Habitat niches suggest that non-crop habitat types differ in quality as source habitats for Central European agrobiont spiders

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A B S T R A C T

Non-crop habitats in agricultural landscapes may differ in their potential to serve as source habitats for natural enemies. To determine this potential for different habitat types, it is crucial to understand habitat preferences and the habitat niche width of natural enemies. In addition, populations of natural enemies are affected by management practices depending on their preferences for habitat strata. Here we analysed agrobiont spider preferences (very common species in arable fields) for different microhabitats (ground, herbaceous, and shrub strata) and non-crop habitats (agroecosystems, forests, scrub, meadows, steppe, and wetlands). We compared guild-specific preferences of cursorial and web-building spiders that inhabit pome fruit orchards and cereal fields using two databases on Central European spider preferences. The majority of agrobiont spiders showed a moderate niche width. Agrobiont spiders from orchards preferred the shrub stratum while spiders from cereal fields preferred the ground and herbaceous strata across habitats. Agrobiont spiders primarily utilized non-crop habitats that were structurally similar to a particular agroecosystem: spiders from orchards utilized mostly woody vegetation while spiders from cereal fields utilized mostly meadows. Moreover, cursorial and web-building spider species from cereal fields differed in their preferences for different non-crop habitats. The results highlight that non-crop habitats have different potential as sources of agrobiont spiders. The composition of non-crop habitats in agricultural landscapes may affect the functional composition and pest control potential of spider communities. Further studies focusing on the effects that landscapes have on natural enemies in local agroecosystem need to account for the identity of non-crop habitats.

1. Introduction

Non-crop habitats in agricultural landscapes support the density and diversity of natural enemies in crops and thereby promote pest suppression (Chaplin-Kramer et al., 2011; Shackelford et al., 2013; Rusch et al., 2016; Martin et al., 2019). The variation in effect-strength between individual studies is high (Karp et al., 2018) and non-crop habitats are sometimes even shown to have negative effects on natural enemies (Chaplin-Kramer et al., 2011; Tscharntke et al., 2016). Various types of non-crop habitats, such as forests or grasslands, can differ in their quality and capability of supporting natural enemy populations (Mansion-Vaquié et al., 2017; Birkhofer et al., 2018; Gallé et al., 2018; Nardi et al., 2019). However, landscape-scale studies investigating the effect of non-crop habitats often do not distinguish between different habitats and instead pool them into a single category (e.g. non-crop or semi-natural habitats). This approach may hamper our ability to identify subsets of non-crop habitats that would be most efficient in supporting an abundant and diverse community of natural enemies and high levels of biocontrol services in the crop fields. It is therefore important to understand the habitat requirements of natural enemies (Waldock et al., 2020).

To a large extent, local biotic communities are assembled through niche filtering as species are selected from a regional pool according to the species adaptations to local abiotic and biotic conditions (Emerson and Gillespie, 2008; Mayfield and Levine, 2010). Therefore, the movement to, and the establishment of, viable populations in a recipient habitat are often facilitated if the conditions in the recipient habitat are similar to conditions in the source habitat (Holt et al., 2005; Emerson and Gillespie, 2008). Spillover of natural enemies between crop and non-crop habitats with highly distinct conditions can be considerably weaker than between two very similar habitat types (Kajak and Oleszczuk, 2004). As crop species create markedly different

environmental conditions (e.g. perennial versus annual crops), it is likely that the potential for different non-crop habitats to be a source of natural enemies also depends on the focal crop species.

As specific functional traits are often filtered along with the species (Poff, 1997), the different composition of non-crop habitats in the landscape may affect not only the species composition but also the functional composition of natural enemy communities in local agroecosystems (Kajak and Oleszczuk, 2004; Birkhofer et al., 2018; Gallé et al., 2018). For example, open habitats such as grasslands and meadows may harbour mostly cursorial spiders (Jocqué and Alderweireldt, 2005; Birkhofer et al., 2015) while non-crop habitats with shrubby vegetation may support a higher number of web-building spiders (Birkhofer et al., 2015; Gómez et al., 2016). Management practices, such as fertilization, insecticide application, or pruning are applied to different habitat strata (e.g., Simon et al., 2011), and therefore may affect the taxonomic and trait composition of natural enemy communities as they are vertically stratified (Abraham, 1983; Arvidsson et al., 2020). Differences in trait composition between natural enemy communities can consequently affect levels of pest suppression (Gagic et al., 2015; Paredes et al., 2015; Greenop et al., 2018).

