



Agriwilding substantially restores butterfly and moth diversity in a European agricultural landscape

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ABSTRACT

Agricultural intensification has caused widespread biodiversity loss, particularly among insects, highlighting the urgent need for strategies that restore biodiversity in human-dominated landscapes. Agriwilding—perennial polycultures that combine productive trees and shrubs with species-rich grasslands while allowing partial ecological succession—has been proposed as a nature-inclusive alternative to conventional agriculture, yet empirical evidence remains limited. We assessed the potential of agriwilding to restore Lepidoptera diversity in an agricultural landscape in Belgium. We combined long-term butterfly observations within a 2-ha agriwilding system following land-use conversion with later standardised surveys of butterflies and moths across different land-management types. Long-term butterfly observations indicate that the agriwilding site supported a high proportion of the regional species pool following land-use conversion. Community composition shifted from mobile generalists towards rarer species associated with woody vegetation, which coincided with ecological succession and increased structural complexity. Standardised monitoring revealed significantly higher butterfly and moth diversity in agriwilding than in conventional agriculture, and similar moth diversity to nature management systems within the study landscape. Overall, agriwilding showed higher species richness, abundance, Shannon diversity, and Hill numbers for both butterflies and moths. Furthermore, species composition differed substantially among all land-management types, showing that agriwilding supports many unique species. The findings from this case study highlight agriwilding as a promising approach for reconciling biodiversity conservation with productive land use and suggest that such multifunctional agricultural systems could be incorporated into biodiversity-focused policy frameworks.

1. Introduction

Worldwide biodiversity loss, particularly in agricultural landscapes, is strongly driven by habitat degradation and fragmentation associated with agricultural intensification (Butler et al., 2007; Green et al., 2005). The European Union's biodiversity restoration plan therefore prioritises the integration of more natural elements into agroecosystems (EU, 2024). Recommended measures include the establishment of wild-flower strips and grassy field margins, as well as the management of hedgerows and low-intensity permanent grasslands (Merckx et al., 2009; Pywell et al., 2004). The success of these implemented measures is evaluated by analysing trends in indicators such as the European grassland butterfly index and the proportion of agricultural land with high-diversity landscape features (EU, 2024; van Swaay et al., 2025a).

So far, these measures have not been able to turn the overall trend of biodiversity loss (Hermoso et al., 2022; Seibold et al., 2019; van Swaay et al., 2025a). Therefore, identifying new approaches to embed nature into agricultural systems may be essential (Cardoso et al., 2020; Fanzo et al., 2020).

One novel approach that explicitly combines biodiversity restoration and agricultural production is agriwilding (Bossuyt, 2024; Corson et al., 2022; Scherr and McNeely, 2008; Vogt, 2021). Agriwilding systems are rationally designed polycultures of productive perennials, in which species-rich grasslands are combined with trees and shrubs that produce high-quality food (Fig. 1, S1) (Kreitzman et al., 2020; Toensmeier, 2024). Agriwilding systems resemble wood pastures and can be viewed as structurally diverse perennial production systems in which farmers actively steer ecological succession through management

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(Bossuyt, 2024). Unlike traditional nature management focused on native species, agriwilding systems combine both native and non-native species that are adapted to the local biome (Moereels et al., 2024). Colonisation and establishment of wild plants and their contribution to succession are partially allowed, resulting in a high diversity of both edible and non-edible plant species with different growth forms (Moereels et al., 2024). Agriwilding systems thus contribute to landscape-scale conservation by creating diverse landscape features and thereby aim to restore and harness ecological and evolutionary processes to obtain resilient and self-sustaining systems that can restore biodiversity while simultaneously producing food (Bossuyt, 2024; Corson et al., 2022). This dual goal of agriwilding is what sets it apart from rewilding practices: where rewilding focuses on restoring self-sustaining native ecosystems by reintroducing keystone species such as large herbivores to create wild nature, agriwilding focuses on the introduction of edible perennials to create wild productive systems (Carver et al., 2021; Vogt, 2021).

While biodiversity loss is apparent across many taxa, the decline of insect diversity is particularly evident, with substantial reductions in both diversity and abundance over recent decades (Wagner et al., 2021). Butterflies and moths (Lepidoptera) are no exception to this ongoing

decline of insect populations (Warren et al., 2021). Butterflies are a conspicuous group of insects that are highly sensitive to environmental conditions and therefore serve as good indicators of the state of a changing ecosystem (Dennis et al., 2003; New, 1997; Warren et al., 2021). While moths have received less attention than butterflies, they are a very diverse ecological group with a wide range of ecological requirements. Both butterflies and moths have a significant role in ecosystem functioning throughout their life cycle: they are pollinators, prey, and herbivores (Merckx and Macdonald, 2015; Ricketts et al., 2001). A reduction in their abundance can therefore have far-reaching consequences on both higher and lower trophic levels (Forister et al., 2019; Yazdanian et al., 2024).

Butterfly abundance across Europe has declined by 50% since 1990, affecting approximately one-third of all species (van Swaay et al., 2025b, 2010; Warren et al., 2021). In Flanders (Belgium), butterfly abundance has declined by 30% since 1992, with one-fourth of butterfly species now extinct, and another fourth threatened with extinction (Maes et al., 2021, 2013; Warren et al., 2021). These numbers place Flanders among the worst-performing regions for butterfly conservation in Europe, largely because of its heavily human-modified landscapes (Maes et al., 2022). Although moths make up the majority of



Fig. 1. – Elements of an agriwilding system. (a) Schematic overview of an agriwilding system. An agriwilding system is a designed wood pasture system that combines natural species-rich grasslands (maintained by a mowing regime or by extensive livestock grazing) with food production in a polyculture of productive perennials (trees, shrubs, hedgerows, different vegetational layers, perennial vegetables, herbs). (b) Photograph of a species-rich grassland and (c) perennial polyculture at the agriwilding study site *De Wildernis* (see also Fig. S1).

Lepidoptera, they have received less scientific attention than butterflies. Moreover, most existing research focuses on macro-moths, while micro-moths remain largely understudied. Despite the current lack of comprehensive Red List data for moths at the European scale, multiple studies have confirmed the decline of macro-moth populations in Europe (Conrad et al., 2006; Fox et al., 2021; Maes et al., 2024). For Flanders, a recent regional Red List analysis highlights the severity of the situation, estimating that 5% of moth species have gone extinct and 23% are threatened with extinction (Veraghtert et al., 2023). In other European countries, regional extinctions range from 4% (Germany) to 9% (The Netherlands), and 27% (Germany) to 39% (The Netherlands) of species are threatened with extinction (Ellis et al., 2013; Nuß, 2011; Trusch et al., 2011; Wachlin and Bolz, 2011). For both butterflies and moths, declines are mostly observed among (oligotrophic) grassland specialists and species with limited dispersal capabilities (Maes et al., 2022; Veraghtert et al., 2023; Warren et al., 2021). Specialist species have primarily declined due to the conversion of extensive grasslands into crop fields, land abandonment, and the loss of species-rich semi-natural grasslands (Eskildsen et al., 2015; Nilsson et al., 2013). Simultaneously, less mobile or sedentary species have primarily declined due to the fragmentation of remaining suitable habitats, which limits their dispersal potential (Maes et al., 2022). With approximately 38% of the EU's total land area (Eurostat, 2022), and up to 50% of Flanders (Borremans et al., 2018) currently under agricultural production, the landscape largely fails to provide the wide variety of resources necessary for lepidopterans to complete their life cycle, posing challenges to eggs, caterpillars, pupae and the adult butterflies and moths.

