Received: 20 June 2025 | Accepted: 19 August 2025

DOI: 10.1111/een.70018

ORIGINAL ARTICLE

Ecological Entomology | Royal Entomological Society

Solar parks provide heterogeneous habitats for winter-active ground-dwelling predatory arthropods

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Funding information

Hungarian National Research, Development and Innovation Office, Grant/Award Number: K 146137 and FK-142926

Associate Editor: Thomas Hesselberg

Abstract

1. Winter-active ground-dwelling spiders and ground beetles mainly inhabit non-crop habitats (e.g., grasslands and forests) with complex-structured vegetation and stable microclimates. In spring, they migrate from non-crop habitats into crop fields, contributing to pest control. Nowadays, there is an increasing number of solar parks in agricultural landscapes. However, the role of solar parks as habitats for winter-active ground-dwelling spiders and ground beetles and thus their potential contribution to pest control has not been studied yet.
2. We investigated how different habitat types (i.e., forest, grassland, habitat between and under solar panels and abandoned farmland) are associated with variation in microclimatic conditions (i.e., air temperature and humidity) and with the diversity of winter-active ground-dwelling spiders and ground beetles across 50 sites in western Hungary. Using pitfall traps, we collected 957 ground-dwelling spiders belonging to 69 species and 327 ground beetles belonging to 40 species. We recorded microclimatic conditions using data loggers simultaneously with arthropod sampling.
3. We showed that patterns in arthropod assemblages likely reflect differences in microclimatic conditions across habitat types. Solar parks hosted species of different habitats (e.g., forest, grassland, wetland) with a relatively strong preference for humidity. Solar parks also supported a high abundance of agrobiont ground-dwelling spiders (i.e., species dominant in agroecosystems). In contrast, grasslands and abandoned farmlands exhibited the most extreme microclimatic conditions, supporting mainly dry-habitat species.
4. Our results demonstrate for the first time that solar parks can serve heterogeneous habitats for diverse assemblages of winter-active ground-dwelling spiders and ground beetles and may positively contribute to biocontrol and biodiversity conservation.

KEYWORDS

Araneae, biodiversity, Carabidae, Hungary, novel ecosystem, photovoltaics

[Corrections added on 23 October 2025, after first online publication: ORCID IDs have been added, and some minor grammatical corrections have been made and figures have been repositioned in the text.]

INTRODUCTION

Intensified agricultural land use has changed ecosystems more dramatically and intensely than ever in human history (Matson et al., 1997). Land-use changes include the conversion of complex non-crop habitats, such as grasslands and meadows, into simplified crop fields or abandoned and degraded habitats. Moreover, the intensification of resource utilisation is characterised by the increased use of agrochemicals (Robinson & Sutherland, 2002; Stoate et al., 2009; Tscharntke et al., 2005). These changes are the main reason for the decline in arthropod biodiversity (Prangel et al., 2023; Raven & Wagner, 2021; Seibold et al., 2019), which negatively affects essential ecosystem services such as biological control (Geiger et al., 2010; Thies et al., 2011). In today's intensified landscape, non-crop habitats are therefore gaining importance as vital habitats for native biodiversity, including natural enemies of crop pests (Gallé et al., 2018; Hamřík & Košulič, 2021; Knapp et al., 2022).

The harvest of annual crops increases predatory arthropod mortality and simplifies microhabitat structures, leading to their movement into surrounding non-crop habitats (Opatovsky & Lubin, 2012; Thorbek & Bilde, 2004). Furthermore, their overwinter survival in crop fields is low due to limited vegetation. Consequently, many predatory arthropods overwinter in adjacent habitats and disperse into the crop fields in the spring (Landis et al., 2000). Non-crop habitats that provide suitable microhabitats and prey resources for winter-active predatory arthropods are therefore crucial for sustaining effective biological control, as they facilitate rapid recolonisation of adjacent crop fields (Tscharntke et al., 2012).

Agrobionts can be defined as species that exhibit dominance in agroecosystems, thereby contributing significantly to biological control (Michalko & Birkhofer, 2021; Rusch et al., 2015; Samu & Szinetár, 2002). Some of the agrobiont predatory arthropods are winter-active, which means that they actively move and feed even during the winter months when temperatures are low (Gajski et al., 2024; Jaskula & Soszyńska-Maj, 2011). These winter-active agrobionts can effectively suppress pest populations during winter and early spring because the pest mortality during this period is not offset by reproduction (Pekár et al., 2015). Habitats that are structurally similar to focal crops and maintain high humidity have the potential to provide microhabitats for winter-active agrobiont predatory arthropods (Holland et al., 2016; Kober et al., 2024; Michalko & Birkhofer, 2021).

Spiders and ground beetles, as dominant generalist predators in terrestrial ecosystems, comprise many winter-active agrobiont species and significantly contribute to biological control by reducing crop pest populations (De Heij & Willenborg, 2020; Kotze et al., 2011; Michalko et al., 2019), especially at the beginning of the season (Birkhofer, Bezemer, et al., 2008; Pekár et al., 2015). Vegetation structure and microclimatic factors such as shading, humidity and temperature are significant determinants of the diversity and composition of ground-dwelling spiders and ground beetles (Entling et al., 2007; Hamřík & Košulič, 2021; Kotze et al., 2011; Lövei & Sunderland, 1996). However, during winter, the effect of microclimatic conditions is stronger than that of habitat structure on winter-active predatory arthropods (e.g., Ingle et al., 2020). Ground beetles overwinter in habitats that offer a more stable microclimate with low temperature fluctuations but relatively high minimum temperatures (Lövei & Sunderland, 1996; Roume et al., 2011). Therefore, winter is a crucial period that affects the survival of these predatory arthropods.

Given the increasing demand for renewable energy, the EU is expected to allocate 0.5%–5% of its land for solar park development by 2050 (Van de Ven et al., 2021). Solar panels are often installed on the ground, altering microclimatic conditions in their surroundings (Armstrong et al., 2016; Lambert et al., 2021; Pisinaras et al., 2014). Solar parks can be regarded as novel ecosystems that provide high microclimatic variability as they host relatively shaded habitats and a humid microclimate under solar panels while relatively open habitats and a drier microclimate exist between the panels (Tölgyesi et al., 2023). Consequently, forest-associated species may prefer habitats under solar panels, whereas grassland-associated and agrobiont species may thrive between the panels. Therefore, solar parks may play an important role not only in biodiversity conservation but also act as important source habitats for natural enemies of pests.

Non-crop habitats such as forests, grasslands and field margins are recognised for providing suitable habitats for winter-active spiders and ground beetles (e.g., Geiger et al., 2009; Ingle et al., 2020; Knapp et al., 2022). Accordingly, most studies on winter-active predatory arthropods have been conducted in forests and agricultural habitats (e.g., Gallé et al., 2018; Ingle et al., 2020; Pekár et al., 2015). The high diversity of microhabitats in solar parks, along with the microclimate buffering provided by solar panels that increases soil humidity (e.g., Armstrong et al., 2016), could positively affect winter-active predatory arthropods. Despite the high potential of solar parks for predatory arthropod conservation, only a few studies on spiders and ground beetles have focused on solar parks (e.g., Armstrong et al., 2021; Zitzmann et al., 2024). The role of solar parks as habitats for winter-active ground-dwelling spiders and ground beetles, as well as their potential for biological control, has not yet been examined. Exploring this could shed light on whether solar parks support biodiversity and biocontrol ecosystem service in agricultural landscapes.

