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Synergistic enhancement of wild bee abundance at the landscape scale through multiple types of agri-environmental interventions

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ABSTRACT

The ongoing biodiversity crisis and increasing land pressure call for efficient strategies that promote biodiversity and sustain ecosystem services while minimizing trade-offs with agricultural production. Here, we examine how the concurrent implementation of two agri-environmental interventions—flower strips and extensively managed meadows—can synergistically enhance wild bees in agricultural landscapes through three nonexclusive mechanisms: (i) habitat heterogeneity, (ii) resource complementarity, and (iii) resource continuity. We sampled plant-bee interaction networks and nest-site availability across all major habitat types in 28 Central European agricultural landscapes to assess landscape-level bee community composition and the spatiotemporal distribution of resources. Landscapes combining both intervention types showed a synergistic increase in wild bee abundance, including key crop pollinators. Consistent with habitat heterogeneity effects, bee species turnover was higher between different intervention types than between patches of the same type, resulting in increased species richness in landscapes with both interventions. Bee communities in landscapes with flower strips were dominated by smaller and more oligolectic species, whereas higher proportions of extensively managed meadows were associated with lower functional specialization and a more balanced bee community composition, likely reflecting alleviated environmental filtering. Extensively managed meadows provided suitable nesting habitat for ground-nesting bees and both interventions independently increased bees' foraging generality toward a broadened diet, indicating resource complementarity. The bees' extinction risk from agricultural landscapes was also reduced by both interventions, likely through measured staggered flowering periods that increased resource continuity. Overall, our findings demonstrate that combining complementary agri-environmental interventions can increase land-use efficiency and enhance ecosystem services by more effectively promoting wild pollinators, thereby reducing trade-offs between biodiversity conservation and agricultural production.

1. Introduction

Several practices that have been introduced during agricultural intensification to optimize crop production are related to ongoing biodiversity loss in agroecosystems (Tscharntke et al., 2012; Kehoe et al., 2017). Low crop (rotation) diversity, high inputs of fertilizers and pesticides, mechanization, field enlargements and landscape simplification all contribute to reduced plant and arthropod diversity (Ekroos et al., 2020; Redlich et al., 2021; Meier et al., 2022; Maurer et al., 2024; Nicholson et al., 2024). To mitigate or reverse biodiversity loss from agricultural landscapes, many European countries introduced agri-environmental schemes (AES) by subsidizing biodiversity-friendly interventions such as the implementation of flower strips (Kleijn and Sutherland, 2003; Batáry et al., 2015). However, despite these efforts, some organism groups continue to experience negative biodiversity trends in agroecosystems within certain regions, and most biodiversity restoration goals have yet to be achieved (European Environment Agency, 2020; Cliquet et al., 2024).

This ongoing biodiversity decline in European agroecosystems calls for strategies that enhance the effectiveness of AES interventions, especially in light of potential trade-offs posed by growing land pressure, opportunity costs, and the increasing demand for food production to support a growing population (Molotoks et al., 2021; Marja et al., 2024). While the local effects of commonly implemented interventions have been evaluated (Batáry et al., 2011; Scheper et al., 2013), potential increases in effectiveness when implemented in combination with other

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types of interventions through synergistic interactions remain largely unexplored (Fahrig et al., 2011). Recent research has demonstrated that the combination of multiple habitat patches in the same landscape can harbor more species and larger populations compared to single patches of the same total area (Riva and Fahrig, 2023). Although small patches have been linked to negative effects, such as increased edge effects and extinction risks for species within individual patches (Chase et al., 2020), these consequences may be offset by several benefits. The assemblage of multiple patches may benefit biodiversity by: 1) increasing environmental heterogeneity, thereby offering diverse habitats for different species, 2) providing resource complementarity, thus offering various essential resources to the same species, and 3) reducing local extinction risk of species from landscapes e.g. through enhanced spatiotemporal resource continuity. These processes have been suggested to positively affect beta diversity and meta-community dynamics, leading to overall enhanced species richness and abundance of mobile species at the landscape level (Riva and Fahrig, 2023).

Bees often use multiple habitats to fulfill their floral resource and nesting requirements, and are particularly vulnerable to agricultural intensification and associated habitat loss (Rivers-Moore et al., 2020; Maurer et al., 2022). Although some crops provide valuable floral resources to bees, they typically offer low plant richness, their flowering time is often too short to cover the bees' entire activity period (Ammann et al., 2024), and most crop fields are relatively poor nesting habitats (Kim et al., 2006; Albrecht et al., 2023; Tschanz et al., 2023). In contrast, AES interventions such as extensively managed meadows or flower strips can provide valuable habitats for bees (Sutter et al., 2017; Albrecht et al., 2020). Different types of interventions could complement each other by offering different resources to distinct species (i.e., increasing habitat heterogeneity) or to the same bee species, thereby promoting their populations (i.e., increasing resource complementarity) (Marja et al., 2021; von Königslöw et al., 2021; Maurer et al., 2022). Moreover, the temporary loss of floral resources from habitat patches (e.g., through mowing) may force dependent species to emigrate, subsequently leading to their disappearance from a landscape (Scheper et al., 2014; Vanbergen et al., 2017). Combining different types of AES interventions with divergent temporal management dynamics and complementary resources across different time periods may therefore enhance the persistence of bee species and other beneficial insects within landscapes (i.e., spreading of extinction risk) (Fig. 1) (Kremen et al., 2007; Iuliano and Gratton, 2020).

Agricultural intensification can reduce nest-site availability for wild bees with consequences for community composition (Albrecht et al., 2023; Eeraerts and Isaacs, 2023; Collins et al., 2025). In contrast, AES interventions - such as flower plantings and extensified grasslands - can provide a relatively high proportion of bare ground that benefits ground-nesting bees, which represent about 75 % of species in Central Europe (Albrecht et al., 2023; Williams et al., 2024). Moreover, many European agroecosystems are characterized by mixed farming systems in which floral resources strongly decline towards summer (Ammann et al., 2024; Harris et al., 2024). This period strongly overlaps with the peak activity of most bee species (Duchenne et al., 2020), making the enhancement of floral resources during summer - such as through the establishment of flower strips - a promising strategy to support wild bee populations. In addition, flower strips have the potential to promote pollination services to crops (Albrecht et al., 2020), but due to direct trade-offs with food production and opportunity costs, they typically cover only a small proportion of arable land, whereas AES interventions on less productive land are more widely implemented. In Switzerland for example, flower strips currently cover 0.3 % of the agricultural area (0.8 % of arable land), whereas extensively managed permanent meadows account for 12.5 % (BLW, 2023). As a result, floral scarcity is particularly pronounced when these meadows are simultaneously mown in June, following the delayed mowing schedules prescribed by AES