Although the productivity of wood pasture agricultural systems is well recognized (Shepard, 2013) and numerous studies have examined the effects of biodiversity measures in agricultural landscapes, empirical evidence for the capacity of agriwilding to enhance or restore biodiversity remains limited. Most studies focus on the inclusion of a single (non-productive) landscape element (e.g., hedgerows) or compare the effects of individual elements in isolation (Merckx et al., 2009). A holistic approach that combines multiple landscape elements into a structurally heterogeneous and productive system is largely missing. Such an approach could contribute to ongoing discussions on land-use planning in Europe aimed at creating multifunctional landscapes. Agriwilding may offer a coherent strategy to support several objectives of the EU's Biodiversity Strategy for 2030 and the Nature Restoration Regulation, including the enhancement of biodiversity and ecosystem functioning, while maintaining food production in an increasingly uncertain socio-political context. To assess the potential of agriwilding for biodiversity restoration, we evaluated butterfly and moth diversity at a developing agriwilding site 15 years after its transition from conventional agriculture, comparing it to areas under conventional agricultural management and nature management within the same valley. We hypothesised that agriwilding systems could have a synergistic effect: harbouring more species in greater abundances than conventional agriculture, with a more diversified species community of both grassland and woodland-associated species as the system matures.

2. Materials and methods

2.1. Study area and sites

The study was performed in the Aerebeek valley in Herne (Pajottegem, Flemish Brabant, Belgium). Most of the valley is under conventional agricultural management, with only a few exceptions. The presence of an agriwilding site located between two Natura2000 sites within this agricultural matrix provides an opportunity to quantify differences in biodiversity restoration among three different land-management types in nearby sites (≤ 3 km apart; Fig. S2): conventional agriculture, agriwilding, and nature management. To capture the range of habitats provided by each system, two local sites were selected per land-management type, representing different habitat components.

De Wildernis is an agriwilding project and research site of 2 ha, which combines the goal of biodiversity restoration and food production in a heterogeneous system resembling a wood pasture (Fig. 1, S1). Until the end of 2009, the site consisted of an arable field under crop rotation and an intensively grazed meadow with sheep, both under conventional management. In the following years, hedgerows, solitary trees, and shrubs were gradually planted, and several ponds were added. Planted trees and shrubs consist of both productive and non-productive species. Productive species include different fruit and nut species such as chestnuts, hazels, blackcurrants, persimmons, apples, and pears, as well as perennial vegetables such as asparagus. Approximately ninety edible species are grown in *De Wildernis*. The grasslands were submitted to a biodiversity-enhancing mowing regime twice a year (including removal of the cuttings, without livestock), while other areas with trees and shrubs were allowed to undergo ecological succession, leading to the current wood pasture-like agriwilding system. *De Wildernis* comprises two sites separated by a meadow under conventional management. Both sites were included in the sampling design for both moths and butterflies (Fig. S2).

The conventional agriculture area monitored for butterflies and moths included arable fields under crop rotation (wheat, maize, and potato during the study period) and a meadow under conventional management with cattle grazing. The two studied arable fields cover 1 ha and 21.5 ha, respectively. Both are located less than 500 m from the agriwilding system, are surrounded by conventionally managed arable land, and are separated by a 1.8 ha poplar forest patch. The meadow (1.3 ha) lies between two agriwilding patches and borders a 0.2 ha poplar stand. Both arable fields and the meadow have been under agricultural management since at least 1770, and are currently managed conventionally, including pesticide use, fertilisation, and crop rotation (Geopunt Vlaanderen, 2025), but detailed information on pesticide types and fertilisation regimes during the sampling years was not consistently available across study sites.

Two protected nature management sites were selected: one for butterfly monitoring and one for moth monitoring (Fig. S2). For butterflies, the site included a natural grassland (12.5 ha), located 2 km east of the agriwilding system, managed by the Flemish government department responsible for nature conservation, Agentschap voor Natuur en Bos (ANB), since 1981 and part of the Natura2000 network (Sitecode BE2400009) (Baeté et al., 2006), together with an annually sown flower field (1 ha) managed by ANB for biodiversity restoration (explicitly including butterflies as a target taxon). Both sites are adjacent to an established mixed deciduous forest under nature management (incl. Poplars, oak, beech, sweet chestnut, and sycamore) of 51 ha (Agentschap voor Natuur en Bos, 2023). For moths, the nature management site consisted of a wood pasture system (2.5 ha), located 2 km west of the agriwilding system. It lies within a mosaic of meadow and forest patches under nature management (45 ha), which are all part of the Natura2000 network (Sitecode BE2400009). The wood pasture contains a permanent pond and a small ephemeral ditch (of approx. 200 m). It is grazed by cattle in the summer, and like the other two systems, is flanked by a forested patch dominated by poplar. Monitoring of moths and butterflies occurred at different sites due to their different habitat requirements, which were both met at the agriwilding site, but not at the separate nature-management sites. Because this prevents direct comparison between butterflies and moths, these data were analysed separately.

The study design thus represents a spatially controlled comparison among land-management contexts within a single agricultural valley. The selected sampling locations were intended to capture habitat heterogeneity within each management type rather than to provide independent replicated agriwilding systems at the landscape scale. Consequently, the study should be interpreted as a detailed case study comparing local management contexts under similar environmental conditions.

2.2. Long-term butterfly data

From 2010 to 2025, the arrival of new butterfly species in agriwilding system *De Wildernis* was recorded ad hoc after baseline monitoring. Baseline monitoring consisted of recording all species observed along a transect walk during the first eight years after land use change (2010–2017). The transect varied between visits but consistently covered the entire agriwilding area. It was surveyed once per visit, with at least one visit a month, but with a varying number of months per year (Table S1). Combined with the ad hoc observations in later years, this dataset allows us to evaluate whether butterfly colonisation is associated with vegetation succession. Because monitoring intensity and standardisation differed between the baseline transect surveys (2010–2017) and the later ad hoc observations, these data were used to document cumulative species detection and colonisation history rather than to quantify standardised temporal trends in species richness or abundance. Species were classified according to broad host-plant categories, and their temporal patterns of arrival were analysed. Host-plant associations for Flanders were based on Maes et al. (2013). Species were assigned to categories according to their known larval host plants and grouped into three broad, simplified categories: (i) grasses and forbs, (ii) trees & shrubs, and (iii) both, in cases where species utilise host plants from multiple categories. The national prevalence of each species was used as a proxy for rarity within Belgium, based on species status data from *Observation.org* (accessed 19 March 2025), a database managed by national and international conservation organisations.