Arthropod species that are classified as agrobionts are dominant components of natural enemy communities in agroecosystems (Luczak, 1979) and are particularly important contributors to the biological control services (Rusch et al., 2015). Agrobiont spider and carabid species are often considered to be habitat generalists (Luczak, 1979; Samu and Szinetár, 2002; Lambeets et al., 2008). Habitat generalists can benefit from diverse landscapes where they can build-up large populations due to high resource availability (Gaston et al., 1997; Krasnov et al., 2004; Miyashita et al., 2012). For such generalists, the habitat composition of the landscape would be of minor importance. In order to determine the potential of different habitat types being source habitats for these natural enemies, it is crucial to understand the habitat preferences and habitat niche width of agrobiont species.

Spiders belong to the most abundant and diverse generalist predators in terrestrial ecosystems (Nyffeler and Birkhofer, 2017) and they reduce pest densities and increase crop yields world-wide (Michalko et al., 2019a). Spiders employ a wide variety of hunting strategies (Cardoso et al., 2011) that ensure utilization of different prey types (Michalko and Pekár, 2016) and have different non-consumptive effects on pests (Schmitz, 2010). Spiders strongly respond to environmental conditions (Entling et al., 2007) and even to small habitat differences such as in canopy openness, for example (Košulič et al., 2016). Effects of non-crop habitats on spiders in focal crop fields are highly variable, ranging from positive (Isaia et al., 2006; Rusch et al., 2014; Lefebvre et al., 2016; Pompozzi et al., 2019) to negative (Öberg, 2009; Havlova et al., 2017), or are generally weak (D'Alberto et al., 2012). Recent studies already indicated that these effects may depend on the major hunting strategy of the spider species (Picchi et al., 2016; Birkhofer et al., 2018), but the identity of potential source habitats has largely been ignored (but see Nardi et al., 2019).

To address this knowledge gap, we quantified habitat niches of agrobiont spiders using a database of independent studies investigating species occurrence across habitats. We also investigated microhabitat niches of agrobiont spiders to identify vegetation strata in crop fields that may be most relevant for management practices to improve biocontrol services of spiders. We tested the hypotheses that [i] non-crop habitats vary in their potential to serve as sources of agrobiont spider species and that this potential depends on the [ii] focal crop type (orchard vs. cereal) and [iii] hunting strategy (cursorial vs. web building spiders). We also expected that [iv] agrobiont cursorial spiders in cereal crops prefer the ground stratum, whereas orchard spiders and web-building spiders in general prefer herbaceous and shrub strata.

2. Material and methods

2.1. Data collection

We compiled a list of known agrobiont spider species from apple and pear orchards (cursorial spiders: N = 9, web-building spiders: N = 11; Table S1) and from cereal fields (mostly wheat, but also barley, oat, and rye; cursorial spiders: N = 20, web-building spiders: N = 11; Birkhofer et al., 2013) from Central Europe. We pooled apple and pear orchards because they host a similar spider fauna (Pekár, 1998; Bogya et al., 1999; Pekár and Kocourek, 2004). We used pome orchards and cereals fields because these crops are common across Central Europe (Eurostat, 2018) and spider communities are frequently studied in these agroecosystems (e.g. Bogya et al., 1999; Diehl et al., 2013; Birkhofer et al., 2016). For orchards, we only selected spider species that were sampled in trees because these species are directly linked to pest suppression (Isaia et al., 2010; Michalko et al., 2017). For cereals we used spiders that were sampled from the ground as well as from the vegetation strata because both are known to contribute to pest control (Birkhofer et al., 2008; Samu et al., 2013; Beleznai et al., 2017).

The list of spiders from orchards was compiled from studies conducted in two regions in the Czech Republic (Pekár, 1998, 1999a,b; Pekár and Kocourek, 2004; Korenko and Pekár, 2010; Michalko et al., 2017; Michalko unpubl.), five regions in Hungary (Bogya et al., 1999), and one region in Germany (Klein, 1988). We used spider species that occurred in all three countries and at least in 50 % of all the regions (i.e. 4 out of 8). The list of herb- and ground-dwelling spider species from cereals follows Birkhofer et al. (2013), which corresponds also with the composition of spiders in cereals in the Czech Republic (Pekár et al., 1997).

We retrieved data on habitat preferences for each agrobiont species from two independent databases. The first database is based on syntheses of faunistic studies conducted in the Czech Republic and is published by Buchar and Růžička (2002). The database has been digitalized and provided online by Kasal and Kalab (2013). The second database is based on a synthesis of faunistic studies from Germany, Switzerland, and Austria and is published by Hänggi et al. (1995). Based on the available classification, we compared six habitat types: agroecosystem, forest, meadow, scrub, steppe, and wetland. We did not compare preferences for anthropocenoses (i.e. buildings), rocks, and coastal habitats that are generally uncommon non-crop habitats in Central Europe. The habitat preference scores for individual species × habitat type combinations in the database were computed as proportions of individuals observed in a given habitat type weighted by the frequency of sampling in that habitat type (Kasal and Kalab, 2013). The habitat preferences were estimated from 25 to 1014 individuals from 18 to 251 independent samples in Buchar and Růžička (2002) and 15–632 individuals from 5 to 153 independent samples in Hänggi et al. (1995).

