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Crop type rather than production method determines functional trait composition of insect communities on arable land in boreal agricultural landscapes

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Abstract

1. To understand the potential consequences of arable land use changes for insect conservation and ecosystem functioning, it is fundamental to know how insect species with different functional traits respond to crop choice and production method.
2. This study examined the effects of crop type and production method on functional traits of butterfly, bumblebee and carabid beetle communities using species abundance data from 78 fields in Southern Finland. Surrounding landscape composition was also accounted for. The studied traits were associated with dispersal capacity, habitat or diet specialization and phenology—the key determinants modifying species responses to agricultural disturbances and land use changes.
3. Butterfly habitat breadth was narrowest and wingspan shortest in long-term fallows. Fallows also supported the highest share of butterflies overwintering in early development stages and bumblebees with late-emerging queens. The tongue length of bumblebees was longest in organic oat fields, probably due to flowering weeds with long corolla.
4. For carabid beetles, the proportion of poor flyers and carnivores was highest in perennial crops and fallows. Carabid beetles overwintering as adults were relatively more abundant in organic than in conventional production, probably due to more intensive tillage in organic fields.
5. In all insect groups, poor dispersers and/or specialists decreased with increasing arable land cover in the surrounding landscape.
6. Increasing the area of long-term fallows and perennial crops and enhancing within-field plant diversity while maintaining landscape heterogeneity would promote insect species sensitive to agricultural disturbances and land use changes and their associated ecosystem services in boreal farmland.

KEYWORDS
bumblebees, butterflies, carabid beetles, community-weighted means, dispersal capacity, fallows, organic production, specialization, species traits

INTRODUCTION

Agricultural land use change and management intensification are among the main drivers of insect decline globally (Wagner, 2020). In agricultural landscapes, insect diversity and abundance have declined due to the loss of semi-natural habitats and landscape heterogeneity (Hendrickx et al., 2007; Tscharntke et al., 2005), and the adoption of high-intensity management practices such as high pesticide and inorganic fertilizer inputs (Geiger et al., 2010; Gossner et al., 2016). While it is clear that intensive agriculture is damaging insect diversity, the effects of various arable land use options on insect community composition are still not well understood.

Arable land can temporarily provide plenty of resources for some insects (Holland et al., 2004; Knapp et al., 2019; Martins et al., 2018). However, in Europe and many other parts of the world, habitats on arable land are mostly homogeneous and ephemeral: the vegetation is typically dominated by few plant species, and the land is regularly disturbed by management such as ploughing, mowing and pesticide use. This leads to insect movement between arable land and adjacent semi-natural habitats that, compared to crops, provide more heterogeneity and temporal continuity in resources and more stable conditions (Knapp et al., 2019; Martínez-Núñez et al., 2022; Martins et al., 2018). Among arable land use types, fallow or set-aside land, that is, land temporarily taken out of production, can host relatively high insect diversity, including species that are not able to persist in more disturbed crop fields (Kovács-Hostyánszki et al., 2011; Toivonen et al., 2015, 2022). In many European countries, farmers are paid agri-environment subsidies for establishing and managing different types of fallows, of which long-term fallows and fallows sown with diverse seed mixtures are probably most beneficial to insect diversity (Alanen et al., 2011; Boetzl et al., 2021; Toivonen et al., 2015).

Insect communities on arable land are constrained by species' functional response traits (i.e., characteristics of species important for their response to the environment) that influence their ability to move, establish, reproduce and tolerate disturbances. Typically, habitat or resource generalists with strong mobility can cope with intensive agricultural land use and homogenous landscapes better than specialist species with poor mobility (Börschig et al., 2013; Gámez-Virués et al., 2015; Kőrösi et al., 2022). The trophic levels of the species may also affect the responses: predators have been suggested to be more dependent on landscape diversity than herbivores that respond more strongly to local habitat type (Woodcock et al., 2010). Furthermore, traits associated with life cycle timing and pace, such as overwintering stage, voltinism and the length of the activity period, may be linked to land use intensity and landscape structure (Börschig et al., 2013; Gámez-Virués et al., 2015; Kőrösi et al., 2022). For example, species with short activity periods have been reported to suffer from intensive management more than species with longer activity periods (Börschig et al., 2013; Gámez-Virués et al., 2015). Insects' resource needs and vulnerability to disturbances also vary depending on their life cycle stage (Kőrösi et al., 2022). Thus, the ability of an insect species to use arable land is dependent on the temporal match between insect life cycle, field operations and resource provision on arable land.

Functional effect traits (i.e., characteristics of species important for their effect on the ecosystem) of insect communities, in turn, affect ecosystem functioning and service provision, such as the suppression of pests and weeds on arable land (Greenop et al., 2018; Guenay-Greunke et al., 2023; Welch & Harwood, 2014) or pollination success of insect-pollinated crops and wild plants (Bommarco et al., 2012; Ehlers et al., 2021; Woodcock et al., 2019). Hence, knowing how insect species with different functional traits respond to arable land use is a prerequisite for understanding the consequences of arable land use change for both insect conservation and insect-driven ecosystem services.

Crop choice and production method are important determinants of habitat quality for many taxa on arable land (Stein-Bachinger et al., 2021; Toivonen et al., 2022). For example, cereal fields, which dominate agricultural land use in most of Europe (Eurostat, 2016), are relatively resource-poor habitats for many insects (Toivonen et al., 2022; Yvoz et al., 2020). The types of crops grown are affected by the production method (Barbieri et al., 2019), and both production method and crop type influence management practices, such as tillage system and agrochemical use. Crop choice and production method are also of high political interest and under pressure for change. For example, in the European Union, increasing domestic plant protein production as well as increasing the share of agricultural land under organic farming have been set as targets (European Commission, 2020). Still, functional traits of insect communities have seldom be compared between various crop types while also accounting for production methods (but see Eyre et al., 2013).

