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Agri-environmental interventions enhance climatic niche complementarity and resilience of wild crop pollinator communities

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ABSTRACT

How diverse pollinator communities may promote resilience of crop pollination services in the face of increased climatic variability and to what extent such climatic resilience could be fostered through management options remains largely unexplored. Here, we address these research gaps using sweet cherry as a model crop. We quantified flower visitation by bee pollinators under the full range of variable temperature conditions throughout cherry flowering in 15 conventionally managed orchards chosen along a gradient of extensively managed agri-environment scheme meadows (AES meadows) in surrounding landscapes. Thermal niches for a total of 17 important cherry pollinator species based on 11’483 flower visits were determined. Thermal niche complementarity and resilience of wild bees visiting cherry (i.e. the summed temperature niches of species weighted by their flower visitation frequency), but not thermal niche breadth, was enhanced by the proportion of AES meadows in the landscape. We identified wild bee diversity and the broad thermal niches of bumblebees as important drivers of an enhanced resilience. Fruit set as a proxy of cherry yield was exceptionally low and not significantly influenced by thermal resilience or other tested bee community variables. We hypothesise that adverse weather conditions during fruit development were the main cause. Our study highlights the important role of thermal niche breadth and complementarity of diverse wild pollinator communities in providing resilience to crop flower visitation under variable climatic conditions. Our findings show that agri-environmental interventions can enhance such climatic response diversity and niche complementarity of wild crop pollinators underpinning resilience of crop pollination.

1. Introduction

Accelerating rates of global change and associated environmental disturbances and loss of biodiversity is threatening ecosystem functioning and the provisioning of vital ecosystem services (IPBES, 2019). Mitigating negative impacts on the stability and resilience of ecosystem services is therefore a key challenge of our time (IPBES, 2019; Mooney et al., 2009). Biodiversity is predicted to play a key role for the provisioning of stable and resilient ecosystem services (Tilman et al., 2014) through functional redundancy (i.e., the diversity of functionally equivalent species) (Feit et al., 2019; Rosenfeld, 2002) providing functional insurance against losses of species (“insurance hypothesis”) (Yachi and Loreau, 1999). Furthermore, biodiversity should underpin ecosystem service resilience through a “portfolio effect” against temporal variability in population dynamics of species in a community (Thibaut and Connolly, 2013), and response diversity (i.e., the diversity in response to changes in environmental conditions and disturbances within a community) (Elmqvist et al., 2003; Mori et al., 2013). Such response diversity could arise for example from different optima of realised environmental niches (niche complementarity) and tolerance range (niche breadth) of different species determining the realised community niche composed of individual species niches (i.e., “functional resilience”) (Kühsel and Blüthgen, 2015). While these concepts are well established in ecological theory, their relevance and the extent to which they may underpin the resilience of key regulating ecosystem services in agroecosystems, such as crop pollination services sustaining crop production in the face of climate change, remains poorly understood.

Crop pollination is an important regulating ecosystem service with more than three-quarters of the world’s major food crops at least partly relying on animal pollination (Klein et al., 2006), including in particular those providing essential micronutrients (Chaplin-Kramer et al., 2014),

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and is thus vital for food security (IPBES, 2016). Animal pollination contributes to both enhanced quantity and quality of crop yields (Gazzea et al., 2023; Reilly et al., 2020) with about half of the global economic contribution to crop pollination provided by wild pollinators (Garibaldi et al., 2013a; Reilly et al., 2024; Scheper et al., 2015). Bees are usually the most important pollinators of crops (Garibaldi et al., 2013b; IPBES, 2016), but their pollination services are jeopardized by multiple interacting pressures including land-use intensification and associated habitat loss, but also exposure to pesticides and climate change (Dick, 2023; Ghisbain et al., 2024; Goulson et al., 2015; IPBES, 2016; Nicholson et al., 2024; Vanbergen and Initiative, 2013).

Ongoing climate change may severely affect pollination services to crops due to the decline or loss of particularly effective pollinator species or homogenization of pollinator assemblages (Grab et al., 2019; IPBES, 2019; Vasiliev and Greenwood, 2020). Moreover, increasing climatic variability with more frequent extreme events, such as heat waves or droughts (Kazenel et al., 2024; Martinet et al., 2021) or asynchronous seasonal shifts of crop bloom and pollinator activity periods may contribute to impaired pollination services (Bartomeus et al., 2013; Duchenne et al., 2020; Forrest and Thomson, 2011).

Diverse crop pollinator communities with a high thermal niche complementarity and niche breadth may play an important role in enhancing the stability and resilience of pollination services in the face of such increased climatic variability (Kühsel and Blüthgen, 2015; Miñarro and García, 2018), but this hypothesis remains largely untested. In early flowering crops in temperate and northern climatic regions, these buffering functions may be particularly important to stabilized pollination services as weather conditions become increasingly variable during bloom. This includes cold periods when key crop pollinators, like managed honeybees, are inactive and unable to pollinate crops (Tuell and Isaacs, 2010; Vicens and Bosch, 2000). Identifying pollinator species and groups occupying particularly important climatic niches thereby ensuring climatic resilience of pollinator communities (Blüthgen and Klein, 2011; Miñarro and García, 2018) could help to guide pollination management strategies towards enhanced stability of pollination services. Therefore, it is crucial to deepen our understanding of how to foster response diversity and pollinator species playing key roles for resilient crop pollination services in the face of increasing climatic variability.

Landscape management through the implementation of agri-environmental schemes (AES) and the maintenance of semi-natural habitats in agricultural landscapes could be a promising way to enhance climatic response diversity of wild crop pollinators communities. Such measures have been shown to contribute to diverse pollinator communities in agroecosystems and improved pollination services (Albrecht et al., 2020; Dainese et al., 2019; Kovács-Hostyánszki et al., 2017; Maurer et al., 2022). For example, grassland extensification programs, which typically involve less frequent mowing and little to no fertilizer use, as promoted by the EU's Common Agricultural Policy (Batáry et al., 2015), can help to increase pollinator diversity in agroecosystems (Albrecht et al., 2007a; Ekroos et al., 2020; Johansen et al., 2022; Maurer et al., 2022). Such extensively managed grasslands generally promote pollinators through higher flower diversity (Albrecht et al., 2007b; Buri et al., 2014; Ekroos et al., 2020) and improved nesting opportunities for ground-nesting bees (Albrecht et al., 2023). However, it remains unexplored whether they also help to enhance the resilience of crop pollination services, for example through enhanced climatic response diversity of wild bee communities.

