Designing tomorrow's farmland: alternative mowing regimes for promoting biodiversity in extensively managed meadowland

Inauguraldissertation

der Philosophisch-naturwissenschaftlichen Fakultät

der Universität Bern

vorgelegt von

Pierrick Buri

von Pampigny (VD)

Leiter der Arbeit

Prof. Dr. R. Arlettaz
Conservation Biology, Institut für Ökologie und Evolution, Universität Bern

Dr. Jean-Yves Humbert
Conservation Biology, Institut für Ökologie und Evolution, Universität Bern

Designing tomorrow's farmland: alternative mowing regimes for promoting biodiversity in extensively managed meadowland

Inauguraldissertation

der Philosophisch-naturwissenschaftlichen Fakultät

der Universität Bern

vorgelegt von

Pierrick Buri

von Pampigny (VD)

Leiter der Arbeit

Prof. Dr. R. Arlettaz
Conservation Biology, Institut für Ökologie und Evolution, Universität Bern

Dr. Jean-Yves Humbert
Conservation Biology, Institut für Ökologie und Evolution, Universität Bern

Von der Philosophisch-naturwissenschaftlichen Fakultät angenommen.

Bern, 29. Oktober 2013

Der Dekan
Prof. Dr. Silvio Decurtins

Content

Abstract

Semi-natural grasslands are widely recognized for their high ecological value and count among the most species-rich habitats in Europe. Yet, in the second half of the 20th century, traditional farming has been progressively replaced by more intensive management and semi-natural grasslands have been systematically converted into arable lands, improved (i.e. intensified), or simply abandoned. As a remedy, agri-environment schemes (AES) have been introduced, yet these schemes could neither halt nor reverse the trend towards conversion, intensification or abandonment. Maintaining and/or restoring semi-natural grasslands is a top priority, but nevertheless represents a real conservation challenge, especially regarding their invertebrate assemblages.

This PhD thesis investigated, at the field scale and through a fully randomized experimental block design, the effects of four different mowing regimes on the biodiversity of extensively-managed meadows. The main aim was to identify mowing regime(s) that could best improve the effectiveness, regarding biodiversity conservation, of current AES grasslands. The four investigated mowing regimes were; 1) mowing regime according to the Swiss AES prescriptions for extensively managed hay meadows, i.e. first cut not before 15 June (control meadows, hereafter C-meadows); 2) first cut not before 15 July (delayed treatment, D-meadows); 3) first cut not before 15 June and second cut not earlier than 8 weeks after the first cut (8W-meadows); and 4) refuge left uncut on 10-20% of the meadow area (R-meadows). These mowing treatments were applied during three years (2010 to 2012), to evaluate direct (after the mow) and cumulative (carry-over from one year to the next) effects. To get a thorough appraisal of the different managements, responses of primary and secondary consumers, as well as pollinators were considered: Auchenorrhyncha and Araneae (chapter 5), orthopterans (chapter 3) and wild and honey bees (chapter 4). In addition, a literature review was carried out at the beginning of the project to synthesize current knowledge and to identify research gaps on the effects of delaying the first mowing date upon plants and invertebrates in European meadowland (Chapter 2).

In July, D-meadows harboured higher abundances of orthopterans, bees, Auchenorrhyncha and Araneae compared to the other mowing regimes, i.e. when all meadows had been cut but D-meadows, confirming a strong direct negative effect of mowing on field invertebrates. A cumulative positive effect could be evidenced for Orthoptera and Araneae, namely that measures implemented a given year had carried-over effects discernable the following spring, before any mowing intervention. Surveys among farmers revealed that 8W- and C-meadows were managed similarly, which was confirmed by similar abundances and species richness of invertebrates between these two mowing regimes. Leaving uncut refuges had several positive effects on the investigated invertebrate populations. In spring, abundance of orthopterans and wild bees were doubled in R-meadows compared to C-meadows, pointing to a cumulative effect from one year to the next. For both taxa, species richness was also higher in these treatments than in controls.

Maintaining and restoring semi-natural grasslands is not only of major conservation concern worldwide, but also one of the most heavily subsidized conservation measures, especially in Europe. The present thesis demonstrates that delaying grass mowing and/or leaving uncut refuges when mowing would improve the effectiveness, and thus return on investment, of current AES. Notwithstanding that the management measures were tested within extensively managed meadows under Swiss AES, conclusions can be applied far beyond the Swiss border and in other grassy habitats other than hay meadows.

1

General introduction

1.1 The green revolution: its impact on farmland and biodiversity

As the 21st century dawned, the growing human population and the increasing purchasing power in emerging countries have been accentuating the need for agricultural goods (Lee *et al.* 2012). Agriculture was traditionally asked to produce food and fibre, but nowadays the production of energy is added to these missions, making expectations for agriculture even higher than before (Pingali 2012). Based on the outcomes of the so-called green revolution, the prolongation of the agricultural revolution of the 17th century, new farming practices took place after the World War II with severe consequences on biodiversity (Krebs *et al.* 1999; Robinson & Sutherland 2002). Nowadays, governments and international NGOs are confronted to a crucial dilemma, namely guaranteeing a productive agriculture while minimising its impact on the environment (Foley *et al.* 2011).

Threats on biodiversity depend on local and historical conditions. Regions where agriculture is developing are facing a problem of land conversion into farmland (Tollefson 2010). This conversion takes roots in the *Borlaug dilemma* (named after the father of the green revolution: Norman Borlaug), where areas are converted into intensive farming with high yield, while biodiversity occurring in other places is preserved. This paradigm was recently reformulated within the *land sharing/land sparing* framework (Balmford, Green & Phalan 2012). Regions that are prone to land sharing are usually areas with traditional farming practices such as European cultural landscapes. Long-established management is withdrawing in favour of new farming practices, and traditional farmland that gives refuge to many species is nowadays threatened (Bignal & McCrackent 1996). Despite that few new areas were recently converted into farmland in Europe, the existing ones were simplified, if not cleared, and became unsuitable for many species (Tscharntke *et al.* 2005).

The green revolution was designed to extirpate famine in the world and to heal the trauma due to food restriction during World War II in Europe. This revolution was made possible with the help of different economic and technological developments. Firstly, products like pesticides and artificial fertilizers were for the first time affordable for a majority of farmers. The second factor is the reasonably cheap machinery (Warren, Lawson & Blecher 2008). Use of heavy machinery required modification of the landscape as a third element of the green revolution, with the removal of semi-natural structures like high-stem orchards or hedgerows, simplifying the landscape and fragmenting the populations of numerous species (Frey-Ehrenbold *et al.* 2013). As a fourth component, numerous crops were abandoned and the remaining ones were strongly selected in order to maximise yield. Therefore, many locally adapted crop species and varieties were definitively lost. These new tools allowed an optimisation and a rationalisation of food production, where places suitable for a certain type of production were completely turned to monoculture (Tscharntke *et al.* 2005). Less productive areas were assigned to less demanding crops or animal husbandry. Ultimately, the less accessible and almost unproductive areas were abandoned.

In some regions, these farming practices were highly subsidized. The Treaty of Rome, establishing the European Economic Community (EEC), gave birth to the oldest European common policy in 1962: the Common Agricultural Policy (CAP). The first version of the CAP aimed to develop the living standard of farmers and to provide stable food supply at an affordable price for consumers. One of the aims of the CAP was also to limit the competition between the members of the EEC and thus to protect the farmers at national level. These improvements were so effective in Europe that overproduction became an issue at the beginning of the 1980's (Donald *et al.* 2002). About at the same time, environmental consciousness arose in the public, calling for a profound shift in the orientation of the CAP.

1.2 Emergence and efficiency of the agri-environment schemes (AES)

The extensification of farming practices ruled by the CAP was an opportunity to mitigate the biodiversity erosion observed in intensified farmland. This took place in the legal framework called agri-environment schemes (AES). All EU members are requested to define their AES aims and procedures for achieving the requirements of the PAC (Anonymous 1985). For countries with intensive farming practices, the main aim is the reduction of environmental risks. These risks are linked to the overuse of fertilizers or other chemicals, soil erosion and biodiversity loss (European Commission 2005).

Although AES are apparently favouring biodiversity, these measures have only mixed benefits (Kleijn *et al.* 2001; Kleijn & Sutherland 2003; Kleijn *et al.* 2006). Different reasons make restoration ecology in farmland challenging, such as increase of nitrogen deposition due to the massive use of fossil fuel (with modification of soil chemistry); landscape fragmentation and limitation of the genetic exchange between populations; disappearance of source populations (Knop, Schmid & Herzog 2008); absence of a truly functional seed bank; no previous experience that could have been used as model in establishing and applying such nature friendly regulations (Bakker & Berendse 1999; Kleijn *et al.* 2001). This gap of knowledge has also favoured a system where subsidies are allocated with respect to the implementation of AES measures (inputs) rather than their actual outcomes for biodiversity (outpus; Gibbons *et al.* 2011). This approach is suitable for some aims of the AES such as the limitation of the application of fertilizers or chemicals or the protection of soils against erosion, because this data could be easily monitored, even on a yearly basis (FOAG 2012). In contrast, evaluation of their effects on biodiversity necessitates a fine-tuned appreciation of the actual outputs of such subsidies.

1.3 The Swiss context

When compared to EU, Switzerland is an exception regarding historical and political aspects, but farming practices encouraged by the green revolution evolved in a comparable way. Even if Switzerland was not directly involved in World War II, food needs were an issue during this time period. Moreover, the particular geographical situation of this mountainous country makes any type of farming difficult. To face the co-occurring problems of the limited domestic production and the restricted access to imported resources, measures to maximise the production of agricultural goods were taken through the *Wahlen plan* (after Friedrich Traugott Wahlen, agronomist). This plan marked the start of the evolution of Swiss farmland toward a cleared landscape that continued after World War II along the development of the green revolution. Intensification of farming practices was also uneven in Switzerland. Relatively flat areas that are easily accessible were intensified first. The region that was mostly affected by this shift in management is the Swiss plateau, an area comprised between Lake Geneva and Lake Constance and representing about 30 % of the national territory. The other regions, especially in the mountainous areas, started to be intensified later, as a result of the technical improvement of machinery, allowing farmers to access and exploit steeper areas.

Another particularity that has to be mentioned is that Switzerland does not belong to the European Union. However, numerous agreements were ratified between EU and Switzerland, and laws and rules that are edited in Switzerland are in compliance with the European norms. The agricultural policies aimed, since the middle of the 1990's, at an extensification of the practices associated to a protection of the environment and are therefore comparable to the European AES. They aim to balance the use of fertilizers on farms, to practice crop rotation and to respect constraining animal welfare norms (Swiss Federal Council 1998). The most particular policy is the obligation for each farmer to have a part of their utilized agricultural area devoted to nature: the so-called ecological compensation areas (ECA). This last point is cited as an example for the greening of the CAP, meaning that Switzerland, though not being an EU member, could serve as a real-scale laboratory for developing future EU agro-ecological policies (Hart & Baldock 2011).

1.4 Semi-natural grasslands and AES

Grassland is a major emblematic habitat of traditional farmland in temperate regions. One of the traditional farming systems based on the co-occurrence of grassland and cropland, the so-called mixed farming management, uses the vicinity between animal husbandry and crops. The outputs generated by livestock, like manure or slurry, were traditionally transferred as inputs to cropland and thus maintained a low nutrient level in grasslands (Warren, Lawson & Blecher 2008).

Benefits of mixed farming became less important due to the availability of artificial fertilizers and this management vanished in numerous places in favour of specialized farming, threatening at the same time the existence of semi-natural grasslands. In the regions where animal husbandry was abandoned, grasslands were converted into cropland. Regions with remaining grasslands were also intensified, meaning earlier and more frequent cuts for meadows (Čop, Vidrih & Hacin 2009). Moreover, the increase in yield due to intensification is associated with an important use of machinery that is harmful for biodiversity and makes it possible to manage much larger areas during a much shorter period of time (Humbert, Ghazoul & Walter 2009). Numerous species that could cope with the traditional management of grasslands, such as grey partridge (*Perdrix perdrix* L., 1758), whinchat (*Saxicola rubetra* L., 1758), ortolan bunting (*Emberiza hortulana* L., 1758) or bats, are nowadays endangered (Donald *et al.* 2002; Britschgi, Spaar

& Arlettaz 2006; Menz & Arlettaz 2012; Frey-Ehrenbold *et al.* 2013). Different reasons might explain not only the disappearance of these organisms, but also their inability to re-establish when alternative managements are in use. Beyond the detrimental effect of the mowing machines, food resources availability has been dramatically reduced, because invertebrates are also massively impacted by intensification (Britschgi, Spaar & Arlettaz 2006). This is true for insectivorous bird species, but numerous if not all granivorous bird species also feed their chicks with insects to guarantee the protein supply needed for growth (Menz & Arlettaz 2012). Another factor related to intensification is the evolution of a homogenous sward cover that reduces prey accessibility to birds (Schaub *et al.* 2010; Tagmann-Ioset *et al.* 2012).

Grassland conservation is therefore of major concern and, not surprisingly, agricultural parcels registered within the Swiss AES are mainly grasslands, especially extensively managed hay meadows, which represent almost half of extant ECAs (FOAG 2012). The management of this type of ECA is regulated by the Swiss agricultural legislation. The main directives are: 1) at least one cut per year, not before 15 June; 2) no fertilizer allowed; 3) if problematic plant species could not be removed mechanically, use of herbicide is allowed, but only by topic spraying of the pest plants; 4) pasture allowed between 1 September and 30 November, as long as grazing is not damaging the meadow; 5) the minimum enrolment duration of these meadows in the AES is six years (Swiss Federal Council 1998). Some other practices remain possible, such as the use of weeder harrow in spring or oversowing with adapted seed mixes for extensively managed grasslands. When compared to intensively managed grassland, some benefits for biodiversity could be evidenced, but they remain tiny to moderate (Knop *et al.* 2006; Jeanneret *et al.* 2010).

1.5 Aim and general design of this thesis

Heterogeneity at temporal and/or spatial scale is considered as a major factor in preserving biodiversity in farmland (Benton, Vickery & Wilson 2003; Vickery & Arlettaz 2012). Notwithstanding the improvements realized with the present AES regulation and the increase of heterogeneity in the landscape, the first mowing suppresses within hours ECA meadows and therefore their attractiveness for biodiversity, leading to a suddenly homogenized landscape. This habit of mowing the great majority of ECA meadows on June 15th has even been termed the *federal hay day* by the farmers, showing the important synchrony of the phenomenon throughout Switzerland. Thus the main aim of this thesis is to test if alternative management regimes could create some heterogeneity capable of improving natural conditions for meadowland biodiversity. Several management regimes that could potentially increase heterogeneity were investigated.

These management measures could serve to improve the present ECA regulations for hay meadows, the most important semi-natural habitat within the Swiss agri-environment scheme. The measures proposed had to be easy to apply and to be fully compatible with modern farming practices so as to ensure their uptake by the ultimate end-users, the farmers. The following management regimes were tested:

1) Extensively managed meadow with first cut not before 15 July, with no restriction on the number and frequency of subsequent cuts (D-meadow, with D for delayed).
2) Extensively managed meadow with a maximum of two cuts per year and at least 8 weeks between the cuts, with first cut not before 15 June (8W-meadow, with 8W for eight weeks).
3) Extensively managed meadow with a rotational uncut refuge on 10–20% of the meadow area, meaning that a corresponding proportion of the area is left uncut each time the meadow is mown, with the location of the refuge being changed from one cut to the next to avoid vegetation succession; otherwise first cut not before 15 June (R-meadows, with R for refuge).
4) Extensively managed meadow with standard Swiss AES regulation, i.e. first cut not before 15 June, but with no restriction on the number and frequency of subsequent cuts. These meadows constitute our control meadows (C-meadows).