We investigated the microhabitat niche using only the database of Buchar and Růžička (2002) because we could not extract the relative sampling effort from Hänggi et al. (1995) as the authors did not provide information how the samples were distributed among habitat strata. We estimated the microhabitat niche based on the collecting method, namely pitfall traps as ground, sweeping as herbaceous, and beating as shrub stratum.

2.2. Statistical analyses

All analyses were performed in the R environment (R Development Core Team, 2019). We used mixed effect models (GLMM) with beta distribution and logit link function (GLMM-beta) or GLMM with gamma distribution and log link (GLMM-g) from the package '*glmmTMB*' (Brooks et al., 2017) to compare the habitat preference scores and test whether they differ between cursorial and web-building spiders. We used GLMM-beta because the data were proportions (Zuur et al., 2015). We used GLMM-g to compare the microhabitat preferences of agrobiont

spiders from cereals. We added the lowest non-zero value to the response variables if it contained zeros because the Gamma distribution is defined only for positive values. The response variable was the preference score of each species. The fixed factors were "habitat type" or "habitat stratum", "hunting strategy", and the interaction terms (Table 1, 2). "Spider species" was included as a random factor. The models were validated by the diagnostic graphs. We used an information–theoretic approach to select the adequate model (Zuur et al., 2015). We built three candidate models including the null model (Table 1, 2). The optimal model i was then selected based on Akaike weights (ω_i) (Zuur et al., 2015). We did not include the model with the additive effect of hunting strategy because the additive effect did not improve the interpretation of the results. The post hoc comparisons are based on treatment contrasts.

We computed the niche width using the standardized Levins' B (Levins, 1968) which can reach values from 0 to 1. We defined the niche width based on intervals [0−0.33], [0.34−0.66], and [0.67−1] as narrow, moderate, and wide, respectively. We compared the niche widths between cursorial and web building spiders (i.e., niche width ~ hunting strategy) using linear models (LM), generalized linear models (GLM) with beta error structure and logit link function (GLM-beta). We used model type according to its suitability for the respective data (Zuur et al., 2015).

3. Results

3.1. Habitat niche

In orchards, cursorial and web-building spiders did not differ significantly in habitat preferences according to both databases (Table 1; Hänggi et al., 1995; Buchar and Růžička, 2002). However, based on both databases, spider preferences differed significantly between habitat types (Table 1; Fig. 1A, B). Agrobiont spiders primarily utilized agroecosystems (contrasts, Buchar and Růžička, 2002: P < 0.040; Hänggi et al., 1995: P < 0.001). For the non-crop habitat types, preferences differed between databases (Fig. 1). Based on Buchar and Růžička (2002; Fig. 1A) orchard spiders mostly utilized scrub but to a similar degree also meadows and steppe (contrasts, P > 0.211). Forests were utilized marginally less than scrub (contrasts, P = 0.055) while wetlands were utilized significantly less than scrub (contrasts, P = 0.024). Based on Hänggi et al. (1995; Fig. 1B) orchard spiders mostly utilized forests and to a similar degree also wetland, scrub, and meadow (contrasts, P > 0.154). Steppe was utilized less than forests and wetlands (contrasts, P < 0.036).

In the cereal fields, according to both databases, the habitat preferences of spiders differed significantly depending on hunting strategy (Table 1; Fig. 1C,D). Although there were some differences among the two databases, they show similar trends. According to Buchar and Růžička (2002; Fig. 1C), cursorial spiders primarily preferred

agroecosystems (contrasts, P < 0.004). Out of the non-crop habitats, cursorial spiders preferred meadows (contrasts, P < 0.002). Web-building spiders also preferred agroecosystems and to a similar degree meadows, wetlands, and forests (contrasts, P > 0.081). Steppe and scrub were then utilized marginally less than meadows (contrasts, P < 0.051). According to Hänggi et al. (1995; Fig. 1D), cursorial spiders utilized mostly agroecosystems and meadows (contrasts, P < 0.001) which were both utilized to a similar degree (contrasts, P = 0.770). Web-building spiders preferred mostly agroecosystems (contrasts, P < 0.018). Web-building spiders utilized meadows more than steppe (contrasts, P = 0.015). The preferences for other habitat types did not differ significantly (contrasts, P > 0.107).

The habitat niche width did not differ significantly between cursorial and web-building spiders in orchards (Buchar and Růžička (2002): LM, $F_{1,18} = 0.6$, P = 0.435; Hänggi et al. (1995): LM, $F_{1,30} = 0.5$, P = 0.501) or in cereal fields (Buchar and Růžička (2002): LM, $F_{1,29} = 2.2$, P = 0.145; Hänggi et al. (1995): LM, $F_{1,29} = 3.2$, P = 0.085). Two thirds of the spider species from orchards as well as from cereal fields had a narrow to moderate habitat niche width (Fig. 2).