Here, we address these questions by examining how increasing amounts of AES areas, i.e. extensively managed meadows, in agricultural landscapes surrounding cherry orchards may promote climatic response diversity of cherry pollinator communities, the climatic resilience of pollination services and consequences on cherry yield. Sweet cherry (*Prunus avium L.*) was chosen as a model crop due to its high dependence on pollination service by wild pollinators and the high climatic variability which is characteristic for the flowering period in central Europe (Eeraerts et al., 2019; Holzschuh et al., 2012). Specifically, we test the following hypotheses: (1) Higher proportion of AES meadows in agricultural landscapes surrounding cherry orchards will enhance the diversity and abundance of wild bee pollinators in these orchards, which (2) translates in positive effects of AES on thermal niche complementarity and breadth, and thus enlarged thermal resilience of wild bee pollinator communities in cherry orchards with higher AES meadow in the surrounding landscape. (3) Enlarged thermal community niches are primarily driven by niche complementarity and the niche breadth of wild bees, with cold-tolerant species such as bumblebees playing a particularly important role. (4) Enlarged thermal community niches of wild cherry pollinators contribute to more stable and thus increased crop pollination services and crop yield, while managed pollinators play an inferior role.

2. Material and methods

2.1. Study system and design

Sweet cherry (*Prunus avium L.)* was chosen as a model crop as (i) its flowering period early in the year, which is mostly in April in the study region, typically exhibits high climatic variability, often including periods with cold temperatures in Central Europe and the study region, (ii) fruit set and yield strongly depends on insect pollination and (iii) wild pollinators and their species diversity can substantially contribute to cherry pollination and yield (Eeraerts et al., 2019; Holzschuh et al., 2012).

Extensively managed meadows were selected as AES interventions since they represent the most implemented type of agri-environment scheme measures to promote farmland biodiversity in Switzerland (BLW, 2023). The major management requirements of these meadows include postponed mowing (no mowing before 15 June in the study region), which also results in an overall reduced number of cuttings per year (typically twice a year, rarely less) and prohibition of any fertilizer applications (Bundesrat, 2013). Conventionally managed meadows, in contrast, are mown the first time considerably earlier and up to five or six times per year (if weather conditions allow it), and are fertilized, typically receiving high nitrogen inputs (Husse et al., 2017; Knop et al., 2006). Compared to conventionally managed meadows, this extensive management has been shown to increase the richness of vascular plant species (Knop et al., 2006; Albrecht et al., 2007b), as well as the richness and abundance of bees and hoverflies (Albrecht et al., 2007a).

A total of 15 conventionally managed cherry orchards (hereafter sites) were chosen in agricultural landscapes on the Swiss northern plateau. This region is characterized by a small-scaled mosaic of crops, agricultural grasslands and semi-natural habitats (SNH; mainly woodland remnants, hereafter forested area), as well as semi-natural grasslands. For the selection of sites, it was ensured that the percentage area covered with AES meadows in the landscape was not correlated with the percentage of the total area covered by grasslands (Pearson correlation: $r = -0.07$ and $p = 0.8$) or forest (Pearson correlation: $r = -0.38$ and $p = 0.16$) based on available GIS information using QGIS (QGIS Development Team, 2023). Based on average considered foraging ranges of wild bees (e.g. Greenleaf et al., 2007) 500 m and 1000 m buffer radii around cherry orchards were initially considered. Explorative analyses revealed that, overall, the proportion of AES meadows in landscapes around cherry orchards explained more variation (based on R^2 values of linear models) in bee community response variables at a 500 m buffer radius than at a 1000 m buffer radius (Table S1); therefore, a 500 m radius was chosen for further analyses. Sites were separated from each other by at least 1 km.

2.2. Sampling of bee pollinators

Bees visiting cherry flowers were sampled in each cherry orchard during three sampling rounds evenly distributed throughout the cherry bloom between April 8 and April 29, 2023. During each sampling round, four separate standardized transect walks (Westphal et al., 2008) of 100 m length were conducted along randomly selected rows of flowering cherry trees. Each transect walk was done in constant pace during 10 min while recording all individual bees (*Hymenoptera: Apoidea*) visiting cherry flowers (i.e. contacting flower reproductive organs). If visual identification on the species level was not possible, the observed bee was collected and identified by a taxonomic expert according to Westphal et al. (2008). Sampling time was paused during handling of bees (catching and transfer to killing jar). The low-trunk cherry trees in our study region are typically 3–4 m tall and are planted with 1–2 m and 3–4 m spacing within and between rows, respectively. During each transect walk, we recorded all the bees on one randomly chosen side of the tree rows. The cherry tree variety was not considered, as sampling was constrained to the short flowering time of cherry and many the orchards consisted of different varieties.

Rarefaction curves of sampling for wild bees showed saturation, indicating a sufficient sampling effort to capture the majority of bee species present (Fig. S1). At the beginning of each transect walk, temperature was recorded with a high-precision hand thermometer (Testo 175-H1) at a height of 1 m above ground in the shade. To be able to adequately determine thermal resilience of bee species, it was ensured that observations were made under the full range of temperature conditions from 7.2 °C to 28.7 °C during the flowering period of cherry (Kühsel and Blüthgen, 2015). Pollinator sampling was only done under dry weather conditions (no rain/snow falling) and no or almost no wind (wind speed < 2 m s^{-1}).

2.3. Measuring fruit set

Fruit set was used as a measure of pollination service delivery to cherry trees (e.g. Eeraerts et al., 2019; Holzschuh et al., 2012; Lech et al., 2008). To this end, sixteen trees were randomly selected in each orchard. From each selected tree, two clusters of ca. 15–30 flowers each (one in the lower part and one in the upper part of the tree) were randomly selected, marked and the number of flowers counted. Approximately five weeks later, developed cherry fruits were counted, and fruit set was determined as the proportion of developed fruits (i.e. the number of developed fruits divided by the number of flowers per cluster). Fruit set was again measured at the right before fruit harvest.

2.4. Determining thermal species and community niche variables

In a first step, the thermal niches of individual bee species were estimated according to Kühsel and Blüthgen (2015). The unimodal thermal niche of each species is characterized by two parameters: The weighted mean temperature at which it was recorded (thermal optimum), and the weighted standard deviation (thermal niche breath). Weighting is based on both the number of individuals recorded for each temperature and the sampling effort per temperature (Kühsel and Blüthgen, 2015).

