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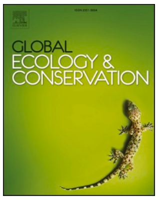

Fragmentation of forest-steppe predicts functional community composition of wild bee and wasp communities

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ABSTRACT

Increased habitat fragmentation in natural areas is one of the causes of declining insect diversity and biomass globally. Wild bees and wasps and their ecosystem functions are not exceptions of the trend. To stop this trend, we need to increase our understanding of interactions between functional traits and the environment for better informing conservation and restoration. Therefore, we studied how habitat fragmentation (i.e., connectivity, fragment size) and flower availability (abundance and species richness) affect functional traits of wild bees and wasps. Forest-steppe is a complex ecosystem ranging from far East of Asia to Eastern Central Europe, consisting of a mosaic of woody and herbaceous vegetation patches. We selected 30 natural forest-steppe fragments along a connectivity gradient in the Hungarian Great Plain region. The size of the selected fragments ranged between 0.16 and 6.88 ha. We collected wild bees and wasps with yellow pan traps. We selected four functional traits: social habit, body size, feeding preference, and nesting location and investigated them in relation to habitat connectivity, patch size, flower abundance and richness. We used RLQ ordination to analyse the pollinators' functional community composition. We found that habitat connectivity supported larger, eusocial and ground nesting wild bees. Fragment size was closely related to larvae feeding preference in both studied groups by positively affecting oligolectic bees and carnivore wasps. Additionally, higher abundance and species richness of flowers maintained polygolectic bees and solitary, ground-nesting wasps. In our study, we described for the first time the relationship between the functional traits and habitat fragmentation of wild bee and wasp communities in a natural forest-steppe habitat. Our findings suggest that improved knowledge about the response of functional traits of wild bee and wasp communities to habitat fragmentation will allow a better understanding and prediction of subsequent effects on ecosystem functioning. We conclude that a combination of large, high-quality and well-connected patches maintains specialist wild bee and wasp communities.

1. Introduction

Habitat fragmentation exists in all habitat types. It increases the risk of insect decline and influences ecosystem functions by

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changing the relative abundance of species (Jacobson et al., 2019; Chase et al., 2020). In recent years, more and more studies indicate that ecosystem functioning can be affected by habitat fragmentation, and changes in ecosystem functioning may also alter ecosystem services (Liu et al., 2018). The functionally important species' negative response to habitat fragmentation would drive an overall decrease in ecosystem function. We know that bees' species richness and abundance decline in agricultural areas where the landscape structure and land use frequently change. Thus pollination ecosystem function and service is also degraded (Potts et al., 2010; Hall et al., 2019; Lanner et al., 2020). The same applies to natural enemy community composition changes (e.g. of parasitoid or predatory wasps), which negatively affect biological control services (Kruess and Tscharntke, 1994; Coudrain et al., 2013; Hoffmann et al., 2018, 2020). We need to understand the response of community composition to environmental variables and subsequent impacts on ecosystem processes. Thus studying the relationships between important organismal traits and higher-level ecosystem processes affords a deeper mechanistic understanding of diversity's role in ecosystem functions and providing services (Nock et al., 2016).

Functional traits are physiological, morphological, and phenological characteristics that impact the fitness of an individual and influence ecosystem functioning (Riemann et al., 2017; Wong et al., 2019). It is challenging to predict the specific responses of functional traits to habitat fragmentation. For example, Larsen et al. (2005) found that large-bodied wild bee species were the most extinction-prone and most sensitive to the decrease and connectivity of their habitat. However, Carrié et al. (2017) showed an opposite result, large-bodied wild bees have good dispersal ability, therefore they are not so sensitive to habitat fragmentation as smaller-bodied species. Small-bodied species have limited dispersal abilities and need to nest closer to floral resources (Greenleaf et al., 2007). These opposite results may be related to semi-natural habitat types, because most of the Hymenoptera functional trait studies focus on agricultural and urban areas (Hoffmann et al., 2018, 2020; Marja et al., 2018; Hall et al., 2019; Lanner et al., 2020), and these environments can affect Hymenoptera functional traits differently. This can be related to body size, which is one of the most commonly studied functional trait because it is easy to measure, but not easy to interpret (Gallé and Batáry, 2019), since it may influence insects' metabolism (Brown et al., 2004) growth rate (Angilletta et al., 2004), movements speed (Sekar, 2012) and forage/prey consummation (Pawar et al., 2012). Furthermore, body size can be correlated with other traits such as diet breadth and sociality (Jauker et al., 2013; Nock et al., 2016).

Wasps regulate arthropod populations including insect vectors of human diseases and limit herbivore population growth, which is also essential in a healthy ecosystem (Sumner et al., 2018). Investigations on the body condition of wasp species related to different levels of fragmentation also show the consequences of altered food availability (Bucher and Entling, 2011; Schüepp et al., 2011). Feeding specialist wasp species with low dispersal ability depend on large and well-connected habitats to fulfil their feeding requirements. Habitat fragmentation directly affects diet as less connected, isolated fragments can offer a lower amount and diversity of food resources. As a consequence, dietary specialist species can disappear, but generalists tend to increase (Tylianakis and Morris, 2017). Another easily identifiable trait is sociality, which is well known for all Hymenoptera groups. Jauker et al. (2013) suggested that eusocial species need more floral resources to feed their numerous larvae and build up food stores for the colony in bad weather conditions. Another functional trait that can be sensitive to habitat fragmentation is nesting location. Nesting location can also be influenced by fragmentation – large fragments offer more nesting places, such as suitable vegetation, deadwood or trees (Potts et al., 2005; Kremen and M'Gonigle, 2015). The high quality of flowering plants positively affects herbivore prey, which can influence the feeding preference of wasps. Ecologically specialised predators are highly dependent on ecologically specialised prey. Therefore, they are more susceptible to local extinction in fragmented landscapes where their prey is either absent or reduced in abundance (Anderson et al., 2019). Thus interactions between ecologically specialised prey and their specialised predators are likely to be deficient in communities in fragmented landscapes (Bagchi et al., 2018).

