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Report on generic model predicting the contribution of pollinator diversity to stability of pollination and crop yield under different land use and climate change scenarios

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Matthias Albrecht[1], Chiara Durrer[1], Anina Knauer[1]
[1] *Agroecology and Environment, Agroscope, Zürich, Switzerland*

SHOWCASE

SHOWCASing synergies between agriculture, biodiversity and Ecosystem services to help farmers capitalising on native biodiversity

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Preface

Loss of biodiversity in agroecosystems is jeopardizing the provisioning and stability of ecosystem services such as pollination and pest regulation services supporting crop production, and importantly in the face of ongoing global change. To be able to better buffer such ecosystem services against increasing environmental disturbances, such as extreme weather events and increased variability of climatic conditions, a better understanding of the role of agrobiodiversity buffering such effects for example through climatic response diversity among species, as well as knowledge how this could be fostered through management options are required. Currently, it remains for example poorly explored how such climatic response diversity and resilience could be fostered by interventions such as agri-environmental measures and landscape management to restore and maintain for biodiversity in agricultural landscapes in Europe. In Task 3.4 we therefore addressed these basic and applied knowledge gaps through different approaches, including data collection in SHOWCASE EBAs used for an in-depth case study analyses and for the contribution to general quantitative synthesis analyses and modelling based on a large compilation of published and unpublished data collected at a total of 296 apple and cherry production sites across major climatic and biogeographic regions of Europe. Here, we report about the main findings of this work and discuss their implications.

Key takeaway messages

- In-depth EBA case study analyses showcase an enhanced climatic response diversity (thermal niche complementarity and thermal resilience of cherry flower visitation by wild bees as important aspects of stable pollination service provisioning under variable climatic conditions with increased proportion of agri-environmental interventions (less intensive meadow management) in landscapes around cherry orchards. Thermal resilience was primarily driven by species groups with broad thermal niches such as bumblebees pollinating cherry also during cool temperatures, as well as thermal niche complementarity among species.

- Quantitative synthesis models based on a total of 28 datasets including 296 apple and cherry production sites across major production regions of Central and Northwestern Europe highlight enhanced apple and cherry pollination services (assessed as fruit set and other measures also representing proxies of crop yield) increased with wild bee communities' thermal niche complementarity, but not thermal resilience.

- Thermal niche complementarity increased with species richness of wild bee communities pollinating apple and cherry, and both wild bee species richness and thermal niche complementarity increased with the proportion of semi-natural habitat in the agricultural landscape around orchards. Our model predicts an increase in thermal niche complementarity of 35% from 0% to 20%, and an increase of 133% to 60% semi-natural habitat in the landscape.

- Thermal niche complementarity of natural enemy communities (aphid regulating hoverflies) increased with the proportion of semi-natural habitat in the agricultural landscape around orchards. But neither thermal niche complementarity or any other tested descriptor of aphidophagous hoverfly communities and their activity in cherry and apple orchards was significantly related to crop yield proxies, potentially due to factors such as high aphid pest regulation through insecticides.

- The findings of this task indicate an important role of thermal niche complementarity of diverse wild bee communities in buffering variability in climatic conditions, thereby increasing climatic stability of pollination services for early flowering cherry and apple crops in Central and Northwestern Europe. Moreover, they showcase how agri-environmental interventions and the restoration and maintenance of semi-natural habitats in agricultural landscapes can support this buffering function of diverse wild bee pollinator communities.

Summary

Enhancing farmland biodiversity is predicted to buffer regulating ecosystem services sustaining crop production, such as crop pollination services, against environmental change, including extreme weather events and increased variability of climatic conditions, for example through enhanced climatic response diversity (niche complementarity) among species and broad niche breadths of communities. However, this remains poorly understood. Moreover, to what extent such buffering functions could be fostered by interventions such as agri-environmental measures and landscape management to maintain habitat for biodiversity remains largely unknown. In this task we addressed these knowledge gaps through different approaches: in a first sub-task, we collected empirical data in SHOWCASE EBAs; in a second sub-task, we addressed these knowledge gaps through a general analysis and modelling approach based on quantitative synthesis of a total of 28 published and unpublished studies including 296 apple and cherry production sites across Central and Northwestern Europe. In the first sub-task, we quantified cherry flower visitation by bee pollinators under the full range of the often highly variable temperature conditions during the flowering period of this crop as a proxy of pollination services throughout the flowering period of this early flowering crop along independent gradients of agri-environmental interventions (extensively managed agri-environment scheme meadows (AES meadows) and woody semi-natural habitat, and assessed consequences on fruit set as a measure of crop yield. Results show that thermal resilience of cherry flower visitation by wild bees increased with the proportion of AES meadows in landscapes around orchards, but not with the proportion of woody semi-natural habitat. Our analysis indicate that this was primarily driven broad thermal niches of bumblebees, which were also actively pollinating cherry during relatively cool temperatures, as well as thermal niche complementarity among wild bee species. Fruit set as a proxy of cherry yield was exceptionally low in this study reflecting the generally exceptionally low fruit set of cherry in the production region and year, and was neither significantly related to thermal resilience nor any other tested flower visitation variable such as visitation frequency, probably due to a strong negative impact of pollination independent unfavourable weather conditions during fruit development. In sub-task two, we were able to calculate thermal niches of 45 bee pollinator species and 11 aphidophagous hoverfly species that can provide important pest (aphid) regulation services in apple and cherry orchards. Preliminary results highlight substantial thermal complementarity among both wild bee pollinator species as well as among aphidophagous hoverfly species. Apple and cherry pollination services, measured as fruit set or other measures directly related or expected to be associated with crop yield, increased with wild bee communities' thermal niche complementarity, irrespective of the crop species, while none of the other tested pollinator community and crop flower visitation variables were significantly related to pollination services. Thermal niche complementarity increased with species richness of wild bee communities, and both, species richness and thermal niche complementarity of wild bees pollinating apple and cherry increased with the proportion of semi-natural habitat in the agricultural landscape around orchards. Our model predicts a non-linear increase of thermal niche complementarity of 42% from 0% to 20% semi-natural habitat in landscapes surrounding orchards, and a 57% increase to 60% semi-natural habitat, respectively. The proportion of semi-natural habitats was also positively related to thermal niche complementarity of aphidophagous hoverflies. However, neither thermal

complementarity or any other tested variable of aphidophagous hoverfly communities was significantly related to tested crop yield proxies.

The findings of this task indicate an important role of enhanced thermal niche complementarity of diverse wild bee communities in buffering variability in climatic conditions during the flowering period of early flowering cherry and apple crops, thereby positively influencing pollination services for these crops in Central and Northern Europe. They also showcase how agri-environmental interventions can enhance climatic response diversity and resilience of crop flower visitation, and how fostering thermal niche complementarity of diverse wild pollinators through restoration and maintenance of semi-natural habitats in agricultural landscapes can support fruit production of apple and cherry crops.