The objective of this study was to evaluate the effect of habitat type (i.e., forest, grassland, habitat between and under solar panels and abandoned farmland) and microclimatic conditions (i.e., air temperature and humidity) on winter-active ground-dwelling spiders and ground beetles, focusing on comparing the effects of solar parks with other habitat types in western Hungary. We hypothesised that (1) the habitats under solar panels exhibit similar microclimatic conditions to those observed in forests, whereas the habitats between solar panels resemble grasslands and abandoned farmlands. This results in similar assemblage compositions of winter-active ground-dwelling predatory arthropods under solar panels and in the forests, as well as between solar panels and in grasslands and abandoned farmlands. We also predicted that (2) solar parks promote higher species richness and support species from different habitats due to their heterogeneous environment and the resulting increased diversity of microclimatic conditions. In contrast, (3) grasslands and abandoned farmlands have a lower species richness of winter-active ground-dwelling predatory arthropods, composed of species preferring drier habitats due to their more homogeneous environment and thus reduced microclimatic variability. Finally, we predicted that (4) solar parks host a high abundance of agrobiont species due to the presence of humid conditions and the structural similarity of these habitats to adjacent crop fields.

MATERIALS AND METHODS

Study site

The study was carried out in western Hungary (Figure 1). The mean annual temperature ranges from 10.5°C to 11.5°C, and the mean annual precipitation from 600 mm to 800 mm. The coldest month's (January) mean temperature ranges from −1°C to 1°C, and the precipitation ranges from 40 mm to 50 mm (Bihari et al., 2018; Hungarian Meteorological Service, 2024). Elevation of the study area ranges from 115 m to 210 m above sea level. The dominant land use is agriculture, followed by settlements and forests.

The study sites are located around five settlements, namely Bicske, Csurgó, Nagyatád, Nyirad and Óhíd (Figure 1). Forests consist of small patches of plantations primarily composed of oak and alder, with no recent forestry activities. Grasslands comprised extensively managed mesic meadows. Abandoned farmlands represent small patches of former arable fields, field margins (Figure S1), degraded grasslands overgrown by shrubs (Figure S2) and other heavily disturbed habitats. Abandoned grasslands overgrown by shrubs due to reduced management often support low species richness of ground-dwelling spiders and ground beetles (Prangel et al., 2023). Including this habitat type allows us to evaluate whether solar parks, as novel and human-modified environments, merely resemble the low-quality disturbed areas commonly found in agricultural landscapes or contribute positively to biodiversity beyond the degraded conditions of the surrounding matrix.

We selected solar parks located 18–180 km apart and 5–10 years old to minimise the impact of construction-related disturbances. The solar park panels are mounted in rows on steel structures and facing south. The distance between the panels and the ground is 60–80 cm at the lowest part. The width of the area under the solar panels is 4 m, and the spacing between the rows of panels is 4–6 m.

Solar parks were established on degraded grasslands with varying amounts of shrubs, except for Bicske, which was established on arable land. They are located within or at the edge of the settlements, surrounded by buildings, infrastructure, as well as arable fields and grasslands. The vegetation in solar parks is composed of plant species that have colonised these areas from the surrounding landscape or have emerged from the soil seed bank. To prevent shading of the solar panels, the solar parks are managed 3–4 times a year by mowing without biomass removal, except for the solar park in Bicske, which is managed by sheep grazing. All sites are managed during the growing season outside the winter months, i.e., outside the studied sampling period.

Study design

Near each settlement, we established two independent sampling sites in each of the following habitat types: forest, grassland and abandoned farmland. In the case of solar parks, two sampling sites were established within each park, placed 100 metres apart. In total, we established 50 sampling sites: 10 in forests, 10 in grasslands, 10 in abandoned farmlands, 10 between solar panels, and 10 under solar panels.

We recorded the following microclimatic variables using data loggers (Optin TH4-32 U): (a) humidity (%), (b) minimum temperature

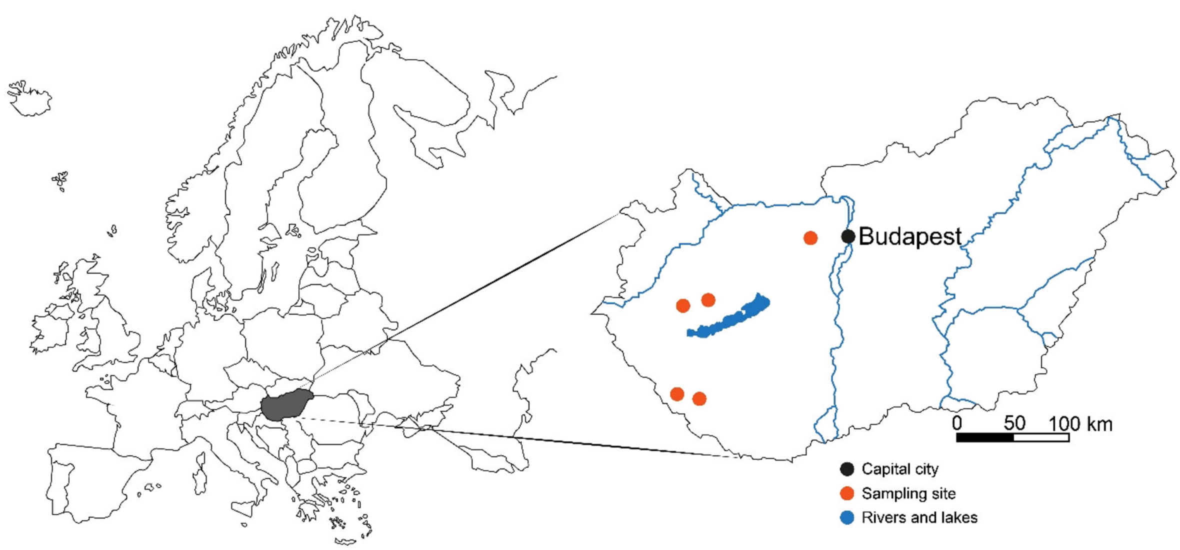

FIGURE 1 Map of the study area with the positions of the five settlements.

(°C), (c) maximum temperature (°C), (d) mean temperature (°C) and (e) temperature variation (max. temperature-min. temperature) (°C). Microclimatic conditions were recorded every 20 minutes for 11 days (from February 23 to March 4—the second arthropod sampling period). Near each settlement, one data logger was placed in each habitat type at one of the two sampling sites. However, the data loggers placed in the forests of Bicske, the habitats between solar panels in Ohid and the abandoned farmlands in Nagyatad were lost.

