Nature Conservation 55: 103–134 (2024)
DOI: 10.3897/natureconservation.55.108688

Review Article

Effects of management, habitat and landscape characteristics on biodiversity of orchard meadows in Central Europe: A brief review

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Abstract

Increasing agricultural intensification, combined with land transformation and fragmentation, poses significant threats to biodiversity. While extensively cultivated landscapes serve as vital refuges against biodiversity loss, they are modified by land abandonment and intensification. Orchard meadows in Central Europe represent traditional extensive land management systems, exhibiting high biodiversity. Comprising cultivated grasslands and scattered fruit trees, orchard meadows feature structures rich in different habitats supporting a diverse flora and fauna. However, their decreasing economic importance in recent decades has resulted in severe degradation or abandonment. Despite their importance for biodiversity conservation, there remains no comprehensive overview of orchard meadow biodiversity and management in Central Europe. This review aims to summarize existing knowledge on orchard meadows' role in biodiversity conservation and the effects of management practices on habitat diversity and quality at both smaller (structure and microhabitats, local scale) and larger scales (surrounding landscape, regional scale). The first part focuses on orchard meadow biodiversity, including both plants and animals and their link to landscape-scale factors. Biodiversity in orchard meadows is predominantly affected by patch size, determining species richness and composition, and connectivity to neighbouring orchard meadows, influencing species migration and recolonization success. The second part evaluates management impacts, illustrating differences in the benefits of mowing versus grazing across taxonomic groups. An intermediate management intensity for orchard meadows determines their conservation value in terms of species composition, varying among different taxonomic groups. To prevent area loss and abandonment of orchard meadows, we advocate for political and public support, along with incentives for farmers to maintain their biodiversity.

Key words: Extensively cultivated landscapes, extensive grassland, grazing, habitat connectivity, mowing, patch size, scattered trees, species richness, Streuobstwiese, structural diversity, traditional orchard

OPEN ACCESS

This article is part of:
Scaling in Nature Conservation
Edited by Reinhard Klenke, Joseph Tzanopoulos, Doug Evans, Małgorzata Grodzińska-Jurczak, Yrjö Haila, William Kunin, Rui Ferreira dos Santos

Academic editor: Reinhard Klenke
Received: 20 July 2023
Accepted: 27 February 2024
Published: 28 March 2024

ZooBank: https://zoobank.org/07647B51-E6E5-4FD8-B494-1B7152DD0D18

Citation: Sattler C, Schrader J, Hüttner M-L, Henle K (2024) Effects of management, habitat and landscape characteristics on biodiversity of orchard meadows in Central Europe: A brief review. Nature Conservation 55: 103–134. https://doi.org/10.3897/natureconservation.55.108688

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Introduction

Habitat loss and fragmentation are main drivers of biodiversity decline, affecting nearly all habitat types and species worldwide (Settele et al. 1996; Stuart et al. 2004; Haddad et al. 2015; Fletcher et al. 2018). Agriculture is a main contributor to habitat loss and fragmentation. In the European Union, for example, agricultural landscapes dominate with ca. 40% coverage (Eurostat 2021). They become increasingly intensified to produce higher yield leading to accelerating use of pesticides and fertilizer (Henle et al. 2008; Lécuyer et al. 2022). In addition, extensive and structurally heterogeneous cultivated land became rare due to abandonment, intensification or transformation to other land-use types. This change in land-use types leads to continuing fragmentation of remaining semi-natural landscapes as well as decreases in fragment size and increases in isolation to next suitable habitats (Haddad et al. 2015). As a consequence, intensive agriculture and biodiversity conservation are difficult to reconcile, representing one of the greatest challenges of global change (Henle et al. 2008; Egli et al. 2018; Lécuyer et al. 2022).

Only few organisms are adapted to intensively used agricultural landscapes, such as crop feeding insects or those adapted to high and continuing disturbance (Henle et al. 2004). The gross of species, however, cannot survive in highly intensified agricultural landscapes requiring natural or semi-natural landscapes (Henle et al. 2008; Guerrero et al. 2012; Tscharntke et al. 2012a; Lécuyer et al. 2022).

For conservation of farmland biodiversity, it is essential to maintain semi-natural habitats (Kleijn et al. 2011; Tscharntke et al. 2012b; Pe'er et al. 2014). This is especially the case for traditionally used landscapes, which can act as refuges, food source or nesting sites for many species (Lichtenberg et al. 2017; Eeraerts et al. 2019). Traditionally farmed orchard meadows in Central Europe present such a refugium for many threatened species (Kajtoch 2017; Schuboth and Krummhaar 2019; Henle et al. 2024). Their value for conservation and management recommendations will be the focus of the present contribution.

Orchard meadows are a combination of planted fruit trees in the overstory and extensively managed grassland in the understory (Stappen 2016; Degenbeck 2021). Orchard meadows as a habitat type is loosely defined (Henle et al. 2024) and they come in different forms and functions (Erlach 1994; Stappen 2016). Here, we concentrate on orchard meadows in the strict sense (Henle et al. 2024); that are, planted fruits trees with an herbaceous and/or graminoid understory that form two distinct strata composed of under- and overstory. It is important to note that orchard meadows are contrasted with fruit plantations by their style of management, which is mainly extensive with limited external input of fertilizer and pesticides in accordance with the EU regulation on ecological/biological agricultural production (EU 2018). Also, tree density is much lower, stem height is higher (at least 180 cm for newly planted trees) and age distribution wider in orchard meadows compared to fruit plantations.

Orchard meadows provide many important ecosystem services and functions, due to their multifaceted structure, the unique combination of two strata and the low to no external input of chemical substances (Bünger 1996; Hoff 2003; Krause et al. 2017; Henle et al. 2024). They have provisioning services like fruits for human consumption and fodder for livestock, but also regulating services like nutrient retention, carbon sequestration and flowering resources. Furthermore, the scattered density of trees in orchard meadows provide many different microclimatic conditions beneficial for animals and plants as trees offer alternating shaded and sunny patches and reduce wind speed. Fruit trees prevent fast surface flow of precipitation reducing soil erosion (Palma et al. 2007; Plieninger et al. 2010).

Despite these apparent values for food provisioning and biodiversity conservation, since the mid-19th century, orchards have declined substantially in

Europe (Herzog 1998; Plieninger et al. 2015; Forejt and Syrbe 2019; Žarnovičan et al. 2021). Also, their management has changed drastically (Poschwitz 2009; Žarnovičan et al. 2020) in line with many other extensively used traditional agricultural systems in Europe (Henle et al. 2008; Lécuyer et al. 2022). However, orchard meadows have received limited attention in scientific conservation biology and no comprehensive study has yet attempted to summarise existing knowledge and point out future research directions.

Here, we set out to fill this gap by reviewing the literature and distil patterns and drivers of species diversity in orchards, the effects of management on structural diversity of orchards and on species composition and the dependence of species in orchards to landscape characteristics that are likely to change when orchards get lost and fragmented. As studies are scarce on biodiversity in orchards, our baseline assumption is that diversity patterns recorded from fragmented habitats and factors affecting diversity in extensively used grasslands are transferrable to orchards. However, it is not our intention to provide a comprehensive literature review on grassland as this has been done in detail by other authors in the past (e.g., Dengler et al. 2014; Tälle et al. 2016). We point out differences and identify future research areas where further research is needed to identify drivers and effects of biodiversity in orchard meadows.

