A multitaxa assessment of the effectiveness of agri-environmental schemes for biodiversity management

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Agri-environmental schemes (AES) aim to restore biodiversity and biodiversity-mediated ecosystem services in landscapes impoverished by modern agriculture. However, a systematic, empirical evaluation of different AES types across multiple taxa and functional groups is missing. Within one orthogonal design, we studied sown flowering AES types with different temporal continuity, size, and landscape context and used calcareous grasslands as seminatural reference habitat. We measured species richness of 12 taxonomic groups (vascular plants, cicadas, orthopterans, bees, butterflies, moths, hoverflies, flower visiting beetles, parasitoid wasps, carabid beetles, staphylinid beetles, and birds) representing 5 trophic levels. A total of 54,955 specimens were identified using traditional taxonomic methods, and bulk arthropod samples were identified through DNA metabarcoding, resulting in a total of 1,077 and 2,110 taxa, respectively. Species richness of most taxonomic groups, as well as multidiversity and richness of pollinators, increased with temporal continuity of AES types. Some groups responded to size and landscape context, but multidiversity and richness of pollinators and natural enemies were not affected. AES flowering fields supported different species assemblages than calcareous grasslands, but assemblages became more similar to those in seminatural grasslands with increasing temporal continuity. Our results indicate that AES flowering fields and seminatural grasslands function synergistically. Flowering fields support biodiversity even when they are relatively small and in landscapes with few remaining seminatural habitats. We therefore recommend a network of smaller, temporally continuous AES flowering fields of different ages, combined with permanent seminatural grasslands, to maximize benefits for biodiversity conservation and ecosystem service delivery in agricultural landscapes.

agriculture | conservation | DNA-metabarcoding | ecosystem services | flower fields

Human societies are facing a worldwide loss of biodiversity with alarming declines of insect diversity in temperate agricultural landscapes (1, 2). This loss of biodiversity is jeopardizing agricultural production as important ecosystem services ensuring crop yields are directly driven by biodiversity (3). Biodiversity, however, requires suitable habitats for species to persist, forage, nest, reproduce, and hibernate (4, 5). This challenge has been recognized and agri-environmental schemes (AES) have been introduced in the European Union and other regions to reverse biodiversity declines, to restore functional diversity, and to harness the benefits of ecosystem services, like pollination and pest control, in agricultural landscapes (6–8).

An important component of AES to fulfill these goals is the establishing of habitats that provide limiting resources, such as food and shelter for a broad range of organisms. Typically, farmers are financially compensated on a per area basis, but the effectiveness of schemes is often unclear. Thus, compensations might not direct farmers' decisions among different AES to the ecologically most meaningful ones (7). A variety of different habitats are created as AES, ranging from hedgerows to sown flower strips or flowering fields, with the latter being widely used due to their flexible applicability and public appreciation (4). Recent assessments, however, found that overall, European AES are not fulfilling their goals (6, 9). Particularly, the value of AES for securing biodiversity is under debate (10, 11). Beneficial effects previously reported focused on single taxonomic or trophic levels or ecosystem services and varied among study designs, taxa, or services assessed (12–14). Conclusive multitaxa approaches assessing potential services and disservices in one design are missing (8). Furthermore, it is unclear how different properties of AES habitats (e.g., their temporal continuity or size) and varying landscape context affect biodiversity across multiple taxonomic groups.

Temporal continuity is an important factor affecting biodiversity. Higher temporal continuity increases heterogeneity within a habitat and creates niches for more species (15, 16). Temporal continuity also enables weak dispersers and higher tropic levels to colonize a habitat, with the latter being dependent on established populations of lower trophic levels (15). In AES habitats, the influence and the effects of temporal

Significance

The loss of biodiversity challenges agriculture as crop yields depend on biodiversity-mediated ecosystem services. Targeted agri-environmental schemes (AES), like sown flowering fields, provide additional food resources and shelter for wild plants and animals. Such AES have been implemented to restore biodiversity in agricultural landscapes and ensure ecosystem services provision. However, little is known about the comparative benefits of different AES for functional biodiversity and whether temporal continuity, covered area, or perennial source habitats in the surrounding landscape limit the success of an AES. Here, we systematically evaluate within one study design how temporal continuity, size, and seminatural habitat cover in the surrounding landscape affect multitaxa diversity in different AES types and assess their potential for biodiversity conservation in agricultural landscapes.

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continuity have so far been neglected. Newly established flowering fields were found to be more attractive to pollinators than older flowering fields, but pollination services in adjacent fields peak 2 y after initial sowing (14, 17). Older AES habitats could potentially also benefit rare and endangered species with specific habitat requirements, if species assemblages in AES habitats change toward those in permanent species-rich seminatural grasslands with time or increased temporal continuity (18).

Apart from temporal continuity, size might be an important predictor for the conservation value of AES habitats. Increasing habitat size leads to an increased species richness as it is accompanied with the establishment of larger, more stable populations and allows higher trophic levels to persist (19–21). It is unclear whether biodiversity in a landscape benefits more from few large habitats or a network of many small habitats (22, 23). Relationships between size and species richness might therefore be essential for the planning and strategic placement of AES habitats.

Source habitats for biodiversity are needed in agricultural landscapes to build up local populations in newly established AES habitats from regional species pools (24). Seminatural habitats embedded in agricultural landscapes have been shown to support farmland diversity (25, 26), and thus AES habitats in complex landscapes with high proportions of seminatural habitats potentially host the highest diversity.