This study examined how key functional traits of insect communities on boreal arable land are influenced by crop type and production method. The studied traits were associated with dispersal capacity, habitat or diet specialization and life cycle timing—the key determinants modifying species responses to agricultural disturbances and land use changes. The crop types included seven common annual and perennial crop types, as well as long-term fallows as an alternative land use option. We expected that (1) the proportional abundance of species with poor dispersal ability is higher in perennial crops and fallows than in annual crops, as persisting in a more disturbed habitat requires a better dispersal ability; (2) the proportional abundance of habitat or diet specialists is highest in fallows, which have more diverse vegetation and a higher share of wild plants than crop fields, and are thus more likely to provide suitable resources for specialist insects and (3) traits associated with life cycle timing, including overwintering stage and spring emergence time differ between arable land use types since these traits affect insects' ability to tolerate disturbances and utilize resources at different times of the year.

MATERIALS AND METHODS

Study design

Data on butterflies, bumblebees and carabid beetles were obtained from a biodiversity study of 78 fields in Southern Finland (60.09936–

61.01251° N, 23.40421–25.14284° E), described in detail by Toivonen et al. (2022). Landscapes in the study region are typically mosaics of arable land and coniferous and mixed forests. The study fields represented a range of arable land use types, called as 'crop types' in this paper: (1) spring cereal (oat; $n = 10$), (2) winter cereal (rye; $n = 10$), (3) faba bean ($n = 10$), (4) spring oilseed crops ($n = 10$), (5) cabbage ($n = 8$), (6) grass ley ($n = 10$), (7) arable pasture ($n = 10$) and (8) long-term fallow ($n = 10$) (Table 1). Fallows are a popular agri-environment measure in the study region and they are often retained in the same place for several years or even decades. The studied fallows had 8–35 years old grassland swards. Five conventionally managed and five organically managed fields were selected for each crop type, except for oilseeds and cabbage, which are uncommon in organic farms. For oilseeds, seven conventionally managed and three organically managed fields were selected. For cabbage, eight conventionally managed fields and no organically managed fields were found. All organically managed study fields were situated in organic farms certified according to the EU regulation (Regulation (EU) 2018/848). Fallows were also selected from organic and conventional farms, although the production method does not affect the management of long-term fallows. The study fields were separated by at least 500 m. For the study fields that represented the same crop type, the minimum distance was 1 km.

Proportions of the areas covered by arable land, forest, built-up area and waters and wetlands were calculated for four radii (100, 250, 500 and 1000 m) around the central points of the study sites using ArcGIS 10.8.1 (Esri, 2020). Data on arable land cover were obtained from the Finnish agricultural land parcel register (Finnish Food Authority, 2021). Data on the other land use types were derived from CORINE Land Cover 2018 dataset (Finnish Environment Institute, 2018). Fallows were situated in landscapes with higher forest cover and lower arable land cover than the other crop types (Table 1). This could not be avoided because farmers prefer to have long-term fallows in field parcels that are low productive, irregularly shaped or located far away from the farm centre and these kinds of parcels are concentrated in forested landscapes.

Insect sampling

Butterflies and bumblebees were counted five times during the summer of 2020 at approximately 2-week intervals, from 27 May until 7 August, in weather conditions allowing insect activity. Counts were performed using the standard line transect method (Pollard & Yates, 1993), in which an observer walks along a fixed route at a steady speed and counts all the individuals within an imaginary box of 5 × 5 × 5 m in front of him or her. In each field, two 50 m-long transects were placed parallel at 5 and 20 m distances from the field edge farthest from the forest. Butterflies and bumblebees were identified as species. An exception was bumblebee individuals belonging to the *Bombus lucorum* group (*B. lucorum* (L.), *Bombus terrestris* (L.), *Bombus cryptarum* (Fabiricius) and *Bombus magnus* Vogt) that were treated as one species, *B. lucorum*, in the analyses.

Carabid beetles were sampled by pitfall trapping between 8 and 25 June 2020, with two consecutive 1-week trapping periods per field. Three pitfall traps (9 cm in diameter, 8 cm in depth, transparent plastic) filled with concentrated NaCl liquid were placed in each field: two traps were placed next to the ends of the pollinator transects, at 5 and 20 m distances from the field edge, and one trap between them, at 12.5 m distance from the edge. The traps were covered with plywood roofs to prevent flooding during rain. All carabid beetles were identified at the species level. In two fields, pitfall trapping could not be conducted, and in one field, the traps were in place only during

TABLE 1 The descriptions of the crop types, the numbers of study fields per crop type and production method and the covers of arable land and forest within the 250-m radius around the central points of the study sites.

		Number of study fields		Land use cover (%) within 250 m, mean	
Crop type	Description	Conventional	Organic	Arable land	Forest
Spring cereal	Oat *Avena sativa* L.	5	5 (4)	68	23
Winter cereal	Rye *Secale cereale* L.	5	5	72	18
Faba bean	*Vicia faba* L.	5	5	66	23
Spring oilseeds	Annual mass-flowering Brassicaceae: oilseed rape *Brassica napus* L. subsp. *oleifera*, turnip rape *Brassica rapa* L. subsp. *oleifera* and camelina *Camelina sativa* (L.) Crantz	7	3	66	24
Cabbage	*Brassica oleracea* L. var. capitata	8 (7)	0	58	30
Grass ley	Mean age of the sward 3.5 years (median 2.5 years), mowing 2–3 times/year	5	5	69	28
Arable pasture	Mean age of the sward 7.5 years (median 4.5 years); various animal types and grazing intensity	5	5 (4)	62	30
Long-term fallow	Mean age of the sward 18.1 years (median 17.5), mowing 0–1 times/year	5	5	30	49

Note: The numbers of study fields in parentheses indicate the fields where full data on carabid beetles were collected, if not collected in all study fields.

one trapping period. These fields were excluded from the analyses of carabid beetle traits.