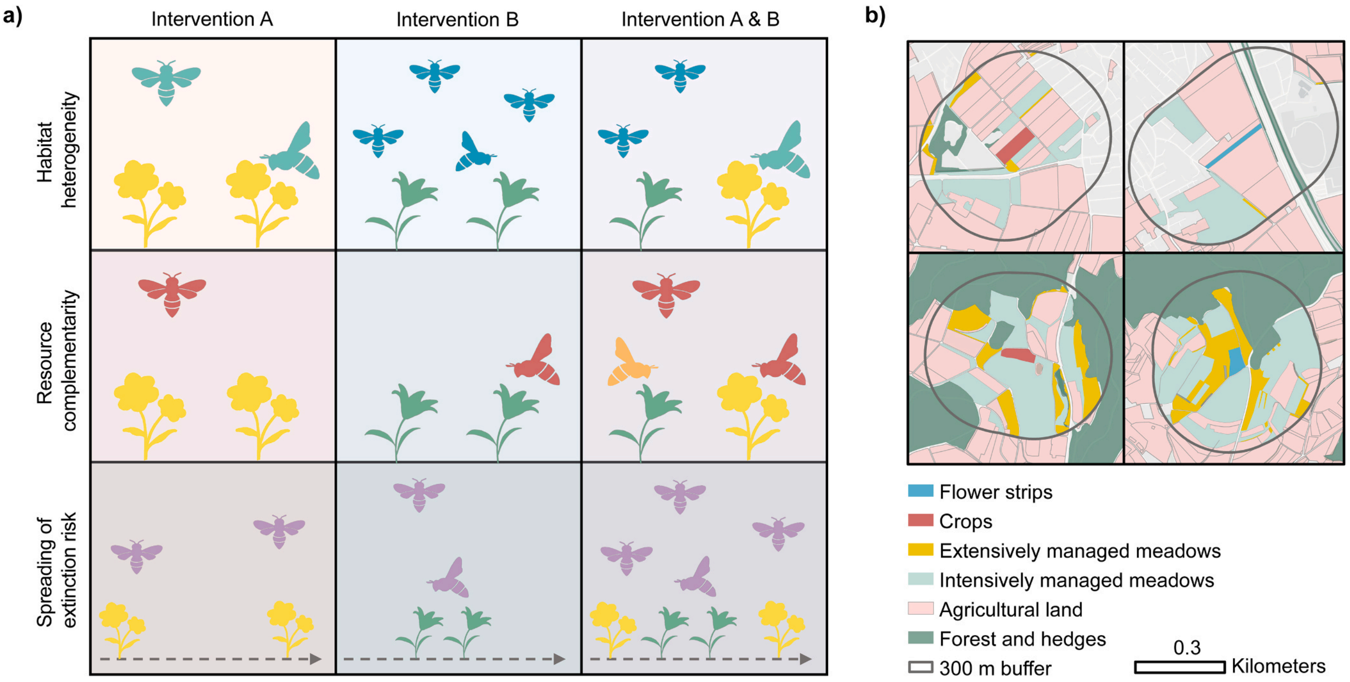

Fig. 1. Hypotheses and study design. a) Hypothesized processes driving synergism between different types of AES interventions in promoting bees without increasing total intervention area. Different intervention types may 1) offer diverse habitats for different bee species, thereby increasing total species richness in agricultural landscapes (i.e., habitat heterogeneity), 2) provide complementary resources (e.g., pollen and nectar) for the same bee species, enabling their persistence in the landscape or supporting population growth (i.e., resource complementarity), 3) enhance spatiotemporal resource continuity for certain bee species through divergent temporal management dynamics or complementary resource availability across different time periods, thereby reducing these species' local extinction risk (i.e., spreading of extinction risk). Dashed arrows represent the timeline. b) Four types of study landscapes to assess landscape-level bee abundance and diversity. Top: pair of landscapes without (left) and with (right) flower strip and low proportions of extensively managed meadows. Bottom: pair of landscapes without (left) and with (right) flower strip and high proportions of extensively managed meadows.

regulations.

In this study, we compared landscapes varying in the proportion of extensively managed meadows, centred around either flower strips or arable crop fields. The main objectives addressed with this design were (i) to test for synergy between extensively managed meadows and flower strips, and (ii) to gain a better understanding of the mechanisms and processes driving potential synergies. To achieve this, we assessed 28 agricultural landscapes in Switzerland, measuring wild bee foraging across all major land-use types relevant to bees. This approach allowed us to account for density-dependent processes such as dilution, concentration, and spillover across local habitat patches (Kleijn et al., 2018). To test for the role of increased habitat heterogeneity, resource complementarity and the spreading of extinction risk for bees in landscapes with concurrent implementation of both AES intervention types (i.e. flower strips and extensively managed meadows), we assessed floral and nesting resource availability, functional bee community composition and floral resource use by bees through the analysis of plant-bee networks.

2. Methods

2.1. Study design

Data on bee abundance and diversity were collected in the summer of 2022 from 28 agricultural landscapes across the lowlands of Northern Switzerland (Fig. S1); 14 landscapes were centered around a perennial flower strip (typically implemented across entire arable fields), while the other 14 landscapes lacked a flower strip and were instead centered around an arable crop field. Landscapes were defined as sectors within 300 m buffers from the edge of the central arable fields. This distance falls well within the typical foraging range of most species in the regional bee community, which had a median body size of 2.1 mm intertegular distance (corresponding to typical foraging distances of less than 500 m; Greenleaf et al., 2007). Landscapes with and without central flower strips were selected to ensure similar proportions of extensively managed meadows (Fig. S2), and comparable compositions of other land-use types including arable crops, intensively managed grasslands and forested areas (no significant differences between treatments).

