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How efficient are late mow measures to preserve grassland biodiversity in the Natura 2000 site "Petite Montagne du Jura"?

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The content of this dissertation is the sole responsibility of the candidate and the host organization and does not engage the scientific responsibility of the tutor and the university

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I – INTRODUCTION

Managed by humans since several centuries to raise cattle and produce forage, grasslands are the remnants of pastoralism and extensive agriculture. When well preserved, these semi-natural habitats can reach important levels of biodiversity and can be amongst the highest species-rich ecosystems on Earth, surpassing even tropical rain forests (Wilson et al., 2012; Tälle et al., 2018). Amongst semi-natural grasslands, hay meadows are used specifically for forage production. While mowing a meadow enables to maintain its openness and preserve its characteristics, it has different impacts on the present wildlife. Benefits may arise directly for predatory vertebrates, the vegetation cut facilitating their access to resources, as for instance for red foxes and buzzards chasing the newly exposed voles. For invertebrates, however, the mow has immediate detrimental effects. Cutting the vegetation can cause direct mortality of the individuals, whichever their life stage, for up to 90% of the grassland population (Van Klink et al., 2019). Moreover, the following period of low resource availability, high predation rates and modified microclimate complicates the recovery of the species. Despite these short-term harmful consequences, mowing enables a long-term preservation of meadows, maintaining a suitable open habitat for these invertebrates (Humbert et al., 2012). Concerning the flora, mowing enables a higher diversity of vascular plants to coexist, if it occurs at a low annual frequency and late enough in the season (Humbert et al., 2012). The floral diversity enabled by extensive mowing and fertilization practices can be in turn profitable to the farmer, as a forage originating from a species-rich meadow has attractive characteristics, such as increased protein and milk production potential yields (Schaub et al., 2020). Functional and diverse meadows are also providing essential services for the ecosystems, among which carbon storage, pollination and reduction of the soil erosion (CBN, s.d.).

Despite their important ecological and agricultural values, grasslands and hay meadows are subject to important degradations, induced by the changes in agricultural practices that occurred in the past decades. The strong intensification of mechanization, fertilization and pesticide usage, implemented in the mid-20th century and publicly justified by the need of food security after the 2nd World War, led to major changes in grassland use (Hopkins & Holz, 2006; Tälle et al., 2018). Indeed, the grasslands that were not easily reachable or manageable were abandoned for their insufficient productivity, thereby often turned into forests through natural succession. On the contrary, naturally productive and accessible grasslands got overly exploited

and lost their semi-natural characteristics (Mauchamp, 2014). Indeed, by increasing fertilization and grazing intensities and selecting the most productive herbaceous species, soil characteristics got deeply affected and floral communities substantially banalized (CBN, s.d.). These different threats and the additional urbanization increase led to a considerable loss of grasslands across Europe in few decades. In France, 20% of semi-natural grasslands were lost since 1980 and as much as 50,000 hectares of grasslands are still disappearing every year (Agreste, 2021; LPO, 2026). As half of European species depend on agricultural habitats, these habitat deteriorations engender serious consequences for the biodiversity (Stoate et al., 2009). As symptoms of these agricultural changes, in France, 32.5% of the farmland birds disappeared in the last 15 years, due to the rarefaction of their nesting and food resources induced namely by massive pesticide use, hedge removal and local grassland disappearance (LPO, 2026).

This generalized grassland degradation and the strong biodiversity decline induced by agriculture intensification raised important concerns during the past decades, which led to the promotion of Agri-environmental schemes (AES) in European countries (Batáry et al., 2015). These schemes, funding famers to change their practices towards better environmental consideration, started to be implemented in 1985 and became compulsory for all countries of the European Union in 1992 (Batáry et al., 2015). As one of the tools of the Rural Development pillar of the Common Agricultural Policy (CAP), AES are mainly funded by the European Union (EU), yet each EU member state designs its own scheme. In France, AES translate into local Agri-environmental programs called ‘PAEC’, led by different structures of the territories (such as environmental organizations, regional parks or public institutions) and last for five years. These structures propose to the farmers a list of Agri-environmental measures called ‘MAEC’, previously selected from a national catalogue by the regional agriculture institution (MASA, 2025). Farmers who sign up for these MAEC engage to respect specifications constraining their practices during the five years of the PAEC. In return, they receive a specific amount per hectare of engaged surface and per year, based on the estimated economical shortfall caused by these management constraints (FPNRF et al., 2020). Since many farmers subscribe to PAEC, these measures represent an important budget for France and Europe and their costs usually equals or exceeds the ones spent on wildlife conservation through other routes (Batáry et al., 2015). Despite this important financial commitment, Batáry et al. (2015) pointed out a lack of positive effects on biodiversity for many of the settled MAECs over Europe, especially when considering large scales.

Therefore, PAEC still must prove themselves; and this study aims to test the efficiency of one measure specifically, the mow delay. While late mow effects on invertebrate and plant communities cannot always be clearly identified, early mowing appear detrimental for grassland invertebrates and floral diversity; thus, postponing the mow could indeed be beneficial for many of the grassland inhabitants (WallisDeVries & Van Swaay, 2009; Humbert et al., 2012; Johansen et al., 2019). In addition, late-mow MAECs constraint the fertilization and grazing intensities, which are known to strongly influence plant diversity, and thereby grassland communities (Mauchamp, 2014). These conditions make late-mow MAECs promising for an efficient preservation of biodiversity, and their ease of implementation explains that it is one of the most widespread and recommended agri-environmental measure in the EU (Johansen et al., 2019; FPNRF et al., 2020). In this context, assessing the efficiency of these measures appear essential.

Evaluating late-mow MAECs could not only highlight but also improve their efficiency for preserving biodiversity, which appears particularly important in Natura 2000 (N2000) sites, designated for hosting habitat and species of concerns. In fact, while managers of N2000 sites often use MAEC as tools to preserve wildlife, they state that more science is needed to make these contracts both adapted for habitat preservation and suitable for farmers (FPNRF et al., 2020). An ongoing French study by Goudet et al. (2025) aims to fill this knowledge gap and specifically to test the efficiency of late-mow MAECs in French N2000 areas.

My study goes along similar lines, concerning specifically the N2000 site “Petite Montagne du Jura”. Similarly to Goudet et al. (2025), butterflies were chosen as indicators of the efficiency of MAECs, for their well-known ecological traits and their ease to monitor (WallisDeVries & Van Swaay, 2009). Specialist butterfly species can inform particularly well on the changes in ecosystem characteristics, as they cannot remain if their resources disappear due to the alteration of habitat conditions. Additionally, because of their sensitivity to environmental changes, butterflies are greatly affected by the agriculture intensification; and European grassland butterfly abundance decreased by 40% in less than 30 years (Van Swaay et al., 2019). Thus, more than using them only as indicators, this study aims to report if late mow measures could help lessen the decline of these emblematic but threatened insects. On top of butterflies and since they are directly impacted by the management methods, flowering plants were monitored to obtain additional community responses and namely for the resources they can provide for butterflies.

For this study, I supported the following hypotheses:

1) Both butterfly and plant diversity are greater in meadows engaged in late mow MAECs, as early mowing appears detrimental to both these taxa (Humbert et al., 2012). A delayed mow enables a longer resource availability for invertebrates during the summer, supporting more individuals of more species to successfully complete their life cycle all over the season (Humbert et al., 2012, Johansen et al., 2019). Similarly for plants, with delayed effects of mowing, I presume that more species can complete their life cycle and produce more seeds within a delayed mow regime (Chaudron et al., 2016).

2) Not only a later mow but other management and environmental conditions, such as the number of mows, fertilization rates, grassland specificities (size, altitude) and its surrounding land cover, have strong effects on grassland communities. I presume that a reduced fertilization and mowing frequency promotes plants and butterflies, influencing on both their diversity and abundance (Zechmeister et al., 2003; Humbert et al., 2012). As for plot conditions, relying on the findings of Öckinger et al. (2006), I predict more diversity in large plots surrounded by a high number of grasslands around. Similarly, since it has been widely demonstrated that the number of species decrease following an elevational gradient (40 species lost each 100m of altitude in the Alps), I expect less species in high-altitude meadows (Körner, 2000).

3) Late-mow MAECs cause variations in both plant and butterflies community compositions, with namely a greater presence of species characteristic of dry grasslands as their habitat would be better preserved with the constraints induced by the contracts (Voirin & Boucard, 2024). The late-mow contract would also enhance a higher functional diversity of butterflies, as intensive practices are known to favour insects with specific characteristics (namely small-sized, generalists and with high dispersal capacities) over others (Van Klink et al., 2019).

2- MATERIALS AND METHODS

2.1- Study area

2.1.1 - Site description

The study was conducted in the Natura 2000 site 'Petite Montagne du Jura' (PMJ), located in the French department of the Jura (Bourgogne-Franche-Comté) and covering 38 towns on a surface of 383 km². Expanding on part of the Jura Mountain range, it is a rolling area crossed by several rivers and whose altitudes varies between 280 and 841 meters. This Natura 2000 site exists since 2001 and is animated by *Terre d'Emeraude Communauté*, an organization originating from the fusion of four federations of municipalities in 2020. The landscapes of the site are dominated by forests (43% of the site surface), as well as meadows and grasslands, covering 25% of the area and hosting remarkable species such as the Woodlark (*Lullula arborea)*, the Red-backed shrike (*Lanius collurio*) and the Marsh fritillary (*Euphydryas aurinia*) (Chaput et al., 2014).

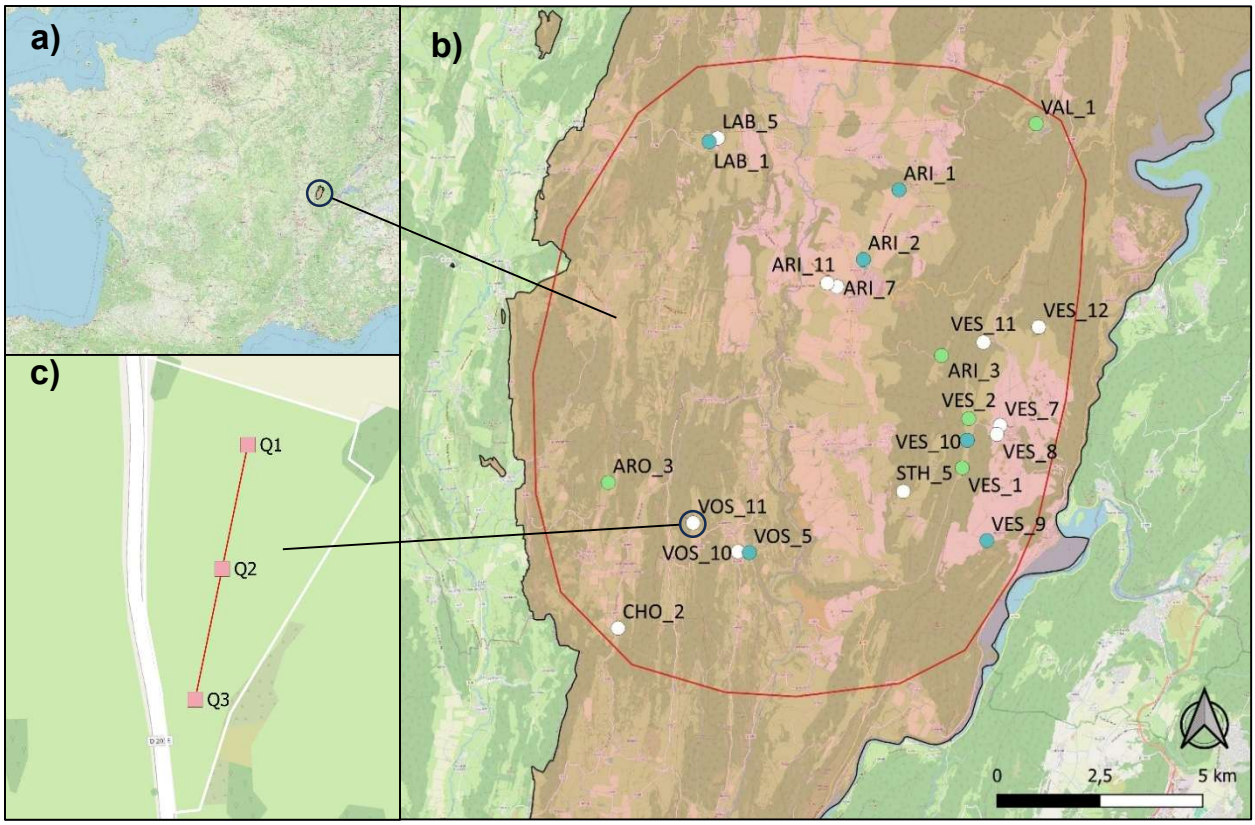

Figure 1 | Maps showing **(A)** the location of the Natura 2000 site *Petite Montagne du Jura* (PMJ) within France; **(B)** the location of the sampling area (red line) and the sampled grasslands (n=24, white dots: non-engaged (NE), coloured dots: late-mown (blue: RF1, from the 16th of June; green: RF3, from the 4th of July)) within the PMJ site (pink surface) **(C)** An example of a surveyed plot (white shape), with the 100-m transect for butterfly inventories (red line) and the three 1m²-quadrats for plant inventories (pink squares).