Here, we investigate the effects of AES differing in temporal continuity, size, and surrounding landscape context over several years on multiple taxonomic groups within one study design. Different types of flowering fields are commonly established by farmers as part of AES to provide additional flower resources. These fields are sown with seed mixtures adapted to local soil properties and taken from regional species pools. After a certain timespan, often varying from 1 to 10 y, flowering fields are returned to crop production. The studied flowering fields differed in temporal continuity from: 1) Newly sown on arable land, over 2) refreshed (i.e., flower fields resown after 5 y) to 3) continuous, 6-y-old flowering fields. Species-rich calcareous grasslands were used as permanent control (Fig. 1 and Table 1). Calcareous grasslands are seminatural biodiversity hotspots in Europe and are preserved by low intensive mowing or grazing (27). We investigated species richness in these 4 AES types across 12 taxonomic groups belonging to 5 trophic levels, including pollinators (bees, butterflies, moths, flower visiting beetles, and hoverflies) and natural enemies (parasitoid wasps, carabid beetles, staphylinid beetles, and birds) as providers of important ecosystem services (3). Species were identified by classic taxonomic techniques (vascular plants, orthopterans, bees, butterflies, moths, flower visiting beetles, carabid beetles, staphylinid beetles, and birds) and DNA metabarcoding (cicadas, hoverflies, and parasitoid wasps). Repeated recordings of a subset of four taxonomic groups (plants, orthopterans, bees, and carabid beetles) within 2 y were performed to clarify whether short-term succession changed assemblages in newly established flowering fields toward those in seminatural calcareous grasslands. Apart from analyses for each taxonomic group, we performed a multidiversity analysis by calculating a diversity index across all taxa, pollinators, and natural enemies (28). Our study aims to judge which types of AES fulfill the goal of restoring biodiversity and ecosystem services in agricultural landscapes best, and should therefore be fostered. Such data are urgently needed to build the scientific basis for a successful transition of

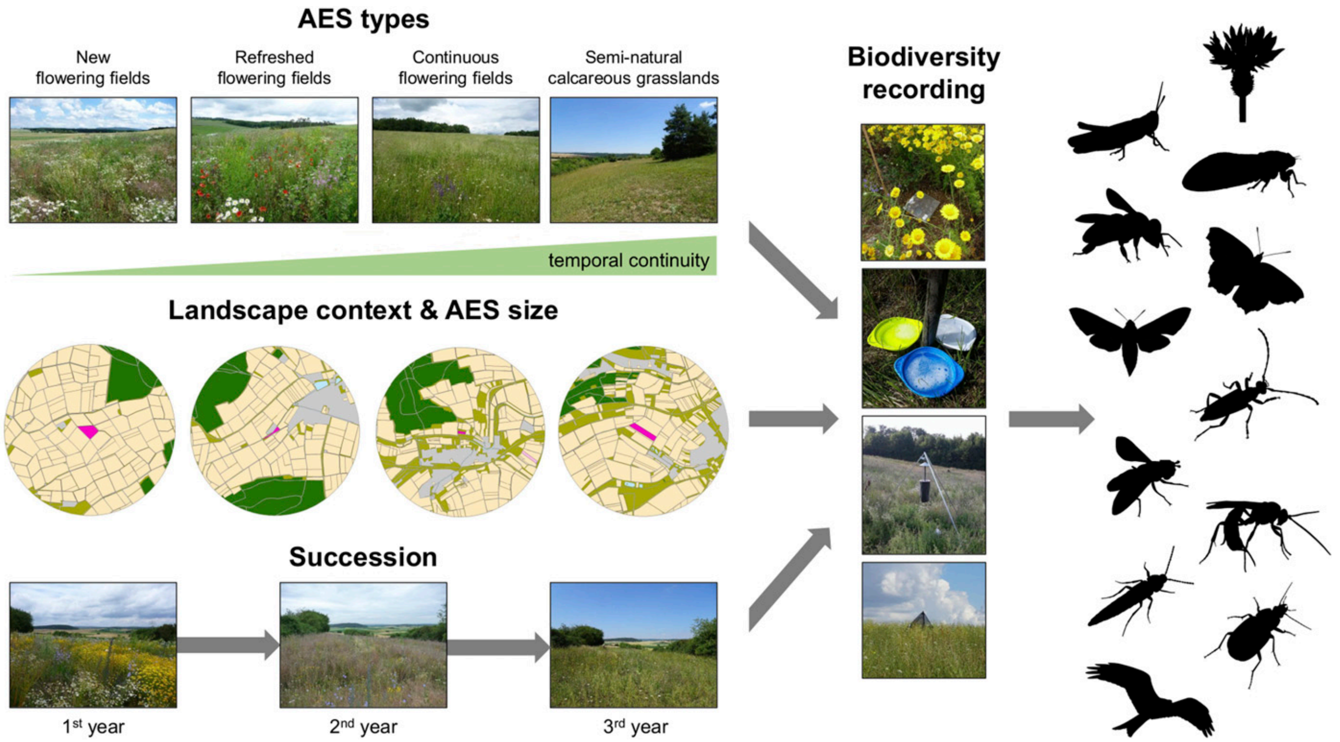

Fig. 1. Study design on the landscape and site level. Biodiversity across 12 different taxonomic levels (from top to bottom: Vascular plants, orthopterans, cicadas, bees, butterflies, moths, flower visiting beetles, hoverflies, parasitoid wasps, carabid beetles, staphylinid beetles, birds) was recorded using a variety of classic methods (pan traps, pitfall traps, transect walks, light traps combined with taxonomic identification) as well as metabarcoding analyses (using samples collected with Malaise traps). The different types of flowering fields and calcareous grasslands were located along a gradient of temporal continuity (Table 1). All AES types covered independent gradients of seminatural habitat in the surrounding landscape and habitat size (purple, AES; yellow, arable land; light green, seminatural habitat; dark green, forest; gray, urban). Repeated recordings over 2 y were performed for vascular plants, orthopterans, bees, and carabid beetles to assess whether succession shifted assemblages in flowering fields toward those in seminatural calcareous grasslands.

Table 1. **Differences in temporal continuity**

	Habitat age, y	Last soil disturbance, y	Temporal continuity	Previous land use	Management	Vegetation
New sown flowering field	1	1	Low	Arable land	None	Customary flower seed mixture; sown in the previous year
Refreshed sown flowering field	>6	1	Low–intermediate	Sown flowering field (5 y)	None	Customary flower seed mixture; sown in the previous year
Continuous sown flowering field	>6	>6	Intermediate–high	Sown flowering field (5 y)	Mulching above ground once per year after June	Customary flower seed mixture sown >6 y ago; strongly shaped by succession
Calcareous grassland	>>20	>>20	High	NA	Grazing or mowing once per year after June	Seminatural xerothermic grassland vegetation

Differences in temporal continuity—resulting from habitat age and management—of the studied AES types in 2016 (first year of the study).