In this study, we investigated a specific and under-studied natural ecosystem, the forest-steppe. Forest-steppe mosaics are widespread habitats at the interface between tree- and grass-dominated ecosystems. Forest-grassland mosaics typically consist of numerous types of forest and grassland patches of various sizes, with strongly different physiognomies and environmental conditions (Gallé et al., 2018; Kuli-Révész et al., 2021). Forest-steppe ecosystems have high nature conservation value, harbouring plenty of rare and protected plant and animal species (Erdős et al., 2018). Forest-steppe offers open grasslands for the grassland species and open forest areas for the forest species (Gallé et al., 2018). These habitats, due to the typical, relatively sparse vegetation, the tendency for the sandy soil to heat up quickly in the sun, and the ease with which burrows can be dug, support diverse wild bee and wasp communities (Benton, 2017).

In Central and Eastern Europe, human activity has mostly converted these mosaics to commercial plantations of native (poplar) and exotic (black locust and pine) tree species (Gallé et al., 2017, 2018). All our study fragments were surrounded mainly by exotic pine tree plantations that create a real barrier for the wild bees and wasps. Non-native pine plantations are low-quality habitats and they probably also pose a dispersal barrier for most forest-steppe Hymenoptera. This brought dramatic changes in landscape structure, as large grasslands and open-canopy of forest patches disappeared, which is a serious conservation problem.

Here we aimed to understand the effects of habitat fragmentation on the functional traits of wild bees and wasps in the forest steppe. Therefore, we studied the effects of size and connectivity of forest-steppe fragments and flower availability (abundance and species richness) on functional community composition of wild bees and wasps by considering body size, social habit, larvae feeding preference and nest location as functional traits.

We expected that the distribution of traits will shift along the studied gradients of fragment size and fragment connectivity. We examined the following hypotheses:

H1. : Local number of flowering species and abundance of flowers affect feeding preference. Flower species-rich fragments and those with high flower abundance support wild bees and wasps with generalist feeding preferences.

H2. : Fragment size affects nest location and social habit. Large fragment size offers more and diverse nesting places. Social species are linked to larger fragments, as they have higher food demand than solitary bees and wasps.

H3. : Connectivity affects the body size of bees and wasps, which is linked to dispersal ability.

2. Materials and methods

2.1. Study area and design

The study area is located in the Hungarian Great Plain, in the centre of the Kiskunság region. The natural vegetation in the forest-steppe is composed of native poplar (*Populus alba*) and hawthorn (*Crategus monogyna*) patches embedded in dry sandy grasslands resulting in a structurally and microclimatically complex ecosystem (Erdős et al., 2018). *Festuca vaginata* and *Stipa borysthenica* are the dominant grass species and *Euphorbia seguieriana* and *Alkanna tinctoria* are the dominant flower species in this area. The climate is continental with 500–550 mm mean annual precipitation and 9.5 and 10 °C mean annual temperature. We selected 30 sampling fragments embedded in a matrix of small-scale forest plantations near the villages of Pirtó (n = 15), Bócsa (n = 7) and Kunfehértó (n = 8) (Appendix, Fig. A1, A2). The study sites were selected based on the size of the fragments (ranged between 0.16 and 6.88 ha) and along a landscape configuration gradient by performing preliminary field visits and GIS calculations. We selected 15 small (0.16–0.48 ha) and 15 large (0.93–6.88 ha) forest-steppe fragments. For quantifying landscape configuration, we calculated Hanski's connectivity index (Hanski et al., 2013) using Google aerial photographs (captured in 2019), the new ecosystem map of Hungary (Tanács et al., 2021) in Quantum GIS 3.6.1 software (Quantum GIS Development Team 2019). We applied a 500 m radius buffer for the calculations. For connectivity calculations we considered all natural habitat fragments (other forest steppe fragments and open sand grasslands) that were situated around the focal fragments. We applied the connectivity index to entire wild bee and wasp communities containing many taxa, thus both scaling parameters α and β were set to the value of 0.5 (Kormann et al., 2015). The connectivity values of the selected fragments ranged from 24 (isolated) to 811 (connected), (mean ± SEM = 394 ± 206).

2.2. Wild bee and wasp sampling and examined their functional traits

We used yellow pan traps for sampling wild bees and wasps. At each sampling fragment we installed four pan traps, two in the interior and two in the edge zone (2 traps × 2 locations × 30 fragments = 120 traps). The minimum distance between traps per fragment was 15 m, and the mean distance was 38 m. The pan traps were open for two 4-day periods from 27th May to 2nd June and from 17th to 23rd June in 2019, and operated in good wheather conditions (sunny days at ca. 20–38 °C, and without strong wind and precipitation). All collected specimens were conserved in 70% ethanol, and subsequently all wild bees and wasps were identified to species level in the laboratory.