We concentrate on Central Europe as this region has comparable biogeographical, climatic and economic conditions and has a long and shared history of cultivation of orchard meadows (Beigel et al. 1995; Handlechner and Schmidthaler 2019) allowing for comparison of existing studies. However, we argue that similar processes may also affect diversity in similar systems outside Europe. Our review is structured in two main parts. In the first part, we focus on patterns of species diversity in orchard meadows across scales and their drivers. In the second part, we concentrate on management options to obtain high biodiversity of orchard meadows in a sustainable way. We introduce each part with ecological theories that explain observed patterns and then review to which extent these theories have been addressed for orchard meadows. Based on our key conclusions, we provide recommendations for further management of orchard meadows to support biodiversity in these unique and fascinating habitats. We further identify knowledge gaps for research to foster their conservation.

Methods

We conducted our literature search in English and German language. We searched across various databases, including the literature database of the German Federal Agency for Nature Conservation, literature references of the Federal Committee for Orchard Meadows of NABU, and searched in Web of Science, and Google Scholar. Our search included the following keywords 'orchard meadows', 'orchard management', 'traditional orchards', 'grazing', 'pruning', 'mowing', 'landscape composition' within the scope of 'Central Europe'.

Because we encountered only a limited number of publications directly focused on the effects of orchard meadow management on biodiversity (totalling 20 publications), we broadened our scope to include studies related to recommendations for grassland management that could be used to understand biodiversity maintenance and change in orchard meadow systems. Our final dataset included 218 publications, which underwent thorough review (see Suppl. material 1 for complete literature list). Subsequently, we identified and selected 127 publications closely associated with orchard meadow management and conservation from this comprehensive set of references, which are cited in the main text.

Part I: Patterns of species diversity in orchard meadows across spatial scales and their drivers

In this part, we discuss the effects of different spatial scales and surrounding landscape configuration on biodiversity in orchard meadows. To this end, we first look at the importance of microhabitats and vegetation structure within orchards. Most species have specific requirements on their environment and their presence may depend on the availability and quality of microhabitats. Next, we turn towards the local scale to discuss the effect of size of individual orchard meadows as well as their isolation to other orchards on their biodiversity. As orchards share many species with other habitat types, such as grasslands, fallow lands and forests, we will look at the structure and diversity of the surrounding landscapes, which also play an important role on the biodiversity in orchards. Finally, we explore the diversity across multiple orchards on a regional or national scale.

Structure and microhabitats

The high amounts of multifaceted habitats and structural diversity of orchards are important drivers of their species diversity (Simon and Rühl 1992; Bösneck and Hampel 2013; Schuboth and Krummhaar 2019; Jagel et al. 2020). Here, an essential element of orchard meadows is the set of fruit trees of different ages. Young trees, planted at successive stages, secure the long-term continuity of orchard meadows. Younger trees with higher vitality also have higher numbers of flowers offering nectar, pollen and fruits for diverse flower visiting insects and fruit feeding vertebrates, compared to older or dying trees (Israel 2002; Steffan-Dewenter and Leschke 2003). Old and dying trees contain many important microhabitats for many arthropods, birds and small mammals like branch holes, cavities, bark injuries, crown and branch breaks, epiphytic mosses, cracks and crevices and deadwood (Braun et al. 2010; Grossmann and Pyttel 2016). Especially existing cavities and branch holes, e.g., created by woodpeckers or fungal heart rot, are essential for secondary cavity users like many bird species (e.g., *Athene noctua*, *Jynx torquilla*, *Otus scops*), mammals (e.g., *Dryomys nitedula*, *Glis*, *Eliomys quercinus*, *Myotis myotis*) and insect groups (e.g., Hymenoptera, Thysanoptera, Coleoptera) (Rösler 1992; Simon and Rühl 1992; Eichler et al. 2001; Israel 2002; Bauschmann 2005; Eckstein and Albrecht 2006; Burger and Creutzburg 2012; Grüebler et al. 2013; Henle et al. 2024). Low numbers of cavities decrease numbers of less competitive bird species, such as common redstart (*Phoenicurus phoenicurus*) and collared flycatcher (*Ficedula albicollis*), and they may lose breeding possibilities completely (Erlach 1994) if old and/or dying trees are removed from orchards. Therefore, dead branches or coarse woody debris on the ground should not be removed.

Dead wood, from trees or branches, is important for hibernating insects and small mammals like garden dormouse (*Eliomys quercinus*) (Ulitzka 2013; Godmann 2016). Insects, especially Thysanoptera, use bark crevices and space between dead bark and wood of older trees for hibernation (Ulitzka 2013), thereby offering food resource for woodpeckers and tree creepers (*Certhia* spp.) during winter. Wild bees and wasps benefit from dead wood as nesting and hibernation habitats (Saure 2016). Dead wood also benefits potential prey of saproxylic parasitoid wasps (Hilszczański 2018).

The heterogeneous habitat structure of orchard meadows favours specialist bird species like Eurasian hoopoe (*Upupa epops*), little owl (*Athene noctua*) and wryneck (*Jynx torquilla*), for which orchards are key habitats. Those species require both a structurally rich arboreal stratum for breeding (e.g., old trees with cavities) and open ground for foraging (Ullrich 1987; Kämpfer-Lauenstein and Lederer 2007).

However, orchard meadows also support generalist species, which feed on a broader range of host plants. For example, Herrmann et al. (2010) found that a structural diverse understory maintained by high plant diversity benefits generalist meadow spiders. Likewise, Szabó et al. (2022) found butterflies with generalist functional and life-history traits more abundant in orchard meadows compared to calcareous grasslands. In contrast, species adapted to more open habitats, such as farmland butterflies, occur in higher numbers and richness in calcareous grasslands (Ernst et al. 2017). It should be noted that the orchard meadows studied by Ernst et al. (2017) seemed to be more intensively managed, as farmland butterflies increased with abandonment, which possibly provide more herbs and flowers. This highlights that specialist species are tightly linked to management intensity, which will be discussed in the second part of this review.

In addition to habitat structure, particularly dead wood, edaphic conditions also significantly affect the diversity of plants and animals in traditional orchard meadows. According to the nutrition indicator values of Central European plants (Ellenberg et al. 2001), nutritionally rich orchard meadows exhibit species-poor plant communities, which in turn affect the species diversity of animal taxa dependent on a species-rich plant community (Kornprobst et al. 1994; Ružičková and Halada 2005; Žarnovičan et al. 2017). In contrast, orchard meadows that are dry and nutritionally poor, either naturally or due to usage-based biomass removal, show high plant and animal diversity (Kornprobst 1994; Thiem and Bastian 2014). Orchard meadows on nutritionally poor soils are rare in many regions of Central Europe (e.g., Kornprobst 1994; Denk and Wittig 1999).

The interplay of shadow and sun, influenced by the spatial distribution of trees and other structures (e.g., woodpiles, fences, and bowers), determines not only potential microhabitats for animals but also the composition of herbaceous plant communities (Langensiepen and Otte 1994; Denk and Wittig 1999; Žarnovičan et al. 2017). For example, Langensiepen and Otte (1994) observed that the number of spring geophytes increased with proximity to shade-providing fruit tree trunks, such as *Gagea lutea*, which only occurred in the vicinity of fruit trees. Spring geophytes grow before the fruit trees develop leaves, thus casting less shadow. They use this advantage in early-season growth over later-growing plants, which then grow in the shade of fruit trees, and their development is reduced by the shade of the fruit trees (Langensiepen and Otte 1994).

How management will influence the flora of orchard meadows will be discussed in the second part of this review.