With only 8% of its surface urbanized, the PMJ is a very rural area, considerably modelled by agriculture, all the more so as it is located inside the Comté Protected Designation of Origin ('AOP Comté'). This label restricts the production of the Comté cheese to a delimited area in Franche-Comté and induces precise specifications such as obligation of outdoor grazing and limitations in fertilization and grazing rates (Mauchamp, 2014). Despite these restrictions made to guarantee a reasonable use of lands, the landscapes of Franche-Comté are subject to strong pressures since several decades to substantially rise the milk production (+1-2% every year since 2009) and thereby answer the increasing demand of Comté cheese (Mauchamp, 2014; CIGC, 2021). The development of this activity in the last decades was made possible by increasing the fertilization and grazing intensities of meadows, with a focus on the more accessible and productive lands for an easier mechanization (Mauchamp, 2014). Additionally, since the priority was set on finding grazing surfaces and not hay making, there was considerable loss of mown grasslands to grazing pastures (-40% of mown grasslands in 15 years in a similar Natura 2000 site of Franche-Comté, mainly for conversion to grazing meadows) (Boucard & Ballaydier, 2017). These authors also revealed a strong decline in grassland conservation state, with more than half of this site's grasslands presenting a bad floral typicity in 2017. Since 80% of farms in the PMJ are specialized on dairy cattle production, this site is indeed particularly subject to these pressures from the cheese production sector (Chaput et al., 2014). In such agricultural context, there are high stakes for conciliating favourable practices for both environmental and economical purposes, hence the implementation of PAECs since about twenty years in the PMJ site.

2.1.2- Agri-environmental measures

The Objective document ('DOCOB') of the Natura 2000 PMJ site synthetises the conservation aims and actions deployed to preserve the habitats and species of interest (Chaput et al., 2014). Within the framework of this document, an Agri-environmental and Climatic Project ('PAEC') is set up every five years to develop contracts with farmers for a better consideration of environmental concerns in their practice. These PAECs propose a list of Agri-environmental and Climatic Measures (MAEC) that farmers can sign for their lands and for which they earn subventions from Europe, as part of the Common Agricultural Policy. The conditions of the late mow MAECs registered for the PMJ area over the different PAECs are summarized in **Appendix 1**. I grouped these late-mow measures under three categories, based on the minimal delay from the mean annual mow date of the territory (fixed at May the 20th): 'RF1', 'RF2' and 'RF3', whose mow

delays are fixed respectively to 25, 35 and 45 days after May the 20th. I excluded the 'RF2' contract from this study as it is new from the PAEC 2023-2027 and only few farmers subscribed to this measure. Additionally, non-engaged grasslands ('NE') include all plots of the study which are not currently engaged in a MAEC contract (control plots). According to local data, these grasslands are mowed on average on the 20th of May, depending on weather conditions, and at least twice during the season. There is no limit in fertilization input, grazing intensity or any specific constraint, except that ploughing is prohibited.

2.2 – Selection of surveyed grasslands

2.2.1 – Habitat selection

In the PMJ, the semi-natural grasslands eligible to the late-mow MAECs belong to four main phytosociological categories, according to the different cartographies of open habitats carried out in the area (Boucard & Voirin, 2011; Voirin & Boucard, 2024). The features and surface covered by these four habitats are summarized in **Appendix 2.** For this study, I selected one habitat only, to analyse strictly the effects of the management on grassland communities without the influence of the differences in habitat composition. While the four habitats are of patrimonial interest, I excluded the *Heracleo sphondylii-Brometum mollis* alliance, as it appeared to be a degraded meadow, originating from an over-fertilization of other alliances with a loss of up to half of the plant diversity (Boucard & Ballaydier, 2017; Voirin & Boucard, 2024). As for *Colchico autumnalis-Festucetum pratensis* and *Mesobrometum erectii*, too little plots of these alliances were engaged in 'RF1' and 'RF3' MAEC contracts to be able to rigorously compare their impacts. Therefore, the *Galio veri – Trifolium repentis* grasslands were chosen as the focus habitat for this study, since they are widespread in the PMJ, thus many of them are engaged in MAEC contracts. Additionally, this alliance presents a strong ecological interest, as it makes the transition between the *Arrhenatherion* mesophile hay meadows, and hosts species of this category in high proportions (e.g. *Tragopogon pratensis, Crepis biennis, Rhinanthus alectorolophus*), and the *Mesobrometum erecti* calcicole grasslands, with numerous typical species (e.g. *Onobrychis viciifolia, Dianthus carthusianorum, Poterium sanguisorba).* As *Galio veri* is a sensitive habitat, extensive practices such as late mowing and low mowing frequency, grazing intensity and fertilisation inputs are particularly recommended for its preservation, which highlights the importance of implementing MAECs in such habitat (Voirin & Boucard, 2024).

2.2.2- Plot selection and characteristics

I selected the grasslands to inventory for this study on the cartographical software QGIS, using three different layers: the phytosociological layer from Boucard & Voirin (2011), its 2023-actualisation (Voirin & Boucard, 2024), and a third layer inventorying the plots engaged in the MAECs for the different PAECs. Using this information, I selected twenty-four plots of *Galio veri* meadows for the study's inventories, among which twelve engaged in a late mow MAEC agreement ('RF') and twelve not engaged ('NE') (**Appendix 3**). Amongst the engaged plots, seven of them were engaged in the 'RF1' measure (mow from the 16th of June) and five in the 'RF3' measure (mow from the 4th of July). For this selection, I prioritized the meadows engaged in MAEC since 2007 to better assess the effects of MAEC engagement, but some of the selected ones are engaged only since 2021. As for the NE plots, all the ones that I selected had never been engaged in MAECs in any of the previous PAEC. I did not include two similar plots located nearby each other and belonging to the same farmer, to avoid pseudo-replicates.

Environmental variables

I chose the plots considering different environmental variables, namely their altitude, surface, locality and landscape openness on the surroundings, since these metrics are known to influence butterfly and plant diversity (Körner, 2000; Öckinger & Smith, 2006; Öster et al., 2007). The plot surface was computed on QGIS using the field calculator, while its altitude was retrieved from the OpenStreetMap raster layer. The selected grasslands were 2.0 ha large on average (ranging from 0.3ha to 6.0ha) and they were all located between 400m and 725m high, with an average of 560m. As for the land openness, it was visually estimated by assessing the forest presence in the direct surroundings of the plots using an orthophotography map, the selected plots being categorized at Open, Semi-Open or Closed. This metric was not used afterwards for data analysis, since a more precise land cover analysis was performed (see below).

Pairing the plots

Since the different metrics could not be standardized for all plots, to limit their variability and compare them in similar conditions, I paired the RF plots with control NE grasslands (cf. **Appendix 3**). Paired plots would have the highest possible similarity in the criteria mentioned above, which was possible for all but two pairs (P8 and P9). These plots were paired despite their mismatching criteria (respectively locality and plot size) since they were very similar in the other

ones. I performed tests on the statistical analysis software RStudio (R Core Team, 2026) to assess whether the pairing was adequate. There were no significant differences in plot surface and altitude between the (Student's t-test, p=0.234 and p=0.07 respectively) neither in the estimated landscape openness (Fisher's test, p=0.870) between the pairs.

Land cover composition

Land cover composition of the study area was retrieved from the THEIA - CES OSO database (10m resolution, 2025) and was computed at 500m and 2km buffers around each sampled grassland of the study area, using QGIS v3.16.7. The percentage of land covered by Prairie was retrieved, as it informs about the availability of potential habitats for butterflies around the studied grassland (Öckinger & Smith, 2006). The Deciduous and Coniferous categories were combined as a single Forest category, used for the analyses, as the presence of forests nearby is known to influence both butterfly and plant diversity (Öster et al., 2007; Ulyshen et al., 2023). Both butterflies and plants are affected by land cover at low and high distance around their habitat, hence the use of the 500m and 2-km buffers (Öster et al., 2007; Ulyshen et al., 2023).

Management methods

Prior to the inventories, I identified the farmers using the selected grasslands thanks to their administrative number from the Common Agricultural Policy and asked for their authorization to survey their lands. At this occasion, I asked whether they fertilized their grasslands, or I obtained this information directly in the field. Additionally, I followed the state of each grassland during the study period and estimated the mowing dates considering the last time I saw it unmown and its state on the day I see it mown. All dates were converted into Julian days for an easier analysis.

2.3- Field surveys

Following the recommendations for butterfly inventories from the French national monitoring scheme (Manil & Henry, 2007), I inventoried the twenty-four selected grasslands three times, once every month, between the 20th of May and the 10th of July 2026, with an interval of minimum 15 days between two surveys on the same plot. I surveyed the two plots of each pair on the same day to limit the influence of weather conditions, and two or three pairs were surveyed per day and in similar locations. Before the first field session, the order of the pair

was randomly attributed and kept the same for the two next ones. To avoid time and weather biases, the order of pair surveyed during the day was switched at each session. For instance, a plot surveyed in the morning during the first session was surveyed in the afternoon during the second one. The same process was applied to NE and RF plots.

2.3.1 – Butterfly inventories

Transects appeared as the most efficient and easy-to-implement method to inventory butterflies for this study, as they enable to evaluate exhaustively the communities present in a specific habitat and measure their response to the farming practices (Sobczyk-Moran & De Flores, 2022). Therefore, following the protocols for national and European butterfly monitoring schemes, I placed 100-meters long transects in each studied plot (Manil & Henry, 2007; Sevilleja et al., 2019). A single transect (except for one plot, very narrow in the centre, where the transect had to be split in two) was set in the centre of each plot, with a minimal distance to the edge of 10 meters, to avoid spill-over effects of other habitats on both plant and butterfly species (Arnold et al., 2026) (cf. **Appendix 4**). The transects were set in the diagonal of the plots so they would go across the slope and be representative as representative as possible of the vegetation of the whole grassland. I did the butterfly counts by walking the entire 100-m transect (measured with a decametre), in 10 minutes of observation (timed with a chronometer). The *Pollard Walk* methodology was used, i.e. walking the transect at a constant speed and counting all individuals seen in an imaginary box of 5x5x5 meters (Pollard, 1977).

All living adult *Rhopalocera* seen during the transect were inventoried, i.e. all species belonging to the *Hesperiidae*, *Papilionidae, Pieridae, Lycaenidae,* and *Nymphalidae* families. The number of individuals seen for each species was retrieved on a survey sheet. When the identity of a butterfly could not be determined from the distance, it was captured thanks to an insect net, then identified either directly through the net (with the wings carefully unfolded), or after a transfer into a transparent tube. If needed, pictures of the upper and lower faces of the wings were taken for a later identification. The captured individuals were released immediately after determination or after taking pictures. I identified all individuals to the most precise taxonomical level (sometimes only Family or Genus) and avoided double counts as much as possible by keeping aware of the individuals going in and out the transect again.

I identified the butterfly species thanks to previous knowledge and using the *Guide for European Butterflies* (Lafranchis, 2010) and specific identification keys (Jacquier, 2017; Ryelandt

& Jugan, 2017; Ryelandt et al., 2022). Additionally, prior to the field sessions, I established a list of species I expected to be present in mown grasslands, thanks to entomological inventories previously conducted in the N2000 PMJ area (Moureau, 2015). I used this list as a baseline for training on the different identification criteria before the field sessions.

2.3.2- Plant inventories

Quadrats of 1m² were used to record the abundance and species richness of plant species present in the grassland. Three quadrats were disposed on the transects used for butterflies; one in the start, one in the middle and one at the end of the transect (cf. **Appendix 4**). The abundance of each species was estimated in each quadrat; the counts being usually rounded to the decade for time constraints, and the numbers of the three quadrats added up afterwards. All forb species, i.e. every herbaceous flowering plant aside from graminoids (Poaceae, Cyperaceae, Juncaceae), were recorded. Grasses were excluded for simplicity and time reasons, as their identification require strong botanical skills. Moreover, the butterflies using *Poaceae* as host plants seem to be unspecific in their choice, thus their precise identification did not appear relevant for this study, neither their abundance, since they were generally largely distributed in all recorded grasslands (Clarke, 2024, Öckinger & Smith, 2006).

Forbs were counted at every life stage and identified to the most precise taxonomical level thanks to previous knowledge and using the *Flora Vegetativa* and *Petite flore de France* guides (Eggenberg & Möhl, 2007; Thomas et al., 2022). Additionally, I sometimes carefully used the automated plant identification application PlantNet for preliminary identification, as its success rate is suggested to be up to 95% within the five first suggestions (Hart et al., 2023). I systematically verified the identification criteria and the ecology of the suggested species.

2.3.3- Meteorological conditions

Following the standardized monitoring schemes, the inventories were conducted only in favourable conditions for butterfly observations according to national protocols (Manil & Henry, 2007; Sevilleja et al., 2019). Therefore, the field sessions took place in warm and sunny days, with a temperature no lower than 13°C in case of sunny weather (less than 10% cloud cover) or greater than 17°C with a 10-50% cloud cover. The actual temperature was retrieved during the field from a mobile weather application, and the cloud cover was visually estimated. The inventories were performed at a wind speed no greater than 30km/h, estimated by the motion of vegetation

according to the Beaufort scale (cf. **Appendix 5**). The inventories were conducted in a period comprised between 9:30am and 5:00pm, with possible adaptations during the days of extreme heat to avoid the hottest hours. These meteorological data were systematically noted down on the survey sheets at the start of the inventories.

2.4- Data analysis

All analyses were performed using the statistical analysis software RStudio v4.6.1 (R Core Team, 2026). I computed abundance and alpha-diversity metrics (Species richness, Shannon, Simpson's and Pielou's indices) of butterflies and plants for each transect (n=72) and used them for all diversity analyses.