We surveyed flower abundance and richness when traps were open. At each sampling site, we designated two 6 × 4 m plots (edge and interior), where we recorded the number of flowering species and number of the flowering shoots (abundance of flowers).

We excluded honeybees (*Apis mellifera*) from the analyses because the abundance of this managed species is likely to be related to local beekeeping activities rather than a direct effect of landscape structure. We selected four functional traits: body size, social habit, larvae feeding preference and nest locationwhich are sensitive to habitat fragmentation. Functional traits information were collected from the following literature: Bees, Wasps and Ants Recording Society BWARS (2021), Evans and Matthews (1973), Witt (1998), Bogusch and Straka (2012), Falk (2015), Yeo and Corbet (2015), Anon (2017) Michez et al. (2019), Agnoli and Rosa (2021).

For the body size we used the mean body length in mm according to literature data (Appendix, Table A1, A2). For social habit, we used three categories in both groups: solitary, parasite, and eusocial. For bees, we defined food specialisation by the number of plant families, from which they collect food for their larvae. We classified them as oligolectic species, which collect pollen from a single plant family, and as polylectic species, which collect pollen from several plant families. In case of wasps, we used the larva prey feeding preference, which resulted in three categories: herbivore (e.g. caterpillar prey), omnivore (e.g. other insects prey) and carnivore (e.g. spider prey). Finally, for both groups we created four categories for the nesting location: soil, herbaceous plant stem, deadwood and wood nesters (Appendix, Table A1, A2).

2.3. Data analysis

For studying the functional community composition, we used RLQ co-inertia analysis to detect the links between wild bee and wasp traits and our predictor environmental variables, i.e. fragment size, connectivity, flower abundance and number of flowering species (Dolédec et al., 1996). We analysed the wild bee and wasp data separately. We used three data matrices: predictor environmental variables × sampling site (R), species × sampling site (L) and traits × species (Q), with the package ade4 (Dray and Dufour, 2007) of the R statistical environment (R Development Core Team 2020). This multivariate analysis provides an ordination plot to summarise the joint structure amongst the three tables (Dray et al., 2014). To determine, which functional traits were responsible for the species distributions according to environmental variables, we conducted a Kendall and Spearman correlation analysis between the scores of the species along the first and second axis of the RLQ analysis and the original values for the functional traits (Benesty et al., 2009).

3. Results

3.1. Wild bee species and traits

We recorded 692 wild bee specimens belonging to 45 species from Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae families (Appendix, Table A1, A2). We excluded 267 *Apis mellifera* individuals from the analysis. The most abundant species were *Nomioides minutissimus* 42% and *Lasioglossum albipes*, representing 15% of all wild bee individuals caught. We also detected some typically rare forest-steppe species: *Andrena combaella*, *Anthidium interruptum*, *Eucera nigrifacies*, *Halictus brunnescens*, *Hoplitis bisulca*, *Hylaeus moricei*, *Megachile melanopyga*. The RLQ analysis of the wild bee data indicated a significant relationship between environmental variables and species trait composition ($p < 0.001$, permutation test). The first two RLQ axes explained 96% of the total inertia (83% and 13%, respectively). The RLQ revealed that connectivity was positively associated with larger body size, eusocial habit and soil nesters along the first axis. The large fragment size positively associated with oligolectic larvae feeding preference. Furthermore, high abundance of flowers and number of flowering species positively associated with polylectic larvae feeding preference (Table 1, Fig. 1) along the second axis.

The most abundant flowering species detected in the flowering plant survey were *Euphorbia seguieriana*, *Euphorbia esula*, *Alyssum toruosum*, *Thymus glabrescens, Gypsophila arenaria*.

3.2. *Wasp species and traits*

We collected 794 wasp specimens belonging to 46 species from a following wasp families Chalcididae, Crabronidae, Mutillidae, Pompilidae, Scoliidae, Sphecidae, Tiphiidae, Vespidae (Appendix, Table A1, A2). The most abundant species was *Tiphia femorata*, representing 63% of all wasp individuals caught. We detected some typical, but rare forest-steppe species: *Aporinellus moestus sericeomaculatus*, *Pemphredon lugens*, *Sphex funerarius*, *Telostegus inermis*, *Tachysphex mediterraneus*, *Tiphia minuta*, *Pseudospinolia uniformis*. The RLQ analysis of the wasp data indicated a significant relationship between environmental variables and species trait composition ($p < 0.001$, permutation test). The first two RLQ axes explained 97% of the total inertia (76% and 21%, respectively). The RLQ plot revealed that large fragment size was positively associated with carnivore prey feeding preference and smaller bodied wasps. Furthermore, high abundance of flowers and high number of flowering species positively linked with soil nester and solitary wasps (Table 2, Fig. 2).

4. Discussion

We found that fragment size, fragment connectivity, and flower availability predict the distribution of functional trait changes. The traits shifted along the gradient of fragment size, fragment connectivity, and flower availability. Large, flower-rich, and well-connected forest-steppe fragments were associated with large-bodied, eusocial, soil nester, oligolectic and soil nester bees but with small-bodied, solitary, carnivore prey and soil nester wasps.