We collected ground-dwelling predatory arthropods using pitfall traps. Pitfall traps were plastic cups (diameter of 8.5 cm), filled with a 50% water-ethylene-glycol solution and a few drops of detergent. We used a plastic funnel to reduce vertebrate catches and prevent arthropods from escaping, and a plastic roof to protect the preservation fluid from dilution by precipitation (Császár et al., 2018). Traps were open for two 14-day periods at the beginning of November (2023) and the end of February (2024). In the forest, grassland and abandoned farmland, two pitfall traps 8–10 m apart were placed in a transect at the centre of each site. In the solar parks, two traps 8 m apart were placed centrally under the solar panel (hereafter referred to as habitat under solar panel) and between the solar panels (hereafter referred to as habitat between solar panels).

Species classification

All adult spiders were identified to the species level following Heimer and Nentwig (1991) and Nentwig et al. (2024). The nomenclature is based on the latest version of the World Spider Catalog (2024). Ground beetle species were identified following Müller-Motzfeld (2004); their nomenclature is based on Szél (2019).

As ground-dwelling spiders and ground beetles are sensitive to changes in microclimatic conditions, we selected two available and accessible species-level traits to characterise assemblage trait composition: humidity preference (1—very dry, 2—dry, 3—semi-humid, 4—humid, 5—very humid) and shading tolerance (1—open, 2—semi-open, 3—partly shaded, 4—shaded). Spider species trait data were obtained from Buchar and Růžička (2002), while ground beetle species traits were obtained from various websites (Appendix S1). If a species was assigned to more than one category, it received an average value. A non-integer between two categories was rounded based on expert knowledge. Traits of the recorded spider species are available in Table S1, and traits of the recorded ground beetle species are in Table S2.

To assess the ecological distribution patterns of the collected species, we categorised them based on their habitat affinities into five groups: grassland-associated, forest-steppe-associated, forest-associated, wetland-associated and agrobiont species (Buchar & Růžička, 2002; Michalko & Birkhofer, 2021; Samu & Szinetár, 2002).

Statistical analyses

Univariate analyses were conducted using R (R Development Core Team, 2024), and multivariate analysis was performed using CANOCO 5 (ter Braak & Šmilauer, 2012).

We tested the effect of habitat type on microclimatic conditions by generalized linear mixed models (GLMMs) with a Gaussian error structure using the 'glmmTMB' function in the 'glmmTMB' package (Brooks et al., 2017). The nonnormality of residuals was corrected by the logarithmic transformation of the response variables (maximum temperature and temperature variation). We collected microclimatic data for each datalogger over 11 days, which resulted in temporal autocorrelation. Therefore, we added an autoregressive correlation structure to each model: ar1 (as.factor(day) + 0 | datalogger ID). To account for repeated observations within the same settlement and datalogger, settlement and datalogger ID (unique for each datalogger) were included as random effects in each model.

The two pitfall traps collected in each sampling site throughout the sampling periods were pooled together, resulting in 50 samples (5 settlements × 5 habitats × 2 sites). The species richness and abundance of agrobiont spider species were determined by the number of species and specimens in the samples pooled across sampling periods. The abundance of agrobionts was evaluated only for spiders due to a lack of data on agrobiont species of ground beetles. Trait composition was evaluated based on the community-weighted mean (CWM), which summarises the average trait value weighted by the relative abundance of each species in the given community (Garnier et al., 2004). The CWMs were calculated within the 'functcomp' function in the 'FD' package (Laliberté et al., 2024).

We compared the species richness of both predatory groups and the abundance of agrobiont species of spiders between habitat types using generalized linear mixed-effects models (GLMMs) with a Poisson error structure (GLMM-p) using the 'glmer' function in the 'lme4' package (Bates et al., 2024). We used GLMMs with a negative binomial error structure (GLMMs-nb) if we detected overdispersion (Pekár & Brabec, 2009). We evaluated the effect of habitat type on trait composition (CWM) by linear mixed-effects models (LMMs) using the 'lmer' function in the 'lme4' package (Bates et al., 2024). We added settlement as a random effect to each model.

Post hoc comparisons were made using the 'glht' function in the 'multcomp' package (Hothorn et al., 2024).

We compared the composition of ground-dwelling predatory arthropod assemblages between habitat types by canonical correspondence analysis (CCA). The pilot detrended correspondence analysis revealed a gradient length greater than 4, suggesting the use of CCA (Šmilauer & Lepš, 2014). Only species with occurrence in more than three samples were selected for the analysis. The Hellinger transformation was applied to the species data before the calculation. The significance of the effects was tested using Monte Carlo permutation tests with 999 permutations within the blocks represented by the settlements. To investigate the effect of habitat type on the species' habitat preferences, the typical habitat of each species was passively projected onto CCA biplots.

To evaluate whether our sampling effort was sufficient to reliably compare predatory arthropod assemblages across habitats, we assessed sample completeness using the coverage-based approach (Chao et al., 2014) implemented through the 'iNEXT' function from the 'iNEXT' package (Hsieh et al., 2020).

RESULTS

Effects of habitat type on microclimatic conditions

The humidity varied significantly among habitat types (GLMM, $\chi^2_4 = 9.84$, $p = 0.043$) and was higher in habitats under solar panels than in grasslands (Figure 2a, Table 1).

The minimum temperature was significantly affected by habitat type (GLMM, $\chi^2_4 = 18.37$, $p = 0.001$). Forests had higher minimum temperatures than grasslands, abandoned farmlands and habitats between solar panels. Habitats under solar panels had higher minimum temperatures than grasslands and abandoned farmlands (Figure 2b, Table 1).

There were significant differences among the maximum temperature values of the habitat types (GLMM, $\chi^2_4 = 26.05$, $p < 0.001$).