Both perennial flower strips and extensively managed permanent meadows are interventions subsidized by the Swiss AES to promote biodiversity, including wild bees (Table S1). AES management requirements for extensively managed meadows include postponed mowing until after June 15 and prohibition of any fertilizer. To enhance plant diversity, hay transfer from diverse source meadows or overseeding with seed mixtures are sometimes applied. Perennial flower strips consist of sown mixtures of wildflowers on arable land and are maintained for at least six years. All investigated perennial flower strips were in their fourth year after establishment and had not been mown. In four landscapes, farmers combined the perennial flower strips with narrow strips of annual flower sowings (e.g., purple tansy, poppy and cornflower). The only bee-attractive crops flowering during the sampling period were sunflowers and faba beans, each present in one landscape with a flower strip and in one control landscape (four landscapes in total).

2.2. Data collection

We followed the methodology proposed by Kleijn et al. (2018), with slight adaptations, to measure landscape-level responses of bees to interventions. In each study landscape (including central fields), flower-visiting bees were sampled during standardized transect walks in all land-use types that offered floral resources during the sampling period: 1) flower strips, 2) extensively managed meadows, 3) intensively managed meadows (temporal or permanent), 4) bee-attractive crops (sunflower or faba bean) (Fig. S3). Forests and hedges were not sampled, as they provide only minor foraging habitats for bees during that time of year (Bartual et al., 2019; Bertrand et al., 2019; Maurer et al., 2022; Rivers-Moore et al., 2023).

Sampling took place between 9 am and 6 pm during dry and warm weather conditions (min. 18°C) with low wind (Westphal et al., 2008). Transects were 40 m long and 2 m wide, and were walked during 4.5 min at a consistent speed. During this time, each flower visiting bee and the corresponding visited plant species were recorded (excluding managed honey bees *Apis mellifera*), allowing for the construction of plant-bee networks (see below). Bees that could not be identified in the field were caught for later identification to species level.

Bees were sampled during two sampling rounds, one before the first cut of extensively managed meadows in mid-June (May 30 to June 15, 2022) and the second after the cut (June 29 to July 25, 2022), when the extensively managed meadows had returned to bloom. Across both sampling rounds, we completed 534 transect walks for a total sampling time of 2403 min. To ensure comparable sampling completeness, total sampling effort was adjusted by land-use type (as shown in Fig. S4). All central perennial flower strips were sampled with four transects per landscape and sampling round, whereas the remaining land-use types (extensively and intensively managed meadows, crops and annual flower strips) were sampled with two to eight transects per landscape and sampling round, depending on available area, plant species richness, and floral cover heterogeneity. For each land-use type, transects were distributed across the whole landscape and randomly assigned to the different fields.

The presence of ground-nesting bee nests and the percentage of bare ground were recorded in each transect during the second sampling round. To locate bee nests, a 1 m^2 plot was placed at the location with the highest percentage of bare ground considered suitable nesting habitat for most ground-nesting bee species (Albrecht et al., 2023). Nests were identified based on the presence of tumuli constructed by the majority of ground-nesting species (Fig. S3) (Albrecht et al., 2023). We focused on tumuli-building bees because their nests are distinctive (e.g., round hole marking the nest entrance and characteristic soil tumuli) and generally well identifiable by a trained person, although some misclassifications cannot be fully ruled out without capturing the nesting bees (Tschanz et al., 2023). As a control, another 1 m^2 plot was placed at the location with the lowest percentage of bare ground, confirming the absence of ground nests in areas with high vegetation cover (no nest detected across all transects).

During each sampling round, we recorded all plant species with entomophilous flowers and estimated their flower cover percentage along each transect used for bee sampling. Additionally, in each study landscape, we combined information on land use with field surveys to characterize each landscape element to the defined land-use types and recorded the presence or absence of floral resources. In total, we sampled bees in 62 % of all habitat patches with floral resources in the first sampling round and 59 % in the second round.

All habitat patches (extensively and intensively managed meadows, flower strips, bee-attractive crops) were digitalized using a geographic information system (ArcGis Pro 10.6, ESRI) to quantify their area. Additionally, to account for the potential immigration of bees from surrounding areas into focal landscapes, we quantified the proportion of AES interventions (flower strips and extensively managed meadows) within a 1 km radius around the center of the study landscapes.

2.3. Testing for interactive effects of AES interventions on bee abundance and species richness

Bee abundance and species richness were calculated for whole landscapes across both sampling rounds. To account for the heterogeneous distribution of bees across different land-use types, landscape-level bee abundance was calculated as $\sum_{r=1}^{m}\sum_{h=1}^{n}\frac{N_{rh}}{S_{rh}} \times A_{rh}$, where r is the sampling round, h the sampled land-use type, N_{rh} the total number of bees across all sampled transects in that land-use type and sampling round, S_{rh} the sampled area, and A_{rh} the total area of the land-use type offering floral resources in that sampling round (fields with no flowers were excluded from the quantification of A_{rh}) (Czechofsky et al., 2025). The identification of key crop pollinators was based on the list of key crop pollinator species for Europe from Kleijn et al. (2015). Flower abundance was calculated with the same formula presented above, but with N representing the total flower abundance.

All statistical analysis were done in R 4.4.2. (R Core Team, 2026). To test for synergistic effects of the two focal AES intervention types on landscape-level bee abundance and species richness, we used (generalized) linear models. For species richness, we fitted a model with a Poisson error distribution, and for abundance, a Gaussian model with log-transformation to fulfill model assumptions. The presence of a flower strip and the proportion of extensively managed meadows in landscapes, as well as their interaction, were included as explanatory variables. Additionally, full models included the total proportion of foraging habitat in landscapes (considering the total area of all patches of flower strips, and flowering meadows and crops), the mean patch size of foraging habitats and the proportion of AES interventions in a 1 km radius as covariates. Model simplification was done based on likelihood-ratio tests (Zuur et al., 2009). We could not include the total area of AES interventions in landscapes as a covariate due to its high correlation with the area of extensively managed meadows. However, an additional model using the total area of AES interventions instead of the area of extensively managed meadows as an explanatory variable confirmed synergistic interactions between the presence of a flower strip and the total AES intervention area, showing that our results were not driven by non-linear relationships between bee community metrics and AES intervention area.

2.4. Testing for habitat heterogeneity, resource complementarity and spreading of extinction risk

To explore the potential processes driving interactive effects across AES intervention types on landscape-level bee abundance and species richness - habitat heterogeneity, resource complementarity, and the spreading of extinction risk - we analyzed resource-use by wild bees, their community functional composition, and the spatiotemporal distribution of bee species and resource availability.