2.4.1- Effects of late-mow MAECs on grassland biodiversity

To identify the effects of late mow contracts, I compared both plant and butterfly diversity metrics between engaged plots ('RF1' and 'RF3') and control non-engaged ('NE') meadows. I used one-way analyses of variance (ANOVAs) or Kruskal-Wallis tests, followed by post-hoc tests, to assess the differences between RF1, RF3 and NE contracts, and Student's t-tests to compare engaged and non-engaged grasslands (NE vs RF). I performed a complementary standardization of these alpha-diversity metrics extrapolated to double the sample size of the highest survey numbers (i.e. 72, twice the number of NE grassland surveys) using the *iNEXT* package (Hsieh et al., 2016).

2.4.2- Effects of late-mow MAECs on grassland communities

I used Non-metric Multidimensional Scaling (NMDS) analyses (R function *metaDMS*) with Bray-Curtis distance to visualize differences between the grassland communities depending on its MAEC contract (Bakker, 2026) and confirmed these assessments by a permutational multivariate analysis of variance (PERMANOVA, R function *vegan::adonis2*).

Moreover, I analysed the functional diversity of butterfly communities for a precise evaluation of the state of communities and to assess if it differed between contracts. For this purpose, the following ecological traits of each observed species were retrieved from the European Butterfly Trait Database (Middleton-Welling et al., 2020): host plant specificity (monophagous -restricted to a species-, oligophagous -restricted to a genus or family- or polyphagous -feeding on species of different families-), ant association (whether it interacts with

ants during its life cycle), adult feeding resource (the food sources used by the adult), average flight period duration (number of months in the year it is observed flying), voltinism (the number of generations per year) and wingspan (the distance between the apices of the two forewings in a set specimen) - these three last criteria characterizing the dispersal abilities of the species (Sekar et al., 2012). Their specialism was also considered, using the list of species depending on dry habitats according to the inventories performed in the PMJ by Moureau (2015).

I used these ecological traits to analyse the functional diversity of the communities, commonly measured by three primary components: functional richness (FRic - the amount of functional space filled by the community), functional evenness (FEve – the evenness of abundance distribution in a functional trait space), and functional divergence (FDiv - how the abundance is spread along a functional trait axis, within the range occupied by the community) (Villéger et al., 2008). I also computed the additional metric of functional diversity proposed by (Villéger et al., 2008), the functional dispersion (FDis), which corresponds to the mean distance of individual species to the centroid of all species in the community. It is closely related to Rao's quadratic entropy (Rao's Q) which expresses the mean distance between two randomly selected individuals. I computed all these functional diversity metrics for each survey session and for the different contracts using the *FD* package developed by Laliberté & Legendre (2010).

I also analysed few plant traits, focusing on the species relevant for butterflies, namely the nectareous and larval host plants using the databases by Clarke (2024) and Lanuza et al. (2025). Additionally, I retrieved the species characteristic of the *Galio veri* habitat mentioned in the phytosociological study from Voirin & Boucard (2024).

2.4.3- Combined effects of farming practices and environmental factors on grassland biodiversity

A Structural Equation Model (SEM) was used for analysing the combined effects of all variables on the observed results. Such models enable to combine all variables in a single network and to test the relationships between them, therefore variables can be potentially both predictors and responses. Variance-covariance SEMs are traditionally used to get a global estimation of the tested model, but I preferred a piecewise SEM (R package *piecewiseSEM)* which performs an estimation at a smaller scale by evaluating each equation separately (Lefcheck, 2016). Following the common method for performing SEMs, I schemed a conceptual diagram which included every variable that I predicted to influence butterfly and plant diversity in the studied grasslands, and

the links that I presumed between these variables (**Appendix 6**). I also aimed to test whether the MAEC contract effectively influenced the farming practices (mow date, fertilization and mowing frequency). However, the mowing frequency was excluded from the analysis as all grasslands were mown once only during the season due to climatic conditions.

I used an assemblage of Generalized Linear Mixed Models (GLMM) with Poisson distributions, as my variables were either independent or dependant, and I defined the plot pairing as the random variable of the models. In total, I included five GLMMs in the piecewise SEM for explaining the following variables: first mow date (predicted by type of contract only), plant abundance, plant species richness, butterfly abundance and butterfly species richness. Original GLMMs for plant and butterfly diversity included farming practices (first mow date and fertilization), survey conditions (whether the grassland had been mown before the survey and the survey session), the contract duration (the number of PAECs for which the grassland has been engaged) and the environmental conditions (plot size, altitude and surrounding land cover). The Akaike Information Criteria (AIC) of each GLMM were computed to choose the best fit, following the principle of parsimony: for each response variable, the model with the lowest AIC and the lowest number of explanatory variables was kept. The global fit of the SEM was computed using a Fisher's C test (Lefcheck, 2016). If the p-value was lower than 0.05, the model did not reflect the relationships implied by the data, thus the GLMMs were changed for a better fit. These changes included the consideration of potentially missing relationships that were not originally predicted to influence the response variables (e.g. the direct effect of mowing practices on butterfly diversity or the direct effect of the contract on plant and butterfly diversities).

3- RESULTS

A total of 838 butterflies of 50 different pseudospecies (42 identified species) and 15,591 plants of 79 pseudospecies (66 identified species) were recorded in the 72 transects performed between the 19th of May and the 10th of July 2026. The list of species, their abundance in the different sessions and their ecological traits are summarized in **Appendices 7 and 8.** The most abundant butterfly species were *Maniola jurtina* and *Melanargia galathea,* accounting together for 36% of all observations, while the most abundant plant species were *Trifolium pratense, Sanguisorba minor, Lotus cornicolatus* and *Plantago lanceolata,* accounting together for 33 % of all observations. Few vulnerable or threatened butterflies at the national level were observed, according to the Butterfly Red list, among which the Marsh fritillary (*Euphydryas aurinia)* (Itrac-Bruneau & Mora, 2026).

The mow dates of the 24 surveyed grasslands are summarized in **Appendix 3**. All grasslands were mown once only, between the 19th of May and the 12th of July. Half of the non-engaged grasslands were mown around the 15th of July, thus similarly to RF1 grasslands.

3.1- Effects of late-mow MAECs on grassland biodiversity

Kruskal-Wallis tests did not reveal any significant impact of late-mow MAEC contracts on butterfly species richness or abundance, neither a difference in diversity indices (Shannon, Simpson and Pielou) between the contracts (**Table 1**). For plants, Kruskal-Wallis tests did not show any significant effect of contract on abundance, but there was moderate evidence of a higher species number in RF3 than NE and RF1 grasslands (Kruskal-Wallis, p=0.02; post-hoc Dunn, p=0.055 and p=0.02 respectively) (**Table 2**). Similarly, there was moderate evidence that Shannon and Simpson's indices were both significantly higher in RF3 than NE or RF1 grasslands (Kruskal-Wallis, p=0.01, respectively p=0.01 and p=0.02).

Species accumulation curves obtained by rarefaction-extrapolation methods (*iNEXT*) appear visually similar for both plant and butterflies whichever the contract (**Appendix 9**). For double the highest sample size (n=72) and for both plants and butterflies, estimates of Shannon and Simpson's indices are slightly greater for RF3 grasslands, followed by NE and then RF1 grasslands; while species richness is predicted to be higher in NE than RF3 and RF1 grasslands (**Appendix 9**).

Table 1 | Summary of alpha-diversity metrics of butterfly communities inventoried in the grasslands of the Petite Montagne du Jura. Means and standard deviation of Abundance, Hill numbers (Species Richness, Shannon and Simpson's indices) and Pielou's index are given for each contract (NE: non-engaged, RF: engaged, RF1 and RF3: engaged respectively in 25-days and 45-days mow delays). There was no significant difference between the contracts for any of the metrics.

Contract	Butterfly Abundance	Butterfly Sp. richness	Butterfly Shannon's	Butterfly Simpson's	Butterfly Pielou's
NE	10.0 ± 6.8	4.5 ± 2.0	1.2 ± 0.5	0.6 ± 0.2	*NA*
RF (RF1 + RF3)	13.3 ± 13.2	4.7 ± 2.3	1.3 ± 0.4	0.6 ± 0.2	*NA*
RF1	11.0 ± 8.9	4.4 ± 1.9	1.2 ± 0.5	0.6 ± 0.2	*NA*
RF3	16.5 ± 17.4	5.1 ± 2.7	1.3 ± 0.4	0.7 ± 0.1	0.9 ± 0.1

Table 2 | Summary of alpha-diversity metrics of plant communities inventoried in the grasslands of the Petite Montagne du Jura. Means and standard deviation of abundance, Hill numbers (Species Richness, Shannon and Simpson's indices) and Pielou's index are given for each contract (NE: non-engaged, RF: engaged, RF1 and RF3: engaged respectively in 25-days and 45-days mow delays). Plant species richness, Shannon and Simpson's indices were significantly higher in RF3 grasslands than RF1 and NE grasslands.

Contract	Plant Abundance	Plant Sp. richness	Plant Shannon's	Plant Simpson's	Plant Pielou's
NE	206.1 ± 159.4	12.1 ± 5.6[a]	1.9 ± 0.5[a]	0.8 ± 0.1[a]	0.8 ± 0.1
RF (RF1 + RF3)	227.0 ± 164.5	12.9 ± 5.7	2.0 ± 0.6	0.8 ± 0.1	0.8 ± 0.1
RF1	187.1 ± 164.2	10.8 ± 5.6[a]	1.8 ± 0.6[a]	0.8 ± 0.2[a]	0.8 ± 0.1
RF3	282.7 ± 153.1	16.0 ± 4.6[b]	2.3 ± 0.3[b]	0.9 ± 0.0[b]	0.8 ± 0.0

3.2 – Effects of late-mow MAECs on grassland communities

According to the NMDS visualization and the PERMANOVA analysis, there was no significant differences in neither butterfly nor plant communities between the contracts (PERMANOVA, p=0.907 for butterflies and p=0.691 for plants) (**Appendix 10**). Additionally, a similar PERMANOVA analysis of the communities present in the unmown grasslands in the first survey session was conducted, to exclude the effect of a recent mow on the biodiversity, but there was no evidence of differences in communities neither (PERMANOVA, p=0.734 for butterflies and p=0.725 for plants).

As for the functional diversity of butterflies, there was also no evidence for a greater diversity in grasslands engaged in late-mown contracts (**Table 3**). Some traits were more specifically analysed, namely the diversity of specialist species, but there was no evidence for

neither a higher abundance nor a higher species richness in late-mown grasslands (Kruskal-Wallis, respectively p=0.54 and p=0.80) (**Table 4**). The average flight period, wingspan and voltinism were retrieved as well to characterize the dispersal ability, but no significant effect of the contract could be assessed (**Table 4**).

As for the plant trait analysis, it revealed a low to moderate evidence of the MAEC contract influence on the richness of all specific plant species, namely the ones characteristics of the *Galio veri* habitat as well as the nectareous and host plants, which were all more diverse in RF3 grasslands. More precisely, there was a higher richness of characteristic plants in RF3 than NE (ANOVA, p=0.04; Tukey, p=0.03), a higher richness of nectareous plants in RF3 than RF1 (Kruskal-Wallis, p=0.05; Dunn p=0.05) and a higher richness of host plants in RF3 than RF1 and NE (Kruskal-Wallis, p=0.01; Dunn, RF3-NE: p=0.03, RF3-RF1: p=0.01) (**Table 5**). However, there was no evidence for any difference in abundance for these specific categories between the contracts.

Table 3 | Summary of functional diversity metrics of butterfly communities for each grassland contract: functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), functional dissimilarity (FDis), and Rao's quadratic entropy (RaoQ). Metrics were computed with *Cailliez* correction method.

Contract	FRic	FEve	FDiv	FDis	RaoQ
NE	0.97	0.82	0.79	0.2	0.05
RF1	0.89	0.8	0.8	0.21	0.06
RF3	1.06	0.82	0.78	0.21	0.05

Table 4 | Summary of main butterfly traits depending on the grassland contract: abundance of specialist species, average flight period (mean number of months the species is seen flying), wingspan (distance between the forewings, in millimetres) and voltinism (number of generations per year). There was no significant difference for any of the metrics between the contracts.

Contract	Abundance of specialists	Average flight period (months)	Wingspan (mm)	Voltinism (nb of generations/year)
NE	3.3 ± 5.2	5.5 ± 0.9	37.7 ± 6.7	1.5 ± 0.3
RF1	3.8 ± 3.6	5.2 ± 1	38.0 ± 7.6	1.4 ± 0.2
RF3	6.7 ± 9.4	5 ± 0.8	38.9 ± 5.6	1.4 ± 0.3

Table 5 | Variation of richness of specific plant categories with the MAEC contract: species characteristic of the habitat, nectareous species and host plants for butterfly larvae. Characteristic plants were more diverse in RF3 compared to NE grasslands (ANOVA, p=0.04; Tukey, p=0.03), nectareous plants more diverse in RF3 than RF1 (Kruskal-Wallis, p=0.05, Dunn p=0.05), and host plants more diverse in RF3 than RF1 and NE (Kruskal 0.01, Dunn: RF3-NE: 0.03, RF3-RF1: 0.01).

Contract	Richness of characteristic plants	Richness of nectareous plants	Richness of host plants
NE	3 ± 1.93[a]	9.2 ± 4.4	7.2 ± 3.0[a]
RF1	3.3 ± 2.11	8.0 ± 4.5[a]	6.4 ± 3.2[a]
RF3	4.7 ± 2.5[b]	11.7 ± 3.2[b]	9.7 ± 2.9[b]

3.3 –Combined effects of farming practices and environmental factors on grassland biodiversity

The final piecewise Structural Equation Model (SEM) showing all significant relationships between the variables is shown in **Figure 2** (Fisher's C, pvalue=0.596). According to the Akaike Information Criteria (AIC) of the Generalized Linear Mixed Model (GLMM), the mow date is indeed delayed with the MAEC contract (RF1: p=0.003, effect estimate: 0.07 and RF3: p<0.001, effect estimate: 0.23).