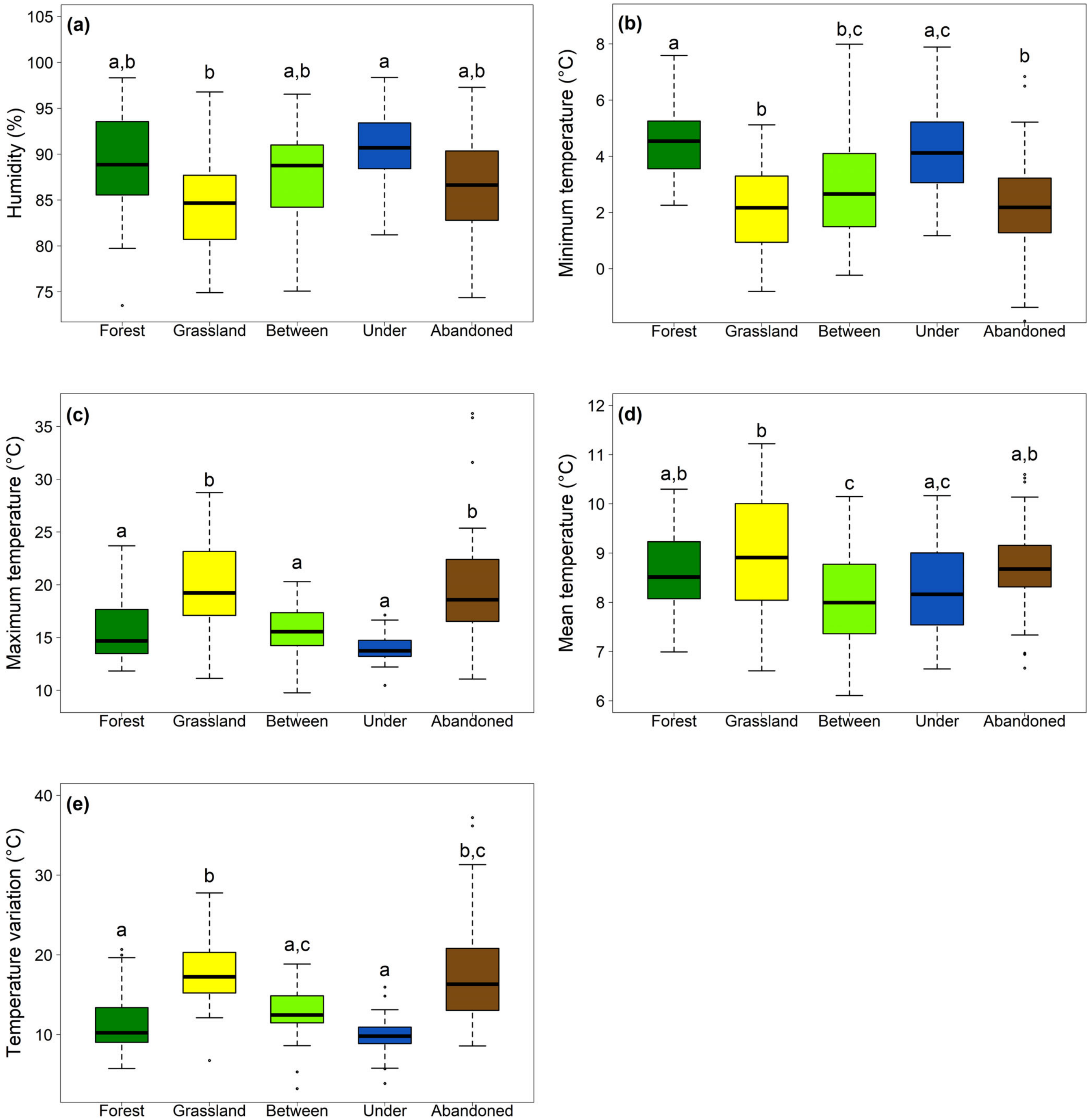

FIGURE 2 The effect of habitat type on microclimatic variables: (a) humidity, (b) minimum temperature, (c) maximum temperature, (d) mean temperature, and (e) temperature variation. The observation unit is a site. Horizontal lines within boxes indicate median values, box boundaries represent quartiles, and whiskers extend to 1.5 times the interquartile range. Statistically significant differences are indicated by different letters ($p < 0.050$).

TABLE 1 Effect of habitat type on microclimatic variables.

Response variable	Habitat type	Estimate	*z*-value	*p*
Humidity	Abandoned–between	−1.097	−0.538	0.983
	Forest–between	1.366	0.670	0.963
	Grassland–between	−3.002	−1.552	0.528
	Under–between	3.001	1.551	0.528
	Forest–abandoned	2.463	1.208	0.746
	Grassland–abandoned	−1.906	−0.985	0.862
	Under–abandoned	4.098	2.119	0.211
	Grassland–forest	−4.368	−2.259	0.158
	Under–forest	1.635	0.846	0.916
	Under–grassland	6.004	3.293	**0.009**
Minimum temperature	Abandoned–between	−0.578	−0.991	0.859
	Forest–between	1.736	2.961	**0.026**
	Grassland–between	−0.751	−1.372	0.645
	Under–between	1.283	2.344	0.131
	Forest–abandoned	2.314	3.964	**<0.001**
	Grassland–abandoned	−0.173	−0.317	0.998
	Under–abandoned	1.861	3.403	**0.006**
	Grassland–forest	−2.487	−4.527	**<0.001**
	Under–forest	−0.453	−0.826	0.923
	Under–grassland	2.034	3.976	**<0.001**
Maximum temperature	Abandoned–between	0.208	3.199	**0.012**
	Forest–between	0.004	0.069	1.000
	Grassland–between	0.243	3.934	**<0.001**
	Under–between	−0.109	−1.766	0.393
	Forest–abandoned	−0.204	−3.128	**0.015**
	Grassland–abandoned	0.035	0.562	0.980
	Under–abandoned	−0.317	−5.136	**<0.001**
	Grassland–forest	0.238	3.862	**0.001**
	Under–forest	−0.113	−1.838	0.351
	Under–grassland	−0.352	−6.046	**<0.001**
Mean temperature	Abandoned–between	0.825	3.343	**0.007**
	Forest–between	0.747	3.031	**0.021**
	Grassland–between	0.941	4.089	**<0.001**
	Under–between	0.256	1.112	0.800
	Forest–abandoned	−0.078	−0.316	0.998
	Grassland–abandoned	0.116	0.503	0.987
	Under–abandoned	−0.569	−2.475	0.096
	Grassland–forest	0.193	0.840	0.918
	Under–forest	−0.492	−2.138	0.203
	Under–grassland	−0.685	−3.200	**0.012**
Temperature variation	Abandoned–between	0.292	2.523	0.085
	Forest–between	−0.128	−1.108	0.802
	Grassland–between	0.358	3.259	**0.010**
	Under–between	−0.246	−2.234	0.167
	Forest–abandoned	−0.421	−3.631	**0.003**

TABLE 1 (Continued)

Response variable	Habitat type	Estimate	*z*-value	*p*
	Grassland–abandoned	0.066	0.600	0.975
	Under–abandoned	−0.538	−4.894	**<0.001**
	Grassland–forest	0.487	4.427	**<0.001**
	Under–forest	−0.117	−1.066	0.824
	Under–grassland	−0.604	−5.827	**<0.001**

Note: The effects were tested using GLMMs. Significant results are shown in bold. Pairwise comparisons were conducted using the 'multcomp' package in R with Tukey's adjustment for multiple comparisons. Values are presented on the model scale.

Grasslands and abandoned farmlands had the highest maximum temperature (Figure 2c, Table 1).

Habitat types showed significant differences in mean temperatures (GLMM, $\chi^2_4 = 14.62$, $p = 0.006$). Habitats between solar panels had a lower mean temperature than forests, grasslands and abandoned farmlands. Habitats under solar panels had a lower mean temperature than grasslands (Figure 2d, Table 1).

There was a significant difference in daily temperature variations among habitat types (GLMM, $\chi^2_4 = 28.24$, $p < 0.001$). Grasslands had higher temperature variations than forests and habitats between and under solar panels. Abandoned farmlands had higher temperature variations than forests and habitats under solar panels (Figure 2e, Table 1).