When comparing the structural diversity of extensively cultivated orchard meadows with intensified fruit plantations, on plantations mainly low-trunk fruit trees are cultivated as those are easier to farm due to their homogenised low-trunk and dense plantation (Rösler 1992; Herzog 1998). Tree crowns start already at a height of <1 m. Tree care is intensive as well as the use of pesticides and fertilizers (Mader 1982; Rösler 2002). Low-trunk fruit trees have less microhabitats and offer less breeding sites for birds and arthropods. Vulnerable bird species and arthropods are more abundant in high-trunk, structurally rich orchards compared to plantations (Rösler 2002; Samnegård et al. 2019). Especially woodpeckers favour orchards with high-trunks (Rösler 2016). Mader (1982) found a much higher species diversity of carabid beetles and spiders in traditionally managed orchard meadow. The availability of ecological niches and habitats is a driver of high species diversity. Low-trunk trees and intensive tree care like use of pesticides are usually associated with low alpha diversity compared to extensively managed high-trunk fruit trees (Mader 1982; Rösler 2002; Samnegård et al. 2019).

Local scale: effects of patch size and isolation

Besides structural differences within orchard meadows, there are also large differences in species diversity and composition between orchard meadows in the same region. To understand these, we will now turn towards effects and drivers at local scale.

Orchard size and isolation from other similar habitats are important drivers of species diversity and composition. Core predictions for species diversity in habitat fragments, such as orchard meadows, can be derived from the Equilibrium Theory of Island Biogeography and metapopulation theory (MacArthur and Wilson 1967; Hanski and Gilpin 1997). Transferring island biogeography theory, which proposes that the number of species coexisting on an island depends on island size and isolation, to fragments on the mainland, it follows that patch size, and the diversity of different habitats therein, is an important factor how many species can coexist. Its distance to other suitable habitats determines how many species can recolonize if they become locally exinct. Similarly, metapopulation theory predicts that numerous smaller patches can secure the survival of a species in the landscape if they are not too isolated from each other, thus allowing constant multidirectional dispersal (Hanski and Gilpin 1997; Frank and Wissel 1998).

In line with these theories, it has been shown that the number of bird species and various insect groups (e.g., bees, wasps and their natural enemies) increases with patch size (Steffan-Dewenter and Leschke 2003; Bauschmann 2005; Amann 2007; Bailey et al. 2010). However, a positive species-area relationship was not found for species at lower trophic level like plants (Steffan-Dewenter 2003). Species-area relationships are assumed to be more pronounced for specialist species and species at higher trophic level (Holt 1996).

As expected, the abundance of solitary wrinkled wasps (Eumeninae) and bees increased with the size of the orchard. However, this was not the case for digger wasps of the family Sphecidae and the parasitisation rate also did not increase with area and connectivity, but depended only on the local and regional abundance of hosts (Steffan-Dewenter 2003). Why the abundance of some taxa and of functional relationships do not increase with patch area is still insufficiently understood.

Bailey et al. (2010) studied the effect of habitat isolation and size on snails, beetles, true bugs, spiders and breeding birds in traditional orchards and found that isolation was more important than patch size. Species richness and abundance decreased with increasing isolation, showing the importance of habitat connectivity. Further, predatory birds and spiders were more affected by patch isolation than herbivore beetles, true bugs and snails. The authors assumed that predators were more sensitive to isolation, which in turn benefit herbivores due to reduced control by predators, which supports the trophic level hypothesis (Holt 1996) and the mesopredator release theory (Henle et al. 2004). This is in line with a study by Herrmann et al. (2010), who found a positive effect of patch isolation on canopy spiders in relation with lower predation pressure of insectivorous birds and spider wasps (Pompilidae and Crabronidae).

Orchard meadows are usually of small size, e.g., ranging from 0.08 to 5.8 ha in southern Lower Saxony, Germany (Steffan-Dewenter 2003), possibly acting as strong filter for species with larger area requirements. Similarly, smaller orchard meadows are more prone to edge effects possibly affecting species composition. While small, isolated orchard meadows can be important as resting and feeding habitats for bird species, only species tolerating anthropogenic disturbance or coping with habitat edges, like blackbirds (*Turdus merula*) or great (*Parus major*) and blue tits (*Cyanistes caeruleus*), breed in small and isolated orchards (Bauschmann 2005). Species with larger area requirements and poorly adapted to edge effects like wryneck (*Jynx torquilla*), little owl (*Athene noctua*) and spotted flycatcher (*Muscicapa striata*) prefer large, interconnected orchards in combination with adjacent structurally similar habitats (Bauschmann 2005; Amann 2007).

The number of studies testing the effects of area and isolation of orchard meadows on the composition and abundance of different taxonomic groups and species within a taxonomic group is still very limited. Clearly, more studies are required to fully understand the contrasting reactions that have been observed for some species and groups in the studies carried out so far. Also, we need more studies that allow derivations of minimum sizes of orchards for providing breeding sites and the longer-term persistence of populations, especially for threatened species and species for which orchard meadows belong to their favoured habitats.

Surrounding landscapes

The surrounding landscape can be an important driver for the community composition in orchard meadows (Ernst et al. 2017). Orchard meadows share many habitats with other, larger ecosystems in Central Europe, such as grasslands, forests and moderately modified anthropogenic landscapes like gardens and suburban habitats. Orchards can draw species from such habitats, and their abundance and configuration in the surrounding landscape likely have a strong effect on the species composition and diversity in orchards. At the same time orchards surrounding other (semi)-natural habitats can serve as temporary refuges for some species when their habitat changes (e.g., deciduous woodlands for saproxylic beetles) (Horák 2014a). However, only few studies investigated the effect of surrounding habitats on orchard meadow diversity, making general claims difficult. The few available studies indicate that surrounding land use types similar in structure to orchard meadows benefit species richness of birds, butterflies (though not for butterflies that are typical for forests) and plants in orchards (Horák et al. 2013). For some bird species (e.g., *Coccothraustes*, *Dendrocopos major*, *Muscicapa striata*), orchard meadows may even complement woodlands or grassland as they can act like transition areas (Šálek et al. 2010; Horák et al. 2013). For snails, the results are contradictory. While terrestrial snails were affected by land use in the surroundings in a study in the Czech Republic (Horák et al. 2013), the surrounding landscape had no effects on snail species richness in a study in Switzerland (Bailey et al. 2010).

Further, it is important to note that the effects of patch size and surrounding landscape composition can be tightly interlinked (see also above). Patch size, matrix quality and amount of suitable patches in the surroundings determine metapopulation dynamics and the survival of species in fragmented habitats (e.g., Settele et al. 1996; Hanski and Gilpin 1997; Frank and Wissel 1998). The sensitivities of species to these effects differ between generalist and specialist species (Henle et al. 2004) and between the core and the periphery of the distribution area of species (Prieto-Ramirez et al. 2020). Specialist insects, like aboveground-nesting bees and eumenid wasps, appear to be more sensitive to habitat fragmentation than unspecialized insects (Steffan-Dewenter 2003).

Here, we regard the lack of studies specifically targeting landscape effects on orchard diversity as the main hindrance to reach clear conclusions. However, such knowledge is of paramount importance to formulate effective conservation measures for orchards at landscape scale. Also, the link of landscape effects on species composition in orchards presents a promising avenue for future research. For instance, it is poorly understood whether orchard meadows with high structural diversity may support non-arboreal species with different traits than tree-less meadows and meadows in intensively used plantations that may only support species with limited trait diversity.

Regional scale

The regional scale describes species diversity across many different orchard meadows, such as in a region, state or country. At this scale, orchards are among the most biodiverse cultivated landscapes in Central Europe (Saure 2016; Schuboth and Krummhaar 2019). For instance, in the German state of Saxony-Anhalt, one third of the nationwide species of wild bees, 19% of wasp species and 22% of hoverfly species (Syrphidae) were found in orchard meadows (Saure 2016). The area of orchards covers approximately 60–70 km^2 (Henle et al. 2024), which is approximately 0.3% of the area of Saxony-Anhalt. A similarly high richness in orchards was reported for the German state Baden-Württemberg and for Upper Austria for wild bee species with >40% and 23% of the state's overall diversity respectively (Schwenninger and Wolf-Schwenninger 2012; Ockermüller 2018). Among these species, 21% of the bee species listed as endangered in Baden-Württemberg were recorded in orchards (Schwenninger and Wolf-Schwenninger 2012).

