



Habitat selection by threatened burrowing spiders (Araneae: Atypidae, Eresidae) of central Europe: evidence base for conservation management

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Abstract

Habitat selection in sedentary, long-lived burrowing spiders is a key life-history event that directly affects their reproductive success. In this study, we analyzed the role of the chemical and physical properties of soil in habitat selection by threatened temperate burrowing spiders. We examined 296 burrows of three *Atypus* spp. and three *Eresus* spp. at 68 sites in Czechia. We found that the study species were associated with soils that have high or very high cation exchange capacity, which allows the presence of a stable and humid microclimate in their burrows. We found that specific bedrock types can be used as predictors of the presence of particular study species. All *Eresus* spp. avoided compacted soils. However, when present in soils with very low penetration resistance, they were limited to sites with high soil cohesion. The burrows of all study species were located at well-drained sites. The study species seemed to be selective for a steppe-like character of their microhabitat but not necessarily for its southward orientation. We found the study species even at sites where steppes were present in the early 1950s and that underwent later afforestation but not extensive landscaping or plowing. What types of disturbances can be sustained by the study species and how long it takes the decreased populations to recover after, e.g., trampling associated with grazing, remain to be investigated.

Keywords Biodiversity conservation · Bioindicator species · Conservation management · *Cirsio-Brachypodium pinnati* · Edaphic conditions · Habitat preferences

Milan Řezáč, Jaroslav Tošner, and Petr Heneberg have contributed equally.

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Introduction

Habitat selection in burrowing spiders is a key life-history event that directly affects their reproductive success. Several factors drive habitat selection; these include microclimatic variables in and around the burrow (e.g., temperature, humidity and solar radiation) as well as intrinsic variables (such as substrate texture and other physical and chemical properties and southern exposure). Combined, these factors determine the burrow microclimate and can consequently alter the costs of reproduction and development (Woodman 2008; Martinez 2009; Mason et al. 2013). Digging a burrow is energetically demanding, and the costs of digging may be positively correlated with burrow depth and the chosen substrate, but the costs may be offset by greater protection from outside conditions, as shown in vertebrates (Cowles and Bogert 1944; Shenbrot et al. 2002; Ke and Lu 2009).

Information on the habitat requirements of temperate burrowing spiders is surprisingly limited. Many studies have provided information that is valid at a local scale (within

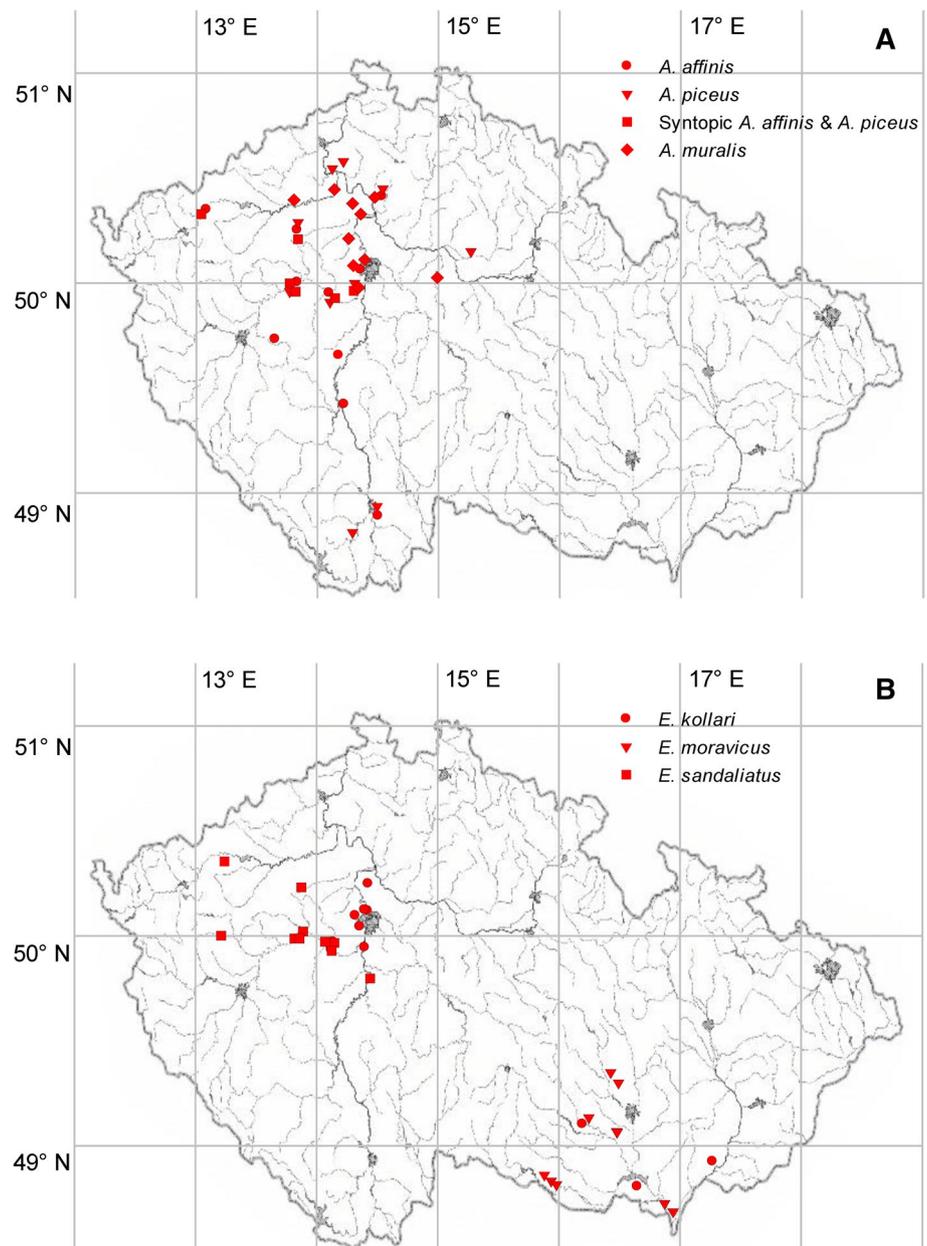
their study area) but not accurate for the rest of the distribution range of the given species. For example, *Eresus kollari* is considered a highly specialized inhabitant of heathlands that requires humus-rich soil (Krause et al. 2013). Such sites are occupied throughout its entire area of distribution, but this species can also be found in aeolian sand deposits and on calcareous steppes and loessic steppes (see the data below). Similarly, *Atypus affinis* is found in only two types of habitats in Denmark and Sweden. These consist of dry, sun-exposed sandy slopes covered by open oak forests and unspoiled coastal slopes with scarce *Prunus spinosa* and *Crataegus* spp. (Pedersen and Loeschcke 2001). Both of these habitats are characterized by their high stability and continuity. However, in central Europe, the same species preferentially occupies other habitats, which, similarly to the habitats occupied in northern Europe, display high stability and continuity (see the data below). Thus, although all these species are strictly stenotopic, their habitat requirements are poorly defined and sometimes misunderstood, which may lead to wrong decisions in the conservation management of the sites at which they occur. The detrimental effects of such conservation management errors are also exacerbated by the low dispersal ability of *Atypus* spp. (except *A. affinis*—Pétillon et al. 2012; Řezáč and Heneberg 2014) and *Eresus* spp. (Baumann 1997a). For example, *E. kollari* was never seen to colonize or recolonize fragmented heathland patches in a large German heathland reserve, where capture–recapture experiments with 1004 individuals of *Eresus* revealed that the offspring built their new burrows in close proximity to their native burrows (Baumann 1997a). Even sexually active males do not usually move farther than 12 m (max 61 m) from their burrows (Baumann 1997a). Krejčí (2012) observed frequent pre-ballooning behavior in *E. kollari* and *Eresus moravicus* juveniles but never observed ballooning itself. Similarly, Ratschker (1995), Baumann (1997a, b) and Pedersen and Loeschcke (2001) reported the absence of ballooning in *E. kollari* and *Eresus sandaliatus* but confirmed ballooning in a Mediterranean species, *Eresus walckenaeri*, which is in agreement with its ability to colonize the Aegean Islands. These data collectively correspond with a decline in *Eresus* abundance following the fragmentation of heathlands (Krause et al. 2011) and with successful outcomes following the transfer of *E. sandaliatus* to putatively suitable habitats in Great Britain (Hughes et al. 2009). Only the first nymphal instar of the most common species, *A. affinis*, has good dispersal ability (Pétillon et al. 2012), but the first nymphal instars of *Atypus piceus* and particularly *Atypus muralis* are much heavier and were never observed to perform ballooning (Řezáč and Heneberg 2014). However, even in *A. affinis*, significant genetic differentiation was found when studying populations at a distance of 1–10 km from each other (Pedersen and Loeschcke 2001), which suggests that the exchange of individuals among such closely located

populations is very limited. Fragmentation may also result in a decrease in the effective population size needed for the maintenance of genetic variation for future adaptation. Such decreases have already been shown for *A. affinis* in northern Europe (Pedersen and Loeschcke 2001) and may likely affect the other study species as well, as they are less abundant and more restricted in their dispersal abilities when compared to *A. affinis*.