To compare butterfly diversity in the agriwilding system with the regional species pool, we collected regional butterfly observation data from the surrounding municipalities (Herne, Galmaarden, Bever, Toll-embeek, Marcq, Hoves, Petit-Engnien, Heikruis, and Vollezele) from the citizen science portal *Observation.org*. Although citizen science data are known to have several limitations, including spatial bias and data quality issues, they are increasingly recognized as valuable sources of large-scale temporal and geographical ecological data (Habel et al., 2025). Since the regional species pool in this study is based on species richness rather than abundance, and because *Observation.org* performs a two-step verification process in collaboration with experts, we consider these data to represent a reliable estimate of the regional species pool. In total, 4727 observations (1995–2025) were retrieved following qualitative filtering performed by the platform. Although the dataset included observations from *De Wildernis*, these represented only incidental records (119 observations; 2.5%) contributed by a single observer, as all systematic monitoring data (both baseline and subsequent monitoring; see section 2.3) were stored in an independent database. To ensure temporal consistency, the regional dataset was further restricted to observations from 2009 onwards ($n = 4704$), i.e., the year preceding land-use change in *De Wildernis*. This restriction did not exclude any species. Regional cumulative species richness was calculated based on all observations, including records from *De Wildernis*. Given the low number of these records and the fact that their inclusion did not affect total species richness, they were retained in the dataset. Based on their occurrence in Flanders, most butterfly species were assumed to be present in the regional species pool prior to 2010. Two exceptions were identified: *Lampides boeticus*, which has been recorded more regularly in Belgium since 2013, and *Pieris mannii*, recorded since 2016 (De Prins and Steeman, 2025). For these species, the year of the first regional observation was used to define their inclusion in the regional species pool.

2.3. Standardised butterfly monitoring

To compare Lepidoptera diversity, standardised monitoring was conducted across three land-management types: conventional agriculture, agriwilding, and nature management (Fig. S2). From early July to early October 2021, butterflies were monitored 38 times using the Pollard walk method (Table S2). This method involves surveying

predefined transects and recording all butterfly individuals observed within an imaginary cage of 125 m³ around the observer (2.5 m on either side and 5 m ahead of the observer) (Pollard and Yates, 1993; van Swaay et al., 2015). Transects were established following guidelines from *De Vlinderstichting* (van Swaay et al., 2018) along existing paths, so as not to disturb natural habitats or interfere with agricultural activities. Multiple transects were defined across each land-management type to capture habitat heterogeneity: meadows and arable land for conventional agriculture; meadows, wood pasture, and an annually resown flower field for nature management; and all habitat components within the agriwilding system (i.e., a species-rich grassland, wood pasture, poplar stand, and perennial flower strip). Transect lengths varied according to habitat availability. However, a total transect length of 480 m (corresponding to a surveyed area of 2400 m²) was covered per land-management type. All surveys were conducted by the same observer. Each land-management type was surveyed on the same day, between 10:00 and 17:00, and only under suitable weather conditions (temperature > 13 °C, wind speed < 5 beaufort, and no precipitation), following established monitoring guidelines (van Swaay et al., 2018). To avoid temporal sampling bias and to achieve evenly distributed sampling efforts across land-management types, the different land-management types were surveyed in random order on each sampling day.

2.4. Standardised moth monitoring

Moth abundance and diversity were monitored using two 12 V SMD 2835 UV (395–405 nm) LED light traps (LedEmmer – *De Vlinderstichting*) in each of the three different land-management types (i.e., six traps in total, Fig. S2) from March 2023 to August 2024 (Table S2). These traps, with an effective attraction radius of 10–30 m, were selected to specifically target local moth assemblages (Merckx and Slade, 2014; Truxa and Fiedler, 2012). Although other trap types, such as Skinner light traps, could greatly increase the catch size per night by attracting individuals over larger distances, this would not correctly represent the species pool present in the systems under study. Moths were monitored for 39 nights using all six traps per sampling night simultaneously. Per night, the two light traps within each land-management type were treated as a single sample because they were located at the same site and therefore did not represent independent samples. This approach was used to characterise local moth communities and allow comparison between land-management types. The following day at sunrise, individuals inside and on the outside of the trap were identified using the ObsIdentify® application (a product of *Observation International*) in combination with field guides on macro-moths and micro-moths (Sterling and Parsons, 2023; Waring and Townsend, 2020). Individuals observed in the surrounding vegetation were excluded. After identification, all animals were released in a well-vegetated habitat at the capture site.

In addition, the bait method – which attracts moths by scent rather than by light – was used 23 times as a monitoring technique from October 2023 to August 2024 (Table S2). For this method, five wooden poles were installed in each study area (Fig. S2), and a bait mixture of wine and sucrose in a 1:1 ratio was applied to the poles before sunset. After a 30–45 min waiting period following bait application, poles were checked for moth presence four times at 15-min intervals and all individuals were photographed. To minimise disturbance, individuals were not captured, which may have resulted in repeated observations of the same individuals across sampling rounds. However, repeated sightings were excluded from subsequent analyses by carefully comparing photographs of individuals observed on the same pole. Moths observed in the surrounding vegetation were also excluded. All study sites were sampled simultaneously on each monitoring night. For the bait method, sampling began 30–45 min before sunset and continued until the four observation rounds were completed. For both methods, monitoring continued during winter (November 2023 – March 2024) to capture the presence of moth species overwintering as imago. Both light

trapping and bait sampling were conducted simultaneously in each system, and observations from both methods were combined in subsequent analyses, unless stated otherwise.

2.5. Species richness and abundance

Species richness and abundance were calculated for each land-management type based on the results of the standardised monitoring. All analyses were performed separately for butterflies and for each moth monitoring method (light trapping and bait sampling). Although sampling effort was equal across land-management types within each monitoring technique, species accumulation curves were first constructed using the *specaccum* function. For butterflies, sampling effort was defined as the number of transect walks, whereas for moths, sampling units corresponded to the number of sampling nights per method.

Species richness, abundance, and diversity of both butterflies and moths were subsequently compared among the three land-management types by calculating the mean and variance of species richness and abundance, as well as the Shannon diversity index, and Hill numbers for each system (Chao et al., 2014). While the Shannon index incorporates both species richness and evenness and is widely used for comparing species diversity across sites, Hill numbers were included due to their improved interpretability and ability to unify diversity measures (Chao et al., 2014). All diversity indices were calculated based on cumulative species assemblages per land-management type to assess overall diversity across the study period. In addition, indices were calculated for each sampling unit per land-management type, and mean values $\pm$ standard deviation (SD) were used to describe temporal variation in diversity between land-management types. Statistical analyses of differences in diversity indices between land-management types were conducted on the full (non-cumulative) dataset to ensure sufficient temporal replication. Linear mixed-effects models (LMMs) were fitted using the *lmer()* function in the *lme4* package, with sampling unit included as a random effect to account for temporal non-dependence. When model residuals deviated from normality (assessed using the Shapiro-Wilk test), generalised linear mixed-effects models (GLMMs) were fitted using the *glmmTMB()* function with a negative binomial distribution. As with the LMMs, sampling unit was included as a random effect. This approach was applied only to the Hill-Simpson ($q = 2$) diversity index. Homogeneity of variances was assessed using the Levene's test. Where slight heterogeneity was indicated, this was further evaluated using Q-Q plots and inspection of residual distributions by the Shapiro-Wilk test. If model assumptions remained violated, the response variable was log-transformed and the LMM was refitted. All analyses were conducted in R version 4.5.2.