For birds, the numbers are similarly high. In Austria, about one third of the 200 species of regular breeding birds, and half of the 103 songbird species were recorded in orchard meadows (Erlach 1994).

Schuboth and Krummhaar (2019) provide a detailed list of species occurring in orchard meadows in the German state Saxony-Anhalt. In their study, the authors recorded a total of 3,623 species in ten orchard meadows, of which

359 species are considered endangered in Germany [Figures from Henle et al. (2024), who used slightly different data from the individual chapters of a few taxonomic groups]. Taxa like mosses (Bryophyta), lichens (Lichenophyta) and fungi were recorded with 95, 72 and 326 species, respectively. The highest diversity was from the phylum Arthropoda, in which the class of Coleoptera dominated with 899 recorded species, followed by butterflies (368), Arachnida (365 species), and Hymenoptera (351 species: bees, ants, wasps).

A study by Zarabska et al. (2009) compared lichens among apple orchards in Poland, Slovakia and Italy and found highest diversity in Slovakia (52), followed by Italy (43) and Poland (32). The authors concluded that each orchard creates its own conditions, leading to a different number of species, as some species favour specific conditions over others (Zarabska et al. 2009).

Only few similar studies exist for Central European orchard meadows, all of them showing a high species richness for many taxonomic groups [see Henle et al. (2024) for studies in Germany]. Most comprehensive studies focussed on one or very few taxonomic groups, mainly on birds, pollinating insects and/or plants. As a consequence, for most regions and other taxonomic groups occurring in orchard meadows, much less is known (Henle et al. 2024). This bias in taxonomic coverage makes it difficult to evaluate whether other taxa, like mammals and other insect groups, are similarly diverse in orchard meadows from the local to the regional scale, which species depend on orchard meadows and how the availability of orchard meadows at the regional scale affects their abundance.

The high species diversity at regional scale can be explained by different factors. Generally, it is important to note that there is no standard appearance among orchard meadows at local scale. Orchard meadows have different sizes, managements, fruit tree compositions, and environmental site conditions, e.g., soil properties and topographic location (e.g., Glück et al. 2004; Bauschmann 2005; Grüebler et al. 2013; Žarnovičan et al. 2017). Differently structured orchard meadows offer more diverse habitat types, food resources and nesting sites, resulting in higher species diversity (Erlach 1994; Wiche et al. 2015; Kajtoch 2017; Tonelli et al. 2017; Schuboth and Krummhaar 2019). Similarly, the surrounding landscape is an important driver for high beta diversity at the regional scale (Horák et al. 2013). All these different local characteristics lead to higher species spatial turnover among orchard meadows contributing to the high alpha diversity observed at regional scale.

However, it is important to note that only few studies assessed the overall species diversity at regional scale and especially across scale. More knowledge is needed to (i) gain better understanding of which taxa are particularly diverse in orchards locally and regionally and (ii) to compare diversity among regions and taxa. This knowledge is important to guide conservation actions in orchards and could potentially serve as a baseline for future monitoring of biodiversity changes in orchards over time. This is of high relevance, since the total area of orchard meadows has declined substantially in most regions of Central Europe since the 1950s (Ullrich 1987; Rösler 1996; Herzog 1998; Žarnovičan et al. 2017; Henle et al. 2024) and their quality as habitat is also in decline due to eutrophication, which refers to nutrient enrichment that can degrade habitat quality (e.g. Kornprobst 1994; Wassen et al. 2021).

The loss of orchard meadows and the reduction of their quality threatens the biodiversity of orchard meadows at the regional scale. This has been well documented for bird species that breed primarily in orchard meadows (Henle et al. 2024). In the region of Havelland, Germany, for example, the population of the hoopoe (*Upupa epops*) has declined sharply and all but a few pairs of the little owl (*Athene noctua*) have disappeared despite support measures (Putze et al. 2009). In Bavaria, wrynecks (*Jynx torquilla*) and ortolan (*Emberiza hortulana*) have declined by more than 50% in the last 25–30 years (Kilian 2016). The declines were probably due to the extensive loss of orchards and rows of fruit trees in the arable farming areas of Franconia (ortolan) and the loss of the meager, patchy vegetation for the wryneck. Species, for which orchard meadows remain the last remaining refuges, such as *U. epops*, *A. noctua* and woodchat shrike (*Lanius senator*) (Ullrich 1987), became threatened with extinction regionally or even extinct nationally (Ullrich 1987; Kilian 2016). Given the large number of threatened species of other taxonomic groups that have been observed in orchard meadows (Henle et al. 2024), similar regional declines likely also occurred for many species in other taxonomic groups but in the absence of targeted long-term monitoring it is difficult to evaluate.

For plants, eutrophication of orchard meadows has led to a rather low species richness of plants across large parts of Franconia in Bavaria (Kornprobst 1994). Global nitrogen-based production of fertilizer has increased by one order of magnitude since the 1950s (Smil 2001). Central Europe is particularly heavily impacted by nitrogen deposition (Ellenberg 1991), which has contributed to a reduction of plant species richness in many parts of Europe (Stevens et al. 2010; Wassen et al. 2021). The understory vegetation in orchard meadows, which strongly influences many taxonomic groups, likely contributed to regional declines in diversity and abundance of numerous animal species due to eutrophication.

Part II: Management of orchards

Extensive management of the under- and overstory is a major driver of the biodiversity of orchard meadows. In this part, we will review and discuss the effects of different management practices on species diversity in orchards. We provide recommendations on the management of orchard meadows for maintaining and increasing biodiversity.

In Central Europe, most open grasslands and scattered tree landscapes are artificial and maintained by people (Mühlenberg and Slowik 1997). Traditionally managed grasslands support high species richness, with one third of all native vascular plant species in Central Europe occurring in grazed or mowed agricultural grassland (Leuschner and Ellenberg 2017). To maintain open grassland, interventions are necessary as otherwise those areas would disappear, driven by succession towards forests. Management interventions in the form of fertilization, grazing and mowing are disturbances affecting species composition and diversity (Leuschner and Ellenberg 2017).

The intermediate disturbance hypothesis by Connell (1978) describes that to a certain (intermediate) degree, disturbance can promote establishment of new and less competitive species into a system and rearrange species composition by changing competitive interactions. For example, vascular plant species richness peaks at moderate grazing levels rather than at complete abandonment of livestock (Yuan et al. 2016). Even for some semi-natural grasslands protected under the Natura 2000 framework in Central Europe, it is assumed that current grazing and mowing intensities are too low compared to the previous traditional management or that the timing of management is not suitable for many species with strong effects on species richness and composition (Diekmann et al. 2019). However, spatio-temporal shifting of management could ameliorate this problem (Kleyer et al. 2007).

In general, too high intensification in the form of high fertilizer use (N fertilization >120 kg N ha^{-1}: eutrophic) either intensive grazing and mowing (3–6 times a year) can lead to decreasing species diversity of grassland (Leuschner and Ellenberg 2017); and presumably also in orchards. The transition from high-diversity grasslands to less diverse plant communities likely has similar effects on the fauna, which may become less diverse and dominated by generalist species (Siemann et al. 1998; Ebeling et al. 2018). For the overstory, tree management is mandatory for maintaining high biodiversity. Appropriate management increases microhabitats in fruit trees that, in turn, leads to high biodiversity, especially in arthropods and birds (see above for the effects of structure and microhabitats on species richness, Asbeck et al. 2021).