To increase the robustness of estimated temperature niches of bee species observed in the cherry orchards, this data was complemented by an additional dataset of pollinators sampled in apple orchards in the same study region in 2017, strongly overlapping in the composition of frequently observed bee pollinators. The general sampling approach and methodology was identical to the one described above for the cherry orchards: in each of the eight apple orchards four sampling rounds were conducted covering the full range of temperature conditions during apple flowering period, which similarly ranged from 6.5°C to 26.8°C. In each orchard, four transects of 75 m length were conducted during 15 min of sampling time per transect. To ensure robust estimates of thermal species niches, they were only estimated for species with a minimum number of observations of at least six observations per species. This yielded in a total 11’483 flower visits by bees (observed during 310 transect walks) across the full range of temperature measured during the flowering period in 15 cherry and 8 apple orchards in the study region that could be used to determine thermal niches for a total of 17 important bee species visiting cherry flowers (see Fig. 1 and Table S3 for details).

In a second step, the calculated species thermal niche values were used to calculate thermal community niche parameters of the bee community of each of the 15 cherry orchard sites according to methodology proposed by Kühsel and Blüthgen (2015). Each community niche is defined by the composition of co-occurring bee species at an orchard site and defined by three parameters: the average species’ thermal niche optima, the variation of these thermal niche optima across the species that defines the thermal complementarity among species irrespective of their niche breadth (response diversity *sensu* Elmqvist et al., 2003) and the mean thermal niche breadths of the species (not considering variation in niche optima among species; Kühsel and Blüthgen, 2015). All measures are weighted by the proportional activity abundance (i.e. flower visitation frequency) of each species in the community (Kühsel and Blüthgen, 2015). Thermal resilience of the community in each orchard is defined as the integral of the summed species niches (community niche area), which is again weighted by the relative abundance of the contributing species. The resilience is standardized by dividing it by the maximum species niche amplitude, resulting in a measure of generality of realised thermal niches in the community with higher values for communities with low thermal specialization (Kühsel and Blüthgen, 2015). Thus, resilience can increase by two drivers: higher niche breadth and higher niche complementarity. Niche complementarity and breadth are not dependent on each other, as complementarity only reflects variation in thermal optima of different species, but not niche overlap (Kühsel and Blüthgen, 2015).

To explore thermal complementarity of individual bee species with honeybees, we additionally calculated their predicted activity, based on the calculated thermal niches, at temperature below 13°C, which was found to be the minimal foraging temperature for honeybees (Delaplane and Mayer, 2000; Winston, 1987)

2.5. Statistical analysis

To assess the effects of extensively managed AES meadows on wild bee diversity and abundance in cherry orchards (research question 1), we fitted separate linear models (LM) with Shannon diversity of wild bees and their abundance as response variable and the proportion of AES meadows as explanatory variable. We use Shannon diversity as it incorporates information about both species richness and evenness. To better understand how landscape composition affected the abundance of key groups of wild bees (with predicted importance for thermal resilience of wild bee communities), the abundance of bumblebees (*Bombus* spp.) and other (non-*Bombus* spp.) wild bees were additionally analysed.

To address research question 2, LMs were used to test for the effects of the proportion of AES meadows on different aspects of thermal niches of wild bee communities, i.e. niche complementarity, niche breadth and thermal resilience.

To explore the importance of wild bee diversity, and some taxonomic groups in particular, in shaping the thermal resilience, thermal complementarity and thermal niche breadth of wild bee communities (research question 3), we fitted separate LMs with wild bee Shannon diversity, abundance of *Bombus* spp. and abundance of non-*Bombus* spp. wild bees as explanatory variables. Thermal complementarity was square-root transformed to improve model fit.

Similarly, to assess the contribution of wild versus managed bees to the different aspects of the total bee communities’ thermal niches, i.e., thermal resilience, thermal niche complementarity and the thermal niche breadth, we fitted LMs with these metrics as response variables and the abundance of the different pollinator groups (*Bombus* spp., non-*Bombus* spp., *Apis mellifera*, *Osmia* spp.) and Shannon diversity as explanatory variables. As Shannon diversity was never a significant term and to reduce the risk of overfitting, this variable was dropped from the