European Union and global policies to biodiversity-friendly and sustainable crop production.

We expected that: 1) Benefits of temporal habitat continuity differ among taxonomic groups, pollinators, and natural enemies; 2) temporal continuity and short-term succession alter species assemblages of sown flowering fields toward those in seminatural grasslands; and 3) multidiversity in sown flowering fields benefits most from the combination of temporal continuity, large habitat size, and high proportion of seminatural habitats in the landscape.

Results

Using different sampling approaches and classic taxonomic identification, we recorded a total of 331 vascular plant species, as well as 746 animal species (5,466 orthopterans of 27 species, 2,441 bees of 143 species, 4,188 flower visiting beetles of 91 species, 3,020 butterflies of 56 species, 798 moths of 120 species, 27,558 carabid beetles of 111 species, 11,151 staphylinid beetles of 141 species, and 666 birds of 57 species) with a total of 55,288 identified specimens. Molecular DNA metabarcoding yielded an additional 2,110 taxa from various, predominantly flying, insect orders, of which we selected cicadas (54 taxa), hoverflies (66 taxa), and parasitoid wasps (322 taxa) for further analyses as these groups are important indicators (cicadas) or ecosystem service providers (hoverflies and parasitoid wasps). A total of 442 taxa from DNA metabarcoding were included in the analyses (*SI Appendix*, Fig. S2 and Tables S2 and S3).

Effects of Temporal Continuity on Multidiversity in AES. Multitaxa diversity [the percentage of species in each site of the total species pool (28)] increased on average by 39% with temporal continuity from new flowering fields to calcareous grasslands, with the latter having a significantly higher multidiversity than all flowering field types (Fig. 2 *A* and *D* and *SI Appendix*, Table S4). Calcareous grasslands supported a higher pollinator diversity than flowering fields, while there were no differences among AES types with different temporal continuity in diversity of natural enemies (Fig. 2 *B*, *C*, *E*, and *F* and *SI Appendix*, Table S4).

Different taxonomic groups showed variable responses to temporal continuity. Plants (in 2016) and carabid beetles (in 2017) were most species-rich in the new and refreshed flowering fields (Fig. 3 *A* and *J* and *SI Appendix*, Table S4). Orthoptera, butterflies, and parasitoid wasps had the highest richness in calcareous grasslands and the lowest richness in new and refreshed flowering fields, with continuous flowering fields being intermediate (Fig. 3 *B* and *E* and *SI Appendix*, Table S4). Moths and birds were more species-rich in calcareous grasslands than in all types of flowering fields (Fig. 3 *F* and *L* and *SI Appendix*, Table S4). For cicadas, bees, flower visiting beetles, hoverflies, and staphylinid beetles we found no differences in richness between the AES types with different temporal continuity (Fig. 3 *C*, *D*, *G*–*I*, and *K* and *SI Appendix*, Table S4).

Effects of Temporal Continuity and Short-Term Succession on Species Assemblages. Ordinations showed that for all taxonomic groups except cicadas, moths, and birds, AES with different temporal continuity shaped species assemblages. In plants, butterflies, parasitoid wasps, carabid beetles, and staphylinid beetles, a gradual increase in the similarity between assemblages along the gradient of temporal continuity was visible (Fig. 4 *A*, *E*, *I*, *J*–*L* and *SI Appendix*, Table S5). Orthopterans, bees, and flower visiting beetles had similar assemblages in all flowering fields but different assemblages in calcareous grasslands (Fig. 4 *B*–*D* and *G* and *SI Appendix*, Table S5).

Short-term succession was measured over 2 y in four selected taxonomic groups (plants, orthopterans, bees, and carabid beetles) with repeated recordings (using the same methodology in both years). Plant assemblages of flowering fields became more similar to those in calcareous grasslands in the second year of recording (Fig. 4*A* and *SI Appendix*, Table S5). Bee assemblages did not differ among AES types but changed essentially between the repeated recordings in all AES types (Fig. 4*D* and *SI Appendix*, Table S5). Assemblages of orthopterans and carabid beetles did not change in any of the AES types between repeated recordings, while carabid richness was higher in the first than in the second year (Fig. 4 *B* and *J* and *SI Appendix*, Fig. S3 and Tables S5 and S6).

Effects of Flowering Field Size and Landscape Context on Local Diversity. Multidiversity, as well as diversity of pollinators and natural enemies, were not significantly affected by flowering field size and seminatural habitat proportion in the surrounding landscape (*SI Appendix*, Table S6). However, increasing flowering field size decreased staphylinid beetle richness (*SI Appendix*, Table S6). An increasing proportion of seminatural habitats in the landscape enhanced the richness of bees (*SI Appendix*, Table S6). All other taxonomic groups showed no significant relation to flowering field size or proportion of seminatural habitats.