List of abbreviations

AES	Agri-environment scheme
EBA	Experimental Biodiversity Areas
EU	European Union
SNH	Semi-natural habitat

1 Introduction

Loss of biodiversity in agroecosystems is threatening the provisioning of vital ecosystem services supporting crop production and their stability and resilience in the face of ongoing global changing (IPBES 2019). Crop pollination is such a key 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., 2007; IPBES 2016) by managed and wild pollinators such as wild bees (Kleijn et al. 2015), contributing to both the quantity and quality of crop yields (Reilly et al. 2020; Gazzea et al. 2023). Aphidophagous hoverflies are important predators of aphids, which are key pests in numerous crops (Hogg et al. 2011), thereby proving important natural pest control services (in addition to pollination services) in agroecosystems (Pekas et al. 2020; Rodriguez-Gasol et al. 2020). Biodiversity of pollinators and natural enemies is predicted to play a key role for the provisioning of stable and resilient ecosystem services (e.g. Tilman et al. 2014), for example by providing insurance against losses of functionally redundant species ("insurance hypothesis"; Yacci & Loreau 1999; Feit et al. 2019) and "portfolio effects" against temporal variability of populations of species in a community (Thibault & Connolly 2013), as well as through response diversity (i.e., the diversity in responses of different taxa within a community to changes in environmental conditions (Mori et al . 2013). Such response diversity could arise for example from complementarity in the optima of realized climatic niches of species and their tolerance ranges (niche breadths) in a community niche, providing "functional resilience" to communities (Kühsel & Blüthgen 2015). Fostering diverse crop pollinator communities could increase climatic response diversity and enhance climatic niche complementarity, which could provide functional resilience and stability to crop pollination services during increasingly variable weather conditions (Tuell et al. 2010).

Both the implementation of agri-environmental interventions and the restoration and maintenance of semi-natural habitats (SNH) in agricultural landscapes are predicted to foster climatic response diversity of wild crop pollinators and natural enemy communities (Feit et al. 2019). In fact, such measures have for example been found to promote pollinator diversity (Maurer et al. 2022). For example, wild bee pollinators have been shown to benefit from increased flower diversity and better nesting opportunities of grassland extensification measures as also promoted through the Common Agricultural Policy of the EU (Batáry et al.

2015), and can help to increase pollinator diversity in agroecosystems (e.g., Albrecht et al. 2007; Ekroos et al. 2020; Albrecht et al. 2023). Furthermore, the restoration and maintenance of woody SNH such as forest lots and hedgerows can help to sustain important crop pollinators and diverse pollinator communities in agroecosystems (Bertrand et al. 2019; Ammann et al. 2024). However, their role in potentially also enhancing climatic niche complementarity and resilience of pollinators communities visiting flowers of crops, crop pollination services and consequences on crop yield remain largely unexplored. Similarly, how such landscape management could affect climatic niche properties of natural enemy communities providing pest control services and consequences on crop yield remains poorly understood.

In Task 3.4, we address these knowledge gaps within two sub-tasks. In a first sub-task, a SHOWCASE EBA in Switzerland was specifically designed to address the task objectives focusing on cherry pollinators and how the resilience of cherry pollination services may be enhanced by agri-environmental interventions and SNH in landscapes around cherry orchards. Specifically we examined the relationships between the proportion of agri-environment scheme meadows (AES meadows) and woody SNH in agricultural landscapes surrounding cherry orchards on the diversity and abundance of wild bee pollinators in these orchards, how the role of predicted increase in wild pollinator diversity with increasing proportions of AES meadows and woody SNH affects thermal niche complementarity among pollinator species thermal community niche breadth and resilience of cherry flower visitation by wild pollinator communities in orchards, and how predicted enhanced thermal niche complementarity and resilience affects cherry yield assessed as fruit set (see section 2.1). Moreover, empirical data on crop flower visitation along with precise temperature measures under variable thermal conditions and the provision of crop pollination services was collected in further SHOWCASE EBAs in which insect-pollinated crops and pollination services were studied (the Netherlands, Spain). Part of this data (see specifications below in section 2.1) was then used for the analyses performed in sub-task two. In sub-task two, a more general understanding of the impact of different scenarios of land use in European agricultural landscapes on the diversity, climatic niche complementary (response diversity) and climatic resilience of pollinators (bees) and providers of natural pest control services (aphidophagous hoverflies) was assessed, as well as the role of thermal niche complementarity and resilience for the provisioning of pollination services and proxies of crop yield. To this end, EBA data were complemented with large number of published and unpublished data collected at a total of 296 apple and cherry production sites across major climatic and biogeographic regions in (see detailed description in section 2.2).

2 Methods

2.1 EBA data collection and case study

To address the objectives of this task, empirical data have been collected in a subset of SHOWCASE EBAs in which insect-pollinated crops were studied (Switzerland, the Netherlands and Spain) across multiple years according to the standardized common SHOWCASE protocols developed in Task 1.2. As aphid regulating hoverflies, as our natural enemy target group for this task, were only measured and identified at species level in one EBA, species thermal niches of aphidophagous hoverfly species, climatic response diversity and resilience how they are affected by landscape management and potential consequences on crop yield were instead quantified using a substantially more robust dataset collected in sub-task two (including data collected in nine primary studies including 55 independent crop production sites across different European region, see section 2.2 below). In addition to data collected in Switzerland to assess how agri-environmental interventions (i.e., meadows with reduced management intensity according to the Swiss agri-environment scheme) in agricultural landscapes around cherry orchards affect pollinator diversity and their role in fostering climatic response diversity and resilience of pollination services and yield of cherry (see detailed study description below), pollinator communities, flower visitation and pollination services were measured in apple orchards with or without interventions (hedgerows and/or extensively managed grasslands) in the Netherlands. This data was used in sub-task two (see section 2.2 below). In Spain, bee pollinators were sampled in plums with or without flowering green covers as intervention as well as in those interventions, and flower visitation, pollination and yield were measured in plum orchards. After careful consideration, it was finally decided not include the Spanish data in the analyses of this task, due to (i) low numbers of wild pollinators compared to very strong dominance of crop flower visitation by managed honeybees bees (which are not or much less depending on interventions and semi-natural habitat management compared to wild pollinators) and (ii) strongly different climatic conditions and study system in the Spanish dataset compared to the other Central and Northwestern European datasets and the decision to focus on comparable datasets from Central and Northwestern climatic regions in which cold periods during the flowering period of the early flowering focal crops and flower visitation by cold-adapted wild pollinators during such periods are predicted to play a central role for the stability and resilience of pollination services (see detailed description below). Thus, while data from other EBAs are considered for the general synthesis and modelling analyses of sub-task two (see section 2.2), the first sub-task described in detail below focuses on an EBA case study (cherry pollination in Switzerland) specifically designed to address the objectives of the task.

2.1.1 Study design and data collection

A total of 15 cherry orchards (sites) separated by at least 1 km were chosen in agricultural landscapes on the northern plateau in Switzerland. Sweet cherry (*Prunus avium* L.) was chosen to address the objectives of this task as it flowers early in the year (a period typically exhibiting high climatic variability in the study region and as well as other Central and Northwestern European production regions), often including periods with cold temperatures, it strongly depends on insect pollination for fruit set and yield, it is visited by a diversity of wild pollinators that provide important contributions to cherry pollination and yield (e.g., Eeraerts et al. 2019). Sites were selected along independent gradients of extensively managed agri-environment scheme meadows (AES meadows as focal intervention type) and forested area as the dominant type of SNH in the agricultural landscapes of the study region. Extensively managed meadows (no fertilizer input, postponed mowing) represent the most commonly implemented type of agri-environment scheme measure to promote biodiversity in agroecosystems in Switzerland (BLW 2023). Gradients were assessed across a range of landscape buffers covering foraging ranges of focal pollinators, but finally a buffer of 250 m around cherry orchards was used in the final models as it fitted the data best, in a line with findings of other studies assessing the influence of landscape composition on pollinators in cherry orchards (e.g., Eeraerts 2023). AES meadow proportion did not correlate with total grassland proportion in the landscape.