The experimental plots were selected across the Swiss plateau, where 48 meadows were selected, distributed in 12 regions (the replication unit). These meadows had to be registered as ECA since latest 2004, and to have a minimal size of 50 x 50 m. A full experimental block design was adopted, where the different management treatments were randomly allocated to one of the four meadows selected in a given region, such that each meadow represented one given management regime. One advantage of such a pragmatic approach, compared to many observational and correlative studies, is the ability to disentangle the effects of our management regimes from other parameters that could influence the results, such as environmental variables or abiotic conditions. Conclusions drawn from such an experimental framework could be considered as extremely reliable and could therefore be extrapolated to a larger scale. Moreover, the potential functional problems of implementation that the farmers could encounter with these novel management regimes could be assessed directly, because the farmers were required to apply these measures by themselves. These treatments were applied during three years (2010 to 2012), to evaluate direct (after the mow) and cumulative, carry-over (from one year to the next) effects. The different taxonomic groups investigated are presented in the overview below.

In order to facilitate the future application of these measures on a wide scale, the gap between science and policy had to be bridged. A pluri-disciplinary group of experts was created at the beginning of the project to build a catalogue of pragmatic evidence-based management recommendations for effective public actions (Sutherland *et al.* 2004; Arlettaz *et al.* 2010; Caudron, Vigier & Champigneulle 2012). Representatives of the local and national environment and agriculture offices were invited to join.

1.6 Overview of the thesis

The second chapter scans the extant literature on the effects of delaying mowing on biodiversity in European meadows. A systematic review approach combined with a meta-analysis was selected to provide an objective and clear assessment of the impact of mowing with respect to the time of the year. Effects on plant species richness, invertebrate species richness and invertebrate abundance were synthesized. Several gaps in knowledge were identified, which will partly be filled by the results of this PhD study.

In the third chapter, the impact on orthopterans of the different management regimes described above was investigated. Orthoptera are a major component of ecological communities and food chains of grassland. The relatively large body size of some species renders them vulnerable to mowing; they could thus benefit from extensified meadow management (Humbert *et al.* 2010).

In the fourth chapter, the impact of our management regimes was studied on solitary bees and bumblebees. The homogeneization of floral resources present in farmland strongly affects wild bees. Numerous AES are designed to boost these profitable pollinators, for instance wild flower strips, but the role that grassland could have in their promotion is understudied. Recommendations for an appropriate meadow management could therefore constitute a valuable complement to the existing schemes and policies.

The last, fifth chapter describes, via mid-term (three years) experiments, the effect of our management regimes on two taxonomic groups considered as highly appropriate for studying grassland biodiversity: Auchenorrhyncha and Araneae. The first group presents a broad range of species ranging from generalist species, quite resilient to management regime and disturbance, to species with high requirements regarding food resources and sensitive to disturbance level (Nickel 2003). Consequently this group is considered as an excellent bioindicator for evaluating the effects of mowing regimes. The second group, Araneae, could provide a valuable ecosystem service because all species are exclusively predators and thus play a crucial role in the control of pest species (Bell, Wheater & Cullen 2001).

These chapters are followed by a general discussion that will summarize the outcomes of the different chapters and draw on perspectives for further research needed and recommendations for stakeholders.

1.7 References

Anonymous (1985) Regulation of the European Parliament and of the Conncil establishing rules for direct payments to farmers under support schemes within the framework of the common agricultural policy. pp. 1-105.

Arlettaz, R., Schaub, M., Fournier, J., Reichlin, T.S., Sierro, A., Watson, J.E.M. & Braunisch, V. (2010) From Publications to Public Actions: When Conservation Biologists Bridge the Gap between Research and Implementation. *BioScience*, **60,** 835-842.

Bakker, J.P. & Berendse, F. (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology & Evolution*, **14,** 63-68.

Balmford, A., Green, R. & Phalan, B. (2012) What conservationists need to know about farming. *Proceedings of the Royal Society B: Biological Sciences*, **279,** 2714-2724.

Bell, J.R., Wheater, C.P. & Cullen, W.R. (2001) The implications of grassland and heathland management for the conservation of spider communities: a review. *Journal of Zoology*, **255,** 377-387.

Benton, T.G., Vickery, J.a. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, **18,** 182-188.

Bignal, E.M. & McCrackent, D.I. (1996) Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology*, **33,** 413-424.

Britschgi, A., Spaar, R. & Arlettaz, R. (2006) Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management. *Biological Conservation*, **130,** 193-205.

Caudron, A., Vigier, L. & Champigneulle, A. (2012) Developing collaborative research to improve effectiveness in biodiversity conservation practice. *Journal of Applied Ecology*, **49,** 753-757.

Čop, J., Vidrih, M. & Hacin, J. (2009) Influence of cutting regime and fertilizer application on the botanical composition, yield and nutritive value of herbage of wet grasslands in Central Europe. *Grass and Forage Science*, **64,** 454-465.

Swiss Federal Council (1998) Verordnung über die Direktzahlungen an die Landwirtschaft. *930.13*, pp. 229-265. Bundesrat.

Donald, P.F., Pisano, G., Rayment, M.D. & Pain, D.J. (2002) The Common Agricultural Policy, EU enlargement and the conservation of Europe's farmland birds. *Agriculture, Ecosystems & Environment*, **89,** 167-182.

European Commission (2005) Agri-environment Measures: Overview on General Principles, Types of Measures, and Application. pp. 24. Brussels, Belgium.

FOAG (2012) Rapport Agricole 2011. pp. 1-284. Federal Office of Agriculture, Bern.

Foley, J.A., Ramankutty, N., Brauman, K.A., Cassidy, E.S., Gerber, J.S., Johnston, M., Mueller, N.D., O/'Connell, C., Ray, D.K., West, P.C., Balzer, C., Bennett, E.M., Carpenter, S.R., Hill, J., Monfreda, C., Polasky, S., Rockstrom, J., Sheehan, J., Siebert, S., Tilman, D. & Zaks, D.P.M. (2011) Solutions for a cultivated planet. *Nature*, **478,** 337-342.

Frey-Ehrenbold, A., Bontadina, F., Arlettaz, R. & Obrist, M.K. (2013) Landscape connectivity, habitat structure and activity of bat guilds in farmland-dominated matrices. *Journal of Applied Ecology*, **50,** 252-261.

Gibbons, J.M., Nicholson, E., Milner-Gulland, E.J. & Jones, J.P.G. (2011) Should payments for biodiversity conservation be based on action or results? *Journal of Applied Ecology*, **48,** 1218-1226.

Hart, K. & Baldock, D. (2011) Greening the CAP: Delivering environmental outcomes through pillar one.

Humbert, J.Y., Ghazoul, J., Sauter, G.J. & Walter, T. (2010) Impact of different meadow mowing techniques on field invertebrates. *Journal of Applied Entomology*, **134,** 592-599.

Humbert, J.Y., Ghazoul, J. & Walter, T. (2009) Meadow harvesting techniques and their impacts on field fauna. *Agriculture, Ecosystems and Environment*, **130,** 1-8.

Jeanneret, P., Walter, T., Birrer, S. & Herzog, F. (2010) Evaluating the performance of the Swiss agri-environmental measures for biodiversity: methods, results and questions. *Aspects of Applied Biology*, **100,** 35-42.

Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M. & Yela, J.L. (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, **9,** 243-254.

Kleijn, D., Berendse, F., Smit, R. & Gilissen, N. (2001) Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature*, **413,** 723-725.

Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40,** 947-969.

Knop, E., Kleijn, D., Herzog, F. & Schmid, B. (2006) Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. *Journal of Applied Ecology*, **43,** 120-127.

Knop, E., Schmid, B. & Herzog, F. (2008) Impact of Regional Species Pool on Grasshopper Restoration in Hay Meadows. *Restoration Ecology*, **16,** 34-38.

Krebs, J.R., Wilson, J.D., Bradbury, R.B. & Siriwardena, G.M. (1999) The second Silent Spring? *Nature*, **400,** 611-612.

Lee, B., Preston, F., Kooroshy, J., Bailey, R. & Lahn, G. (2012) Resources Futures. *Chatham House Report* (ed. C. House). The Royal Institute of International Affairs, London.

Menz, M.H.M. & Arlettaz, R. (2012) The precipitous decline of the ortolan bunting Emberiza hortulana: time to build on scientific evidence to inform conservation management. *Oryx,* **46,** 122-129.

Nickel, H. (2003) *The Leafhoppers and Planthoppers of Germany (Hemiptera, Auchenorrhyncha): Patterns and strategies in a highly diverse group of phytophagous insects*. Pensoft.

Pingali, P.L. (2012) Green Revolution: Impacts, limits, and the path ahead. *Proceedings of the National Academy of Sciences,* **109,** 12302-12308.

Robinson, R.A. & Sutherland, W.J. (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology,* **39,** 157-176.

Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi, F., Zbinden, N., Jenni, L. & Arlettaz, R. (2010) Patches of Bare Ground as a Staple Commodity for Declining Ground-Foraging Insectivorous Farmland Birds. *PLoS ONE,* **5,** e13115 (13115 pages).

Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. (2004) The need for evidence-based conservation. *Trends in ecology & evolution (Personal edition),* **19,** 305-308.

Tagmann-Ioset, A., Schaub, M., Reichlin, T.S., Weisshaupt, N. & Arlettaz, R. (2012) Bare ground as a crucial habitat feature for a rare terrestrially foraging farmland bird of Central Europe. *Acta Oecologica,* **39,** 25-32.

Tollefson, J. (2010) The Global Farm. *Nature,* **466,** 554-556.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters,* **8,** 857-874.

Vickery, J. & Arlettaz, R. (2012) The importance of habitat heterogeneity at multiple scales for birds in European agricultural landscapes. *Birds and Habitat: Relationships in Changing Landscapes* (ed. R.J. Fuller), pp. 177-204. Cambridge University Press, Cambridge.

Warren, J., Lawson, C.S. & Blecher, K. (2008) *The Agri-Environment*. Cambridge, United Kingdom.

2

Does delaying the first mowing date benefit biodiversity in meadowland? A meta-analysis

Does delaying the first mowing date benefit biodiversity in meadowland? A meta-analysis

Jean-Yves Humbert[a], Jérôme Pellet[a, b], Pierrick Buri[a], and Raphaël Arlettaz[a]

[a] Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland
[b] A. Maibach Sàrl, CP 99, Ch. de la Poya 10, 1610 Oron-la-Ville, Switzerland

Manuscript:
Published in *Environmental Evidence*, 2012, 1:9
doi:10.1186/2047-2382-1-9

2.1 Abstract

1. **Background**

Meadows are regularly mown in order to provide fodder or litter for livestock and to prevent vegetation succession. However, the time of year at which meadows should be first mown in order to maximize biological diversity remains controversial and may vary with respect to context and focal taxa. We carried out a meta-analysis on the effects of delaying the first mowing date upon plants and invertebrates in European meadowlands.

2. **Methods**

We followed the review methodology of the Collaboration for Environmental Evidence partnership. ISI Web of Science, Science Direct, JSTOR, Google and Google Scholar were searched. We recorded all studies that compared the species richness of plants, or the species richness or abundance of invertebrates, between grassland plots mown at a postponed date (treatment) vs plots mown earlier (control). In order to be included in the meta-analysis, compared plots had to be similar in all management respects, except the date of the first cut that was (mostly experimentally) manipulated. They were also to be located in the same meadow type. Meta-analyses applying Hedges'*d* statistic were performed.

3. **Results**

Plant species richness reacted differently with respect to the date to which mowing was postponed. Delaying mowing from spring to summer had a positive effect, while delaying either from spring to fall, or from early summer to later in the season had a negative effect. Invertebrates were expected to show a strong response to delayed mowing due to their dependence on sward structure, but only species richness showed a clearly significant positive response. Invertebrate abundance was positively influenced in only a few studies.

4. **Conclusions**

The present meta-analysis shows that in general delaying the first mowing date in European meadowlands has either positive or neutral effects on plant and invertebrate biodiversity. Overall, there was also strong between-study heterogeneity, pointing to other major confounding factors, the elucidation of which requires further field experiments with both larger sample sizes and a distinction between taxon-specific and meadow-type-specific responses.

Keywords: cutting; grassland; restoration; systematic review

2.2 Background

Farmland biodiversity has been dramatically affected by the green revolution [1] and concern about its decline already emerged in the late 1960s [2]. Concern has amplified during the past decade [e.g. 3, 4-7] as it is now recognized that farmland biodiversity plays a major role in many agroecosystem processes, such as grassland productivity, crop pollination, pest control and soil fertility [e.g. 8, 9-12]. As a response, most countries have implemented agri-environment schemes (AES), in which farmers are subsidised to modify their farming practice to provide environmental benefits. AES mostly aim at protecting and restoring farmland biodiversity [13, 14]. They are voluntary programmes in which farmers usually receive direct payments for providing services that go beyond conventional agricultural practices, such as management of semi-natural habitats. Currently, about 30% of European farmland is under some sort of agri-environmental contract [15].

Low input (extensively managed) hay and litter meadows are among the most commonly implemented agri-environmental measures [13, 16]. The most important management action on these grasslands is mowing. Mowing vegetation at least once a year has a positive effect on vascular plant species richness, especially when cuttings are removed [17, 18]. However, since it has been demonstrated that early-summer mowing often has a detrimental effect on species richness of flowering plants, as it hampers completion of the reproductive cycle [17], later mowing is generally found to be more favourable for vascular plant biodiversity [19, 20].

Annual mowing has a contrasting effect on invertebrates [21, 22]. Although detrimental to many insects in the short term [23-28], mowing has a largely positive long term effect because it prevents the growth of bushes and trees and thus maintains semi-natural grasslands that are beneficial to a large number of heliophilous and thermophilous species [29]. It has also been suggested that delaying the date of first mowing could be positive for a multitude of invertebrates, including butterflies, spiders, grasshoppers and ground beetles that depend on various vegetation structures [30-35]. For vertebrates, the situation is different: mowing renders food resources suddenly available (e.g. insects and rodents) that were previously hidden in the sward. Foragers may congregate towards these rich, although ephemeral food supplies [36, 37]. On the other hand, ground-breeding birds are likely to be heavily penalised by early mowing [e.g. 38].

While most AES have the clear objective of restoring biodiversity and ecosystem services [13, 14, 39], they often bind farmers to threshold dates for agricultural operations. The date of the first mowing of meadows is usually defined as a trade-off between expected agricultural yield and supposed effects on wildlife. Given that this first mowing date is the most easily changed management practice [7, 31], it is the most likely to provide environmental benefits at little economical cost. Using a meta-analytical framework, we studied the currently available scientific literature about the pros and cons for biodiversity of delaying mowing in farmed European meadowland; we also identified major gaps in knowledge related to this theme. The synthesis will be useful to both agro-ecologists and policy-makers involved in farmland management.

2.3 Methods

We followed the review methodology of the Collaboration for Environmental Evidence partnership [40, 41].

2.3.1 Search strategy

The following web databases were searched for relevant documents: ISI Web of Science, Science Direct, JSTOR, Google (100 first hits), Google Scholar (100 first hits). Searches were conducted in English, French and German using translations of the following logical search string: (mowing OR cutting) AND (meadow OR grassland) AND (biodiversity OR richness). The term "Europe" was not included in the search keywords as stated in the Review Protocol [41], because European studies that do not mention the term Europe may have been missed. Studies originating from extra European regions were excluded from the analyses. Any apparently relevant citations or links were followed one step away from the original hit. In addition, national and international experts on the subject were asked for any relevant literature and unpublished data.

2.3.2 Study inclusion criteria

All references retrieved from the web search (367) were scanned at the title, abstract and full text filter level by a first reviewer. From the 367 initial references, 200 (randomly selected) were rescanned by a second reviewer in order to check for inclusion consistency. The following inclusion criteria were used:

- Relevant subjects: semi-natural grasslands that are mown annually, including conventionally managed grasslands, AES meadows, hay or litter meadows.
- Types of intervention: first mowing date delayed (treatment).
- Types of comparator: comparison with similar meadows or plots that are first mown on an earlier date (control). Treatment and control plots must be similar in all management respects, except the date of the first cut, and must be located in the same habitat type.
- Types of outcome: species richness and/or abundance.