Species traits

For each insect group, three species traits associated with dispersal capacity, habitat or diet specialization and life cycle timing were selected. These traits were selected because they have been shown to be key determinants modifying insects' responses to agricultural land use (Börschig et al., 2013; Gámez-Virués et al., 2015; Kőrösi et al., 2022; Toivonen et al., 2016) and because previously published measures of these traits were available for all three insect groups.

Butterfly species traits were wingspan (as a measure of dispersal capacity; Kuussaari et al., 2014; Sekar, 2012), adult habitat breadth and overwintering stage. The average wingspan of females was based on Marttila et al. (1990). Adult habitat breadth (an inverse measure of habitat specialization) was expressed as the number of habitat types occupied by adult butterflies, as in Komonen et al. (2004). Overwintering stage (Marttila et al., 1990) was an ordinal variable describing the development stage and ranging from 1 (egg) to 4 (adult).

Bumblebee species traits were body size (a measure of dispersal capacity; Greenleaf et al., 2007), tongue length (a measure of diet specialization; Goulson & Darvill, 2004) and spring emergence time. Body size, measured as the average body length of females (from the front edge of the head to the tip of the abdomen), was based on Söderman and Leinonen (2003), supplemented by Scheuchl and Willner (2016) for some species. Tongue length was according to Ranta and Lundberg (1980) and Goulson et al. (2005, 2008). Spring emergence time of queens (Scheuchl & Willner, 2016; Söderman & Leinonen, 2003) was expressed as month and it ranged from 4 (April) to 6 (June).

Carabid beetle species traits were flight ability, feeding preference and overwintering stage. All three traits were categorical with two levels. The categorization of species was according to Hanson et al. (2016), supplemented by information from Lindroth (1985, 1986). Species with no or reduced wings, dimorphic species and those for which flight observations are missing or rare, were classified as poor flyers, while the species with fully developed wings and documented flight ability were classified as good flyers. Based on feeding preference, carabid beetles were divided into species with mainly carnivorous diet and those with omnivorous or herbivorous diets. Furthermore, the species were grouped into those overwintering in adult stage and those overwintering in larval stage.

Statistical analyses

Prior to statistical analyses, insect observations of each field were pooled over the season (five transect counts for butterflies and bumblebees and two trapping periods for carabid beetles) and the locations within the field (two transects for butterflies and bumblebees and three traps for carabid beetles). The pooled abundance data were used to calculate community trait values for each field. For butterflies and bumblebees, the trait values of individuals observed on a field were averaged to get the community-weighted mean for the field (following, e.g., Kuussaari et al., 2021; Toivonen et al., 2016). For carabid beetles, the proportions of individuals in the groups of poor dispersers, carnivores and adult hibernators were calculated for each field.

The effects of crop type and production method on the community trait values were analysed using generalized linear mixed models. The response variables were the mean wingspan, adult habitat breadth and overwintering stage of butterflies; the mean body size, tongue length and spring emergence time of bumblebees and the logit-transformed proportions of carabid beetles in the groups of poor dispersers, carnivores and adult hibernators. The models were fitted using the glmmTMB function of the R package *glmmTMB* (Brooks et al., 2017) with Gaussian error distribution.

Two types of models were fitted. Firstly, to analyse the effects of crop type on the insect traits, all eight crop types were compared using models with crop type as a fixed factor, the percentage cover of arable land in the landscape as a covariate and farm as a random factor. For the percentage cover of arable land, the radius of 250 m was used for butterflies and carabid beetles and the radius of 500 m for bumblebees. The landscape variables were selected by comparing the correlations of species richness and abundance of the insect groups with arable land and forest covers within four landscape radii (100, 250, 500 and 1000 m; Toivonen et al., 2022). For each insect group, a landscape variable with the highest correlation with species richness and/or abundance was used in the analyses.

Secondly, the effects of production method and the interaction effects of production method and crop type on the insect traits were analysed using models with crop type, production method and their interaction as fixed factors, arable land cover as a covariate and farm as a random factor. These models were fitted to data from five crop types: oat, rye, faba bean, grass ley and arable pasture. For oilseeds and cabbage, the production methods could not be compared because only three organic oilseed fields and no organic cabbage fields were studied. Fallows were excluded because the management of long-term fallows is not affected by the production method.

The residuals for the models were checked using simulateResiduals() function of the *DHARMa* package (Hartig, 2020). Due to residual heteroscedasticity in the model predicting bumblebee tongue length with crop type, ln-transformed values of tongue length were used in that model. Type II Wald χ^2 tests with the function Anova() of the R package *car* (Fox & Weisberg, 2019) were used to test the statistical significance of the parameters in the models. If the landscape variable of arable land cover had no statistically significant effect, it was removed from the model. In case of non-significant interaction of production method and crop type, the interaction effect was removed, and the final model included production method and crop type as single factors. Values of $p < 0.05$ were considered statistically significant. The sequential Bonferroni correction was not used to control the Type I errors due to the multiple tests, as it substantially increases the risk of Type II errors (Moran, 2003). Where a significant effect of crop type or a significant interaction effect of production method and crop type was found, post-hoc pairwise comparisons with

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Tukey *p*-value adjustment for multiple comparisons were conducted using emmeans() function of the package *emmeans* (Lenth, 2021) to determine which crop types or crop type production method combinations differed from each other.