4.1. *Abundance of flowers and number of flowering species*

As expected, the abundance of flowers and the number of flowering species were positively linked with oligolectic/polylectic feeding preference. We found that a high abundance of flowers and diverse flowering species supported polylectic, i.e. generalist wild bees, confirming our first hypothesis. These generalist species are flexible regarding habitat quality and have a wide range of foraging areas. In contrast, oligolectic, i.e. specialist bees are morphologically and behaviourally adapted to effectively collect pollen on their host plants. Their foraging behaviour is fine-tuned to their host plants, the degree of specialisation depends on the composition of plant species at the local landscape (Konzmann et al., 2020). Based on floral resources limitation the specialist species are the most sensitive to interspecific food competition (Rasmussen et al., 2021). Generalists are attracted by flowering plants, and might prefer flower-rich microhabitats for successful larval development, they might in turn displace the specialist species (Konzmann et al., 2020). Therefore, it is important to focus on specialist, oligolectic bee species. They should be taken into consideration when formulating conservation plans to promote viable populations.

The solitary habit of wasps was positively related to the high abundance of flowers. Solitary wasps need to nest closer to the floral resource, as they do not have any helpers or workers to share the food collection/foraging in the closely surrounded landscape

Table 1
Correlations between the first two RLQ axes with environmental variables and wild bee traits. Correlation coefficient (corr. coeff.) for factorial variables is Kendall's tau, for the only continuous variable (body size) is Spearman's rho.

	First RLQ axis		Second RLQ axis	
	corr. coeff.	P-value	corr. coeff.	P-value
Forest steppe, environmental variables				
Connectivity	0.803	< 0.001	-0.411	0.023
Fragment size (small, large)	-0.162	0.389	0.558	0.001
Number of flowering species	-0.309	0.096	-0.750	< 0.001
Abundance of flowers	-0.149	0.431	-0.767	< 0.001
Wild bee traits				
Social habit (parasite, solitary, eusocial)	0.842	< 0.001	0.284	0.055
Nesting (soil/herbaceous plants stem/dead wood/wood)	-0.685	< 0.001	0.171	0.255
Feed preference (oligolectic, polylectic)	0.131	0.385	-0.883	< 0.001
Body size (mm)	0.390	0.007	0.202	0.177

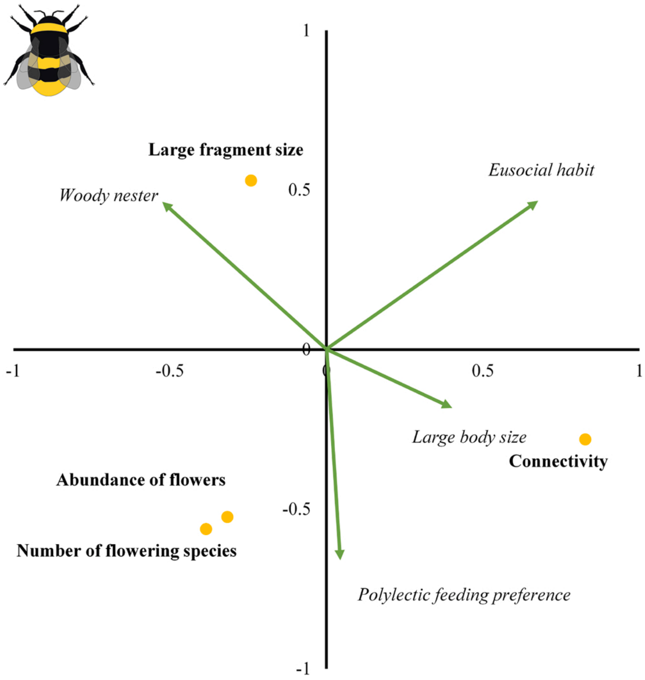

Fig. 1. Ordination plot of environmental variables (yellow points) and wild bee species traits (arrows) along the two first axes of the RLQ analysis. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 2
Correlations between the first two RLQ axes with environmental descriptors and wasp traits. Correlation coefficient (corr. coeff.) for factorial variables is Kendall's tau, for the only continuous variable (body size) is Spearman's rho.

	First RLQ axis		Second RLQ axis	
	corr. coeff.	P-value	corr. coeff.	P-value
Forest steppe, environmental variables				
Connectivity	0.225	0.230	-0.321	0.083
Fragment size (small, large)	-0.882	< 0.001	0.482	0.006
Number of flowering species	0.117	0.535	-0.793	< 0.001
Abundance of flowers	-0.059	0.753	-0.785	< 0.001
Wasp traits				
Social habit (parasite, solitary, eusocial)	0.220	0.140	0.457	0.001
Nesting (soil/herbaceous plants stem/dead wood/wood)	-0.147	0.326	0.732	< 0.001
Larvae prey feed preference (herbivore, omnivore, carnivore)	-0.708	< 0.001	-0.012	0.936
Body size	0.530	< 0.001	-0.693	< 0.001

(Palladini and Maron, 2014). Fabian et al. (2014) found a positive effect of plant diversity on the richness and abundance of soil-nester spider-hunting wasps. Flower-rich habitats, such as wildflower strips, might represent attractive foraging sites not only for adults feeding on nectar but also for their carnivorous larvae by offering a larger diversity and abundance of spiders. To optimise foraging, they need to nest closer to floral resources, where suitable prey is also available (Kovac et al., 2018).