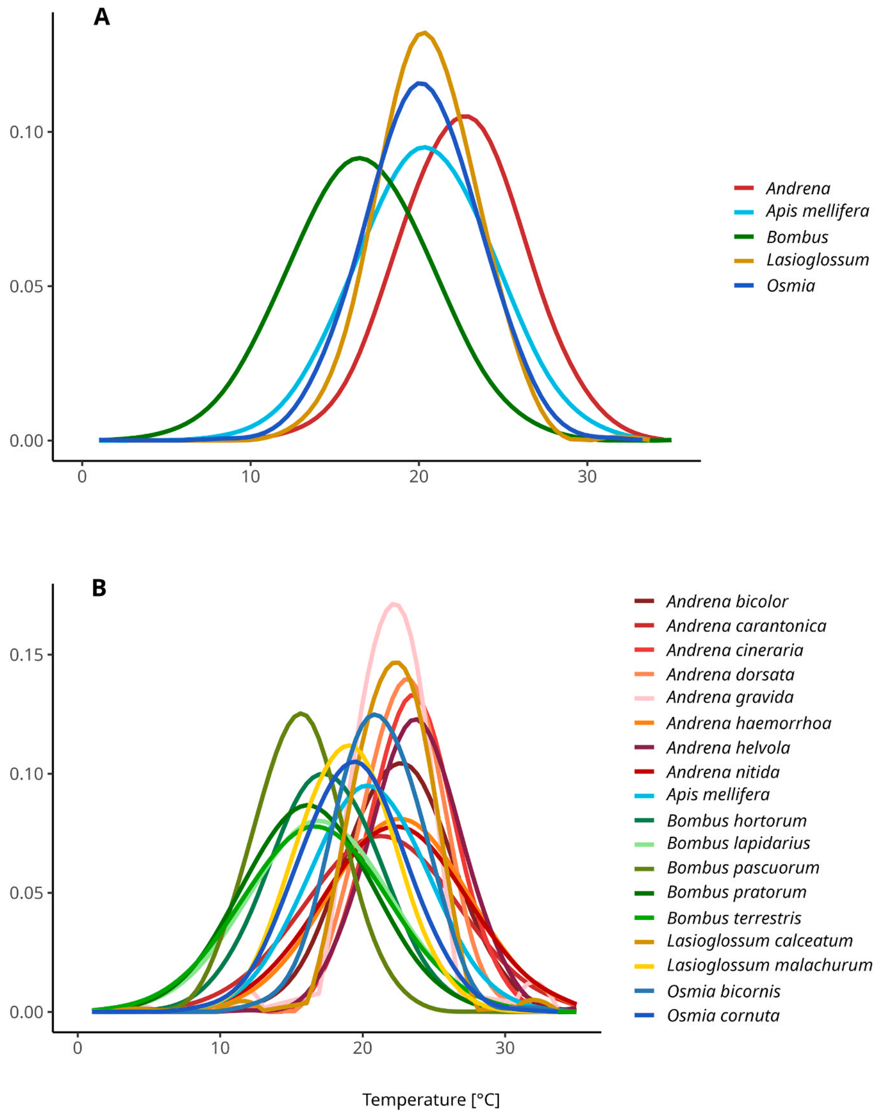

Fig. 1. Calculated average realised thermal niches for the major bee pollinator genera (A) and major bee pollinator species (B) in cherry orchards. Calculations are based on 11'483 flower visits of species (see methods for details). *Apis* (represented by the Western honeybee, *Apis mellifera*) and *Osmia spp.* (represented by *O. bicornis* and *O. cornuta*) were used as managed pollinators in the study orchards.

models. Again, thermal niche complementarity was transformed to increase model fit (log-transformation).

To address research question 4, i.e. to assess the role of thermal niches covered by wild and managed bee pollinators for the provisioning of cherry pollination services, three separate generalized linear models (GLM) with binomial error distribution were fit with fruit set as response variable (log-transformed) and the three thermal community descriptors (thermal community niche, thermal niche complementarity and thermal niche breadth of wild bees) as well as the abundance of managed bee pollinators as explanatory variables and the mean observed temperature as covariate. For this model, the thermal niches were quantified for the bee communities that were actively foraging during the day while the flowers used to measure fruit set were in bloom.

All statistical analyses were performed in R version 4.3.2 (R R Core Team, 2024). For LMs, assumptions of normality and homoscedasticity of residuals were assessed visually (Zuur et al., 2007, 2009a) and if needed the response variables were transformed for model fit. GLMs were checked for overdispersion, but fulfilled model assumptions. Outliers were removed from the analysis based on Cooks distance (calculated with the *performance* package with function check_outliers (Lüdecke et al., 2021). Type II ANOVA for LMs and likelihood ratio tests for GLMs were used for statistical inference (Zuur et al., 2009b).

3. Results

3.1. Bee pollinator communities and thermal resilience

A total of 6837 bees (6093 honeybees (*Apis mellifera*) 285 mason bees (*Osmia* spp.), 273 bumblebees (*Bombus* spp.) and 186 other wild bees) reflecting a total of 24 different bee species were observed in the 15 cherry orchards investigated. Mean thermal niches of bee genera (averaged across all species in each genus) and individual species are shown in Fig. 1 and exact values of calculated thermal optima and niche breaths in Table S2.

The optimal observed temperature for *A. mellifera* was 19.9°C (sd = 4.2). At temperatures below 13°C only 3.8 % of all *Apis mellifera* (Table S2) individuals were found to be active, corroborating findings of previous studies that honeybees generally do not forage at temperatures below 13°C (Delaplane and Mayer, 2000; Winston, 1987). In contrast, 20.9 % of all observed bumblebees were visiting flowers at temperatures below 13°C (Fig. 1A). The genus *Bombus* spp. showed the lowest optimal temperature (average across all species) of 16.0°C (sd = 4.36) and the broadest temperatures niches of the observed genera (Fig. 1A,B; Table S2). At the other end of the temperature spectrum were several species of the genus *Andrena* spp. (Fig. 1A,B; Table S2). The species of the remaining observed genera, *Lasioglossum* spp. and *Osmia* spp., ranged at intermediate average optimal temperatures (Fig. 1B, Table S2).

Further analysis of the species-specific temperature optima (Table S2) revealed that, besides all five *Bombus* species, *Lasioglossum malachurum* (18.34°C) and *Osmia cornuta* (18.8°C) showed lower temperature optima than *A. mellifera* (19.9°C) (Fig. 1B; Table S2).

3.2. Effects of AES meadows on thermal niches of wild bee communities

A high proportion of extensively managed AES meadows in the agricultural landscape surrounding cherry orchards increased the Shannon diversity ($F_{1,12}=10.92$, $p < 0.05$; Fig. 2; Table S3) and had a marginally significant positive effect on the abundance of wild bees visiting cherry flowers ($F_{1,13}=4.62$, $p = 0.051$; Table S3). Further in-depth analyses showed that the abundance of bumblebees (*Bombus* spp.) was not significantly related to AES meadows (Table S3), while non-*Bombus* spp. wild bees showed a positive relationship ($F_{1,12}=8.19$, $p < 0.05$; Table S3).

The thermal resilience and the thermal niche complementarity of wild bee communities in cherry orchards were positively associated with the proportion AES meadows around cherry orchards, ($F_{1,12}= 10.77$, $p < 0.05$; Fig. 3A; $F_{1,12}=7.50$, $p < 0.05$; Fig. 3B; Table S3), while thermal niche breath of wild bees showed a negative association ($F_{1,12}=4.68$, $p < 0.05$; Fig. 3C; Table S3). In each of the models for Shannon diversity, non-Bombus wild bees and thermal properties one statistical outlier was removed.

3.3. Bee community properties affecting thermal niches

Shannon diversity increased the thermal resilience and thermal niche complementarity of the wild bee community ($F_{3,10}=7.75$, $p < 0.05$, one statistical outlier removed; Fig. 4, Table S3, and $F_{3,11}=8.28$, $p < 0.05$; Table S3). Thermal niche breadth of the wild bee community was increased by the abundance of non-*Bombus* spp. wild bees ($F_{3,11}=20.57$, $p < 0.05$, Table S3).