2.6. Community composition

Species composition was analysed based on data from standardised monitoring of moths and butterflies. Differences in species composition between the three land-management types were assessed separately for butterfly and moth communities. For moths, bait and light-trapping observations were combined for community composition analyses because the two methods target partly complementary assemblages and together provide a more comprehensive representation of the local moth community within each land-management type. In contrast, richness and abundance analyses were performed separately for each monitoring method to avoid confounding differences in detectability between trapping approaches.

First, species communities were explored using non-metric multidimensional scaling (NMDS) based on a species-by-land-management type matrix in which rows represent sampling units across land-management types. NMDS was performed using Bray-Curtis dissimilarity and the *metaMDS* function. Because the moth dataset contained many species with low (or zero) abundances across sampling units, inclusion of all data resulted in ordination artifacts. Therefore, the moth NMDS was

restricted to species occurring in at least three sampling units, reducing the dataset from 241 to 96 species.

To test for differences in species composition among land-management types over time, permutational multivariate analysis of variance (PERMANOVA) was performed separately for butterflies and moths (bait and light-trapping data combined). Because repeated observations within sampling sites over time violate the assumption of independence, permutations were constrained within time points using the *adonis2* function in the *vegan* package with the *strata* argument. Unlike NMDS, PERMANOVA is robust to sparse matrices; therefore, no prior reduction of the moth dataset was required. Prior to the PERMANOVA, the homogeneity of multivariate dispersion assumption was checked using the *betadisper* function. A post-hoc test was performed to identify where differences in species communities occurred, using the *pairwise.adonis2* function (Martinez Arbizu, 2020).

Additionally, community weighted means (CMWs) were calculated for body size and national prevalence. Body size was approximated using forewing length (in millimetres, mm), which is closely linked to species mobility (Ovaskainen et al., 2019; Sekar, 2012; Slade et al., 2013). Forewing length data were obtained from Cook et al. (2021), Eskildsen et al. (2015), and Sterling and Parsons (2023). The total number of observed individuals within Belgium on *Observation.org* from 2010 to 2025 was taken as a measure of each species' national prevalence. While this metric is based on observation frequency, rather than ecological rarity, it represents the current probability to encounter a species within Belgium given similar sampling efforts.

CMWs were calculated separately for the monitored butterfly community and the moth communities monitored by the bait method and the light trapping. To test whether differences in community weighted traits between land-management types were significant, an analysis of variance (ANOVA) was carried out when all assumptions were met. However, when normality was violated, a Kruskal-Wallis test was carried out (as determined by a Shapiro-Wilk normality test). When the assumption of homogenous variances was not met, a Welch ANOVA was used. All analyses were performed in R version 4.5.2.

3. Results

3.1. Evolution of butterfly diversity in the agriwilding system

A total of 30 species belonging to 5 families were recorded in *De Wildernis* after 15 years of agriwilding management. The cumulative number of detected butterfly species increased from 19 species recorded after the land-use change in spring 2010 to 30 species by late 2022 (Fig. 2, Table S3), reflecting the progressive colonisation of the site over time. In the early years after the land-use change, butterfly assemblages were dominated by species common in Belgium (based on *Observation.org*), with a few relatively common species present (Fig. 2a). These early colonisers were primarily mobile species, including the peacock (*Aglais io*), red admiral (*Vanessa atalanta*), and whites (*Pieris* spp.), although less mobile species, such as some skippers (Hesperiidae), were also recorded. Additional species colonised the agriwilding site over time (Fig. 2a), including mobile but less widespread species, classified as relatively common (e.g., the brown hairstreak, *Thecla betulae*, and large tortoiseshell, *Nymphalis polychloros*) as well as rare species (e.g., the white-letter hairstreak, *Satyrion w-album*, and lesser purple emperor, *Apatura ilia*). About ten years after the transition from conventional to agriwilding management, there was a marked increase in species associated with trees and shrubs (Fig. 2b). Retrieval of regional species-pool data resulted in 4704 observations of 39 butterfly species from 2009 to 2025 across an area of 42,000 ha (the regional species pool increased by two species, *Pieris mannii* and *Lampides boeticus*, over this period). In comparison, *De Wildernis* (2 ha) supported 30 of the 39 regionally recorded species (Table S3).

3.2. Species richness and abundance

We conducted standardised monitoring across the three land-management types for butterflies (38 surveys from July to September 2021) and moths (63 surveys from March 2023 to August 2024). In total, 4875 individuals belonging to 260 Lepidoptera species were observed (Table S4). An overview of the observed species per land-management type is provided in Table S5. A total of 19 butterfly species were observed, of which 10 occurred across the three land-management types. Species richness was highest in the agriwilding system (19 species), followed by the nature management site (12 species) and conventional agriculture (10 species) (Table S4). Butterfly abundance also varied among systems, with 1893 individuals recorded in the agriwilding system, 569 in the nature management site, and 343 in conventional agriculture (Table S4, Fig. S3). A total of 241 species of moths (147 macro- and 94 micro-moths) were recorded, 231 of which were detected using light trapping and 68 using bait trapping (Table S4). A total of 160 moth species were observed in both the nature management and agriwilding systems, whereas 82 species were observed in conventional agriculture. A total of 2070 moth individuals were observed, with abundance varying between sites. The lowest abundance was observed in conventional agriculture ($N = 253$), with higher abundances in the agriwilding ($N = 800$) and nature management systems ($N = 1017$) (Fig. 3, Table S4).

3.3. Diversity indices

Species accumulation curves (Fig. S4) indicated similar sampling completeness across land-management types for each monitoring method, while revealing differences in species richness. Due to the seasonality of Lepidoptera, the influence of weather conditions and the stochastic nature of spatially fixed bait and light-trapping methods for moths, mean values were generally low and variances high (Table S6). Therefore, diversity was assessed using the Shannon index (H) and Hill numbers. Diversity indices based on the cumulative community matrix all showed consistent patterns for butterflies and moths: Diversity was highest in the agriwilding system (butterflies $H = 2.06$; moths $H = 4.39$), followed by the nature management system (butterflies $H = 1.77$; moths $H = 4.08$), and lowest in conventional agriculture (butterflies $H = 1.67$; moths $H = 3.88$) (Table S7). When investigating diversity patterns across sampling units, mean butterfly diversity was highest in the agriwilding system, followed by the nature-management system, and lowest in the agricultural system (Fig. 4, Table S7). All pairwise differences were statistically significant ($p < 0.05$, Table S8). For moths, mean diversity indices over time were consistently lowest in the agricultural system ($p < 0.001$ for all diversity indices, Fig. 4, Table S9), whereas values for the nature-management and agriwilding systems were similar, although their relative ranking varied depending on the diversity index used (no statistical differences, Table S9).

