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Rows make the field: Winter wheat fields with manipulated crop architecture show potential for ecological intensification based on higher natural pest and weed seed control

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ABSTRACT

Ecological intensification aims to reduce environmental costs of agricultural production by increasing biodiversity and using the associated ecosystem services instead of, or in combination with, external inputs, so that yields are maintained at high levels or increased. However, to date there are few measures available for which such benefits have already been demonstrated in the field.

In this study, the seeding pattern in winter wheat fields was manipulated to create a diversified crop architecture consisting of 'unsown-rows' and 'densely-sown-rows' in treatment fields in comparison to 'conventionally-sown-rows' in control fields to assess whether (i) in-field structural and microclimatic conditions are more heterogeneous in fields with manipulated crop architecture compared to conventionally managed fields, (ii) a change in crop architecture is related to higher species richness, activity density and altered body size distribution of carabid communities, (iii) this in turn increases natural pest and weed seed control, but (iv) does not lead to yield loss.

In-field structural and microclimatic conditions were more heterogeneous in treatment fields compared to control fields, which was associated with significantly increased body sizes of predatory carabids and a trend for increased predatory carabid species richness (in the 'unsown-rows' of treatment fields). These changes were related to significantly stronger pest suppression in the 'densely-sown-rows' of treatment fields compared to 'conventionally-sown-rows' in control fields, with 10 % higher experimental pest predation rates and 56 % reduced crop damage caused by cereal leaf beetles. Moreover, carabids known to consume weed seeds showed significantly higher activity densities in 'unsown-rows' compared to 'conventionally-sown-rows', which was related to significantly higher experimental weed seed predation in 'densely-sown-rows'. Wheat yields were not significantly different in fields with or without manipulated crop architecture.

The results suggest that the simple measure of manipulating the seeding pattern in winter wheat fields creates a diversified crop architecture, thereby promoting carabid diversity and altering their community composition and activity density such that important ecosystem services are increased without yield losses. Thus, beyond fostering biodiversity, this measure has, although not directly tested here, the potential for being used for ecological replacement of pesticides through enhanced ecosystem services without entailing agronomic and economic disadvantages such as land opportunity costs or increased workload.

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1. Introduction

Globally, intensive agriculture threatens farmland biodiversity and biodiversity-associated ecosystem services (Foley et al., 2005). One of the main drivers are external inputs, such as fertilizers or pesticides, which are used to increase yield or avoid yield loss, but which have detrimental effects on biodiversity (Tilman et al., 2001; Kleijn et al., 2019). For example, pesticides have been shown to cause declines in non-target beetles (Lee et al., 2001), bees (Alston et al., 2007) and birds (Hart et al., 2006).

In particular, crop-dominated areas are characterized by high pesticide inputs (Hossard et al., 2014), with winter wheat fields accounting for more than 25 % in Europe (based on FAO statistics 2021). Thus, the development of sustainable alternatives to pesticides in such areas is among the major current challenges, also addressed in the EU Green Deal on pesticide reduction (EU Commission, 2019). Particularly challenging is to achieve this without reductions of overall crop production and yield, as the demand for agricultural products is steadily rising (Glamann et al., 2017). Organic farming, while mitigating many negative environmental impacts, is usually accompanied by yield losses and thus requires more land for the same production volume, which entails negative impacts on biodiversity and hence may not be sufficient to solve all these problems (Tscharntke et al., 2021).

In contrast, ecological intensification strives to minimize adverse environmental impacts and simultaneously meet the growing demands for farmland products (Bommarco et al., 2013). The concept aims to replace or complement external inputs with services delivered by biodiversity, such as substitution of pesticides by natural pest regulation through natural enemies. Based on the assumption that specific components of biodiversity can be managed and used to either increase productivity further (ecological enhancement) or to replace external inputs without negatively impacting productivity (ecological replacement), ecological intensification aims to lower environmental costs of agricultural production, such as negative impacts on biodiversity (Kleijn et al., 2019). Despite the growing number of studies targeting ecological intensification, to date there are few effective and easy applicable measures for ecological intensification available, of which benefits for biodiversity and associated ecosystem services have been demonstrated in the field (Bommarco et al., 2013; Lyu et al., 2021). Even fewer studies include yield assessments and consider the demands that measures place on farmers, making large-scale adoption difficult. Particularly, demonstrations of successful ecological intensification measures that promote biodiversity and associated natural pest control services in wheat production systems without significant negative agronomic or economic costs, remain scarce (but see Tschumi et al., 2016; Pywell et al., 2015).

One such management option might be the manipulation of crop architecture, i.e., specifically designed seeding patterns with different crop densities within the field, which result in an increased diversity of the crop architecture. According to the structural heterogeneity hypothesis (Tews et al., 2004), one might expect a bottom-up effect of such an increased diversity of the crop architecture on the diversity of higher trophic levels, such as arthropods, providing important ecosystem services such as pest control or weed seed predation (Kromp, 1999; Menalled et al., 2006). Species-specific habitat preferences of such beneficial arthropods may be better met in fields with higher structural heterogeneity and various microclimatic conditions. Consequently, composition of species' functional traits (e.g., body size) may be modified, with positive ramifications for pest control services, for example through higher *per capita* consumption of pests by larger natural enemies (Rouabah et al., 2014). Knowledge about effects of crop architecture on arthropod agrocoenoses, however, is limited to the recognition of different preferences of few species in few crops (Kromp, 1998; Honek and Jarosik, 2000). Thus, there is an applied research gap how higher field heterogeneity affects arthropod diversity and community composition, and the consequences of such altered metrics of community composition such as diversity, abundance, and body size distribution for the delivery of biological functions and ecosystem services.

Among beneficial arthropods, carabids are considered important natural enemies of pests, including predators of the larvae of cereal leaf beetles (Kromp, 1999; Meindl et al., 2001; Kheirodin et al., 2019), which are among the major cereal pests in Europe, Asia, and North America. Their larvae can cause substantial crop damage (Buntin et al., 2004) which is mainly counteracted with insecticides, the use of which might further increase in near future, since climate change promotes phenological mismatch between cereal leaf beetles and their parasitoid (Evans et al., 2013). Moreover, carabids are known to be important predators of weed seeds (Menalled, 2006). Thus, crop management promoting carabids without entailing agronomic and economic disadvantages could be a promising example of ecological replacement of pesticides by ecosystem services provided by carabids in winter wheat.

In this study, we thus tested whether a simple manipulation of the crop architecture (by keeping some sowing coulters closed at sowing, without reducing seed quantity and without further implications on conventional farming) results in more heterogeneous winter wheat fields with positive consequences for carabid biodiversity and pest and weed seed control without reducing yield. Thus, the aim was to test, whether the measure has, beyond biodiversity promotion, the potential for ecological intensification. Specifically, we hypothesized that 1) fields with manipulated crop architecture offer more heterogeneous structural and microclimatic conditions compared to conventionally managed fields, which 2) is related to higher diversity, activity density and altered body size distribution of carabid communities, and 3) increases ecosystem service provisioning (pest and weed seed control), without 4) leading to significant yield losses.