Inclusion consistency was checked with kappa statistics, and agreement between the reviewers was satisfactory (k = 0.81) [42].

2.3.3 Data extraction

Some studies reported more than one treatment (two or more delayed cuts) or more than one type of measurable outcome (e.g. species richness and abundance, or different taxonomic groups such as plants and invertebrates). In these cases, all comparisons were recorded as independent data points, and this is why there are more data points (units of analysis) than references [43, 44] (Fig. 1; Table 1).

The following information was extracted from the studies for each data point: (1) taxon, (2) species richness or abundance, (3) standard deviation, (4) sample size, (5) study duration in years, (6) plot size of vegetation relevés or sampling methodology for invertebrates, (7) ordinal days of the early cut and (8) delayed cut, and finally (9) meadow type, classified as dry, mesophilous or wet. Additional potential sources of heterogeneity were also extracted such as fertilizer application, number of cuts per year, grazing activity, and biogeographical region where the study was carried out. Diversity indexes such as the Shannon index were recorded when present, but did not lead to sufficient data points for a meta-analysis (MA).

Taxa were plants, invertebrates or a specific group of invertebrates. Standard deviations (SD) were usually retrieved from standard errors (SE) or variances. If no estimate of variance was provided, we requested it from the original authors. If original authors could not provide SD, or sample size was equal to one (i.e. no variance), the corresponding study was included only in the unweighted analyses (see statistical analysis section below). The ordinal days (day 1 = January 1st) of the early cut (control) and delayed cut (treatment) were used to calculate the number of days between the two mowing regimes. If the exact date of the early or delayed cut was unknown, but only the month was given, then the 15th of the month was used for calculations. If the terms "early" or "late" in a given month were mentioned, then the 7th or 24th, respectively, of that corresponding month were used.

Delaying cutting is often studied within a broader context of agricultural extensification for biodiversity, including reduced number of mowing events, changes in fertilizer inputs and/or type of fertilizer, oversowing, etc. Studies of cases in which delaying mowing occurred in the presence of such confounding factors could not be included in the MA as the effect of delaying the first cut cannot be separated from these other confounding factors [e.g. 32].

2.3.4 Statistical analysis

Meta-analyses were conducted on three groups of studies according to their measurable outcomes: 1) plant species richness; 2) invertebrate species richness; 3) invertebrate abundances. Studies on plant species richness lasted between two and 40 years, and if multiple time-points were available along the time series, only the data for the last year (longest time period) were considered. Studies on invertebrates were usually shorter, mostly three to four years, and due to a high inter-annual variation, these studies often reported biodiversity responses averaged across the years. Here we used these reported average values.

The Hedges'*d* statistic was used to estimate effect size, Hedges'*d* equalling to the standardized mean difference between delayed and early cuts [45]:

$$\mathrm{d} = \frac{(\overline{\mathrm{X}}^{\mathrm{D}} - \overline{\mathrm{X}}^{\mathrm{E}})}{\mathrm{S}}\mathrm{J}$$

Where $\overline{\mathrm{X}}^{\mathrm{D}}$ and $\overline{\mathrm{X}}^{\mathrm{E}}$ are the means of the delayed and early cut outcomes, S is their pooled standard deviation, while the term J corrects for small sample bias [46]. It was calculated using the function *escalc* of the R package *metafor* [47].

Random- and mixed-effects models (mixed-effects models are random-effects models with covariates) were chosen as it is now common practice for this kind of analysis [46]. Under random- and mixed-effects models, the true effect size, i.e. the effect size as if there were no sampling errors, can vary from study to study, but usually do so under a normal distribution [48, 49]. Here the Q test and I^2 statistic were used to assess heterogeneity between studies. The Q test is the test of significance, and the I^2 statistic estimates how much of the total variability in the mean effect size (composed of heterogeneity and sampling error) can be attributed to heterogeneity among the true effect size [47, 49].

First, the null model was generated. Then all univariate models including the following moderators were tested: ordinal day, time lapse (in days) between the early and the delayed cuts, study duration (in years), meadow type and plot size of the vegetation relevés. Multivariate models (various combinations of the above mentioned variables) were also explored. Further subgroup analyses were conducted to investigate the influence of key moderators separately. Models were ranked based on their AIC values (Akaike Information Criterion) and on the level of significance of the estimates [50]. Permutation tests were not always possible due to an insufficient number of data points, which limits the number of possible iterations. Therefore test statistics of the effect sizes and corresponding confidence intervals (CIs) referred to the normal distribution (Z test). Publication bias was assessed using funnel plots, by applying a regression test for funnel plot asymmetry [45, 47].

In addition to the proper weighted meta-analyses, unweighted meta-analyses were performed using the response ratio as effect size. Response ratio (*lr*) is equal to the natural logarithm of the ratio of the delayed on the early cut date [45]. Note that this way a positive value means a positive effect of delaying mowing.

$$\mathrm{lr} = \ln\left(\overline{\mathrm{X}}^{\mathrm{D}}/\overline{\mathrm{X}}^{\mathrm{E}}\right)$$

Although less powerful than proper-weighted meta-analyses, this approach allows the inclusion of studies that did not report SD or where sample size was one, i.e. studies for which no Hedges'*d* could be calculated. Bootstrapping was used to calculate 95% confidence intervals (CI); if CI overlapped zero, the effect size was considered to be non significant. All statistics were performed using R version 2.13.0 [51].

2.4 Results and discussion

367 references were retrieved from the web search; using these as a database, the influence on biodiversity of delaying the first mowing date could be investigated in 27 articles that matched inclusion criteria (Fig. 1). Subsequently, twelve references were excluded due to duplication or unsuitable data for an MA. Duplication happened when it was obvious that two studies based on the same experimental set up were looking at the same metric while either addressing different questions or considering different times. For example, the studies [52] and [53] investigated the impact of different mowing regimes on plant species richness in the same experimental set up, same plots, but one after 15 years, and the other after 22 years of management, respectively. In such cases, only the latest study (longest duration) was included in the MA. Nine additional studies were found in bibliography sections of the selected papers or obtained after contacting experts, which makes a total of 24 suitable studies submitted to the present MA (Fig. 1). In some studies more than one delayed cut or more than one invertebrate group were investigated, resulting in a total of 55 data points (Table 1). From these 55 data points, 35 deal with plant species richness, ten with invertebrate species richness, and ten with invertebrate abundance. In eleven cases (nine for plant species richness, one for invertebrate species richness and one for invertebrate abundance), the study did not reported SD, or sample size equalled one. Consequently, these data points could only be included in the MA assessing response ratio. Two suitable studies on seed shed and seed bank were also found, but not included because their very specific focus was too marginal with respect to our main research question [20, 54]. An additional file shows the included data points in more detail [see Additional file 1].

Postponing the first mowing date is a widespread agri-environmental measure in Europe, though it is usually coupled with other measures such as reduction of fertilizer applications. This makes sense from an agronomical point of view since postponing mowing must be accompanied by reduced hay productivity in order to avoid over-mature grass laying on the ground and/or mouldering at the time of mowing. It would then be difficult to separate the effects of postponing mowing from the effect of fertilizer reduction. Therefore, most of the studies included in the present MA concern extensively managed grasslands with no fertilizer application and a single cut per year.

2.4.1 Effects on plant species richness

Results based on the response ratio qualitatively converged with the Hedges'*d* estimates. Therefore, only the results of the weighted meta-analysis based on the Hedges'*d* are presented below due to their superior explanatory power. An additional file shows the results of the unweighted meta-analysis based on the response ratio [see Additional file 3].

In the null model, no overall significant effect of delaying the first mowing date was found as regards plant species richness (mean Hedges'*d* = 0.017 with 95% CI -0.237 – 0.2716, z = 0.134, P = 0.882, Fig. 2). However, heterogeneity between studies was significant (Q = 56.88, d.f. = 25, $P < 0.001$, I^2 = 54%), indicating that the true effect size does vary from one study to the next. With study duration (in years) included in the model as a moderator, no significant influence of that moderator on the effect size was discerned (slope = 0.016 with 95% CI -0.019 – 0.051, z = 0.878 P = 0.380, Fig. 3a).

In further univariate models, a significant negative influence of the date of the early cut (control) was established (slope = -0.015 with 95% CI -0.025 – -0.005, z = -2.878, P = 0.004, Fig. 3b). This means that the earlier the cut in the year, the more pronounced the effect on biodiversity of delaying the first cut. On the other hand, when the early cut occurred late in the season (July to August), delaying it had no, or even a negative, effect on plant species richness. Between studies heterogeneity was significant (Q = 43.12, d.f. = 24, P = 0.010), indicating again that other moderators may also influence the effect sizes. On the contrary, the date of the delayed cut did not significantly influence the effect size (slope = -0.007 with 95% CI -0.013 – 0.001, z = -1.805, P = 0.071), although it did explain some of the heterogeneity.

In order to further investigate this issue and to evaluate the extent to which heterogeneity can be explained by variation in this moderator (first mowing date), two subset MAs were conducted. The first included only the data points with an early cut in spring (before July 1) associated with a delayed cut in summer (July to September); the second included all other combinations of early and delayed cuts (spring to fall, early summer to late summer and summer to fall, but excluded one early spring to late spring study [55]). In the first case, mean Hedges'*d* became significantly positive (mean Hedges'*d* = 0.388 with 95% CI 0.092 – 0.684, z = 2.569, P = 0.010, Fig. 2b). Between studies heterogeneity was significant (Q = 24.88, d.f. = 14, P = 0.036), while I^2 (40%) was not. In the second case, mean Hedges'*d* became significantly negative (mean Hedges'*d* = -0.504 with 95% CI -0.763 – -0.246, z = -3.828, P < 0.001, Fig. 2c). Heterogeneity was not significant (Q = 4.56, d.f. = 9, P = 0.871), indicating that these latter studies provided consistent results.

Note that none of the models including one or more moderators (study duration, mowing date, time interval between mowings, habitat type, and plot size of the vegetation relevés) performed better that the null model according to AIC values [Additional file 4]. In addition, no asymmetry was detected in any funnel plots, which rules out any publication bias effect [Additional file 2].

2.4.2 Effects on invertebrate species richness

A significant positive effect of delaying the first mowing date on invertebrate species richness was found (mean Hedges'*d* = 0.511 with 95% CI 0.129 – 0.893, z = 2.6217, P = 0.009, Fig. 4). Heterogeneity was not significant (Q = 14.97, d.f. = 8, P = 0.060). No significant influence was found concerning the number of years during which a study was carried out (slope = 0.154 with 95% CI -0.074 to 0.382, z = 0.117, P = 0.186). No models including a moderator performed better that the null model according to AIC values [Additional file 4]. No asymmetry was detected in funnel plots [Additional file 2].

2.4.3 Effects on invertebrate abundance

Delaying the first mowing date was found to have no significant effect on invertebrate abundance (mean Hedges'*d* = -0.053 with 95% CI -0.889 – 0.783, z = -0.1249, P = 0.901, Fig. 5). However, the resulting Q-Q plot was not satisfactory, while the funnel plot showed a significant asymmetry in the distribution of the data points due to the two outlying studies of Morris [56, 57]. Excluding Morris's studies from the analysis resulted in model assumptions and funnel plot becoming satisfactory, with a significant positive effect of delaying the first mowing date (mean Hedges'*d* = 0.533 with 95% CI 0.222 – 0.844, z = 3.3564, P = 0.001, Fig. 5a), even in the absence of heterogeneity (Q = 6.59, d.f. = 6, P = 0.360). The apparent generality of this result must be treated with caution, however, as it is based on only two independent experiments. Model ranking accounting for all studies, including Morris's studies, showed that the model that included the dates of both early and delayed mowing had a lower AIC value, with a negative effect for early mowing (slope = -2.130 with 95% CI -3.017 – -1.241, z = -4.6989, P < 0.001) and a positive effect of delayed mowing (slope = 5.607 with 95% CI 3.283 – 7.930, z = 4.730, P < 0.001) [see Additional file 4]. This means that effect size is greater the earlier the first mowing and later the delayed mowing. The influence of study duration was not investigated because all study durations were either 3 or 4 years.

2.4.4 Limitations of available information

The main limitation of this systematic review is the low number of data points stemming from an even lower number of studies (Table 1), which precluded investigations on specific invertebrate taxa, and on the influence of several moderators. As a consequence, only the main general effects of postponing mowing could be clearly investigated. Moreover, in the MA there was great heterogeneity in plant species richness, indicating that other factors (moderators) than delaying the first mowing probably influence the effect size. While the date of the first mowing was found to be an important factor, study duration was not (Fig. 3). It was also expected that heterogeneity would be influenced by the great variety of meadow types involved. However, no analyses could be conducted on this factor due to the highly unbalanced distribution of the habitats among the data points (n = 36 mesophilous meadows; 16 wet meadows; 3 dry meadows). Moreover, from the sixteen wet meadow data points, nine could not be included in the weighted MA. Additional management factors such as fertilizer application, occurrence of a second cut, seed oversowing, and autumn grazing would also influence the effect size, but they could not be investigated for the same reasons. Note that the most common management practice (42 data points out of 55) was no fertilizer application, no grazing and a single cut per year.

Study design could also play a role. While most studies were experimental, three used a purely observational approach [31, 58, 59]. Experimental frameworks also differed greatly in sample sizes, plot sizes and sampling methodologies, which additionally affect the probability of detecting changes. Publication bias was not apparent from the funnel plots; however, some biogeographical bias might be present as most studies originated from the UK [see Additional file 1].

2.5 Conclusions

The present study shows that, overall, delaying the first mowing date in European meadows has either positive or neutral effects on plant and invertebrate biodiversity. Our MA also provides evidence for a sheer between-study heterogeneity, emphasizing that factors other than mowing date might play an important role, a topic which deserves further investigations. These findings have particular relevance to all agri-environment schemes (AES) where the date of first mowing is strictly regulated. They are also important for the management of low input meadows, where delaying mowing may improve and secure primary production. It is known that primary productivity in more diverse plant communities is more stable and resilient to disturbances [60]. In addition to agricultural grasslands, open nature reserves are often mown [e.g. 61, 62]. When conservation is the primary goal of such management, the first possible mowing date should be considered carefully.

Plant species richness reacted differently according to the way mowing was postponed. Delaying mowing from spring to summer had a positive effect, while delaying either from spring to fall, or from early summer to late summer, or from summer to fall had a negative effect (Fig. 2). The time interval between two mowing events was expected to have a greater positive impact the longer the time interval between cuts, though the time interval, in fact, appeared to be not significant.

Invertebrates were expected to show an even stronger response to delayed mowing than plants, due to their heavy dependence on vegetation structure [33, 63, 64] and high susceptibility to mechanized harvesting processes [65]. However, only invertebrate species richness showed a clear overall significant positive response (Fig. 4), while no effect was detected on invertebrate abundance. It was only after removing two studies [56, 57] contradicting basic MA assumptions that delaying the first mowing date was found to have a positive effect on invertebrate abundance (Fig. 5).

The types of meadow considered in this review – both from a phytosociological viewpoint (e.g. Arrhenatherion, Mesobromion, Filipendulion or Caricion) and a functional perspective (e.g. hay or litter meadow) – are also believed to interact with the effects of delaying mowing. Unfortunately, the variety of meadow types across studies yielded an insufficiently balanced sample to enable investigation of the influence of that moderator. For the same reason, we had to renounce analysing specific invertebrate taxa, notwithstanding that responses are also expected to vary with respect to taxa body size, mobility, and life history traits [27, 61, 66, 67].

Extensification of grassland management practices is known to positively affect general plant and invertebrate biodiversity [e.g. 32, 68, 69], which is confirmed by this MA. However, contrary to some other studies [e.g. 70], we could not evidence any conservation conflicts between our two main focal taxa (plants and invertebrates), when some practices benefit one taxon to the detriment of the other.