Discussion

We show that flowering fields support biodiversity and ecosystem services in agricultural landscapes. However, they cannot replace species-rich seminatural grasslands as they support different species assemblages and for most taxa lower diversity. The parallel or contrasting responses of different taxonomic groups, representing multiple trophic levels (plants, herbivores, predators), functional groups (pollination and pest control services), species traits (e.g., body size and mobility), and conservation

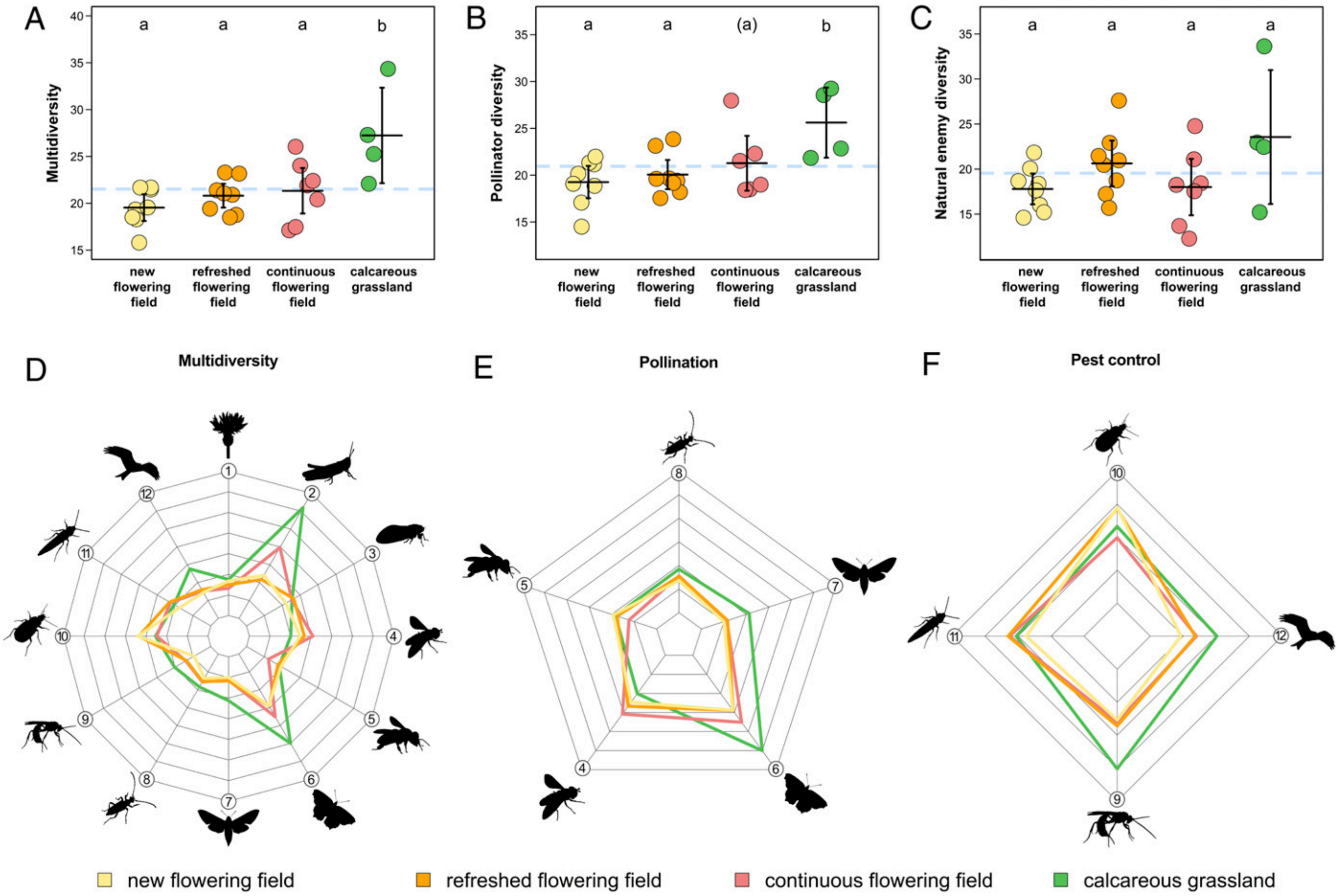

Fig. 2. (*A*) Overall multidiversity, (*B*) diversity of pollinators, and (*C*) diversity of natural enemies in the different AES types along a gradient of temporal continuity (increasing from left to right; percentages of species in each site of the total species pool ± 95% confidence interval; blue dashed lines indicate means across all sites). Proportion of species present in each AES type (mean) for (*D*) all taxa, (*E*) pollinators, and (*F*) natural enemies. In radar charts, one interval equals 10% starting from the center of the chart. Taxonomic groups were 1) vascular plants 2) orthopterans, 3) cicadas, 4) hoverflies, 5) bees, 6) butterflies, 7) moths, 8) flower visiting beetles, 9) parasitoid wasps, 10) carabid beetles, 11) staphylinid beetles, and 12) birds. Different letters in *A*–*C* indicate significant differences ($P < 0.05$), brackets indicate marginally significant differences ($P < 0.1$). For statistics, see *SI Appendix*, Table S4.

status broaden the scientific basis for evidence-based designs of AES, regional prioritizations, and allocation of subsidies.

The Importance of Temporal Continuity. We found temporal continuity of AES habitats to be important: Multidiversity, as well as pollinator diversity, benefited from flowering fields with higher temporal continuity and permanent seminatural grasslands, while natural enemy multidiversity was unaffected by temporal continuity.

The investigated taxonomic groups reacted differently to temporal continuity. Carabid beetles as important natural enemies had the highest richness in newly established flowering fields. Orthopterans, butterflies, moths, parasitoid wasps, and birds, however, benefitted from older, more temporally continuous habitats, and richness peaked in calcareous grasslands. Many species of these taxonomic groups are endangered habitat specialists with habitat requirements that younger AES types fail to fulfill. AES with higher temporal continuity are more heterogeneous in structural aspects due the successional change than uniformly sown young flowering fields. Furthermore, grasslands provide, for example, shrubs for birds or specific food plants for orthopterans or butterflies and moths, which are not present in seed mixtures and potentially increase their suitability for these taxa (4, 5).

Consequently, species assemblages of these groups in continuous flowering fields were more similar to those in calcareous grasslands than to those in young flowering fields. This trend was also visible in the assemblage structures of plants, carabid beetles, and staphylinid beetles, although no differences in richness were visible. Short-term succession overall did not change species assemblages of younger AES toward assemblage structures of AES with higher temporal continuity. We assume that the observed changes in plant and bee assemblages in all AES types were mainly driven by different weather conditions between the years. Both 2017 and 2018 were exceptionally warm years in the study region, which could have shifted assemblages when compared to 2016.