The model predicts that plant abundance is positively influenced by several variables, the most important ones being the MAEC contract (effect estimate: 0.66, p<0.001 for RF1; 0.20, p=0.06 for RF3), the plot surface (0.13, p<0.001) and the plant species richness (0.13, p<0.001). Plant abundance appears negatively affected by a recent mow (-0.11, p=0.009) and by the duration of the engagement (-0.16, p<0.001). The survey session impacted negatively plant abundance as well, with S2 accounting for a lower presence of plants (-0.12, p<0.001), while forest and prairie cover at 500m around the plot both reduced plant abundance (-0.04 for both, p<0.001). Plant species richness is driven mainly by a recent mow of the grassland (-0.63, p<0.001) and the survey session (effect estimate for S2: 0.16, p=0.059). Additionally, the duration of the engagement has a slight negative influence on plant richness (-0.07, p=0.004).

As for butterflies, their abundance is strongly predicted by a recent grassland mow (-0.77, p<0.001), the survey session (0.87 for S2 and 0.42 for S3, p<0.001 for both) and butterfly species richness (0.14, p<0.001). Butterfly species richness itself is only explained by a slightly positive influence of the plant species richness (0.05, p<0.001).

Moreover, to assess the influence of plant resource availability on butterfly diversity, I tested the GLMMs excluding the plants which are not used by butterflies (i.e. considering only the diversity of nectareous and host plants). Since these new models gave similar predictions, I kept the first model with all plant species for a better representativity of the grassland diversity.

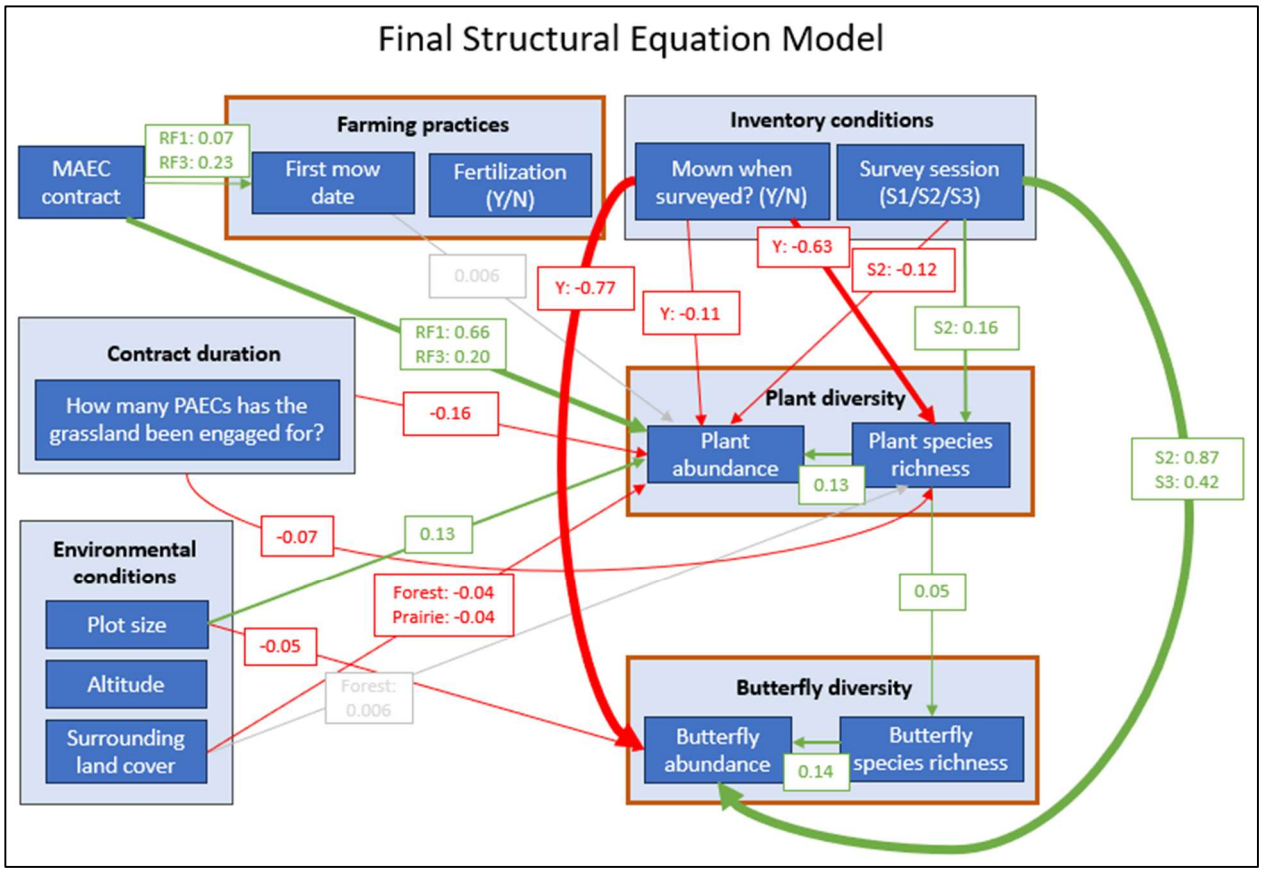

Figure 2 | Final piecewise Structural Equation Model (SEM) showing all significant interactions between the variables (blue boxes) which explain the variations in plant and butterfly diversities in the surveys. GLMMs were built and tested for each response variables to find its predictors, the model with the lowest Akaike Information Criterion being kept as the most probable. Arrows represent the significant effect of a predictor on a response variable (green: positive interaction, red: negative interaction, value: effect estimate of the variable). The final piecewise SEM has a p-value of 0.596, which means that it is likely to be representative of all significant relationships.

Influence of the survey session

As the survey session has the most significant effects after the grassland mow, I specifically analysed the influence of this factor on grassland biodiversity. The butterfly abundance significantly differed between the survey sessions (ANOVA, $p<0.01$), with a higher abundance in S2 than S1 and S3 (Tukey, $p=0.02$ and $p<0.01$ respectively) (**Appendix 11**). Additionally, in S2, this abundance varied with the grassland contract (ANOVA, $p=0.01$) with a higher abundance in RF3 grasslands than NE or RF1 (Tukey, $p<0.01$ and $p=0.056$) (**Appendix 11**). Species richness did not differ between the survey sessions.

As for plant diversity, both the abundance and species richness differed between sessions (ANOVA, $p<0.01$ for abundance; Kruskal-Wallis, $p<0.01$ for richness) with a lower diversity in S3 than S1 or S2 (Tukey, $p<0.01$ and $p=0.04$ for abundance; post-hoc Dunn, $p<0.01$ and $p=0.01$ for

species richness) (**Appendix 11**). In S2, plant abundance differed between the contracts (ANOVA, p=0.02) with a higher abundance in RF3 grasslands than in RF1 (Tukey, p=0.02)

Moreover, the PERMANOVA analyses revealed that both butterfly and plant communities differed between the survey sessions (p=0.001 for butterflies and p=0.008 for plants). Indeed, some species appear predominant in some sessions, as *Maniola jurtina* and *Melanargia galathea* which were predominant in S2 (60% of the observed individuals) (**Appendix 7**)**.**

4- DISCUSSION

4.1 – Effects of late-mow MAECS on grassland biodiversity

While the mow date is indeed positively influenced by the MAEC contract, there is a low effect of contract on mow delay for RF1. In fact, half of non-engaged grasslands were mown at about the same time than RF1 grasslands, which goes against the fact that the 20th of May is considered as the average mowing date of the territory (**Appendix 3**). This can explain the difficulties to obtain evidence for a greater biodiversity in RF1 grasslands.

Neither the one-way analyses of variance (ANOVAs) nor the piecewise Structural Equation Model (SEM) showed any evidence of an effect of MAEC contracts on butterfly diversity. In fact, there was a generally low butterfly diversity in all surveys, with a mean of 4 to 6 species and 10 to 15 individuals per transect. Only in June survey session ('S2'), there was evidence for a higher butterfly abundance in grasslands mown on the 4th of July ('RF3'), with an average of 35 individuals observed in these grasslands.

Plant diversity was more clearly influenced by the MAEC contracts than butterflies. I observed a higher number of species in RF3 grasslands than the other ones (16 versus 12 species on average). Similarly, Shannon and Simpson's indices for plant diversity were both significantly higher in RF3 grasslands than in the others. This difference among contrast appears particularly evident in June surveys, with a mean of almost 20 species in RF3 grasslands while only 10 in the grasslands mown on the 16th of June ('RF1'). However, when considering the other conditions thanks to the piecewise SEM, there was no evidence of an effect of late-mow contracts or a later mow date on plant species richness. In fact, if a later mow could improve plant diversity by

allowing certain species to produce more seeds in the season, this effect can vary depending on the species ecology and late mow can sometimes have low efficiency in promoting species richness (Chaudron et al., 2016).

As for plant abundance, ANOVAs did not reveal any evidence of differences between the contracts, with a mean abundance varying between 180 to 280 individuals. However, the piecewise SEM showed strong evidence that late-mow contracts have a positive influence on plant abundance (effect estimates: 0.25 and 0.20 for the two different contracts). There was also a positive, but very weak effect of a later first mow date on plant abundance. In fact, I expected the mow date to have more influence than the contract itself, namely since half the non-engaged grasslands were mown on the same time than RF1 grasslands (i.e. around the 16th of June). This suggests that not only the mow delay but other contract conditions impact grassland diversity.

Among the other conditions, I expected the limitations of N/P/K inputs (none allowed for RF3 grasslands, only 20 units/ha of N allowed in RF1 grasslands) to preserve a higher species diversity, as the *Galio veri* alliance is particularly sensitive to fertilization and can be subject to species loss if too intensively fertilized (Voirin & Boucard, 2024). However, the piecewise SEM did not show evidence of an effect of fertilization on the grassland diversity, which could be due to counterbalancing effects of nutrient inputs on plant diversity. While high fertilization rates tend to homogenize communities towards nitrophilous and competitive species, an absence of fertilization can lead to the disappearance of these nitrophilous species (which can also be indicators of quality hay meadows, such as *Crepis biennis,* characteristic of *Galio veri* grasslands) (Mauchamp et al., 2016; Cordier et al., 2025). This can explain that the effects of the reduction in fertilization rates on plant communities are not always clear and can strongly vary depending on the ecosystem (Zechmeister, 2003; Hopkins & Holz, 2006).

Another constraint set by the late-mow contract which could impact plant diversity is the grazing period. Grasslands engaged in MAECs cannot be grazed before the mow, while non-engaged grasslands are sometimes grazed in spring already. This early grazing as well as the grazing intensity after the mow could both impact the diversity of plants and butterflies (Hopkins & Holz, 2006). As grazing period and pressure can vary strongly depending on the yearly conditions, their long-term effect on the grassland might be hard to assess but can have an important influence on the actual diversity.

Moreover, the MAEC contract has an indirect impact on mowing frequency, as a delayed first mow date reduces the frequency to only one mow (especially in RF3 grasslands) versus two or even three mows in non-engaged grasslands (Chaput, 2014). Exceptionally, in summer 2026, all grasslands were mown once only, but the mowing frequency might have a long-term effect on the grassland communities and invertebrates are known to be particularly affected by a high frequency of mows (WallisDeVries & van Swaay, 2009; Humbert et al., 2012).

The duration of the engagement in MAEC contracts can also have an important influence on the biodiversity, as the measures have effects on the long-term and it can take more than 10 years to obtain changes in the communities (Cordier et al., 2025). The negative correlation between plant abundance and contract duration highlighted by the piecewise SEM is hardly explainable considering that the MAEC have rather positive effects.

Ultimately, it is probable that it is the combination of the different constraints set by the MAECs that engender their positive effects on plant diversity.

4.2 – Effects of late-mow MAECs on grassland communities

PERMANOVA analyses did not show any evidence of differences in community composition for butterflies or plants with the MAEC contracts. The diversity metrics computed for butterfly communities (Functional richness, evenness, divergence and dissimilarity as well as Rao's quadratic entropy), based on species' ecological traits, did not differ neither between the MAEC engagements. These results could not validate my prediction that the different mowing regimes impact specific species more than the others, probably because of the overall low number of butterflies observed. With more records, I suppose to observe changes in the communities towards more specialist grassland butterflies in late mow regimes, as they can benefit from a longer availability of resources in their preferred habitat (Johansen et al., 2019).

For plants, there was evidence for a higher number of characteristic species in RF3 grasslands, suggesting that these grasslands have a better typicity and a better conservation state. Indeed, the constraints induced by late-mow MAECs seem particularly adapted to preserve the ecological richness of this habitat (Voirin & Boucard, 2024). There was also a higher richness of resource plants for butterflies (nectareous and larval host plants) in the grasslands mown on the 4th of July, which shows that this increased diversity in RF3 grasslands does benefit the butterflies by providing a greater availability of resources. This link between plant and butterflies is further explored in the next section.