Maintenance of structural diversity of the understory

The understory of orchard meadows, which consists of grasses and herbs, can be managed through grazing, mowing, fertilization, mulching, or a combination of these methods. Each management form has specific effects on the plant community composition of the understory and likely also its fauna. It is important to note that orchard meadows can include dry, moderate, or wet grasslands, and nutrient poor or eutrophic grasslands (Kornprobst 1994), which changes the plant community and subsequently the meadow management. However, due to the scarcity of literature, we did not differentiate between grassland types (such as gradients in wetness of nutrients) in orchard meadows within our management categorization. This gap in knowledge is a distinct need for future research.

Grazing mainly promotes species richness of grasses, whereas mowing increases richness of herbs (Steffan-Dewenter and Leschke 2003). Characteristic plant species found in extensive managed orchard meadows are grasses such as *Arrhenatherum elatius*, *Dactylis glomerata* and in warmer stands *Bromus erectus* (Langensiepen and Otte 1994; Denk and Wittig 1999; Čejka et al. 2018). However, it is important to note that plant communities highly depend on the location (and its associated environmental conditions) and management which determine the species composition and plant community in the understory. For example, in grazed orchards, the herb layer is typically lower than in mown ones, mainly comprising low grasses (such as *Cynosurus cristatus*, *Lolium perenne*), along with herbs tolerant to grazing and trampling (e.g. *Bellis perennis*, *Plantago major*, *Prunella vulgaris*). While on nutrient-rich soils, species of the *Molinio-Arrhenatheretea* class are common (e.g. *Acetosa pratensis*, *Festuca pratensis*, *Ranunculus acris*), nutrient-poor and semi-arid meadows will feature more *Festuco-Brometea* species (e.g. *Galium verum*, *Medicago lupulina*, *Securigera varia*) (Denk and Wittig 1999).

Fertilization or mulching can be important for nutrients repatriation (Degenbeck 2021). All methods have their pros and cons, and these depend on their type and intensity (Fig. 1).

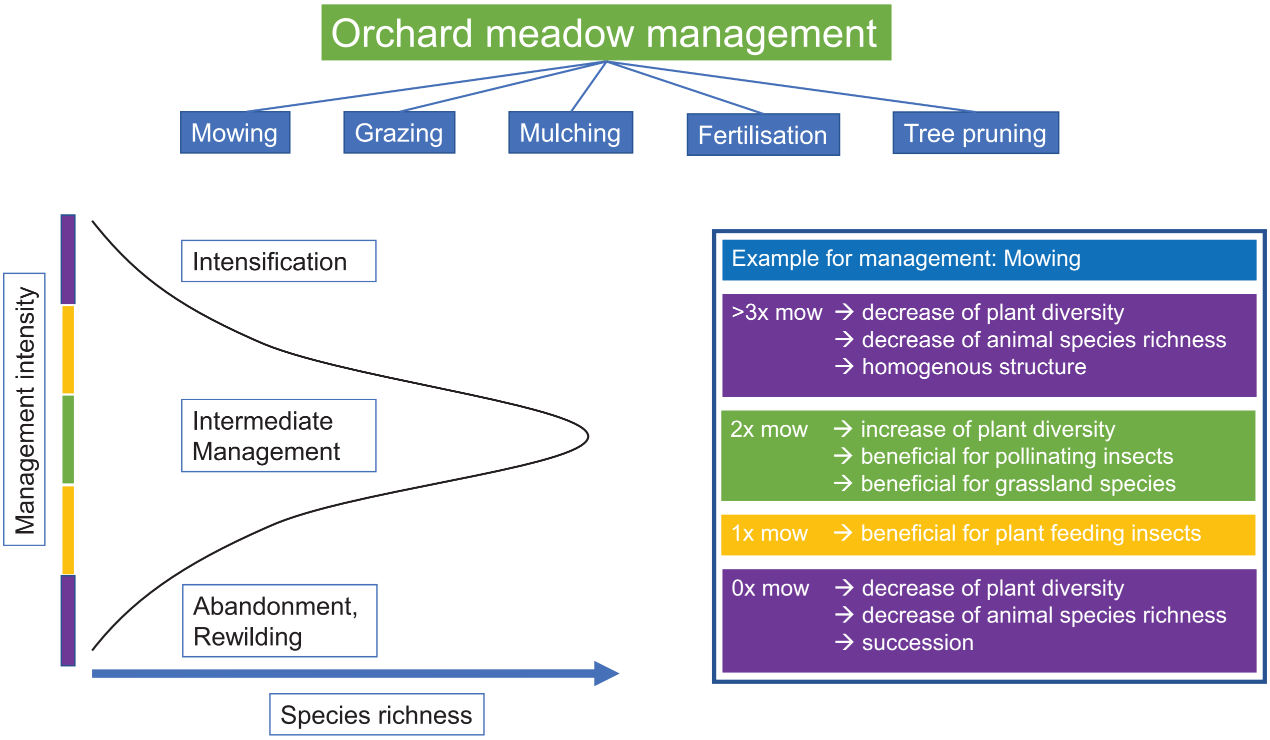

Figure 1. Schematic figure illustrating the effects of management intensification on species richness. The graph illustrates the potential effect of management intensity (from high over intermediate to abandonment/rewilding) on species richness in orchard meadows. As an example, the effect of mowing intensity on species richness is shown in a box.

Grazing as management option

Grazing can ensure that meadows remain structurally diverse by creating a mosaic of damaged and undamaged vegetation (Schoof et al. 2019). Cattle, sheep, horses and goats have different feeding behaviour, with different effects on vegetation (Carvell 2002; Öckinger et al. 2006; Rook and Tallowin 2011; Schoof et al. 2019). Sheep and goats bite off vegetation, whereas cattle tear it off, leaving more vegetation intact (Schoof et al. 2019).

Öckinger et al. (2006) found that grasslands being grazed by sheep support less plant and butterfly species compared to grasslands grazed by horse or cattle. These results were mirrored by Carvell (2002), who found that cattle grazed grasslands supported higher bumble bee abundance than those grazed by sheep. Sheep have a highly selective feeding behaviour, which can lead to a floristic impoverishment as only certain plant species are affected. Also, temporal scale of grazing is crucial for plant species composition. A short time period of grazing with a high number of sheep can lead to an evenly grazed vegetation. In contrast, a small number of sheep grazing over a long time period in the same meadow can lead to selective feeding behaviour (Zahn and Tautenhahn 2016). Selective grazing by sheep can be partly compensated by combining sheep with goats or cattle as not only sheep-selected plants are grazed (Zahn and Tautenhahn 2016). Goats can modify their feeding behaviour depending on the seasonal change of vegetation. They also feed on woody plants suppressing the potential development of shrubs and therefore prevent succession (Elias and Tischew 2016). Cattle, however, are unselective in their choice of plants and support higher structural and floristic diversity (Zahn and Tautenhahn 2016). Low to moderate cattle grazing can be beneficial for butterflies by creating more structural diversity and potentially be used as conservation tool for disturbance-dependent grasslands (Bussan 2022) like orchard meadows. Furthermore, a structurally diverse meadow created by extensive grazing with areas excluded for livestock promotes orthopteran diversity and abundance (Gardiner 2018).

Timing of grazing can also highly influence the grassland community. Paesel et al. (2019) found that when the grazing period starts late and fast-growing competitive species spread and reach a certain height (120 cm and more), grazers most likely avoid them due to lignification of plant tissue. Therefore, in their study, grazing did not increase vegetation heterogeneity (Paesel et al. 2019).