3.2. Microhabitat niche

In orchards as well as cereal fields, web-building and cursorial spiders did not show significantly different preferences for habitat strata (Table 2). The preferences of spiders from orchards and cereal fields differed significantly among the habitat strata (Table 2; Fig. 3). Spiders from pome orchards preferred shrub strata, followed by herbaceous, and ground strata (contrasts, P < 0.001; Fig. 3A). Agrobiont spiders from cereal fields did not show significantly different preferences between the ground and herbaceous strata (contrasts, P = 0.605) and they preferred both strata more than the shrub stratum (contrasts, P < 0.018; Fig. 3B).

The width of microhabitat niches did not differ between cursorial and web-building spiders in orchards (GLM-beta, $\chi^2_2 = 1.2$, P = 0.278) or cereal fields (GLM-beta, $\chi^2_2 = 0.9$, P = 0.343). More than 90 % of all spider species from orchards had a narrow to moderate microhabitat niche width (Fig. 4A). In contrast, two thirds of spider species from cereals had a moderate to wide microhabitat niche width (Fig. 4B).

4. Discussion

Here we investigated whether preferences for non-crop habitat types differed between cursorial and web-building agrobiont spider species and between pome-fruit orchards and cereal crops. Agrobiont spiders occupied the whole range of the habitat niche width, but most of the orchard species showed a narrow to moderate niche width. Preferences for non-crop habitats differed between spiders from orchards and spiders from cereal fields and between web-building and cursorial species from the cereal fields.

Table 1

Comparison of the beta mixed effect models investigating the effect of the factors, habitat type (Habitat) and hunting strategy (Strategy), on habitat preferences of agrobiont spiders from pome-fruit orchards and cereal fields using two independent databases. ΔAIC and ωi refer to AIC difference and AIC weights, respectively. The optimal model is highlighted in bold.

Agroecosystem / database	Model	Predictor	d.f.	AIC	ΔAIC	ω_i
	1	Habitat*Strategy	14	−241.4	8.6	0.01
Orchard / Buchar and Růžička (2002)	**2**	**Habitat**	**8**	**−250.0**	**0.0**	**0.99**
	3	Null	3	−237.9	12.1	0.00
	1	Habitat*Strategy	14	−254.1	10.3	0.01
Orchard / Hänggi et al. (1995)	**2**	**Habitat**	**8**	**−264.4**	**0.0**	**0.99**
	3	Null	3	−192.2	72.2	0.00
	1	**Habitat*Strategy**	**14**	**−432.4**	**0.0**	**0.99**
Cereals / Buchar and Růžička (2002)	2	Habitat	8	−423.2	9.2	0.01
	3	Null	3	−350.5	81.9	0.00
	1	**Habitat*Strategy**	**14**	**−437.0**	**0.0**	**0.92**
Cereals / Hänggi et al. (1995)	2	Habitat	8	−432.2	4.8	0.08
	3	Null	3	−333.2	103.8	0.00

Table 2

Comparison of the mixed effect models investigating the effect of factors, habitat stratum (Stratum) and hunting strategy (Strategy), on microhabitat preferences of agrobiont spiders from pome-fruit orchards and cereal fields using two independent databases. ΔAIC and ω_i refer to AIC difference and AIC weights, respectively. The optimal model is highlighted in bold.