2. Methods

2.1. Study design

To examine the impact of altered crop architecture on carabid communities and the delivery of pest control and seed predation services, as well as effects on cereal leaf beetle densities and crop damage, a total of 38 winter wheat fields (pairs of 19 fields with and 19 fields without manipulated crop architecture) were experimentally established. Field experiments were conducted between April and July in 2019 and 2020. The 19 conventionally managed winter wheat field pairs (six in 2019, 13 in 2020) were selected in intensively used agricultural landscapes in the Swiss lowlands. Each pair was close to one another, and experienced similar abiotic and environmental conditions (e.g., soil type, water table, climatic conditions, and surrounding landscape composition). However, it was not possible to also control for the wheat variety within a pair. Crop management (preceding crop in the rotation, soil cultivation, fertilization, and application of fungicides, herbicides, and growth regulators; no application of insecticides) was similar but differed in crop architecture, i.e., seeding pattern. One winter wheat field in each pair served as control with all sowing coulters remaining open during sowing, resulting in a homogeneous seeding pattern typical of conventionally grown wheat crops in central Europe with row spacings slightly varying between 12.5 and 16.6 cm depending on the seed drill (Abichou et al., 2019). The other winter wheat field in a pair represented the altered crop architecture treatment, where the seeding pattern was manipulated by closing two or three sowing coulters, depending on the seed drill and given row spacing, per 4 m working width without reducing seed rate, e.g., for a row spacing of 12.5 cm: 29 sown rows followed by three unsown ones and so on; or e.g., for a row spacing of 16.6 cm: 22 sown rows followed by two unsown ones and so on. Thus, the manipulated crop architecture created included both 'unsown-rows' that remained unsown (where sowing coulters have been closed) and 'densely-sown-rows' (where sowing coulters have been open) that were sown slightly more densely as seed rates in treatment areas were not changed (400 seeds m-2) and thus the leftover seeds from the 'unsown-rows' were distributed to these areas (Fig. 1A). Field size

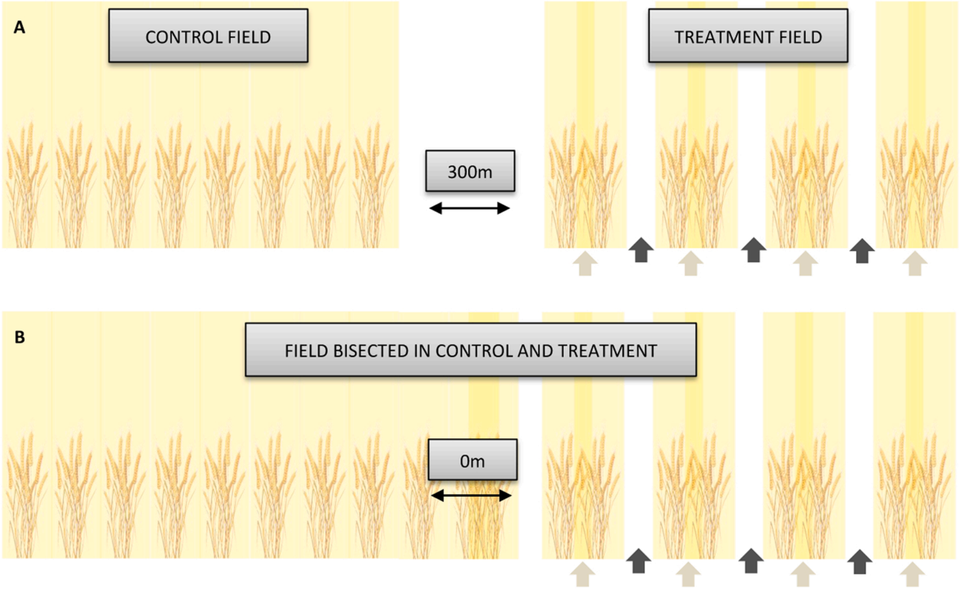

Fig. 1. Schematic illustration of winter wheat seeding patterns with and without manipulated crop architecture. In the control areas (left), all sowing coulters were open, resulting in a regular seeding pattern of 'conventional-rows'. In the treatment areas (right), the seeding pattern was manipulated by closing two or three sowing coulters per 4 m working width without reducing the seed rate. Thus, the manipulated crop architecture created included both 'unsown-rows' that remained unsown (where sowing coulters have been closed) and 'densely-sown-rows' (where sowing coulters have been open). Dark arrows point to 'unsown-rows' and light arrows point to 'densely-sown-rows' in treatment fields. Row spacing for both control and treatment areas was between 12.5 and 16.6 cm, depending on the seed drill, which corresponds to the standard row spacing of conventionally grown wheat crops in central Europe (Abichou et al., 2019). **(A) Independent control and treatment fields.** To avoid spillover effects of mobile organisms, control and treatment fields of a pair were established with a minimum distance of 300 m from each other. All assessments concerning mobile organisms (i.e., carabid pitfall sampling, predation experiments, pest level and crop damage observation) and the according microclimatic and structural measurements were conducted on such independent control and treatment fields. **(B) Bisected fields (one half with the control-seeding pattern, one half with the treatment-seeding pattern).** To avoid factors influencing yields other than the seeding pattern, control and treatment areas of a pair were established on the same field for yield measurements.

was 4.93 ha (± 3.36 ha) on average and the minimum distance between fields of field pairs was 300 m to guarantee independence of sites (mean ± s.e.: 733 ± 482 m), except for six field pairs where similarity of fields in pairs was favored over a minimum distance. Experiments were conducted in three plot types ('unsown-rows' and 'densely-sown-rows' in treatment fields; 'conventionally-sown-rows' in control fields), and in the center of fields to avoid edge effects.

A slightly different design was used to assess effects of altered crop architecture on yields. Yields of wheat production under the two different crop architecture types were assessed on 17 different fields. In one half of each field the manipulated wheat architecture was established (treatment), while the other half had the conventional architecture (control) (Fig. 1B), with both halves of the field forming a pair. These fields were established between 2017 and 2021 in the same study region with same management as above, except that the wheat variety within a pair was the same here (but still differed between pairs). Field size was 15.48 ha (± 4.90 ha) on average. Yield assessment was conducted in two plot types (treatment areas with 'unsown-rows' and 'densely-sown-rows'; control areas with 'conventionally-sown-rows').

The reason for studying impacts of crop architecture on yield within the same field was to minimize factors that may vary across different field sites and may influence yield other than crop architecture (e.g., nutrient and water availability, wheat variety etc.). The reason for studying the effects of crop architecture on carabids and the delivery of pest control and seed predation services on different fields, keeping a minimum distance between treatment and control fields, was to minimize potential exchange of carabids and other mobile arthropods and thus potential spillover effects between treatment and control fields.

2.2. Assessing microclimatic and structural characteristics of fields

To test whether fields with manipulated crop architecture showed different microclimatic and structural characteristics, leading to higher heterogeneity within fields (hypothesis 1), temperature, moisture and vegetation data were collected.

Temperature and moisture loggers (TMS-4, TOMST, Prague, Czechia) were installed in each of the three plot types in the 13 field pairs in 2020. Loggers provided microclimatic measurements by simultaneously measuring soil moisture (6 cm below the soil surface) and soil surface temperature (2 cm above the soil surface) every 15 min between April and July (Wild et al., 2019).