Plant-bee networks were built at the landscape-level considering all interactions across different land-use types (García et al., 2018). The abundance of each interaction was calculated equivalent to landscape-level bee abundance, but with N representing the total number of a certain plant-bee interaction (Castro-Urgal et al., 2012). The following network metrics were calculated using the bipartite package in R (Dormann et al., 2008):

(i) Bee generality: weighted mean effective number of plant species per bee species standardized by the plant's marginal totals (Tylianakis et al., 2007). Generality is expected to increase as complementary floral resources become more available to bees, thereby enhancing resource complementarity. To test for the simultaneous use of complementary resources by bees, generality was calculated separately for each sampling round.

(ii) Bee robustness to extinction risk: area below the extinction curve as a measure of network robustness to plant species loss. The curve represents the number of secondary bee extinctions based on 1000 simulated random primary extinction sequences of plant species. In this simulation, bees go extinct only if all their food plants have disappeared from the landscapes (Memmott et al., 2004). We used a random extinction scenario for food plants rather than one based on abundance as the temporary disappearance of plant species from landscapes depends mainly on management practices, affecting both abundant and rare plant species. While flower strips and crops may fully disappear from landscapes due to field rotation across years, the mowing of meadows causes seasonal losses of floral resources. To analyze robustness to extinction risk throughout the season, plant-pollinator networks were built across both sampling rounds.

We calculated two metrics to describe the functional composition of landscape-level bee communities: mean pairwise distance (MPD) and functional specialization. Functional MPD is the mean weighted distance in the functional space between all pairs of species present in a community. Functional specialization is the weighted mean distance of a bee community to the centroid of the global species pool across all communities (Magneville et al., 2022). Both metrics are little affected by species richness and are suitable to test whether bees are disappearing from agroecosystems due to their traits (Laliberté and Legendre, 2010). Here we linked those metrics to flower strips and extensively managed meadows to test whether these interventions can relax environmental filters imposed by agroecosystems (Weekers et al., 2022). Functional MPD and specialization were calculated with the mFD package (Magneville et al., 2022) using the Gower multi-trait dissimilarity matrix obtained with the gawdis function in R (package gawdis; de Bello et al., 2021). We considered potential response traits (Table 1), which were collected from a European database (Miličić et al., in prep.). Synergistic effects of the two AES intervention types on functional community composition would imply that bees with specific traits benefit from the concurrent implementation of interventions, highlighting resource complementarity. In contrast, single intervention effects may highlight the importance of habitat heterogeneity, with specific interventions supporting bee species with particular traits.

To test for the effects of flower strips and extensively managed meadows on robustness to extinction risk and functional community composition, we used (generalized) linear models. For functional specialization, we fitted a model with a Gamma distribution. The remaining models were fit with a Gaussian error distribution, applying a square root transformation of robustness to extinction risk to fulfill model assumptions. Generality, which was calculated for each sampling round separately, was analyzed with a linear mixed model that included landscape identity as a random term. The structure and simplification of full models was done as described above for the landscape-level analysis on bee abundance and species richness, except that for generality, full models also included the sampling round and its interaction with AES interventions.

The probability of wild bee species to persist in landscapes across both sampling rounds was analyzed with a generalized linear model with a Binomial distribution, classifying species detected in both sampling rounds as persistent and those only found in one sampling round as non-persistent. Species identity and landscape identity were included as crossed random terms. The structure of explanatory variables and the simplification of full models were done as described above for the landscape-level analysis on bee abundance and species richness. Species only found in one of the two sampling rounds throughout the whole study were excluded from this analysis.

To test for differences in floral and nesting resource availability across land-use types and sampling rounds, we analyzed transect-level data with (generalized) mixed effect models. Land-use type, sampling round, and their interaction were included as explanatory variables, with landscape and field as random terms. For species richness of bees and plants, we fitted models with a Poisson error distribution, whereas the presence of flowers and bee nests was analyzed with a Binomial error distribution. Log transformation was used for flower abundance, bee abundance and bare ground to fulfill assumptions of models with Gaussian error distributions. We used the emmeans package to conduct post-hoc comparisons across land use types and sampling rounds.

Finally, we measured bee species turnover across patches of different AES intervention types in comparison to patches of the same intervention to test for habitat heterogeneity. Turnover is the dissimilarity in species composition across habitat patches due to the replacement of some species by others, and was calculated across all pairs of AES intervention types in the subset of landscapes with concurrent implementation of both interventions as Jaccard pair-wise dissimilarity using

Table 1
Bee species traits and their hypothesized response to the implementation of AES interventions.

Trait	Scale	Measurement	Expected impact of AES interventions on bees with different traits
Body size	Continuous	Intertegular distance	Due to their smaller foraging ranges, small bees depend more on the continuity of floral resources and the proximity between these resources and suitable nesting sites (Greenleaf et al., 2007). Therefore, small bees may particularly benefit from increased resource continuity and complementarity in AES interventions.
Lecty	Binary	Oligolectic Polylectic	Oligolectic bees, being less flexible in switching to alternative food sources, may suffer more from a decline in flowering plant diversity, especially if it includes the loss of their specific food plants (Michener, 2000). Therefore, oligolectic bees are likely to benefit from increased plant diversity from AES interventions.
Floral resource access	Continuous	Proboscis length	Flower choice of bees is, among other factors, constrained by a lack of morphological trait matching shaped by the fit of corolla and proboscis length (Andersson et al., 2014). Landscapes with increased plant diversity from AES interventions may also support bee communities with greater variation in proboscis length. Short-tongued species, in particular, may profit from high flower diversity as they rely on open and short-tubed flowers to reach floral resources such as nectar, limiting their ability to access floral resources of certain plants (Borrell, 2005).
Sociality	Ordinal	Social Communal or facultative social Solitary	Social bees typically have long activity periods and therefore depend on continuous floral resources (Maurer et al., 2022). They should benefit from increased resource continuity, especially through the combined implementation of AES interventions.
Nesting	Binary	Above Below	Ground-nesting bees prefer habitats with bare ground and low vegetation cover, such as those found in extensively managed grasslands (Albrecht et al. 2023). Cavity-nesting bees rely on structures like hollow stems or insect burrows (Michener, 2000). Perennial flower strips include large perennial plant species that can provide such structures.
Kleptoparasitism	Binary	No kleptoparasite Kleptoparasite	Kleptoparasitic bee species can be negatively affected by habitat loss both directly (e.g., decline of floral food resources) and indirectly through the decline of their hosts. Therefore, they may particularly benefit from AES interventions.

the R package betapart (Baselga, 2010). Turnover was analyzed with multiple regression on distance matrices (MRM) including the geographic Euclidean distance across each pair of intervention patches as a covariate (McLean et al., 2019).