RESULTS

The insect data used to calculate the community trait values consisted of 559 butterflies representing 27 species (Table S1), 835 bumblebees representing 15 species (Table S2) and 4208 carabid beetles representing 63 species (Table S3). Several functional traits of the studied insect communities in the study fields were correlated with each other based on the community-weighted mean values (Table S4): Large mean wingspan of butterflies was associated with butterfly overwintering in advanced development stages (adult or pupa). For bumblebees, late mean emergence time was associated with long mean tongue length and small body size. For carabid beetles, the proportion of poor flyers was positively correlated with the proportion of carnivores and negatively correlated with the proportion of adult hibernators.

Effect of crop type

Crop type affected the measured species traits of the studied insect communities except bumblebee size and the overwintering stage of carabid beetles (Table S5). The mean wingspan of butterflies was shortest in fallows and longest in rye and faba bean fields (Figure 1a). Adult habitat breadth of butterflies was narrowest in fallows and pastures and broadest in oilseed and cabbage fields (Figure 1b). Fallows had the highest share of butterflies overwintering in early development stages (Figure 1c).

The mean tongue length of bumblebees was longest in oat and fallow fields and shortest in oilseed and rye fields (Figure 2b). The mean emergence time of bumblebee queens was earliest in oilseed fields and latest in fallows (Figure 2c).

The proportions of carabid beetles with poor flight ability and carnivorous diet were highest in leys and fallows and lowest in cabbage fields (Figure 3a,b). Pastures did not significantly differ from leys and fallows in these traits (Figure 3a,b).

The cover of arable land in the surrounding landscape was significantly related to bumblebee size, the flight ability and diet of carabid beetles (Table S5). The mean size of bumblebees increased with increasing arable land cover in the 500 m buffer (Figure 4). For carabid beetles, the proportion of poor flyers and carnivores decreased with increasing arable land cover in the 250 m buffer (Figure 4).

Effects of production method and the interaction of production method and crop type

The overwintering stage of carabid beetles differed between the production methods (Table S6). The proportion of adult hibernators was higher in organically than in conventionally managed fields (Figure 5).

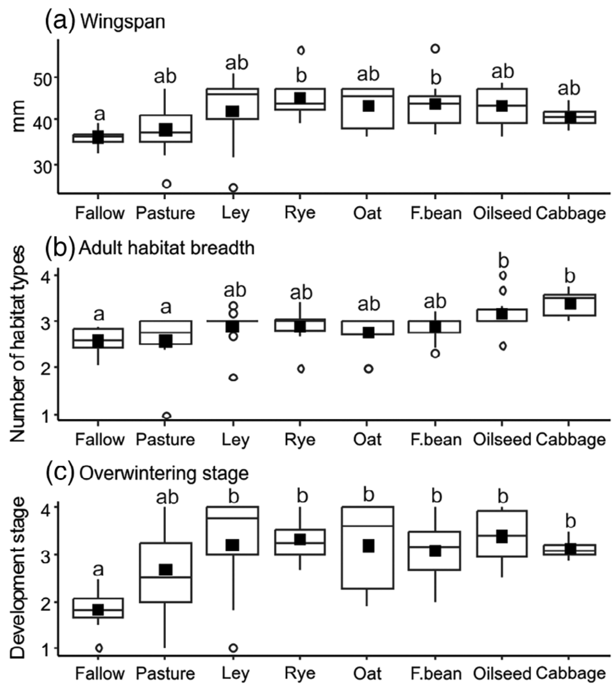

FIGURE 1 Wingspan (a), adult habitat breadth (b) and overwintering stage (c) of butterflies in eight crop types. Overwintering stages were 1 = egg, 2 = larva, 3 = pupa and 4 = adult. Statistically significant differences between the crop types in post-hoc tests ($p < 0.05$) are indicated by different letters. Mean values are indicated by black squares. The boxes display median values and upper and lower quartiles, with whiskers extending to minimum and maximum values within 1.5 times the interquartile range. Outliers are shown as circles.

Interaction between crop type and production method affected the studied species traits except butterfly habitat breadth, carabid beetle diet and overwintering stage (Table S6). For the wingspan and overwintering stage of butterflies, post-hoc pairwise tests found no significant difference between the crop type-production method combinations due to the *p*-value adjustment for multiple comparisons. On average, the wingspan of butterflies was shorter, and the proportional abundance of species overwintering as egg or larva was higher in organically managed oat fields than in conventional oat fields (Figure 6a,b). In the other crop types, differences between the production methods were small or non-existent (Figure 6a,b).

The mean size of bumblebees was largest in organic rye fields and lowest in organic ley, oat and faba bean fields (Figure 6c). The mean tongue length of bumblebees was longest in organic oat fields (Figure 6d). For the emergence time of bumblebee queens, post-hoc pairwise tests found no significant difference between the crop type production method combinations. On average, the emergence time of bumblebee queens was latest in organically managed pastures (Figure 6e).

The proportion of carabid beetles with poor flight ability was highest in conventionally managed leys and lowest in oat fields, conventional pastures and organic rye and faba bean fields (Figure 6f).