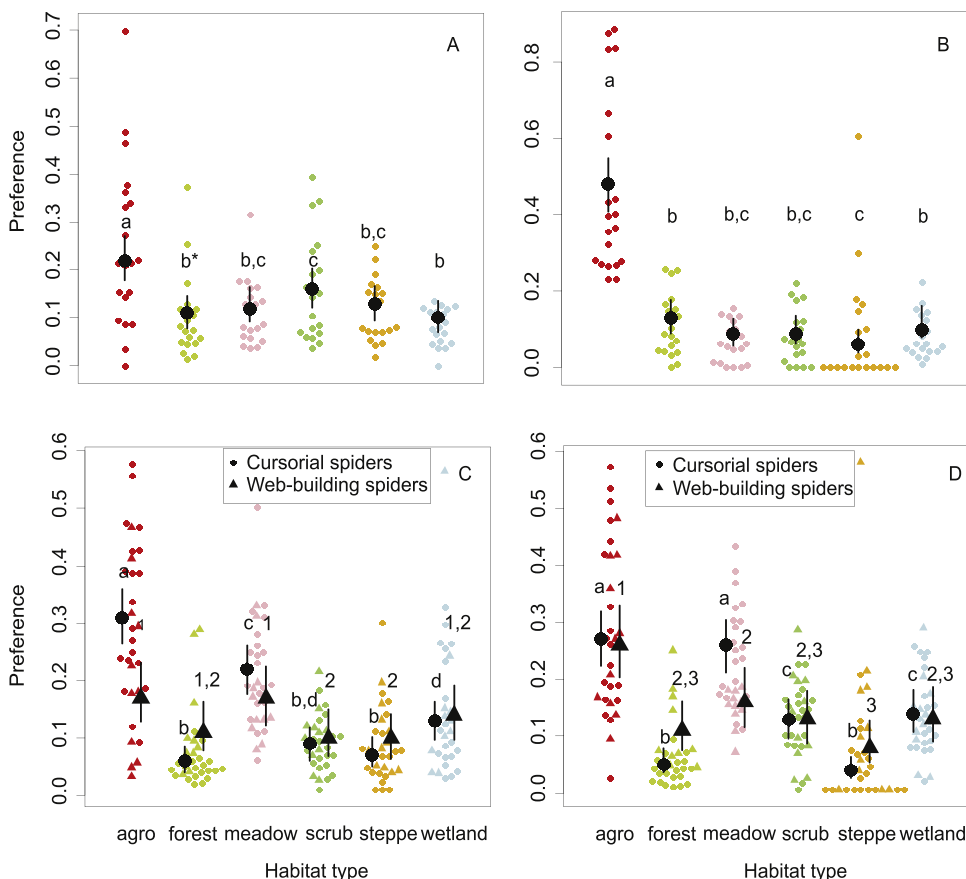| Agroecosystem / Database	Model	Model type	Predictor	d.f.	AIC	ΔAIC	ω_i
Orchard / Buchar and Růžička (2002)	1	GLMM-beta	Stratum*Strategy	8	−82.1	5.7	0.05
	2	**GLMM-beta**	**Stratum**	**5**	**−87.8**	**0.0**	0.95
	3	GLMM-beta	Null	3	−24.7	63.1	0.00
Cereals / Buchar and Růžička (2002)	1	GLMM-gamma	Stratum*Strategy	8	−9.8	3.9	0.11
	2	**GLMM-gamma**	**Stratum**	**5**	**−13.7**	**0.0**	0.81
	3	GLMM-gamma	Null	3	−9.1	4.6	0.08

Fig. 1. Habitat preferences of agrobiont spiders from pome-fruit orchards (A, B) and cereal fields (C, D) in Central Europe. The analyses of habitat preferences are based on two independent databases: Buchar and Růžička (2002; A, C) and Hänggi et al. (1995; B,D). The analyses are based on 20 spider species (cursorial spiders: N = 9, web-building spiders: N = 11) from orchards and 31 species (cursorial spiders: N = 20, web-building spiders: N = 11) from cereal fields. The large points show means, vertical lines are 95 % confidence intervals. The coloured small points are individual measurements. The different superscripts (in C, D letters for cursorial spiders, numbers for web-building spiders) show difference at P < 0.05. The asterisk in the panel A means that the habitat preference between forests and scrubs was marginally significant (P = 0.055).

4.1. Differences between the two databases

The two independent databases mostly provided comparable results, with a few exceptions. For example, according to Buchar and Růžička (2002) agrobiont spiders from orchards utilized mostly scrub as non-crop habitats while according to Hänggi et al. (1995) these species utilized scrub and forests similarly. Moreover, the preferences for agroecosystems were higher according to Hänggi et al. (1995) compared to Buchar and Růžička (2002). This discrepancy between databases was probably caused by differences in habitat classification. Hänggi et al. (1995) classified commercial orchards and wild growing fruits (e.g. from the genus *Prunus*) as one category, i.e. as fruit woods. We then classified the fruit woods as agroecosystems to unify the habitat classification between the two databases. Wild growing fruits could, however, also be classified as scrub. Wild growing fruits are common habitats of agrobiont spiders such as *Philodromus* spp. (Philodromidae), *Neottiura bimaculata* (L.) (Theridiidae), and *Phylloneta* spp (Theridiidae) (Michalko and Pekár, 2015). The classification of "fruit woods" from Hänggi et al. (1995) as an agroecosystem might result in an inflated

preference score for agroecosystems at the expense of scrub. Moreover, Buchar and Růžička (2002) classified forest clearings and forest edges as scrub because they are scrub dominated rather than tree dominated. Hänggi et al. (1995) did not distinguish between forests and forest clearings. The open canopy patches within forests host distinctively different spider communities compared to the forest patches with closed canopies (Košulič et al., 2016; Černecká et al., 2020). Other potential causes of the discrepancy between the two databases might be, for example, the differences in the proportional representations of sampling methods. Nevertheless, results based on both databases generally support that the agrobiont spiders from orchards primarily utilized non-crop habitats with woody vegetation.