2.5.1 Evidence of effectiveness and management recommendations

This review confirms that postponing of mowing from spring (May-June) to summer (July-September) is appropriate to promote plant and invertebrate diversity. In contrast, postponing mowing from spring to fall (October-November) or from early summer (July) to late summer or fall should be avoided as it will have a negative impact on the vegetation. Invertebrates might still benefit from it but these two postponing schemes could not be differentiated due to a too small sample size. Regarding wet and litter meadows, a late cut (September or later) is usually recommended [71], but unfortunately we are not in a position to confirm this recommendation, in the absence of habitat specific analyses.

When postponing mowing cannot be done at the field scale, leaving uncut grass areas within the cultivated landscape matrix can be an alternative solution to favour plants and animals [see also 72, 73-75]. At the landscape scale, creating a mosaic of different mowing regimes will increase species diversity, as there is no single appropriate mowing time that suits all organisms [33, 53, 76]. In addition to the date of first mowing, a low annual cutting frequency also promotes wild plants [77] and invertebrates [78, 79]. There was no single study on birds that complied with our selection criteria. In effect, none of the studies consisted of field experiments, accounting for potential confounding factors. However, all studies on ground-nesting birds recommend postponing mowing until after fledglings have left the nests [e.g. 80, 81-84]. These management recommendations do not apply everywhere and must be related to the socio-economic context. For example, in highly fertilized systems (high intensity management) biodiversity is generally too low for these measures to have positive effects [e.g. 85].

2.5.2 Further research

Our review focuses solely on the general effect of delaying the first mowing date upon plant and invertebrate species richness as well as invertebrate abundance. Some general trends could be extracted from the scientific literature, but there is still considerable uncertainty concerning the estimated effect sizes, since the influence of several moderators has barely been investigated. Altogether, invertebrates were far less documented than plants, with only seven studies of the impact of delaying mowing on species richness and/or abundance, and even these showed a major geographical bias (six studies from the UK and one from Finland). Clearly this is not sufficient to get the full picture: further long-term, experimental investigations of target taxonomic groups and species regarding responses to mowing regimes are needed. This lack of invertebrate studies is true not only for mowing but also for all factors that may influence grassland invertebrates, such as grazing, habitat fragmentation and management intensity [86]. Only experimental work can disentangle the effects of various, often concommitant management practices (e.g. mowing date and fertilizer application). Additionally, landscape characteristics are known to influence communities of plants and animals within farmland, and should therefore be accounted for in any attempt to model the effects of management practices on those communities [87].

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

JYH and JP carried out the literature search, JYH performed the statistical analyses and wrote the manuscript. JP conceived the systematic review, wrote the protocol and advised on the analyses. PB checked for consistency in the study inclusion (second reviewer). RA supervised the work and provided thorough editing of the manuscript. All authors commented and approved the final manuscript.

Acknowledgements

We are grateful to Judith Wunderlin for a pre-literature research on the topic. We would like to thanks all the following authors who provided extra information on their studies: Barbara Pietragalla (former B. Köhler), Ben A. Woodcock, Carol A. Marriott, Jure Čop, Kalle Hellström, Robin A. Blake, Robin Pakeman, Simon G. Potts, Stein J. Hegland, and Stephanie Bissels.

2.6 References

1. Wilson JD, Morris AJ, Arroyo BE, Clark SC, Bradbury RB: **A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change.** *Agric Ecosyst Environ* 1999, **75:**13-30.
2. Carson R: *Silent Spring.* Boston: Houghton Mifflin; 1962.
3. Kleijn D, Kohler F, Baldi A, Batary P, Concepcion ED, Clough Y, Diaz M, Gabriel D, Holzschuh A, Knop E, et al: **On the relationship between farmland biodiversity and land-use intensity in Europe.** *P Roy Soc B-Biol Sci* 2009, **276:**903-909.
4. Krebs JR, Wilson JD, Bradbury RB, Siriwardena GM: **The second silent spring.** *Nature* 1999, **400:**611-612.
5. Robinson RA, Sutherland WJ: **Post-war changes in arable farming and biodiversity in Great Britain.** *J Appl Ecol* 2002, **39:**157-176.
6. Scherr SJ, McNeely JA: **Biodiversity conservation and agricultural sustainability: towards a new paradigm of 'ecoagriculture' landscapes.** *Philos T R soc B* 2008, **363:**477-494.
7. Chamberlain DE, Fuller RJ, Bunce RGH, Duckworth JC, Shrubb M: **Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales.** *J Appl Ecol* 2000, **37:**771-788.
8. Altieri MA: **The ecological role of biodiversity in agroecosystems.** *Agric Ecosyst Environ* 1999, **74:**19-31.

9. Bianchi F, Booij CJH, Tscharntke T: **Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control.** *P Roy Soc B-Biol Sci* 2006, **273:**1715-1727.
10. Carvalheiro LG, Veldtman R, Shenkute AG, Tesfay GB, Pirk CWW, Donaldson JS, Nicolson SW: **Natural and within-farmland biodiversity enhances crop productivity.** *Ecol Lett* 2011, **14:**251-259.
11. DeHaan LR, Weisberg S, Tilman D, Fornara D: **Agricultural and biofuel implications of a species diversity experiment with native perennial grassland plants.** *Agric Ecosyst Environ* 2010, **137:**33-38.
12. Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, van Ruijven J, et al: **High plant diversity is needed to maintain ecosystem services.** *Nature* 2011, **477:**199-202.
13. Kleijn D, Sutherland WJ: **How effective are European agri-environment schemes in conserving and promoting biodiversity.** *J Appl Ecol* 2003, **40:**947-969.
14. Aviron S, Nitsch H, Jeanneret P, Buholzer S, Luka H, Pfiffner L, Pozzi S, Schupbach B, Walter T, Herzog F: **Ecological cross compliance promotes farmland biodiversity in Switzerland.** *Front Ecol Environ* 2009, **7:**247-252.
15. Gay SH, Osterburg B, Baldock D, Zdanowicz A: **Recent evolution of the EU Common Agricultural Policy (CAP): state of play and environmental potential.** *Research report MEACAP WP6-D4b*. Available at: http://www.ieep.eu/assets/224/WP6D4B_CAP.pdf.
16. Herzog F, Dreier S, Hofer G, Marfurt C, Schüpbach B, Spiess M, Walter T: **Effect of ecological compensation areas on floristic and breeding bird diversity in Swiss agricultural landscapes.** *Agric Ecosyst Environ* 2005, **108:**189-204.
17. Parr TW, Way JM: **Management of roadside vegetation: the long-term effects of cutting.** *J Appl Ecol* 1988, **25:**1073-1087.
18. Bakker JP, Elzinga JA, de Vries Y: **Effects of long-term cutting in a grassland system: perspectives for restoration of plant communities on nutrient-poor soils.** *Appl Veg Sci* 2002, **5:**107-120.
19. Smith RS, Shiel RS, Millward D, Corkhill P: **The interactive effects of management on the productivity and plant community structure of**

an upland meadow: an 8-year field trial. *J Appl Ecol* 2000, **37:**1029-1043.

20. Smith RS, Shiel RS, Millward D, Corkhill P, Sanderson RA: **Soil seed banks and the effects of meadow management on vegetation change in a 10-year meadow field trial.** *J Appl Ecol* 2002, **39:**279-293.
21. Morris MG, Rispin WE: **Abundance and diversity of the coleopterous fauna of a calcareous grassland under different cutting régimes.** *J Appl Ecol* 1987, **24:**451-465.
22. Völkl W, Zwölfer H, Romstöck-Völkl M, Schmelzer C: **Habitat management in calcareous grasslands, effects on the insect community developing in flower heads of Cynarea.** *J Appl Ecol* 1993, **30:**307-315.
23. Erhardt A: **Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland.** *J Appl Ecol* 1985, **22:**849-861.
24. Feber RE, Smith H, Macdonald DW: **The effects on butterfly abundance of the management of uncropped edges of arable fields.** *J Appl Ecol* 1996, **33:**1191-1205.
25. Valtonen A, Saarinen K: **A highway intersection as an alternative habitat for a meadow butterfly: effect of mowing, habitat geometry and roads on the ringlet (*Aphantopus hyperantus*).** *Ann Zool Fenn* 2005, **42:**545-556.
26. Humbert J-Y, Ghazoul J, Richner N, Walter T: **Hay harvesting causes high orthopteran mortality.** *Agric Ecosyst Environ* 2010, **139:**522–527.
27. Humbert J-Y, Ghazoul J, Sauter GJ, Walter T: **Impact of different meadow mowing techniques on field invertebrates.** *J Appl Entomol* 2010, **134:**592–599.
28. Thorbek P, Bilde T: **Reduced numbers of generalist arthropod predators after crop management.** *J Appl Ecol* 2004, **41:**526-538.
29. Grime JP: *Plant Strategies, Vegetation Processes, and Ecosystem Properties.* 2nd edition. Chichester, UK: John Wiley; 2001.
30. Gardiner T, Hassall M: **Does microclimate affect grasshopper populations after cutting of hay in improved grassland?** *J Insect Conserv* 2009, **13:**97-102.
31. Valtonen A, Saarinen K, Jantunen J: **Effect of different mowing regimes on butterflies and diurnal moths on road verges.** *Anim Bio Conserv* 2006, **29:**133-148.

32. Knop E, Kleijn D, Herzog F, Schmid B: **Effectiveness of the Swiss agri-environment scheme in promoting biodiversity.** *J Appl Ecol* 2006, **43:**120-127.
33. Morris MG: **The effects of structure and its dynamics on the ecology and conservation of arthropods in British grassland.** *Biol Conserv* 2000, **95:**129-142.
34. Koller N, Pearson S, Pozzi S, Godat S, Herzog F, Wermeille E: **Evaluation des mesures de compensation écologique sur la diversité de la flore et des papillons dans la région de Nuvilly-Combremont.** *Revue suisse Agric* 2000, **32:**265-271.
35. Pozzi S: **Evaluation des mesures de compensation écologique dans la région de Nuvilly-Combremont par le biais des araignées.** *Revue suisse Agric* 2004, **36:**57-64.
36. Arlettaz R: **Feeding behaviour and foraging strategy of free-living mouse-eared bats, Myotis myotis and Myotis blythii.** *Anim Behav* 1996, **51:**1-11.
37. Hoste-Danylow A, Romanowski J, Zmihorski M: **Effects of management on invertebrates and birds in extensively used grassland of Poland.** *Agric Ecosyst Environ* 2010, **139:**129-133.
38. Tyler GA, Green RE, Casey C: **Survival and behaviour of Corncrake *Crex crex* chicks during the mowing of agricultural grassland.** *Bird Stud* 1998, **45:**35-50.
39. Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C: **Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management.** *Ecol Lett* 2005, **8:**857-874.
40. Centre for Evidence-Based Conservation: **Guidelines for Systematic Review in Environmental Management. Version 4.0.** *Environmental Evidence* 2010, **www.environmentalevidence.org/Authors.htm**.
41. Pellet J, Wunderlin J: **Does delaying the first mowing date increase biodiversity in European farmland meadows? CEE protocol 09-011 (SR72).** *Collaboration for Environmental Evidence* 2009, **www.environmentalevidence.org/SR72.html**.
42. Pullin AS, Stewart GB: **Guidelines for systematic review in conservation and environmental management.** *Conserv Biol* 2006, **20:**1647-1656.

43. Prieto-Benitez S, Mendez M: **Effects of land management on the abundance and richness of spiders (Araneae): A meta-analysis.** *Biol Conserv* 2011, **144:**683-691.
44. Barrientos R, Alonso JC, Ponce C, Palacin C: **Meta-analysis of the effectiveness of marked wire in reducing avian collisions with power lines.** *Conserv Biol* 2011, **25:**893-903.
45. Gurevitch J, Curtis PS, Jones MH: **Meta-analysis in ecology.** *Adv Ecol Res* 2001, **32:**199-247.
46. Gurevitch J, Hedges LV: **Meta-analysis: combining the results of independent experiments.** In *Design and Analysis of Ecological Experiments.* 2nd edition. Edited by Scheiner SM, Gurevitch J. New York: Chapman and Hall; 2001: 347-369
47. Viechtbauer W: **Conducting meta-analyses in R with the metafor package.** *J Stat Softw* 2010, **36:**1-48.
48. Perera R: **Interpreting meta-analyses in systematic reviews.** *Ann Intern Med* 2009, **150**.
49. Borenstein M, Hedges LV, Higgins JPT, Rothstein HR: *Introduction to Meta-Analysis.* Chichester, UK: Wiley; 2009.
50. Johnson JB, Omland KS: **Model selection in ecology and evolution.** *Trends Ecol Evol* 2004, **19:**101-108.
51. R Development Core Team: **R: A language and environment for statistical computing. R Foundation for Statistical Computing.** Vienna, Austria.
52. Ryser P, Langenauer R, Gigon A: **Species Richness and Vegetation Structure in a Limestone Grassland after 15 Years Management with Six Biomass Removal Regimes.** *Folia Geobot Phytotax* 1995, **30:**157-167.
53. Köhler B, Gigon A, Edwards PJ, Krüsi B, Langenauer R, Lüscher A, Ryser P: **Changes in the species composition and conservation value of limestone grasslands in Northern Switzerland after 22 years of contrasting managements.** *Perspect Plant Ecol Evol Syst* 2005, **7:**51-67.
54. Smith RS, Pullan S, Shiel RS: **Seed shed in the making of hay from mesotrophic grassland in a field in northern England: Effects of hay cut date, grazing and fertilizer in a split-split-plot experiment.** *J Appl Ecol* 1996, **33:**833-841.

55. Cop J, Vidrih M, Hacin J: **Influence of cutting regime and fertilizer application on the botanical composition, yield and nutritive value of herbage of wet grasslands in Central Europe.** *Grass Forage Sci* 2009, **64:**454-465.
56. Morris MG: **Responses of grassland invertebrates to management by cutting. II. Heteroptera.** *J Appl Ecol* 1979, **16:**417-432.
57. Morris MG: **Responses of grassland invertebrates to management by cutting. III. Adverse effects on Auchenorhyncha.** *J Appl Ecol* 1981, **18:**107-123.
58. Bissels S, Holzel N, Otte N: **Population structure of the threatened perennial Serratula tinctoria in relation to vegetation and management.** *Appl Veg Sci* 2004, **7:**267-274.
59. Hegland SJ, Van Leeuwen M, Oostermeijer JGB: **Population structure of Salvia pratensis in relation to vegetation and management of Dutch dry floodplain grasslands.** *J Appl Ecol* 2001, **38:**1277-1289.
60. Tilman D, Downing JA: **Biodiversity and stability in grasslands.** *Nature* 1994, **367:**363-365.
61. Cattin M-F, Blandenier G, Banašek-Richter C, Bersier L-F: **The impact of mowing as a management strategy for wet meadows on spider (Araneae) communities.** *Biol Conserv* 2003, **113:**179-188.
62. Bobbink R, Willems JH: **Impact of different cutting regimes on the performance of Brachypodium pinnatum in Dutch chalk grassland.** *Biol Conserv* 1991, **56:**1-21.
63. Dennis P, Young MR, Gordon IJ: **Distribution and abundance of small insects and arachnids in relation to structural heterogeneity of grazed, indigenous grasslands.** *Ecol Entomol* 1998, **23:**253-264.
64. Woodcock BA, Potts SG, Tscheulin T, Pilgrim E, Ramsey AJ, Harrison-Cripps J, Brown VK, Tallowin JR: **Responses of invertebrate trophic level, feeding guild and body size to the management of improved grassland field margins.** *J Appl Ecol* 2009, **46:**920-929.
65. Humbert J-Y, Ghazoul J, Walter T: **Meadow harvesting techniques and their impacts on field fauna.** *Agric Ecosyst Environ* 2009, **130:**1-8.
66. Reinhardt K, Kohler G, Maas S, Detzel P: **Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany.** *Ecography* 2005, **28:**593-602.