The intensity of grazing and thus the number of livestock is crucial when aiming at high biodiversity. Grazing intensity measured on sward height (Jerrentrup et al. 2014) showed that an intermediate lenient grazing (12 cm) by cattle results in higher species richness of grasshopper and butterflies compared to moderate (6 cm) and very lenient (18 cm) grazing intensity. The authors recommend a stocking rate of ~1 SLU ha^{-1} [standard livestock unit (SLU) = 500 kg] to maintain heterogenous sward structure, which is beneficial for less mobile insects and insects sensitive to grassland structure like grasshoppers (Jerrentrup et al. 2014).

The management should aim towards a structurally diverse understory created by intermediate grazing intensity and meadow areas excluded for livestock to offer undisturbed areas for, e.g., breeding birds. However, if the whole meadow is grazed by livestock, a grazing break of 2–4 months should be included to create regeneration time for fauna inhabiting the understory (Zahn and Tautenhahn 2016). In any case, tree protection (e.g., bite protection by fencing off trunks) is recommended when orchard meadows are grazed by livestock as goats, cattle and sheep debark trees (López-Sánchez et al. 2020). Debarking can lead to damage of fruit trees, which in turn can harm crown health and development (López-Sánchez et al. 2020).

Dung of livestock can be an important fertiliser and is also crucial for dung living and visiting organisms like several dipteran families (e.g., Syrphidae, Dolichopodidae, Muscidae) and dung beetles (e.g., Scarabaeidae, Geotrupidae) (Young 2015; Schoof and Luick 2019). Orchard meadows are usually not treated with pesticides or other chemical input (Rösler 1992; Erlach 1994). However, husbandry of livestock is mostly associated with the use of veterinary medicine, like, e.g., antiparasitics and antibiotics, which are highly debated due to, e.g., antibiotic resistance and their environmental impact on ecosystems (Van Puyvelde et al. 2018; Sebestyén et al. 2018; Lalouckova and Skrivanova 2019).

Veterinary medicine or their metabolites in dung of livestock negatively affects dung living insects (Tonelli et al. 2017; Schoof et al. 2019). It can reduce biomass, abundance, functional diversity and species richness of dung beetle communities, which are important decomposers and also serve as food source for a range of animals (Tonelli et al. 2017; 2020). Numerous bird species (e.g., *Turdus merula*, *Lanius collurio*), bats (e.g., *Rhinolophus ferrumequinum*) and hedgehogs (*Erinaceus europaeus*, *Erinaceus concolor*) feed on dung living insects [see Young (2015) for a comprehensive list of predators of dung living insects], which in turn are affected by the reduction of dung organism.

Römbke et al. (2019) recommended risk mitigation measures to protect dung and soil organisms from antiparasitics. The following recommendations were made to protect dung organisms: (i) a selected instead of strategic use (e.g., common practice is that prophylactically all animals are treated) of anti-parasitic treatments as well as (ii) restricting strategic treatments to seasons when diversity and abundance of dung organisms are not at their highest. There should be (iii) no treatment of livestock on the same pasture in the successive season (e.g., spring and summer of the same year). If possible, (iv) animals should be in the shed during the treatment period. The effect of veterinary medicine on biodiversity of dung living insects and other non-target organisms is little studied and generally not considered in conservation management plans yet (Römbke et al. 2019; Schoof et al. 2019).

Management by mowing

When the understory of orchards is managed by mowing, the timing and frequency of mowing strongly determines vegetation structure. Ideally, plants should have reached seed maturity or be capable of vegetative propagation by the time of cutting. This will increase their chances of persistence and propagation under a mowing regime with a constant temporal sequence. Plant species not adapted to frequent mowing, either due to low build-up of energy reserves, damage before seed production or sudden change in microclimate, may not persist long-term under unfavourable mowing management. However, plant species with low competitive ability, such as slow growing species or those adapted to high disturbances, depend on regular clearing or removal of more competitive, fast-growing plants for their survival (Oppermann and Briemle 2009; Schoof et al. 2019).

In orchard meadows, the type and structure of the understory has a strong effect on faunal diversity. Hence, mowing time and frequency also determines which animals persist and establish. For wild bees, early mowing that removes flower buds of spring flowers depletes important flowering resources, such as pollen and nectar (Schwenninger and Wolf-Schwenninger 2012). Therefore, Schwenninger and Wolf-Schwenninger (2012) recommended mid of June as orientation date for the first mowing occasion and from the end of August for the second mowing date, when most summer plants already withered.

Besides timing, the frequency of mowing is also crucial. Intermediate cut frequencies, such as twice a year, support high species richness of vascular plants (Fig. 1) (Socher et al. 2013). Subdominant plant species can establish, as resources essential for them, such as light, become available. However, Wiche et al. (2015) found that mowing twice a year already negatively affected species richness of cicada. Mowing, in particular, enhances the survival of smaller, less competitive plant species on which relatively few cicada species are specialised. Therefore, the authors recommended a single annual mowing to maintain high cicada species richness. To maintain high wild bee diversity, in contrast, Schwenninger and Wolf-Schwenninger (2012) suggested staggered and twice mowing to maintain high flower supply. However, Steffan-Dewenter and Leschke (2003) found that above-ground nesting bee and wasp species were less effected by mowing frequency. The authors assumed that the studied insect communities are only indirectly dependent on the vegetation layer as food supply as flowering fruit trees provide additional pollen and nectar as well as attract prey for hunting wasps. This was similarly observed in a study of Horák (2014b) who found that butterfly species richness was not associated with management (mowing) but with flowering intensity. The author suggested that flowering fruit trees and the surrounding areas might compensate for the effect of mowing on the understory vegetation. Nonetheless, as tree blossoms are temporary and mainly in spring, targeted understory management for bee, wasp and cicada fauna is necessary.

To account for the diverging effects of different mowing schemes on different taxonomic groups, a spatial and temporal mosaic of mowing regimes could be implemented (Kleyer et al. 2007; Johst et al. 2015). For example, a spatio-temporal mowing scheme benefits the survival of the scarce large blue butterfly (*Phengaris teleius*) in grassland systems (Johst et al. 2006). Likewise, asynchronous mowing of grassland likely is a key process governing the high density of white stork in an extensively managed farming landscape of east-central Poland (Golawski and Kasprzykowski 2021). Johst et al. (2015) developed a model to assess the effects of different spatial-temporal mowing schemes on butterfly and bird species. This approach was extended by Sturm et al. (2018) towards a decision-support software, which calculates the effect of grazing and mowing regimes on endangered bird and butterfly species, to determine ecologically and cost-effective agri-environment schemes. Although spatial-temporal mosaic mowing schemes are occasionally implemented in the management of orchards at small scales (Fig. 2), we are not aware of any study applying this model to orchards or that analysed the effects of spatio-temporal mosaic mowing schemes for species in orchards.

Figure 2. Example of a spatio-temporal mosaic mowing regime in an orchard in Rutesheim-Perouse, southern Germany. Photo: Klaus Henle.

To date, there are no studies comparing the combined effect of different management methods in orchard meadows. Similarly, most studies focus on management effects on plants, birds and pollinating insects, which makes it difficult to develop conservation strategies that also account for the needs of the wide range of species from other taxonomic groups or ecological guilds for which orchard meadows are important (Mader 1982; Schuboth and Krummhaar 2019; Henle et al. 2024). The focus on the conservation of a single species group can be detrimental for other taxa. As most studies cited by us were done in grasslands lacking trees, there is an urgent need for studies covering simultaneously several taxa inhabiting orchard meadows for the development of management guidelines that account for synergistic and antagonistic needs of different taxonomic groups and for interactions between the understory and the tree story.