4.2. Habitat niches of agrobiont spiders

The agrobiont spider species in the studied agroecosystems shared similar preferences for agroecosystems and for habitats that are structurally similar to the agroecosystems. This means that there was a significant realized niche-environment interaction, which is a signal of
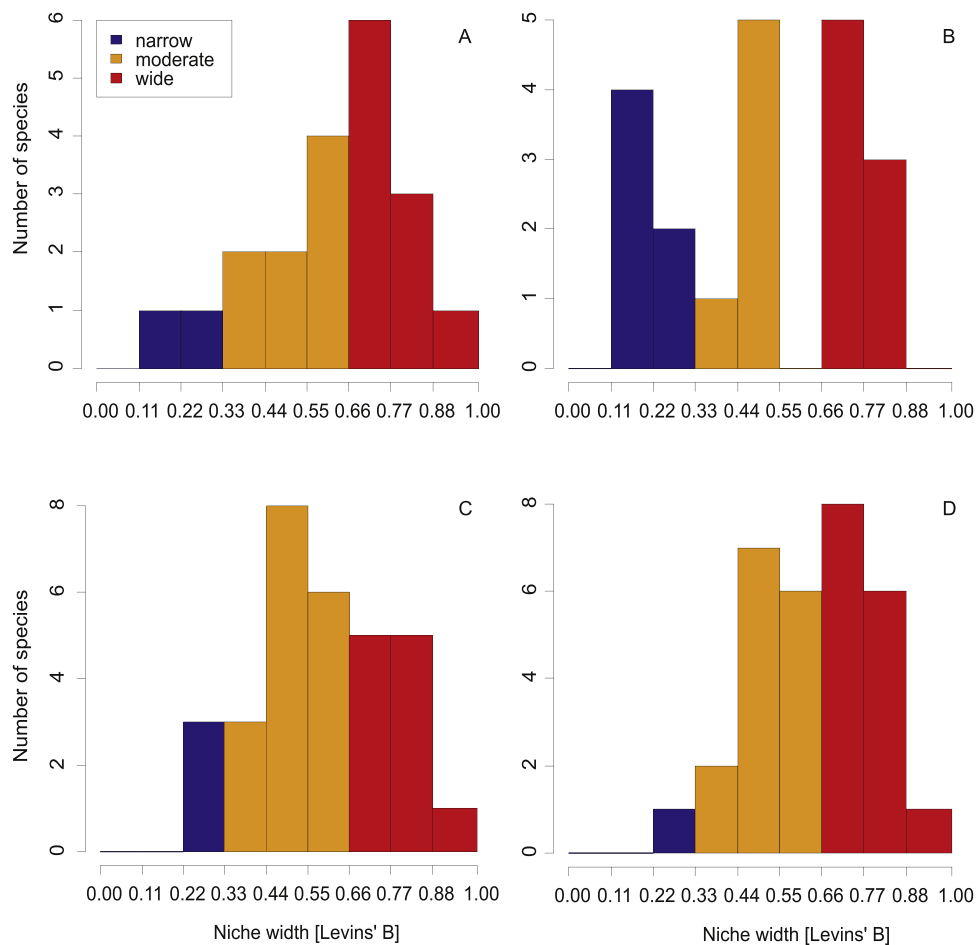
Fig. 2. Distribution of habitat niche width values among agrobiont spider species from pome-fruit orchards (A, B) and cereal fields (C, D) in Central Europe. The analyses of habitat niche widths are based on two independent databases: Buchar and Růžička (2002; A, C) and Hänggi et al. (1995; B, D). The niche width is defined based on intervals [0–0.33], [0.34–0.66], and [0.67–1] as narrow, moderate, and wide, respectively.
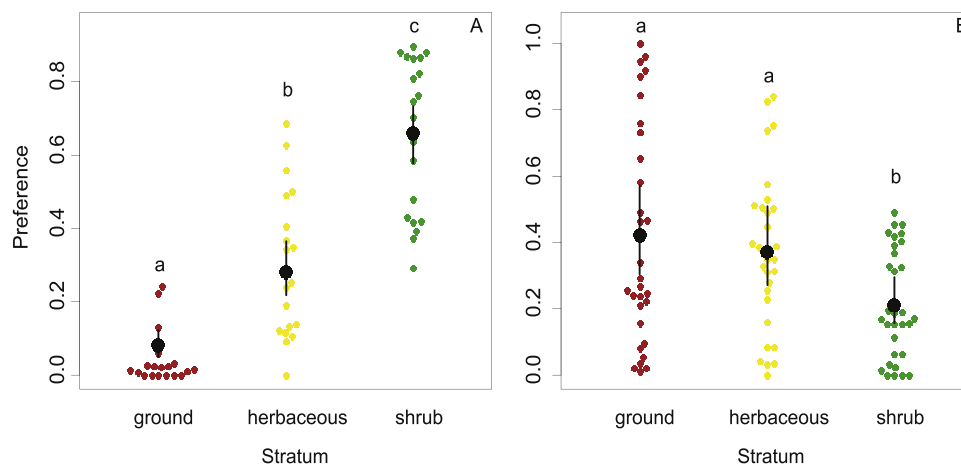