Vegetation structure was measured by assessing wheat density once a month between April and July in 2019 and 2020 in each field of the 19 pairs. Four sub-plots of 0.2 × 2.5 m plots were established in every plot type of every field and the percentage cover of wheat was assessed visually.

2.3. Sampling of natural enemies

To test whether manipulation of crop architecture translated into altered activity density, species richness and body size distribution of carabid beetle communities (hypothesis 2), carabids were sampled in treatment and control fields using pitfall traps (two pitfall traps in each plot type per field; 10 cm funnel diameter; 70 % ethanol, minimum distance of 10 m between each trap). Pitfall sampling was run during four sampling rounds of one week each from beginning of April to beginning of July in 2019 and 2020. One trap per plot type, field, and round was analyzed. Adult carabid individuals were identified to species level and characterized according to body size and trophic level (carnivorous, omnivorous, or phytophagous) from literature (detailed information in Table S1). Trophic levels were used to form guilds relevant for each type of natural control studied, i.e., carnivorous-omnivorous guild for pest control, phytophagous-omnivorous guild for weed seed control.

2.4. Measuring natural pest and weed seed control using surrogate prey

Surrogate prey items (i.e., sentinels) were used to measure predation rates in treatment and control fields in 2020, following a standardized QuESSA (http://www.quessa.eu/) protocol (Holland et al., 2017). Two experiments, a pest predation experiment (using insect sentinel prey) and a weed seed predation experiment (using seed sentinel prey), were conducted to collect data on natural pest and weed seed control under manipulated and non-manipulated crop architecture (hypothesis 3) and to disentangle processes shaping interactions between carabid community metrics (activity density, species richness, body size distribution) and their role as providers of pest and weed seed predators.

2.4.1. *Pest predation experiment*

Larvae of the bluebottle fly (*Calliphora vomitoria* L., Diptera) were selected because they fit the prey pattern of general predators (own observations) similar to cereal leaf beetle larvae (Kheirodin et al., 2020), but are easier to handle. Ten third instar bluebottle fly larvae were pinned (entomological pins, no. 1) alive on a 7.5 cm × 15 cm Styrofoam plate, forming a 'larval-plate'. Three 'larval-plates' were dug into the soil congruent with the soil surface in a transect of 3 m. Nails were used to secure the 'larval-plates' to the ground. In each plot type of each field two transects were set up. 'Larval-plates' were exposed for 12 h during day and night in late June and early July 2020 on 13 treatment and 13 control fields. Altogether, 9360 larvae were exposed (thirteen field pairs, three plot types (sampled twice), three 'larval-plates' with each ten larvae per transect, two daytimes, two repetitions). Partially or totally consumed prey items were recorded as predated directly in the field.

Concurrent with the exposure of the 'larval-plates', additional pitfall samples were collected within 1 m of each transect to assess the active carabid predator community for each transect. This allowed to relate activity density, species richness, and body size distribution to predation rates in each transect. Identification and characterization were identical to the procedure for weekly samples (see 2.3 *Sampling of natural enemies*). Only carnivorous and omnivorous carabids with minimum body sizes of 5.0 mm were considered as potential predators of bluebottle fly larvae in the analysis.

2.4.2. *Weed seed predation experiment*

Seed sentinels comprised *Capsella bursa-pastoris* (Brassicaceae, 0.1 mg per seed), *Tripleurospermum inodorum* (Asteraceae, 0.3 mg per seed), *Stellaria media* (Caryophyllaceae, 0.4 mg per seed), *Poa annua* (Poaceae, 0.4 mg per seed), and *Lamium purpureum* (Lamiaceae, 0.8 mg per seed). Those species are among the most important weeds in arable crops in the study region (Häni et al., 2008). Twenty of each seed species were randomly scattered and glued to 'seed-cards', made of firm sandpaper (4 cm × 9.5 cm, K80) sprayed with repositionable glue, modified after Brust and House (1988). 'Seed-cards' were buried ca. 5 mm below the soil surface and attached with nails to the ground. They were exposed for seven days during four sampling rounds between April and July 2020. Thus, 60 sample units (five species with 20 seeds each, three plot types (sampled once), four repetitions) were established in 13 treatment and control fields, using a total of 15,600 seeds. The collected 'seed-cards' were evaluated in the laboratory by counting the number of seeds removed per seed species with binoculars.

To assess the present seed predator community, 'seed-cards' were exposed congruent with weekly pitfall trap sampling (see 2.3 *Sampling of natural enemies*), in 1 m distance to pitfall traps. Carabid body size restricts potential seed prey since the size of a seed a carabid can grasp is mostly determined by the gape of its mandibles. Thus, body size limits the upper and lower limit of a seed a carabid can feed on (Forsythe, 1982; Honek et al., 2007). Therefore, only phytophagous and omnivorous carabids with body sizes between 2.5 and 8.0 mm were considered as potential predators of the seed species used in this experiment.

2.5. *Assessing cereal leaf beetle density and crop damage*

While the pest predation experiment allowed for controlled examination of surrogate pest control under different crop architectures, the assessment of cereal leaf beetle density and associated crop damage allowed to assess also natural pest (control) levels under non-experimental field conditions in fields with and without manipulated crop architecture, further supporting hypothesis 3.

While feeding of cereal leaf beetle adults on small young grain plants doesn't affect yield, cereal leaf beetle larvae eat long strips of parenchyma tissue skeletonizing the leaf decreasing the wheat plant's ability to photosynthesize, which can cause substantial crop damage (Buntin et al., 2004).

All cereal leaf beetle larvae of the flag leaves of 2 × 25 wheat tillers in each plot type (wheat plants adjacent to the 'unsown-rows' for 'unsown-rows') of each field were recorded three times during the peak of larval appearance (end of May/mid-June) known from literature (Schärer, 1994; Ihrig et al., 2001) in the 13 treatment and control fields in 2020. In the study year, however, cereal leaf beetle larvae developed earlier, thus only the first record was analyzed. Crop damage caused by cereal leaf beetle larvae was assessed from the flag leaf of the same 2 × 25 wheat tillers used for the sampling of cereal leaf beetle larvae in mid-June as percentage damage. Adult cereal leaf beetles were sampled once per plot type in early to mid-July on 13 and four treatment and control fields in 2020 and 2019, respectively, using standardized sweep netting (40 sweeps, 40 cm net diameter). Thus, the second generation of cereal leaf beetles that developed from larvae in early July was assessed, whose density reflected the overall impact of natural enemies on cereal leaf beetle eggs, larvae, and pupae.

2.6. *Assessing crop yields*

To collect data on yields under different crop architectures (hypothesis 4), yield surveys were conducted using combines equipped for yield mapping on the 17 fields between 2017 and 2021 (see 2.1 *Study design*). Homogenous zones were identified based on soil maps, yield maps and topographical characteristics of fields (Bobryk et al., 2016). According to the overlaying experimental design, neighboring sub-plots were assigned to the corresponding crop architecture design. Standardized mean values of grain yield (14.5 % H_2O) were calculated within each subplot using the program package of Quantum GIS ver. 3.14 (QGIS.org, 2022).