4.3 –Combined effects of farming practices and environmental factors on grassland biodiversity

Link between plant and butterfly diversities

As previously mentioned, I found evidence for a higher diversity of resources in late-mown RF3 grasslands, which could in turn benefits the butterflies. There was indeed a low but positive correlation between plant and butterfly richness (effect estimate: 0.05), which in turn influenced butterfly abundance (effect estimate: 0.14), but there was no evidence for any effect of plant abundance on butterfly diversity. Even when considering only plant species which offer resources for butterflies (i.e. nectareous and larval host plants), the model predictions did not differ. In fact, plant diversity might not exhaustively reflect the resource availability, and a more important influence of plants on butterflies would be the phenological state of the resource plants, and namely the flowering stage for nectareous plants. Therefore, an inventory of the floral resources could have better highlighted the link between plant and butterfly diversity and thereby the influence of late-mow contracts on the grassland attractivity for butterflies (Öckinger & Smith, 2006; Johansen et al., 2019).

Effect of a recent mow

More than being influenced by the variation in plant diversity with the MAEC contract, butterflies were directly impacted by the vegetation cut, which caused a drastic reduction in their abundance (effect estimate: -0.77). The reduction in vegetation height and in resource availability (namely flowers) are the most probable reasons for this important direct effect. Additionally, the mow causes a strong direct mortality of eggs and caterpillars (up to 90% of the individuals) which can induce a reduction of population due to a loss of reproductive potential in the following weeks (Van Klink et al., 2019). These deleterious effects should be more important for specialist species, which depend on the habitat for their entire life cycle, than for species which larval stages do not occur in the meadows, as *Aporia crataegi* which lay its eggs on the hawthorn.

Effect of the survey session

The survey period had an important impact on both butterfly and plant diversity. Butterfly abundance was always higher in the surveys performed in June than the ones in May or July. This observation can be explained by different factors, and namely a higher resource availability with more plants flowering at this period. This also impacted butterfly community composition, which differed in May, June and July as many species emerge in late May-early June, at the peak of the

flowering period (Lafranchis, 2010). The switch in plant community composition between the three sessions did certainly drive butterfly community composition, as species synchronize their adult emergence with the availability of their specific feeding and larval host plants (Navarro-Cano et al., 2015). In turn, the emergence of certain butterfly species could strongly influence the overall abundance, and it was the case for two species, *Maniola jurtina* and *Melanargia galathea*, which were almost absent in May but became predominant in the grasslands in June (60% of the observations).

The survey session also influenced indirectly the importance of late-mown grasslands for the biodiversity. I obtained evidence of a higher plant species richness and butterfly abundance in RF3 grasslands in June, suggesting that late-mown grasslands have a particularly important role for supporting butterflies and plants in their peak activity. Indeed, late-mown plots stay intact until July and thus act as refugee areas for biodiversity when all other grasslands are mown. Both RF1 and RF3 appears particularly important in this context, as non-engaged grasslands are mown in the core of the breeding season (mean mowing date considered to be on the 20th of May).

Effect of meteorological conditions

The meteorological conditions of the summer 2026 were particularly harsh and unprecedented in the region. The spring was the hottest ever recorded in France, with an exceptionally early heat wave in the end of May, followed by the hottest months of June and July ever recorded (Météo-France, 2026). The several heat waves that occurred were particularly early, long and intense, namely the heat wave of 14 days in June. Aside from these very hot temperatures, the summer was also extremely dry, with very rare rain events after mid-May. Thus, in the Jura department, there was a 30% rain deficit on the period from the January 1st to the 10th of July (compared to the average of 1997-2022) (Info-climat, 2026).

These weather conditions were unfavourable for plants and especially for their regrow after the mows and that explains their significantly lower diversity in July. In a few plots, some flowers grew after the mow, maybe due to favourable local conditions (e.g. topography, orientation towards the sun, presence of water nearby), but most grasslands stayed very poor in plants once mown. Indeed, the absence of resources must have affected butterflies, hence their very poor diversity in July, where less than 10 individuals were seen per transect on average. The

meteorological conditions themselves impact butterfly presence, as they adapt their behaviour in case of high temperatures. Above 30°C, butterflies flight activity decrease and they concentrate on cooling activities, by seeking for shade, using abdominal hyperventilation and looking for shelters (Clench, 1966; Hayes et al., 2024). The prolongation of days with temperature above 35°C can bring butterfly to keep a reduced activity on a relatively long period, which could also reduce the fitness of the populations (Hayes et al., 2024). Therefore, it is probable that the meteorological conditions explain for a great part the low abundance of butterflies in all surveys.

Effect of other environmental factors

If I did not find any evidence of an effect of altitude, both land cover and plot size affected plant and butterfly diversity. While I observed only a very weak positive effect of forest cover on plant species richness (effect estimate: 0.006), the presence of both forest and prairie in a 500m radius around the grasslands was negatively correlated with plant abundance, but with a weak effect (-0.04 for both). In fact, such weak or unclear effects of the landscape context on plant diversity are common in other studies (Öster et al., 2007). Plant diversity appears to be influenced more by a very local scale (plot conditions) than by nearby patches. As for butterflies, surprisingly, the piecewise SEM did not highlight any influence of the landscape, while they are usually affected by the habitats at a 2-km radius around the plot due to their dispersal abilities (Öckinger & Smith, 2006).

While a greater plot size usually has a positive influence on plant species richness by increasing the heterogeneity in soil conditions (Öster et al., 2007), I did not record such effect in this study. I sometimes observed a heterogeneity in soil conditions (slope, wet features in some parts) for the largest grasslands, but there was no evidence for any impact on plant richness. As explained by the authors, small samples such as my quadrats might not be sufficient to reveal this relationship. However, I found a positive correlation between plot size and plant abundance, which can be a consequence of an easier colonization of plants in a homogeneous habitat and management type (Öster et al., 2007). On the contrary, there was evidence that a greater plot size negatively affected butterfly abundance (effect estimate: -0.10). This goes against usual observations, as smaller grasslands have greater edge effect and it usually reduces the presence of grassland butterflies (Öckinger & Smith, 2006). This negative correlation could in fact indirectly result from the unfavourable meteorological conditions. Many of the plots were surrounded by hedges, which can serve as refuge during the hottest hours of the day (Dover & Sparks, 2000). By

being closer to the edge in small grasslands, butterflies might have benefited from the shading conditions and the shelter provided by the hedges. A more specific analysis on the presence of hedge around the plot would have been ideal to test this hypothesis.

4.4 – Improving the adequacy of MAECs

Ecological efficiency

Results of this study suggest that many factors others than mow delay do influence grassland biodiversity and that the direct effect of mow could be considered as predominant, especially for butterflies. If this can be partly explained by the meteorological conditions, it might also suggest that the ecological efficiency of late-mow MAECs could be improved.

Regarding grasslands mown from the 16th of June ('RF1'), except from a positive correlation with plant abundance, I did not find much effect of such contract compared to no engagement. Indeed, the fact that half of non-engaged grasslands were mown in similar dates did not help for showing its efficiency. Nonetheless, authors of a large-scale analysis on MAEC efficiency deplore that a 20-days mow delay has very little impact on ecosystems (FPNRF et al., 2020). In this sense, the 45-days delays contracts ('RF3') should be promoted more, as they can have greater positive impacts on grassland biodiversity. Indeed, I found a higher plant diversity in such grasslands, which also supports a higher butterfly diversity, especially in the peak of the flowering season. In fact, late-mow MAECs should not be considered as efficient only for their potential to promote biodiversity but for that they support a greater panel of mowing dates and thus they help maintaining resources available throughout the summer. In this sense, both RF1 and RF3, as well as the new RF2 measure (mow from the 25th of June), are of equal interest, and a balanced number of grasslands engaged in these three measures should be aimed.

Indeed, apart from the mow delay, MAECs are ecologically valuable for their constraints on grazing and fertilization rates. However, these conditions are regularly changed with the PAECs, which might limit their efficiency as effects of such limitations arise in the long-term (Cordier et al., 2025). A higher stability in these constraints should be aimed for a better efficiency and for a better understanding of the MAEC conditions for the farmers (FPNRF et al., 2020).

Adequacy for farmers

As MAECs are voluntary measures, they need to be attractive for farmers, especially since they need to engage for a period of five years. Engaging in late-mow contracts for such period might be complicated for farmers as their yields strongly depend on the meteorological conditions of the year. Farmers already deplore the fixed mowing date of the MAECs and suggest that the date of first mow should be defined annually (FPNRF et al., 2020). Indeed, the constancy in the mow date can appear hardly compatible with unsure meteorological conditions, especially since the droughts and heat waves will become more frequent in the upcoming years (IPCC, 2023). However, changing contract conditions every year seems unrealistic to apply, and might reduce the ecological benefits of the mow delays.

The extreme climatic events appear particularly detrimental for farmers engaged in RF3 contracts, as the repetitive droughts can cause the grass to dry earlier in the season and thus to lower the yields prematurely. This probably occurred during the survey period, as all non-engaged grasslands had been already mown in mid-June, suggesting that there was no benefit to wait for a later mow. Indeed, there is a clearly lower number of grasslands engaged in RF3 than RF1 contracts, which suggests that they are less attractive to farmers. The RF2 measure (35-days delay), newly implemented in the actual PAEC, appears as an interesting compromise, as it might have higher ecological interest than RF1 grasslands, but is less constraining than a 45-days delay. Therefore, I expect some farmers to switch from a 45-days to a 35-days delay in the upcoming PAECs, even if the ideal would be to increase the number of both contracts to support diversified mowing dates and thereby ensure the presence of unmown grasslands all summer long. In this aim, reevaluating the shortfall due to the mow delay and increasing the subventions for RF3 and RF2 could be a way to make these measures more attractive.

MAECs and other agroecological practices

In addition to improving the MAECs efficiency, a combination of the mow delay with other agroecological practices could increase the grassland's ability to preserve biodiversity. Batáry et al. (2015) suggest combining in-production schemes, as the mow delay, with out-of-production schemes that concern field boundaries or wildflower strips. Indeed, maintaining an unmown strip on the edge of the grassland can provide crucial resources for butterflies and all pollinators when the grassland has been mown (Cordier et al., 2025). Additionally, the presence of hedges along the grassland support plants and butterflies as it increases the diversity of conditions, namely by

providing shade and a protection against wind. Moreover, hedges can also be used as larval foodplant for some butterfly species (e.g. *Aporia crataegi* using the hawthorn) and can act as ecological corridors between high-quality meadows (Van Klink et al., 2019). If more constraints could reduce the attractivity of MAECs for farmers, adding for instance the preservation of a wildflower strip in the late-mow MAEC conditions could improve their efficiency for preserving butterflies and other pollinators which depend on floral resources for their survival.

5- CONCLUSION

While hay meadows of the Natura 2000 site 'Petite Montagne du Jura' are ecosystems with high ecological value, they are threatened by agriculture intensification, as all semi-natural grasslands. By conditioning mowing practices, fertilization and grazing intensities in exchange for subventions, late-mow agri-environmental measures (MAECs) appear as an efficient tool to support agroecological practices valuable for both farmers and grassland biodiversity. Able to promote plant diversity, late-mow MAECs can thereby ensure a greater forage quality and increase the yields; but they also provide a higher availability of resources for insects such as butterflies. For them, the benefits of these MAECs lie namely in the heterogeneity of mowing dates that is supported, as it enables to provide a landscape with continuous resource availability and helps compensating the direct detrimental effects of mows on the populations.

The study was conducted in a particularly harsh meteorological context, with an unprecedented number and intensity of droughts and heat waves that strongly affected plant and butterfly populations. The fact that such extreme meteorological events are predicted to become increasingly common in the upcoming years (IPCC, 2023) appears highly concerning for farmland biodiversity, which is already threatened by intensive agricultural practices. The changing climatic conditions appear also challenging for farmers' activities as it engenders less favourable farming conditions and more meteorological uncertainties. This context could make it harder to engage for five-years contracts such as the MAECs. Nonetheless, the implementation of MAECs and other agroecological practices appears crucial for more sustainable agricultural practices that are also compatible with the preservation of biodiversity.

6- SWOT ANALYSIS

STRENGTHS	WEAKNESSES
• My previous internship experience helped me for the methodology, the diversity and community analyses and I could reuse some methods I learned back then • I had already great knowledge on butterfly ecology and skills in butterfly identification of common species, which helped me to quickly learn the identification criteria of all species • Similarly, I was already able to recognize some grassland plants and that helped me to learn the other species	• I sometimes struggled for plant determination and could not always identify them to species level • I took much time to choose a protocol for plant inventories as I was doubting on the choice of categories (only flowering or host plants, all forbs, …) and the counting method • I contacted the farmers a bit late and since I struggled to reach them, I could not ask for all information I planned to
OPPORTUNITIES	**THREATS**
• I had the time to practice butterfly and plant determination both theoretically and on the field prior to inventories, and I had great field guides and identification keys at my disposal • My university tutor was available and helped me much for the protocol choice and the data analysis • The field sessions took less time than expected thus I could write the report on the go	• I changed supervisor in the middle of the internship, which caused a period of uncertainty and difficulties. Moreover, the replacement was new to the region, to the context and was at the start of his professional career • The methodological help from the supervisors was limited regarding scientifical approach and data analysis • The meteorological conditions (droughts, heat waves) were not ideal to record effects of management conditions on the communities

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8- APPENDICES

Appendix 1 | Summary of the conditions of late-mow MAEC measures for mesophile mown grasslands, across the different PAEC instructed in the Natura 2000 area "Petite Montagne du Jura" since 2007 (DDT39, 2023). Maximal fertilization rates are expressed in units per hectares and per year of nitrogen (N), phosphate (P) and potassium (K). RF2 was not considered for this study since it is a new measure.