3. Results

Altogether, we observed 2693 flower-visiting wild bees across 88 species. Of these, 24 % were exclusively found in extensively managed meadows, 22 % exclusively in flower strips, and 38 % visited both interventions (Fig. 2). The abundance of bees at the landscape-level was synergistically increased by the concurrent implementation of flower strips and high proportions of extensively managed meadows in agricultural landscapes ($F = 5.0$, $p = 0.035$; Fig. 2). This result was confirmed when only key crop pollinators were considered ($F = 9.2$, $p = 0.006$; Fig S5). While extensively managed meadows and flower strips also had a positive impact on wild bee species richness at the landscape level, the positive effect of flower strips on bee species richness declined with increasing proportions of extensively managed meadows ($\lambda_{LRT} = 6.6$, $p = 0.010$; Fig. 2). In contrast, species richness of key crop pollinators was additively increased by the two types of AES interventions (flower strips: $\lambda_{LRT} = 12.9$, $p < 0.001$; extensively managed meadows: $\lambda_{LRT} = 8.4$, $p = 0.004$; Fig. S5), as was plant species richness (flower strips: $\lambda_{LRT} = 65.4$, $p < 0.001$; extensively managed meadows: $\lambda_{LRT} = 16.6$, $p < 0.001$; Fig. S6).

3.1. Habitat heterogeneity

Bee species turnover was greater across different types of interventions than across patches of the same intervention ($p = 0.010$; Fig. 3), confirming the role of habitat heterogeneity in shaping wild bee species richness at the landscape scale. Plant species turnover across intervention types was much stronger than turnover of bees ($p < 0.001$; Fig. S6).

Both types of AES interventions affected the functional composition of bee communities, but in an independent manner, indicating habitat heterogeneity rather than functional complementarity. Functional specialization decreased with increasing proportions of extensively managed meadows in landscapes ($\chi^2 = 4.8$, $p = 0.029$; Fig. 3). This indicates that extensively managed meadows can relax different types of environmental filters imposed by agricultural landscapes, resulting in functionally more balanced community composition and more similar communities across landscapes (Fig. S7). Flower strips, in contrast, increased functional MPD ($F = 31.1$, $p < 0.001$; Fig. 3) due to an extended range of PC2 representing small, short-tongued and oligolectic bees (Fig. 3, Fig. S8 and S9). Plant species in flower strips supporting small and oligolectic bees are listed in Table S1.

3.2. Resource complementarity

The presence of flower strips and the proportion of extensively managed meadows in landscapes additively increased the bees' foraging generality throughout the season, with consistent effects across sampling rounds (no significant interaction between intervention and sampling round) (flower strips: $F = 16.0$, $p < 0.001$; extensively managed meadows: $F = 6.8$, $p = 0.015$; Fig. 4, see also Fig. S10), indicating that both interventions promote a complementary use of floral resources by bees. Additionally, extensively managed meadows, but not flower strips, had a higher percentage of bare ground and more nests of ground-nesting bees than intensively managed meadows (Fig. 4), confirming their important function as nesting habitat.

3.3. Spreading of extinction risk

A bee species' probability of persisting within landscapes throughout the summer period (early June to late July) was additively increased by the presence of flower strips and the proportion of extensively managed meadows (flower strips: $\lambda_{LRT} = 4.5$, $p = 0.034$; extensively managed meadows: $\lambda_{LRT} = 11.5$, $p < 0.001$; Fig. 5). Network-analysis further revealed that both intervention types reduced the extinction risk of bee species in agricultural landscapes (flower strips: $F = 34.1$, $p < 0.001$; extensively managed meadows: $F = 34.5$, $p < 0.001$; Fig. 5).

The importance of land-use types in terms of floral resources provided varied between early and mid-summer, resulting in greater