Bee pollinators were sampled according to standard SHOWCASE protocols (Task 1.2) in each cherry orchard during the full range of variable weather conditions (i.e., strongly variable temperature conditions (range: 7.2°C to 28.7C°) during the flowering period of this early flowering crop across three sampling rounds. All specimens were identified to species level. At the beginning of each transect walk, temperature was recorded with a high-precision hand thermometer. It was ensured that pollinator sampling was only done under dry weather conditions (no rain/ snow falling) and no or almost no wind (velocities wind speed).

Fruit set was used as a measure of pollination service dependent yield (e.g., Eeraerts et al. 2019) measured from a total of sixteen trees randomly selected in each orchard.

2.1.2 Analysis of data

The realized observed thermal niches of bee pollinator species were calculated according to Kühsel & Blüthgen (2015) only considering species with at least six observations per species visiting cherry crops. To further increase the robustness of estimated thermal niches of bee pollinator species observed in the cherry orchards, this data was complemented by a similar dataset of pollinators sampled in eight apple orchards during four sampling rounds (pollinator communities visiting cherry and apple strongly overlap in the study region) according to an identical sampling approach in the same study region. In total, 11`483 crop flower visits by bees could be used for these calculations. Flower visitation has been found to be a robust proxy of pollination service delivery (e.g., Vazquez *et al.* 2005). In a second step, thermal niche properties of entire bee pollinator communities observed to visit cherry flowers were calculated according to Kühsel and Blüthgen (2015): the average species' thermal niche optima and their variation across the species that defines their complementarity (or response diversity; hereafter niche complementarity); the mean thermal niche breadths of species in a community that together with thermal niche complementarity affect "functional resilience" (*sensu* Kühsel and Blüthgen 2015), defined as the integral of the summed species niches weighted by the proportional contribution of a species to a community. To facilitate comparisons of different communities that differ in the amplitude of different species niches, functional resilience is standardized by dividing it by the maximum species niche amplitude. All measures are weighted by the proportional activity-abundance (flower visitation frequency) of each species in the community at a site.

Linear and general linear models were used to (i) assess the effects of extensively managed AES meadows and SNH on wild bee diversity and abundance and (ii) thermal niche properties of cherry pollinator communities, (iii) explore the role of wild bee diversity on the thermal resilience of the community niche of wild bee communities in cherry orchards and drivers of such a relationships, (iv) assess the different contributions of wild bee pollinators compared to managed bees (the Western honeybee *Apis mellifera* and the two mason bee species that were used as managed bee species *Osmia cornuta* and/or *O. bicornis* in some cherry orchards) to thermal resilience and (v) assess the role of thermal resilience of wild and managed bee pollinators for pollination service dependent cherry yield.

All statistical analyses were performed with the statistical software package R (version 4.3.2; R Development Core Team 2023). Assumption of normality and homoscedasticity of residuals for linear models were assessed visually (Zuur et al. 2009). General linear models were checked for overdispersion, but none of the models were overdispersed. Cooks distance was used to assess the presence of outliers (using the car package; Fox and Weisberg 2011). For linear models type II ANOVA and likelihood ratio tests for general linear models were used for statistical inference (Zuur et al. 2009).

2.2 Quantitative synthesis analyses and modelling

2.2.1 Dataset

To gain a general understanding of the impact of different scenarios of land use in terms of levels of SNH in European agricultural landscapes on the diversity and climatic niche complementary and resilience pollinators (bees) and providers of natural pest control services (aphidophagous hoverflies), as well as their role for pollination services and proxies of crop yield, a database of datasets collected in a wide range of European crop production regions and agricultural landscape types has been compiled. We searched for studies that quantified (i) crop pollinator community composition (focusing on bees) and (ii) crop pollination services, (iii) and/ or community composition of aphidophagous hoverflies, and, if available, (iv) records of temperature along with activity measures of pollinators (crop flower visitation) and/ or aphidophagous hoverflies, (v) land use around crops with respect to the local presence or absence of interventions and/or landscape-level proportion of SNH and (vi) crop yield. We focused this search on the two most important early flowering and insect pollination dependent fruit crops of Central and Northwestern Europe: apple and cherry, sharing to a large extent bee pollinator and aphidophagous hoverfly communities. We focused on early flowering crops geographically on Central and Northwestern Europe as early flowering crops in these climatic zones typically show particularly high variation in climatic conditions during crop flowering, which is predicted to further increase, where a high climatic niche complementarity in the activity of pollinators and natural enemies is predicted to play a particularly important role in buffering such effects that contribute to the stability and resilience of ecosystem service provision. We identified suitable datasets (i) from synthesis and modelling work on crop pollinators and crop pollination services performed in previous and ongoing EU framework and Horizon 2020 projects, (ii) screened the extensive recently compiled global crop pollination data base ("CropPol"; Allen-Perkins et al. 2022) and (iii) performed a systematic Web of Science and Scopus search. Identified datasets were then checked for further criteria for inclusion of dataset in the analyses: (i) minimum number of replication (≥ 6 study sites), (ii) minimum sampling effort of bee pollinators and/or aphidophagous hoverflies, (iii) sampling of pollinators and natural enemies through direct observations (i.e., transect walks, timed observations) in crops (excluding methods such as pan trapping). This search resulted in a total of 28 studies fulfilling these criteria, including data from 296 sites (Table 1). At 241 sites, temperature measures were available in addition to pollinators and pollination services, whereas at an additional 47 sites pollinator flower visitation and temperature was measured in the same study regions using the same sampling approach (but not pollination services; Table 1), which could be used as complementary data for the calculation of thermal niches of species. Data in primary studies were collected between 2008 and 2023. We defined a study as data collected by the same group of researchers across a replicated set of different study sites for a particular crop species in one region and year (Albrecht et al., 2020; Dainese et al., 2019).

2.2.2 Determining climatic species and community niche variables

Bee and aphidophagous hoverfly communities were sampled from focal apple or cherry orchards in timed transect walks or plot observations. While bee communities were sampled at all 296 focal sites, hoverflies were sampled at a subset of 82 sites from 9 studies (Table 1). Based on the raw data we calculated species richness and bee abundance per sampling time. The thermal niche of different bee species was calculated using data from 288 sites, where air temperature was recorded during transect walks or observations while thermal niches of hoverflies were obtained from 55 sites (Table 1). Species' thermal niches were calculated as described in Kühsel & Blüthgen (2015) with slight adaptations. The thermal optima and niche breadth of the species were calculated separately for each study where the species was found, to avoid bias from differences in observers, orchard structures, and overall bee abundance across regions. Therefore, proportional weights $w_{S,T}$ were calculated as $\frac{A_{S,T}}{\sum A_{S,T}}$ per study, where $A_{S,T}$ is the activity rate of a species at temperature T, and the obtained optima and niche breath from the different studies were subsequently averaged. Averaging across studies was done by weighted means with weights w_S as $\frac{N_S}{N}$, whereas N_S is the total number of individuals observed per study and N the total number of individuals observed across all studies. We used weighted means to consider reliability (based on number of observations) of different optima and niche breath values. Moreover, to increase reliability of thermal niche calculations, we only considered a species' thermal optima and niche breath from studies, where the species was observed at least three times. Realized thermal niches could be quantified for 45 of the total 82 bee species visiting apple and cherry flowers and for 11 aphidophagous hoverfly species of the total 28 hoverfly species observed in apple and cherry orchards. Additionally we calculated thermal complementarity and resilience of bee pollinator and aphidophagous hoverfly communities as described in section 2.1.2 above, according to Kühsel & Blüthgen (2015), based on the individual species' thermal niches and their relative abundances.