Furthermore, thermal resilience of total bee communities (including the managed bees *Apis mellifera* and *Osmia* spp.) increased with the abundance of *Bombus* spp. ($F_{4,10}=60.15$, $p < 0.001$; Fig. 5A; Table S3) and with the abundance of non-*Bombus* spp. wild bees ($F_{4,10}=7.83$, $p < 0.05$; Fig. 5B; Table S3), while it decreased with the abundance of honeybees *Apis mellifera* ($F_{4,10}=17.20$, $p < 0.001$; Fig. 5C; Table S3). In contrast, the abundance *Osmia* spp. was only marginally related to the thermal resilience of bee communities ($F_{4,10}=4.29$, $p = 0.065$; Fig. 5D; Table S3). The thermal niche complementarity of the total bee community was positively related to the abundance of *Bombus* spp. ($F_{4,9}=62.37$, $p < 0.001$; Fig. 6A; Table S3) and non-*Bombus* spp. wild bees ($F_{4,9}=13.38$, $p < 0.001$; Fig. 6B; Table S3), but decreased with the abundance of *Apis mellifera* ($F_{4,9}=31.02$, $p < 0.001$; Fig. 6C; Table S3), while it was not significantly related to the abundance of *Osmia* spp. (Fig. 6D; Table S3) (one statistical outliner removed in these models). Thermal niche breadth of the total bee community was positively related to the abundance of *Bombus* spp. ($F_{4,10}=22.40$, $p < 0.001$; Fig. S3A; Table S3) and tended to be positively related to the abundance of *Apis mellifera* ($F_{4,10}=4.76$, $p = 0.054$; Fig. S3C; Table S3), while thermal niche breath decreased with the abundances of non-*Bombus* spp. wild bees ($F_{4,10}=15.77$, $p < 0.05$; Fig. S3B; Table S3) and *Osmia* spp. ($F_{4,10}=82.66$, $p < 0.001$; Fig. S3D; Table S3). In all three models, the Shannon diversity did not explain significant variation in the investigated thermal niche variables, thus it was dropped from the final models.

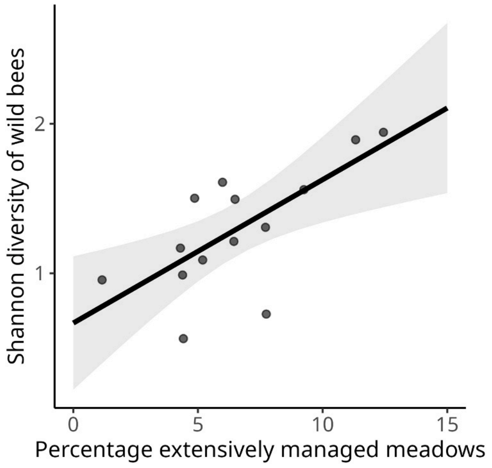

Fig. 2. Relationship between the proportion (%) of extensively managed agri-environmental meadows in landscapes surrounding cherry orchards (500 m radius) and Shannon diversity of wild bees visiting cherry flowers. The solid regression line shows a significant predicted linear relationship with 95 % confidence intervals (shaded areas). Points show raw data.

3.4. Cherry yield

Initial cherry fruit set was 45.7 %, which reduced to 11.8 % after abscission at the time of fruit harvest. Cherry fruit set was not significantly related to any descriptor of bee communities' thermal niches nor to the abundance of managed bees or the mean observed temperature (all p-values >0.17). Fruit set was not significantly related to the proportion of AES meadows in the surrounding landscape (Table S4).

4. Discussion

Our study shows that cherry orchards with higher amounts of less intensively managed meadows under the Swiss agri-environment scheme for meadow extensification in surrounding agricultural landscapes was associated with enhanced thermal resilience and complementarity of wild bee communities visiting cherry flowers. Our findings indicate overall diversity of bee communities and particularly the preference of bumblebees for cool temperatures and their broad thermal niches play a key role for thermal resilience and complementarity. Managed bee species, in contrast, did not significantly contribute to an increased thermal resilience. This highlights the importance of AES interventions to promote resilience of crop flower visitation under variable climatic conditions with potential implications for stability of pollination services and food safety.

4.1. Positive effects of AES meadows on diversity and thermal resilience of wild pollinator communities in cherry orchards

Maintenance and restoration of habitat quality of agricultural grasslands are considered to play an important role to sustain wild bee pollinators in European agroecosystems (e.g. Albrecht et al., 2007a; Ammann et al., 2024; Maurer et al., 2022; Öckinger and Smith, 2007). Meadow extensification schemes including postponed and less frequent mowing and abandonment of fertilizer inputs generally result in more diverse plant communities and high availability of floral resources (e. g. Albrecht et al., 2007b; Humbert et al., 2012; Johansen et al., 2019), which has been shown to be positively associated with wild bee abundance and diversity (Albrecht et al., 2007b; Buri et al., 2014), including both rare species (Ekroos et al., 2020; Sutter et al., 2017) as well as important crop pollinators (Sutter et al., 2017). Such AES meadows can also be substantially for more suitable nesting habitat of ground-nesting wild bees, including species frequently observed as cherry pollinators in the present study, such as several *Andrena* species or *Lasioglossum*