The cover of arable land in the surrounding landscape was significantly related to the wingspan and adult habitat breadth of butterflies

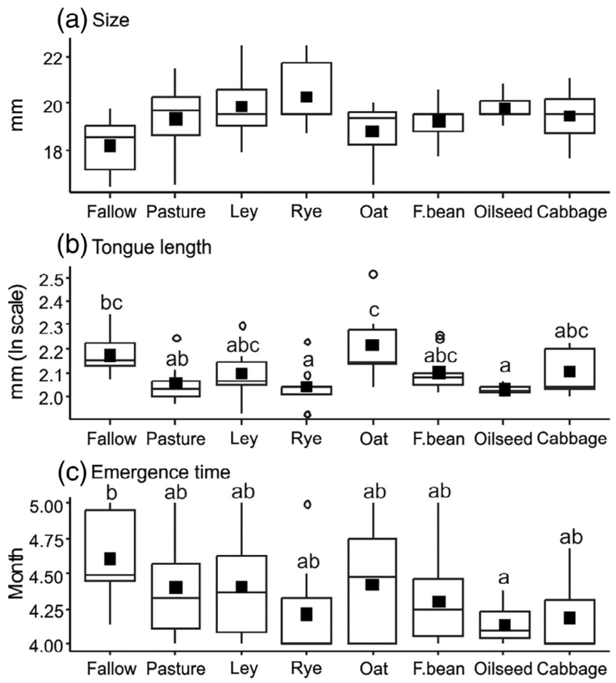

FIGURE 2 Size (a), tongue length (b) and spring emergence time (c) of bumblebees in eight crop types. Emergence time was expressed as month number and ranged from April (4) to June (6). Statistically significant differences between the crop types in post-hoc tests are indicated by different letters. Mean values are indicated by black squares. For description of boxplot features, see Figure 1 legend.

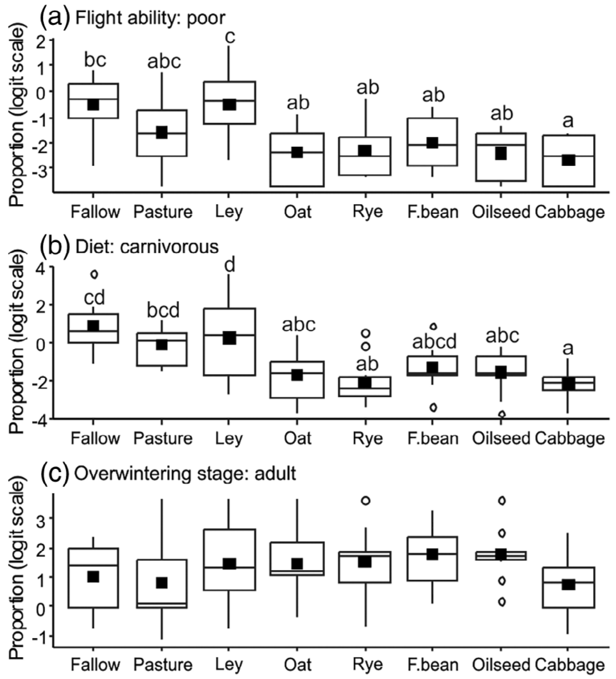

FIGURE 3 The logit-scaled proportion of carabid beetles with poor flight ability (a), carnivorous diet (b) and overwintering as adult (c) in eight crop types. Statistically significant differences between the crop types in post-hoc tests are indicated by different letters. Mean values are indicated by black squares. For description of boxplot features, see Figure 1 legend.

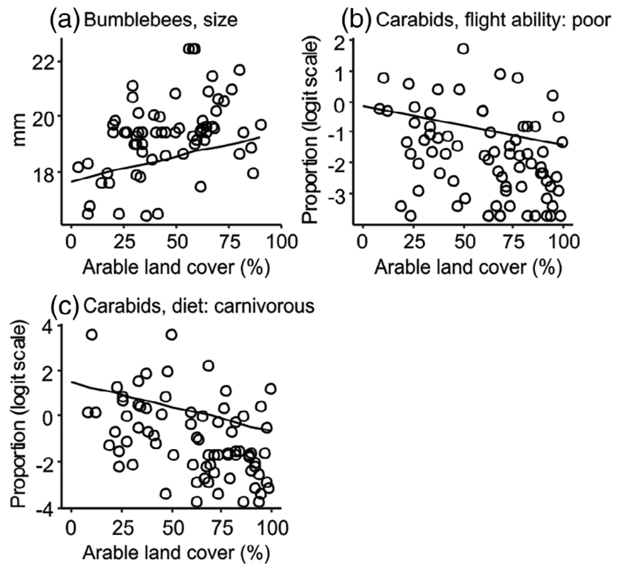

FIGURE 4 Bumblebee size (a) and the proportion of carabid beetles with poor flight ability (b) and carnivorous diet (c) in relation to arable land cover within 500 m radius (bumblebees) or 250 m radius (carabid beetles). Lines depict predicted values based on the models with all crop types and arable land cover as a statistically significant covariate (Table S5).

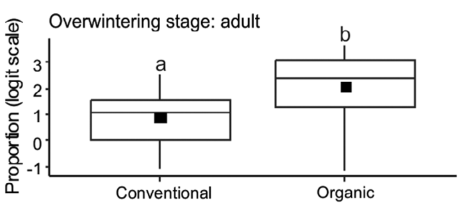

FIGURE 5 The logit-scaled proportion of carabid beetles overwintering as adult in conventionally and organically managed fields. Statistically significant differences are indicated by different letters. Mean values are indicated by black squares. For description of boxplot features, see Figure 1 legend.

and the flight ability and diet of carabid beetles (Table S6). With increasing arable land cover in the 250 m buffer, the mean wingspan and habitat breadth of butterflies increased, and the proportion of carabid beetles with poor flying ability and carnivorous diet decreased (Figure 7).