2.2.3 Quantification of pollination service, yield proxies and land-use variables

Different measures of pollination service were used in the primary datasets (Table 1). In apple, early fruit set (i.e., the proportion of flowers setting fruits directly depending on adequate pollination) was used as a measure of pollination services instead of late fruit set, since thinning of fruits (mechanically or chemically) is commonly applied in intensive apple production to maximise fruit quality and constant yield across years (e.g., Garratt et al. 2021). If early fruit set was not available (four studies), seed set (i.e., the number of seeds per fruit) or fruit size was used as proxies for pollination services (Garratt et al. 2021; Olhnuud et al. 2022), and final fruit set was used in a single study where these measures were not available (Table 1). In cherry, in contrast, final fruit set was used mostly as measure of pollination service as no thinning was used. Values of pollination service were scaled (z-score) within measurement to obtain comparable scales for subsequent statistical analysis.

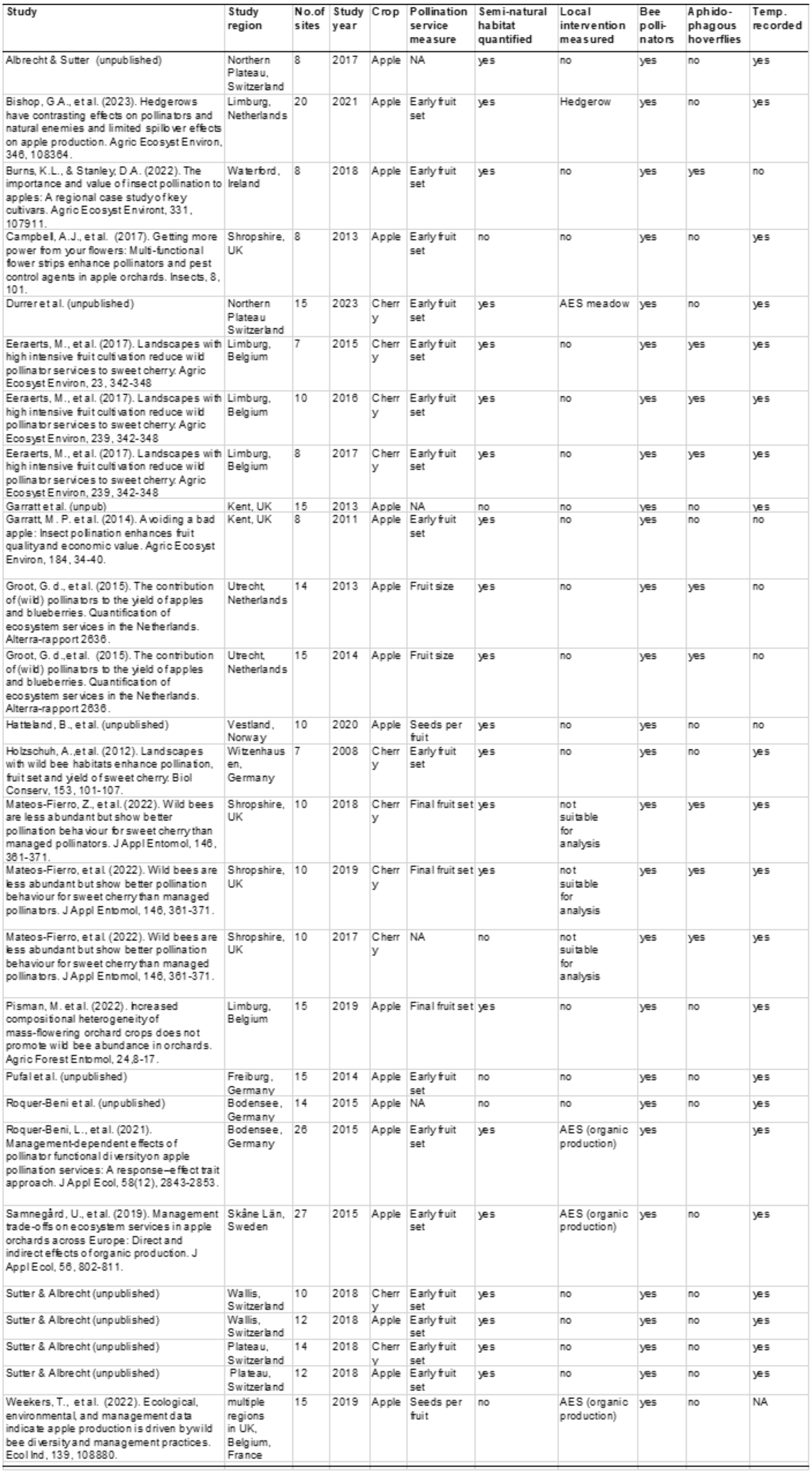
The proportion of SNH in agricultural landscapes was provided by holders of primary datasets, which has the advantage that the classification of bee-relevant SNH was based on local expert knowledge. SNH was obtained mostly on a radius of 500 m around focal fields and included forests, hedgerows, extensively managed grasslands, and floral enhancements under agri-environment schemes (Table 1). Data on landscape composition was available for 238 sites from 19 studies. Only for four studies information on present or absent local interventions was available (Table 1). Due to this very low number of studies and the high heterogeneity of interventions implemented (e.g., organic production, hedgerows, extensively managed meadows), no reliable analysis of effect of local interventions was possible.

2.2.4 Statistical analysis

All statistical analysis were done with (generalized) linear mixed-effects models including the study as random term. To test for effects of bee community metrics on pollination services, original models included wild bee communities' thermal complementarity and resilience, as well as honeybee abundance, wild bee abundance and species richness as predictors. However, honeybee abundance, wild bee abundance, species richness and thermal resilience did not explain significant variation in pollination services based on likelihood ratio tests and were therefore dropped from the final models (Zuur et al., 2009). Crop species (apple or cherry) and the interaction between crop thermal complementarity was included in the model to test whether effects differ between apple and cherry. Moreover, models were fit to test if thermal complementarity and resilience depend on wild bee abundance and species richness and how these metrics are affected by the proportion of SNH in landscapes surrounding apple and cherry orchards. For species richness we fitted a generalized model with a Poisson error distribution.

The same modelling approach and model structures as described above was used to test for effects of SNH proportion around study orchards on thermal complementarity, thermal resilience abundance and species richness, of aphidophagous hoverfly communities in focal orchards, and the relationships between the later variables with fruit set or fruit size of apple, or fruit set of cherry, respectively.

Table 1: Datasets used for quantitative synthesis analyses and modelling.