4.2. *Fragment size*

Our results showed that larger fragment size was positively related with specialist, oligolectic wild bees and small-bodied wasps whose larvae prefer carnivore prey. So our second hypothesis was not confirmed. Foraging ranges are related to feeding preferences in bees (Greenleaf et al., 2007). Floral specialist bees, which collect pollen from a limited number of plant species, are known to be more sensitive to the loss of natural habitats because they may be incapable of switching to alternative food resources in the landscape (Tscharntke et al., 2002; Cane and Sipes, 2006). However, specialist species more successfully pollinate specific plants and maintain plant diversity. Additionally, the specialist species, in general, do not have active dispersal behaviour because the level of specialisation and dispersal behaviour is often related (López-Uribe et al., 2019). Consequently, large fragments can sustain specialist wild bees and their floral resources.

Large forest-steppe fragments offer special resources for the specialist species, e.g., open habitat and suitable flowers for the wild

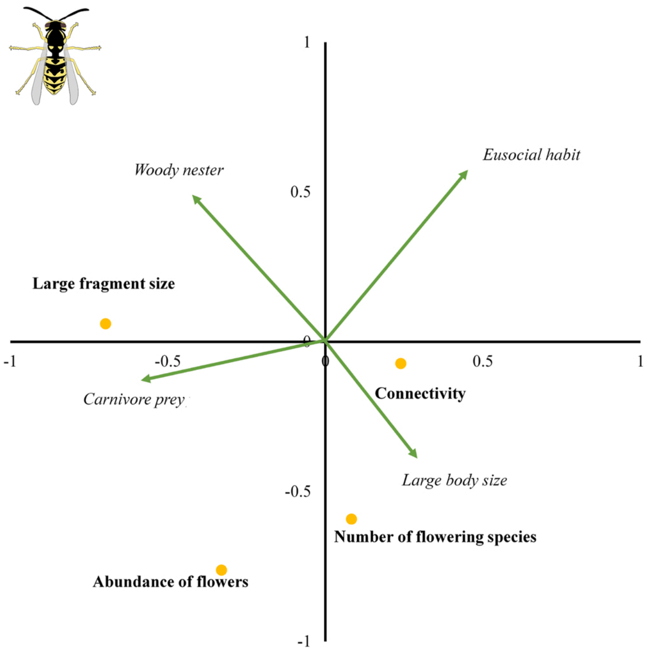

Fig. 2. Ordination plot of environmental variables (yellow points) and wasp species traits (arrows) along the two first axes of the RLQ analysis. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

bees and space for the carnivore wasps to hunt for their prey (e.g., spiders). Furthermore, large habitat patches support high insect species richness and abundance (Chase et al., 2020), e.g., these large forest-steppe patches with their species-rich and abundant spider community (Gallé et al., 2018) can support carnivore wasps. Carnivore wasps are very sensitive to environmental disturbances, and previous studies have shown that wasp diversity increases with the quality of the habitat (Tscharntke et al., 1998, 2002). Quantifying food availability to a species is difficult due to factors, such as fluctuating spatial and temporal prey abundance and the species' ability to prey on them (Coudrain et al., 2013). However, larger fragments, in general, can offer more prey than small fragments.

Large-fragments are positively linked with small-bodied wasps, which can be explained by the behaviour of wasps. They optimise either the intake rate or the energetic efficiency of a foraging trip for maximising the benefits for their larvae (Kovac et al., 2018, Buschini et al., 2010). In this sense, small-bodied wasp species have limited foraging ranges, and the energy required to find resources further from the nest site may reduce their reproductive potential (Peterson and Roitberg, 2006; Zurbuchen et al., 2010). Small-fragments can offer less food availability for small-bodied low dispersal ability wasps, which can easily become extinct.

4.3. *Connectivity*

Our results showed that connectivity shaped wild bee functional traits more than those of wasps. Habitat fragmentation reduced the connectivity of habitat fragments, which affects the body size, social habit, and nesting preference of wild bees. As expected in our third hypothesis, we found that body size trait is closely related to connectivity. Wild bees of different body sizes, and foraging ranges, can respond differently to fragmentation depending on the resources available in the fragments. Our results showed that habitat fragmentation negatively influenced the large-bodied bees, indicating that these species are the most sensitive and vulnerable to habitat fragmentation (Larsen et al., 2005). However, the home ranges of large-bodied bees are usually larger than those of small-bodied bees. On the one hand, the larger home range sizes of larger species may indicate that body size and dispersal ability are positively correlated with each other (Gaston, 2003). On the other hand, larger-bodied species are usually rarer, have greater resource requirements, and are therefore more vulnerable to fragmentation (Millien and Damuth, 2004; Wray et al., 2014). For instance, when natural landscape fragments become too small compared to the species' home range, larger-bodied species may have reduced reproductive output and higher extinction risk. However, the large-bodied species may use several habitat fragments if these fragments are well connected. They need to feed more frequently, but the food resources available in small and isolated fragments are limited. In addition, isolated patches may have increased food competition and predation pressures (Lovegrove, 2000). So despite being less mobile, small-bodied species are less sensitive to habitat fragmentation than large ones (Rossetti et al., 2017; Gallé et al., 2020). Small-bodied wild bee species might need less energy and resources, thus, they have smaller home ranges than large-bodied wild bee species (Greenleaf et al., 2007).

Overall, our results showed that well-connected forest-steppe fragments were positively associated with large-bodied, eusocial, and soil-nester wild bees. These characters correspond to traits typical of bumblebees. Based on social life, the workers of a bumblebee colony have to optimise the energetic efficiency in foraging trips, therefore, the individuals probably save more energy in well-connected fragments. Making wrong decisions and crossing large unsuitable patches is energetically very costly (Goulson, 2003).