2.7. *Statistical analyses*

Generalized linear mixed models or linear mixed models, depending on error distribution of response variables were fitted. Generalized linear mixed models were checked for overdispersion by including an observation-level random factor (unique for each observation) in each model and comparing it to the original model, which was retained if it significantly improved the model. Model assumptions for Gaussian distributions were checked according to graphical validation procedures recommended by Zuur et al. (2009). All numerical explanatory variables were standardized prior to the analyses. Unique field IDs nested within unique field pair IDs were included as random factors in all models. Analyses were performed using R ver.4.0.2 (R Core Team, 2020).

For variables of ecological interest and their effects (microclimatic and structural characteristics of fields, natural enemies, predation of sentinels, cereal leaf beetle density and crop damage), the focus was on the three plot types ('conventionally-sown-rows' in control fields, 'unsown-rows' in treatment fields, 'densely-sown-rows' in treatment fields) to analyze local effects in plot types and to see how and with which effects these three areas formed different niches in the fields. Differences between 'conventionally-sown-rows' and 'unsown-rows', 'conventionally-sown-rows' and 'densely-sown-rows', respectively were used for conclusions. For yields, the whole treatment area (consisting of 'unsown-rows' and 'densely-sown-rows') was compared to the control area (consisting of conventionally-sown-rows) to gain relevant information on yield per ha.

Effects were defined as significant when $p < 0.05$ or marginally significant when $0.05 \leq p < 0.10$.

2.7.1. *Microclimatic and structural characteristics of fields*

To test whether treatment fields offered more heterogeneous structural and microclimatic conditions (hypothesis 1), data from TMS loggers and visually observed crop cover of the different plot types were compared.

Microclimatic conditions in fields with and without manipulated crop architecture were analyzed using soil moisture and temperature on the soil surface as separate response variables, assuming a Gaussian distribution. Temperature was log-transformed to achieve normally distributed residuals and avoid heteroscedasticity. Structural conditions were analyzed using crop cover as response variable, assuming a Gaussian distribution. Models included crop architecture (three levels: 'conventionally-sown-rows', 'unsown-rows', 'densely-sown-rows') as fixed factor. Point in time of data collection was nested in the established field pair/field ID random factor.

2.7.2. Natural enemies

To test whether crop architecture shaped natural enemy communities, it was analyzed how activity density, species richness and community weighted means of body size were influenced by crop architecture (hypothesis 2). Separate models for each mentioned response variable were fitted for the different predator communities: carnivorous-omnivorous carabids (relevant for pest control), phytophagous-omnivorous carabids (relevant for weed seed control). Generalized linear mixed models, assuming a Poisson distribution for activity density and species richness, and linear mixed models, assuming a Gaussian distribution, for community weighted means of body sizes were used. Models included crop architecture (three levels: 'conventionally-sown-rows', 'unsown-rows', 'densely-sown-rows') as fixed factor.

2.7.3. Predation of sentinel preys

The effect of crop architecture on the predation of sentinels was analyzed to test whether natural pest and weed seed control was increased in fields with manipulated crop architecture (hypothesis 3). Predated or non-predated bluebottle fly larvae and weed seeds, respectively, were used as binary response variable, assuming a Binomial distribution of data. Different descriptors of relevant carabid communities were included as explanatory variables in the models to better understand their role in predation events. Thus, the model for bluebottle fly-predation included crop architecture (three levels: 'conventionally-sown-rows', 'unsown-rows', 'densely-sown-rows') and daytime (two levels: day, night) as fixed factors, and activity density, species richness, and community weighted means of body sizes of carnivorous and omnivorous carabids with body sizes of at least 5.0 mm as continuous variables.

The model for weed seed-predation included crop architecture (three levels: 'conventionally-sown-rows', 'unsown-rows', 'densely-sown-rows') as fixed factor and activity density and species richness of phytophagous and omnivorous carabids with body sizes between 2.5 and 8.0 mm. Seed species was included as random factor.

Data on species richness, activity density and community weighted means were obtained from the associated pitfall trap sample of each 'larval-plate' and 'seed-card', respectively. Since the upper body sizes of potential weed seed predators were restricted, community weighted means of body sizes were included only for the pest predation experiment analysis.

2.7.4. Cereal leaf beetle density and crop damage

To test whether natural pest levels were reduced in fields with manipulated crop architecture (hypothesis 3), the effect of crop architecture on cereal leaf beetle larvae, the second generation of cereal leaf beetle adults and crop damage (each as separate response variable) was analyzed, assuming Poisson distribution of errors. Models included crop architecture (three levels: 'conventionally-sown-rows', 'unsown-rows', 'densely-sown-rows') as fixed factor.

2.7.5. Crop yields

The effect of crop architecture on yield (hypothesis 4) was analyzed using a model with Gaussian error distribution and treatment as fixed factor (two levels: control, treatment).

3. Results

3.1. Effect of crop architecture on microclimatic and structural conditions

Mean temperature on soil surface was significantly higher in 'unsown-rows' of treatment fields compared to 'conventionally-sown-rows' in control fields between April and July (5.9 % on average) but this didn't translate into significant changes in soil moisture. Crop cover was significantly lower in 'unsown-rows' compared to 'conventionally-sown-rows' within the same period (92.2 % on average). Microclimatic and structural conditions in the 'densely-sown-rows' and 'conventionally-sown-rows' were not significantly different from each other. See Table 1 for model summaries and Table S2 for mean ± se of raw data.

3.2. Effect of crop architecture on natural enemies

In fields with manipulated crop architecture, species richness of potential pest predators was marginally significantly higher in 'unsown-rows' by an average of 10.6 % compared to 'conventionally-sown-rows' in control fields (Fig. 2A), while activity density didn't differ significantly between the plot types in treatment and control fields. Body sizes of potential pest predators were on average 6.5 % larger in communities caught in 'unsown-rows' compared to 'conventionally-sown-rows' (significant; Fig. 2C). See Table 2 for model summaries and Table S3 for mean ± se of raw data.

Contrarily, activity density of potential seed predators was increased by an average of 45.5 % and 30.7 % in 'unsown-rows' (significant) and 'densely-sown-rows' (marginally significant), respectively, compared to 'conventionally-sown-rows' (Fig. 3A). Species richness of this guild was not affected significantly by crop architecture, but communities showed an averagely 13.9 % and 7.7 % increase in body size in 'unsown-rows' and 'densely-sown-rows' (both significant), respectively, compared to 'conventionally-sown-rows'. See Table 2 for model summaries and Table S3 for mean ± se of raw data.

3.3. Effect of crop architecture and carabid communities on natural control in pest and weed seed predation experiments

Pest predation was significantly increased in 'densely-sown-rows' of treatment fields by an average of 10.1 % compared to 'conventionally-sown-rows' of control fields (Fig. 4C). Predation rate was on average 5.0 % higher at night than during daytime (significant). Higher species richness (Fig. 2B), activity densities and body sizes (Fig. 2D) of predatory carabids with body sizes of at least 5.0 mm were significantly positively related to sentinel pest suppression. See Table 3 for model summaries and Table S4 for mean ± se of raw data.

Weed seed predation was also significantly increased in treatment fields in comparison to control fields, again significantly only in 'densely-sown-rows' (by 6.5 % on average; Fig. 4D). Species richness and activity density (Fig. 3B) of potential seed predators with body sizes between 2.5 and 8.0 mm had significantly positive effects on weed seed suppression. See Table 3 for model summaries and Table S4 for mean ± se of raw data.