In the present study, we address in detail the habitat requirements of six burrowing spider species. These include *A. affinis*, the *Atypus* species with the northernmost geographic distribution in Europe (Kraus and Baur 1974); its distribution extends to the north up to Denmark and southern Sweden and to the east up to Belarus, western Ukraine and Moldova (Mikhailov 1997). We also studied *A. piceus*, which is distributed throughout central Europe and the Balkans (Schwendinger 1989). The third species, known from Czechia and included in this study, is *A. muralis*, the distribution range of which is centered around the Black Sea but also extends to central Europe and northern Italy (Kraus and Baur 1974; Schwendinger 1989). It is thought that each of these species colonized central Europe from different glacial refugia, a model that is still somewhat reflected in the microclimatic conditions characteristically associated with the habitats of each of these three species (Řezáč et al. 2007). Of the *Eresus* spp., the study area hosts populations of four species—*E. kollari*, *E. moravicus*, *E. sandaliatus* and *Eresus illustris* (*Eresus hermani*), the latter of which was recently identified in southeastern Czechia (Kůrka et al. 2015). Here, we analyzed the habitat requirements of the first three species. The distribution range of *E. kollari* (formerly also called *Eresus cinnaberinus*) extends from Spain and France through most of Europe up to Kyrgyzstan, Kazakhstan and Russian Novosibirsk. The distribution range of *E. moravicus* spans the entire Pannonian region (including the type locality in southeastern Czechia). The distribution range of *E. sandaliatus* extends from England and France to eastern Germany and Czechia (Řezáč et al. 2008). All the study species are considered threatened in Czechia (Řezáč et al. 2015).

In the present study, we analyzed the role of chemical and physical properties of the soil in habitat selection by threatened burrowing spiders of temperate central European landscapes. We answered the following questions: (1) Does water evaporation or its proxy in the form of cation exchange capacity play a role in the known link between some burrowing spider species and calcareous and igneous bedrock? (2) Could any of the physical or chemical properties be used as a proxy to indicate the suitability of a given soil for particular burrowing spiders? (3) Are there any proxies for the presence of burrowing spiders that can be used in applied conservation?

Fig. 1 Locations of study sites in Czechia occupied by *Atypus* spp. (a) or *Eresus* spp. (b)



Materials and methods

Study area and sampling sites

We conducted the study at 68 sampling sites (Fig. 1) distributed across Czechia (48°48′–50°37′ N, 13°31′–17°31′ E), reflecting the distribution ranges of each study species. The study sites consisted of 10 sites occupied by *A. affinis*, 10 sites occupied by *A. piceus*, 10 sites occupied by *A. muralis*, 6 sites occupied syntopically by *A. affinis* and *A. piceus*, 12 sites occupied by *E. kollari*, 10 sites occupied by *E. moravicus* and 10 sites occupied by *E. sandaliatus*. The occurrence of *Atypus* at a large proportion of the study sites

was previously summarized by the first author of this study (Řezáč 2009); the distribution of *Eresus* was examined by our student, Tomáš Krejčí, in his Master's Thesis (Krejčí 2012).

Sampling

Two researchers examined each sampling site for at least 1 h in order to analyze the burrow density of the examined species. During this time period, we primarily focused on microhabitats close to rocks or boulders lying on the soil, under fallen tree trunks or under plants, such as shrubs of *Calluna vulgaris*, tufts of grass or leaf litter (Řezáč and

Heneberg 2014). At each sampling site, we measured at least three burrows of each species found (unless we found fewer than three burrows), preferentially burrows that hosted adult individuals.

We examined the plant cover and species composition by phytocenologic relevés performed in 25 m² areas (5×5 m) where the examined spider burrows occurred. We performed phytocenologic relevés from 21 July to 4 November 2011 and from 17 September to 25 October 2012. We quantified the vegetation cover using standardized ranks (Braun-Blanquet 1932; Podani 2006) and used botanical nomenclature according to Kubát (2002). The vascular plant species included on the Czech Red List were termed as threatened, and these consisted of the following categories of species: critically endangered (C1), endangered (C2), vulnerable (C3), near-threatened (C4a) and data deficient (C4b). The C1 and C2 species were further divided according to the formal reasons leading to their inclusion in the Red List based on rarity and population decline (C1b, C2b), population decline (C1t, C2t), or rarity (C1r, C2r) (Grulich 2012).

Measurement of physical parameters of the soil

We measured the effective cation exchange capacity using the Van der Marel method (1961). We used 2.5 g of soil, which was sieved through a mesh with 2.00 mm openings into a glass tube closed by a glass stopper. We flushed the sample with 300 ml of 500 mM sodium acetate to saturate the exchange capacity with sodium cations. Next, we flushed the sample with 300 ml of 80% ethanol to remove the residues of sodium acetate and then with 300 ml of ammonium chloride to extract the exchangeable sodium ions. We measured the content of sodium in the last extract by flame atomic emission spectrometry. Recalculation of the sodium content in the percolate gave the cation exchange capacity value.

We measured the pH of a suspension of soil in water (pH-H₂O) and in a 10 mM CaCl₂ solution (pH-CaCl₂) potentiometrically using a suspension with a 1:5 ratio (v:v) according to ISO 10390:1994. We mixed the suspension of soil and water for 5 min, left to equilibrate (2–24 h), briefly mixed, and then measured. As the analysis of the first 40 soil samples revealed that the results of pH-H₂O and pH-CaCl₂ were linearly correlated, we present only the data resulting from the pH-CaCl₂ measurements only.

We measured the orientation of the sampling sites based on maps and aerial photographs available at <http://www.mapy.cz> (accessed 16 January 2017). We retrieved the bedrock types from 1:50,000 geological maps available at <http://www.geologicke-mapy.cz/> (accessed 6 February 2017). We retrieved information on the history of vegetation cover from aerial photographs taken from 1949 to 1956 available at <http://kontaminace.cenia.cz/> (accessed 6 February 2017).

As the study area was affected by dramatic changes in agriculture schemes beginning at the onset of communism and later again after the fall of the communist regime, we quantified the tree cover that was present at each sampling site in 1949–1956 based on aerial photographs of these sites. We assumed that the forest cover detected at that time better represents the landscapes that were present at each site for several previous centuries, and, as shown above, such landscapes differ strongly from those currently present at most of the examined sites. We quantified the landscape type using a numerical scale that included the following categories: 0: field, 1: forest, 2: dense shrubs, 3: forest-steppe, orchard or sparse forest, 4: steppe or other uncultivated area without trees or shrubs. We expressed the change in afforestation during the last 60 years on a numerical scale where –1 indicated deforestation, 0 indicated no change, +1 indicated an increase in the cover of shrubs or trees and +2 indicated complete overgrowth with dense forest. We measured the slope angles of the macrorelief using an optical reading clinometer to the nearest 0.5°. We measured soil penetration resistance and soil shear strength resistance as described by Srba and Heneberg (2012). Soil penetration resistance identifies areas with restrictions due to compaction, whereas shear strength resistance is a result of friction and interlocking of particles, as well as possibly of cementation or bonding at particle contacts. Increases in these variables result in mechanical impedance for burrowing. We used the dry sieve method to analyze the soil texture (Heneberg 2001) using sieves with mesh sizes of 0.072, 0.125, 2.00 and 4.00 mm.