3.4. Community composition

Based on shared and unique species among land-management types, the community composition of both butterflies and moths differed across systems (Fig. 5). NMDS ordination of butterflies shows overlapping species communities, but with separated centroids, suggesting potential differences in species composition among land-management types (Fig. S5, stress = 0.23). For moths, NMDS (stress = 0.08) was based on a reduced dataset excluding species occurring at low abundances or unique to a single management type. Here, species communities largely overlapped (Fig. S5). However, given the relatively high stress value for butterflies and the reduced dataset for moths, both ordinations should be interpreted with caution.

Multivariate dispersion was homogenous among the three land-management types for both butterflies ($p = 0.063$, Table S10) and moths ($p = 0.295$, Table S11), supporting the use of PERMANOVA,

which indicated that the community composition differed significantly among land-management types for both butterflies ($p = 0.001$, Table S10) and moths ($p = 0.001$, Table S11). Post-hoc tests for butterflies revealed significant differences between all pairwise comparisons ($p < 0.005$, Table S10). For moths, species communities differed between nature management and conventional agriculture ($p = 0.001$, Table S11) and between agriwilding and conventional agriculture ($p = 0.002$, Table S11), but not between agriwilding and nature management ($p = 0.194$, Table S11).

Differences in community composition were not clearly reflected in community-weighted means (CWM). For butterflies, the mean body size was significantly larger in conventional agriculture than in the nature management ($p = 0.040$) and agriwilding system ($p = 0.020$; Fig. S6, Table S12). For moths, body size did not significantly differ between land-management types. Community-weighted national prevalence did not differ significantly among land-management types for either butterflies or moths, irrespective of the moth monitoring method.

4. Discussion

4.1. Substantial butterfly restoration during 15 years of agriwilding

Butterfly monitoring after fifteen years of agriwilding demonstrates that *De Wildernis* has transitioned from a conventionally managed agricultural landscape into a habitat capable of sustaining a diverse butterfly community comprising 30 out of the 39 regionally present species (Fig. 2, Table S3). This temporal trajectory illustrates how biodiversity can recover in a productive system when perennial vegetation, structural heterogeneity, and partial ecological succession are allowed to develop. Because the long-term dataset combines baseline transect surveys with later ad hoc observations, the observed trajectory should be interpreted as cumulative colonisation and species detection over time rather than as a standardised annual time-series of butterfly richness or abundance.

In the early years following the land-use change, butterfly assemblages were dominated by widespread and mobile species, a pattern consistent with colonisation dynamics observed in other restoration contexts (Heneberg et al., 2026; Woodcock et al., 2012). Over time, however, species richness continued to increase through the arrival of rarer taxa, including several species associated with woody vegetation. This gradual shift in community composition towards tree- and shrub-dependent species coincided with the maturation of woody elements in *De Wildernis*, suggesting that butterfly colonisation tracks vegetation development. If this pattern is confirmed in future studies, it would show that agriwilding promotes a successional pathway in which increasing structural complexity expands the range of available niches, while agricultural productivity is maintained. This suggests that biodiversity recovery may be compatible with productive perennial land use, rather than being mutually exclusive. Continued shifts in species composition are likely as succession proceeds, and the system increasingly resembles a wood pasture mosaic (Habel et al., 2019). Such a habitat configuration is suitable for woodland, edge-associated, and open-habitat species. Moreover, because agriwilding also incorporates thickets and extensively managed grasslands, it is likely to remain suitable for grassland species. This is an important aspect for the conservation of grassland specialists, as these generally face greater challenges than woodland specialists (Maes et al., 2024; Merckx et al., 2012). Maintaining open grassland elements within agriwilding systems will be essential to support these vulnerable Lepidoptera in north-western Europe (van Swaay, 2002; van Swaay et al., 2025b).

The potential for biodiversity restoration within a given area is strongly constrained by the size of the regional species pool. Despite its small size (2 ha), the agriwilding site currently supports more than three-quarters of the regional butterfly species pool, even though records from the site represent only 2.5% of all regional butterfly

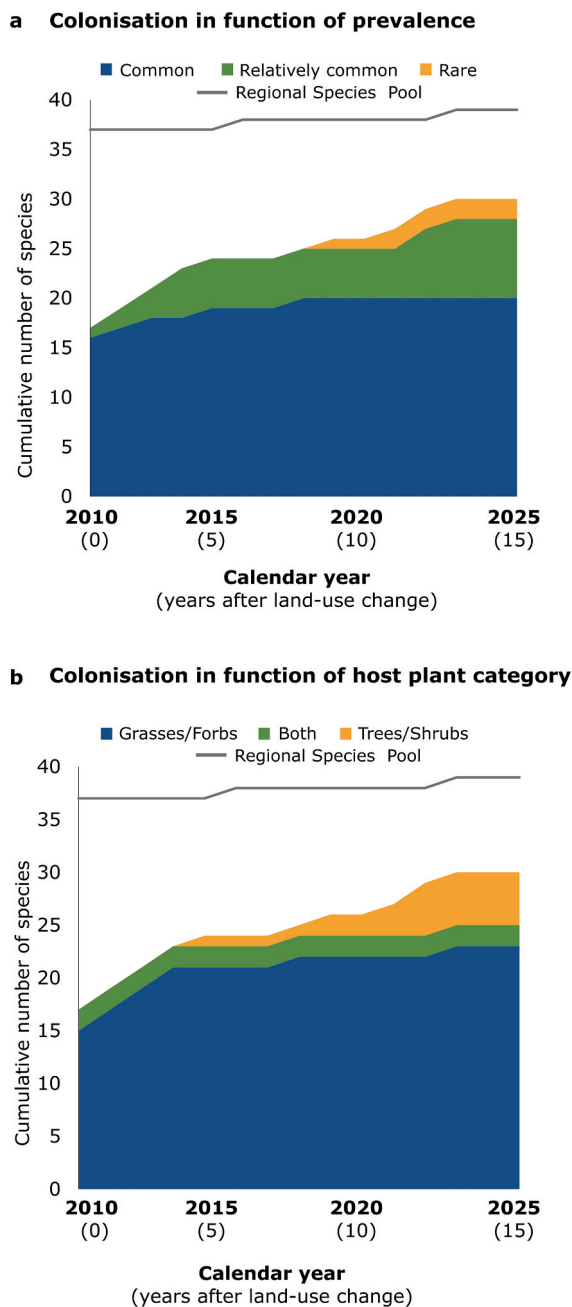


Fig. 2. – Butterfly colonisation of the agriwilding study site over the first 15 years after land-management change. (a) Cumulative colonisation according to species prevalence in Belgium (cf. section 2.2. in Materials & methods) in the agriwilding system based on baseline monitoring and ad hoc observations. The time axis represents the calendar years as well as the number of years since the start of the land-use transition in 2010 (year zero), shown in brackets. The regional species pool is indicated by a solid line. (b) Cumulative colonisation according to host plant category (grasses and/or forbs, trees and/or shrubs, or species that have host plants in both categories), based on Maes et al. (2013)). This shows an increase in woodland species (i.e., with trees and/or shrubs as host plants) as the system matures.