Effects of abandonment and management intensification

Orchard meadows that are neither grazed nor mowed and left fallow rewild and lose their typical structure of semi-open grasslands with scattered trees. Important habitats disappear, floral as well as faunal species richness decrease (Žarnovičan et al. 2017). Grass and herbal cover of the understory decrease and succession starts to develop (increase of shrub and tree abundance) (Steffan-Dewenter and Leschke 2003; Wiche et al. 2015; Vowinkel 2017). Such forms of abandonment of orchard meadows can lead to a short increase of butterfly and bird diversity as additional resources like forbs and shrubs as well as dead wood become available (Ernst et al. 2017; Kajtoch 2017). In the long term, however, open structures vanish followed by habitats and forage resources unsuitable for species requiring (semi-)open environments (Ernst et al. 2017; Čejka et al. 2018). Horák et al. (2018) found that the number of lichens, butterflies, beetles, and orthopteran species increased when abandoned orchard meadows were restored. These results show that maintenance or restauration has positive effects on species biodiversity and successional changes argue against rewilding of extensively used agricultural landscapes like traditional orchard meadows.

Intensification of orchard meadows towards fruit plantations is the opposing effect of abandonment. Intensification aims at increasing economic output by increasing external inputs like fertiliser and pesticides and by more intensive management like removing old and/or less productive trees. Permanent transition towards intensive grazing and/or high disturbance by mowing in combination with high nutrient input leads to a decrease of taxonomic and functional diversity of pollinating insects (e.g., species of Hymenoptera, Lepidoptera and Diptera) and orthopteran species as well as in alteration of vegetation communities toward highly competitive and disturbance-adapted species (Gardiner 2018; Rakosy et al. 2022). Similarly, high fertilizer rates and frequent mowing can lead to homogenisation of plant communities (Kornprobst 1994; Hammel and Arnold 2012; Socher et al. 2013; Kilian 2016). Addition of fertiliser favours dominant plant species; especially threatened species are lost by high N and P inputs (Harpole et al. 2016; Hautier et al. 2020; Wassen et al. 2021) as many of the Central European threatened plant species depend on nutrient poor soils (Ellenberg 1991; Ellenberg et al. 2001) and are threatened because of the substantial increase of N-emission and P-input across most areas in Central Europe (Ellenberg 1991; Wassen et al. 2005).

Similarly, accumulation of dung due to overstocking of livestock and mulching (cut vegetation left on the meadow) can lead to accumulation of nutrients and rotting processes. This in turn can lead to a change and homogenisation of the flora and vegetation structure in the longer term (Pavlů et al. 2016). However, mulching or fertilising can be important for the replenishment of nutrients for fruit trees, which can have an undersupply of phosphor, potassium and magnesium if, e.g., regularly harvested (Degenbeck 2021). Pavlů et al. (2016) found no significant changes of nutrient concentration in herbs or soil when cuttings were either left or removed in upland grassland in the Czech Republic. Nonetheless, the authors reported a tendency towards higher nutrient concentrations in grasslands treated by mulching than grassland with cuttings removed. Mulching or fertilising should be considered based on the location and abiotic factors, e.g., soil properties. While mulching can benefit plant species and functional trait diversity in a nutrient-poor mountain meadow (Doležal et al. 2011), it can decrease plant species richness in an nutrient-rich upland grassland (Gaisler et al. 2019). Beside the need to change from intensive to extensive cultivation, a grassland study in Germany showed that variation of land-use intensification (mowing, grazing, fertilisation) across years can be a complementary strategy to enhance biodiversity (Allan et al. 2014).

If extensive management like grazing or mowing with cut vegetation removed cannot be maintained, temporarily mulching twice a year seems to be a good option to conserve plant diversity and depress succession (Römermann et al. 2009; Gaisler et al. 2019).

Effects of extensive tree management on species richness

The diversity of microhabitats is a useful indicators for species richness as it is assumed that microhabitats such as dead wood, cavities and branch holes, correlate with the abundance and diversity of organisms living on and in trees (Grossmann and Pyttel 2016; Asbeck et al. 2021). Therefore, the maintenance of high-trunk trees in form of occasional pruning is very important as pruning promotes the formation of natural cavities beneficial for cavity users like many bird and insect species (see chapter structure and microhabitats) (Eckstein and Albrecht 2006; Grüebler et al. 2013; Henle et al. 2024). Especially, removing of main branches leads to large pruning wounds, which in turn lead to decay cavities (Grüebler et al. 2013). Extensive tree care, such as leaving dead branches, promotes deadwood and notably increases decay-induced tree cavities (Eckstein and Albrecht 2006).

Quality and quantity of microhabitats further depend on the tree species and tree associated properties, such as bark structure and trunk diameter. Eckstein and Albrecht (2006) found that trunk and branch hollows were mostly associated with apple trees whereas moss cushions were mostly found on pear trees. Lichens are most common on pear and plum trees. Grossmann and Pyttel (2016) found more microhabitats in walnut trees compared to apple trees and a correlation of tree diameter with microhabitats. Larger tree diameter is associated with more microhabitats as trees are usually older. Older trees are more likely to be exposed to natural disturbances resulting in injuries or rot infestation, which favours development of microhabitats (Bobiec 2002; Vuidot et al. 2011; Grossmann and Pyttel 2016). Although walnut trees seem to offer many microhabitat structures because of their high tree diameter, they are not common in orchard meadows in Central Europe (Degenbeck 2003; Schuboth and Krummhaar 2019).

The importance of different tree species and varieties is also shown by different susceptibility to diseases. Apple trees are affected by higher rates of fungal heart rot infestation. This, in turn, attracts high numbers of woodpeckers and consequently leads to higher numbers of woodpecker-cavities (Grüebler et al. 2013). Other studies also showed that especially apple trees contain higher numbers of tree holes (Amann 2007), which might be because of the softer bark of apple trees, which is easier to penetrate compared to other fruit trees (Eckstein and Albrecht 2006). To obtain a high quantity of microhabitats new tree plantings should include a high proportion of apple trees (Grüebler et al. 2013). At the same time, nesting possibilities in the form of artificial nesting boxes are also an important conservation strategy to promote birds, small mammals and insects (Amann 2007).

Summary conservation and management recommendations

The species diversity of orchard meadows is very closely connected to the maintenance and management of the under- and overstory, which determines structural diversity. However, it is evident from the studies reviewed above that management recommendations depend on and differ among targeted taxa, and thus each may be detrimental for non-target taxa (Wiche et al. 2015; Schoof et al. 2019). In any case, rewilding, a strategy for biodiversity conservation recently increasingly promoted also for cultural landscapes in the form of land abandonment (Navarro and Pereira 2015), is not an appropriate conservation strategy for orchard meadows. Rewilding will lead to the disappearance of plants and animal species that depend on the combination of open diverse grassland with trees (Ernst et al. 2017; Žarnovičan et al. 2017). Likewise, intensification with high interventions will be detrimental to many taxa and will result in the loss of the biodiversity conservation value of orchards (Pavlů et al. 2016; Gardiner 2018; Rakosy et al. 2022).

Similar to the understory, the maintenance of the overstory by extensive tree pruning leads to high numbers of microhabitats, which offers manifold ecological niches for different species. Management of trees prevent premature ageing. For the maintenance of orchard meadows adding young trees of different species and varieties are important. Similarly, dead wood, e.g., standing trees contain many microhabitats and are crucial for cavity users (Eckstein and Albrecht 2006; Grüebler et al. 2013; Grossmann and Pyttel 2016). Although fruit trees contain many microhabitats, nesting boxes should be provided to support secondary cavity users like several bird, mammal and insect species (Amann 2007).