Effect of habitat type on ground-dwelling spider diversity

We collected and identified 957 specimens belonging to 69 species (Table S1). The most abundant group was agrobionts, with 424 individuals representing 16 species. The most abundant species were the habitat generalist *Centromerus sylvaticus* (Blackwall, 1841) ($n = 204$; Linyphidae) and the agrobionts *Trochosa ruricola* (De Geer, 1778) ($n = 178$; Lycosidae), *Pachygnatha degeeri* Sundevall, 1830 ($n = 164$; Tetragnathidae).

Habitat type had no significant effect on species richness (GLMM-p, $\chi^2_4 = 2.61$, $p = 0.625$). However, habitat type had a significant effect on the abundance of agrobiont ground-dwelling spider species (GLMM-nb, $\chi^2_4 = 24.03$, $p < 0.001$), with the lowest abundance in forests (Figure 3, Table 2).

Habitat type significantly affected the ground-dwelling spider assemblage composition (CCA, pseudo-$F = 2.1$, $p = 0.001$; Figure 4) and explained 8.9% (adjusted R^2) of the compositional variability. The CCA biplot reveals ground-dwelling spider assemblages form four distinct groups: forest, grassland, abandoned farmland and solar park habitats [Correction added on 23 October 2025, after first online publication: the words 'and solar park habitats' have been reinstated.]. Forests were preferred by forest-

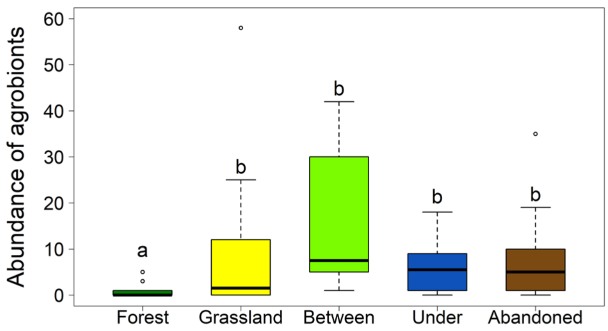

FIGURE 3 The effect of habitat type on the abundance of agrobiont ground-dwelling spiders. The observation unit is a site. Horizontal lines within boxes indicate median values, box boundaries represent quartiles, and whiskers extend to 1.5 times the interquartile range. Statistically significant differences are indicated by different letters ($p < 0.050$).

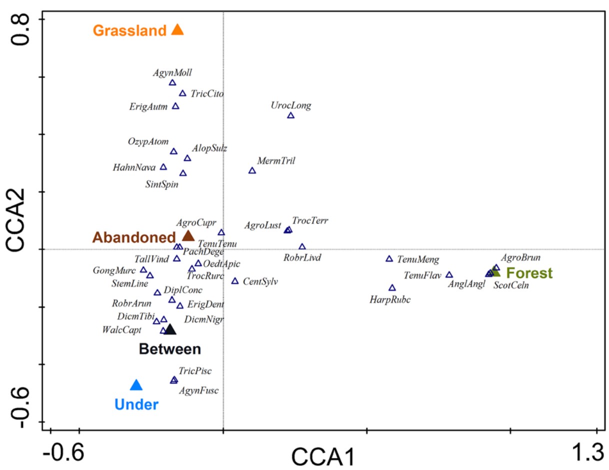

FIGURE 4 Ordination diagram of Canonical Correspondence Analysis showing the effect of habitat type on the assemblage composition of ground-dwelling spiders, which explains 8.9% (adjusted R^2) of the compositional variability. The first four letters of the genus and species names are shown.

TABLE 2 Effect of habitat type on the biodiversity of winter-active ground-dwelling spiders.

Response variable	Habitat type	Estimate	*z*-value	*p*
Abundance of agrobionts	Abandoned–between	−0.578	−1.512	0.550
	Forest–between	−2.790	−5.517	**<0.001**
	Grassland–between	−0.826	−2.124	0.206
	Under–between	−0.870	−2.232	0.165
	Forest–abandoned	−2.212	−4.286	**<0.001**
	Grassland–abandoned	−0.248	−0.610	0.973
	Under–abandoned	−0.293	−0.711	0.953
	Grassland–forest	1.964	3.825	**0.001**
	Under–forest	1.919	3.652	**0.002**
	Under–grassland	−0.044	−0.107	1.000
Species richness	Abandoned–between	−0.047	−0.264	0.999
	Forest–between	−0.201	−1.095	0.809
	Grassland–between	0.073	0.427	0.993
	Under–between	−0.095	−0.535	0.984
	Forest–abandoned	−0.154	−0.832	0.921
	Grassland–abandoned	0.120	0.691	0.958
	Under–abandoned	−0.049	−0.271	0.999
	Grassland–forest	0.274	1.517	0.551
	Under–forest	0.105	0.562	0.980
	Under–grassland	−0.168	−0.961	0.872
CWM of humidity	Abandoned–between	−0.105	−0.842	0.918
	Forest–between	0.052	0.402	0.995
	Grassland–between	−0.387	−3.104	**0.016**
	Under–between	−0.107	−0.855	0.913
	Forest–abandoned	0.156	1.220	0.740
	Grassland–abandoned	−0.282	−2.263	0.157
	Under–abandoned	−0.002	−0.013	1.000
	Grassland–forest	−0.438	−3.420	**0.006**
	Under–forest	−0.158	−1.233	0.732
	Under–grassland	0.280	2.250	0.162
CWM of shading	Abandoned–between	0.025	0.153	1.000
	Forest–between	0.605	3.663	**0.002**
	Grassland–between	−0.059	−0.365	0.996
	Under–between	0.120	0.744	0.946
	Forest–abandoned	0.580	3.514	**0.004**
	Grassland–abandoned	−0.083	−0.518	0.986
	Under–abandoned	0.095	0.591	0.976
	Grassland–forest	−0.663	−4.018	**<0.001**
	Under–forest	−0.485	−2.939	**0.027**
	Under–grassland	0.178	1.109	0.802

Note: The effects were tested using LMMs and GLMMs. Significant results are shown in bold. Pairwise comparisons were conducted using the 'multcomp' package in R with Tukey's adjustment for multiple comparisons. Values are presented on the model scale.

associated species (e.g., *Agroeca brunnea* (Blackwall, 1833)), and forest-steppe-associated species (e.g., *Scotina celans* (Blackwall, 1841)). Grasslands were preferred by grassland-associated species (*Trichopterna cito* (O. Pickard-Cambridge, 1873)), and habitat generalist species (e.g., *Agyneta mollis* (O. P.-Cambridge, 1871)), while abandoned farmlands were associated with agrobionts (e.g.,