observations. This highlights the importance of habitat quality and internal heterogeneity over sheer area, particularly in fragmented agricultural landscapes (Poniatowski et al., 2018; Seibold et al., 2019). However, the absence of certain grassland specialists from the agriwilding site may also reflect the influence of the surrounding agricultural matrix. Intensive land use, habitat fragmentation, eutrophication, and pesticide application in adjacent fields may reduce landscape

connectivity and potentially act as dispersal barriers for specialist and less mobile species, thereby limiting colonisation even where local habitat conditions are suitable. For example, the small heath (*Coenonympha pamphilus*), a characteristic species of oligotrophic grasslands, is sensitive to eutrophication (Bink, 1992) and exhibits limited dispersal in fragmented landscapes (Deppe et al., 2024). Although this species occurs within the regional species pool, its colonisation of *De Wildernis* is less likely, as it would need to cross intensively managed arable fields and grasslands. This highlights that, while agriwilding can substantially enhance local biodiversity, its full potential depends on the scale at which it is implemented, as well as on landscape-scale connectivity and coordinated land-use planning.

4.2. Agriwilding supported high Lepidoptera diversity relative to nearby land-management types

By standardising monitoring of Lepidoptera across a representative variation in habitats in an agriwilding site, conventional agricultural land, and nature management within the same valley, we were able to conduct a spatially controlled comparison. We therefore infer that observed differences in species richness and abundance are likely to be explained by the land-management type. Our results suggest that agriwilding has the potential to achieve biodiversity outcomes comparable to nature management areas.

Species richness varied among the three land-management types, with the lowest number of species observed in the conventional agricultural system. The restored agriwilding site supported all butterfly species observed during standardised monitoring in the study area, thereby substantially exceeding the species richness in protected natural habitat (Fig. 3c). Ten butterfly species that we found as common to the three land-management types were also observed in *De Wildernis* during the initial years after land-use change, and these consisted mainly of common mobile generalists (as indicated by the highest community weighted body size and national prevalence, Table S12). The absence of monitoring in spring may explain the absence of species that only occur during those months. However, in the focal region, this primarily concerns the common species *Anthocharis cardamines* (orangetip), the only species with a flight period preceding the study period, meaning its inclusion would not substantially alter species richness patterns across land-management types.

The monitoring results are even more pronounced in terms of abundance: the number of individuals observed at the agriwilding site was more than three times that of the nature management system, and almost six times greater than in conventional agriculture (Fig. 3d, Table S4). Diversity indices (Shannon index and Hill numbers, Fig. 4, Tables S7 & S8) confirm that the agriwilding site has a significantly higher butterfly diversity than both nature management and conventional agriculture systems. These results indicate that structurally complex, perennial systems can outperform some protected areas in supporting Lepidoptera diversity.

Although annually resown flower fields are semi-natural systems, the flower field in this study was included within the nature-management system because it was established to promote biodiversity by the Flemish government department responsible for nature conservation (ANB). Annually resown flower fields are also supported by the Flemish government and the European Union as an agri-environmental measure to support agrobiodiversity. However, such measures generally do not achieve comparable landscape complexity, and often provide lower plant and resource diversity, resulting in limited success in restoring biodiversity while simultaneously removing land from production (Bartholomée et al., 2020; Erisman et al., 2016). Similar to conventional arable systems, they can introduce annual disturbances (e.g., harvest or reseeding), potentially creating ecological traps that reduce habitat quality for early emerging butterflies (Ganser et al., 2019; Schmied et al., 2022). In contrast, agriwilding maintains continuous structural complexity, supporting stable resources and diverse communities. This

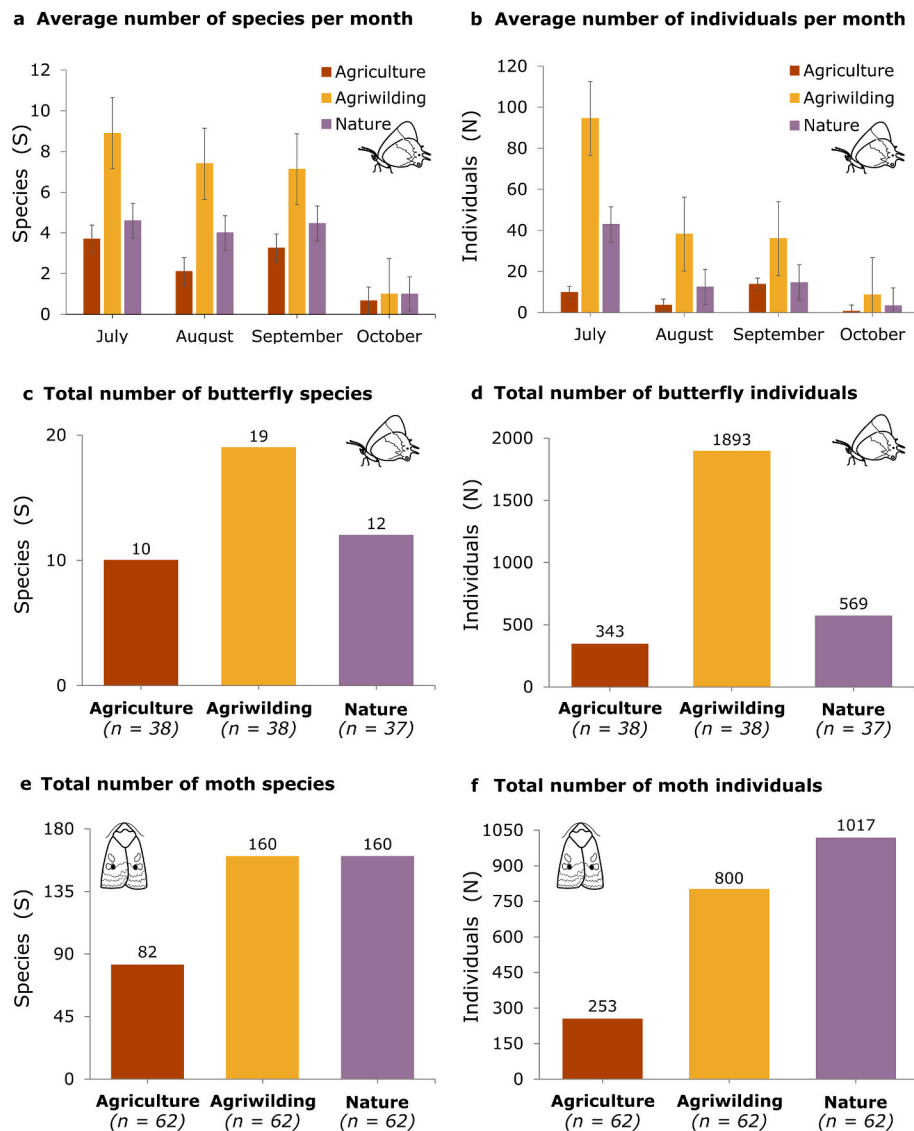


Fig. 3. – Comparison of observed species richness and abundance between land-management types during standardised monitoring. Average number of butterfly species (a) and individuals (b) observed per month. Error bars represent standard errors. Total butterfly species richness (c) and abundance (d), and total moth species richness (e) and abundance (f) across the full standardised monitoring period, including sampling effort between brackets below each graph.

continuity is ecologically relevant, as many *Lepidoptera* require stable host plants, overwintering sites, and microclimatic refugia that are rarely available in systems subject to regular tillage, reseeding, or mowing.