67. Walter T, Schneider K, Gonseth Y: **Schnittzeitpunkt in Ökowiesen: Einfluss auf die Fauna.** *Agrarforschung* 2007, **14:**114-119.
68. Klimek S, Kemmermann ARG, Hofmann M, Isselstein J: **Plant species richness and composition in managed grasslands: The relative importance of field management and environmental factors.** *Biol Conserv* 2007, **134:**559-570.
69. Britschgi A, Spaar R, Arlettaz R: **Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management.** *Biol Conserv* 2006, **130:**193-205.
70. Kruess A, Tscharntke T: **Contrasting responses of plant and insect diversity to variation in grazing intensity.** *Biol Conserv* 2002, **106:**293-302.
71. Wettstein W, Schmid B: **Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers.** *J Appl Ecol* 1999, **36:**363-373.
72. Dover JW, Rescia A, Fungariño S, Fairburn J, Carey P, Lunt P, Dennis RLH, Dover CJ: **Can hay harvesting detrimentally affect adult butterfly abundance?** *J Insect Conserv* 2010, **14:**413-418.
73. Marini L, Fontana P, Battisti A, Gaston KJ: **Agricultural management, vegetation traits and landscape drive orthopteran and butterfly diversity in a grassland-forest mosaic: a multi-scale approach.** *Insect Conserv Diver* 2009, **2:**213-220.
74. Schmidt MH, Rocker S, Hanafi J, Gigon A: **Rotational fallows as overwintering habitat for grassland arthropods: the case of spiders in fen meadows.** *Biodiversity Conserv* 2008, **17:**3003-3012.
75. Humbert J-Y, Ghazoul J, Richner N, Walter T: **Uncut grass refuges mitigate the impact of mechanical meadow harvesting on orthopterans.** *Biol Conserv* 2012*, in press*. DOI: 10.1016/j.biocon.2012.1003.1015.
76. Cizek O, Zamecnik J, Tropek R, Kocarek P, Konvicka M: **Diversification of mowing regime increases arthropods diversity in species-poor cultural hay meadows.** *J Insect Conserv* 2011.

77. Zechmeister HG, Schmitzberger I, Steurer B, Peterseil J, Wrbka T: **The influence of land-use practices and economics on plant species richness in meadows.** *Biol Conserv* 2003, **114:**165-177.
78. Helden AJ, Leather SR: **Biodiversity on urban roundabouts-Hemiptera, management and the species-area relationship.** *Basic Appl Ecol* 2004, **5:**367-377.
79. Blake RJ, Woodcock BA, Ramsay AJ, Pilgrim ES, Brown VK, Tallowin JR, Potts SG: **Novel margin management to enhance Auchenorrhyncha biodiversity in intensive grasslands.** *Agric Ecosyst Environ* 2011, **140:**506-513.
80. Olsson O, Brady M, Hart R: **Optimal delay of harvest – implications for bird populations and economic compensation.** *Asp Appl Biol* 2010, **100:**1-8.
81. Green RE: **Factors affecting the population density of the corncrake Crex crex in Britain and Ireland.** *J Appl Ecol* 1996, **33:**237-248.
82. Müller M, Spaar R, Schifferli L, Jenni L: **Effects of changes in farming of subalpine meadows on a grassland bird, the whinchat (*Saxicola rubetra*).** *J Ornithology* 2005, **146:**14-23.
83. Bretagnolle V, Villers A, Denonfoux L, Cornulier T, Inchausti P, Badenhausser I: **Rapid recovery of a depleted population of Little Bustards *Tetrax tetrax* following provision of alfalfa through an agri-environment scheme.** *Ibis* 2011, **153:**4-13.
84. Nocera JJ, Parsons GJ, Milton GR, Fredeen AH: **Compatibility of delayed cutting regime with bird breeding and hay nutritional quality.** *Agric Ecosyst Environ* 2005, **107:**245-253.
85. Haddad NM, Haarstad J, Tilman D: **The effects of long-term nitrogen loading on grassland insect communities.** *Oecologia* 2000, **124:**73-84.
86. Littlewood NA, Stewart AJ, Woodcock BA: **Science into practice – how can fundamental science contribute to better management of grasslands for invertebrates?** *Insect Conserv Diver* 2012, **5:**1-8.
87. Schmidt MH, Roschewitz I, Thies C, Tscharntke T: **Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders.** *J Appl Ecol* 2005, **42:**281-287.

88. Beltman B, van den Broek T, Martin W, ten Cate M, Gusewell S: **Impact of mowing regime on species richness and biomass of a limestone hay meadow in Ireland.** *Bull Geobot Inst ETH* 2003, **69:**17-30.
89. Fenner M, Palmer L: **Grassland management to promote diversity: creation of a patchy sward by mowing and fertiliser regimes.** *Field Studies* 1998, **9:**313-324.
90. Hellstrom K, Huhta AP, Rautio P, Tuomi J: **Search for optimal mowing regime - slow community change in a restoration trial in northern Finland.** *Ann Bot Fenn* 2006, **43:**338-348.
91. Kirkham FW, Tallowin JRB: **The influence of cutting date and previous fertilizer treatment on the productivity and botanical composition of species-rich hay meadows on the Somerset Levels.** *Grass Forage Sci* 1995, **50:**365-377.
92. Marriott CA, Bolton GR, Fisher JM: **Changes in species composition of abandoned sown swards after imposing seasonal cutting treatments.** *Grass Forage Sci* 2003, **58:**37-49.
93. Smith RS, Buckingham H, Bullard MJ, Shiel RS, Younger A: **The conservation management of mesotrophic (meadow) grassland in northern England .1. Effects of grazing, cutting date and fertilizer on the vegetation of a traditionally managed sward.** *Grass Forage Sci* 1996, **51:**278-291.
94. Woodcock BA, Potts SG, Pilgrim E, Ramsay AJ, Tscheulin T, Parkinson A, Smith REN, Gundrey AL, Brown VK, Tallowin JR: **The potential of grass field margin management for enhancing beetle diversity in intensive livestock farms.** *J Appl Ecol* 2007, **44:**60-69.
95. Oomes MJM, Mooi H: **The effect of cutting and fertilizing on the floristic composition and production of an Arrhenatherion elatioris grassland.** *Vegetatio* 1981, **46-7:**233-239.
96. Selinger-Looten R, Muller S: **Restoration of grassland in old maize-cultivated land: impact of mowing and role of soil seed bank.** *Revue D Ecologie-La Terre Et La Vie* 2001, **56:**3-19.
97. Potts SG, Woodcock BA, Roberts SPM, Tscheulin T, Pilgrim ES, Brown VK, Tallowin JR: **Enhancing pollinator biodiversity in intensive grasslands.** *J Appl Ecol* 2009, **46:**369-379.

Table 1: Data points and respective references included in the meta-analysis.

All 55 data points (unit of analysis) and their respective references included in the meta-analysis. Rows are ordered by taxon and specific outcome measures. Note that rows with two outcomes (species richness and abundance) count as two data points. The time (month) of the early and delayed first cut are given for both control and treatment plots, as well as the duration of the study in years and the sample size. Studies where the Standard Deviation (SD) was not provided could only be included in meta-analyses based on the response ratio. See Additional file 1 for more details on each data points.

Taxon	Outcomes		Early cut (control)	Delayed cut (treatment)	Study duration in years	Sample size	SD provided	Reference
	Species richness	Abun-dance						
Plants	x		May	July	11	4	yes	Beltman et al. 2003 [88]
Plants	x		June	Sept	20	9	yes	Bissels et al. 2004 [58]
Plants	x		June	Aug	2	8	yes	Bobbink and Willems 1991, exp.1 [62]
Plants	x		June	Nov	2	8	yes	Bobbink and Willems 1991, exp.1 [62]
Plants	x		Aug	Nov	2	8	yes	Bobbink and Willems 1991, exp.1 [62]
Plants	x		Aug	Nov	4	2	yes	Bobbink and Willems 1991, exp.2 [62]
Plants	x		Early June	Late June	6	16	yes	Cop et al. 2009, exp.2 [55]
Plants	x		June	Aug	13	3	yes	Fenner and Palmer 1998 [89]
Plants	x		Late June	Late July	40	9	yes	Hegland et al. 2001 [59]
Plants	x		June	Aug	5	10	yes	Hellström et al. 2006 [90]
Plants	x		May	July	2	6	yes	Kirkham and Tallowin 1995 [91]

Plants	x	May	Aug	2	6	yes	Kirkham and Tallowin 1995 [91]
Plants	x	May	Sept	2	6	yes	Kirkham and Tallowin 1995 [91]
Plants	x	July	Aug	2	6	yes	Kirkham and Tallowin 1995 [91]
Plants	x	July	Sept	2	6	yes	Kirkham and Tallowin 1995 [91]
Plants	x	Aug	Sept	2	6	yes	Kirkham and Tallowin 1995 [91]
Plants	x	July	Oct	22	6	yes	Köhler et al. 2005 [53]
Plants	x	June	Oct	6	24	yes	Marriott et al. 2003 [92]
Plants	x	June	July	11	8	yes	Parr and Way 1988 [17]
Plants	x	June	July	4	18	yes	Smith et al. 1996b [93]
Plants	x	June	Sept	4	18	yes	Smith et al. 1996b [93]
Plants	x	July	Sept	4	18	yes	Smith et al. 1996b [93]
Plants	x	June	July	8	36	yes	Smith et al. 2000 [19]
Plants	x	June	Sept	8	36	yes	Smith et al. 2000 [19]
Plants	x	July	Sept	8	36	yes	Smith et al. 2000 [19]
Plants	x	May	July	3	12	yes	Woodcock et al. 2007 [94]
Plants	x	July	Sept	25	1	no	Bakker et al. 2002 [18]
Plants	x	May	June	7	4	no	Oomes and Mooi 1981 [95]
Plants	x	May	Aug	7	4	no	Oomes and Mooi 1981 [95]
Plants	x	May	Sept	7	4	no	Oomes and Mooi 1981 [95]
Plants	x	June	Aug	7	4	no	Oomes and Mooi 1981 [95]
Plants	x	June	Sept	7	4	no	Oomes and Mooi 1981 [95]
Plants	x	Aug	Sept	7	4	no	Oomes and Mooi 1981 [95]
Plants	x	May+Sept	June+Sept	7	4	no	Oomes and Mooi 1981 [95]
Plants	x	Early June	Late June	4	1	no	Selinger-L. and Muller 2001 [96]

Auchenorrhyncha	x	x	May	July	3	12	yes	Blake et al. 2011 [79]
Invertebrates	x		June	Aug	13	3	yes	Fenner and Palmer 1998 [89]
Heteroptera	x	x	May	July	3	4	yes	Morris 1979 [56]
Auchenorhyncha	x	x	May	July	3	4	yes	Morris 1981a [57]
Bumblebees	x	x	May	July	4	12	yes	Potts et al. 2009 [97]
Butterflies	x	x	May	July	4	12	yes	Potts et al. 2009 [97]
Butterfly larvae		x	May	July	4	12	yes	Potts et al. 2009 [97]
Butterflies	x	x	July	Aug	unknown	18	yes	Valtonen et al. 2006 [31]
Diurnal moths	x	x	July	Aug	unknown	18	yes	Valtonen et al. 2006 [31]
Beetles	x	x	May	July	3	12	yes	Woodcock et al. 2007 [94]
Coleoptera	x	x	May	July	2	4	no	Morris and Rispin 1987 [21]

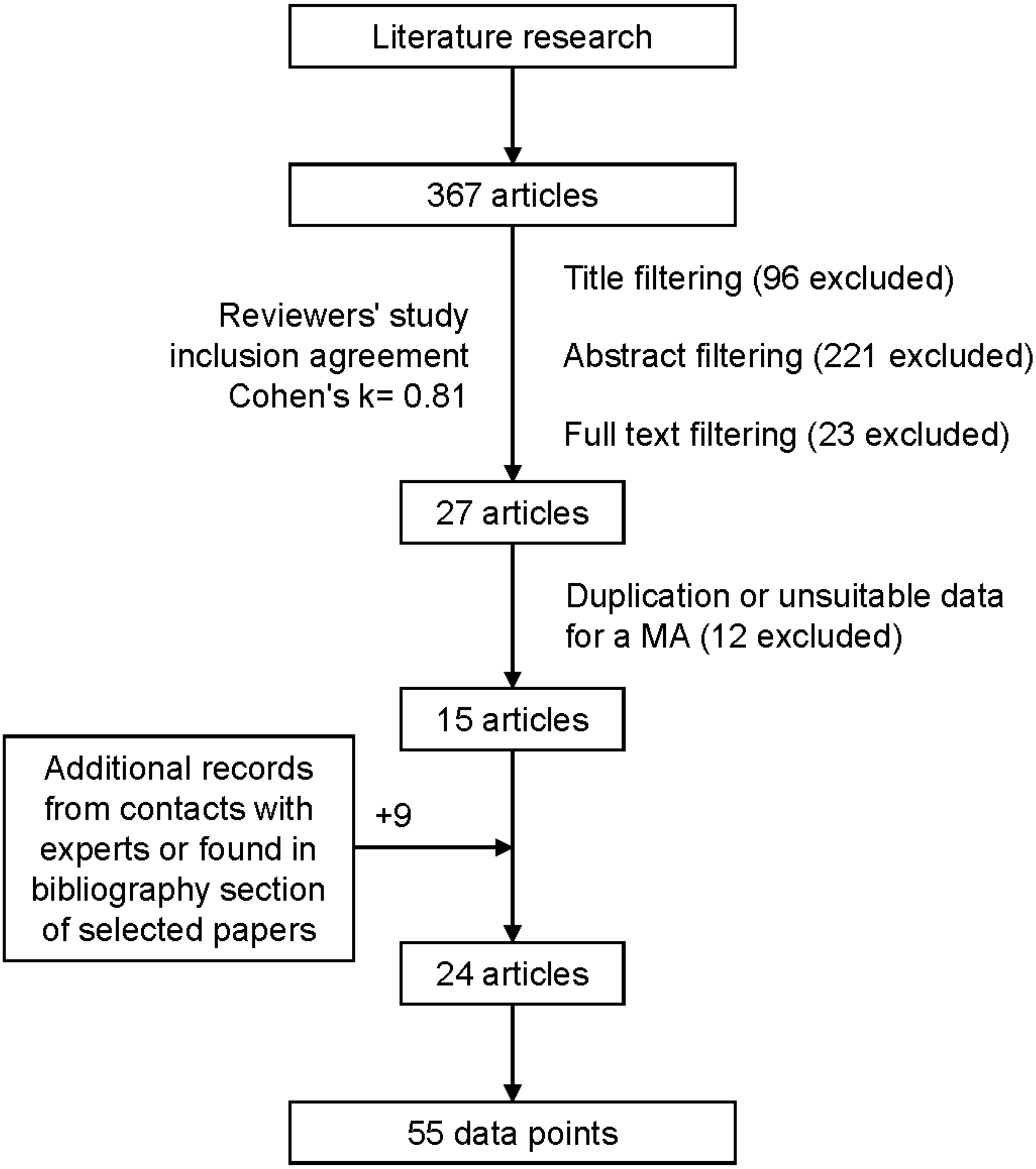


Figure 1. Flow diagram reporting the number of records identified, excluded and added during the literature research process.