Data analyses

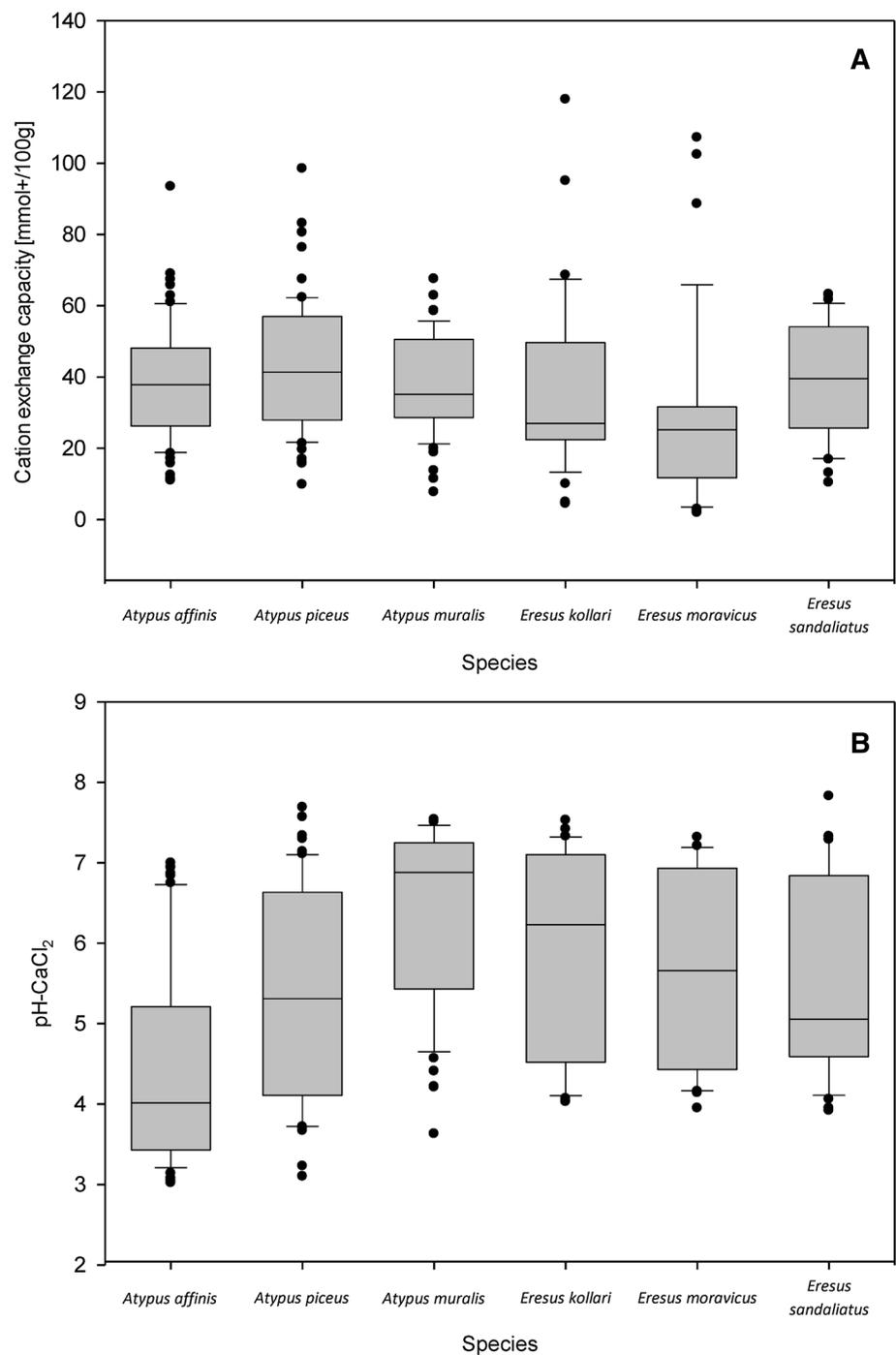
We performed the cation exchange capacity and pH analyses in triplicates. We assessed the reproducibility of the cation exchange capacity assay by means of the intra-assay coefficient of variability, which was calculated for triplicates of raw cation exchange capacity values, reaching 0.28% (range 0.05–0.69%), which suggested good reproducibility of the assay. We tested the significance of species-specific differences by one-way ANOVA. We tested the differences in soil penetration resistance, soil shear strength resistance and soil texture by Kruskal–Wallis one-way ANOVA on ranks followed by Dunn's pairwise post-tests. We performed the calculations in SigmaPlot 12.0 and PAST 2.14. Data are shown as the mean ± SD unless stated otherwise.

Results

Soil chemistry

Burrows of all the examined species were limited to soils with high or very high cation exchange capacity. However,

Fig. 2 Cation exchange capacity (a) and pH-CaCl₂ (b) of soils occupied by *Atypus* and *Eresus* spp.



the species differed in the strictness of their requirements (one-way ANOVA $p < 0.001$, $F = 3.952$). We identified the highest cation exchange capacity values as being associated with *A. piceus* (42.6 ± 18.4 mmol+/100 g), which was followed by four other species with mutually similar requirements for cation exchange capacity, with mean species-specific values of 37.1–38.5 mmol+/100 g. However, two *Eresus* species, *E. kollari* and *E. moravicus*, were not sensitive to cation exchange capacity, and their burrows were dug

in a very broad range of substrates, with cation exchange capacity values ranging from 4.5 to 117.9 mmol+/100 g and from 1.9 to 107.2 mmol+/100 g, respectively (Fig. 2a).

Based on the Hofmeister series paradigm, the cation exchange capacity of the soil is affected by its pH, with higher cation exchange capacity values observed under acidic conditions. However, the pH of soils obtained from the nest sites of *E. kollari* and *E. moravicus* was not lower than that of soils from the nest sites of most other species.

The highest pH-CaCl₂ was associated with nest sites of *A. muralis* (6.4 ± 1.1), while the lowest was associated with those of *A. affinis* (4.4 ± 1.2), which is directly related to the bedrock of the characteristic sites of occurrence for these species. The pH-CaCl₂ of unoccupied habitat patches was also lower than that associated with all species except *A. affinis* and reached only 5.0 ± 1.0 . Although the study species were associated with specific pH ranges (one-way ANOVA $p < 0.001$, $F = 13.820$), all were tolerant of extremely acidic soils, and we found at least a few burrows of each of the six spider species in such soils (Fig. 2b). However, only burrows of *A. affinis* were characteristically located in extremely acidic soils. Acidic soils (pH-CaCl₂ 4.6–5.5) were associated with *E. sandaliatus*, and more than half of the burrows of *A. piceus* were located in such soils. Soils of mild acidity (pH-CaCl₂ 5.6–6.5) were characteristically associated with *E. kollari* and *E. moravicus* and with nearly half of the burrows of *A. piceus*. Soils of neutral pH (pH-CaCl₂ 6.6–7.2) were associated with *A. muralis*, while alkaline soils (pH-CaCl₂ ≥ 7.3) were rarely occupied by any of the analyzed species (Fig. 2b).

Physical parameters of the soil

Burrows of *Eresus* spp., particularly those of *E. sandaliatus*, were associated with low soil penetration resistance. This is related to their frequent presence in rendzina with moder-type humus or in fine-grained talus (rock debris) below vertical slopes. Soils with burrows of *E. sandaliatus* reached a penetration resistance of just 0.9 ± 0.4 kg/cm², with a maximum value of 1.75 kg/cm². In contrast to the *Eresus* spp., the *Atypus* spp. were not limited to soft soils, and they often occupied more compacted soils, particularly loess and loessic soils. Characteristic examples of nest sites are loessic slopes, which have very high values of penetration resistance (Fig. 3a). The species-specific differences in soil penetration resistance were statistically significant (Kruskal–Wallis one way ANOVA on ranks $H = 21.559$, $d_f = 5$, $p < 0.001$). Dunn's pairwise post-tests revealed that the most prominent differences were between *A. muralis* and *A. affinis* ($Q = 4.07$), *E. sandaliatus* ($Q = 3.08$), and *E. kollari* ($Q = 3.0$, $p < 0.05$ each), whereas the differences between *A. muralis* and *E. moravicus* and between *A. affinis* and *A. piceus* were nonsignificant ($p > 0.05$ each). All other differences were smaller than those discussed above.