DISCUSSION

Our results showed that crop type has an important role in shaping the functional trait composition of insect communities on arable land. Despite a wide array of research conducted on the influence of agricultural land use on insect traits, few earlier studies have focused on the effects of crop types (but see Eyre et al., 2013). One reason for this gap may lie in the emphasis of previous research on the effects of agricultural management intensity

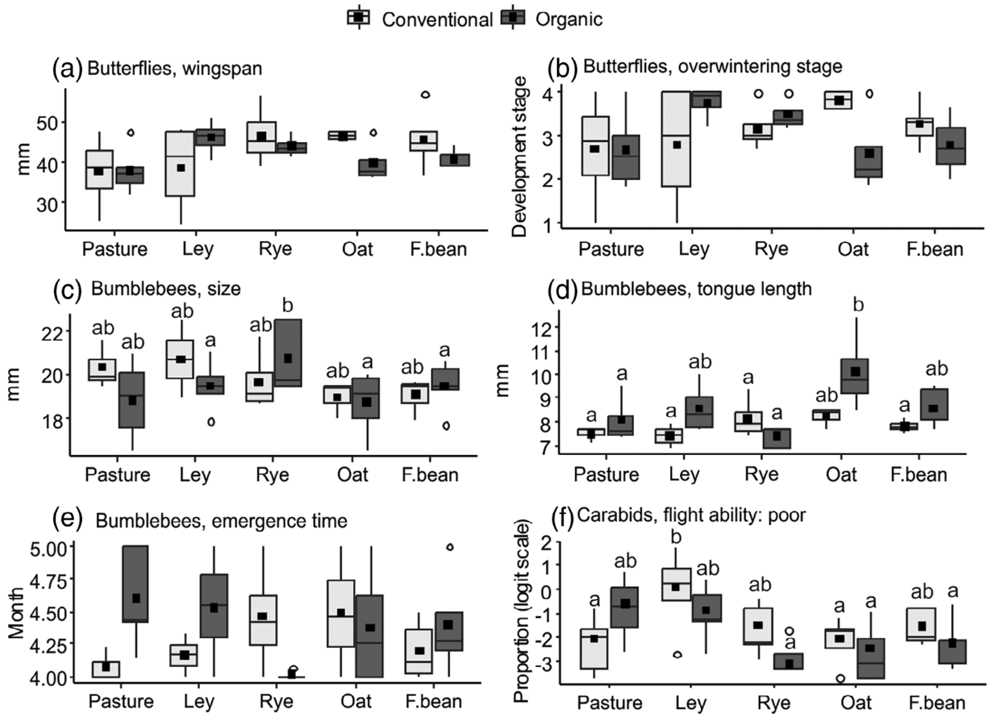

FIGURE 6 Butterfly wingspan (a) and overwintering stage (b); bumblebee size (c), tongue length (d) and spring emergence time (e) and the logit-scaled proportion of carabid beetles with poor flight ability (f) in five crop types under conventional and organic production. Butterfly overwintering stages were 1 = egg, 2 = larva, 3 = pupa and 4 = adult. Bumblebee emergence time was expressed as month number and ranged from April (4) to June (6). Statistically significant differences between the groups in post-hoc tests are indicated by different letters. Mean values are indicated by black squares. For description of boxplot features, see Figure 1 legend.

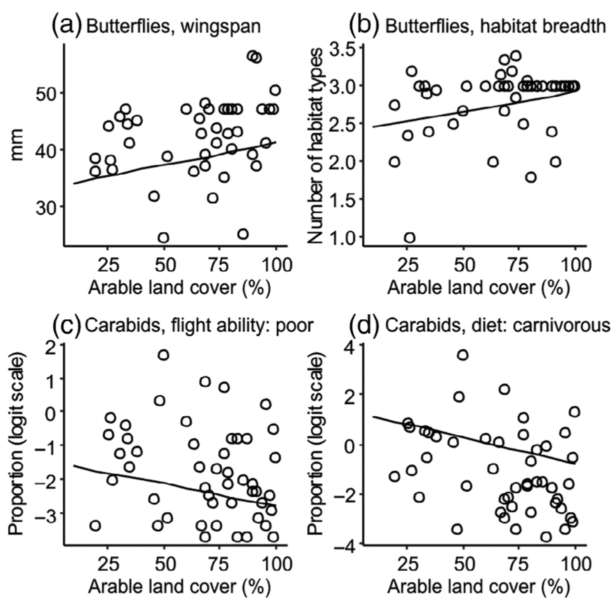

FIGURE 7 Wingspan (a) and adult habitat breadth (b) of butterflies, and the proportion of carabid beetles with poor flight ability (c) and with carnivorous diet (d) in relation to arable land cover within 250 m radius. Lines depict predicted values based on the models without oilseed, cabbage and fallow fields, and with arable land cover as a statistically significant covariate (Table S6).

instead of crop type, resulting in many studies reporting functional traits to modify insects' responses to changes in agricultural intensity (Hanson et al., 2016; Rader et al., 2014; Rusch et al., 2013). However, changes in management intensity are usually associated with changes in crop type, and thus, the effects of the two can easily be confounded with each other.

Importance of fallows for insect functional diversity

Among the studied crop types, long-term fallows had the most distinct trait composition of insect communities. Fallows promoted poor dispersers, habitat and diet specialist species, and species of which life cycle timing was not typical to cultivated fields. This strengthens the evidence that long-term fallows have an important role in protecting not only taxonomic but also functional diversity of insects on arable land (Alanen et al., 2011; Feng et al., 2021; Toivonen et al., 2016), similarly to other extensive grasslands (Börschig et al., 2013). To fully understand the contribution of fallows to insect conservation and insect-driven ecosystem services, more studies on functional trait differences between fallows and cultivated fields are needed. For example, in our study fields, the species richness of bumblebees did not differ between oilseed fields and fallows (Toivonen et al., 2022). However, oilseed fields were strongly dominated by short-tongued and early emerging species, whereas fallows harboured more long-tongued and late-emerging species. The latter are of special conservation interest due to their documented declines in several countries (Bommarco et al., 2012; Dupont et al., 2011; Goulson et al., 2005). Furthermore, the loss of long-tongued species may reduce pollination success of flowers with long corollas with negative implications for the yields of certain crops (Bommarco et al., 2012).