Study	Study region	No.of sites	Study year	Crop	Pollination service measure	Semi-natural habitat quantified	Local intervention measured	Bee polli-nators	Aphido-phagous hoverflies	Temp. recorded
Albrecht & Sutter (unpublished)	Northern Plateau, Switzerland	8	2017	Apple	NA	yes	no	yes	no	yes
Bishop, G.A., et al. (2023). Hedgerows have contrasting effects on pollinators and natural enemies and limited spillover effects on apple production. Agric Ecosyst Environ, 346, 108364.	Limburg, Netherlands	20	2021	Apple	Early fruit set	yes	Hedgerow	yes	no	yes
Burns, K.L., & Stanley, D.A. (2022). The importance and value of insect pollination to apples: A regional case study of key cultivars. Agric Ecosyst Environt, 331, 107911.	Waterford, Ireland	8	2018	Apple	Early fruit set	yes	no	yes	yes	no
Campbell, A.J., et al. (2017). Getting more power from your flowers: Multi-functional flower strips enhance pollinators and pest control agents in apple orchards. Insects, 8, 101.	Shropshire, UK	8	2013	Apple	Early fruit set	no	no	yes	no	yes
Durrer et al. (unpublished)	Northern Plateau Switzerland	15	2023	Cherry	Early fruit set	yes	AES meadow	yes	no	yes
Eeraerts, M., et al. (2017). Landscapes with high intensive fruit cultivation reduce wild pollinator services to sweet cherry. Agric Ecosyst Environ, 23, 342-348	Limburg, Belgium	7	2015	Cherry	Early fruit set	yes	no	yes	yes	yes
Eeraerts, M., et al. (2017). Landscapes with high intensive fruit cultivation reduce wild pollinator services to sweet cherry. Agric Ecosyst Environ, 239, 342-348	Limburg, Belgium	10	2016	Cherry	Early fruit set	yes	no	yes	yes	yes
Eeraerts, M., et al. (2017). Landscapes with high intensive fruit cultivation reduce wild pollinator services to sweet cherry. Agric Ecosyst Environ, 239, 342-348	Limburg, Belgium	8	2017	Cherry	Early fruit set	yes	no	yes	yes	yes
Garratt et al. (unpub)	Kent, UK	15	2013	Apple	NA	no	no	yes	no	yes
Garratt, M. P. et al. (2014). Avoiding a bad apple: Insect pollination enhances fruit quality and economic value. Agric Ecosyst Environ, 184, 34-40.	Kent, UK	8	2011	Apple	Early fruit set	yes	no	yes	no	no
Groot, G. d., et al. (2015). The contribution of (wild) pollinators to the yield of apples and blueberries. Quantification of ecosystem services in the Netherlands. Alterra-rapport 2636.	Utrecht, Netherlands	14	2013	Apple	Fruit size	yes	no	yes	yes	no
Groot, G. d.,et al. (2015). The contribution of (wild) pollinators to the yield of apples and blueberries. Quantification of ecosystem services in the Netherlands. Alterra-rapport 2636.	Utrecht, Netherlands	15	2014	Apple	Fruit size	yes	no	yes	yes	no
Hatteland, B., et al. (unpublished)	Vestland, Norway	10	2020	Apple	Seeds per fruit	yes	no	yes	no	no
Holzschuh, A.,et al. (2012). Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. Biol Conserv, 153, 101-107.	Witzenhausen, Germany	7	2008	Cherry	Early fruit set	yes	no	yes	no	yes
Mateos-Fierro, Z., et al. (2022). Wild bees are less abundant but show better pollination behaviour for sweet cherry than managed pollinators. J Appl Entomol, 146, 361-371.	Shropshire, UK	10	2018	Cherry	Final fruit set	yes	not suitable for analysis	yes	yes	yes
Mateos-Fierro, et al. (2022). Wild bees are less abundant but show better pollination behaviour for sweet cherry than managed pollinators. J Appl Entomol, 146, 361-371.	Shropshire, UK	10	2019	Cherry	Final fruit set	yes	not suitable for analysis	yes	yes	yes
Mateos-Fierro, et al. (2022). Wild bees are less abundant but show better pollination behaviour for sweet cherry than managed pollinators. J Appl Entomol, 146, 361-371.	Shropshire, UK	10	2017	Cherry	NA	no	not suitable for analysis	yes	yes	yes
Pisman, M. et al. (2022). Increased compositional heterogeneity of mass-flowering orchard crops does not promote wild bee abundance in orchards. Agric Forest Entomol, 24,8-17.	Limburg, Belgium	15	2019	Apple	Final fruit set	yes	no	yes	no	yes
Pufal et al. (unpublished)	Freiburg, Germany	15	2014	Apple	Early fruit set	no	no	yes	no	yes
Roquer-Beni et al. (unpublished)	Bodensee, Germany	14	2015	Apple	NA	no	no	yes	no	yes
Roquer-Beni, L., et al. (2021). Management-dependent effects of pollinator functional diversity on apple pollination services: A response–effect trait approach. J Appl Ecol, 58(12), 2843-2853.	Bodensee, Germany	26	2015	Apple	Early fruit set	yes	AES (organic production)	yes		yes
Samnegård, U., et al. (2019). Management trade-offs on ecosystem services in apple orchards across Europe: Direct and indirect effects of organic production. J Appl Ecol, 56, 802-811.	Skåne Län, Sweden	27	2015	Apple	Early fruit set	yes	AES (organic production)	yes	no	yes
Sutter & Albrecht (unpublished)	Wallis, Switzerland	10	2018	Cherry	Early fruit set	yes	no	yes	no	yes
Sutter & Albrecht (unpublished)	Wallis, Switzerland	12	2018	Apple	Early fruit set	yes	no	yes	no	yes
Sutter & Albrecht (unpublished)	Plateau, Switzerland	14	2018	Cherry	Early fruit set	yes	no	yes	no	yes
Sutter & Albrecht (unpublished)	Plateau, Switzerland	12	2018	Apple	Early fruit set	yes	no	yes	no	yes
Weekers, T., et al. (2022). Ecological, environmental, and management data indicate apple production is driven by wild bee diversity and management practices. Ecol Ind, 139, 108880.	multiple regions in UK, Belgium, France	15	2019	Apple	Seeds per fruit	no	AES (organic production)	yes	no	NA

3 Results

3.1 Results from EBA case study

3.1.1 Thermal niches of important cherry pollinators

A total of 6837 bees reflecting a total of 24 different bee species were observed in the 15 studied cherry orchards. Thermal species niches could be determined for a total of 17 important bee cherry pollinator species frequently visiting cherry flowers. As predicted, bumblebees showed lowest temperature optima as well as largest thermal niche breadth of bee pollinators of cherry (optima between 15.5°C and 16.5°C (range: 7.1-27.4°C), followed by *Osmia cornuta* and *O. bicornis*, while intermediate values were found for the managed western honeybee, highest temperature optima for mining bees (*Andrena* sp.), and variable optima for different *Lasioglossum* species.

3.1.2 Effects of AES meadow interventions on pollinator diversity, climatic complementarity, niche breadth and resilience of cherry flower visitation

Shannon diversity of wild bees ($p < 0.001$), but not their abundance, increased with the proportion of extensively managed agri-environment scheme meadows (AES meadows) in the surroundings of cherry orchards. Furthermore, thermal resilience (Fig. 1; $p = 0.002$) and niche breadth of wild bees (Fig. 2; $p = 0.001$) in cherry orchards were positively related to the proportion of AES meadows around cherry orchards, and there was a trend for such a positive relationship also for thermal niche complementarity of wild bees visiting cherry crops (Fig. 2; $p = 0.069$). No such positively relationships with thermal niche properties of wild cherry pollinators and the proportion woody SNH in the landscape around cherry orchard were found (all $p > 0.19$).