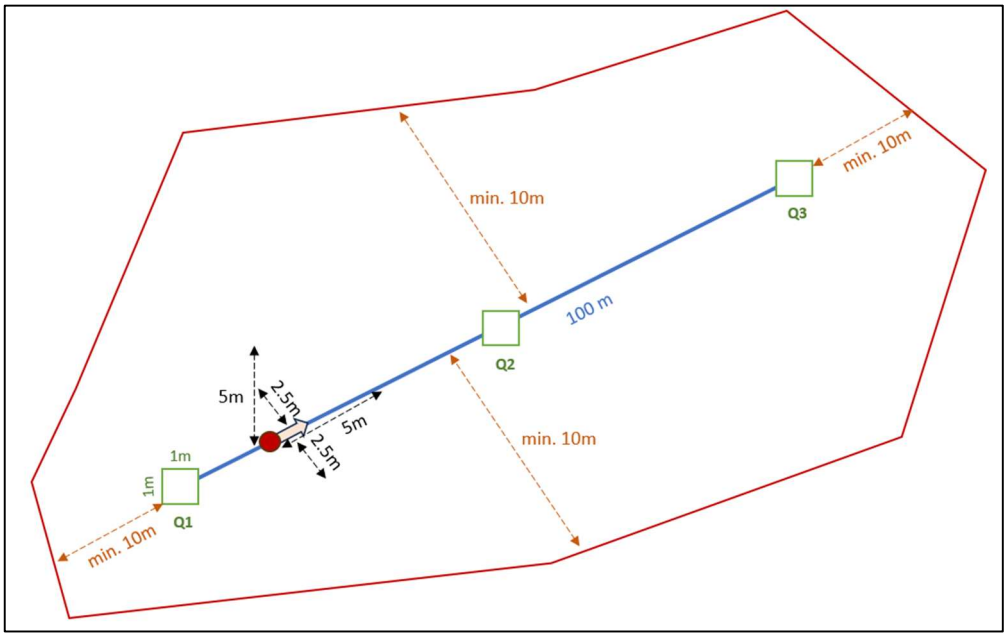
Category	Measure code	PAEC	Mowing date	Maximal fertilization rates	Maximal grazing intensity
'RF1'	ESP02	2023-2027	June 15th	Zero P/K input 20 U/ha of N	-
	PF01	2021 & 2022 2015-2020	June 16th	*No limit*	0.8 UGB/ha/year
	PF03	2021 & 2022 2015-2020	June 16th	Zero N/P/K input	0.8 UGB/ha/year
	PF1	2007-2014	June 16th	80 U/ha of N/P/K	-
'RF2'	*ESP03*	*2023-2027*	*June 24th*	*Zero N/P/K input*	-
'RF3'	ESP04	2023-2027	July 4th	Zero P/K input 1 N input of 40 U/ha	-
	PF02	2021 & 2022 2015-2020	July 2nd	-	0.8 UGB/ha/year
	PF04	2021 & 2022	July 2nd	Zero N/P/K input	0.8 UGB/ha/year
	PF2	2007-2014	July 2nd	80 U/ha of N/P/K	-
'NE'	-	-	-	-	-
			(average: May 20th)		

Appendix 2 | Description of mowed grasslands in the Natura 2000 area "Petite Montagne du Jura" (PMJ) according to Voirin & Boucard (2024). Characteristic species of each habitat are given as examples, refer to Voirin & Boucard (2024) for an exhaustive list. The surface covered by each habitat in the PMJ site is given in hectares, according to Boucard & Voirin (2011). The *Galio veri-Trifolietum repentis* habitat (highlighted in bold) was chosen for this study for its ecological importance and since it is the most frequent.

Habitat name	Natura 2000 code	Corine Land Cover code	Characteristic species	Surface in PMJ (ha)
Mesophile hay meadow *Colchico autumnalis-Festucetum pratensis* J. Duvign. 1958.	6510-4	38.22	*Colchicum autumnale* *Schedonorus pratensis* *Tragopon pratensis*	81.99
Mesophile hay meadow ***Galio veri-Trifolietum repentis*** **Sougnez 1957**	**6510-6**	**38.22**	***Tragopon pratensis*** ***Crepis biennis*** ***Onobrychis viciifolia***	**773.97**
Eutrophic mesophile hay meadow *Heracleo sphondylii-Brometum mollis* B. Foucault 1989 *ex* 2008	6510-7	38.22	*Bromus hordeaceus* *Poa trivialis* *Rumex obtusifolius*	223.06
Mesophile calcicole grassland *Mesobrometum erecti* W. Koch 1926	6210-15	34.322B	*Thymus* gr. *pulegioides* *Salvia pratensis* *Onobrychis viciifolia*	436.71

Appendix 3 | List of the 24 surveyed grasslands and their characteristics: their attributed pairing, the MAEC contract in which they are engaged (NE: non-engaged, RF1 and RF3: engaged in a mow delay to respectively the 16th of June and the 4th of July), their estimated mow date, the numbers of PAEC for which they are engaged and whether it is fertilized (Y: yes, N: no), the plot altitude (in meters), surface (in hectares) and estimated landscape openness (O: open, SO: semi-open and C: close).

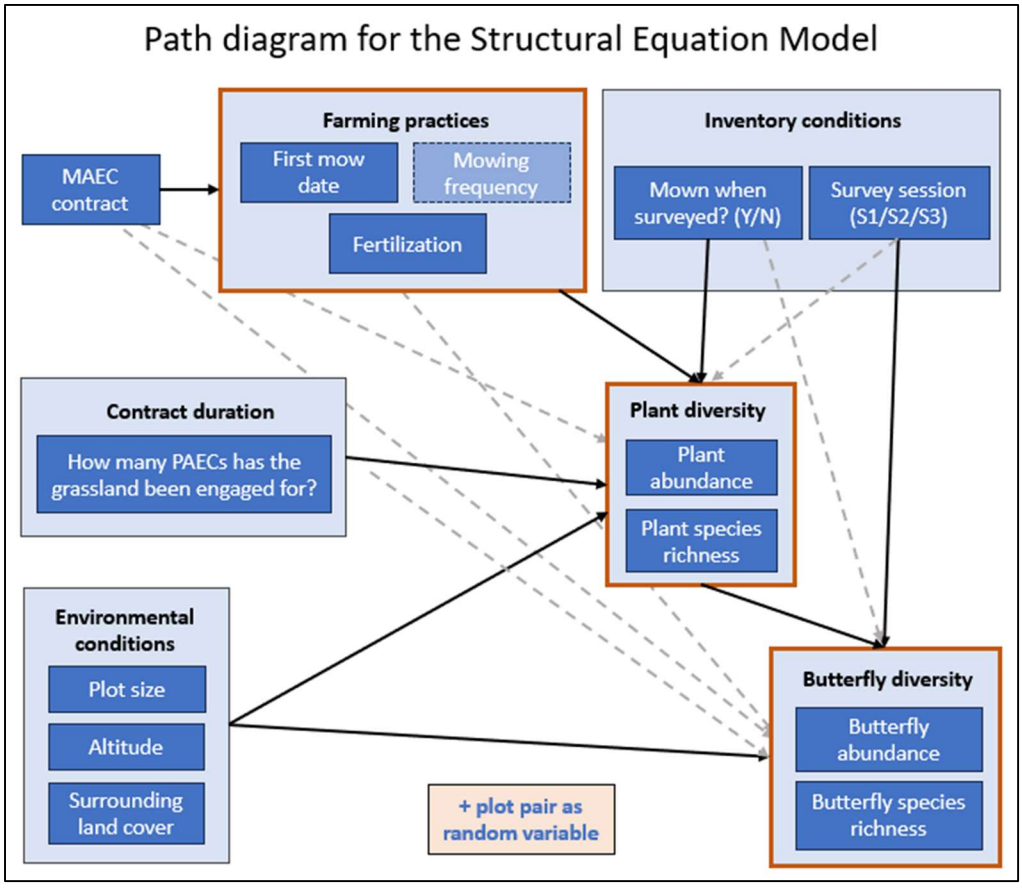
Site ID	Pair	Contract	Mow date	Number of PAECs	Fertilization	Altitude (m)	Surface (ha)	Landscape
ARI_1	P1	RF1	17/06	4	Y	440	1.56	SO
ARI_7	P1	NE	15/06	-	Y	400	1.16	O
LAB_1	P2	RF1	17/06	4	N	520	2.89	C
LAB_5	P2	NE	17/06	-	N	525	1.99	C
VOS_5	P3	RF1	17/06	4	N	480	0.47	SO
VOS_10	P3	NE	22/05	-	Y	490	0.93	SO
VES_9	P4	RF1	16/06	2	N	620	2.23	SO
VES_8	P4	NE	15/06	-	N	570	2.66	O
VES_10	P5	RF1	16/06	3	N	655	1.02	SO
VES_11	P5	NE	15/06	-	N	630	1.66	SO
ARI_3	P6	RF3	04/07	4	N	725	1.67	C
STH_5	P6	NE	20/05	-	Y	690	4.66	C
ARO_3	P7	RF3	04/07	4	N	520	3.04	O
CHO_2	P7	NE	19/05	-	Y	490	6.02	O
VAL_1	P8	RF3	12/07	4	N	660	1.52	SO
VOS_11	P8	NE	15/06	-	N	620	1.35	SO
VES_1	P9	RF3	04/07	3	N	670	5.37	C
VES_12	P9	NE	15/06	-	N	680	0.63	C
VES_2	P10	RF3	16/06	2	N	640	0.3	SO
VES_7	P10	NE	25/05	-	N	560	0.97	O
ARI_2	P11	RF1	16/06	3	Y	425	2.27	O
ARI_11	P11	NE	16/06	-	Y	400	3.23	O
VOS_4	P12	RF1	16/06	4	N	505	0.71	SO
VOS_12	P12	NE	28/05	-	N	560	1.2	SO



Appendix 4 | Schematic representation of the plant and butterfly inventory methods implemented for this study, based on common protocols for butterfly inventories (Pollard, 1977; Manil & Henry, 2007; Sevilleja et al., 2019). The 100-m transect (blue line), set in the middle of the surveyed plot (red shape), at a minimal distance to the edge of 10m, was walked for about 10 minutes at a constant speed to record all butterflies observed in an imaginary box of $5m^3$. Plant abundance was recorded in three vegetation quadrats of $1m^2$ set in the beginning, the middle and the end of the transect (green squares).

Appendix 5 | Beaufort scale for wind speed measurement, following RMetS (s.d.), used to estimate wind speed. Surveys were not performed in case of wind speed greater than 30km, i.e. a Beaufort number of 5 or more.

Beaufort number	Wind speed (km/h)	Description	Effects on vegetation
0	<1	Calm	Immobility
1	1 - 5	Light air	Immobility
2	6 - 11	Light breeze	Leaves rustle
3	12 - 19	Gentle breeze	Small twigs in constant motion
4	20 – 28	Moderate breeze	Small branches moved
5	29 - 38	Fresh breeze	Small trees in leaf start to sway
6	39 - 49	Strong breeze	Large branches in motion
7	50 - 61	Moderate gale	Whole trees in motion



Appendix 6 | Path diagram used to draw the equations for the piecewise Structural Equation Model. The response variables (blue boxes included in brown frames) were tested with different GLMMs including all predictors (blue boxes in black frames), following the predicted relationships (black arrows). Dashed arrows represent the potentially missing relationships, added to the model if not significant without. The mowing frequency (transparent box) was not included in the final model as all grasslands were mown once only.

Appendix 7 | List of the 50 pseudospecies of butterflies recorded during the survey sessions and their characteristics: Family, Host plant specificity (HP, oligo G: oligophagous on a genus, oligo F: oligophagous on a family, poly: polyphagous), Ant Association (AnA, Y: yes, N: no), Average flight period (FP, in months), Voltinism i.e. the mean number of generations per year (V) and Wingspan, i.e. the average wing length (WS, in millimetres), as well as their red list status at national level. The abundance of each species is given for each survey session (S1, S2, S3). Species highlighted in bold are dry grassland specialists. References for species traits are Moureau (2015), Middleton-Welling et al. (2020) and Itrac-Bruneau & Mora (2026).