The differences between fallows and the other crop types in the functional traits of butterfly and bumblebee communities can be explained by several reasons. Relatively high plant diversity in fallows (Toivonen et al., 2022) supported the diversity of floral resources and butterfly larval host plants, which, along with the longevity of sward and the low level of disturbance, allowed species with narrow diet or habitat specialization and poor dispersal capacity to colonize and persist. For dispersal capacity, the differences between the crop types were found for butterflies but not for bumblebees. Bumblebees are relatively mobile central place foragers, which can efficiently find rewarding floral resources in the landscape around their nest, as far as the resources are within their foraging range (Osborne et al., 2008). Many butterfly species, instead, are relatively sedentary, and thus, more dependent on permanent and long-term habitats (Alanen et al., 2011; Toivonen et al., 2016). The overwintering stage of butterflies was coupled with dispersal capacity: species overwintering in advanced development stages had, in average, larger wingspan than species overwintering in earlier stages. In addition, species overwintering as egg or larvae spend a relatively long time from autumn to spring in stages with very limited mobility and high vulnerability to habitat disturbances (Kőrösi et al., 2022). This may explain the high proportion of species overwintering in early development stages in fallows compared to most other crop types, even perennial leys.

For bumblebees, fallows probably provided a relatively good availability of nesting sites and floral resources throughout the season. These resources are most critical for late-emerging bumblebee species that, compared to early species, have harder to find free nesting sites and suffer more from the scarcity of mid- and late-season flower resources in contemporary agricultural landscapes (Blasi et al., 2023; Fitzpatrick et al., 2007; Persson et al., 2015). Besides, fallows in our study were rich in Fabaceae, such as *Lathyrys pratensis* L., *Vicia* sp. and *Trifolium* sp., which are important pollen and nectar sources for bumblebees and, in particular, for late-emerging and long-tongued species (Goulson et al., 2005).

In our study, fallows were situated in landscapes with higher forest cover and lower arable land cover than the other crop types. Due to the landscape difference, it is not possible to reliably distinguish the effect of fallow from the effect of forested landscape. For example, grassland butterflies with poor dispersal capacity and narrow habitat breadth have been reported to benefit from forest matrix (Berg et al., 2011; Öckinger et al., 2012; Toivonen et al., 2017). However, our results show that long-term fallows, as they are typically located in our region, are highly valuable for insect functional diversity on arable land.

Differing effects of annual and perennial crops on insect functional traits

Among actual crop fields, long-tongued bumblebees were proportionally most abundant in organic oat fields. This can be explained by the occurrence of flowering weeds with long corolla, such as *Galeopsis* sp. and *Vicia* sp. in some of these fields in late summer (Toivonen et al., 2022). In organic pastures and leys, the proportional abundance of late-emerging bumblebee species tended to be high, which may be due to the occurrence, and sometimes abundance, of clovers and other legumes with long flowering periods in these fields. The results corroborate the importance of maintaining weeds at tolerable levels (Nicholls & Altieri, 2013) and growing legumes (Bommarco et al., 2012; Dupont et al., 2011; Goulson et al., 2005) for maintaining bumblebee diversity on arable land.

The functional traits of carabid beetle communities were more affected by the perenniality of the sward than any specific crop type. Besides long-term fallows, pastures and leys promoted species with poor flight ability and carnivorous diet, whereas annual crops were dominated by good flyers, omnivores and herbivores. Carabid beetles have generally lower dispersal capacity than bees and butterflies. Flightless species can move a few hundreds of meters by walking but dispersal over longer distances requires flying (den Boer, 1990). Therefore, it can be expected that the occurrence of carabid beetles in such ephemeral habitats as annual crops is restricted by species-specific flight ability. However, the results of previous studies on the effects of management intensity, or associated crop type, on carabid beetles with different flight abilities have been mixed. Ribera et al. (2001) reported higher frequency of long-winged species with increasing land use intensity, whereas Rusch et al. (2013) showed that the mitigation of agricultural intensification increased the proportion of species with good flight ability, and Hanson et al. (2016) found higher proportion of good flyers in perennial grasslands than in winter wheat and sugar beet fields. The differences between the studies may stem from differences in landscape composition, and in particular, the cover of grasslands. The share of carabid beetles with good flight ability increases in grasslands with grassland fragmentation, and thus, isolated grasslands are dominated by good flyers (Hanson et al., 2016; Hendrickx et al., 2009). In our study region, landscapes are relatively rich in perennial grasslands, fallows and field margins, which probably allowed poor dispersers to persist in grasslands.

The high proportion of carabid beetles with carnivorous diet in the perennial crop types contrasts with some previous studies that have reported carnivores to be proportionally more common in annual crops than in perennial grasslands and grassy field margins (Birkhofer et al., 2014; Hanson et al., 2016; but see Eyre et al., 2013). Furthermore, in an earlier study in Finland, perennial fallows were characterized by a high number of individuals of the genus *Amara*, which are predominantly herbivorous (Kinnunen & Tiainen, 1999). The differences between the studies are likely to reflect variation in the availability of food resources for carabid beetles within crop types. Annual crops can offer ample prey in the form of arthropod pests such as aphids, which can attract a high number of predatory carabid beetles to the fields (Holland et al., 2004; Knapp et al., 2019). If the sampling of carabid beetles coincides with high pest abundance (as in Birkhofer et al., 2014), carnivores may be particularly abundant. Similarly, weeds increase the availability of plant-derived food resources for herbivores and omnivores (Diehl et al., 2012). In our study, 65% of the annual crop fields were managed without chemical weed control, and 19% were undersown with grass-clover mixtures, sometimes supplemented with other annual and/or perennial plants. The relatively high plant diversity in the annual crop types probably increased the abundance of carabid beetles with omnivorous and herbivorous diets. Dietary traits of carabid beetle communities have implications for pest and weed control. From pest control perspective, supporting carnivores in annual crop types is important, as annual crops are typically associated with higher pest damage than perennial crops. This could be done by creating perennial habitats next to annual crops, for example, by widening field margins or creating in-field perennial strips (Kromp, 1999; Toivonen et al., 2018).