Futile and time-consuming foraging will result in a net loss of resources. The best nesting location is always close to the food, i.e., floral resource. A bumblebee queen who makes a poor decision about the location of the nesting place will quickly starve, whereas an inefficient worker will drain the resources gathered by her nestmates.

Social species, such as bumblebee workers, share floral resource information. Bumblebees use pheromones to inform the other workers where currently available floral resources are (Granero et al., 2005). Furthermore, bees are central place foragers, the distance between nest sites and food resources in fragmented habitats will probably affect offspring provisioning and may influence population size (Cane, 2001; Williams and Kremen, 2007; Marja et al., 2018). In general, the queens choose the nesting place's location based on fragment-connectivity and avoid isolated fragments (Hall et al., 2019; Lanner et al., 2020). Another explanation why well-connected fragments positively affect bumblebees is the intracolony competition (Dramstad, 1996). This increases if many workers stay close to their colony in a resource-poor environment. Bumblebee workers cover ca. 1000 m (a maximum of 1500 m) when crossing unsuitable habitats when foraging for food (Osborne et al., 2008). Consequently, the most economical strategy for a colony is to distribute its foragers widely in the landscape, i.e., connected fragments.

5. Conclusion

Understanding fragmentation effects (i.e. connectivity, fragmentation size) on functional traits are crucial for future conservation planning as it allows a more inclusive perspective of landscape alteration effects on ecosystem processes. Different fragmentation effect combinations are likely indicate changes in availability of resources that affect ecosystem functions, such as pollination and predation. Communities in highly modified landscapes might provide weaker functions and different services. We suggest that careful conservation planning would aim to protect existing large and well-connected forest-steppe fragments to protect wild bee and wasp communities as well as pollination and predation.

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. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2021.e01988.

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Appendix: Supplementary material data

Table A1: Species list of collected wild bees from forest steppe study sites including information on species functional traits. Functional traits information after Bees, Wasps & Ants Recording Society (BWARS); Bogusch & Straka, 2012; Falk, 2015; Michez et al., 2019.

Taxa	Social habit	Nest location	Larvae feeding preference	Body size (mm)
1. *Amegilla quadrifasciata* (de Villers, 1789)	Solitary	Soil	polylectic	11
2. *Andrena combaella* Warncke, 1966	Solitary	Soil	oligolectic	12
3. *Andrena niveata* Friese, 1887	Solitary	Soil	oligolectic	11.5
4. *Andrena oralis* Morawitz, 1876	Solitary	Soil	polylectic	12
5. *Anthidium interruptum* (Fabricius, 1781)	Solitary	Soil	polylectic	12
6. *Anthidium manicatum* (Linnaeus, 1758)	Solitary	Woody plant	polylectic	11.5
7. *Bombus humilis* Illiger, 1806	Eusocial	Soil	polylectic	12
8. *Bombus pascuorum* (Scopoli, 1763)	Eusocial	Soil	polylectic	12
9. *Bombus ruderatus* (Fabricius, 1775)	Eusocial	Soil	polylectic	12.5
10. *Bombus terrestris* (Linnaeus, 1758)	Eusocial	Soil	polylectic	14
11. *Coelioxys quadridentata* (Linnaeus, 1758)	Parasitic	Dead wood	polylectic	8
12. *Halictus confusus* Smith, 1853	Eusocial	Soil	polylectic	7
13. *Halictus semitectus* Morawitz, 1874	Solitary	Soil	polylectic	6
14. *Hoplitis bisulca* (Gerstäcker, 1869)	Solitary	Soil	oligolectic	10
15. *Hylaeus angustatus* (Schenck, 1861)	Solitary	Dead wood	polylectic	4
16. *Hylaeus brevicornis* Nylander, 1852	Solitary	Herbaceous plants	polylectic	5
17. *Hylaeus communis* Nylander, 1852	Solitary	Woody plant	polylectic	6.5
18. *Hylaeus gibbus* Saunders, 1850	Solitary	Herbaceous plants	polylectic	7
19. *Lasioglossum albipes* (Fabricius, 1781)	Eusocial	Soil	polylectic	8
20. *Lasioglossum bluethgeni* Ebmer, 1971	Solitary	Soil	oligolectic	7
21. *Lasioglossum brevicorne* (Schenck, 1869)	Eusocial	Soil	oligolectic	6.5
22. *Lasioglossum calceatum* (Scopoli, 1763)	Eusocial	Soil	polylectic	8.5
23. *Lasioglossum leucozonium* (Schrank, 1781)	Eusocial	Soil	polylectic	9
24. *Lasioglossum mesosclerum* (Perez, 1903)	Solitary	Soil	polylectic	4
25. *Lasioglossum minutissimum* (Kirby, 1802)	Solitary	Soil	polylectic	4.5
26. *Lasioglossum politum* (Schenck, 1853)	Eusocial	Soil	polylectic	4.5
27. *Lasioglossum punctatissimum* (Schenck, 1853)	Solitary	Woody plant	polylectic	6.5
28. *Lasioglossum puncticolle* (Morawitz, 1872)	Eusocial	Soil	polylectic	6.5
29. *Lasioglossum semilucens* (Alfken, 1914)	Solitary	Soil	polylectic	5.5
30. *Lasioglossum sexstrigatum* (Schenck, 1869)	Solitary	Soil	polylectic	6.5
31. *Lasioglossum tarsatum* (Schenck, 1870)	Solitary	Soil	polylectic	5.5
32. *Lasioglossum xanthopus* (Kirby, 1802)	Solitary	Herbaceous plants	polylectic	12
33. *Lasioglossum zonulum* (Smith, 1848)	Solitary	Soil	polylectic	9.5
34. *Megachile centuncularis* (Linnaeus, 1758)	Solitary	Dead wood	polylectic	9
35. *Megachile circumcincta* Kirby, 1802	Solitary	Dead wood	polylectic	10