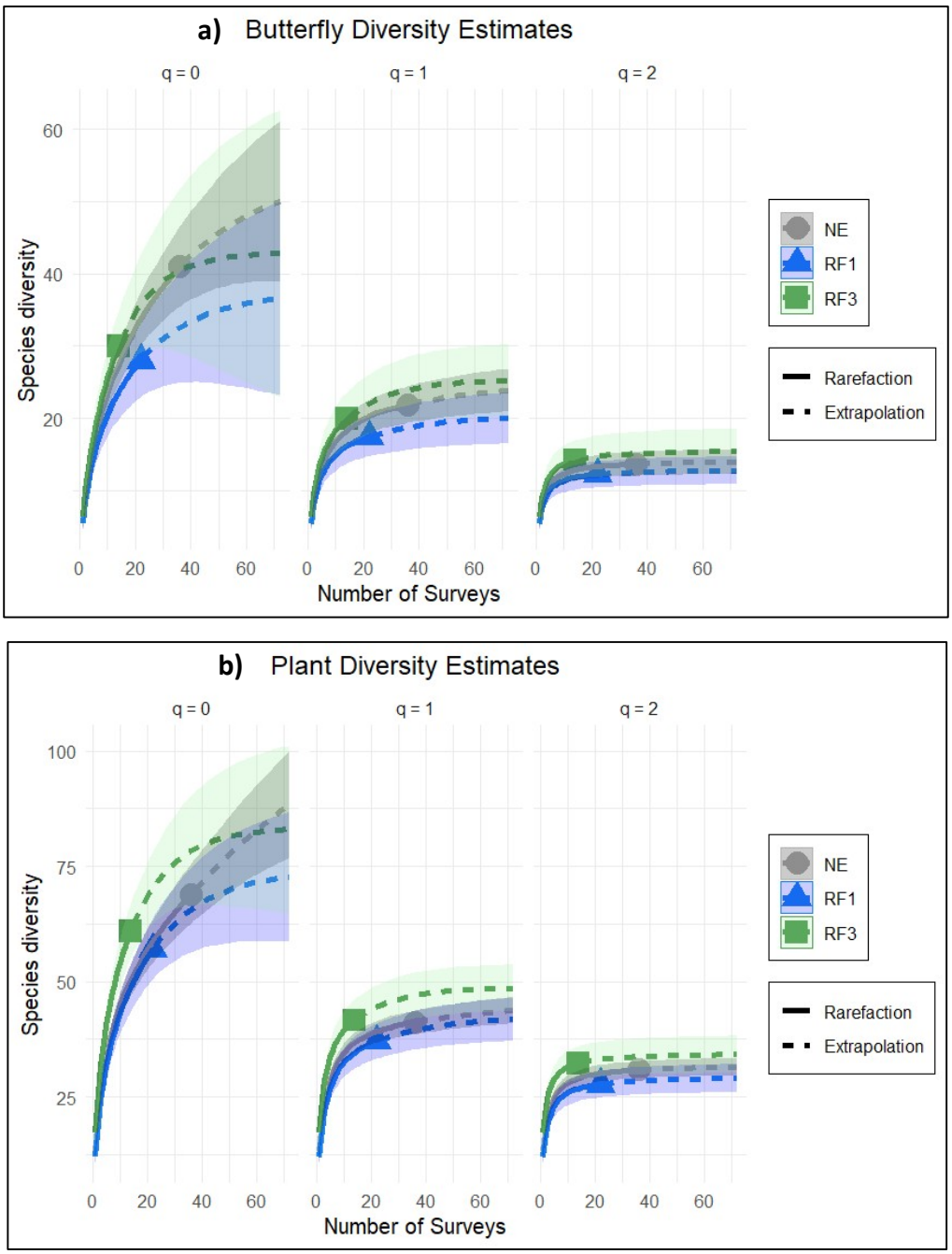
Latin name	Family	Abundance				HP	AnA	FP	V	WS	RL status
		S1	S2	S3	Total						
Aglais urticae	*Nymphalidae*	4	0	0	4	oligo G	N	7	2	46.5	LC
Aporia crataegi	*Pieridae*	17	45	0	62	oligo F	N	3.5	1	60	LC
Aricia agestis	*Lycaenidae*	1	0	3	4	poly	Y	7	2	25	LC
Azuré sp.	*Lycaenidae*	4	0	4	8	-	Y	-	-	28	-
Boloria dia	*Nymphalidae*	0	5	2	7	oligo G	N	5.5	2.5	33	LC
Brenthis daphne	*Nymphalidae*	0	0	1	1	oligo G	N	3.5	1	47	LC
Brenthis ino	*Nymphalidae*	0	1	0	1	oligo F	N	2.5	1	35.5	NT
Brintesia circe	*Nymphalidae*	0	3	4	7	oligo F	N	4.5	1	73	LC
Carterocephalus palaemon	*Hesperidae*	1	0	0	1	oligo F	N	2.5	1	26.5	NT
Coenonympha pamphilus	*Satyridae*	67	63	19	149	oligo F	N	7	2	27	LC
Colias crocea	*Pieridae*	0	0	3	3	oligo F	N	7	3	46.5	LC
Cyaniris semiargus	*Lycaenidae*	17	2	20	39	oligo F	Y	6	1.5	28	LC
Erynnis tages	*Hesperidae*	0	0	10	10	poly	N	4	1.5	30	LC
Euphydryas aurinia	*Nymphalidae*	3	0	0	3	poly	N	3.5	1	35	VU
Gonepteryx rhamni	*Pieridae*	4	0	4	8	oligo F	N	8	1	58	LC
Hamearis lucina	*Riodinidae*	1	0	0	1	oligo G	Y	6	1	31.5	NT
Hesperidae sp.	*Hesperidae*	3	0	0	3	-	N	-	-	25	-
Iphiclides podalirius	*Papilionidae*	0	0	9	9	oligo F	N	6	2	73.5	LC
Lasiommata megera	*Nymphalidae*	0	0	1	1	oligo F	N	6.5	2	42.5	LC
Leptidea sinapis/reali	*Pieridae*	0	1	1	2	oligo F	N	6	2	37	DD
Lycaena phlaeas	*Lycaenidae*	2	0	0	2	oligo G	N	9.5	2	25.5	LC
Lycaena tityrus	*Lycaenidae*	4	0	1	5	poly	N	7	2	30	LC
Lycaenidae sp.	*Lycaenidae*	1	1	2	4	-	-	-	-	28	-
Lysandra bellargus	*Lycaenidae*	1	0	0	1	oligo F	Y	7	2	31	LC
Maniola jurtina	*Satyridae*	3	112	13	128	oligo F	N	5	1	41	LC
Melanargia galathea	*Satyridae*	0	147	24	171	oligo F	N	3.5	1	47.5	LC
Melitaea athalia/ celadussa	*Nymphalidae*	7	12	0	19	poly	N	3	1.5	36	DD
Melitaea cinxia	*Nymphalidae*	5	0	0	5	oligo G	N	4	1.5	36	LC
Melitaea didyma	*Nymphalidae*	1	0	0	1	poly	N	5.5	2	37	LC
Melitaea parthenoides	*Nymphalidae*	58	3	0	61	oligo G	N	3	1.5	33	LC
Melitaea phoebe	*Nymphalidae*	1	0	0	1	poly	N	4.5	1.5	44.5	LC
Melitée sp.	*Nymphalidae*	25	2	0	27	-	N	-	-	36	-
Nymphalidae sp.	*Nymphalidae*	2	4	1	7	-	N	-	-	45	-
Papilio machaon	*Papilionidae*	1	0	0	1	poly	N	6.5	2	72.5	LC
Pieris brassicae	*Pieridae*	0	0	1	1	oligo F	N	7	2.5	5	LC
Pieris rapae	*Pieridae*	0	2	0	2	poly	N	9.5	2	44.5	LC
Pieridae sp.	*Pieridae*	0	1	0	1	-	N	-	-	50	-
Plebejus sp.	*Lycaenidae*	2	0	4	6	poly	Y	4	1.5	26	LC
Polyommatus icarus	*Lycaenidae*	4	2	27	33	oligo F	Y	7	2	29	LC
Pyrgus armoricanus	*Hesperidae*	2	0	0	2	poly	N	5.5	1.5	26	LC
Pyrgus malvae/ malvoides	*Hesperidae*	1	1	0	2	oligo F	N	3.5	1.5	22.5	NT

Pyrgus sp.	*Hesperidae*	1	0	0	1	-	N	-	-	24	-
Pyronia tithonus	*Nymphalidae*	0	0	4	4	oligo F	N	3.5	1	36	LC
Speyeria aglaja	*Nymphalidae*	0	1	0	1	oligo G	N	3.5	1	52	LC
Spialia sertorius	*Hesperidae*	0	1	0	1	oligo G	N	7	2	24	LC
Thymelicus lineola	*Hesperidae*	0	3	1	4	poly	N	3.5	1	25	LC
Thymelicus sp.	*Hesperidae*	0	6	0	6	-	N	4	1	25.5	LC
Thymelicus sylvestris	*Hesperidae*	0	5	2	7	oligo F	N	4.5	1	26.5	LC
Vanessa atalanta	*Nymphalidae*	0	1	0	1	oligo F	N	8.5	2	56	LC
Vanessa cardui	*Nymphalidae*	1	8	1	10	poly	N	8	2	53.5	LC
TOTAL		**244**	**432**	**162**	**838**						

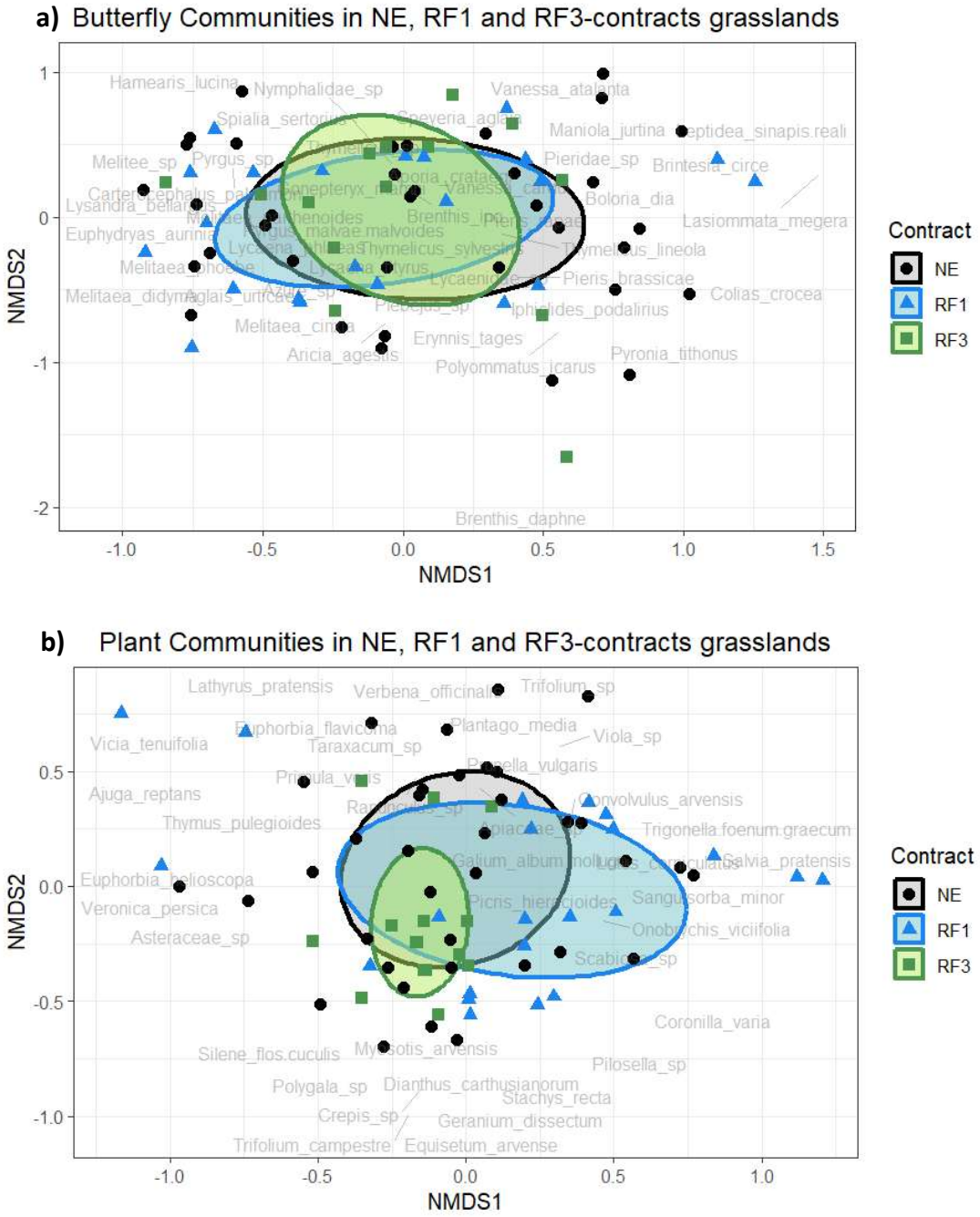
Appendix 8 | List of the 79 pseudospecies of plants recorded during the inventory sessions and their characteristics: Family, source of nectar for butterflies (NP) and potential host plant for butterflies (HP). The abundance of each species is given for each survey session (S1, S2, S3). Species highlighted in bold are the ones characteristics of the *Galio veri – Trifolietum repentis* habitat. References for habitat specialism and traits are Clarke (2024), Voirin & Boucard (2024) and Lanuza et al. (2025).