3.4. Effect of crop architecture on cereal leaf beetle density and crop damage

The number of cereal leaf beetle larvae in 'densely-sown-rows' of treatment fields was marginally significantly reduced (by 50 %, on average) compared to 'conventionally-sown-rows' in control fields. Moreover, crop damage caused by cereal leaf beetle larvae and the number of re-emerged cereal leaf beetle adults were significantly reduced in 'densely-sown-rows' and marginally significantly reduced in

Table 1
Summaries of mixed linear models explaining differences in temperature on the soil surface, moisture in the soil and crop cover between different crop architectures (conventional for ‘conventionally-sown-rows’ in control fields (without manipulated crop architecture); dense for ‘densely-sown-rows’ and unsown for ‘unsown-rows’ in treatment fields (with manipulated crop architecture)). Est. = estimate, SE = standard error, DF = degrees of freedom. P ≤ 0.05 are presented in bold.

Model	Terms	Est.	SE	DF	T Value	P Value
Temperature	Conventional (intercept)	15.14	0.18	19.50	82.64	**<0.001**
	Dense	-0.14	0.19	12.02	-0.76	0.462
	Unsown	0.59	0.19	12.02	3.16	**0.008**
Moisture	Conventional (intercept)	2112.05	85.00	23.99	24.85	**<0.001**
	Dense	-8.49	120.21	23.99	-0.07	0.944
	Unsown	-91.38	120.21	23.99	-0.76	0.455
Crop density	Conventional (intercept)	48.79	3.41	31.47	14.32	**<0.001**
	Dense	-4.89	3.53	24.94	-1.39	0.178
	Unsown	-44.07	3.53	24.96	-12.49	**<0.001**

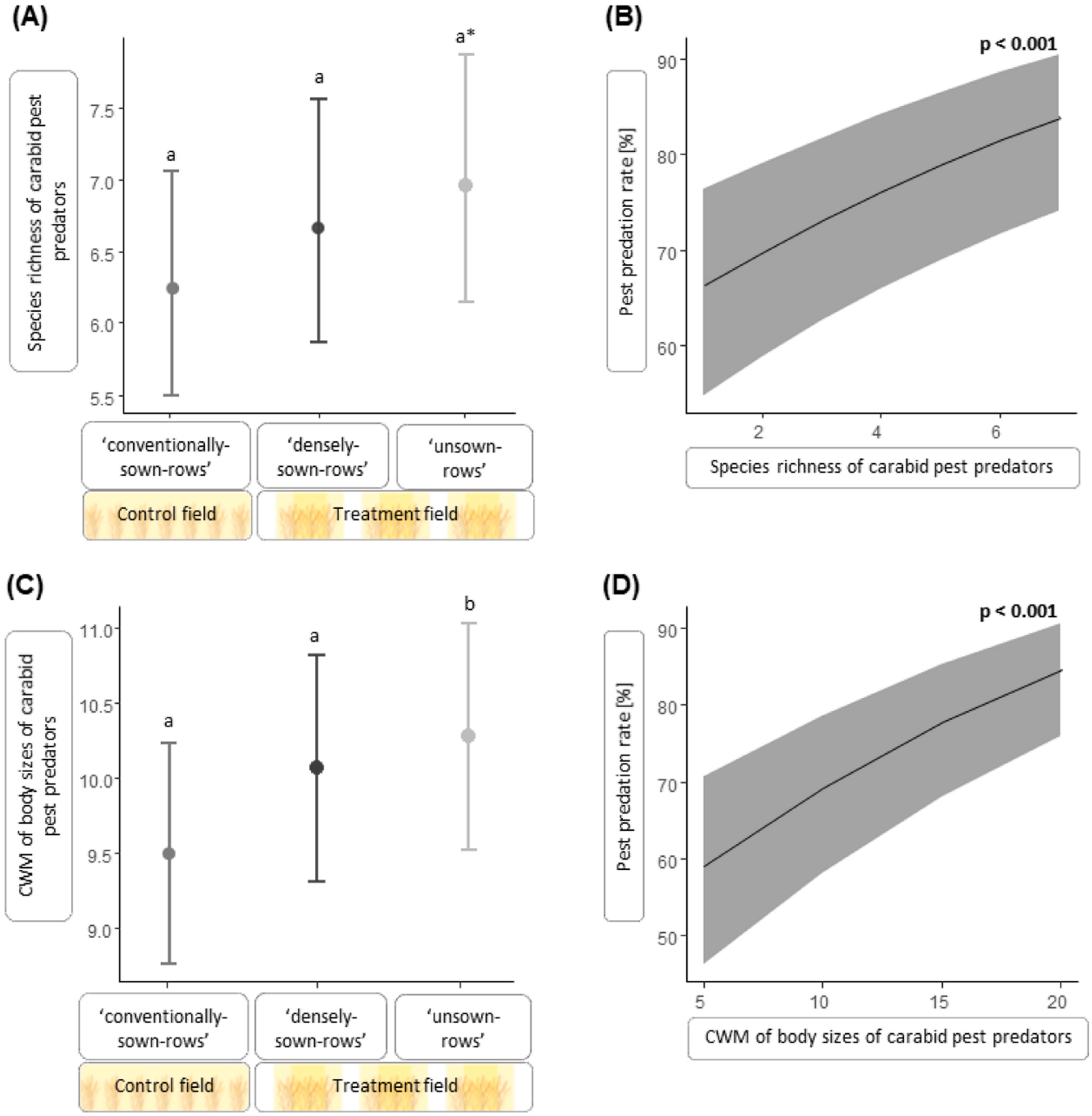

Fig. 2. Species richness and body size distribution of carabid pest predator communities under different winter wheat crop architectures and how these community descriptors affect pest predation. Mean predicted values from (generalized) linear mixed effect models. Error bars show 89 % CI. ‘Conventionally-sown-rows’ in control fields had a homogeneous seeding pattern; treatment fields were established with a heterogeneous seeding pattern, consisting of ‘unsown-rows’ and ‘densely-sown-rows’. **(A)** Effect of crop architecture on species richness of carabid pest predators. Species richness was marginally significantly higher in ‘unsown-rows’ (a*) than in ‘conventionally-sown-rows’ (a). **(B)** Significantly positive relationship of carabid pest predators’ species richness and percentage of predated pest sentinels. **(C)** Effect of crop architecture on body size distribution of carabid pest predators. Community weighted means (CWM) of body sizes were significantly higher in ‘unsown-rows’ (b) than in ‘conventionally-sown-rows’ (a). **(D)** Significantly positive relationship of carabid pest predators’ CWM of body sizes and percentage of predated pest sentinels.

Table 2

Summaries of (generalized) mixed linear models explaining differences in activity density, species richness and community weighted means (CWM) of body sizes of pest predators (carnivorous and omnivorous carabids) or seed predators (phytophagous and omnivorous carabids), respectively, from different crop architectures (conventional for 'conventionally-sown-rows' in control fields (without manipulated crop architecture); dense for 'densely-sown-rows' and unsown for 'unsown-rows' in treatment fields (with manipulated crop architecture)). Data from the pitfall sampling conducted once a month (April to July) for one week. Est. = estimate, SE = standard error, DF = degrees of freedom. P ≤ 0.05 are presented in bold.