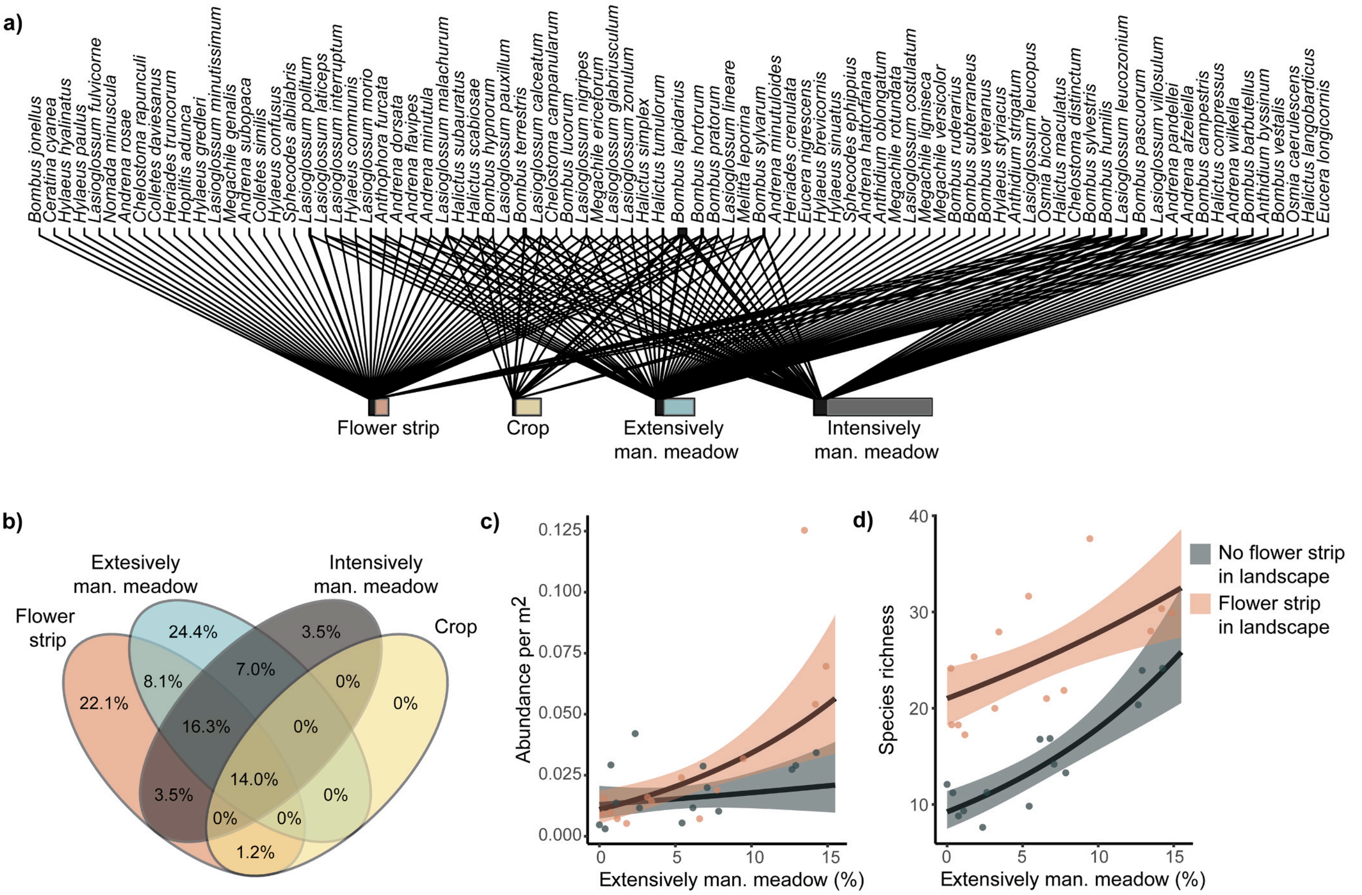

Fig. 2. Foraging patterns of bee species across land-use types and effect of AES interventions on wild bee abundance and species richness at the landscape level. a) Bee-habitat network showing the interactions of all bee species with different land use-types for foraging (across all landscapes). Colored bars represent average proportional area of a land-use type across landscapes, black bars represent interaction strength. b) Percentage of bee species found per land-use type, c) Landscape-level mean wild bee abundance in response to AES interventions, d) Landscape-level species richness in response to AES interventions.

resource continuity in landscapes with concurrent implementation of AES intervention types. Shortly before the cut in mid-June, 79 % of extensively managed meadows offered floral resources for bees, while only 61 % rebloomed by July after about three weeks lacking any floral resources. The second bloom showed comparable flower richness but relatively low floral cover (Fig. 5). In contrast, flower abundance and richness in flower strips increased over this period (Fig. 5). The proportion of flower strips offering floral resources increased from 57 % to 97 % from early to mid-summer. Due to frequent mowing, intensively managed meadows had a relatively high proportion of fields lacking floral resources throughout the whole sampling period, with 57 % in early summer and 52 % in mid-summer. Compared to AES interventions, intensively managed meadows reached similar floral cover, but with substantially lower richness of flowering plant species (Fig. 5). In line with floral resource availability, extensively managed meadows were most important in promoting high abundance and species richness of foraging bees in early summer, while flower strips were most important in mid-summer (Fig. S11).

4. Discussion

Landscape-scale assessments of wild bee communities across major bee-relevant land-use types enabled us to examine how AES interventions act synergistically to promote wild bees. We identified three non-exclusive processes shaping different aspects of bee community composition: (1) habitat heterogeneity, (2) resource complementarity, and (3) reduction of extinction risk. While their individual effects on bee community metrics were additive (e.g., generality, persistence), together these effects appear to drive a synergistic increase in wild bee abundance in agricultural landscapes. Although the positive effect of flower strips on bee species richness became weaker as extensively managed meadows in agricultural landscapes expanded, the turnover of bee species was more pronounced across intervention types than across different patches of the same intervention. This result indicates that on a given area of AES interventions, a combination of the two intervention types can promote more bee species than one type alone. These processes can be addressed in the management guidelines of different interventions and their concurrent implementation within agricultural landscapes to increase the efficiency of pollinator promotion in agroecosystems.

Flower strips provided floral resources mainly after extensively managed meadows were cut in mid-June, thereby creating greater resource continuity in landscapes with both interventions (Ouvrard et al., 2018; Maurer et al., 2022) and promoting the persistence of bee species in agricultural landscapes (i.e., spreading of extinction risk). Continuity of floral resources is especially crucial for social bees with long activity periods, which frequently include important crop pollinators such as bumblebees (Mandelik et al., 2012; Rundlöf et al., 2014; Kleijn et al., 2015; von Königslöw et al., 2021). Increasing resource continuity through a targeted combination of AES interventions may therefore be a promising strategy to promote greater species richness and to better support populations of wild bees and key crop pollinators.

Flower strips and extensively managed meadows offered complementary resources to wild bees. Many generalist species visited plants in both AES intervention types, which increased the bees' generality in landscapes with flower strips and high proportions of extensively

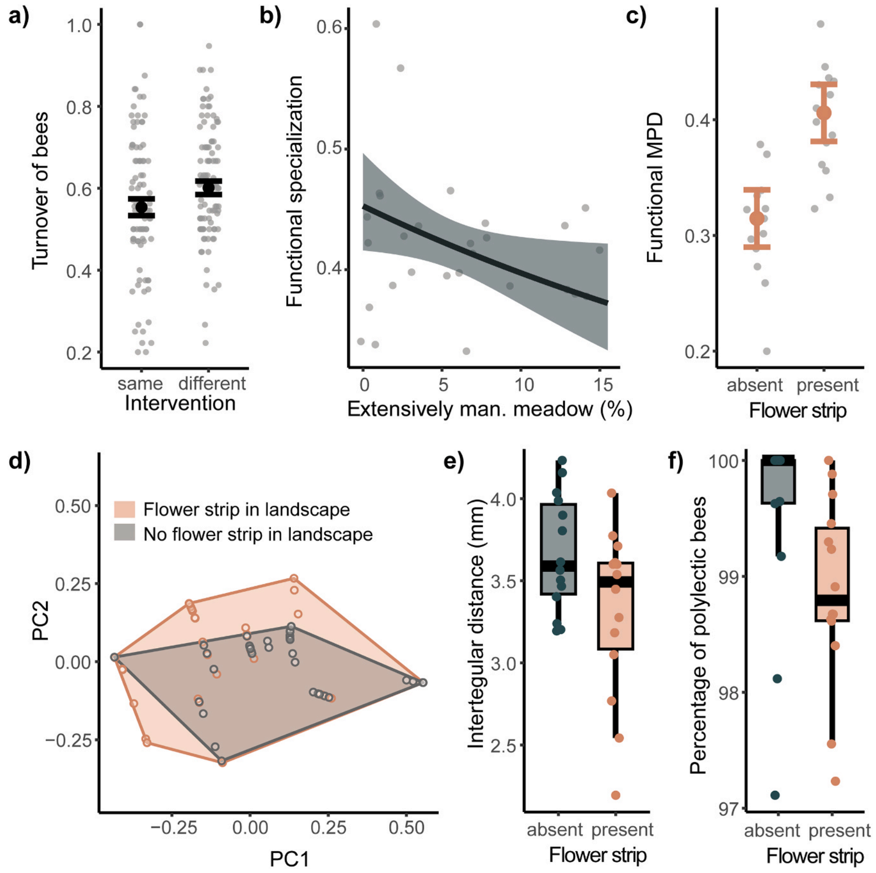

Fig. 3. Evidence for habitat heterogeneity. a) Turnover of bee species across patches of the same AES intervention (flower strip or extensively managed meadow) and across patches of different AES interventions,.