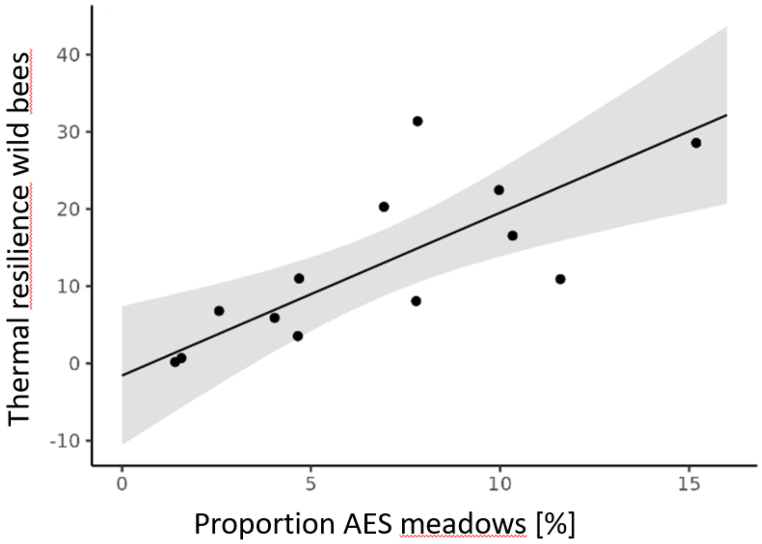


Figure 1: Positive relationship between the proportion of AES meadows (extensively managed agri-environment scheme meadows) in landscapes around cherry orchards and thermal resilience of cherry flower visitation by wild bee pollinators.

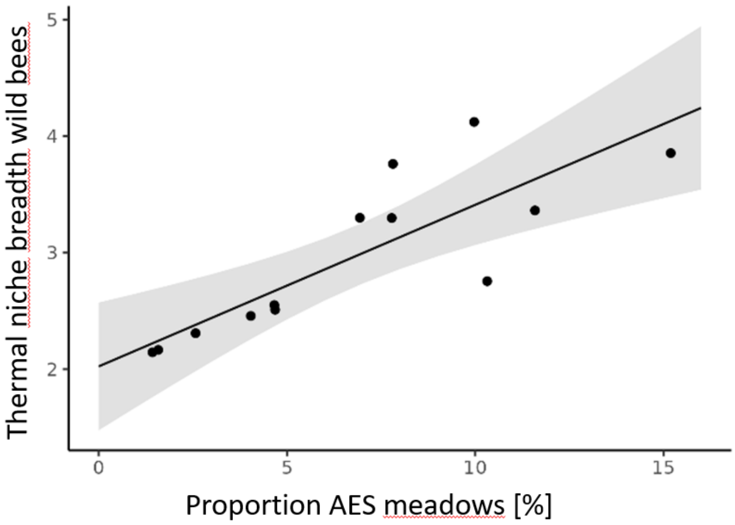


Figure 2: Positive relationship between the proportion of AES meadows (extensively managed agri-environment scheme meadows) in landscapes around cherry orchards and mean thermal niche breadth of cherry flower visiting wild bee pollinators

3.1.3 Wild bee diversity and thermal niche breadth of bumblebees as drivers of thermal resilience of cherry flower visitation

Thermal resilience of wild bee communities visiting cherry flowers was positively affected by the diversity of wild bee species ($p < 0.001$), and tended to be positively related to thermal niche breadth of bumblebees ($p = 0.05$). Thermal resilience of the entire cherry bee pollinator community, including manged bees, was mainly driven by a positive influence of the thermal niche breadth of wild ($p = 0.02$) but not to managed bees ($p = 0.31$).

3.1.4 No evidence for consequences on cherry yield likely due to factors masking pollination effects

Cherry yield measured as fruit set was not significantly influenced by any of the tested explanatory variables, neither by any thermal bee pollinator community property, nor by flower visitation frequency or diversity of bee pollinators (all $p > 0.1$). It is important to note, however, that fruit set was exceptionally low, probably due to pollination independent unfavourable weather conditions during fruit development, which likely masked any effects of pollination service variables on fruit set.

3.2 Results from general predictions based on quantitative synthesis

3.2.1 Thermal niches of crop pollinators and natural enemies

Pollinators (bees)

Realized thermal niches of 45 of total of the 82 bee species pollinating apple and cherry could be quantified. Bee pollinator species' thermal optima greatly varied in a range between 12.6°C and 28.5°C (Fig. 3). Low optima were found for different species of bumblebees (*Bombus* sp.), a certain mining bee (Andrena sp.) and nomad bee (*Nomada* sp.) species, while high optima were found for certain long-horned bee (*Eucera* sp.), sweat bee (*Lasioglossum* sp.) and mining bee (*Andrena* sp.) species (Fig. 1)

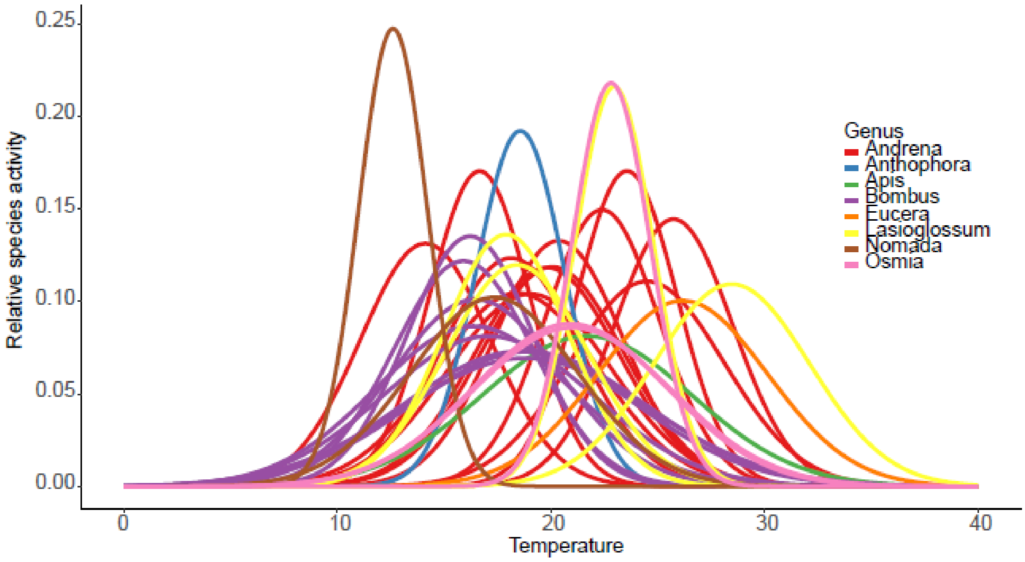


Figure 3: Thermal niches of different bee pollinators of cherry and apple crops. Each curve represents the estimated realize thermal niche of a specific species, different colours represent different bee genera.

Natural enemies (aphidophagous hoverflies)

Realized thermal niches of 11 aphidophagous hoverfly species of the total 28 hoverfly species observed in apple and cherry orchards could be quantified. Thermal niches of aphidophagous hoverflies varied strongly from very generalist wide thermal niches (e.g., *Syrphus ribesii*) to narrow ones (e.g., *Epistrophe eligans*). Lower thermal optima were found for e.g. *Syrphus vitripennis*, while *Platycheirus* sp. (e.g., *P. scutatus*) species had generally higher optima (Fig. 4).