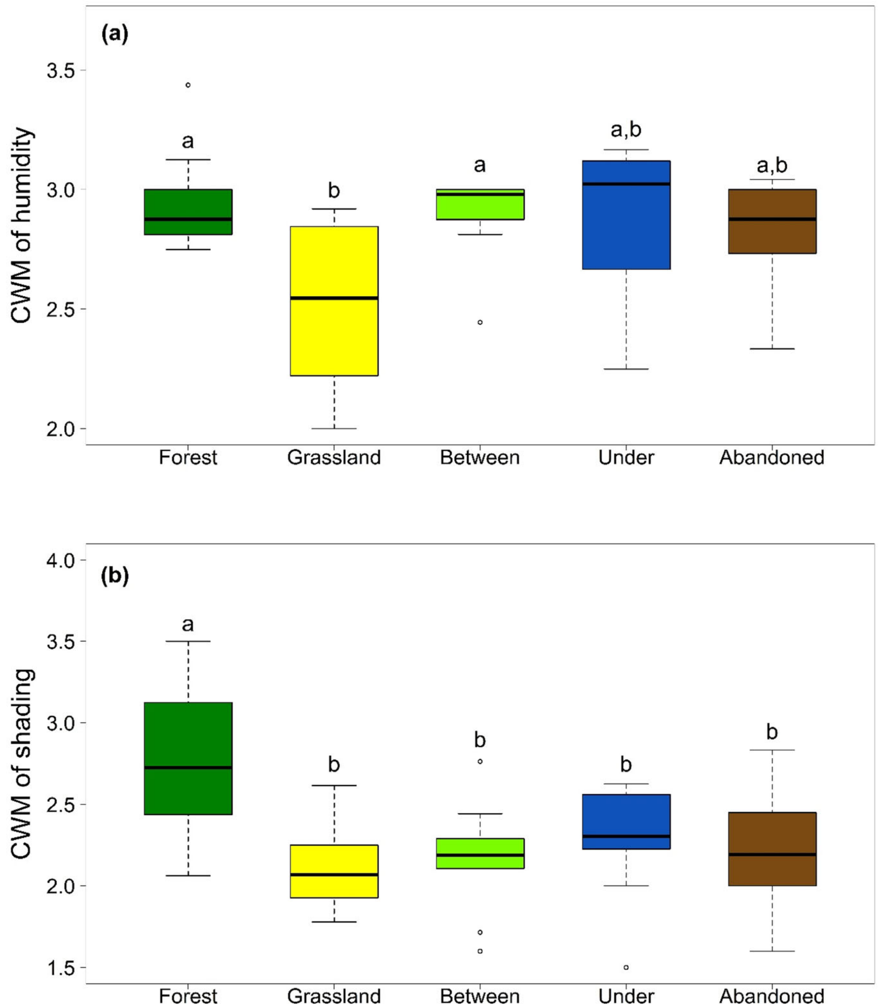

FIGURE 5 The effect of habitat type on community-weighted mean (CWM) of ground-dwelling spiders: (a) CWM of humidity preference and (b) CWM of shading tolerance. The observation unit is a site. Horizontal lines within boxes indicate median values, box boundaries represent quartiles, and whiskers extend to 1.5 times the interquartile range. Statistically significant differences are indicated by different letters ($p < 0.050$).

Tenuiphantes tenuis (Blackwall, 1852)). Solar parks were preferred by grassland-associated species (e.g., *Agyneta fuscipalpus* (C. L. Koch, 1836)), forest-associated species (*Dicymbium tibiale* (Blackwall, 1836)), wetland-associated species (*Dicymbium nigrum* (Blackwall, 1834)) and agrobionts (e.g., *Erigone dentipalpis* (Wider, 1834); Figures 4 and S3).

The CWM of humidity preference differed significantly among habitat types (LMM, $\chi^2_4 = 12.53$, $p = 0.014$). The forests and habitats between solar panels had higher values than grasslands (Figure 5a, Table 2). The CWM of shading tolerance was significantly different among habitat types (LMM, $\chi^2_4 = 17.23$, $p = 0.002$). Forests had the highest values (Figure 5b, Table 2).

Effect of habitat type on ground beetle diversity

We collected and identified 327 specimens belonging to 40 species (Table S2). The most abundant species were the agrobiont *Harpalus distinguendus* (Duftschmid, 1812) ($n = 36$), the grassland-associated *Trechus quadristriatus* (Schrank, 1781) ($n = 26$) and the wetland-associated *Bembidion properans* (Stephens, 1828) ($n = 26$).

There was no significant effect of habitat type on species richness (GLMM-nb, $\chi^2_4 = 7.56$, $p = 0.109$, Table 3).

Habitat type significantly affected the ground beetle assemblage composition (CCA, pseudo-F $= 1.5$, $p = 0.001$; Figure 6) and explained 5.4% (adjusted R^2) of the compositional variability. Ground beetle assemblages also form four distinct groups: forest, grassland, abandoned farmland and solar park habitats. Forests were preferred by forest-associated species (*Notiophilus rufipes* Curtis, 1829), while grasslands were preferred by habitat generalist species (*Bembidion obtusum* Audinet-Serville, 1821). Abandoned farmlands were associated with agrobiont species (*Anchomenus dorsalis* (Pontoppidan, 1763)). Solar parks were preferred by grassland-associated species (e.g., *Amara lucida* (Duftschmid, 1812)), and wetland-associated species (e.g., *Pterostichus strenuus* (Panzer, 1797); Figures 6 and S4).

TABLE 3 Effect of habitat type on the biodiversity of winter-active ground beetles.

Response variable	Habitat type	Estimate	z-value	p
Species richness	Abandoned–between	0.395	1.800	0.372
	Forest–between	−0.164	−0.651	0.966
	Grassland–between	−0.164	−0.655	0.966
	Under–between	0.141	0.607	0.974
	Forest–abandoned	−0.560	−2.368	0.123
	Grassland–abandoned	−0.560	−2.380	0.120
	Under–abandoned	−0.254	−1.181	0.761
	Grassland–forest	0.000	0.000	1.000
	Under–forest	0.305	1.230	0.732
	Under–grassland	0.305	1.235	0.730
CWM of humidity	Abandoned–between	−0.143	−0.514	0.986
	Forest–between	0.854	2.843	**0.036**
	Grassland–between	−0.114	−0.418	0.994
	Under–between	0.193	0.661	0.965
	Forest–abandoned	0.996	3.483	**0.005**
	Grassland–abandoned	0.028	0.107	1.000
	Under–abandoned	0.335	1.168	0.769
	Grassland–forest	−0.968	−3.356	**0.007**
	Under–forest	−0.661	−2.135	0.205
	Under–grassland	0.307	1.078	0.817
CWM of shading	Abandoned–between	−0.048	−0.172	1.000
	Forest–between	0.573	1.902	0.316
	Grassland–between	0.013	0.047	1.000
	Under–between	−0.164	−0.563	0.980
	Forest–abandoned	0.621	2.172	0.190
	Grassland–abandoned	0.061	0.228	0.999
	Under–abandoned	−0.116	−0.403	0.994
	Grassland–forest	−0.561	−1.941	0.295
	Under–forest	−0.737	−2.371	0.123
	Under–grassland	−0.176	−0.620	0.972

Note: The effects were tested using LMMs and GLMMs. Significant results are shown in bold. Pairwise comparisons were conducted using the 'multcomp' package in R with Tukey's adjustment for multiple comparisons. Values are presented on the model scale.