Fig. 3. Microhabitat preferences of agrobiont spiders from pome-fruit orchards (A) and cereal fields (B) in Central Europe for habitat strata. The analyses of microhabitat preferences are based on two independent databases: Buchar and Růžička (2002). The large points show means, vertical lines are 95 % confidence intervals. The coloured small points are individual measurements. The different superscripts show difference at P < 0.05.

habitat filtering (Waldock et al., 2020). Therefore niche filtering processes significantly structure spider communities in pome-fruit orchards and cereal fields in Central Europe. This contrasts with studies that suggest that in disturbed ecosystems, stochastic processes, such as ecological drift, should override niche processes at spatial scales larger than microhabitats (Ulrich et al., 2010; Sattler et al., 2010; Larsen and Ormerod, 2014). Instead, our results support studies that show that niche filtering is an important driver of spider community assemblages (e.g., Entling et al., 2007; Jiménéz-Valverde et al., 2010; Michalko and Pekár, 2015; Samu et al., 2018). However, whether environmental conditions (DeVito et al., 2004), interspecific interactions (Marshall and Rypstra, 1999), and interactions between both processes (Černecká
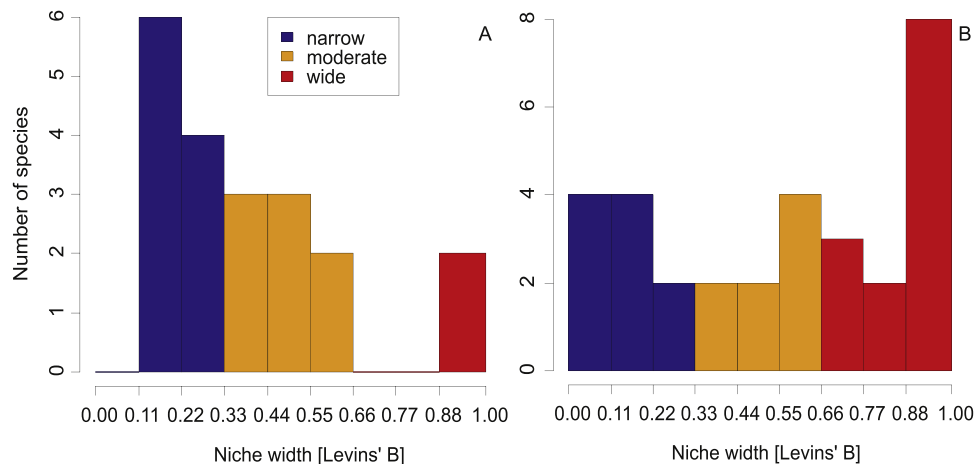
Fig. 4. Distribution of microhabitat niche width values among agrobiont spider species from pome-fruit orchards (A) and cereal fields (B) in Central Europe. The analyses on microhabitat niche widths are based on the database by Buchar and Růžička (2002). The niche width is defined based on intervals [0–0.33], [0.34–0.66], and [0.67–1] as narrow, moderate, and wide, respectively.

et al., 2017) drive the habitat filtering (Mayfield and Levine, 2010; Kraft et al., 2015; Cadotte and Tucker, 2017) in these spider assemblages remains unknown.

The results showing that agrobiont spider species shared habitat preferences indicate that not all non-crop habitats have the same value for supporting spiders in pome-fruit orchards and cereal fields. The most utilized non-crop habitats support a diverse and abundant community of agrobiont spiders. Habitat types, that were utilized less frequently only support a limited number of agrobiont spiders. The least utilized habitat types may even act as sinks with limited spillover to crop fields (Herrmann et al., 2010). For pome-fruit orchard spiders the average ranking of the non-crop habitats across the two databases based on their significance was (ranked from high to low): 1.) scrub, 2.) forest, meadow, and wetland, and 3.) steppe. For cursorial spiders in cereal fields the ranking was: 1.) meadow, 2.) wetland, 3.) scrub, and 4.) forest and steppe. For web-building spiders in cereal fields the ranking was: 1.) meadow, 2.) scrub, and wetland, and forest, and 3.) steppe.

Differences in the utilization of non-crop habitats, however, may not translate into differences in spillover to crop habitats. Structurally similar non-crop and crop habitats share similar spider communities (e. g., Hogg and Daane, 2010) and higher emergence in non-crop habitats leads to higher spillover to crops in cursorial (Birkhofer et al., 2018) as well as ballooning spiders (Bianchi et al., 2017). A high preference for certain non-crop habitats, therefore, most likely also results in high spillover of agrobiont species from those habitats to nearby crop fields.