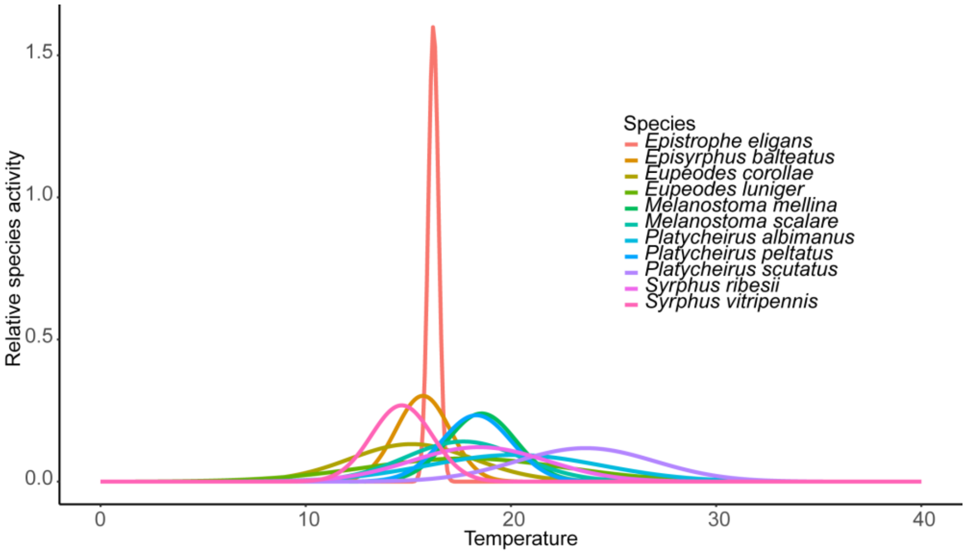


Figure 4: Thermal niches of adults of different aphidophagous hoverfly species active in cherry and apple orchards. Each curve represents the estimated realize thermal niche of a specific species, different colours represent different bee genera.

3.2.2 Apple and cherry pollination services increase with thermal complementarity of wild bee pollinators

Apple and cherry pollination services increased with wild bee communities' thermal complementarity ($p < 0.001$), irrespective of the crop species (interaction term crop species x thermal complementarity: $p = 0.85$). None of the other tested bee pollinator community variables (species richness of wild bees, abundance of wild bees, abundance of managed honey bees, thermal resilience) were significantly related to pollination services (all $p > 0.1$). Further, neither thermal complementarity or thermal resilience, nor abundance or species richness of aphidophagous hoverflies was significantly related with cherry or apple fruit production variables (all $p > 0.1$).

3.2.3 Relationships between landscape proportion of semi-natural habitat with diversity and thermal niche complementarity of pollinators and natural enemies

Thermal niche complementarity of wild bees, to best predictor variable of apple and cherry pollination services (3.2.2) was positively affected by the species richness of wild bees ($p < 0.001$), and both species richness (Fig. 5; $p = 0.002$) and thermal niche complementarity of wild bees ($p = 0.027$) increased with the proportion of SNH in landscapes around orchards. Our model predicts non-linear increases in species richness of wild bees visiting apple and cherry flowers of 18% from 0% SNH around orchards (lowest range limit) to 20%, and an increase of 66% to 60% SNH, respectively (upper range limit). Predicted increases of thermal niche complementarity from 0% to 20% or 60% SNH are 35% or 133%, respectively.

Similarly, thermal complementarity of aphidophagous hoverfly communities ($p = 0.049$), but not their species richness ($p > 0.1$) was positively related to the proportion of SNH in landscapes around apple and cherry orchards.

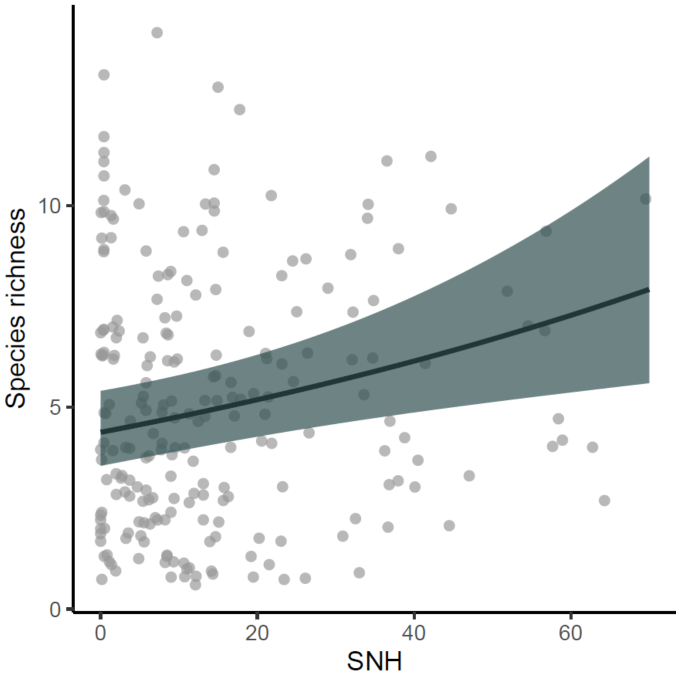


Figure 5: Relationship between the proportion of semi-natural habitat in landscapes (SNH) and the species richness of wild bees visiting flowers of apple or cherry crops.

4 Discussion and implications for policy and management

The findings of both the in-depth analyses of the EBA case study specifically designed to address the objectives of this task and the quantitative synthesis models based a total of 28 datasets including 296 apple and cherry orchards across major production regions of Central and Northwestern Europe indicate an important role of thermal niche complementarity of wild bee communities. Thermal niche complementarity, reflecting climatic response diversity of wild bee communities, can enhance climatic resilience of cherry flower visitation (findings of EBA case study) and pollination services to apple and cherry crops in major European production regions (findings of quantitative synthesis models). Furthermore, our findings showcase how increased amounts of extensively managed meadows under agri-environment schemes (AES meadows) in agricultural landscapes surrounding cherry orchards can foster thermal resilience of cherry flower visitation by wild bee pollinators. Moreover, high amounts of SNH in European agricultural landscapes around apple and cherry orchards enhance thermal niche complementarity of wild bee pollinators and aphidophageous hoverflies found in orchards.

4.1 EBA case study: agri-environmental interventions increased thermal complementarity and resilience in cherry flower visitation by wild bees

The positive effects of meadow extensification measures, primarily consisting of postponed and less frequent mowing and abandonment of fertilizer inputs, and thermal resilience and niche complementarity in cherry flower visitation by wild bees, was likely driven by more diverse flowering plant communities and associated increased availability and diversity of floral resources for wild bee pollinators (e.g. Albrecht et al., 2007; Humbert et al. 2012; Buri et al., 2014) together with more suitable nesting habitat for ground-nesting wild bees (Albrecht et al. 2023). In addition to positive effects of such meadow extensification on thermal niche complementarity, our findings also show positive relationships with thermal niche breadth, which contributed to observed enhanced thermal resilience in cherry flower visitation by wild bees.

Interestingely, managed bees, namely honeybees (*Apis mellifera*) and the two mason bee species *O. cornuta* and O. *bicornis,* did not significantly contribute to thermal resilience of cherry flower visitation by bee communities, which was primarily driven by flower visitation by wild bees. This underpins the important role of diverse wild bee communities for climatic stability and resilience of cherry pollination services. Different bumblebee (*Bombus* sp.) species strongly contributed to the communities' niche breath and resilience, which confirms predictions based on the high thermoregulation ability of bumblebees allowing them to forage also under relatively cool temperatures (Heinrich 1975; Tuell et al. 2010). However, bumblebees are particularly vulnerable to increasingly occurring heat waves and climate warming, which poses a threat to their important contribution to stable pollination services to crops and wild plants (Martinet et al. 2021; Kazanel et al. 2024). The observed broad thermal niches of bumblebees were in contrast to the narrow thermal tolerance of managed honeybees (Miñarro & Garcia 2018). The thermal niche of the latter was actually nested within the substantially wider niche of bumblebees (Miñarro & Garcia 2021).