Habitat type had a significant effect on the CWM of humidity preference (LMM, $\chi^2_4 = 12.67$, $p = 0.013$). Forests had higher values than grasslands, habitats between solar panels and abandoned farmlands (Figure 7, Table 3). The CWM of shading tolerance was comparable among habitat types (LMM, $\chi^2_4 = 4.37$, $p = 0.358$, Table 3).

Sample completeness

The sample completeness curves indicated that the observed samples captured a high proportion of each assemblage in all habitat types (>88.5% sample coverage for spiders and >77.3% for ground beetles), suggesting that the sampling effort was sufficient (see Appendix S2).

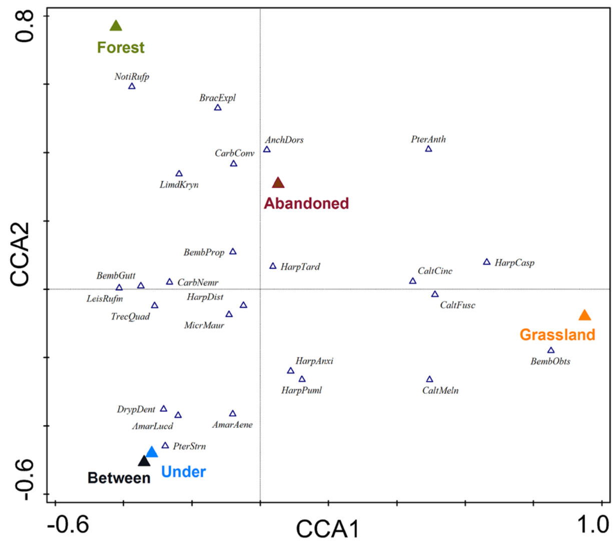

FIGURE 6 Ordination diagram of Canonical Correspondence Analysis showing the effect of habitat type on the assemblage composition of ground beetles, which explains 5.4% (adjusted R^2) of the compositional variability. The first four letters of the genus and species names are shown.

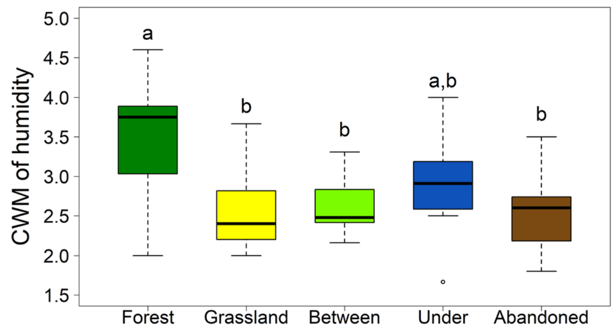

FIGURE 7 The effect of habitat type on community-weighted mean (CWM) of humidity preference of ground beetles. The observation unit is a site. Horizontal lines within boxes indicate median values, box boundaries represent quartiles, and whiskers extend to 1.5 times the interquartile range. Statistically significant differences are indicated by different letters ($p < 0.050$).

DISCUSSION

We compared microclimatic conditions, ground-dwelling spider and ground beetle assemblages between solar parks and surrounding habitat types (i.e., forests, grasslands, and abandoned farmlands). Our first hypothesis, that the habitats under solar panels resemble forests and the habitats between solar panels resemble grasslands, was partly supported. Microclimatic conditions under the panels were similar to forests, and both harboured a high proportion of species with a preference for higher humidity. Our second hypothesis, that solar parks promote higher species richness and support species from different habitats, was also partly supported. Higher humidity and more heterogeneous conditions in solar parks likely enabled the coexistence of species typical of various habitats, including forests, grasslands and wetlands. The third hypothesis, predicting lower species richness in grassland and abandoned farmland due to reduced microclimatic diversity, was partly confirmed. These habitats showed more extreme temperatures and lower humidity, favouring dry-habitat species. Finally, the fourth hypothesis, that solar parks support abundant agrobionts due to humid microclimates and structural similarity to crop fields, was supported.

Solar parks support diverse assemblages of winter-active ground-dwelling predatory arthropods

We showed that habitat type influences the assemblage composition of ground-dwelling spiders and ground beetles during the non-growing season, likely due to variations in microclimatic conditions. This is consistent with findings from other studies investigating habitat preferences of these groups during a growing season (e.g., Gallé et al., 2024; Kirichenko-Babko et al., 2020; Kriegel et al., 2021; Ziesche & Roth, 2008). Habitats under solar panels exhibited stable temperatures (i.e., low temperature variation) and high humidity with similar values to forests. Like a dense canopy in forests, the panel shading reduces temperatures, reduces wind speed and minimises soil moisture loss (Armstrong et al., 2016; De Frenne et al., 2013). As a result, we revealed a high humidity preference of ground-dwelling spiders and ground beetles in habitats under solar panels, with values comparable to those in forests. Closed forests, as shown in previous studies, are characterised by ground-dwelling spider assemblages with high humidity preference (e.g., Hamřík, Gallé-Szpisjak, et al., 2023; Hamřík, Košulič, et al., 2023). However, the ground-dwelling predatory arthropods under solar panels differed from those in forests and hosted a lower proportion of shaded-tolerant and forest-associated species. This could be explained by the lack of leaf litter, which is an important overwintering site and the habitat of forest-associated species of ground-dwelling spiders, ground beetles and their prey (e.g., Hamřík et al., 2024; Huhta, 1971; Koivula et al., 1999; Magura et al., 2003; McIver et al., 1992; Niedobová et al., 2024). Leaf litter also offers conditions that protect against extreme winter temperatures (Pywell et al., 2005). Likely, these species cannot find sufficient shade and shelter in other habitat types. Furthermore, the amount of forests and their proximity play an important role in shaping ground-dwelling spider assemblages in nearby habitats (Hamřík, Gallé-Szpisjak, et al., 2023; Huhta, 1971). Therefore, the relatively small amount of forests in the surrounding landscape and the large distance between forests and solar parks could limit the presence of forest-associated species in the solar parks.

Habitats in solar parks showed a higher proportion of ground-dwelling spider species that prefer more humid conditions compared to grasslands. Accordingly, habitats under the solar panels had higher humidity than grasslands. Although the humidity in habitats between solar panels was not significantly different from that in grasslands, we suggest that the shading effect of the solar panels, which increases humidity under them, may influence the surrounding areas, thereby supporting wetland-associated species.

Unexpectedly, both between and under-panel habitats in solar parks supported similar ground-dwelling predatory arthropod assemblages. A plausible explanation is that the observed patterns reflect the movement of ground-dwelling predatory arthropods between solar park habitats. This may apply to ground beetles, which often exhibit broad and variable habitat preferences and can disperse more readily across the landscape (Kotze et al., 2011). In contrast, ground-dwelling spiders are typically more tightly associated with specific habitat conditions. Once suitable microhabitats are found, they tend to remain within them, leading to distinct assemblages even across small habitat patches (e.g., Hamřík & Košulič, 2021).