36. *Megachile leachella* Curtis, 1828	Solitary	Soil	polylectic	9.5
37. *Megachile maritima* (Kirby, 1802)	Solitary	Woody plant	polylectic	14.5
38. *Megachile melanopyga* Costa, 1863	Solitary	Woody plant	oligolectic	11.5
39. *Megachile versicolor* Smith, 1844	Solitary	Herbaceous plants	polylectic	11.5
40. *Nomioides minutissimus* (Rossi, 1790)	Solitary	Woody plant	polylectic	4.5
41. *Osmia brevicornis* (Fabricius, 1798)	Solitary	Dead wood	oligolectic	11
42. *Osmia melanogaster* Spinola, 1808	Solitary	Dead wood	oligolectic	9
43. *Sphecodes puncticeps* Thomson, 1870	Parasitic	Soil	polylectic	6
44. *Trachusa interrupta* (Fabricius, 1781)	Solitary	Soil	polylectic	12
45. *Xylocopa iris* (Christ, 1791)	Solitary	Dead wood	polylectic	16.5

Table A2: Species list of collected wasps from forest steppe study sites including information on species functional traits. Functional traits information after Agnoli & Rosa, 2021; Bees, Wasps & Ants Recording Society (BWARS); Evans & Matthews, 1973; Witt, 1998; Yeo & Corbet, 2015.

	Taxa	Social habit	Nest location	Wasp preys	Larvae feeding preference	Body size (mm)
1.	*Ancistrocerus gazella* (Panzer 1798)	Solitary	Herbaceous plants	Caterpillars (Lepidoptera)	herbivore	11
2.	*Aporinellus moestus sericeomaculatus* (Kohl, 1888)	Solitary	Soil	Spiders (Araneae)	carnivore	4
3.	*Arachnospila abnormis* (Dahlbom, 1842)	Solitary	Herbaceous plants	Spiders (Araneae)	carnivore	9
4.	*Arachnospila minutula* (Dahlbom,1842)	Solitary	Soil	Spiders (Araneae)	carnivore	8
5.	*Arachnospila spissa* (Schiødte,1837)	Solitary	Soil	Spiders (Araneae)	carnivore	8
6.	*Arachnospila trivialis* (Dahlbom,1843)	Solitary	Soil	Spiders (Araneae)	carnivore	6
7.	*Astata boops* (Schrank,1781)	Solitary	Soil	True bugs (Hemiptera)	herbivore	11
8.	*Bembecinus tridens* (Fabricius, 1781)	Solitary	Soil	True bugs (Hemiptera)	herbivore	10
9.	*Chrysis illigeri* Wesmael,1839	Parasitic	Soil	Wasps (Hymenoptera: Vespidae)	carnivore	2.5
10.	*Chrysis rutilans* Olivier, 1790	Parasitic	Herbaceous plants	Wasps (Hymenoptera: Vespidae)	carnivore	8
11.	*Chrysura dichroa* (Dahlbom, 1854)	Parasitic	Woody plant	Bees (Hymenoptera: Apidae)	herbivore	3
12.	*Crabro scutellatus* (von Scheven,1781)	Solitary	Woody plant	Dolichopodidae (Diptera, Aphidae predators)	herbivore	7
13.	*Crossocerus wesmaeli* (Vander Linden,1829)	Solitary	Soil	Small flies (Diptera)	herbivore	5
14.	*Diodontus minutus* (Fabricius, 1793)	Solitary	Herbaceous plants	Aphids (Aphidoidea)	herbivore	5
15.	*Dipogon bifasciatus* (Geoffroy, 1785)	Solitary	Herbaceous plants	Spiders (Araneae)	carnivore	6
16.	*Ectemnius dives* (Lepeletier de Saint Fargeau & Brullé, 1835)	Solitary	Dead wood	Hoverflies (Syrphidae), true flies (Tachinidae)	herbivore	8
17.	*Episyron albonotatus* (Costa, 1881)	Solitary	Soil	Spiders (Araneae)	carnivore	13

