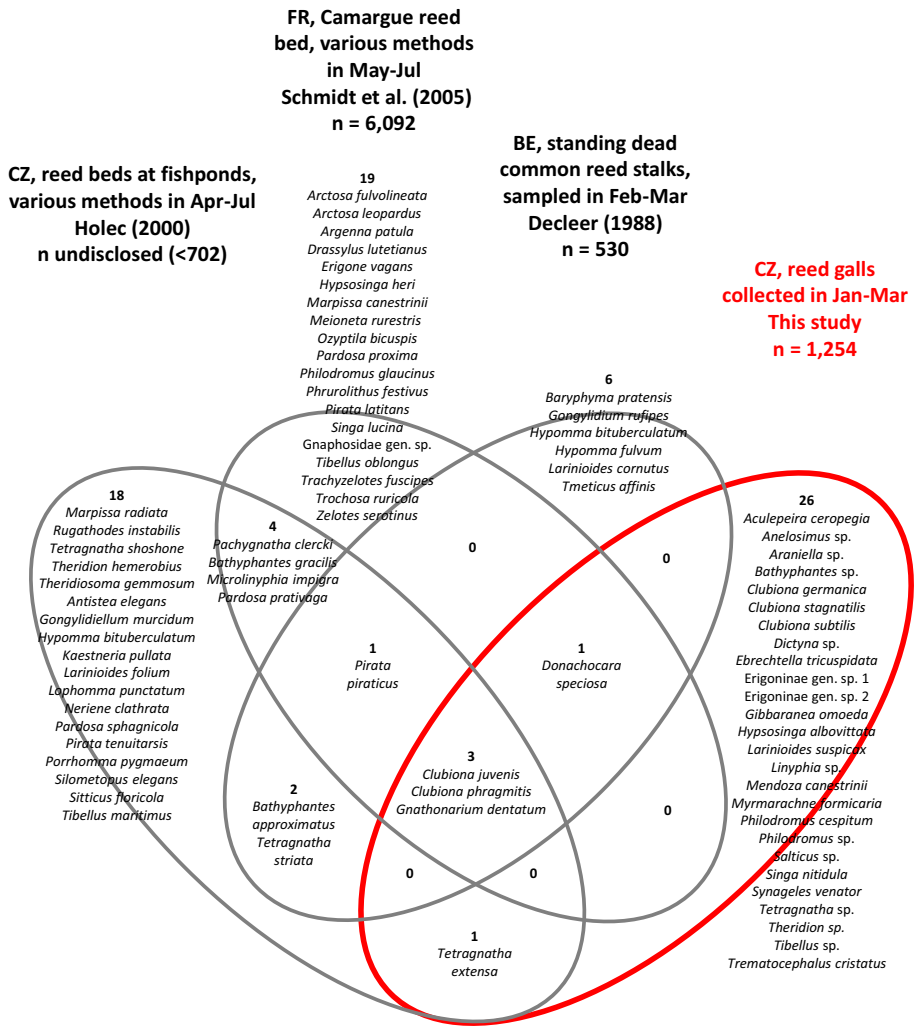


**Fig. 7** Species composition of local microhabitat-specific reed bed-associated component communities of spiders strongly differed from each other as shown by the Venn diagram. Four datasets are compared: (*1*) spiders of Czech reed beds at fishponds, collected by various methods in April–July (Holec 2000; n < 702), (*2*) spiders of French reed beds in Camargue, collected by various methods in May–July (Schmidt et al. 2005; n = 6092), (*3*) spiders collected from common reed stalks in Belgium in February–March (Decleer 1988; n = 530) and (*4*) spiders identified in course of this study in the Czech Republic, which emerged from reed galls collected in January–March (n = 1254)

stable member of the Czech entomofauna. *Haplogonatopus oratorius* (Dryinidae) is also a parasitoid of Delphacidae planthoppers (Guglielmino and Olmi 1997, 2006; He and Xu 2002) with a Palearctic and Oriental distribution. In Europe, it has been only rarely found, reported from Karelia, Romania, Italy, Austria and England (Olmi 1984, 1999). *Gasteruption phragmiticola* (Evanioidea: Gasteruptiidae) was described a decade ago as a new species from Germany (Saure 2006) and confirmed in Germany by Westrich (2008), who reported it from the galls induced by *Lipara lucens* as a parasitoid of *Hylaeus* spp.