Standardised monitoring revealed about twice as many moth species at the nature management and agriwilding areas (Fig. 3e, Table S4) than in conventional agriculture, and about three to four times as many individuals (Fig. 3f, Table S4). Although the nature management site exhibited a slightly higher abundance of moths, cumulative diversity indices were higher for the agriwilding system. This suggests a more even distribution of dominant species in the agriwilding system, whereas the nature management moth community appears more dominated by a subset of highly abundant species and contained a higher proportion of rare species. However, there was no significant difference in diversity between the nature management system and the agriwilding system over time (Fig. 4, Table S7 & S9). The slightly higher, but non-significant, Hill-Simpson index for agriwilding is consistent with this pattern, suggesting a marginally more even distribution of dominant species. Overall, higher diversity indices based on cumulative species community data are an inherent result of accumulating species

over time, highlighting the importance of calculating and comparing diversity indices between land-management types across timepoints. The PERMANOVA further indicated that there was no statistical difference in moth community composition between the nature management and agriwilding system (Table S11), which is likely due to the fact that they share a core set of highly abundant species, while the unique species occurred in lower abundances, which reduces their weight within the PERMANOVA. Since these unique species were largely omitted from the NMDS, it does not represent the full moth community but rather the structure of the more consistently occurring species assemblage. Nevertheless, we observed a high number of butterfly and moth species unique to both the nature management and agriwilding systems (Fig. 5). Despite their lower abundances and the insignificant difference in community composition, these unique species could mean that the studied nature management system supports a different set of less abundant species than the agriwilding system. In this case, agriwilding would be most effective for biodiversity when it coexists with sites dedicated solely to nature conservation.

The presence of species unique to agriwilding (seven butterflies, 62 moths) underscores its ability to provide habitat for taxa not supported

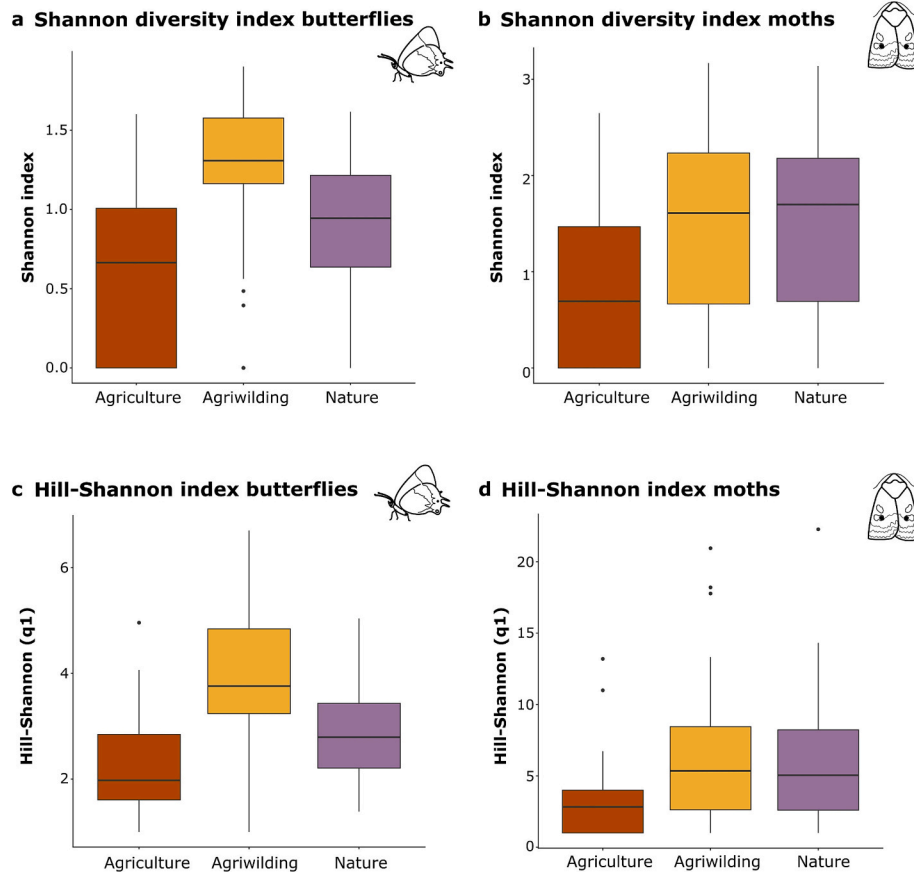


Fig. 4. – Distribution of Shannon and Hill-Shannon indices. Distribution of the Shannon diversity index for (a) butterflies and (b) moths, and of the Hill-Shannon diversity index for (c) butterflies and (d) moths, per land-management type over time. Mean and standard deviations of the Shannon, Hill-Shannon, and other diversity indices are provided in Table S7.

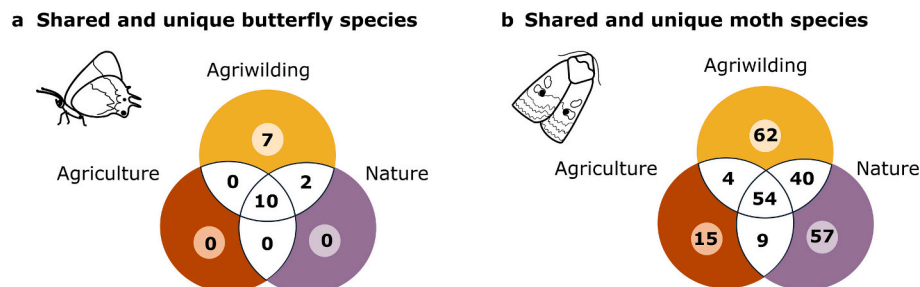


Fig. 5. – Comparison of the community composition between land-management types during standardised monitoring. Venn diagrams representing the species composition of (a) butterflies, and (b) moths, indicating the number of shared and unique species between land-management types.