Agrobionts were the most dominant group of ground-dwelling spiders, with the lowest abundance in forests. Correspondingly, the CCA showed that the agrobiont species of ground-dwelling spiders primarily preferred solar parks and abandoned farmlands. The habitats between solar panels and abandoned farmlands also exhibited similarities in some microclimatic conditions, such as humidity, minimum temperature and temperature variation. The high presence of agrobionts likely reflects favourable microclimatic conditions (e.g., higher humidity) and the availability of their prey. Springtails belong to the dominant prey group of agrobionts (Roubinet et al., 2017), and these winter-active insects could also serve as prey for winter-active ground-dwelling spiders (e.g., Hågvar, 2010), potentially contributing to their activity during the winter in the studied solar parks.

Although we did not directly assess biocontrol ecosystem service, the presence of winter-active agrobiont ground-dwelling spiders in solar parks may indicate a potential for early-season biocontrol in adjacent agricultural fields. These habitats could potentially act as source habitats from which winter-active agrobionts disperse into nearby cereal crops by active movement or passive ballooning early in the spring (Bianchi et al., 2017; Birkhofer et al., 2018). Such early dispersal may contribute to pest suppression before the arrival of specialist natural enemies (Athey et al., 2016; Birkhofer, Gavish-Regev, et al., 2008). Additionally, as some pest species also overwinter near crops (e.g., Samu et al., 2013), early predation by generalist predators such as agrobiont ground-dwelling spiders may help reduce pest populations even during winter (Pekár et al., 2015). These patterns warrant further investigation into the potential of solar parks to contribute to biocontrol in agricultural landscapes.

Solar panels create stable microclimatic conditions

Abandoned farmlands and grasslands exhibited similar microclimatic conditions, characterised by high temperature extremes. Accordingly, ground-dwelling spider assemblages in grasslands resembled those in abandoned farmlands. This suggests that during winter, the effects of habitat degradation and vegetation structure may be less pronounced, while abiotic factors play a more significant role in shaping ground-dwelling spider diversity, which aligns with previous findings (e.g., Ingle et al., 2020).

Solar park habitats had relatively low mean temperatures, likely due to the buffering effect of the solar panels. In addition, habitats under solar panels exhibited lower temperature variation compared to both grasslands and abandoned farmlands, suggesting more stable and balanced microclimatic conditions. This observation is consistent with findings from other studies, which emphasise the role of solar panels in moderating extreme temperature values (e.g., Lambert et al., 2021; Zitzmann et al., 2024). Habitats under solar panels also had higher minimum temperatures than grasslands and abandoned farmlands. The high minimum temperatures under solar panels during winter can be explained by the limited visible sky fraction, which reduces net longwave radiation loss from the surface, and panels also reduce air turbulence, preventing the cooling of the surface area, thus leading to a warmer environment under the panels (Armstrong et al., 2016; Vervloesem et al., 2022).

CONCLUSIONS

We showed that winter-active ground-dwelling spiders and ground beetles are influenced by habitat type through microclimatic variations. However, compared to ground-dwelling spiders, the winter activity of ground beetles was lower, which resulted in less robust and detailed conclusions regarding their diversity. Therefore, ground-dwelling spiders are a more suitable model group for studying the winter activity of predatory arthropods. We demonstrated that habitats under solar panels had more stable microclimatic conditions compared to grasslands and abandoned farmlands. Furthermore, shading by the solar panels presumably enhanced moisture retention, not only in habitats directly under the solar panels but also in the habitats between them, which would likely exhibit microclimatic conditions more similar to those of grasslands and abandoned farmlands in the absence of shading. This created a heterogeneous environment within solar parks, which in turn supported species with differing habitat affinities. In contrast, abandoned farmlands exhibited an extreme microclimate similar to that of grasslands and supported species with less diverse habitat affinities. These habitat types lack features that buffer microclimate, resulting in more extreme and unstable microclimatic conditions. Our results show that solar parks, as novel and heterogeneous ecosystems, provide favourable microclimates during winter, supporting diverse assemblages of winter-active ground-dwelling predatory arthropods. This environmental heterogeneity may promote both taxonomic and trait beta-diversity, thereby enhancing gamma-diversity and contributing to biodiversity conservation and biocontrol ecosystem service at the agricultural landscape level.

AUTHOR CONTRIBUTIONS

Tomáš Hamřík: Investigation; formal analysis; visualization; writing–original draft. **Márton Zoltán Szabó:** Data curation; writing–review and editing. **Nikolett Gallé-Szpisjak:** Data curation; visualization. **Radek Michalko:** Writing–review and editing; formal analysis. **Csaba Tölgyesi:** Writing–review and editing; investigation. **Attila Torma:** Investigation; writing–review and editing. **Róbert Gallé:** Writing–review and editing; conceptualization; methodology; investigation; funding acquisition; project administration.

ACKNOWLEDGEMENTS

We thank the Associate Editor and the two anonymous reviewers for their constructive comments and valuable suggestions on the manuscript. The study was financially supported by the Hungarian National Research, Development and Innovation Office (FK-142926 and K 146137).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are openly available in the Dryad Digital Repository (Hamřík et al., 2025) at https://doi.org/10.5061/dryad.rbnzs7hr8.

DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

During the preparation of this work, the authors used ChatGPT to correct English grammar. After using this tool, the authors reviewed and edited the content as needed and took full responsibility for the content of the published article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Websites providing ground beetle species trait data.
Appendix S2. Sample completeness.
Figure S1. A field margin.
Figure S2. An overgrown grassland.
Figure S3. Ordination diagram of Canonical Correspondence Analysis showing the effect of habitat type on the assemblage composition of ground-dwelling spiders, which explains 8.9% (adjusted R^2) of the compositional variability. The passively projected preferred habitat of each species is shown.
Figure S4. Ordination diagram of Canonical Correspondence Analysis showing the effect of habitat type on the assemblage composition of ground beetles, which explains 5.4% (adjusted R^2) of the compositional variability. The passively projected preferred habitat of each species is shown.
Table S1. List of recorded ground-dwelling spiders with species traits. Humidity preference: very dry (1), dry (2), semi-humid (3), humid (4), very humid (5); shading tolerance: (1) open, (2) semi-open, (3) partly shaded, (4) shaded.
Table S2. List of recorded ground beetles with species traits. Humidity preference: very dry (1), dry (2), semi-humid (3), humid (4), very humid (5); shading tolerance: (1) open, (2) semi-open, (3) partly shaded, (4) shaded.

How to cite this article: Hamřík, T., Szabó, M.Z., Gallé-Szpisjak, N., Michalko, R., Tölgyesi, C., Torma, A. et al. (2026) Solar parks provide heterogeneous habitats for winter-active ground-dwelling predatory arthropods. *Ecological Entomology*, 51(1), 59–73. Available from: https://doi.org/10.1111/een.70018