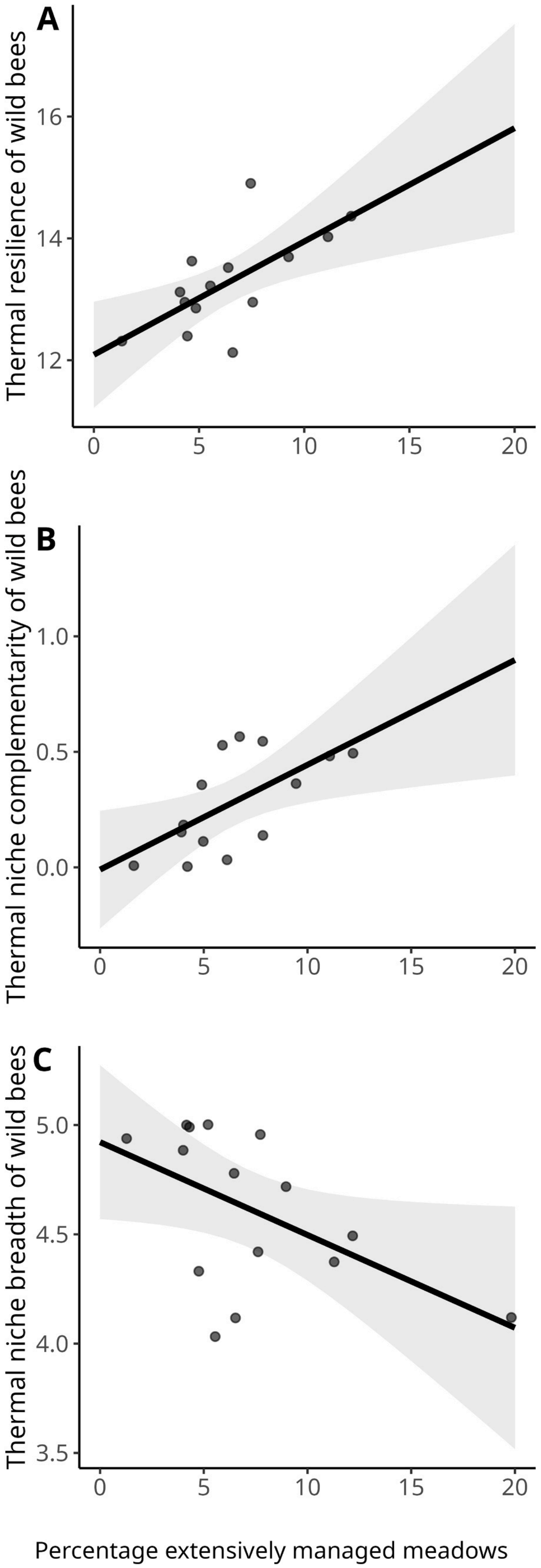

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Fig. 3. Relationships between the proportion (%) of extensively managed agri-envrionmental scheme meadows in landscapes surrounding cherry orchards (500 m radius) and (A) thermal resilience, (B) thermal niche complementarity and (C) thermal niche breadth of wild bee communities visiting cherry flowers. Solid regression lines show significant predicted relationships with 95 % confidence intervals (shaded areas). Points show raw data. Removing outliers were based on Cook's distance tests, but this did not change the outcoming result (see Fig. S2).

malachurum (Albrecht et al., 2023). Our study highlights that higher amount of AES meadows around cherry production sites, can, beyond increasing pollinator diversity within AES meadows themselves, enhance the taxonomic diversity, and importantly also thermal complementarity and ultimately thermal resilience of wild crop pollinators of cherry crops. Considering that the abundance of bumblebees, playing an important role through there broad niche also covering cool temperature (see below), did not significantly increase with the proportion of AES meadows, in contrast to wild bee diversity, which strongly increased, these findings highlight the important role of enhanced wild bee diversity in orchards surrounded by high amounts of AES meadows as a key driver of thermal niche complementarity and resilience in such orchards. These results demonstrate the potential of agri-environmental measures to foster climatic response diversity of crop pollinator communities driving the resilience of crop flower visitation as a key prerequisite for stable pollination services in the face of climate change and concomitant increased climatic variability and frequency of extreme weather events (Mori et al., 2013). These findings should therefore encourage producers to implement such agri-environmental measures on their farmland to promote stable pollination of their crops.

In contrast, we found a negative relationship between AES proportion and average thermal niche breadth, although it should be noted that one data point reflecting a particularly low mean niche breadth at an orchard with a high proportion of AES meadows in the surrounding landscape had a strong influence on this relationship, which therefore should be interpreted with adequate caution. A possible explanation for this finding might be that along with the increase in bee species with increasing AES meadow proportion there was an over proportional increase in species with relatively low niche breadth. As there was no significant relationship between the thermal niche breadth of a species and the number of times it was observed (Pearson correlation analysis, p-value = 0.63), such a potential methodological artefact can be ruled out as a possible explanation.

4.2. The important role of diverse wild bee communities for thermal resilience in crop pollination

From the calculated thermal species niches (Fig. 1B, Table S2), we could confirm that the Western honey bee, *Apis mellifera,* is a poor visitor to crop flowers below the often-cited critical minimum temperature of 13°C (Abou-Shaara, 2014; Delaplane and Mayer, 2000; Winston, 1987), as only 3.6 % of all recorded flower visits by honey bees were recorded below this threshold. In contrast, 20.9 % of all recorded bumblebee visits were below 13°C, highlighting the important role of bumblebees for cherry pollination services during periods of cool temperatures. This finding is consistent with previous studies, which showed that bumblebees have evolved to be active under cooler temperature conditions (Dehon et al., 2019). They may therefore play a key role in supporting the thermal resilience of pollination services for crops that flower early in spring, when temperature fluctuations and cold periods are common (Fründ et al., 2013; Miñarro and García, 2018). In contrast, *Andrena* spp. showed foraging activity at the higher end of the observed temperature spectrum, thereby also contributing to thermal complementarity and resilience of wild pollinator communities (Fig. 1B).

Our findings provide insights into the underlying drivers of climatic resilience of flower visitation by pollinators in cherry orchards. They

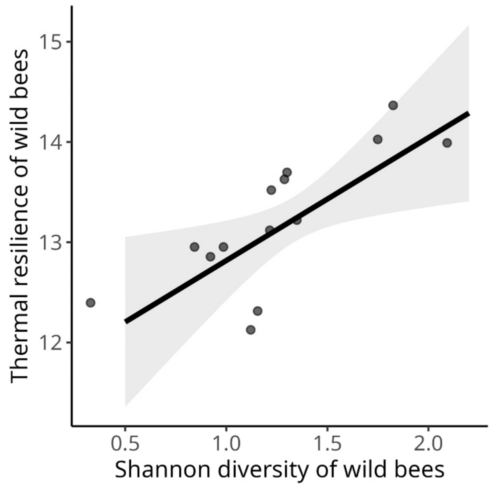

Fig. 4. Relationship between thermal resilience of wild bee community and Shannon diversity of wild bees and the thermal niche complementarity of wild bees visiting cherry flowers. The solid regression line shows a significant predicted linear relationship with 95 % confidence interval (shaded areas). Points show raw data.

indicate that thermal resilience and complementarity was primarily driven by wild pollinator communities, while managed pollinators did not significantly contribute. The thermal resilience of cherry bee pollinators can be interpreted as a measure of the niche generality of a community. In our study, in particular bumblebees, *Bombus* spp., but to lesser extent also non-*Bombus* spp. wild bees played a key role in contributing to such thermal niche generality and resilience of cherry flower visitation. These results demonstrate the important contribution of wild bees to potentially more resilient ecosystem services and more stable pollination under variable temperature conditions through a higher diversity of thermal responses (Elmqvist et al., 2003), thereby contributing to a portfolio effect (Thibaut and Connolly, 2013). While we focused on bee flower visitors as the most important pollinator group of cherry pollinators (e.g. Eeraerts et al., 2017), it would be interesting to also explore the role of non-bee flower visitors for climatic complementarity and resilience in future studies (Garratt et al., 2014, 2016).