Regarding the increasing use of the mason bees (*Osmia* sp.) as managed pollinators in cherry, apple and other early flowering fruit and berry crops, our findings show that *Osmia cornuta* had a clear higher thermal tolerance range towards cool temperatures compared to *Osmia bicornis* (and managed honeybees; Vicens & Bosch 2000). This provides an important argument to use *O. cornuta* instead of *O. bicornis* to increase climatic resilience of pollination services to early flowering crops that frequently experience cool temperatures during their bloom. Release of *O. cornuta* however, should be restricted to regions, where the species already naturally occurs (the species should not be introduced to regions it does not already occur).

Fruit set as a proxy of cherry yield was exceptionally low in the EBA case study region in the study year, very likely due to pollination independent unfavourable weather conditions during fruit development, and should therefore be interpreted with great caution. There is therefore only limited evidence for a lack of effects of thermal resilience and other pollination service predictors on yield. This is corroborated by the fact that we found no significant impact of any of the tested flower visitation measures, not even of flower visitation frequency and richness of pollinator communities, which were robust predictors of cherry fruit set in different European cherry production systems in Europe (Holzschuh et al. 20212; Eeraerts et al. 2019; Osterman et al. 2024).

4.2 Quantitative synthesis: Apple and cherry pollination services are enhanced by thermal niche complementarity of wild bee pollinators, increasing with semi-natural habitat amount around orchards

This study provides, to our knowledge, the first comprehensive estimation of realized thermal niches of 45 wild bee species pollinating apple and cherry crops in Central and Northwestern Europe. These species represent the most common species observed in orchards, likely playing a more important role than those 35 wild bee species, for which thermal niches could not be estimated since they are very rare visitors of apple or cherry flowers. Thermal complementarity among those species was substantial, and increased with the species richness of wild bee communities visiting crop flowers in orchards. Of the tested explanatory variables (manged honeybee abundance, abundance and species richness of wild bees, thermal niche complementarity and thermal resilience), thermal complementarity of wild bees was the only significant predictor of apple and cherry pollination services. These findings highlight the important role of thermal niche complementarity among wild bees for pollination services and yield in apple and cherry as economically import early flowering crops in Central and Northwestern Europe. These findings indicate that high response diversity of wild pollinator may play a crucial role in buffering climatic variability during the flowering period of crops and should be considered as a potentially critical factor of stable pollination service and yields in these crops. They also highlight that relying on a single pollinator species with relatively narrow climatic tolerance and niche breadth, such as managed honeybees, is an inherently risky strategy (Winfree 2008; Breeze *et al.* 2011), which, according to our analyses, is not adequate to ensure high and stable pollination services for cherry and apple in Central and Northwestern Europe.

Future in-depth analyses, building upon our findings and the estimated thermal niches of bee species, will aim to identify those species that largely contribute to thermal niche complementarity, i.e., by covering important climatic niches in particularly cool or warm temperature ranges or niches in unique areas of the niche space with little overlap with other species niches (Blüthgen & Klein 2011; Kühsel & Blüthgen 2015). Based on ecological knowledge of the specific habitat requirements - such as important forage plant species (Bertrand et al. 2019; Eckerter et al. 2022; Maurer et al. 2022; Ammann et al. 2024) and nesting habitat requirements (e.g., Albrecht et al. 2023) specific management recommendations to promote these key species can be developed. However, considering typically strong year-to year variation in wild crop pollinator populations, including variation in dominant species (Senapathi et al. 2021), also high redundancy in thermal niches covered by different species likely plays an important role in stabilising crop pollination services across years (Miñarro & Garcia 2018; Lemanski et al. 2022). In this respect, higher wild bee pollinator diversity should also secure greater inter-annual stability of the communities' thermal niche and the provisioning of pollination services (Senapathi et al. 2021; Lemanski et al. 2022).

The findings of this work further suggest, that the restoration and maintenance of SNH contributes to high climatic response diversity by promoting diverse wild bee communities pollinating crops. In addition to the role of extensively managed grasslands, also other types of SNH considered in this analysis play an important role in sustaining wild bee populations in agricultural landscapes and likely contributed to the observed positively effects on wild bee pollinator richness and thermal niche complementarity in cherry and apple orchards (e.g., Campbell et al. 2017; Sutter et al. 2017; Maurer et al. 2022). For example, forest remnants and hedgerows can provide nesting sites to both ground- and cavity-nesting bees (Eeraerts & Isaacs, 2023) and alternative flower resources to important groups of wild cherry and apple pollinators, such as different bumblebee species (Mallinger et al., 2016; Bertrand et al. 2019; Timberlake et al. 2019; Eearaerts et al. 2019; Ammann et al. 2024). Moreover, flower strips can support wild crop pollinator populations and diverse wild bee communities in agroecosystems (e.g., Albrecht et al. 2021; Ganser et al. 2021), which could have positive functional spillover effects for the pollination of nearby crops (Albrecht et al. 2020; Mateos-Fierro et al. 2023). It will be a promising next step to build upon this work to identify the specific types of habitats and interventions that contribute particularly strongly to thermal niche complementarity and other aspects of climatic response diversity and functional redundancy of wild pollinator communities conferring stability and resilience to crop pollination services. Our model predicts an increase in thermal niche complementarity of 35% from 0% to 20% SNH, and an increase of 133% from 0% to 60% SNH in the landscape. Our findings provide additional arguments for increasing native habitats to at least 20% in heavily modified landscapes, where the proportion of SNH is below this minimum required for sustainable food production, food security and sufficient levels of nature's contributions to people. Our results further support the call for maintaining native habitat at higher levels where present given that restoration of even more than 50% of native habitat is needed in particular landscapes (Garibaldi et al. 2020). However, there are likely trade-offs among such benefits associated with high amounts of SNH in agricultural landscapes around orchards and land opportunity costs, i.e., lower area that can be dedicated to agricultural production and associated economic losses (e.g., Brussaard et al. 2010). The assessment of such trade-offs was beyond the scope this study and should be addressed in future research.

A similar positive relationship between the proportion of SNH and thermal complementarity of aphid regulating hoverfly communities were found, but no evidence that this affected the studied proxies of cherry and apple yield such as fruit set. Possible reasons for this lack of a significant effect may be low aphid pressures and /or a control of aphids through insecticides, masking any potential influence of natural pest regulation by aphidophagous hoverflies. Furthermore, other groups of natural enemies of aphids likely contributed to aphid regulation in addition to hoverflies.

4.3 Conclusions and implications for policy and management

The findings of this task indicate an important role of enhanced thermal niche complementarity of diverse wild bee and aphid predating hoverfly communities in buffering variability in climatic conditions during the flowering period of early flowering cherry and apple crops. Our results indicate that in particular wild bee thermal niche complementarity contributing to climatic response diversity positively influences pollination service provision to cherry and apple crops in Central and Northwestern Europe. The identified species and groups of wild bee pollinators providing disproportionally important contributions to climatic niche complementarity and breadth will help to guide specific pollination management strategies towards enhanced climatic resilience of regulating ecosystem services and sustaining stable and sustainable crop production. Importantly, the findings also showcase how agri-environmental interventions such as meadow extensification measures can enhance climatic response diversity and resilience of crop flower visitation, and how fostering thermal niche complementarity of diverse wild pollinators through restoration and maintenance of SNH in agricultural landscapes can support fruit production of apple and cherry crops in Central and Northwestern Europe. These findings should therefore encourage farmers and land managers to implement such measures, and decision makers to foster them through policies.

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