18. *Episyron rufipes* (Linnaeus 1758)	Solitary	Soil	Spiders (Araneae)	carnivore	11
19. *Evagetes pectinipes* (Linnaeus,1758)	Parasitic	Soil	Wasps (Hymenoptera: Vespidae)	carnivore	5
20. *Gorytes quinquecinctus* (Fabricius, 1793)	Solitary	Soil	Small leafhoppers (Auchenorrhyncha)	herbivore	10
21. *Meria tripunctata* (Rossi, 1790)	Parasitic	Dead wood	Black beetle (Tenebrionidae)	herbivore	14
22. Nemka viduata (Pallas, 1773)	Parasitic	Herbaceous plants	Wasps (Hymenoptera: Vespidae)	carnivore	16
23. *Oxybelus quatordecimnotatus* Jurine, 1807	Solitary	Soil	Muscids (Diptera: Muscidae)	herbivore	6
24. *Passaloecus gracilis* (Curtis, 1834)	Solitary	Herbaceous plants	Aphids (Aphidoidea)	herbivore	4
25. *Passaloecus pictus* Ribaut, 1952	Solitary	Soil	Aphids (Aphidoidea)	herbivore	6
26. *Pemphredon inornata* (Say 1824)	Solitary	Woody plant	Aphids (Aphidoidea)	herbivore	1.5
27. *Pemphredon lethifera* (Shuckard, 1837)	Solitary	Woody plant	Aphids (Aphidoidea)	herbivore	1.5
28. *Pemphredon lugens* (Dahlbom 1842)	Solitary	Woody plant	Aphids (Aphidoidea)	herbivore	1.5
29. *Philanthus venustus* (Rossi, 1790)	Solitary	Soil	Bees (Hymenoptera: Apidae)	herbivore	2
30. *Polistes nimpha* (Christ, 1791)	Eusocial	Herbaceous plants	Spiders (Araneae)	carnivore	8
31. *Pompilus cinereus* Fabricius, 1798	Solitary	Soil	Spiders (Araneae)	carnivore	6
32. *Pseudomalus auratus* (Linnaeus,1758)	Parasitic	Woody plant	Wasps (Hymenoptera: Vespidae)	carnivore	5
33. *Pseudomalus pusillus* (Fabricius, 1804)	Parasitic	Herbaceous plants	Wasps (Hymenoptera: Vespidae)	carnivore	4
34. *Scolia hirta* (Schrank, 1781)	Solitary	Dead wood	Scarabaeidae	herbivore	24
35. *Sphex funerarius* Gussakovskij, 1934	Solitary	Soil	Grasshoppers, crickets (Orthoptera)	herbivore	20
36. *Stenodynerus chevrieranus* (Saussure, 1855)	Solitary	Soil	Other insects	omnivore	7
37. *Symmorphus gracilis* (Brullé, 1832)	Solitary	Herbaceous plants	Leaf beetle (Chrysomelidae)	herbivore	10
38. *Tachysphex mediterraneus* Kohl, 1883	Solitary	Soil	Grasshoppers, crickets (Orthoptera)	herbivore	8
39. *Tachysphex obscuripennis* (Schenck, 1857)	Solitary	Soil	Grasshoppers, crickets (Orthoptera)	herbivore	8
40. *Tachysphex pompiliformis* (Panzer,1805)	Solitary	Soil	Grasshoppers, crickets (Orthoptera)	herbivore	6
41. *Tachysphex psammobius* (Kohl, 1880)	Solitary	Soil	Grasshoppers, crickets (Orthoptera)	herbivore	5
42. *Tachysphex unicolor* (Panzer,1809)	Solitary	Soil	Acrididae	herbivore	6
43. *Telostegus inermis* (Brullé, 1832)	Solitary	Soil	Spiders (Araneae)	carnivore	7

44. *Tiphia femorata* Fabricus,1775	Parasitic	Soil	Scarabs (Scarabaeidae: Amphimallon)	herbivore	10
45. *Trypoxylon scutatum* Chevrier 1867	Solitary	Herbaceous plants	Spiders (Araneae)	carnivore	10
46. *Vespula germanica* (Fabricius,1793)	Eusocial	Herbaceous plants	Spiders (Araneae) and other insects	omnivore	13

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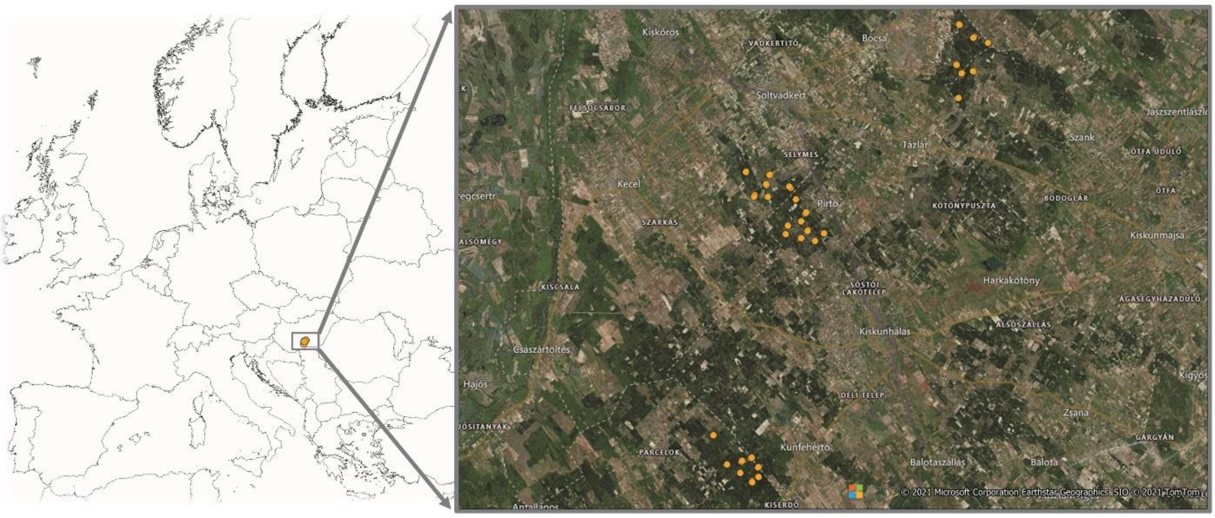

Figure A1. Location of study regions in Hungary, in Europe and sampling sites.

Figure A2. Forest-steppe habitat photo from the Hungarian Great Plain region.