b) Functional specialization along increasing proportions of extensively managed meadows in landscape, c) Functional mean pairwise distance (MPD) between landscapes with and without flower strips, d) Functional space occupied in landscapes with and without flower strip. Each circle within the polygons represents a species positioned along PC1 and PC2 of the Principal Coordinates Analysis, e) Community weighted mean intertegular distance in landscapes with and without flower strips, f) Percentage of polylectic bees in landscapes with and without flower strips.

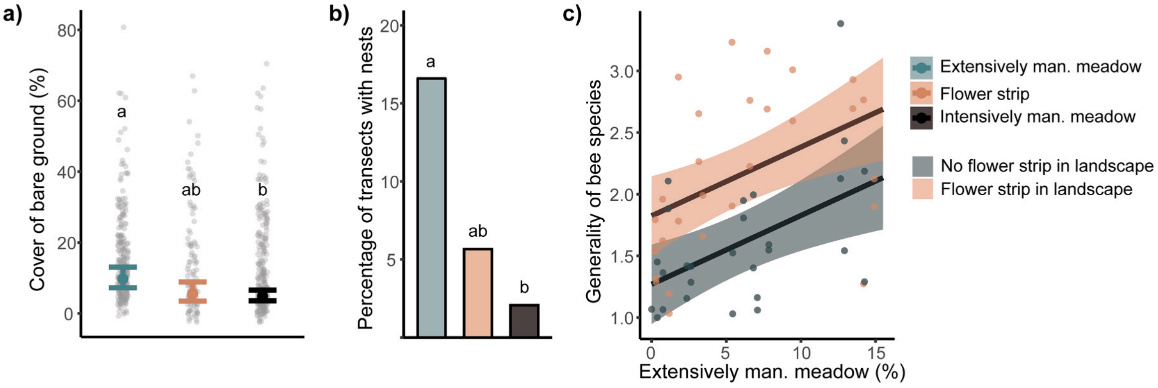

Fig. 4. Evidence for resource complementarity. a) Difference in the percentage of bare ground between flower strips and extensively and intensively managed meadows, b) Difference in the occurrence frequency of ground-nesting bee nests between flower strips and extensively and intensively managed meadows, c) generality of floral resource use in response to AES interventions.

managed meadows. Moreover, extensively managed meadows – and, to a lesser extent, flower strips - offered valuable nesting habitats for ground-nesting bees, potentially complementing nesting resources for bees that primarily forage in other land-use types. These results confirm recent findings that management strategies promoting bare soil constitute promising tools to support ground-nesting bees (Potts et al., 2005; Albrecht et al., 2023; Collins et al., 2025). Although nest-site availability for cavity-nesting bees was not addressed in this study, perennial flower strips provide various plant species with pithy hollow stems, such as thistles, which may offer good nesting sites for certain cavity-nesting species (Orr et al., 2015; Müller et al., 2024) – especially since these stems remain uncut and in place over winter. The complementarity of floral and nesting resources in flower strips and extensively managed meadows may therefore help alleviate resource limitation and promote larger populations of wild bees (Collins et al., 2025).