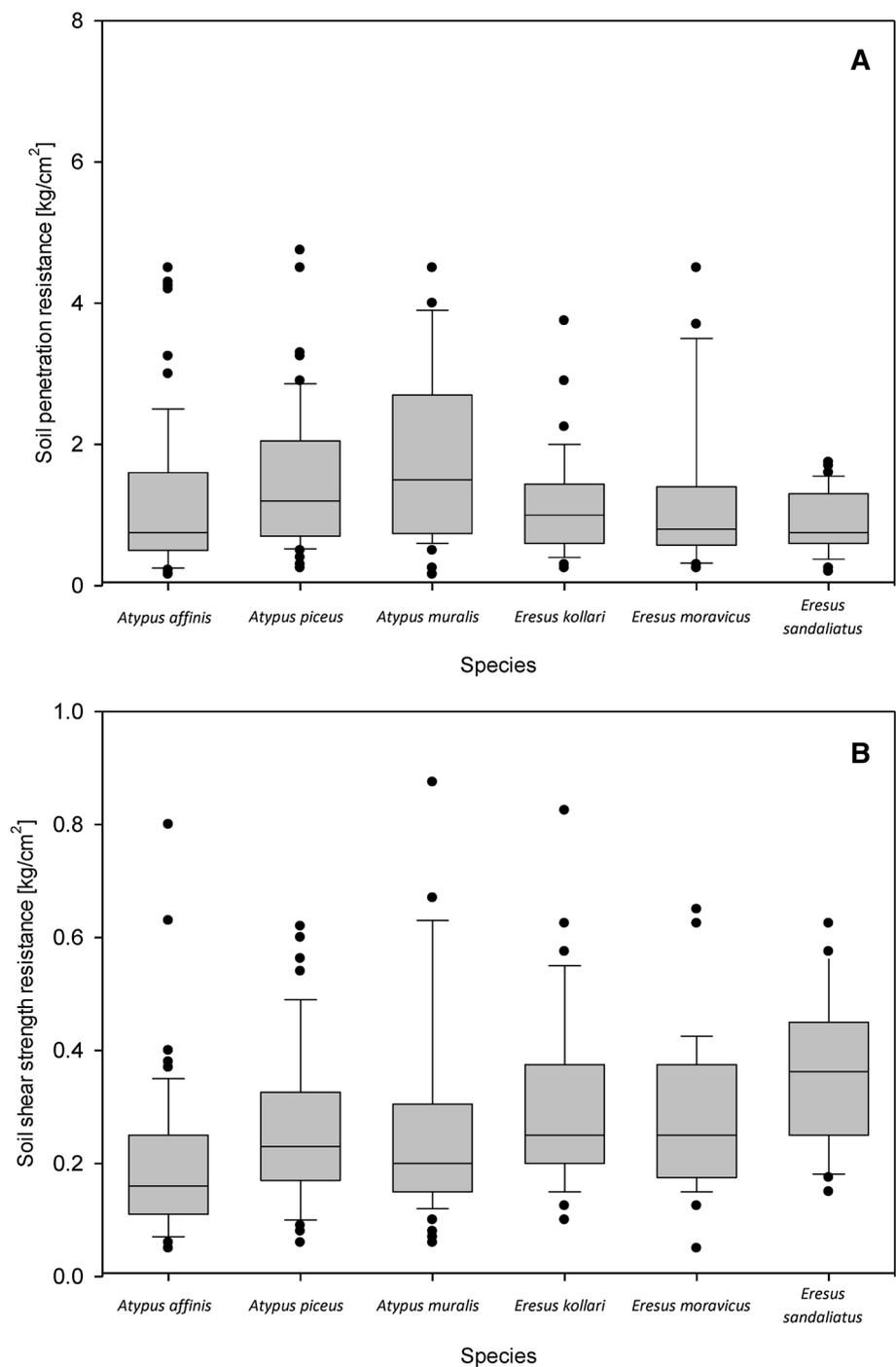
Importantly, soil cohesion, dilatancy and friction, which are responsible for the ability of soil to resist failure and sliding, were high at nest sites of *Eresus* spp. These variables, measured as shear strength resistance, explained why the *Eresus* spp. are able to dig their burrows in soft substrates without the risk of collapse of the burrow particularly during the time when it is dug out. We found the highest shear strength resistance in soils occupied by *E. sandaliatus*

(0.4 ± 0.1 kg/cm²). This species completely avoided soils with shear strength under 0.15 kg/cm². Other species, particularly all the *Atypus* spp., were less prone to avoiding low shear strength. In particular, *A. affinis* was able to dig its burrows in soils with shear strength of 0.05 kg/cm² or less (mean 0.2 ± 0.1 kg/cm²) (Fig. 3b). The species-specific differences in soil shear strength resistance were statistically significant (Kruskal–Wallis one way ANOVA on ranks $H = 37.350$, $d_f = 5$, $p < 0.001$). Dunn's pairwise post-tests revealed that the most prominent differences were between *E. sandaliatus* and *A. affinis* ($Q = 5.49$), followed by differences between *E. sandaliatus* and *A. muralis* ($Q = 3.37$) and *A. piceus* ($Q = 2.97$, $p < 0.05$ each); significant differences were also observed between *A. affinis* and *E. kollari* ($Q = 4.07$), *E. moravicus* ($Q = 3.12$) and *A. piceus* (2.96 , $p < 0.05$ each). The differences between *E. sandaliatus* and *E. moravicus* and between *A. affinis* and *A. muralis* were nonsignificant ($p > 0.05$ each). All other differences were smaller than those discussed above.

The *Atypus* and *Eresus* spp. differed in their soil preferences. All three *Atypus* spp. tolerated higher contents of clay and silt; the highest content of particles < 0.072 and 0.072 – 0.125 mm was associated with *A. muralis*. All the analyzed species were tolerant of a high content of cobbles and boulders (Fig. 4a), which is directly related to their frequent nesting in steep slopes with only thin strata of immature soils, which contribute to the limited vegetation outgrowth. The species-specific differences in the contents of particles < 0.072 mm were statistically significant (Kruskal–Wallis one way ANOVA on ranks $H = 24.322$, $d_f = 5$, $p < 0.001$). Dunn's pairwise post-tests revealed that the most prominent differences were between *A. piceus* and *E. sandaliatus* ($Q = 4.18$) and *E. kollari* ($Q = 3.47$, $p < 0.05$ each); significant differences were also observed between *A. affinis* and *E. sandaliatus* ($Q = 3.04$, $p < 0.05$). The differences between *A. piceus* and *E. moravicus*, between *A. affinis* and *E. kollari*, and between *A. muralis* and *E. sandaliatus* were nonsignificant ($p > 0.05$ each). All other differences were smaller than those discussed above.

There were species-specific differences in the preferred bedrock type. *Atypus affinis* and *E. sandaliatus* completely avoided unconsolidated sediments (such as sand and loess). However, this was not due to their chemistry, as they frequently occupied sites with bedrock consisting of consolidated sediments (sandstone or limestone). The other four species of *Atypus* and *Eresus* occupied both of these bedrock types. *Eresus sandaliatus* was absent from locations with metamorphic bedrock (migmatite, gneiss or marble). *Eresus moravicus* was absent from sites with extrusive magmatic bedrock (pyroclastics, tuff or basanite), and in particular, the nest sites of *E. sandaliatus* were located preferentially in association with this bedrock type. All species except *E. moravicus* were absent from