As biodiversity directly drives pest control and pollination services (3), maintaining biodiversity in agricultural landscapes is essential to ensure ecosystem service provision. We show that in this context, temporal continuity is an essential component. Implementing AES habitats over the span of several years is therefore important, but not a silver bullet for biodiversity conservation due to their eventual discontinuation. Flowering fields only support a subset of the total regional biodiversity, likely rather common species (4). Seminatural calcareous grasslands, however, support and conserve additional species and host the highest overall diversity. Habitats with increased temporal continuity allow slow colonizers to establish populations and are shaped by natural processes, like succession and selection of better adapted species from the regional species pool and thus become gradually more similar to calcareous grasslands.

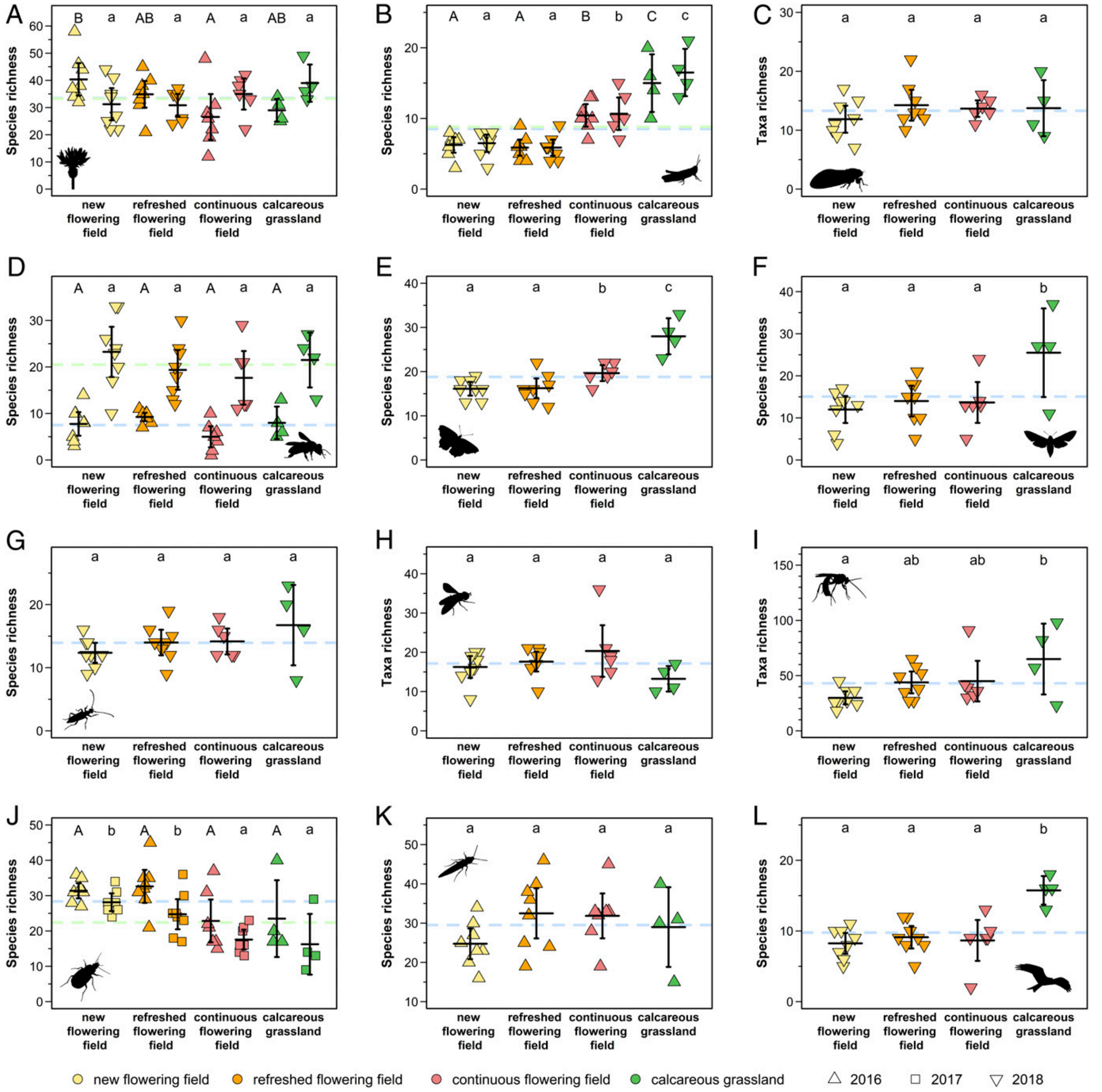

Fig. 3. Species richness of 12 taxonomic groups in the 4 studied AES types along a gradient of temporal continuity (increasing from left to right). Taxonomic groups were (*A*) vascular plants, (*B*) orthopterans, (*C*) cicadas, (*D*) bees, (*E*) butterflies, (*F*) moths, (*G*) flower visiting beetles, (*H*) hoverflies, (*I*) parasitoid wasps, (*J*) carabid beetles, (*K*) staphylinid beetles, and (*L*) birds (*A*, *B*, *D*, and *J* were recorded over two seasons, all other groups over one season). Means ± 95% confidence interval. Dashed lines indicate means across all sites (in groups with recordings over 2 y, blue lines indicate means of the first and green lines means of the second year). For statistics, see *SI Appendix*, Table S4. Different letters indicate significant differences ($P < 0.05$).

Therefore, they can harbor both the species of the agricultural landscape, as well as species with more specific habitat requirements, which makes habitats with higher temporal continuity especially important for conservation efforts (29).

While AES habitats with higher temporal continuity promote pollinator diversity, natural enemy diversity was equally high in newly established habitats. Together with calcareous grasslands, flowering fields also provide shelter to buffer disturbances occurring regularly in adjacent agricultural fields (e.g., soil management, application of pesticides, harvest), as they remain comparatively undisturbed. Both flowering fields and calcareous grasslands together function synergistically and thus maximize benefits for biodiversity if provided simultaneously in a landscape.