Latin name	Family	Abundance				NP	HP
		S1	S2	S3	Total		
Achillea sp.	*Asteraceae*	15	20	15	50	Y	N
Ajuga reptans	*Lamiaceae*	86	26	17	129	Y	N
Anthyllis vulneraria	*Fabaceae*	43	7	3	53	Y	Y
Apiaceae sp.	*Apiaceae*	26	68	0	94	Y	Y
Asteraceae sp.	*Asteraceae*	0	12	0	12	Y	-
Bellis perennis	*Asteraceae*	16	32	0	48	Y	N
Betonica officinalis	*Lamiaceae*	2	7	10	19	Y	N
Campanula glomerata	*Campanulaceae*	25	16	0	41	Y	N
Centaurea jacea	*Asteraceae*	249	365	186	800	Y	Y
Cerastium arvense	*Caryophyllaceae*	23	0	0	23	N	N
Cerastium fontanum	*Caryophyllaceae*	111	62	0	173	N	N
Cirsium arvense	*Asteraceae*	2	12	30	44	Y	Y
Colchico autumnalis	*Liliaceae*	0	2	0	2	N	N
Convolvulus arvensis	*Convolvulaceae*	0	15	33	48	Y	N
Coronilla varia	*Fabaceae*	0	0	11	11	Y	Y
Crepis biennis	*Asteraceae*	19	0	0	19	Y	N
Crepis sp.	*Asteraceae*	10	1	1	12	Y	N
Daucus carota	*Apiaceae*	12	65	77	154	Y	Y
Dianthus carthusianorum	*Caryophyllaceae*	12	4	0	16	Y	N
Equisetum arvense	*Equisetaceae*	20	0	0	20	N	N
Euphorbia flavicoma	*Euphorbiaceae*	0	57	35	92	N	N
Euphorbia helioscopa	*Euphorbiaceae*	80	14	5	99	N	N
Galium album	*Rubiaceae*	258	385	249	892	Y	N
Galium boreale	*Rubiaceae*	0	15	30	45	N	N
Galium verum	*Rubiaceae*	470	45	5	520	Y	N
Geranium dissectum	*Geraniaceae*	23	0	0	23	Y	Y
Hippocrepis comosa	*Fabaceae*	0	40	0	40	N	Y
Knautia arvensis	*Dipsacaceae*	199	118	75	392	Y	Y
Knautia arvernensis	*Dipsacaceae*	69	0	10	79	Y	N
Lathyrus pratensis	*Fabaceae*	0	53	8	61	Y	Y
Leucanthemum vulgare	*Asteraceae*	131	118	43	292	Y	N
Lotus corniculatus	*Fabaceae*	395	369	456	1220	Y	Y
Lotus tenuis	*Fabaceae*	0	0	10	10	N	N
Medicago lupulina	*Fabaceae*	625	141	60	826	Y	Y

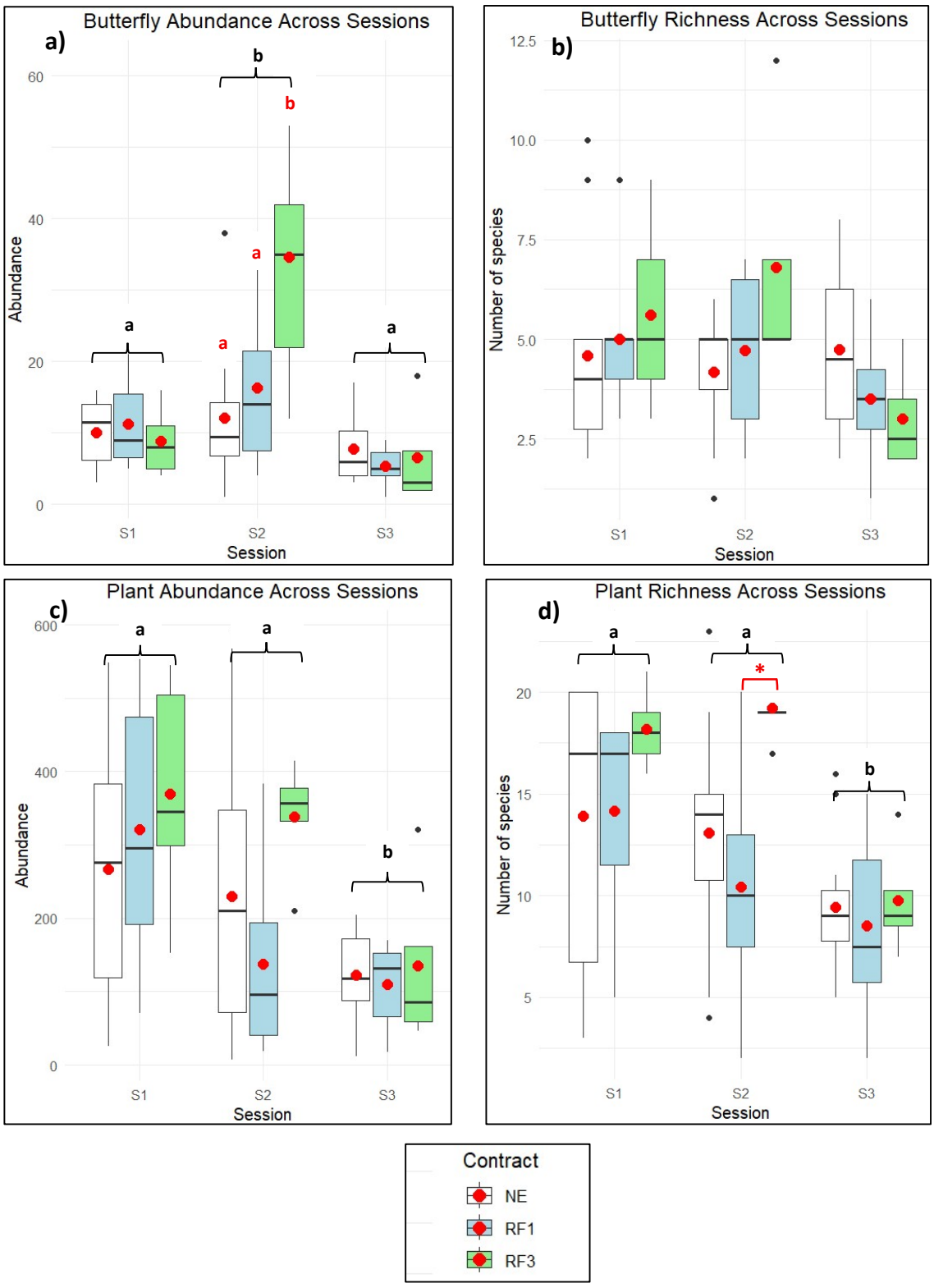
Myosotis arvensis	*Boraginaceae*	184	4	11	199	Y	N
Onobrychis viciifolia	*Fabaceae*	55	12	20	87	Y	Y
Ononis spinosa	*Fabaceae*	1	25	2	28	N	Y
Orobanche minor	*Orobanchaceae*	0	6	0	6	N	N
Phyteuma orbicularia	*Campanulaceae*	0	22	0	22	Y	N
Picris hieracioides	*Asteraceae*	10	0	12	22	Y	N
Pilosella sp.	*Asteraceae*	3	0	0	3	Y	N
Pimpinella saxifraga	*Apiaceae*	0	8	0	8	N	Y
Plantago lanceolata	*Plantaginaceae*	633	392	162	1187	N	Y
Plantago major	*Plantaginaceae*	13	7	0	20	N	Y
Plantago media	*Plantaginaceae*	0	5	2	7	N	Y
Polygala sp.	*Polygalaceae*	10	0	0	10	Y	N
Potentilla erecta	*Rosaceae*	5	15	0	20	Y	Y
Primula veris	*Primulaceae*	21	13	0	34	Y	Y
Prunella vulgaris	*Lamiaceae*	5	112	74	191	Y	N
Ranunculus acris	*Ranunculaceae*	387	130	25	542	Y	N
Ranunculus bulbosus	*Ranunculaceae*	294	0	0	294	Y	N
Ranunculus sp.	*Ranunculaceae*	23	167	131	321	Y	N
Rhinanthus alectorolophus	*Scrophulariaceae*	315	183	0	498	N	Y
Rumex acetosa	*Polygonaceae*	110	152	29	291	N	Y
Salvia pratensis	*Lamiaceae*	91	62	151	304	Y	N
Sanguisorba minor	*Rosaceae*	414	429	462	1305	N	Y
Scabiosa sp.	*Dipsacaceae*	0	40	12	52	Y	Y
Senecio sp.	*Asteraceae*	1	1	4	6	Y	N
Sherardia arvensis	*Rubiaceae*	21	35	0	56	N	N
Silene flos-cuculis	*Caryophyllaceae*	8	0	0	8	Y	N
Stachys recta	*Lamiaceae*	10	0	0	10	N	Y
Succisa pratensis	*Dipsacaceae*	4	0	8	12	Y	Y
Taraxacum sp.	*Asteraceae*	72	139	24	235	Y	N
Thymus pulegioides	*Lamiaceae*	122	98	10	230	Y	Y
Tragopon pratensis	*Asteraceae*	36	15	6	57	Y	N
Trifolium campestre	*Fabaceae*	10	0	0	10	Y	Y
Trifolium pratense	*Fabaceae*	868	433	106	1407	Y	Y
Trifolium repens	*Fabaceae*	88	500	40	628	Y	Y
Trifolium sp.	*Fabaceae*	120	114	155	389	Y	Y
Trigonella foenum-graecum	*Fabaceae*	0	0	5	5	N	N
Verbena officinalis	*Verbenaceae*	0	0	10	10	Y	N
Veronica arvensis	*Scrophulariaceae*	16	13	0	29	Y	Y
Veronica chamaedrys	*Scrophulariaceae*	186	126	30	342	Y	Y
Veronica persica	*Scrophulariaceae*	0	1	0	1	N	Y
Veronica sp.	*Scrophulariaceae*	0	12	0	12	-	Y
Vicia cracca	*Fabaceae*	0	30	14	44	Y	Y
Vicia sativa	*Fabaceae*	233	43	0	276	Y	N
Vicia tenuifolia	*Fabaceae*	0	0	13	13	N	Y
Viola sp.	*Violaceae*	0	1	0	1	N	Y
TOTAL		**7290**	**5414**	**2887**	**15,591**		



Appendix 9 | Standardized estimations of butterfly and plant diversity obtained by rarefaction-extrapolation methods (iNEXT), for the different MAEC contracts (NE: non-engaged, RF1 and RF3: engaged respectively in 25-days and 45-days mow delays). Hill numbers (q=0: species richness, q=1: Shannon index, q=3: Simpson's index are estimated for double the highest sample size (n=72).



Appendix 10 | Non-metric multidimensional scaling representing butterfly (a) and plant (b) communities in the grasslands of different contract types (NE: non-engaged, RF1 and RF3: engaged respectively in 25-days and 45-days mow delays). Both communities were represented in three dimensions (k=3) with a stress of 0.15 for butterflies and 0.19 for plants. There was no evidence for a difference in community composition for neither butterflies nor plants (PERMANOVA, respectively p=0.907 and p=0.691).



Appendix 11 | Variation of butterfly and plant diversity in the surveyed grasslands according to the survey session (S1: May, S2: June, S3: July) and the MAEC contract (NE: non-engaged, RF1 and RF3: engaged respectively in 25-days and 45-days mow delays). Boxplots represent a) butterfly abundance across sessions, with a significantly higher abundance in RF3 grasslands in June sessions (ANOVA, p=0.01); b) butterfly species richness across sessions; c) plant abundance across sessions; d) plant species richness across sessions, with a significantly higher richness in RF3 grasslands than RF1 grasslands in June session (ANOVA, p=0.02).

Abstract: Hay meadows are rich semi-natural ecosystems of important agricultural and ecological values. However, since few decades, changes in agricultural practices lead to their abandonment or to the intensification of their use, thereby threatening their rich biodiversity. By funding more extensive practices, late mow agri-environmental measures (MAECs) appear as promising tools to preserve hay meadows. However, their efficiency for preserving biodiversity remains unsure. This study evaluates the effect of MAECs on grassland communities of the Natura 2000 site "Petite Montagne du Jura". Butterflies and plant were surveyed thanks to 100-m long transects and 1m² quadrats implemented in 24 grasslands, engaged or not in 25-days and 45-days mow delays. Diversity and community analyses revealed a higher plant diversity in the grasslands mown with a 45-days delay, which benefits both farmers and grassland biodiversity. As for butterflies, their diversity was globally low in all grasslands and they seemed rather impacted by the direct effect of mows and the intense droughts that occurred during the survey periods, which reduced the availability of resources. While late-mow contracts do not evidently promote butterfly diversity, they support heterogeneity in the mowing dates that can only benefit them by enabling a continuous access to plant resources throughout the summer. With a better stability in conditions, a greater attractivity for farmers and a combination with other agroecological measures, the efficiency of late-mow MAECs could be enhanced to preserve even more the ecological richness of hay meadows.

Key words: agri-environmental measures – late mow – grasslands – biodiversity

Résumé : Les prairies de fauches sont des écosystèmes semi-naturels de grandes valeurs agricole et écologique. Cependant, depuis plusieurs décennies, les changements de pratiques agricoles amènent à abandonner ou exploiter plus intensivement ces habitats, menaçant fortement leur riche biodiversité. En subventionnant des pratiques plus extensives, les mesures agro-environnementales (MAEC) de fauche tardive semblent être un outil prometteur pour préserver les prairies de fauche. Leur efficacité pour préserver la biodiversité reste toutefois incertaine. Cette étude cherche à évaluer les effets des MAECs sur la biodiversité des prairies au sein du site Natura 2000 « Petite Montagne du Jura ». Les plantes et papillons de jour ont été inventoriés dans 24 prairies, engagées ou non en retard de fauche de 25 et 45 jours, grâce à des transects de 100-m et des quadrats de 1m². Les analyses de diversité et de communautés ont révélé une plus grande diversité de plantes dans les prairies fauchées avec un retard de 45 jours, ce qui profite à la fois aux agriculteurs et à la biodiversité des prairies. Quant aux papillons, leur diversité était globalement faible dans toutes les prairies et ils semblent plutôt avoir été impactés par les effets directs de la fauche et des fortes sécheresses de la saison, réduisant la disponibilité de leurs ressources. Ainsi, si les contrats de fauche tardive n'augmentent pas de façon évidente la diversité de papillons, ils encouragent une hétérogénéité des dates de fauche qui ne peut que leur profiter car elle permet un accès continu aux ressources végétales durant l'été. Avec une meilleure stabilité dans les conditions, un plus grand attrait pour les agriculteurs et en les combinant avec d'autres mesures agroécologiques, l'efficacité des MAECs retard de fauche pourrait être améliorée pour préserver encore mieux la richesse écologique des prairies de fauche.

Mots clés : mesures agro-environnementales – fauche tardive – prairies – biodiversité