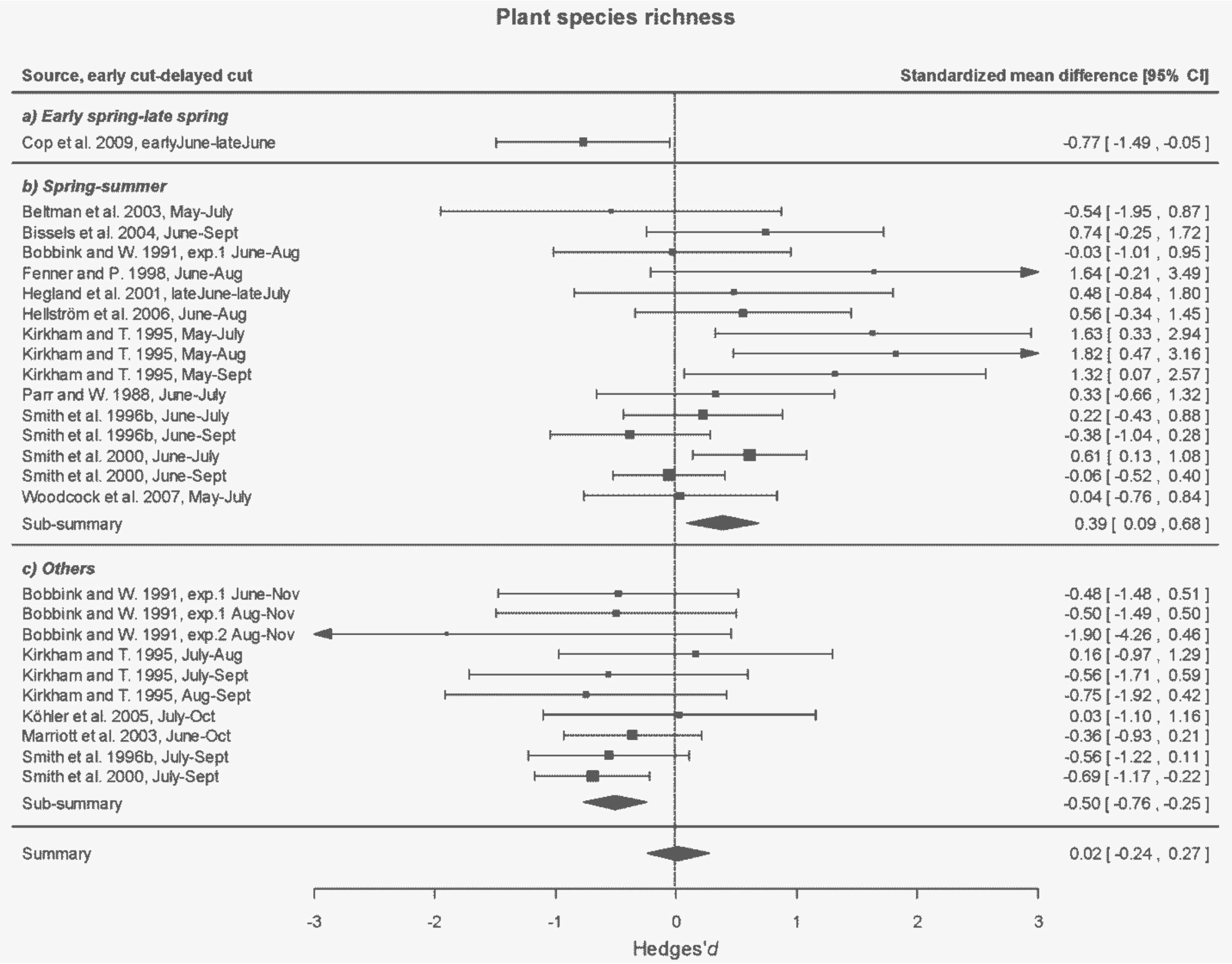


Figure 2. Forest plot showing the effect of delaying the first mowing date on plant species richness. The Forest plot is divided in three sections according to postponing schedule: a) study that delayed the first cut from early spring to late spring, b) studies that delayed the first cut from spring (May-June) to summer (July-August-September), and c) studies that delayed the first cut from spring to fall, early summer to late summer or summer to fall. Effect sizes are Hedges'*d*, i.e. the standardized mean differences between delayed and early cuts. The squares and bars represent the mean values and 95% confidence intervals of the effect sizes, while the size of the squares reflects the weight of the studies. The combined effects (sub-summary and summary) appear as diamonds and the vertical dashed line represents the line of no effect.

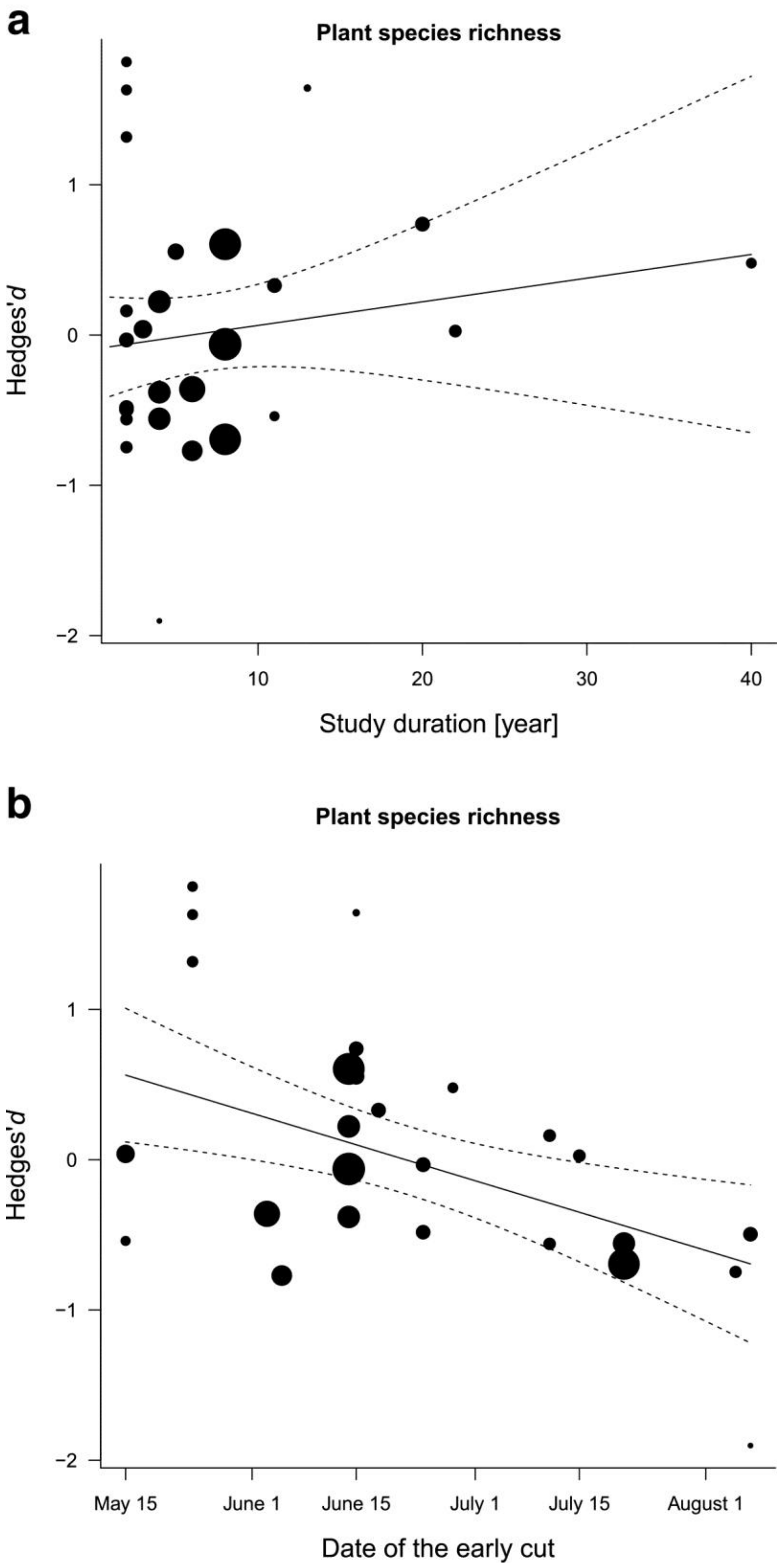


Figure 3. Standardized mean differences (Hedges'*d*) of the effect of delaying the first mowing date on plant species richness as a function of a) study duration (in years), or b) the date of the early cut (control plot). The size of the dots reflects the weight of the study.

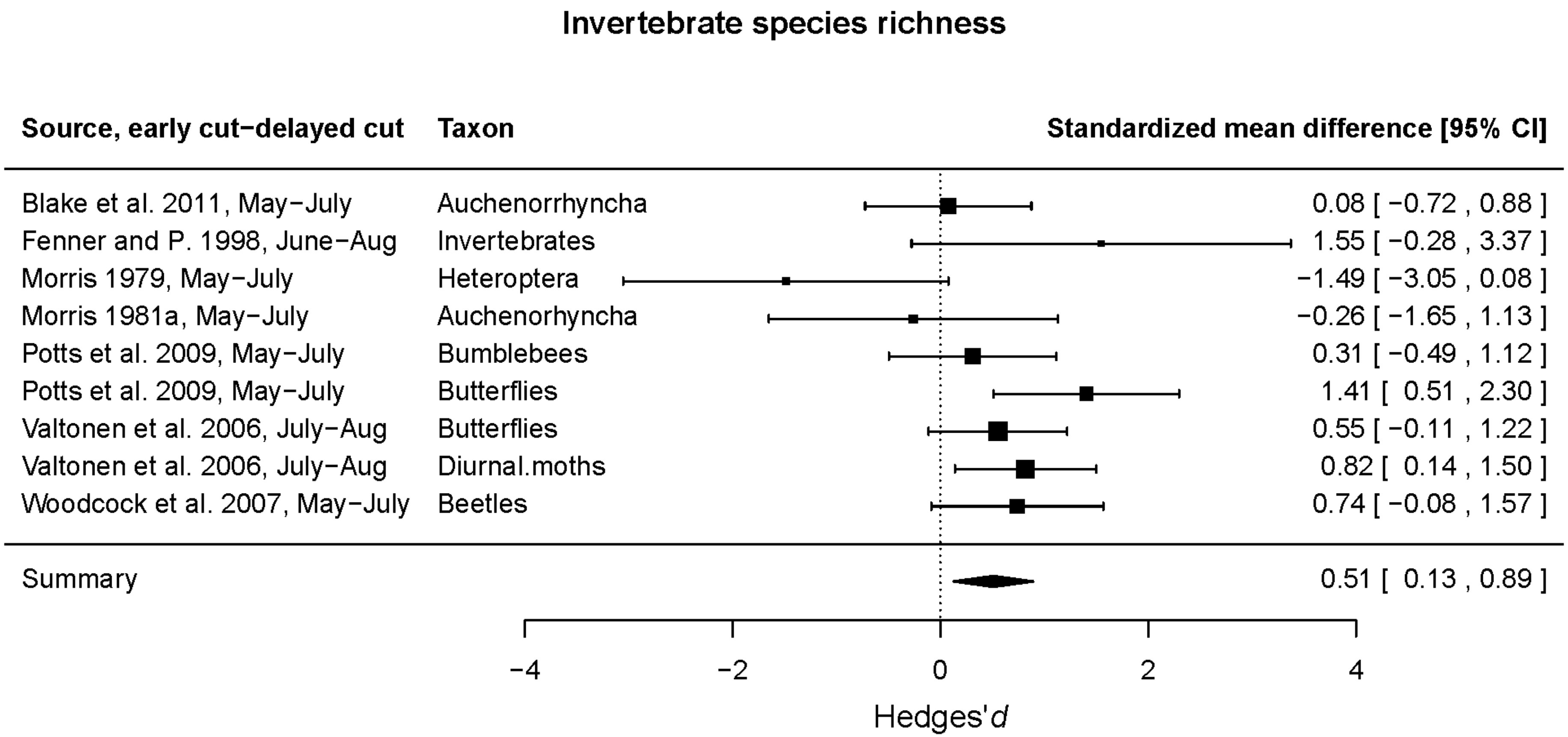


Figure 4. Forest plot showing the effect of delaying the first mowing date on invertebrate species richness. See legend of Fig. 2 for more details on the Forest plot structure.

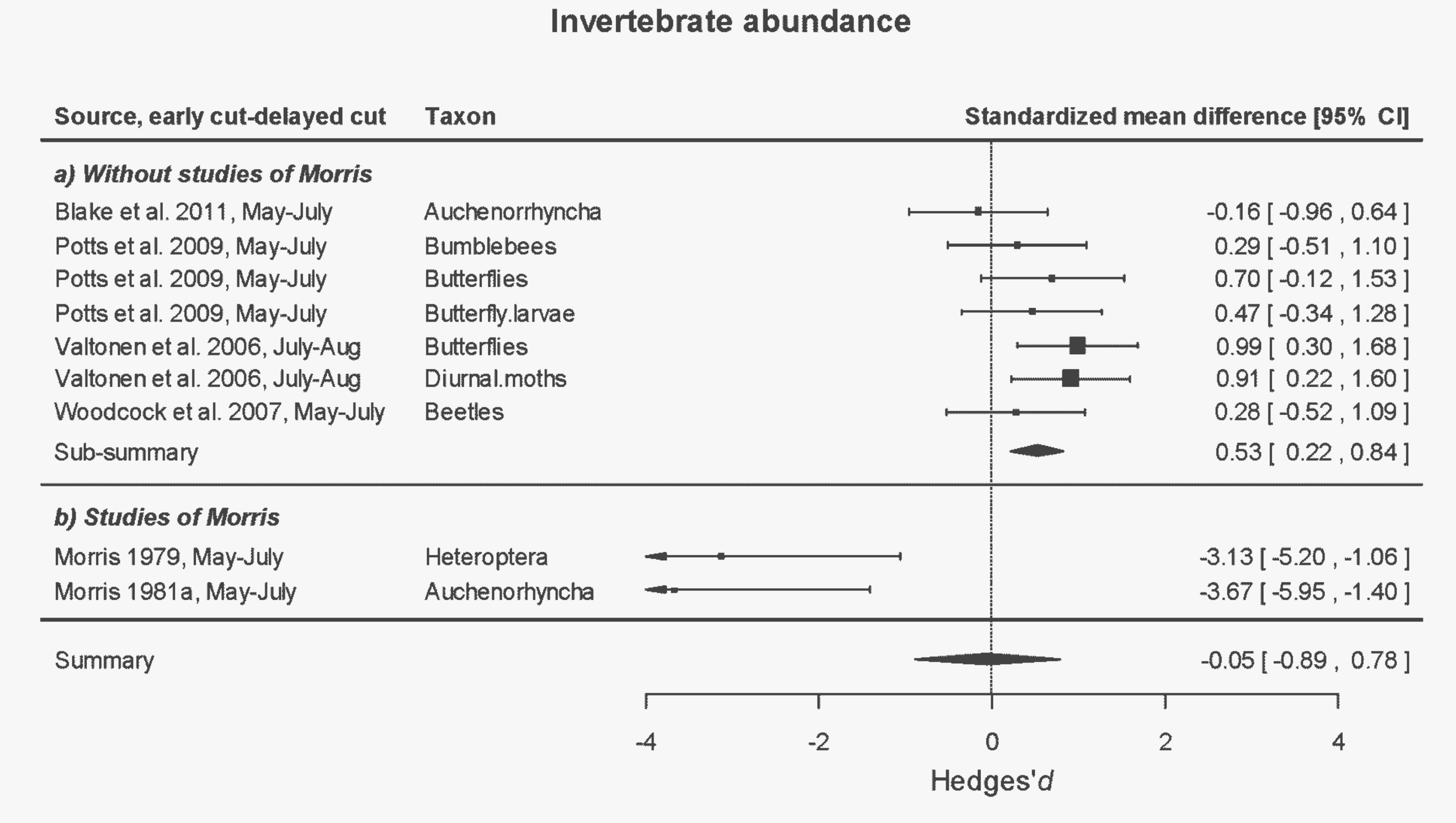


Figure 5. The Forest plot is divided in two sections: a) without the two studies of Morris, and b) the two studies of Morris (see text in the Result and discussion section). The overall combined effect (summary) includes all studies, while the sub-summary does not include Morris's studies. See legend of Fig. 2 for more details on the Forest plot structure.