Single Large or Several Small? The size of a habitat often determines the number of species it contains (20). Especially in biodiversity conservation, the last decades have been dominated by the debate whether single large or several small habitat patches in a landscape were to be preferred (22, 23). Within our gradient from 0.29 ha to 2.92 ha, flowering field size affected neither

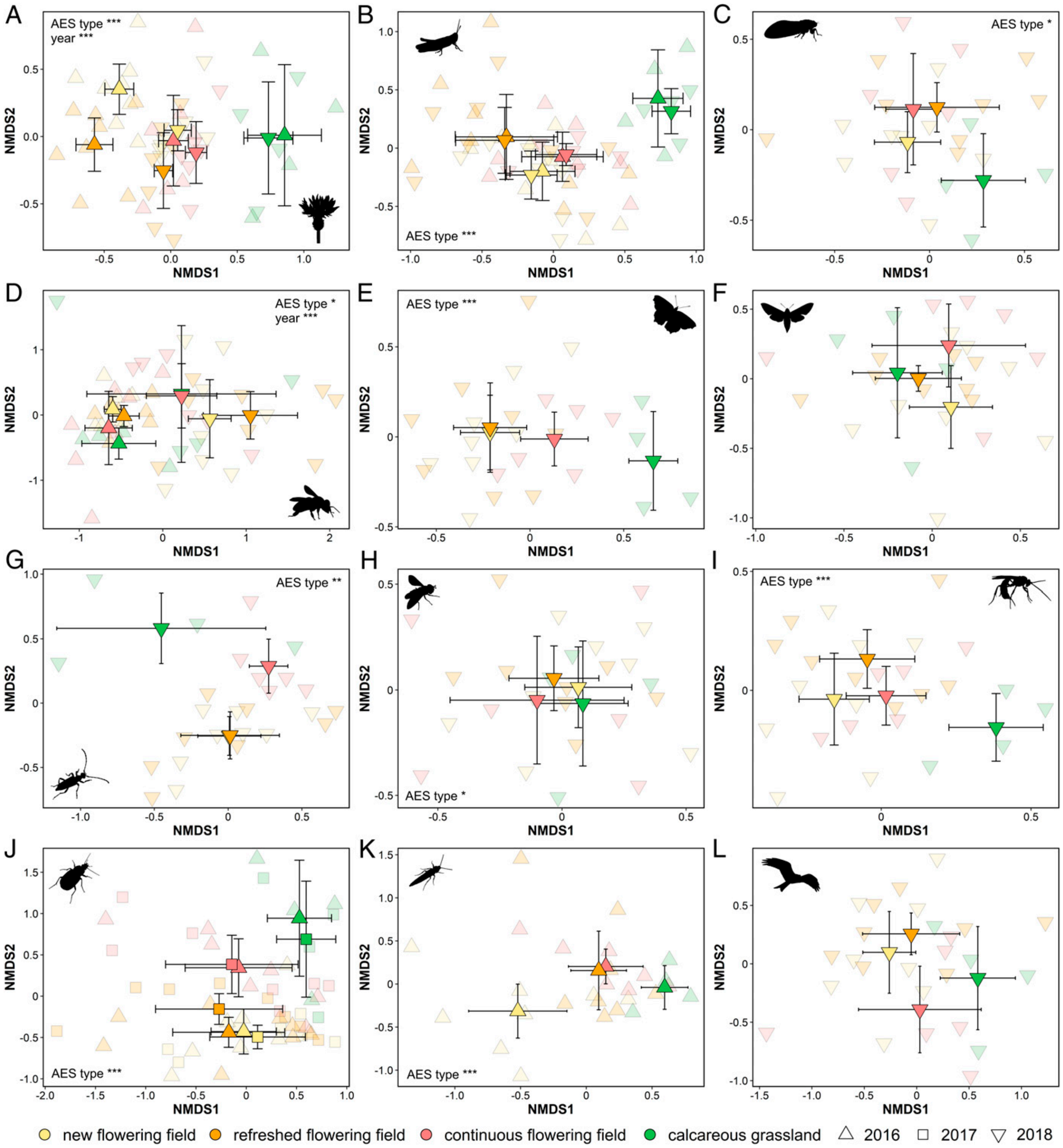

Fig. 4. Species assemblages of 12 taxonomic groups (NMDS ordination) in the four studied AES types; partly for 2 y (*A*, *B*, *D*, and *J*). Taxonomic groups were (*A*) vascular plants, (*B*) orthopterans, (*C*) cicadas, (*D*) bees, (*E*) butterflies, (*F*) moths, (*G*) flower visiting beetles, (*H*) hoverflies, (*I*) parasitoid wasps, (*J*) carabid beetles, (*K*) staphylinid beetles, and (*L*) birds. Centroids of the four AES types ± 95% confidence interval. NMDS and PERMANOVA used Bray–Curtis distances except for taxa recorded and identified by DNA metabarcoding on a presence absence level (*C*, *H*, and *I*), which used Jaccard distances. Significant factors in PERMANOVA tests indicated in the corners of the respective panels ($^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$). For statistics see *SI Appendix*, Table S5.

multitaxa diversity nor the diversity of pollinators or natural enemies. The richness of most of the taxonomic groups was unaffected by flowering field size but staphylinid beetle richness decreased with flowering field size.

Our results indicate that overall, within the range investigated, the size of flowering fields is not limiting the biodiversity they can harbor (this might be different for very small fields below 0.29 ha). Within the studied range, a network of small flowering fields could be more beneficial for agricultural landscapes than single large fields, as beneficial effects within crops (e.g., for pest control) are limited by distance from AES habitats (13, 14, 30). With such a network, edge areas promoting beneficial spillover and edge-effects into adjacent crop fields in the landscape increase (14, 17, 30). This network would also increase overall landscape heterogeneity, which was shown to benefit ecosystem functioning and biodiversity (26, 31). In such networks, AES could comprise habitats of different age with a certain proportion being renewed or replaced and reestablished elsewhere every year. This would ensure that undisturbed habitats for overwintering are continuously available at reachable spatial distances in a landscape. In order to implement such landscape planning policies, further clarification is needed on how beneficial connectivity between AES habitats is, how different types of AES interact with adjacent crop fields, and how dense such a green network in agricultural landscapes should ideally be.