Ongoing climate change is predicted to be even more pronounced in the future with more extreme weather events such as more frequent and prolonged heat waves and cold spells, with likely negative consequences for pollinator communities and pollination services to crops (Hemberger et al., 2023; IPBES, 2016; Walters et al., 2022). Our study corroborates expectations that different pollinator taxa will show distinct responses to changing climatic conditions (Walters et al., 2022). Certain cherry pollinator taxa such as the studied *Andrena* species may benefit from warmer temperatures. In contrast, the relatively low thermal optima of bumblebees, *Bombus* spp., suggests that this genus is well adapted to cold spells, but will be particularly vulnerable to warming and heat waves (Martinet et al., 2021b; Soroye et al., 2020). A high number of wild bee species with wide and complemental thermal niches may stabilize pollination services under climate change (Kühsel and Blüthgen, 2015).

Beside temperature as a key aspect of climatic conditions determining the activity of insects (Kühsel and Blüthgen, 2015), also other factors such as wind could affect pollinators' responses and consequences on crop flower visitation and pollination services (Brittain et al., 2013a, 2013b; Winfree and Kremen, 2008). Future studies could therefore further explore the role of response diversity to various aspects of climatic conditions and its contribution to promote the resilience and stability of flower visitation and pollination services to crops.

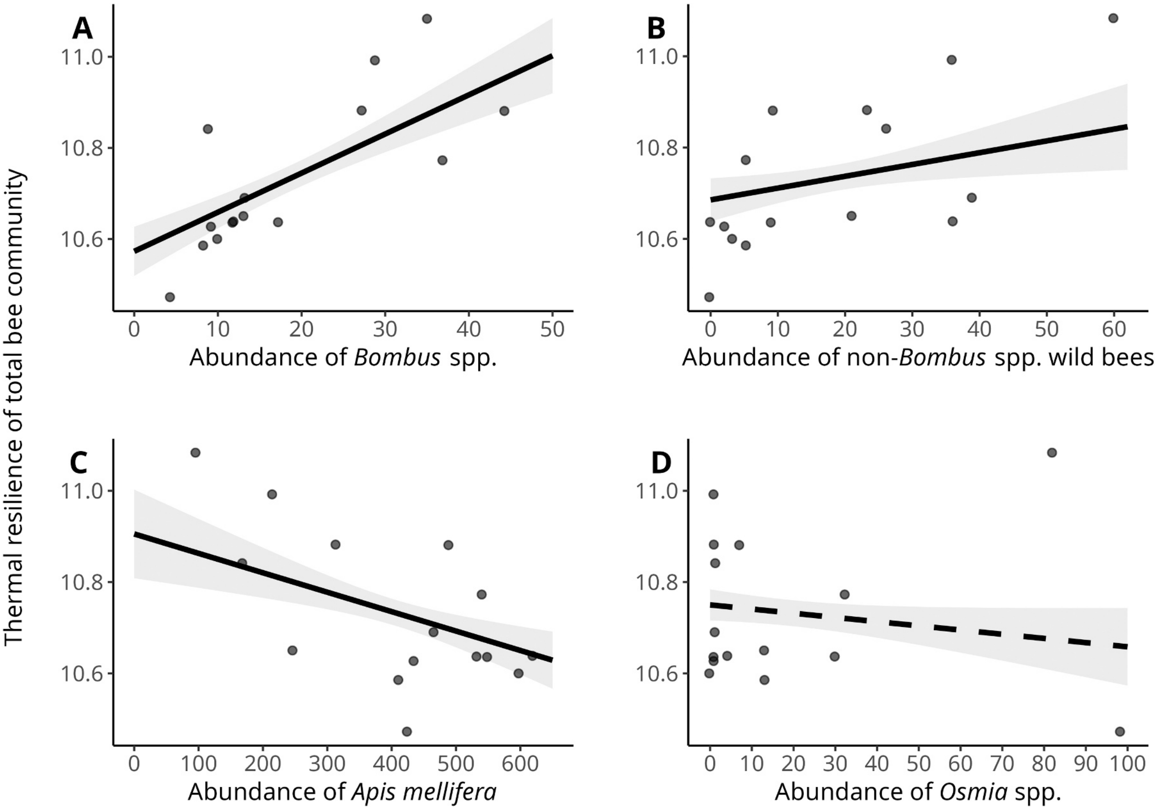

Fig. 5. Relationships between thermal resilience of the total bee community and the abundance of *Bombus* spp. (A), non-*Bombus spp.* wild bees (B), *Apis mellifera* (C) and *Osmia* spp. (D). visiting cherry flowers. Solid regression lines show significant predicted linear relationships with 95 % confidence intervals (shaded areas), the dashed line shows a trend ($p < 0.1$). Points show raw data.