Different land-use types can harbor distinct sets of species and

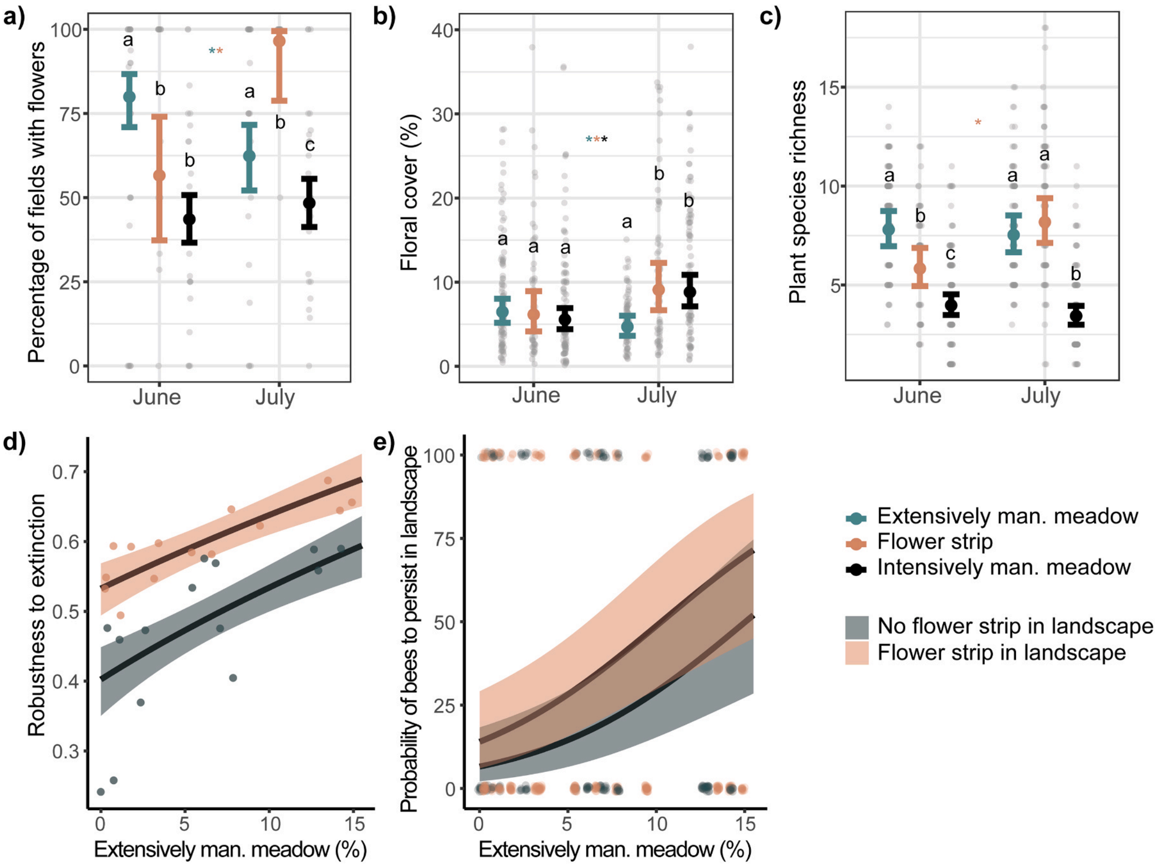

Fig. 5. Evidence for spreading of extinction risk. a) Proportion of patches with floral resources in different land-use types throughout the summer period, b) Flower abundance in in patches with floral resources of different land-use types throughout the summer period, c) flowering plant richness in different land-use types throughout the summer period, d) robustness of bees to risk of extinction from a landscape due to loss of food plants in response to AES interventions, e) Probability of bee species to persist in landscapes throughout the summer period in response to AES interventions.

increase species richness in heterogeneous landscapes (Maurer et al., 2022). Increasing habitat heterogeneity by combining different types of interventions may therefore be a promising tool to support more species within agricultural landscapes without increasing the total area allocated to AES interventions. In fact, we found that flower strips and extensively managed meadows shared only a small number of forage plant species and additively increased the richness of floral resources in landscapes in which they were both implemented (Klaus et al., 2023). Accordingly, each intervention also hosted unique sets of foraging bee species not found in other habitats, with species turnover being more pronounced across intervention types than across different patches of the same intervention. However, this difference in turnover was much weaker than that of flowering plant species, and the additional species contributed by flower strips decreased as the proportions of extensively managed meadows in landscapes increased. This suggests that flower strips and extensively managed meadows increasingly share bee species as extensively managed meadows in landscapes expand, possibly because different patches of extensively managed meadows vary in plant species composition, thereby also enhancing habitat heterogeneity. However, within a given area under AES interventions, species richness should still benefit from concurrent implementation, as suggested by the higher turnover across patches with different intervention types.

Several practices that have been introduced or expanded during agricultural intensification can negatively affect wild bees (Potts et al., 2016). Among the most important are landscape simplification and reduced floral resource availability resulting from improved weed control in crops, or from intensified fertilizer inputs and mowing regimes in grasslands (Dainese et al., 2019; Ekroos et al., 2020; Kline and Joshi, 2020). Bees with different traits may vary in their susceptibility to these stressors and, therefore, be selectively lost from agricultural landscapes (Hopfenmüller et al., 2014; Forrest et al., 2015; Persson et al., 2015). In contrast, AES interventions may help alleviate these selective pressures through the restoration of habitats. Here, we found that landscapes with flower strips particularly supported small, short-tongued and oligolectic species, which aligns with previous findings (Hevia et al., 2021; Kuppler et al., 2023). As central place foragers, small bees with short flight distances are particularly vulnerable to local food scarcity, and both oligolectic and short-tongued species have a limited ability to exploit certain floral resources as they rely on specific taxonomic groups or on short-tubed flowers to reach nectar (Borrell, 2005). Our findings therefore highlight the important role of flower strips in providing floral resources for bees during the summer, a period often marked by a general scarcity of floral resources in the agricultural landscapes of Central European agroecosystems (Harris et al., 2024). In contrast, landscapes with high proportions of extensively managed meadows were characterized by lower functional specialization, resulting in communities with more balanced response trait compositions. These findings suggest that extensively managed meadows provide an important habitat to a wide set of bee species and can alleviate various environmental filters that may vary between landscapes depending on the cultivated crops and the cropping system.

While the ongoing biodiversity deficit in agricultural land highlights the need to expand land area designated to biodiversity promotion (Garibaldi et al., 2021), such an increase directly conflicts with food production, particularly in high-productivity areas dominated by arable cropping systems. In Switzerland, for example, recent efforts to expand AES intervention areas on arable land to increase its severely deficient biodiversity (Richner et al., 2017; Meier et al., 2021) were rejected due to the direct trade-offs with food security and opportunity costs. Our findings highlight how AES can enhance the efficiency of biodiversity promotion per unit of land in agricultural landscapes through the targeted implementation of multiple, synergistically interacting intervention types. Such strategies may additionally reduce trade-offs with agricultural production by supporting ecosystem services to crops. Our study shows that the establishment of flower strips in combination with the extensive management of grasslands can synergistically increase the abundance of key crop pollinators in agricultural landscapes, which may alleviate pollination limitation and increase the yield of insect pollinated crops (Garibaldi et al., 2013; Kleijn et al., 2015; Turo et al., 2024).

Management strategies aimed at increasing the efficiency of biodiversity promotion through synergistic interactions among intervention types may be particularly effective when combining measures that provide distinct and complementary resources (e.g., different floral or nesting resources) and ensure a staggered supply of resources over time (e.g., shifted flowering peaks). Moreover, the effectiveness of specific intervention combinations, as well as their optimal scaling and spatial arrangement within agricultural landscapes, likely depends on the resource requirements and mobility of the targeted taxonomic groups (Riva and Fahrig, 2023). While our study focused on small-scale Swiss agricultural landscapes, the period of greatest resource scarcity for bees, and the two most relevant interventions during this period, future research should consider a broader set of interventions across different regions and throughout the full season. Such studies could assess how the connectivity, relative representation, and spatial configuration of interventions contribute to synergistic effects across multiple taxonomic groups. Understanding how intervention types interact across space and time may help identify combinations that maximize benefits for diverse taxa, determine the landscape contexts in which such synergies are most effective, and inform evidence-based guidelines for the design and spatial placement of agri-environmental measures.

CRediT authorship contribution statement

Chiara Durrer: Writing – review & editing, Investigation. **Anina Knauer:** Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Ahlam Sentil:** Writing – review & editing, Data curation. **Denis Michez:** Writing – review & editing, Data curation. **Matthias Albrecht:** Writing – review & editing, Methodology, Conceptualization.

Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2026.110281.

Data availability

The processed data supporting the findings of this study are available on figshare at: 10.6084/m9.figshare.26972566.

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