How Effective Are Flowering Fields in Different Agricultural Landscapes? After establishment, AES habitats need to be colonized by organisms from source habitats in the surroundings. While different types of seminatural habitats serve as potential source habitats, it is unclear how much and which types of source habitats are needed. AES were previously found to be especially effective in landscapes with few remaining seminatural habitats (32, 33).

In our study, multidiversity in flowering fields was independent from the amount of seminatural habitat in the landscape. While landscape level seminatural habitat positively affected the richness of bees, most of the taxa investigated did not benefit from landscapes with high seminatural habitat proportions. This indicates that relatively small amounts of seminatural habitats as sources in a 1-km landscape were sufficient to proliferate biodiversity into newly established flowering fields. We, however, did not investigate agricultural landscapes with very small amounts of seminatural habitat left and the effectiveness of flowering fields in such landscapes could be lower (the minimum seminatural habitat cover was 3.6%). In contrast to our results within flowering fields, multidiversity in agricultural fields is driven by seminatural habitat cover in the surrounding landscape (25). While agricultural fields constantly need recolonization after major disturbances (such as soil management or harvest), flowering fields can remain undisturbed for a longer period and are therefore less dependent on continuous influx from source habitats. After an initial colonization phase, they provide continuous shelter and are assumed to act as source habitats for adjacent agricultural fields. Our results indicate that in this phase, landscape-level seminatural habitat is less important, presumably because the subset of the regional species pool that can prosper in AES habitats already reached them. Seminatural habitats, however, support many species, which were not present in flowering fields and therefore will not colonize and establish populations there. This emphasizes 1) that AES habitats can restore diversity in rather simple landscapes with low proportion of seminatural habitat, and 2) that seminatural habitats cannot be replaced by temporary AES to secure biodiversity.

Conclusion

Using a unique dataset comprising 1,519 taxa across 12 taxonomic groups on several trophic levels, we showed that temporal continuity is an important factor driving multidiversity in AES habitats. According to our results, flowering fields cannot replace permanent seminatural grasslands as flowering fields only support a subset of biodiversity from the regional species pool. Seminatural grasslands, on the other hand, provide habitat for species that do not occur on flowering fields and therefore are a valuable addition to these. A combination of both flowering fields and seminatural grasslands is needed to maintain a high overall biodiversity in agricultural landscapes. Increasing heterogeneity in agricultural landscapes benefits biodiversity conservation and can be achieved through the strategic placement of AES (31). Our results indicate that the size of flowering fields and landscape level proportion of seminatural habitats are of lesser importance for the multitaxa diversity they harbor, whereas the diversity of bees, which often is of crucial interest in AES programs, benefits from seminatural source habitats in the landscape. Overall, even small habitats in landscapes with low remaining seminatural habitats can therefore be beneficial and support biodiversity, as well as promote ecosystem service provision.

Many studies have pointed out that AES habitats should be tailored more precisely to the specific targets they aim at fulfilling (34–36). For this, the specific local habitat structures supporting different ecosystem service agents (e.g., nesting structures and locations, habitat requirements, food resources) need to be identified. While younger flowering fields are richer in flowers, and therefore raise attractiveness and acceptance for these structures in the general public and among farmers, the provision of pollination in adjacent croplands increases with flowering field age (14). Our results show that more continuous flowering fields and seminatural grasslands support higher pollinator diversities, while natural enemies were equally diverse also in younger habitats. As pollinators operate on a wider spatial range within the landscape than the predominantly soil-dwelling natural enemies, a network of few, more continuous AES habitats and seminatural grasslands to support pollinator populations supplemented by a variety of more evenly distributed smaller and more frequently rotating flowering fields to foster local natural enemy populations in adjacent fields could be most effective [similar to the interconnected network of habitats proposed by Cole, et al. (36) for pollinators]. With a combination of these measures, landscape complexity is simultaneously increased, which allows more species to persist, benefits functional biodiversity, and ultimately enhances crop yields (3, 26). We conclude that AES can be an important and successful component to restore biodiversity in agricultural landscapes that face a severe decline in insects and other taxa (2). However, a more fundamental transformation of farmland management, including large-scale restoration of permanent seminatural grasslands, are mandatory for long-term preservation of biodiversity and its multiple functions.

Methods

Study Design. To assess the effectiveness of different AES for biodiversity conservation, we established a study design comprised of three different flowering field types, as well as species-rich and permanent calcareous grasslands as controls. The flowering fields differed in size and were located within separated landscapes covering a gradient of landscape-scale cover of seminatural habitats (Fig. 1).

The study was conducted between 2016 and 2018 in 27 study sites within a 60-km radius around Würzburg (Bavaria/Germany) (*SI Appendix*, Table S1). Diversity across 12 different taxonomic groups was recorded in four types of AES habitats (3 types of flowering fields and seminatural calcareous grassland habitats under AES management; in the following “AES types”). The four different AES types included: 1) New flowering fields ($n = 8$), 2) refreshed flowering fields ($n = 8$), 3) continuous flowering fields ($n = 7$), and 4) seminatural calcareous grasslands ($n = 4$). The studied AES types were characterized by differences in current and past management (Table 1): Temporal continuity increased from 1) to 4). Flowering fields 1) and 2) were subsidized under governmental AES and sown with a specific customized flower mixture adapted to local flora, soil, and microclimatic limitations in fall of 2015 and subsequently remained unmanaged for 5 y. Both flowering fields 1) and 2) differed in site history: While 1) had been regular agricultural fields previously used for crop production, 2) had already been flowering fields for 5 y and were plowed and then resown as flowering fields under the same program, which results in an extended seed bank already present in their soils. The continuous flowering fields 3) had also been flowering fields under the same AES for 5 y but were transformed without soil disturbance into ecological focus areas under the Common Agricultural Policy of the European Union (CAP) in 2013 to 2015. Plant communities on the continuous flowering fields were shaped by succession but vegetation was mulched once per year above ground to prevent the growth of shrubs. Calcareous grasslands 4) are protected seminatural habitats that were created due to extensive human land-use and are nowadays often highly fragmented and considered as biodiversity hotspots in Europe (27). While calcareous grasslands are not established under AES, their conservation involves management under AES, mostly mowing once a year or extensive grazing by sheep or goats to prevent succession. Calcareous grasslands are typically rich in different structures and contain, for example, open soil patches and shrubs (mostly juniper).