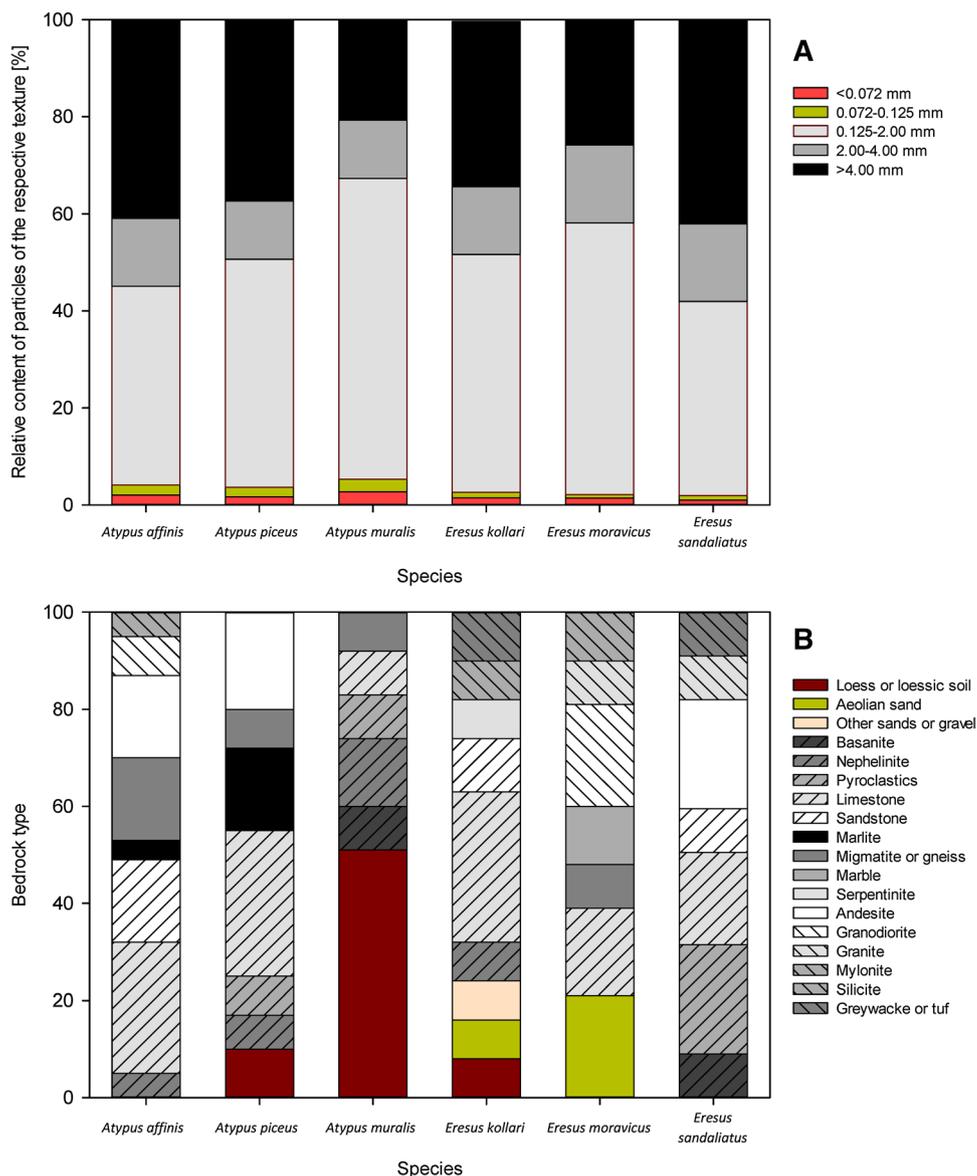
Fig. 3 Penetration resistance (a) and shear strength resistance (b) of soils occupied by *Atypus* and *Eresus* spp.



sites with intrusive magmatic bedrock (granite, granodiorite), with occasional findings of *A. affinis* and *E. sandaliatus*. Considering the distribution of bedrock types across the study area, the distributions of all species except *E. moravicus* were concentrated at sites with the presence of extrusive magmatic or metamorphic bedrock or sites with mineral-rich sediments. *Eresus moravicus* differed from all the other species in terms of its preference for well-drained sites formed on granodiorite bedrock or in

areas with aeolian sands, but it also occasionally occurred at sites with other bedrock types (Fig. 4b; Table S1). The *Eresus* spp. (but not *Atypus* spp.) frequently occurred in association with bedrock of Proterozoic origin. Most of the study sites occupied by any of the burrowing species were located where bedrock of Paleozoic origin occurs. Sites with Mesozoic and Tertiary bedrock were predominantly occupied by *A. piceus*, *A. muralis* and *E. sandaliatus* and were completely avoided by *E. moravicus*. Quaternary

Fig. 4 Soil texture (a) and bedrock (b) occupied by *Atypus* and *Eresus* spp.



bedrock was avoided by *A. affinis* and *E. sandaliatus*, while it was found at over half of the nest sites of *A. muralis* (Table S1).

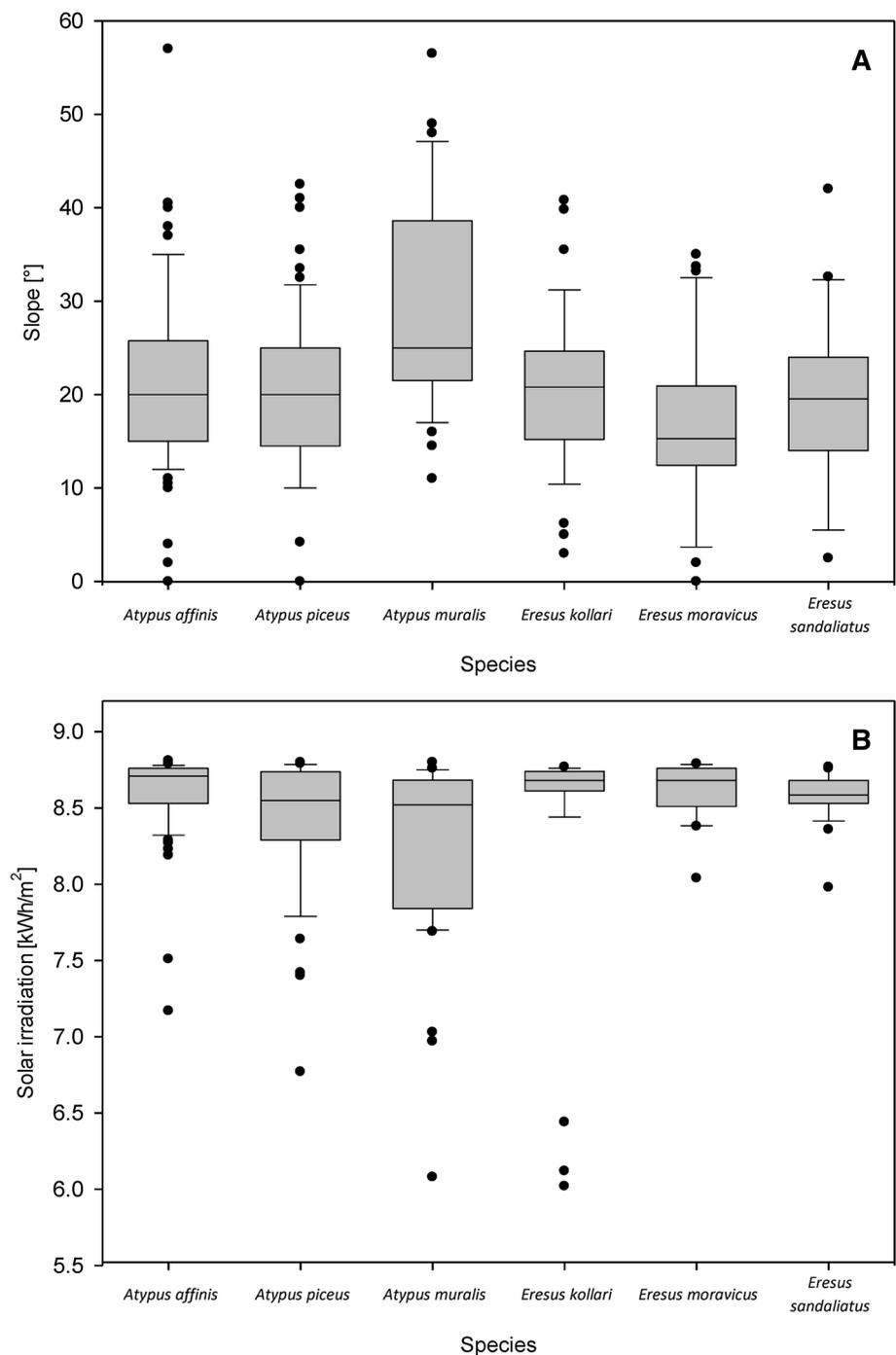
Other physical and biotic factors

The steppes and forest steppes of Czechia are mostly limited to well-drained slopes with southern exposures. Similarly, the nesting habitats of all the examined species were located in terrain with high inclination, which particularly applied to *A. muralis* (mean $29.5 \pm 10.8^\circ$; Fig. 5a). Most of the occupied slopes faced south. The species most sensitive to southward orientation were *A. affinis* and *E. moravicus*, while *A. piceus* was the least sensitive species (Table S2). Both these variables, together with the coordinates and altitude, affect solar irradiation. We calculated the theoretical solar

irradiation for 1 July (not reflecting the vegetation cover), and the results suggested that all the examined species preferred sites with high solar irradiation, with mean values for each species ranging from 8.3 to 8.6 kWh/m². In particular, *E. moravicus* and *E. sandaliatus* were very strict in their solar irradiation requirements, whereas the other species tolerated sites with less irradiation. The less-irradiated sites were associated in particular with *A. muralis* and *A. piceus* (Fig. 5b), which was surprising when considering their preference for regions with the highest annual temperature within the study area.