Grazing, mowing and tree maintenance are key management aspects for biodiversity in orchard meadows. However, there is no "silver-bullet strategy" for an optimal management regime that fits all taxa as it is highly dependent on the location and the targeted species groups. For instance, a mowing frequency of twice per year can already lead to a decrease of cicada species (Wiche et al. 2015), whereas bee species richness may benefit (Schwenninger and Wolf-Schwenninger 2012). As such, we recommend a combination and time-shifted implementation of different management regimes, like grazing and mowing, as this seems to be a promising way to create an understory suitable for taxa with different ecological requirements as grasses and herbs will be in different growth stages. A caveat is that such schemes can be implemented effectively only in very large orchards or at the landscape scale with many orchards in close vicinity to each other.

Compared to other livestock, cattle, with their unselective feeding behaviour, seem to have the best effect on plant, butterfly and bee diversity (Carvell 2002; Sheil and Wunder 2002; Öckinger et al. 2006; Schoof et al. 2019). However, when livestock is involved, fruit trees should be protected with fences to avoid debarking (López-Sánchez et al. 2020). Similarly, risk mitigation measures, e.g., a selected use of antiparasitic treatments, to protect dung living insects should be considered when using veterinary medicine (Römbke et al. 2019).

Mowing times should be adjusted to the surrounding landscapes (e.g., timing of mowing in the neighbouring landscape) to prevent synchronous mowing and maintain alternative areas for the fauna (Kleyer et al. 2007; Johst et al. 2015; Golawski and Kasprzykowski 2021). Especially habitats similar to orchard meadows seem to be beneficial for species richness and should be considered as well (Horák 2014b; Ernst et al. 2017). Generally, conservation schemes should take place on the landscape scale rather than the local scale to promote interconnectivity and landscape diversity. This will provide flower resources during a longer time period for flower visiting insects and structural diversity thereby promoting nesting, foraging or hunting sites for different taxa (e.g., grassland birds, small mammals). If mowing or grazing cannot be afforded, temporarily mulching is also an option to maintain plant diversity and prevent successions (Römermann et al. 2009; Gaisler et al. 2019).

Further, traditional ecological knowledge about orchard meadows in a specific region can be very helpful in optimizing management regimes, as it has been verified by generations of farmers (Babai and Molnár 2014).

Conclusions

To conserve and halt the decline of orchard meadows in Central Europe, we argue that it is paramount to acknowledge their importance for biodiversity at a political, cultural and societal level. There is a need for a clear definition of orchard meadows to create a common term in Europe, which would make the assessment as well as their protection more straightforward (see Henle et al. 2024). Orchard meadows should be listed in the Habitats Directive of the Council of the European Union and farmers should get incentives for maintaining orchard meadows; see Henle et al. (2024) for comprehensive conservation recommendations at the political, economic, cultural and societal level from the local to the European level.

While we highlighted the important ecological role of orchard meadows in Central European landscapes (Table 1), our review also points out the limitation of available studies on orchard meadows in Central Europe. Most studies focused on plants, birds and pollinating insects, and only a few studies are available on other taxonomic groups. Even for plants, the knowledge depends to a large extent on an extrapolation from studies of tree-less grasslands to orchards, which contains uncertainty on the extent of the robustness of the extrapolation. Conservation strategies on single taxonomic groups, e.g., bird

Table 1. Key conclusions.

1. Biodiversity in Orchard Meadows	Selected References
Orchard meadows are one of the most biodiverse agricultural habitats in Central Europe explained by their high structural diversity. (See chapter: Structure and microhabitats)	Kilian (2016), Saure (2016), Schuboth and Krummhaar (2019)
Species richness in orchard meadows increases with patch size. (See chapter: Local scale: effects of patch size and isolation)	Amann (2007), Bauschmann (2005), Steffan-Dewenter (2003)
Habitat surroundings, landscape composition and connectivity of orchard meadows determines species composition. (See chapters: Surrounding landscapes, regional scale)	Ernst et al. (2017), Horák et al. (2013), Steffan-Dewenter (2003)
2. Management in Orchard Meadows	
Extensive grazing and mowing promote structural diversity of the understory. (See chapter: Maintenance of structural diversity of the understory)	Schoof et al. (2019), Jerrentrup et al. (2014), (Gilhaus et al. 2017)
Fertilization and intensive mowing or grazing leads to homogenisation of plant communities. (See chapter: Effects of abandonment and management intensification)	Hammel and Arnold (2012), Kilian (2016), Leuschner and Ellenberg 2017
Extensive tree management promotes animal species richness. (See chapter: Effects of extensive tree management on species richness)	(Rösler 2002), Samnegård et al. (2019), Erlach (1994), Eckstein and Albrecht (2006), Grüebler et al. (2013)

or pollinator insect species, might be detrimental for other taxonomic groups. Studies on the management effects on neglected taxonomic groups is a major research need for improving applied conservation of biodiversity in orchard meadows as is the effect of spatially and temporally asynchronous understory management. Similarly, very few studies investigated the landscape scale effects on orchard meadows, and comparisons with other extensive agricultural landscapes are lacking. Those studies could help to understand the function of orchard meadows as extensive agricultural habitat on the landscape scale and what effect it has for other land use types and vice versa.

Here, we will briefly outline future research directions.

Research gaps and directions:

- Alpha diversity is closely linked to structural diversity of orchard meadows highlighted by the high diversity of different taxa inhabiting the under- and overstory of orchard meadows. However, to this date there are only a limited number of studies comparing orchard meadows to other extensive cultivated landscapes like grasslands or woodlands in the same landscapes. Comparing other extensively cultivated landscapes to orchard meadows could help to better understand species composition in orchard meadows, especially for which species orchard meadows belong to their preferred habitats. Studies on the effects of the presence of trees with their shading, leaf fall and fruit availability on diverse taxonomic groups, and how extensively managed landscapes can substitute or supplement each other at a landscape scale are very rare. Similarly, knowledge about the interactions of orchard meadows with the surrounding matrix in the conservation of species is rather limited, including an assessment of the relative importance of orchard meadow and the matrix for the presence of species in orchard meadows. There is evidence that orchard meadows can be important for specialist and generalist species.
- We see an urgent need to invest in research addressing area requirements of different species. Great promise lies in the discipline of functional ecology

where species occurrences in orchards of different size and isolation can be linked to their traits and other indices of their life-history strategy. For instance, the link of species traits and their occurrence in differently sized and isolated orchard meadows is largely unknown. Here, future research may test whether species with high dispersal capacity, such as winged insects or birds, are overrepresented in small and/or isolated orchard meadows.

- Area requirements of species in orchards are poorly known, rendering it speculative whether species with large area requirements are mostly absent in orchards. Future research should link such questions with habitat connectivity of different orchard meadows. For instance, even smaller but well-connected orchard meadows may allow species with larger area requirements to persist more likely than isolated but larger orchard meadows. Such questions are also of great relevance for conservation and management strategies that we discuss in detail under conservation and management recommendations.

Acknowledgements

We thank Dr. Markus Rösler, Naturschutzbund Deutschland, Gerlingen, Jennifer Krämer, Naturschutzbund Deutschland, Berlin, and Volker Scherfose, BfN, Bonn-Bad Godesberg, for constructive discussions and information on orchard meadows.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This study was funded by The German Federal Agency for Nature Conservation (BfN) (Project reference: FKZ 3520 83 0100).

Author contributions

CS and KH conceived the ideas. CS and MLH conducted literature research. CS wrote the main text of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

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Link: https://doi.org/10.3897/natureconservation.55.108688.suppl1