The areas of the flowering fields ranged from 0.29 ha to 2.92 ha (mean ± SE: new flowering field: 1.32 ± 0.38 ha; refreshed flowering field: 1.05 ± 0.30 ha; continuous flowering field: 1.12 ± 0.25 ha). The minimum distance between study sites was 2.1 km. The amount of seminatural habitat (forest edges, field margins, bank borders, roadside vegetation, small wood groves, hedgerows, orchard meadows, and extensive pastures, calcareous grasslands, and grassland taken out of agricultural production) (17) in a 1-km radius around study sites ranged from 3.6 to 25.0%. (*SI Appendix*, Table S1).

Data Collection. On the 27 sites, we recorded biodiversity at different trophic levels over 3 y. In total, we recorded 12 different taxonomic groups using classic taxonomic methods, as well as identifications based on sequenced data (metabarcoding). The taxa recorded included groups predominantly ranked to one of five different trophic and functional groups: 1) primary producers (vascular plants; recorded with Braun Blanquet Plots); 2) herbivores (orthopterans [Orthoptera; recorded with variable transect walks], cicadas [Auchenorrhyncha; recorded with Malaise traps and identified by metabarcoding]); 3) pollinators with herbivorous larvae (bees [Apoidea; recorded with variable transect walks and pan traps], butterflies and moths [Lepidoptera; recorded with variable transect walks and light traps], flower visiting beetles [several families; recorded with pan traps]); 4) pollinators with predatory larvae (hoverflies [Syrphidae; recorded with Malaise traps and identified by metabarcoding]); and 5) predators (carabid beetles [Carabidae; recorded with pitfall traps], staphylinid beetles [Staphylinidae; recorded with pitfall traps], parasitoid wasps [several families; recorded with Malaise traps and identified by metabarcoding], and birds [Aves recorded with point counts]). Four of the taxa (vascular plants, orthopterans, bees, and carabid beetles) were recorded in 2 of the 3 y using the same methodology. Detailed sampling protocols for all taxa are given in *SI Appendix*.

Statistical Analyses. All statistical analyses were performed in R 3.6.1 for Windows (37). We calculated species richness for taxonomic groups identified by taxonomists and taxa richness for taxonomic groups identified by metabarcoding for all taxa on each site and year as response variables. On each site, all recordings over the course of the year and subplots were pooled for each taxonomic group. Additionally, an index of multidiversity was calculated following Allan, et al. (38): In a first step, we calculated the proportion of species for each site out of the total species pool across all sites recorded for each taxon. In a second step, we calculated the mean of these proportions across all taxa recorded for each site resulting in the multidiversity index. Apart from overall multidiversity, we also calculated multidiversity of potential pollinators (bees, butterflies, moths, flower visiting beetles, and hoverflies; henceforth "pollinator diversity") and natural enemies (parasitoid wasps, nongranivorous carabid beetles, staphylinid beetles, and nongranivorous birds; henceforth "natural enemy diversity").

In a first step, all response variables were tested against AES type using linear models (LM) to detect possible differences between the four AES types (in separate models for each year a taxonomic group was recorded). In a second step, we tested for the flowering fields only (excluding seminatural calcareous grasslands) whether richness was dependent on seminatural habitat proportion and flowering field size (response ~ "flowering field type" × "seminatural habitat proportion" + "flowering field size"). In this step, we performed LMs for taxonomic groups recorded in only one year and linear mixed-effects models [LMER; "lmer" from the "lme4" package (39)] for taxonomic groups recorded over 2 y, including "year" as fixed effect to account for annual fluctuations and "site" as random intercept to account for pseudoreplication in each site. Excluding the calcareous grasslands was necessary as: 1) They were located in landscapes with high seminatural habitat proportion. As a result, the factor "AES type" was correlated with seminatural habitat proportion (which was not the case if calcareous grasslands were excluded); 2) we intended to test the effects of seminatural habitat proportion on biodiversity in established AES habitats and not on permanent seminatural habitats managed under AES that cannot be newly established (i.e., calcareous grasslands).

To assess the effects of different temporal continuity and short-term succession on species assemblages, we compared species assemblages using nonmetric multidimensional scaling (NMDS, "metaMDS", 999 permutations). We tested for the effects of AES type as a measure of temporal continuity and, in case of taxa that were recorded over 2 y, assemblage homogenization over time in the different AES types [species matrix ~ AES type (+ year)]. Prior to ordinations and analyses, species matrices were standardized using the proportions of the species. In datasets obtained from metabarcoding (cicadas, hoverflies, and parasitoid wasps), species observations were treated as presence/absence data and therefore, Jaccard dissimilarities were used in ordinations and statistical testing. For all other groups we tested for differences between obtained clusters in NMDS ordinations using a PERMANOVA ["adonis" from the "vegan" package (40), 9,999 permutations, Bray–Curtis distances].

All models were checked graphically and fulfilled model assumptions. All models were analyzed using type 2 SS ANOVA tests [for LMs with "Anova" from the "car" package (41) and for LMERs with "anova" from the "lmerTest" package (42) using "Kenward-Roger" approximation of denominator degrees of freedom]. Models comparing all four AES types were subsequently tested with Tukey post hoc tests ["glht" from the "multcomp" package (43)].

Data Accessibility. All data associated with this manuscript is available via the Dryad Digital Repository https://doi.org/10.5061/dryad.hdr7sqvh1 (44).

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