Model	Terms	Est.	SE	DF	T Value	Z Value	P Value
Activity density of carabid pest predators	Conventional (intercept)	3.58	0.15			23.96	**<0.001**
	Dense	0.23	0.16			1.45	0.147
	Unsown	0.05	0.16			0.30	0.762
Species richness of carabid pest predators	Conventional (intercept)	1.83	0.06			28.80	**<0.001**
	Dense	0.07	0.07			1.01	0.315
	Unsown	0.11	0.06			1.69	0.091
CWM of carabid pest predators' body sizes	Conventional (intercept)	9.50	0.37	29.01	25.34		**<0.001**
	Dense	0.57	0.36	29.37	1.57		0.126
	Unsown	0.78	0.36	28.95	2.16		**0.039**
Activity density of carabid weed seed predators	Conventional (intercept)	1.84	0.21			8.84	**<0.001**
	Dense	0.30	0.16			1.87	0.062
	Unsown	0.39	0.16			2.42	**0.015**
Species richness of carabid weed seed predators	Conventional (intercept)	1.13	0.11			10.64	**<0.001**
	Dense	0.10	0.09			1.15	0.250
	Unsown	0.11	0.09			1.22	0.222
CWM of carbid weed seed predators' body sizes	Conventional (intercept)	7.78	0.49	26.48	15.99		**<0.001**
	Dense	1.11	0.41	28.13	2.70		**0.012**
	Unsown	1.43	0.41	27.21	3.50		**0.002**

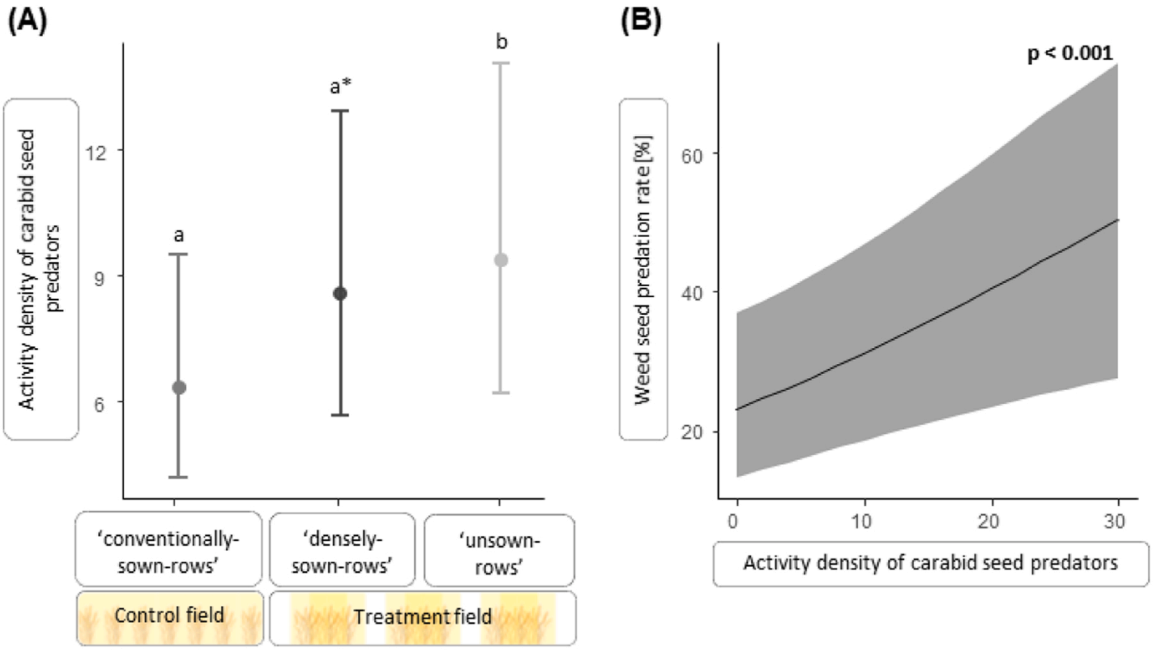

Fig. 3. Activity density of carabid seed predators under different winter wheat crop architectures and its relationship with seed predation. Mean predicted values from generalized linear mixed effect models. Error bars show 89 % CI. **(A)** Effects of crop architecture on activity density of carabid seed predators. 'Conventionally-sown-rows' in control fields had a homogeneous seeding pattern; treatment fields were established with a heterogeneous seeding pattern, consisting of 'unsown-rows' and 'densely-sown-rows'. Activity density was significantly (b) or marginally significantly (a*) higher in 'unsown-rows' or 'densely-sown-rows' than in 'conventionally-sown-rows' (a). **(B)** Significantly positive relationship between carabid seed predators' activity density and percentage of predated weed seed sentinels.

'unsown-rows' compared to 'conventionally-sown-rows' (crop damage: 'densely-sown-rows' 56.3 % reduction; 'unsown-rows': 33 % reduction; Fig. 4B. Cereal leaf beetle adults: 'densely-sown-rows': 52.1 % reduction; 'unsown-rows': 34.1 % reduction). See Table 4 for model summaries and Table S5 for mean ± se of raw data.

3.5. *Effect of crop architecture on yield*

Yields in fields with and without manipulated crop architecture did not differ significantly from each other (Fig. 4A). See Table 5 for model summaries and Table S6 for mean ± se of raw data.

4. Discussion

Modification of seeding pattern led to more heterogenous crop architecture, which was related to changes in the carabid community, increased natural pest and weed seed control, lower densities of cereal leaf beetles, and lower crop damage. At the same time productivity of the treatment fields was maintained. Even though different input levels of pesticides were not directly tested in this study, these results point towards the potential to replace pesticides by harnessing biodiversity to increase natural pest and weed seed control services, especially in areas with high pest densities and resulting crop damage (Bommarco et al.,