Additional file 1: Detailed information on each data point, including weighted and unweighted effect sizes

	Source (reference)	Journal	Months of early cut-delayed cut
1	Beltman et al. 2003	Bull. Geobota. Inst. ETH	May-July
2	Bissels et al. 2004	Appl. Veg. Sci.	June-Sept
3	Bobbink and Willems 1991, exp. 1	Biol. Conserv.	June-Aug
4	Bobbink and Willems 1991, exp. 1	Biol. Conserv.	June-Nov
5	Bobbink and Willems 1991, exp. 1	Biol. Conserv.	Aug-Nov
6	Bobbink and Willems 1991, exp. 2	Biol. Conserv.	Aug-Nov
7	Cop et al. 2009	Grass Forage Sci.	earlyJune-lateJune
8	Fenner and Palmer 1998	Field Studies	June-Aug
9	Hegland et al. 2001	J. Appl. Ecol.	lateJune-lateJuly
10	Hellström et al. 2006	Anna. Bot. Fennici	June-Aug
11	Kirkham and Tallowin 1995	Grass Forage Sci.	May-July
12	Kirkham and Tallowin 1995	Grass Forage Sci.	May-Aug
13	Kirkham and Tallowin 1995	Grass Forage Sci.	May-Sept
14	Kirkham and Tallowin 1995	Grass Forage Sci.	July-Aug
15	Kirkham and Tallowin 1995	Grass Forage Sci.	July-Sept
16	Kirkham and Tallowin 1995	Grass Forage Sci.	Aug-Sept
17	Köhler et al. 2005	Perspect. Plant Ecol. Evol. Syst.	July-Oct
18	Marriott et al. 2003	Grass Forage Sci.	June-Oct
19	Parr and Way 1988	J. Appl. Ecol.	June-July
20	Smith et al. 1996b	Grass Forage Sci.	June-July
21	Smith et al. 1996b	Grass Forage Sci.	June-Sept
22	Smith et al. 1996b	Grass Forage Sci.	July-Sept
23	Smith et al. 2000	J. Appl. Ecol.	June-July
24	Smith et al. 2000	J. Appl. Ecol.	June-Sept
25	Smith et al. 2000	J. Appl. Ecol.	July-Sept
26	Woodcock et al. 2007	J. Appl. Ecol.	May-July
27	Bakker et al. 2002	Appl. Veg. Sci.	July-Sept
28	Oomes and Mooi 1981	Vegetatio	May-June
29	Oomes and Mooi 1981	Vegetatio	May-Aug
30	Oomes and Mooi 1981	Vegetatio	May-Sept
31	Oomes and Mooi 1981	Vegetatio	June-Aug
32	Oomes and Mooi 1981	Vegetatio	June-Sept
33	Oomes and Mooi 1981	Vegetatio	Aug-Sept
34	Oomes and Mooi 1981	Vegetatio	MaySept-JuneSept
35	Selinger-Looten and Muller 2001	Rev. Ecol (Terre Vie)	earlyJune-lateJune
36	Blake et al. 2011	Agric. Ecosyst. Environ.	May-July
37	Fenner and Palmer 1998	Field Studies	June-Aug
38	Morris 1979	J. Appl. Ecol.	May-July
39	Morris 1981	J. Appl. Ecol.	May-July
40	Potts et al. 2009	J. Appl. Ecol.	May-July
41	Potts et al. 2009	J. Appl. Ecol.	May-July
42	Valtonen et al. 2006	Anim. Bio. Conserv.	July-Aug
43	Valtonen et al. 2006	Anim. Bio. Conserv.	July-Aug
44	Woodcock et al. 2007	J. Appl. Ecol.	May-July
45	Morris and Rispin 1987	J. Appl. Ecol.	May-July
46	Blake et al. 2011	Agric. Ecosyst. Environ.	May-July
47	Morris 1979	J. Appl. Ecol.	May-July
48	Morris 1981	J. Appl. Ecol.	May-July
49	Potts et al. 2009	J. Appl. Ecol.	May-July
50	Potts et al. 2009	J. Appl. Ecol.	May-July
51	Potts et al. 2009	J. Appl. Ecol.	May-July
52	Valtonen et al. 2006	Anim. Bio. Conserv.	July-Aug
53	Valtonen et al. 2006	Anim. Bio. Conserv.	July-Aug
54	Woodcock et al. 2007	J. Appl. Ecol.	May-July
55	Morris and Rispin 1987	J. Appl. Ecol.	May-July

continued

Additional file 1 (continued)
* Plot size, only for vegetation relevés

	Country	Taxa	Outcome metric	Habitat	Plot size [m²]*
1	Ireland	Plants	sp. richness	meso	1
2	Germany	Plants	sp. richness	wet	1
3	Netherlands	Plants	sp. richness	meso	0.25
4	Netherlands	Plants	sp. richness	meso	0.25
5	Netherlands	Plants	sp. richness	meso	0.25
6	Netherlands	Plants	sp. richness	meso	0.0625
7	Slovenia	Plants	sp. richness	wet	0.49
8	UK	Plants	sp. richness	meso	0.25
9	Netherland	Plants	sp. richness	dry	4
10	Finland	Plants	sp. richness	dry	0.25
11	UK	Plants	sp. richness	wet	0.25
12	UK	Plants	sp. richness	wet	0.25
13	UK	Plants	sp. richness	wet	0.25
14	UK	Plants	sp. richness	wet	0.25
15	UK	Plants	sp. richness	wet	0.25
16	UK	Plants	sp. richness	wet	0.25
17	Switzerland	Plants	sp. richness	meso	36
18	UK, Scotland	Plants	sp. richness	meso	0.25
19	UK	Plants	sp. richness	meso	0.0225
20	UK	Plants	sp. richness	meso	1
21	UK	Plants	sp. richness	meso	1
22	UK	Plants	sp. richness	meso	1
23	UK	Plants	sp. richness	meso	4
24	UK	Plants	sp. richness	meso	4
25	UK	Plants	sp. richness	meso	4
26	UK	Plants	sp. richness	meso	1
27	Netherlands	Plants	sp. richness	meso	4
28	Netherlands	Plants	sp. richness	wet	2
29	Netherlands	Plants	sp. richness	wet	2
30	Netherlands	Plants	sp. richness	wet	2
31	Netherlands	Plants	sp. richness	wet	2
32	Netherlands	Plants	sp. richness	wet	2
33	Netherlands	Plants	sp. richness	wet	2
34	Netherlands	Plants	sp. richness	wet	2
35	France	Plants	sp. richness	wet	0.0625
36	UK	Auchenorrhyncha	sp. richness	meso	NA
37	UK	Invertebrates	sp. richness	meso	NA
38	UK	Heteroptera	sp. richness	meso	NA
39	UK	Auchenorhyncha	sp. richness	meso	NA
40	UK	Bumblebees	sp. richness	meso	NA
41	UK	Butterflies	sp. richness	meso	NA
42	Finland	Butterflies	sp. richness	meso	NA
43	Finland	Diurnal.moths	sp. richness	meso	NA
44	UK	Beetles	sp. richness	meso	NA
45	UK	Coleoptera	sp. richness	meso	NA
46	UK	Auchenorrhyncha	abundance	meso	NA
47	UK	Heteroptera	abundance	meso	NA
48	UK	Auchenorhyncha	abundance	meso	NA
49	UK	Bumblebees	abundance	meso	NA
50	UK	Butterflies	abundance	meso	NA
51	UK	Butterfly.larvae	abundance	meso	NA
52	Finland	Butterflies	abundance	meso	NA
53	Finland	Diurnal.moths	abundance	meso	NA
54	UK	Beetles	abundance	meso	NA
55	UK	Coleoptera	abundance	meso	NA

continued

Additional file 1 (continued)

	Ordinal day of the first cut			Sample size	
	Early cut (control)	**Delayed cut (treatment)**	**Nb. of days between**	**Control**	**Treatment**
1	135	196	61	4	4
2	166	258	92	9	8
3	175	219	44	8	8
4	175	311	136	8	8
5	219	311	92	8	8
6	219	311	92	2	2
7	156	176	20	16	16
8	166	227	61	3	3
9	179	204	25	9	3
10	166	227	61	10	10
11	144	192	48	6	6
12	144	217	73	6	6
13	144	245	101	6	6
14	192	217	25	6	6
15	192	245	53	6	6
16	217	245	28	6	6
17	196	288	92	6	6
18	154	276	122	24	24
19	169	198	29	8	8
20	165	202	37	18	18
21	165	244	79	18	18
22	202	244	42	18	18
23	165	202	37	36	36
24	165	244	79	36	36
25	202	244	42	36	36
26	135	196	61	12	12
27	196	258	62	1	1
28	135	166	31	4	4
29	135	227	92	4	4
30	135	258	123	4	4
31	166	227	61	4	4
32	166	258	92	4	4
33	227	258	31	4	4
34	135	166	31	4	4
35	158	175	17	1	1
36	135	196	61	12	12
37	166	227	61	3	3
38	142	198	56	4	4
39	142	198	56	4	4
40	135	196	61	12	12
41	135	196	61	12	12
42	190	217	27	18	18
43	190	217	27	18	18
44	135	196	61	12	12
45	142	198	56	4	4
46	135	196	61	12	12
47	142	198	56	4	4
48	142	198	56	4	4
49	135	196	61	12	12
50	135	196	61	12	12
51	135	196	61	12	12
52	190	217	27	18	18
53	190	217	27	18	18
54	135	196	61	12	12
55	142	198	56	4	4

continued

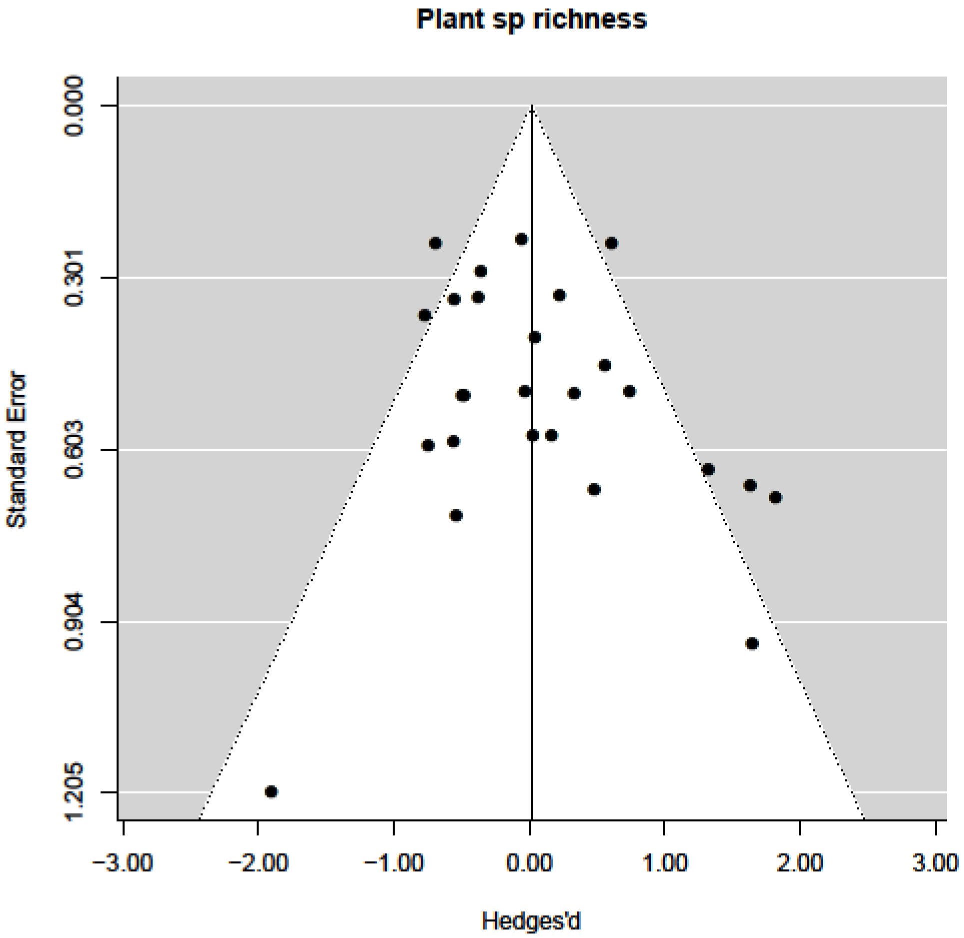
Additional file 1 (continued)

			Effect sizes		
	Study duration in year	**SD provided**	**Hedges'*d***	**Response ratio**	**Variance of Hedges'*d***
1	11	Yes	-0.5398	-0.0817	0.5182
2	20	Yes	0.7387	0.1523	0.2522
3	2	Yes	-0.0321	-0.0056	0.2500
4	2	Yes	-0.4815	-0.0938	0.2572
5	2	Yes	-0.4950	-0.0882	0.2577
6	4	Yes	-1.9021	-0.6838	1.4522
7	6	Yes	-0.7695	-0.1509	0.1343
8	13	Yes	1.6436	0.2247	0.8918
9	40	Yes	0.4789	0.1429	0.4540
10	5	Yes	0.5555	0.1767	0.2077
11	2	Yes	1.6316	0.1194	0.4443
12	2	Yes	1.8181	0.1322	0.4711
13	2	Yes	1.3182	0.0800	0.4057
14	2	Yes	0.1612	0.0128	0.3344
15	2	Yes	-0.5594	-0.0393	0.3464
16	2	Yes	-0.7459	-0.0521	0.3565
17	22	Yes	0.0272	0.0037	0.3334
18	6	Yes	-0.3585	-0.1594	0.0847
19	11	Yes	0.3302	0.0392	0.2534
20	4	Yes	0.2229	0.0287	0.1118
21	4	Yes	-0.3794	-0.0600	0.1131
22	4	Yes	-0.5555	-0.0887	0.1154
23	8	Yes	0.6062	0.1532	0.0581
24	8	Yes	-0.0597	-0.0128	0.0556
25	8	Yes	-0.6920	-0.1661	0.0589
26	3	Yes	0.0397	0.0121	0.1667
27	25	No	NA	0.0741	NA
28	7	No	NA	0.0000	NA
29	7	No	NA	-0.0370	NA
30	7	No	NA	-0.0370	NA
31	7	No	NA	-0.0370	NA
32	7	No	NA	-0.0370	NA
33	7	No	NA	0.0000	NA
34	7	No	NA	-0.0561	NA
35	5	No	NA	-0.0445	NA
36	3	Yes	0.0769	0.0188	0.1668
37	13	Yes	1.5481	0.1823	0.8664
38	3	Yes	-1.4870	-0.2651	0.6382
39	3	Yes	-0.2598	-0.0198	0.5042
40	4	Yes	0.3114	0.6217	0.1687
41	4	Yes	1.4059	1.1507	0.2078
42	NA	Yes	0.5539	0.2036	0.1154
43	NA	Yes	0.8208	0.2573	0.1205
44	3	Yes	0.7430	0.1159	0.1782
45	2	No	NA	-0.0721	NA
46	3	Yes	-0.5986	-0.2631	0.1741
47	3	Yes	-3.1328	-1.2231	1.1134
48	3	Yes	-3.6746	-0.8692	1.3439
49	4	Yes	0.6201	2.9832	0.1747
50	4	Yes	0.2931	0.7309	0.1685
51	4	Yes	0.7318	0.5729	0.1778
52	NA	Yes	0.9912	0.5616	0.1248
53	NA	Yes	0.9095	0.5058	0.1226
54	3	Yes	0.6619	0.2269	0.1758
55	2	No	NA	-0.3185	NA