The overwintering stage of carabid beetles did not differ between perennial and annual crop types. Based on earlier studies, adult hibernators may be more resistant to intensive land use and soil disturbance than species overwintering in their larval form (Kinnunen & Tiainen, 1999; Müller et al., 2022; Ribera et al., 2001). However, tillage regime may be a more important determinant of overwintering success than crop perenniality: species vulnerable to conventional ploughing may tolerate reduced tillage and favour no-till systems (Müller et al., 2022). Tillage also modifies microclimate at soil surface. In spring and early summer, ploughed fields may provide suitable microclimate for breeding for adult hibernating species, which are mostly day-active and thermophilic (Hatten et al., 2007; Kinnunen & Tiainen, 1999). In our study, organically managed fields were mostly ploughed, whereas, in conventionally production, the main tillage method was reduced tillage. This possibly explains why adult hibernators were relatively more abundant in organically than in conventionally managed fields. The high proportion of adult hibernators may benefit pest control services in organic crop fields: adult hibernators are active in spring and early summer, when pest numbers are low, and thus, they can effectively prevent or delay the pest population growth (Welch & Harwood, 2014).

Our study focused on the effects of crop type and production method on dominant traits in insect communities. Besides dominant traits, functional diversity of the traits influences ecosystem resilience and ecosystem service provision (Greenop et al., 2018; Woodcock et al., 2019) and may also differ between crop types and production methods (Feng et al., 2021; Goded et al., 2019). On a landscape scale, increasing crop diversity, along with increasing the area of crop types with the most distinct trait composition, is likely to support functional diversity across insect taxa. Further studies comparing both dominant traits and trait diversity of insects across various crop types and production methods would contribute to our understanding of how arable land use changes affect insect conservation and ecosystem functioning.

Role of the surrounding landscape

Besides crop type and production method, surrounding landscape affected the functional traits of insect communities. Landscapes with low arable land cover supported poor dispersers as well as carnivorous carabid beetles and habitat specialist butterflies. This highlights the importance of non-arable habitats in the landscape in buffering insect communities, and especially poor-dispersing and specialist species, against the adverse effects of intensive arable farming (Gámez-Virués et al., 2015; Kőrösi et al., 2022; Tscharntke et al., 2005). Landscapes with low arable land cover supported largely similar traits as long-term fallows, suggesting that the lack of non-arable habitats in intensively cultivated landscapes can be partly compensated by increasing fallow area.

CONCLUSIONS

Our study shows that crop choice affects functional trait compositions of butterfly, bumblebee and carabid beetle communities on boreal arable land, which has potential implications for pollination and pest control services. Long-term fallows harboured the most distinct insect communities, with high relative abundance of poor dispersers, specialist species and species with differing life cycle timing compared to cultivated fields. This shows the high value of long-term fallows in conserving functional diversity of insects on boreal arable land. Among cultivated fields, annual and perennial crops differed from each other especially in terms of functional traits of carabid beetle communities. However, differences between the results of this and previous studies suggest that the effects of agricultural management on carabid beetle communities are strongly context-dependent. The effects of production method were less clear than those of crop type. Still, certain management practices that are influenced by, yet not entirely tied to production method, such as ploughing, sowing legumes in grasslands or refraining from the use of herbicides, probably affect functional traits of insect communities. To promote insect species sensitive to agricultural disturbances and land use changes, and their associated ecosystem services, it is recommended to increase the area of long-term fallows and perennial crops and enhance within-field plant diversity while maintaining landscape heterogeneity.

AUTHOR CONTRIBUTIONS

Marjaana Toivonen: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; visualization; writing – original draft. **Erja Huusela:** Conceptualization; funding acquisition; investigation; methodology; writing – review and editing. **Terho Hyvönen:** Conceptualization; funding acquisition; investigation; methodology; writing – review and editing. **Ari Järvinen:** Investigation; writing – review and editing. **Mikko Kuussaari:** Conceptualization; funding acquisition; methodology; project administration; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study is available in the Knowledge Network for Biocomplexity (KNB) Data Repository at https://doi.org/10.5063/F11N7ZK5.

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SUPPORTING INFORMATION

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

Table S1. The list of butterfly species observed in 78 fields, their functional traits and the number of individuals.

Table S2. The list of bumblebee species observed in 78 fields, their functional traits and the number of individuals.

Table S3. The list of carabid beetle species sampled in 75 fields, their functional traits and the number of individuals.

Table S4. Correlations between the functional traits of bumblebee, butterfly and carabid beetle communities in 78 study fields. The correlations were calculated using community-weighted means for the fields. Missing values were replaced by the mean of the non-missing values of the respective trait. In the trait names, 'B' refer to bumblebee traits, 'L' to butterfly traits and 'C' to carabid beetle traits. Statistically significant correlations ($p < 0.05$) are bolded.

Table S5. χ^2 test results, and marginal and conditional R^2 for the models with all crop types included.

Table S6. χ^2 test results, and marginal and conditional R^2 for the models without oilseed, cabbage and fallow fields.

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