The nest sites of all the examined species experienced an increase in afforestation during the last 60 years. We identified the most intense changes at nest sites of *E. sandaliatus* (1.0 ± 0.6), *A. affinis* (0.9 ± 0.7) and *A. piceus* (0.9 ± 0.6). The nest sites of *E. moravicus* (0.6 ± 0.8), *E.*

Fig. 5 Slope inclination (a) and estimated solar irradiation (b) of microhabitats occupied by *Atypus* and *Eresus* spp.

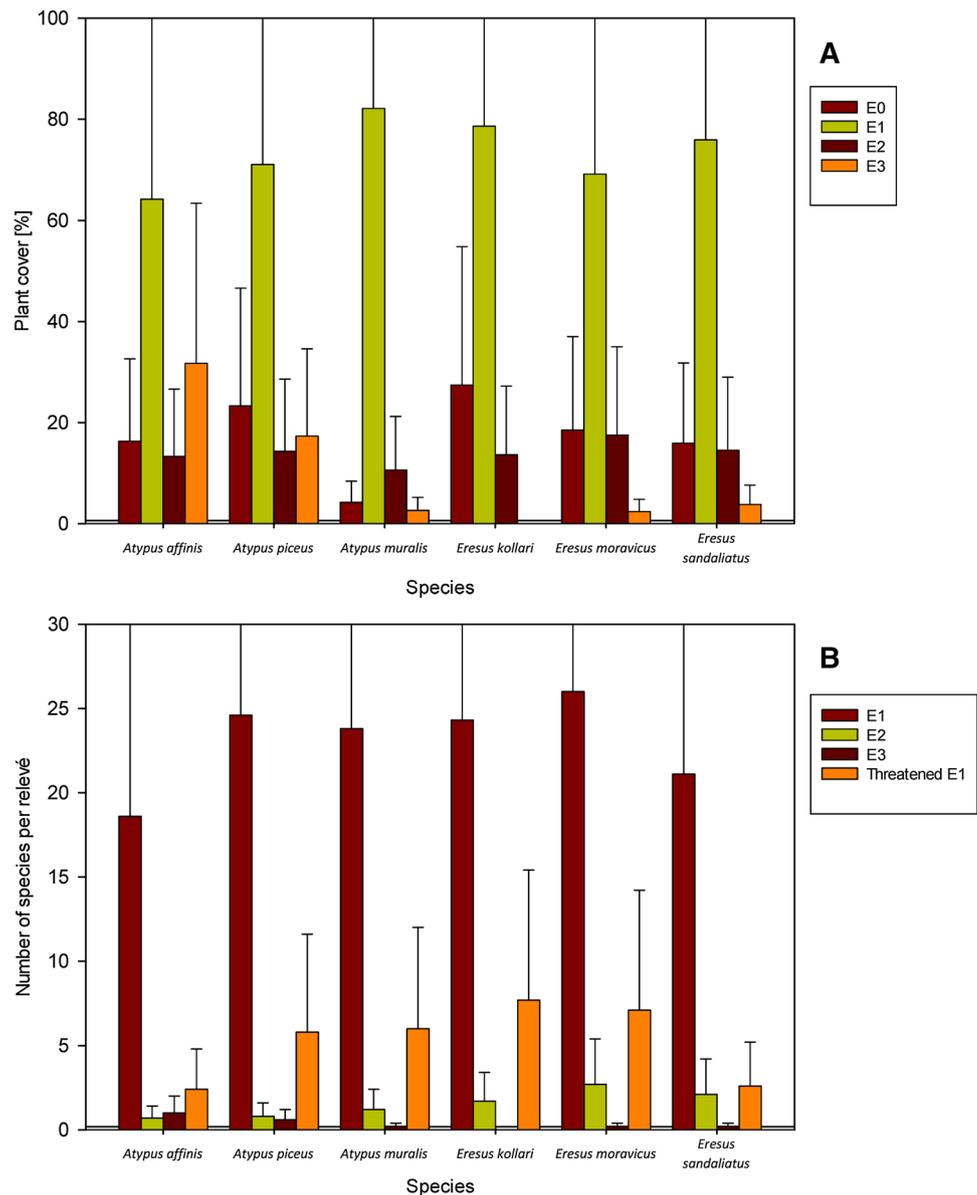


kollari (0.6 ± 0.6) and *A. muralis* (0.5 ± 0.7) were subject to less-intense change, but the same problematic trend towards afforestation was also recorded at their nest sites. Two species, *A. muralis* and *E. kollari*, completely avoided sites with forests and dense shrubs present in 1949–1956; all species were absent at sites of former fields. *Atypus muralis* was nearly exclusively present in steppes, with a single sampling site being located in a forest steppe; the other species occupied both steppe and forest-steppe habitats (Table S2). Note

that these data differ to a large extent from those on the current vegetation cover. Most of the sites of occurrence of any of the six species are now overgrown with shrubs, sparse trees or even dense forests.

Atypus affinis and *A. piceus* frequently occurred at sites with high cover of the tree layers (31.7 ± 27.4 and $17.3 \pm 24.1\%$, respectively). In contrast, the sampling sites hosting the other four species were associated with just a few trees, if any, and all sites where *E. kollari* occurred lacked a

Fig. 6 Plant cover (a) and number of plant species per phytocenological relevé (b) at microhabitats occupied by *Atypus* and *Eresus* spp. E0 through E3 denote vegetation layers (E0: moss, E1: herbs, E2: shrubs and E3: trees)



tree layer (Fig. 6a). The nest sites of all the examined species were associated with shrubs—the mean cover of the shrub layer ranged from 10.6% (*A. muralis*) to 17.5% (*E. moravicus*) (Fig. 6a). The mean cover of the herb layer ranged from 69.1% (*E. moravicus*) to 82.1% (*A. muralis*) (Fig. 6a). The mean cover of the moss layer varied highly; the moss layer was nearly absent at nest sites of *A. muralis* ($4.2 \pm 3.2\%$) but was present at the nest sites of all other species, with means ranging from 15.9% (*E. sandaliatus*) to 27.4% (*E. kollari*) (Fig. 6a). The vascular plant species richness was similar at the nest sites of all six species, ranging from 18.6 (*A. affinis*) to 26.0 (*E. moravicus*) herb species per relevé (Fig. 6b). Importantly, the nest sites differed in the numbers of threatened species of vascular plants. The nest sites of *A. affinis* and *E. sandaliatus* were associated with low numbers

of threatened herb species (2.4 ± 2.7 and 2.6 ± 1.8 threatened herb species per relevé, respectively). The other four spider species nested at sites with high diversity of threatened herb species, ranging from 5.8 (*A. piceus*) to 7.7 threatened herb species per relevé (*E. kollari*) (Fig. 6b). We observed corresponding differences in the numbers of threatened shrub species (Fig. 6b).

All study species were associated with plant species characteristic of stable natural xerothermic habitats. *Atypus affinis* was the species that was least dependent on a warm (micro)climate, as its distribution range also included sites at high altitudes, and it tolerated partly shaded habitats. It mainly occurred in xerothermophilous open oak forests on rocks (*Quercetea pubescentis*, *Quercetea robori-petraeae*). It was often associated with the oak *Quercus petraea*, the

shrub *C. vulgaris* and the grass *Festuca ovina*. *Atypus piceus* preferred calcium-rich compact soils, which are characteristic of Cirsio-Brachypodium pinnati and xerothermophilous Geranium sanguinei forest fringes. It also survived in habitats secondarily overgrown by woody vegetation. It was often associated with the grass *Brachypodium pinnatum* and the herb *Galium verum*. *Atypus muralis* was restricted to relatively deep calcium-rich soils of the chernozem type. It exclusively occurred in continental steppes (Festucion valesiaca). It was associated with the grass *Festuca valesiaca* and the herb *Eryngium campestre*.

Eresus kollari is restricted to areas with the historical occurrence of chernozem steppes in the early Holocene; it occurred in the mineral-rich soils of continental steppes (Festucion valesiaca). It was associated with the grass *F. valesiaca* and the herb *Echium vulgare*. *Eresus sandaliatus* occurred on the edges of the distribution area of *E. kollari*, but these areas did not overlap in Czechia. It appeared that *E. sandaliatus* occurred only in areas that were too cold and/or humid for *E. kollari*. It occurred in steppe grasslands (Festucion valesiaca) dominated by the grass *Festuca rupicola* or the sedge *Carex humilis*. In comparison with *E. kollari*, *E. moravicus* occurred in warmer and drier habitats and only in the Pannonian part of Czechia. It occurred in well-drained sandy soils. Its habitats were usually characteristic of steppe grasslands (Festucion valesiaca) often dominated by the grasses *Bothriochloa ischaemum* or *Stipa capillata* (Table S3).