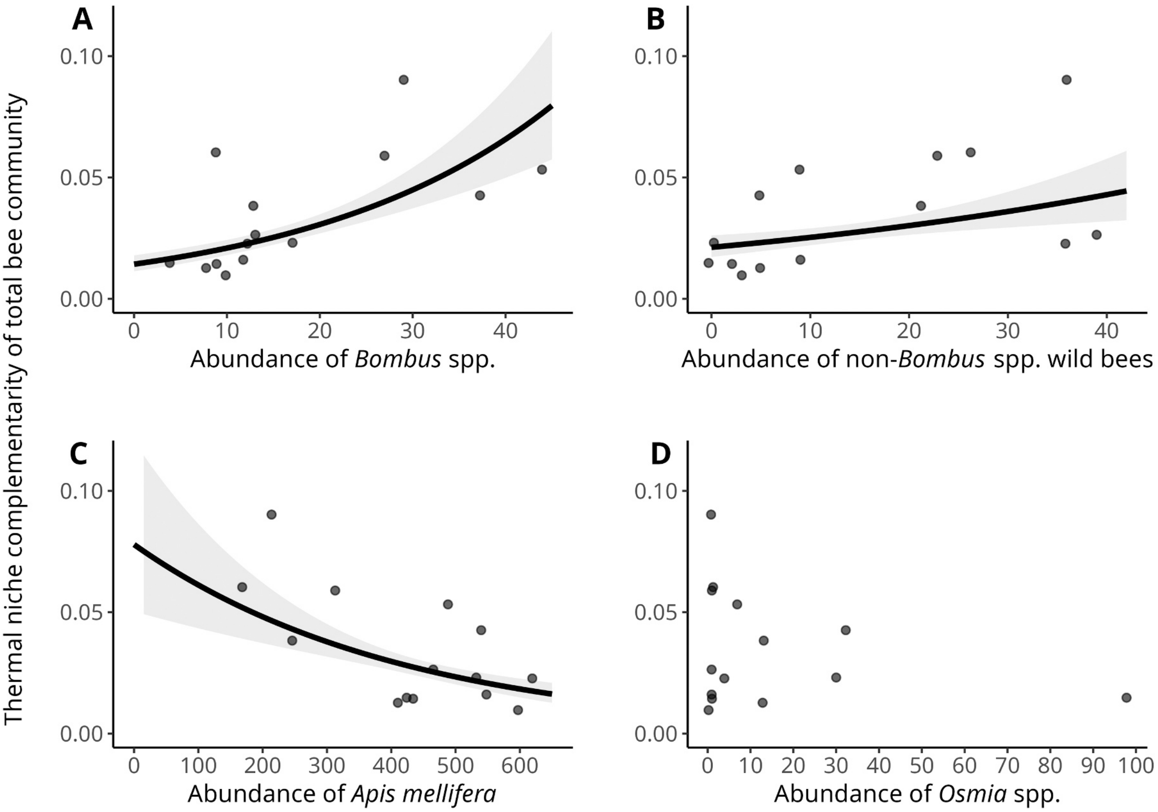

Fig. 6. Relationships between thermal niche complementarity of the total bee community and the abundance of *Bombus* spp. (A), non-*Bombus* spp. wild bees (B), *Apis mellifera* (C) and *Osmia* spp. (D). visiting cherry flowers. Solid regression lines show significant predicted linear relationships with 95 % confidence intervals (shaded areas). Points show raw data.

4.3. The role of managed bees for thermal resilience in crop pollination

Although honeybees clearly dominated cherry pollinator communities in terms of flower visitation rates, their dominance was limited to specific thermal conditions. As a result, thermal resilience and complementarity decreased with increasing honeybee abundance. However, our study highlights that wild pollinator diversity can contribute to increased overall thermal resilience of pollinator communities and more stable pollination services to crops (Blitzer et al., 2016; Eeraerts et al., 2019; Garibaldi et al., 2013a; Holzschuh et al., 2012; Martins et al., 2015; Woodcock et al., 2019). Wild bees may even compensate for the absence of *A. mellifera,* thereby contributing crucially to the stability of pollination services (Guler and Dikmen, 2013; Vicens and Bosch, 2000).

In the study region, *Osmia cornuta* and/or *O. bicornis* are commonly released in orchards to improve pollination of fruit trees. From those two species, *Osmia cornuta* showed foraging activity in cherry orchards at lower temperatures (optimum at 18.8°C) than *O. bicornis* (20.6°C) or honeybees (19.9°C) and thus provides further insurance of pollination services during cold periods in addition to wild bee species (Vicens and Bosch, 2000). Despite this advantage as a cherry pollinator species, and in addition to its high per visit pollination efficiency (Eeraerts et al., 2020), their use as managed pollinators should be treated with caution owing to several risks: large introduced populations may (i) result in resource competition with local populations of wild bee species (Ings et al., 2006), (ii) cause genetic hybridization with wild *O. cornuta* populations (Velthuis and Van Doorn, 2006) and (iii) promote the spread of pathogens spilling over to wild bees — similar to observation for pathogen spillover from managed bumblebees (Graystock et al., 2013) – with unknown-long term consequences on their populations.

4.4. No effects of enhanced thermal community niche detected on cherry yield

Several studies have reported positive effects of wild bee abundance, species richness, and functional diversity on cherry fruit set and yield (Eeraerts et al., 2019; Garratt et al., 2014; Holzschuh et al., 2012; Pisman et al., 2022), demonstrating the generally high pollinator dependence of cherry production. In the present study, however, cherry fruit set was neither related to the abundance of managed bees nor the abundance or diversity of wild bees or any thermal community metric. This contrasting result could be due to several factors. First, pollination deficits in species poor sites may have been compensated partially by the release of managed *Osmia bicornis and/or O. cornuta* into cherry orchards. These *Osmia* species have been shown to be highly efficient in pollinating cherry crops (e.g. Eeraerts et al., 2020; Magnin et al., 2025), in particular *O. cornuta,* which is also active at low temperatures, like bumblebees (Fig. 1B, Table S2), and typically exhibits high fidelity to *Rosaceae* fruit crops (Knauer et al., 2024). However, our analyses do not support this explanation as no such positive relationships between flower visits by *Osmia* bees, or any other group of cherry pollinators, was found in our study. Thus, most likely, highly unfavourable climatic conditions during the study year have caused damage to developing fruits. Late spring temperatures were clearly below the average of the last 30 years including several frost nights and 140 % of the average rainfall (MeteoSchweiz, 2023). In fact, only 45.7 % of flowers developed into fruits, and this proportion declined further with fruit abscission to just 11.8 % of harvestable fruits. These values are extraordinarily low compared to normal harvests of e.g. 31.3 ± 13.9 % harvestable fruits in the year 2008 (N = 192 flower clusters of 24 cherry orchards; Cereghetti 2019). Moreover, as it was not possible to focus on a single variety for fruit set measures due to the high variability of variety composition across orchards, this could have further contributed to the unexplained variation in fruit set. The absence of a significant effect of thermal niche metrics on cherry yield should therefore be interpreted with caution, and rather as a strong direct — pollination independent— impact of adverse weather conditions during fruit development, masking any impact of pollination services and drivers of on yield.

4.5. Conclusions and implications for policy and management

Our study showcases how agri-environmental interventions such as meadow extensification measures can enhance climatic response diversity of wild bee pollinators, complementarity, and the resilience of crop flower visitation, likely providing buffering and insurance functions underpinning stable crop pollination services. Our findings highlight, in addition to the key role of a high diversity of wild bee pollinators, the important contribution of bumblebees with their particularly broad thermal niches to this buffering effect in the face of climatic variability including cool temperature periods in early flowering crops such as cherry. These findings should therefore encourage farmers and land managers to implement agri-environmental and other measures to promote wild pollinators, and decision makers to foster them through respective policies.

CRediT authorship contribution statement

Anina Knauer: Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Chiara Durrer:** Writing – original draft, Methodology, Investigation, Formal analysis. **Matthias Albrecht:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Jaboury Ghazoul:** Writing – review & editing, Supervision.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Matthias Albrecht reports financial support was provided by Agroscope. If there are other authors, they 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.2025.110047.

Data availability

Data will be made available on request.

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