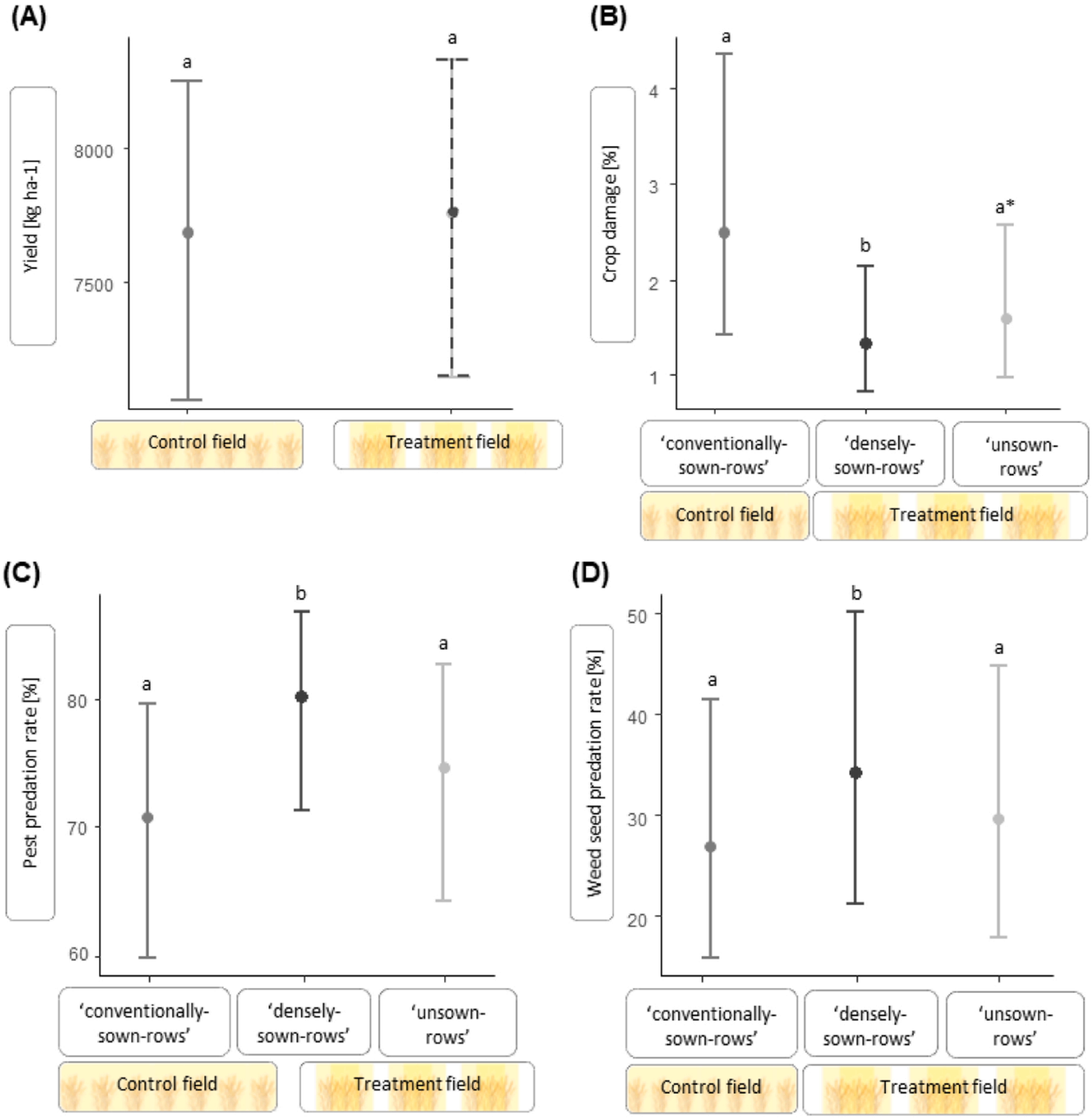

Fig. 4. Effects of winter wheat crop architecture on yield, crop damage by cereal leaf beetles and sentinel pest and weed seed predation. Mean predicted values from generalized linear mixed effect models. Error bars show 89 % CI. Yield was measured in control fields (homogeneous seeding pattern, consisting of 'conventionally-sown-rows') and treatment fields (heterogeneous seeding pattern, consisting of 'unsown-rows' and 'densely-sown-rows'). Crop damage, and natural pest and weed seed control was measured in 'conventionally-sown-rows' in control fields as well as in 'densely-sown-rows' and 'unsown-rows' in treatment fields. **(A)** No significant difference in wheat yield of control and treatment fields. **(B)** Crop damage, measured as percentage of flag leaf damage, was significantly lower (b) or marginally significantly lower (a*) in 'densely-sown-rows' or 'unsown-rows' than 'conventionally-sown-rows' (a). **(C)** Pest predation, measured as percentage predated sentinel pests, was significantly higher in 'densely-sown-rows' (b) than 'conventionally-sown-rows' (a). **(D)** Weed seed predation, measured as percentage predated sentinel weed seeds was significantly higher in 'densely-sown-rows' (b) than 'conventionally-sown-rows' (a).

2013). To what extent, however, needs to be tested by further studies.

Results from the pitfall sampling and the pest predation experiment suggest that pest control benefits (e.g., reduced crop damage) could be driven by higher species richness and larger body sizes of predatory carabids. This would be in line with previous studies, showing that agricultural pest suppression can be strengthened by presence of large carabids (Rouabah et al., 2014) and higher species richness of natural enemies (Cardinale et al., 2003). According to Rouabah et al. (2014), larger carabids can increase pest suppression due to higher *per capita* consumption rates. The sampling effect also known for predatory communities (Ives et al., 2005), the complementarity effect (see Dainese et al., 2019), respectively, may be the reason why pest suppression was positively related to species richness. Indeed, the potentially increased complementarity of more diverse predator communities (i.e., increased diversity with respect of target food items (i.e., cereal leaf beetle eggs, larvae, pupae)) might explain why the number of second generation of cereal leaf beetle adults, crop damage, respectively, were stronger reduced than would be expected from the negative relationship between predator diversity and predation rates in the predation experiment. Crop damage was the result of cereal leaf beetle larvae feeding on wheat plants during their development in the field, thus, suppression of natural enemies on cereal leaf beetle eggs and larvae was reflected. The second generation of cereal leaf beetle adults additionally comprised the pupae life stage as potential food item for predators. On the other hand, in the pest predation experiment solely suppression of larval stages was examined. Altogether, the results suggest that the manipulation of crop architecture results in more efficient pest predator communities and enhanced natural pest control services, which may help to reduce

Table 3
Summaries of generalized mixed linear models explaining differences in the predation rates on pest and weed seed sentinels, respectively. Effects of daytime, crop architecture (conventional for ‘conventionally-sown-rows’ in control fields (without manipulated crop architecture); dense for ‘densely-sown-rows’ and unsown for ‘unsown-rows’ in treatment fields (with manipulated crop architecture)), species richness, activity density and community weighted means (CWM) of body sizes of potential pest predators (carnivorous and omnivorous carabids with body sizes of at least 5.0 mm) on the predation rate of pest sentinels (bluebottle fly larvae). Effects of crop architecture (conventional for ‘conventionally-sown-rows’ in control fields (without manipulated crop architecture); dense for ‘densely-sown-rows’ and unsown for ‘unsown-rows’ in treatment fields (with manipulated crop architecture)), species richness and activity density of potential weed seed predators (phytophagous and omnivorous carabids with body sizes between 2.5 and 8.0 mm) on the predation rate of weed seed sentinels (*Capsella bursa-pastoris* (Brassicaceae, 0.1 mg per seed), *Tripleurospermum inodorum* (Asteraceae, 0.3 mg per seed), *Stellaria media* (Caryophyllaceae, 0.4 mg per seed), *Poa annua* (Poaceae, 0.4 mg per seed), *Lamium purpureum* (Lamiaceae, 0.8 mg per seed)). According to the respective experimental set up, carabid data for the pest predation experiment came from 12 h pitfall samples and carabid data for the weed seed predation experiment came from the 7 d pitfall samples. Est. = estimate, SE = standard error. $P \leq 0.05$ are presented in bold.