Population characteristics and the density and length of burrows

The examined species formed abundant colonies. The mean maximum density of burrows reached 212 ± 360 burrows/m² for *A. affinis*, 143 ± 314 burrows/m² for *A. piceus* and 136 ± 281 burrows/m² for *E. sandaliatus*. The other species displayed a lower maximum density of burrows, with the lowest values recorded for *E. kollari* (13 ± 27 burrows/m²) (Table S2). However, the mean densities of all the species were much lower, usually below 1 burrow/m².

Some of the sampling sites represented syntopic colonies. The most frequent were syntopic colonies of *A. affinis* with *A. piceus* (seven cases). In addition, *E. kollari* often occurred syntopically with other spider species, namely with *A. affinis* (two cases), *A. piceus* (three cases) and *A. muralis* (five cases). Other species interactions were rare; we noticed one case each of syntopic *A. affinis* with *E. moravicus*, *A. affinis* with *E. sandaliatus* and *A. piceus* with *E. sandaliatus* (Table S2).

Regarding the little-known phenology and sex ratios of burrowing spiders, for *A. affinis*, we recorded a single adult male in its own burrow on 1 November. In terms of subadult *E. moravicus*, we found numerous subadult individuals of

both sexes at a ratio of 9 F:2 M (females: 2 on 4 October, 6 on 5 October, 1 on 19 October; males: 1 on 5 October and 1 on 19 October). For adult *E. sandaliatus*, we recorded a sex ratio of 19 F:4 M (males: 1 on 17 September, 1 on 25 September and 2 on 12 October). In burrows with adult females of *A. affinis*, we recorded the presence of adult males (three cases, 9% of all burrows with adult females of *A. affinis*—all on 1 November); adult males were not present in burrows with females of any other species. In burrows with adult females of *A. affinis*, we recorded the presence of nests with eggs (three cases, 9% of all burrows with adult females of *A. affinis*—all on 21 July); eggs were not present in burrows with females of any other species. In burrows of all six species, we repeatedly recorded the presence of nests with juveniles of the first or second instar together with remains of their dead mother. We found the juveniles of the first or second instar in 4 burrows (9%) of adult females of *A. affinis*, 8 burrows (19%) of adult females of *A. piceus*, 12 burrows (40%) of adult females of *A. muralis*, 2 burrows (9%) of adult females of *E. kollari*, 5 burrows (100%) of adult females of *E. moravicus*, and 3 burrows (16%) of adult females of *E. sandaliatus*.

The burrows of adult females of *Atypus* spp. were several times longer than those of adult females of *Eresus* spp. In *Atypus* spp., the burrow length of adult females reached 16.2 ± 6.3 cm (*A. affinis*), 12.6 ± 3.7 cm (*A. piceus*) and 25.2 ± 8.5 cm (*A. muralis*). In *Eresus* spp., the burrow length of adult females reached 6.3 ± 2.3 cm (*E. kollari*), 7.9 ± 2.1 cm (*E. moravicus*) and 6.3 ± 1.8 cm (*E. sandaliatus*). The burrows of adult males were of similar length—they reached 21.0 cm in *A. affinis* and 5.1 ± 1.2 cm in *E. sandaliatus*. The burrow length was affected by the bedrock type. Specifically, the length of burrows of *A. muralis* decreased in size from those located in unconsolidated sediments (28.4 ± 7.8 cm long), through metamorphic bedrock (21.7 ± 1.9 cm long) and extrusive magmatic bedrock (17.8 ± 2.6 cm long) to the length of just 9.0 cm in consolidated sediments.

In *Atypus* spp., we analyzed the reproductive ability based on the numbers of larvae in burrows examined in course of the present study and previously (Řezáč, unpubl.). All the three *Atypus* spp. had roughly similar number of larvae (*A. affinis*: 97 ± 49 larvae, range 53–193 larvae, n = 5 burrows; *A. piceus* 100 ± 38 larvae, range 55–168 larvae, n = 9 burrows; *A. muralis* 89 ± 37 larvae, range 31–150, n = 10 burrows). However, the three species differed in a weight of their larvae, with those of *A. affinis* weighing the least (mean of means of weight of larvae within each clutch 1.07 ± 0.06 mg, range 0.97–1.16 mg, n = 5 burrows), followed by those of *A. piceus* (1.50 ± 0.06 mg, range 1.37–1.58 mg, n = 9 burrows) and with *A. muralis* larvae being the heaviest (2.03 ± 0.12 mg, range 1.85–2.17 mg, n = 10 burrows). The number of larvae and their weight in

individual burrows were not correlated in any of the three species examined (Pearson's correlation coefficient $p > 0.05$ each) and were highly variable even within individual examined sites where we excavated multiple burrows containing larvae.

Discussion

Does water evaporation or its proxy in the form of cation exchange capacity play a role in the known link between some burrowing spider species and calcareous and igneous bedrock?

Soil organic matter directly affects the amount of water in soil by influencing water infiltration, percolation, and evaporation rates and increasing the soil water holding capacity. The stable fraction of soil organic matter (humus) is considered to be the most important fraction contributing to the cation exchange capacity of soil. The cation exchange capacity of the humus itself is within the range of 40–200 mmol+/100 g. The cation exchange capacity of sand ranges only of 1–5 mmol+/100 g, and most soils within the study area are within the range of 8–12 mmol+/100 g (considered low cation exchange capacity) to 25–30 mmol+/100 g (considered high cation exchange capacity). In this study, we have shown that the analyzed species typically dig their burrows in soils with high or very high cation exchange capacity. We found that four of the six analyzed species preferred soils with very high cation exchange capacity and avoided soils with intermediate or low cation exchange capacity. The association with soils having high cation exchange capacity has direct implications for the stability of the burrow microclimate and humidity (Churchman and Burke 1991; Torrent et al. 2015), which is important in allowing the survival of these long-lived spiders in habitats that are otherwise subject to extreme diurnal temperature variation. One of the two species tolerant to soils with intermediate or low cation exchange capacity, *E. moravicus*, occurred in such soils only in microhabitats with no inclination of the ground. We speculate that the low cation exchange capacity at these sites prevents the accumulation of water at sites that are not subject to the simple surface drainage of steep slopes, where this species otherwise occurs.

The effects of high cation exchange capacity can be strengthened by low pH of the soil. However, the species that were least sensitive to the cation exchange capacity values of the soil were not identical to those nesting in soils with the lowest pH values (Fig. 2). Soil pH itself has been repeatedly indicated as a driver of the composition of spider assemblages (e.g., Ziesche and Roth 2008, but see Ferreira and Martins 1998). It is still unclear whether there are any

direct effects or whether the effects of pH are mediated by affecting the composition of plants, microbes and fungi and thus the food sources for the prey of spiders.

The direct measurement of water evaporation is problematic. We constructed a system allowing the measurement of water evaporation from intact or tamped soil specimens under a nitrogen atmosphere. However, the measurements were severely affected by the formation of cracks in soil samples with high silt or clay content, and only sand and sandy soils provided useful data. Under the forced flow of nitrogen at 1660 cm³/min ($t = 30$ °C, $p = 1013.25$ hPa), the control aeolian sand quickly reached the evaporation rate of ~ 1.7 mg H₂O/dm³ of N₂/g of soil. In contrast, the soils occupied by the burrowing spiders gradually progressed from the very low evaporation rate of ~ 0.2 mg H₂O/dm³ of N₂/g of soil and reached the rate of evaporation found for sand only after losing as much as $\sim 20\%$ of the initial wet soil weight (Tošner and Heneberg unpubl.). The variability among the replicates of the above experiments did not allow the differences among the soil samples from the sampling sites to be analyzed except for those taken from completely different environments, such as loess, rendzina and aeolian sand. Further research should, however, focus on the improvement of these measurements, as the understanding of water evaporation capacity seems to be crucial to our understanding of soil type selection in burrowing spiders and other arthropods.

Could any of the physical or chemical properties be used as a proxy to indicate the suitability of a given soil type for particular burrowing spiders?