This study documents that non-crop habitats that are more similar to the focal crop species are most suitable to be potential source habitats of agrobiont spiders. Spiders occurring in orchard trees frequently utilize non-crop habitats with woody vegetation. Both web-building and cursorial species characteristic for cereal fields utilized mostly meadows among all non-crop habitats. Indeed, the composition of functional traits is more similar between spider communities in grasslands and cereal fields than in forest communities (Birkhofer et al., 2015). The structural similarities and the nature of anthropogenic disturbances such as annual mowing are more similar between grasslands and cereal fields and therefore filtered for comparable subsets of traits.

As expected, agrobiont spiders preferred crop habitats over any non-crop habitats. However, we do not suggest that crop dominated landscapes are most suitable for these species, as habitats can act in complementary ways (Miyashita et al., 2012). The complementary function of habitats can arise, for example, because habitat preferences change during a spider's lifespan (Edgar, 1971) or because the habitats provide overwintering sites or refuges during disturbance (Gallé et al., 2018). In line with these arguments, it has been shown that an increasing

proportion of arable crops in agricultural landscapes can lead to reduced diversity of cursorial and web-building spiders (Mader et al., 2017).

The functional composition of spider communities can affect pest suppression (Rusch et al., 2015; Michalko et al., 2019b). Based on our results, an increasing proportion of non-crop habitats other than meadows might increase the relative proportion of web-building spiders in spider communities of cereal fields. Agrobiont web-building spiders in this study were mostly small linyphiid species that capture few prey in their webs compared to the larger cursorial or web-building spider species (Birkhofer et al., 2008; Opatovsky et al., 2012; Mader et al., 2016). The predicted higher densities of small linyphiids in spider communities with a high proportion of non-crop habitats other than meadows would probably have limited impact on pest suppression (Birkhofer et al., 2018).

4.3. Microhabitat niches of agrobiont spiders

Spider species in trees of orchards preferred the shrub stratum. In contrast, spiders from cereal fields preferred ground and herb strata to a similar degree and preferred both over the shrub stratum. The similar preferences of agrobiont spiders from cereal fields for ground and herb strata and the moderate to wide niche widths means that several of these species have the ability to move between these strata. Spiders have been documented to move between strata to avoid intraguild predation (Rypstra et al., 2007; Sitvarin and Rypstra, 2014), to select prey (Alderweireldt, 1994), and due to behavioural thermoregulation (Abraham, 1983).

4.4. Niche width of agrobiont spiders

We found that agrobiont spider species from pome-fruit orchards and cereal fields in Central Europe were habitat generalists with rather moderate niche width. This only partially agree with the point of view that the agrobiont natural enemies like spiders and carabids have relatively wide niche width (Luczak, 1979; Lambeets et al., 2008). While species characteristic of cereal fields have moderate to wide microhabitat niche width, spiders from orchards are more specialized with rather narrow to moderate microhabitat niches. Species common in cereal fields might have wider niches than spiders from orchards because they occur in a highly variable environment. Annual cereal crops are more frequently and severely disturbed than perennial orchards. The unstable environment and frequent disturbances select for species with wider niches, while a relatively stable environment with low disturbance selects for specialists with relatively narrow niches (Futuyma and Moreno,

1988; DeVictor et al., 2008; Ibarra and Martin, 2015; Sexton et al., 2017). However, further studies with more refined experimental approaches are necessary to support this hypothesis.

4.5. Conclusions

In conclusion, agrobiont spiders from pome-fruit orchards and cereal fields, as an important group of natural enemies, utilized non-crop habitat types differently. As higher spider numbers in non-crop habitats can translate into higher spillover to adjacent crop fields (Bianchi et al., 2017; Birkhofer et al., 2018), non-crop habitat types can vary in their potential to serve as sources of agrobiont spiders for the pome-fruit orchards and cereals fields. The highest potential to serve as a source habitat is provided by habitats with properties structurally similar to the focal crop, namely woody vegetation for spiders in pome-fruit orchards, and meadows for spiders in cereal fields. Therefore, future studies investigating landscape effects on natural enemy communities in local agroecosystems should not pool all non-crop habitat types into a simplified "semi-natural" category. A more refined approach, treating landscape data and habitat types as multidimensional, would provide a much-improved understanding of potential spillover effects with beneficial consequences for biological control services. Such detailed knowledge will help provide recommendations on the composition of multifunctional landscapes that aim to optimize the provision of ecosystem services (Landis, 2017).

Data availability statement

Data are available in the public databases referenced within the text: Kasal and Kalab (2013) and Hänggi et al. (1995).

Declaration of Competing Interest

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

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.agee.2020.107248.

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