Model	Terms	Est.	SE	Z Value	P Value
Predation rate on bluebottle fly larvae	Conventional & day (intercept)	0.79	0.25	3.19	**<0.001**
	Night	0.55	0.07	8.10	**<0.001**
	Dense	0.51	0.25	2.08	**0.038**
	Unsown	0.19	0.25	0.78	0.435
	Species richness[a]	0.23	0.05	4.46	**<0.001**
	Activity density[a]	0.13	0.05	2.45	**0.014**
	CWM body size[a]	0.23	0.04	6.10	**<0.001**
Predation rate on weed seeds	Conventional (intercept)	-1.01	0.33	-3.01	**<0.001**
	Dense	0.35	0.15	2.27	**0.023**
	Unsown	0.14	0.15	0.89	0.375
	Species richness[b]	0.24	0.09	2.80	**0.005**
	Activity density[b]	0.38	0.09	4.45	**<0.001**

[a] Carnivorous and omnivorous carabids with body sizes of at least 5.0 mm

[b] Phytophagous and omnivorous carabids with body sizes between 2.5 and 8.0 mm

Table 4
Summary of generalized mixed linear models explaining differences in the density of cereal leaf beetle larvae on the flag leave, adults of the second generation and crop damage between different crop architectures (conventional for ‘conventionally-sown-rows’ in control fields (without manipulated crop architecture); dense for ‘densely-sown-rows’ and unsown for ‘unsown-rows’ in treatment fields (with manipulated crop architecture)). Est. = estimate, SE = standard error. $P \leq 0.05$ are presented in bold.

Model	Terms	Est.	SE	Z Value	P Value
Cereal leaf beetle larvae density	Conventional (intercept)	0.88	0.28	3.20	**<0.001**
	Dense	-0.66	0.34	-1.92	0.055
	Unsown	-0.19	0.33	-0.57	0.572
Cereal leaf beetle adult density	Conventional (intercept)	-0.06	0.42	-0.13	0.894
	Dense	-0.81	0.24	-3.33	**<0.001**
	Unsown	-0.48	0.26	-1.85	0.064
Crop damage	Conventional (intercept)	0.91	0.29	3.17	**<0.001**
	Dense	-0.63	0.27	-2.36	**0.018**
	Unsown	-0.45	0.27	-1.70	0.088

Table 5
Summary of the mixed linear model explaining differences in yield between control fields without manipulated crop architecture (control) and treatment fields with manipulated crop architecture (treatment). Est. = estimate, SE = standard error, DF = degrees of freedom. $P \leq 0.05$ are presented in bold.

Model	Terms	Est.	SE	DF	T Value	P Value
Yield	Control (intercept)	7759.02	305.82	15.60	25.37	<0.001
	Treatment	-73.81	140.28	72.46	-0.53	0.600

insecticide inputs and thus environmental costs of agricultural production, but this needs to be further tested in future studies.

Weed seed predators’ activity density showed strong positive response to manipulated crop architecture and was related to increased weed seed predation in the sentinel experiment. This supports findings of a previous study, that showed a positive correlation between seed removal rates and the number of carabid seed predators (Menalled et al., 2007). While activity density was highest in ‘unsown-rows’, seed predation was highest in ‘densely-sown-rows’. Probably, carabids use ‘unsown-rows’ for unhindered movement, which increased the likelihood that they are caught by pitfall traps, while ‘densely-sown-rows’ offered protection during feeding activity. In summary, the results suggest that a higher number or activity of seed predators in winter wheat fields with manipulated crop architecture could help to reduce the amount herbicides used.

A potential explanation for the effects of the manipulated crop architecture on carabid communities is, that they were caused by different within-crop microclimatic conditions which in turn were caused by different crop densities. It is known that carabids are influenced by temperature and moisture conditions prevailing at the soil surface and the ability to thermoregulate through sunlight exposure (Honek, 1988). The data of this study indicated similar abiotic conditions in the ‘densely-sown-rows’ of the treatment fields as compared to the ‘conventionally-sown-rows’ of the control fields. In general, dense crop stands have a cool and moist microclimate and no sunspots below the canopy (Honek and Jarosik, 2000). In contrast, as expected, the ‘unsown-rows’ of the treatment field were significantly warmer, with sunlight reaching the soil surface (own observation), indicating that fields with manipulated crop architecture offered more variable microclimatic conditions. Thus, these heterogeneous conditions might have caused the carabid community changes observed in this study, as carabids are known to have species-specific preferences regarding abiotic conditions (Honek and Jarosik, 2000). As climate change continues with extreme weather conditions, fields which offer different microclimatic (micro-)habitats could become even more important in the future.

To actually reduce (rather than merely shift) the environmental costs of agricultural production through ecological intensification, yields must not be reduced by the measures. Previous studies indicated that wheat plants can compensate for differences in row spacing, for example by changing the numbers of tillers or final leaves (Abichou et al., 2019). This might explain why there was no yield loss in fields with manipulated crop architecture: While a single wheat plant in ‘densely-sown-rows’ probably yielded less due to reduced access to light and water, a single wheat plant adjacent to the ‘unsown-rows’ probably yielded higher due to increased access to resources, which might be expected to offset each other. However, since it was beyond the scope of this study to also test different pesticide application schemes, the extent to which such plasticity of wheat plants or higher biological control and associated lower crop damage contributed to the constant yields, cannot be completely disentangled. Nevertheless, crop damage and pest levels in the study fields were relatively low from the outset, so that stronger positive effects from an increased natural control could be expected in years and regions with higher pest levels.

From a practical point of view, manipulation of crop architecture has little impact on conventional farming operations. Closing sowing coulters before sowing is the only (one-time) effort that needs to be performed, which is possible with standard seed drills. No further adjustments to conventional farming methods are required, nor are there land opportunity costs that might discourage farmers from implementing this measure (Bailey et al., 2015; Kleijn et al., 2019). Thus, our findings should facilitate and encourage the adoption of this measure, which may also generally contribute to increased awareness of ecological intensification measures.

Further, it can be expected that manipulation of crop architecture might also be a promising approach for promoting other services (e.g., pollination) as well as for other crops that show similar plasticity in plant growth as wheat, for example sunflowers and soybeans (Junior et al., 2018; Pereira and Hall, 2019). As well, other threatened species such as ground-breeding farmland birds could benefit from such a measure, which creates open and accessible areas in cereal fields throughout the season (Wilson et al., 2005). Also, the manipulation of crop architecture in combination with supplementary measures, such as conservation agriculture (Palm et al., 2014), might lead to further enhancement of biodiversity and associated ecosystem services. However, further studies are needed to test these ideas.

In conclusion, the studied manipulation of crop architecture has the potential to become an effective tool for ecological intensification in winter wheat, as benefits for biodiversity promotion and enhancement of ecosystem services are shown, which do not come at the cost of agronomic or economic disadvantages. Particularly in study areas with high pest abundance, increased natural pest control services might help farmers to reduce pesticide applications, which would help resulting in lower economic and environmental costs per production unit and could also help farmers and the agricultural sector to achieve pesticide reduction plans as e.g., currently targeted by the EU Green Deal (EU Commission, 2019). Further field studies with different pesticide input levels are needed to test this and to quantify the potential of the studied crop architecture manipulation as a measure for ecological replacement in wheat production.

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.

Data Availability

Data will be made available on request.

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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.agee.2023.108404.

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