elsewhere. We hypothesise that the integration of diverse plant species and structural elements in agriwilding enhances landscape heterogeneity, potentially providing a broader range of microhabitats and resources on a small surface area, and supporting a higher insect diversity (Merckx, 2015; Weibull et al., 2000). Proximity (relative to the mobility of the species) of resources and high-quality habitat is known to be important for creating a functional habitat for Lepidoptera (Dennis et al., 2006). Adult Lepidoptera need a combination of sunny spots to bask (butterflies only), sheltered spots for egg-laying, to hide from predators or as a hibernaculum, moist or wet areas to hydrate, host plants to reproduce, and nectar plants to feed on (Dennis et al., 2003). For smaller, less mobile species (characterised by a reduced wingspan, see Sekar (2012)), the spatial configuration of habitats is crucial to ensure that essential resources—host plants, nectar, shelter, mates, and

microclimatic refuges—are accessible within their limited flight range (Vanreusel and Van Dyck, 2007). The importance of a diverse set of available resources at site- and landscape-scale has also been raised within conservation efforts of other important pollinator groups such as wild bees and hover flies (Scheper et al., 2013; Tonietto and Larkin, 2018). However, these resources are typically not readily available in a homogenous agricultural landscape, characterised by annual disturbances such as tillage and the application of fertilisers and pesticides that further reduce survival potential (Hahn et al., 2015). In contrast, the perennial polyculture of agriwilding ensures a consistent availability of necessary resources, and we hypothesise that this stability allows it to sustain large and diverse lepidopteran populations throughout the year. As a result, the agriwilding site can harbour a species community with a higher proportion of smaller-sized species, whereas agricultural systems

are usually characterised by more common and larger (and therefore more mobile) species (Ekroos et al., 2010; Körösi et al., 2022).

Our results demonstrate that agriwilding may not only conserve rare species but can also maintain abundant populations of common species, which is crucial for ecosystem functioning and resilience. Lepidoptera are widely acknowledged as a crucial element of ecosystem functioning, contributing to pollination, acting as important primary consumers, and serving as prey for higher trophic levels (Merckx and Macdonald, 2015). Such trophic interactions underpin essential ecosystem services, including pollination and pest regulation, while functional redundancy enhances the stability and resilience of agroecosystems (Merckx, 2015). While declines in biodiversity were once thought to primarily affect rare species, the abundances of common species are also declining, threatening ecosystem stability across the globe (Conrad et al., 2006; Wagner et al., 2021). Long-term conservation of large populations of both rare and common species could therefore be another major contribution of agriwilding for both butterflies and moths, as demonstrated in this case study.

4.3. Potential implementation and policy

From a policy and land management perspective, our findings suggest that agriwilding has the potential to complement both conventional agriculture and nature management by delivering high biodiversity within working landscapes that provide for human needs while conserving ecosystem integrity (Kremen and Merenlender, 2018). Agriwilding could be included as a subsidised measure for farmers, either as an integral component of productive land or alongside annual crops, thereby supporting biodiversity and enhancing ecosystem services, such as pollination and natural pest control. Unlike annually disturbed agri-environment schemes, agriwilding emphasises perennial structure, reduced disturbance, and internal habitat heterogeneity, aligning closely with emerging agroecological and nature-based solution frameworks (Bartholomée et al., 2020; Erisman et al., 2016; EU, 2013). Across a range of landscape contexts, the inclusion of agriwilding areas within the matrix could reduce pressures from conventional agriculture on biodiversity and enhance habitat connectivity (Marcantonio et al., 2024).

In this case study, several elements of agriwilding appear particularly important for supporting Lepidoptera diversity. The combination of perennial vegetation, the presence of woody structures, and reduced disturbance regimes likely contributed to the observed increases in species richness and diversity. In particular, the establishment of shrubs and trees coincided with the arrival of butterfly species associated with woody host plants, while the continuous availability of resources in perennial vegetation likely supported both butterfly and moth communities. In addition, the extensive management of grasslands, characterised by low fertilisation and adapted mowing regimes, likely contributed to maintaining suitable conditions for grassland-associated species by preventing eutrophication and preserving host-plant diversity. The integration of these elements within a structurally heterogeneous system therefore appears to be a key driver of the observed biodiversity outcomes and from a policy perspective, agriwilding measures could realistically be supported within existing agricultural frameworks. Expanding and better targeting such measures to promote structurally diverse, low-disturbance systems could help align agricultural policy more closely with biodiversity conservation goals.

When implemented as a stand-alone agricultural system, the polyculture aspect of agriwilding offers multiple benefits, including diversified yields, which are advantageous under increasingly variable climatic conditions, while its perennial structure enhances ecosystem stability (Raveloaritiana and Wanger, 2026; Sridhar et al., 2026). Especially for orchard-crop farmers, this may provide a viable and future-proof strategy to increase farm-level resilience. However, despite growing market volatility for commodity crops, incentives for fundamentally transforming food systems remain limited (Sridhar et al.,

2026), largely due to restricted market access and persistent yield gaps compared to conventional farming systems (Sridhar et al., 2026). Policymakers should therefore integrate the growing body of scientific and practical knowledge on alternative agricultural systems to support the transition towards agricultural landscapes that restore, rather than further degrade, ecological functioning (Raveloaritiana and Wanger, 2026). A holistic approach is required to ensure that policy changes go hand in hand with evolving distribution networks, market structure, and access to knowledge (HLPE, 2020).

In any scenario, policies will need to accommodate the diversity of agriwilding approaches by increasing flexibility regarding the integration of trees and shrubs, as well as features such as water retention ditches or ponds, without increasing the administrative burden for farmers. Overall, integrating agriwilding into policy could enhance biodiversity outcomes by shifting the focus from short-term interventions to structurally diverse, self-sustaining agroecosystems. Such approaches may be particularly valuable in fragmented agricultural regions where space for strict nature protection is limited, but where biodiversity gains within farmland are urgently needed.

5. Conclusion

Our results demonstrate that agriwilding can support high species richness, abundance, and diversity of Lepidoptera, despite its small spatial extent and location within an intensively managed agricultural matrix. The agriwilding system, which supported lepidopteran diversity comparable to, or higher than, nearby nature management areas highlights the potential of productive landscapes to contribute meaningfully to biodiversity restoration. While protected areas remain indispensable for biodiversity conservation, ecological recovery can also be achieved within agricultural systems by prioritising structural heterogeneity and ecological continuity. Agriwilding therefore provides a promising pathway to reconcile agricultural productivity with healthy ecosystem functioning, amid widespread insect population declines and growing land-use pressure for food production. It is critical to integrate perennial, biodiversity-rich production systems within future agri-environmental policy frameworks, including the European Common Agricultural Policy, as a core component of broader strategies to restore ecosystem functioning and enhance ecological resilience across agricultural landscapes.

CRedit authorship contribution statement

Fien Debusscher: Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Frederik Van Den Eeckhaut:** Writing – review & editing, Methodology, Formal analysis. **Joke Baekeland:** Writing – review & editing, Methodology, Formal analysis. **Hans Van Dyck:** Writing – review & editing, Methodology, Conceptualization. **Thomas Merckx:** Writing – review & editing, Supervision, Formal analysis, Conceptualization. **Franky Bossuyt:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Data curation, Conceptualization.

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Declaration of competing interest

The author(s) declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2026.111965>.

Data availability

Summarised monitoring data obtained in the framework of this research article are available through Mendeley Data—doi: [10.068.224/y4gk5m7y5f.1](https://doi.org/10.068.224/y4gk5m7y5f.1).

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