(Hymenoptera: Aculeata: Colletidae). We also found an unidentified member of the genus *Enclisis* (Ichneumonidae) for the first time in the Czech Republic. *Enclisis* is a small Palearctic genus with only six European and one Chinese species. The information on their biology is limited; all members of this genus are considered idiobiont ectoparasitoids of various Coleoptera and Hymenoptera nesting in wood (Bordera and Hernández-Rodríguez 2003).

Due to the quantitative and non-discriminatory nature of the rearing method used, the collected material provides a unique opportunity to evaluate unbiased species-specific sex ratios. We found skewed ratios across multiple taxonomic groups, including the *Lipara* flies and parasitic hymenopterans (Fig. 3). To our knowledge, the sex ratios in *Lipara* spp. and *Cryptonevra* spp. were not previously studied. In parasitic hymenopterans, the sex ratio is subject to complicated regulation, many species are arrhenotokous, and sometimes females only mate as soon as they emerge with the males emerging in the same host nest. Therefore, more females are produced under these conditions, generating only sufficient numbers of males to fertilize the females (Godfray 1994). The host size, ratio of different hosts, rate of oviposition and even temperature extremes can influence the sex ratio in Parasitica (Fisher et al. 1999). Regarding spiders, some, such as *Dysdera hungarica*, may develop parthenogenetic clones (Řezáč et al. 2007). It remains to be investigated, whether the absence of males in the examined reed bed populations of *Clubiona subtilis* was due to the yet undiscovered parthenogenesis or whether their males simply overwinter in different microhabitats.

## Conclusions and conservation implications

Reed beds are often subject to cutting, herbicide treatment and complete eradication. In some parts of the world, they are considered alien. With widespread eutrophication they often invade formerly nitrogen- and nutrient-poor habitats even in their native distribution range, including the Czech Republic. Reed harvesting allows the silting of reed beds and enhances plant species diversity in the undergrowth (Decleer 1990; Cowie et al. 1992; Hawke and José 1996; Schmidt et al. 2005), but limits the nesting resources of early breeding passerines (Baldi and Moskat 1995; Poulin and Lefebvre 2002) and removes overwintering stages of arthropods (Pühringer 1975; Ditlhogo et al. 1992; Schmidt et al. 2005). The early ecological succession of arthropods in reed beds encompassing very small areas was studied by Athen and Tscharntke (1999), who showed that the keystone species, *Lipara pullitarsis*, colonizes nearly all of the available reed beds just within a few years after their formation, followed shortly by the dominant parasitoids, such as *Stenomalina liparae*. In this report, we addressed, for the first time, long-term changes of arthropod assemblages associated with *Lipara*-induced reed galls. We identified a cyclic and long-term nature of the succession (Fig. 6). The reed beds formed in recent decades host a diverse assemblage of pioneer species that are only rarely found in later stages of the reed bed succession. We assume that such newly formed reed beds may occur at active river terraces, which are freshly formed from sand or gravel-sand in regions where the rivers are not subject to extensive regulations such as in Central Europe. In an intensively cultivated central European cultural landscape with channelized rivers, such newly forming habitats are available nearly exclusively in post-industrial areas, which thus play a key role in the survival of the pioneer species of arthropods associated with reed galls. The later stages of the ecological succession of the studied assemblages are associated with a different

spectrum of species, which are typically found in the Czech Republic in the vicinity of ancient fishponds that are nowadays largely protected as nature reserves and form also key hotspots of diversity of reed passerines. However, the reed gall assemblages in these centuries old habitats still differ from the reed beds that occur in floodplains along rivers and streams and probably have the longest historical continuity, going back perhaps to the last glacial period. When subject to a severe disturbance, or when a new reed bed is formed, the pioneer species absent near both the fishpond- and river-associated reed beds emerge again, completing the cyclic succession nature of the *Lipara*-induced reed gall arthropod assemblages. Efficient evidence-based conservation of such assemblages thus should focus on the whole spectrum of reed beds, including recently formed ones (particularly those stressed by drought or other factors), as well as on the large reed beds that have been present for a long period of time. Of particular importance are the ecotones and the availability of diverse food sources in the vicinity of reed beds (bogs, dry grasslands, shrubs and trees) because numerous species of the *Lipara*-induced reed gall arthropod assemblages utilize the galls only as a shelter or a nesting resource but do not depend on the common reed as a food source.

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**Compliance with ethical standards**

**Conflict of Interest** The authors declare that they have no conflict of interest.

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