We did not identify any variable exclusively associated with just one or a few of the studied burrowing species. However, some soils were preferred or completely avoided by some of the analyzed species. All *Eresus* spp. avoided compacted soils with high penetration resistance (Fig. 3a), and their burrows dug into soils with very low penetration resistance were limited to sites with high soil cohesion measured as shear strength resistance (Fig. 3b). Usually, soil shear strength resistance increases with increasing soil penetration resistance; thus, such a preference can be viewed as an important limitation in the habitat selection of these species. Previous analyses even suggested an equation allowing the prediction of shear strength resistance based on the penetration resistance, which was as follows: $SSR = 0.019 + 0.016 PR$, where SSR denotes shear strength resistance and PR means penetration resistance (Ekwue and Stone 1995). Using the same methodology as in the present study, we also previously obtained several datasets where shear strength resistance and penetration resistance were correlated with one another (Srba and Heneberg 2012; Heneberg et al. 2016). The limitation of *Eresus* spp. to soils that differ from the

above is thus considered a major limitation in habitat selection by these species.

Another predictor that is of practical use is the selection of bedrock types by particular spider species. In previous studies, Řezáč et al. (2007) noticed that *A. piceus* and *A. muralis* were limited to agglutinate calcareous soils. In this study, we further developed this paradigm and analyzed the preferences of other study species. We found that *A. affinis* and *E. sandaliatus* avoided unconsolidated sediments, including any types of sand, loess or loessic soils. *Eresus sandaliatus* also avoided metamorphic bedrock. Most of the species tended to avoid igneous bedrock types, which were occupied only by *E. moravicus*, with occasional findings of *A. affinis* and *E. sandaliatus*. The selective use of particular bedrock types was very prominent, particularly in areas with the prevalent occurrence of one bedrock type, where the occurrence of the study species was limited only to tiny remnants (marlite at sandstone, loess at schist), outcrops (marble in schist) or run-offs (loess at sandstone) of other bedrock types (Table S1).

All burrows were at well-drained sites, either on steep slopes or, less frequently, at less inclined sites, but in those cases, the localities were limited to well-drained bedrock, such as aeolian sand. Most of the sampling sites were oriented towards the south, southeast or southwest. However, occasionally, we also identified localities oriented in other directions (except for those of *E. moravicus* and *E. sandaliatus*). These sites were occupied largely by *A. muralis* and *A. piceus*. As *A. muralis* was strictly limited to habitats where steppes were present in the mid-twentieth century, it seems that it is not the orientation towards the south but the absence of trees and shrubs that defines the appropriate habitat for this species. The second species occupying slopes facing directions other than south, *A. piceus*, is more shade-tolerant, but all sampling sites where this species occurred also consisted of steppes, forest-steppes and shrubby pastures in the mid-twentieth century (Table S2). The present habitat types are not as strictly defined because of their severe overgrowth with shrubs and trees during recent decades following the change in agricultural regimes. Thus, it appears that all the study species are tolerant of some degree of shade, but they do not actively search for such sites, their populations are weak at such sites, and they often tend to occupy the last remaining forest clearings or forest edges (Řezáč and Heneberg unpubl.).

Are there any variables that can be used as proxies of the presence of burrowing spiders in applied conservation?

Each of the burrowing spider species is associated with specific plant communities (Řezáč et al. 2007; Krejčí 2012; Řezáč and Heneberg 2014). Previous authors have

characterized in detail the plant communities associated with particular species. These communities differ from one another. However, when actively searching for spider burrows in the field, it is not only the presence of specific plant communities that indicates the presence of particular spider species. The burrows of all *Atypus* spp. were typically associated with patches of *B. pinnatum*, whereas the *Eresus* spp. were typically found in microhabitats with *F. rupicola*. *Brachypodium pinnatum* is a species of sunny forest fringes and forest-steppe slopes. It is characteristic of humic, often calcareous soils. *Festuca rupicola* is a characteristic species of dry steppe grasslands, also growing in floodplains and meadows that periodically flood but later dry out. It prefers deep, heavy, nutrient-rich soils, usually on limestone or loess, and less frequently also occurs on sandbanks. In addition to these two species, there are also numerous other vascular plant species that indicate the possible presence of one or more burrowing spider species. Among them are both common and threatened species. The threatened species are represented by, e.g., *S. capillata*, which is characteristically associated with nest sites of *A. muralis*, and *Stipa borysthena*, which is characteristically associated with nest sites of *E. kollari*. *Stipa capillata* is a species of dry rocky hillsides, steppes and hedgerows, while *S. borysthena* is considered a rare postglacial relict species of sandy soils and grows at sunny and dry sites in lowlands.¹ For the identification of potential nest sites of burrowing spiders, the species composition of vascular plant assemblages is invaluable.

Another form of guidance that is broadly applicable is knowledge of the bedrock units forming the study area. The examined spider species were strict in their bedrock requirements. In regions containing isolated populations of a particular species, this species is usually bound to a specific bedrock type that is absent in the surrounding landscape. In particular, the distributions of marlite, limestone, loess and tuff overlap with the distribution areas of *A. piceus* and *A. muralis*. Often, tiny areas with these bedrock types encompassing just a few tens of square meters are occupied by these species that are, however, absent from large areas of the surrounding landscape. It is of interest in this regard that there are burrowing organisms already known to specifically live in particular sediment types. A classic example is the bee-eaters (Aves: Meropidae), the mid-sized burrowing birds that specifically nest in loess deposits across the world as documented by Ian Smalley and his team for *Merops apiaster* (Smalley et al. 2013, 2016b), *Merops nubicus* (McLaren et al. 2014), *Merops ornatus* (Smalley et al. 2016a), *Merops orientalis* and *Merops persicus* (Smalley et al. 2016b). In the present study, we document a similar relationship for *A. muralis*, the population of which is associated strictly with

¹ <http://www.botany.cz>; cited as 6 February 2017.

loess deposits and extrusive igneous rocks (Fig. 4b). Like the coincidence of distribution maps of nesting bee-eaters and of loess deposits, the similar coincidence is present between the known sites of occurrence of *A. muralis* (Řezáč et al. 2007) and the Scheidig (1934) map of loess deposits in Europe.

Soil characteristics are of limited use in the applied conservation of burrowing spiders. They are difficult to measure, and individual species have relatively broad valence (cf. the previous subchapter for the most striking differences). Generally, the *Atypus* spp. avoid rock steppes, or if present in such steppes, they are restricted to microhabitats containing deep pockets of soil that allow them to construct appropriately long burrows. The *Eresus* spp. are not as selective in terms of the depth of the soil, but they prefer soils with low penetration resistance, often with high soil cohesion. When previous nest sites of these burrowing spiders are affected by plowing or trampling, the spiders disappear and do not reappear for at least several consecutive decades (Řezáč and Heneberg pers. obs.). It remains to be examined to what extent these species can survive disturbances, what are the key effects that cause the population decline in the study species and how long it takes the decreased population to recover after, e.g., trampling associated with grazing. While we have never seen these spiders return to sites affected by plowing, it seems that residual populations can survive trampling, e.g., under shrubs or fallen trunks, from which they can potentially recolonize the affected area once the disturbance is over. However, the adverse effects of newly formed pastures are obvious, as the numbers of burrows outside fenced areas and inside of them differ dramatically even within a single year since the onset of grazing (as at the sampling site Oblík et al.; Řezáč and Heneberg pers. obs.). This issue needs to be resolved in the future, as grazing is one of the key forms of management of steppes and forest-steppes that were once devoid of any shrubs or trees and that represent the key habitats of the analyzed species.

Conclusions

The importance of a stable and humid microclimate for the nesting of burrowing spiders in temperate regions was suggested decades ago (Coyle and Shear 1981; Miyashita 1992; Řezáč et al. 2007; Buchholz 2010), but direct evidence was lacking. In this study, we showed that all the analyzed burrowing spider species are typically associated with high or very high cation exchange capacity values and that four species avoided any soils with intermediate or low cation exchange capacity. As a high cation exchange capacity of the soil is the key characteristic allowing the stability of the burrow microclimate and burrow humidity, we provided the first direct evidence for the association of these variables with the nest sites of the analyzed spider species. The study

species were associated with specific bedrock types, which could be used as predictors of their presence within a particular landscape. Specific plant communities and individual plant species associated with the study species can be used as proxies for the presence of intact terrain, as extensive landscaping and particularly plowing, have led to the long-term abandonment of the microhabitats by all of the study species.

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Compliance with ethical standards

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