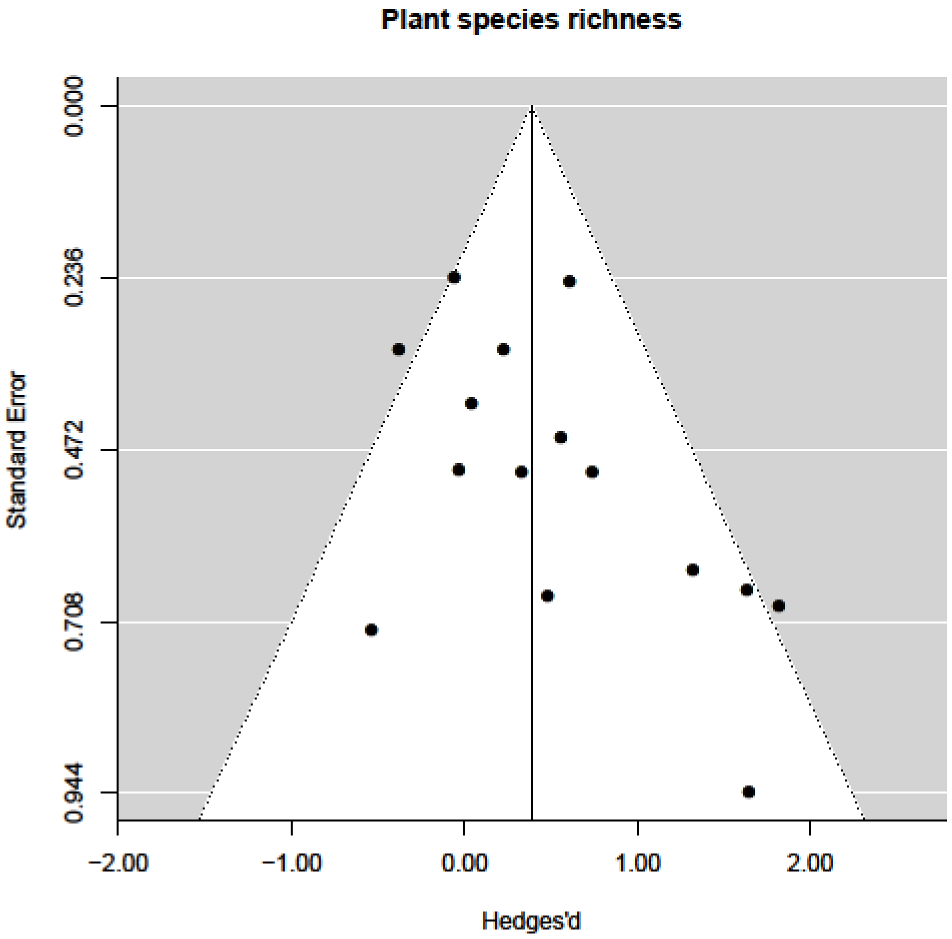
Additional file 2: Funnel plots of the meta-analyses

Effects of delaying the first mowing date on plant species richness

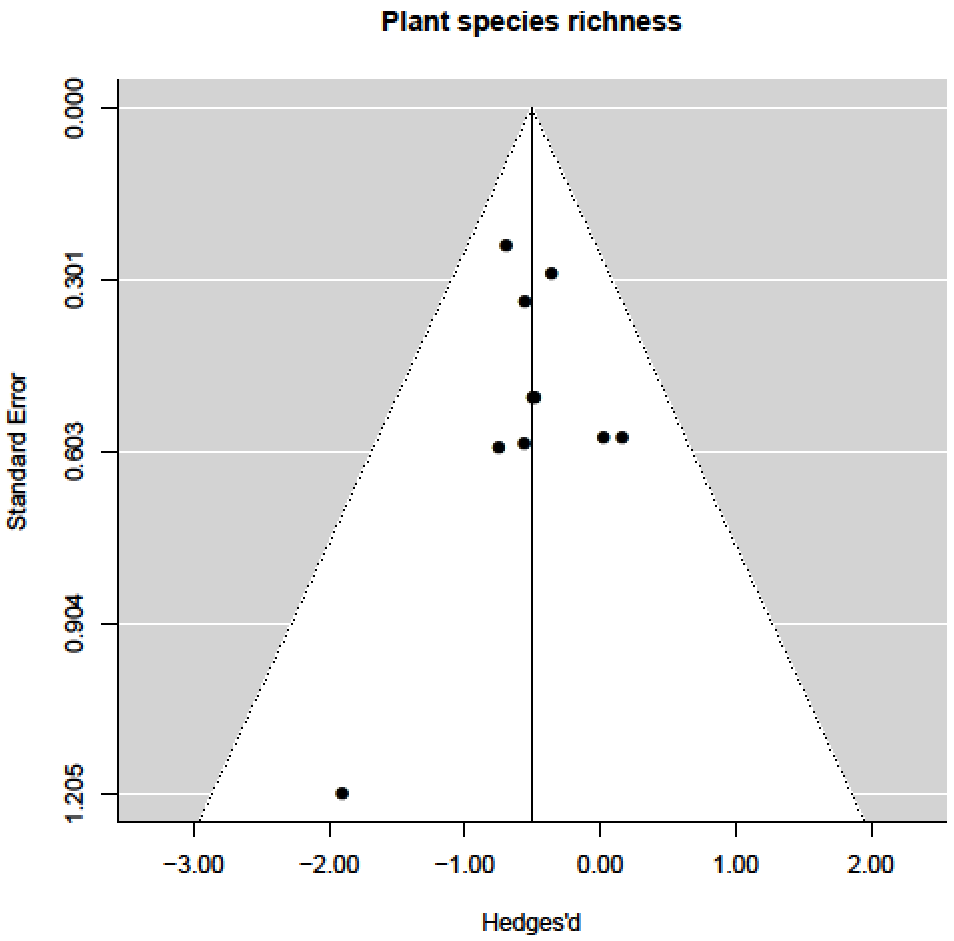
Funnel plot 1: Refers to all studies of the Forest plot Fig. 2 of the article. The study effect sizes (Hedges'*d*) are plotted as a function of their standard errors.



Funnel plot 2: Refers to the studies that delayed the first cut from spring (May-June) to summer (July-August-September) of the Forest plot Fig. 2b of the article.

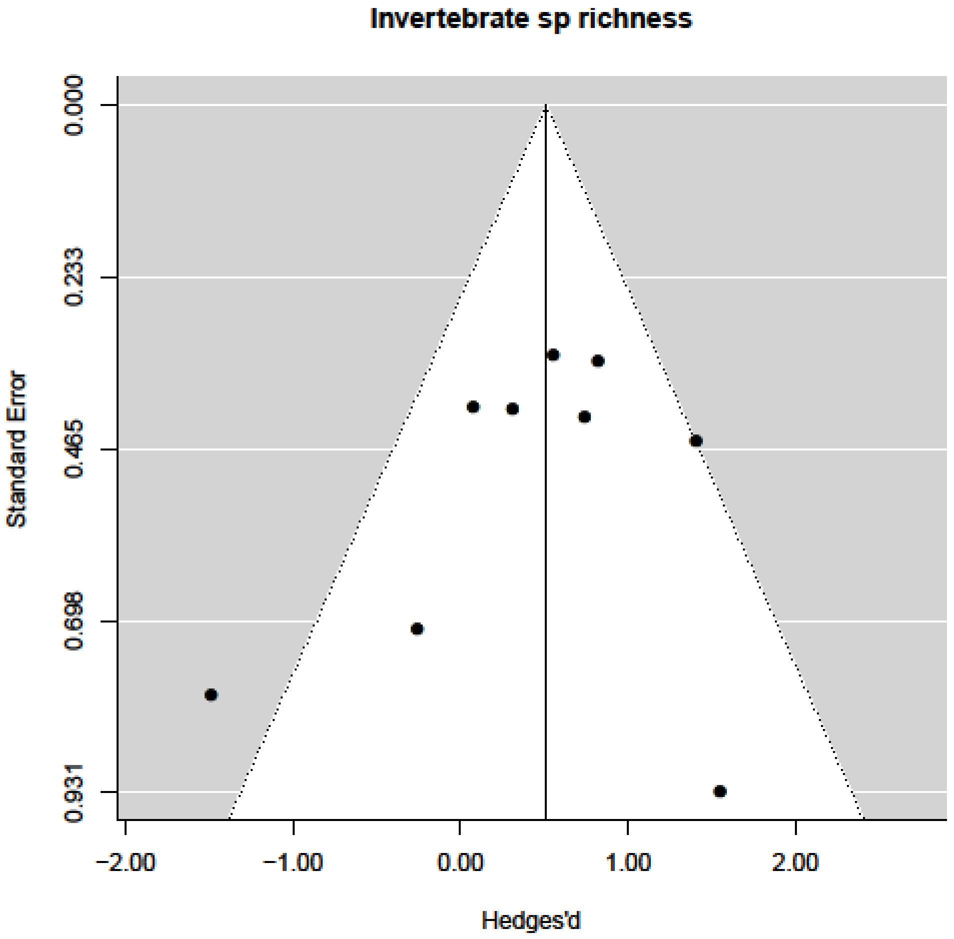


Funnel plot 3: Refers to the studies that delayed the first cut from spring to fall, early summer to late summer or summer to fall of the Forest plot Fig. 2c of the article.



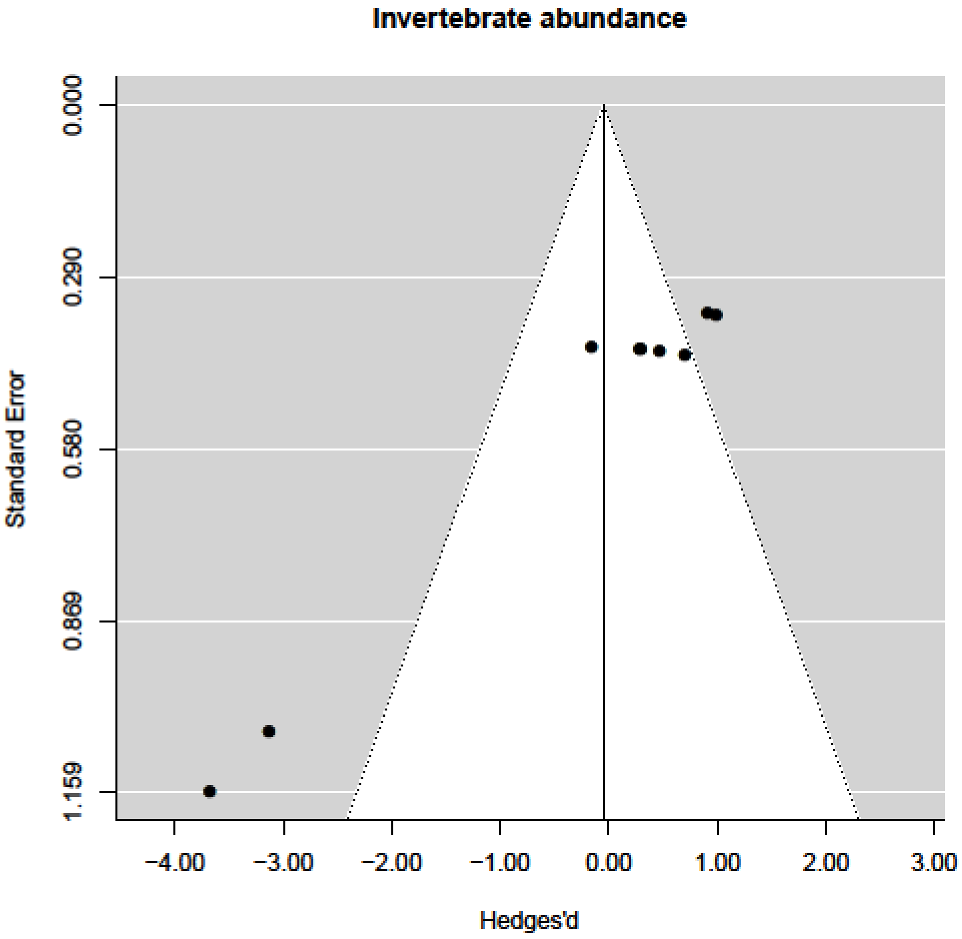
Effects on invertebrate species richness

Funnel plot 4: Refers to all studies of the Forest plot Fig. 4 of the article.

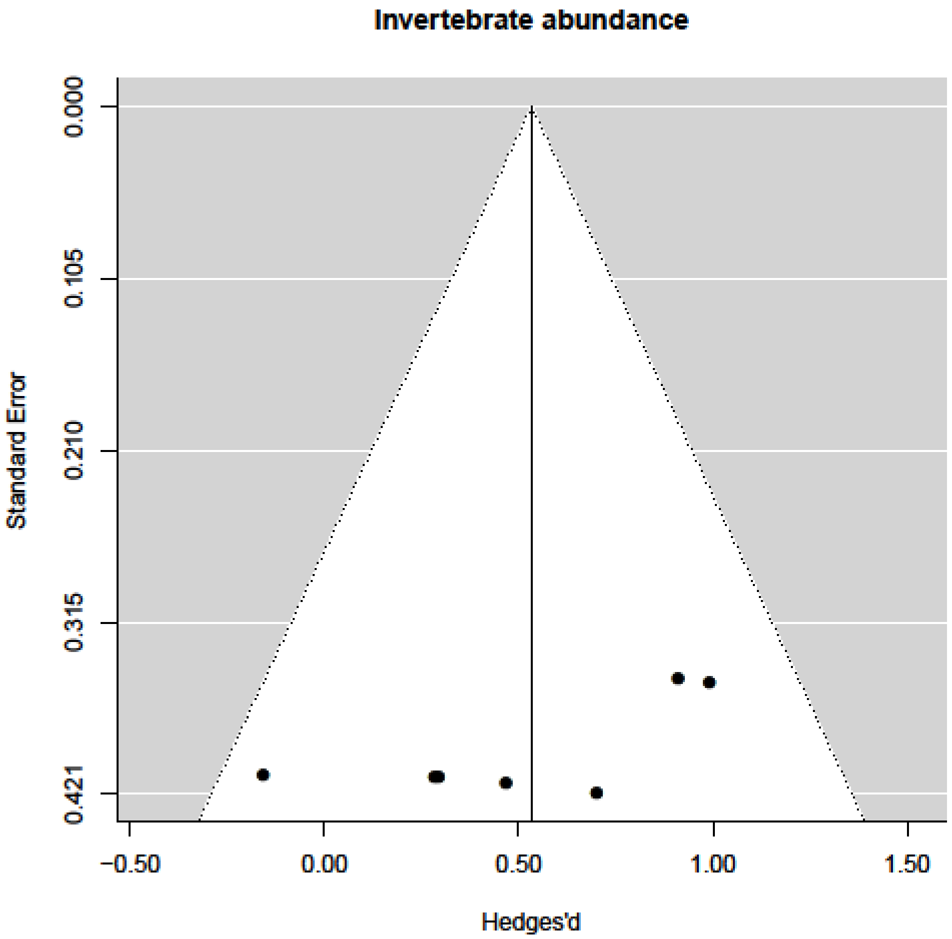


Effects on invertebrate abundance

Funnel plot 5: Refers to all studies of the Forest plot Fig. 5 of the article.



Funnel plot 6: Refers to all studies of the Forest plot Fig. 5a of the article.



Additional file 3: Results of the unweigthed meta-analyses

In addition to the proper weighted meta-analyses (see main text), unweighted meta-analyses were performed using the response ratio as effect size. Response ratio (*lr*) is equal to the natural logarithm of the ratio of the delayed on the early cut date (Gurevitch et al. 2001). Note that this way a positive value means a positive effect of delaying mowing.

$$lr = ln(\bar{X}^D/\bar{X}^E)$$

Although less powerful than proper-weighted meta-analyses, this approach allows the inclusion of studies that did not reported SD or where sample size was one, i.e. studies for which no Hedges'*d* could be calculated. In our case it allowed the inclusion of nine extra studies on plants species richness and one extra study on invertebrate (Coleoptera) species richness and abundance (see Table 1 main text for references). All studies were given the same weight and bootstrapping was used to calculate 95% confidence intervals (CI); if CI overlapped zero, the mean effect size was considered non significant. The original effect sizes (*lr*) of each study are provided in the "Additional file 1".

Effects of delaying the first mowing date on plant species richness

No overall significant effect of delaying the first mowing date on plant species richness was found (mean *lr* = 0.017 with 95% CI -0.070 – 0.028, Fig. 1).

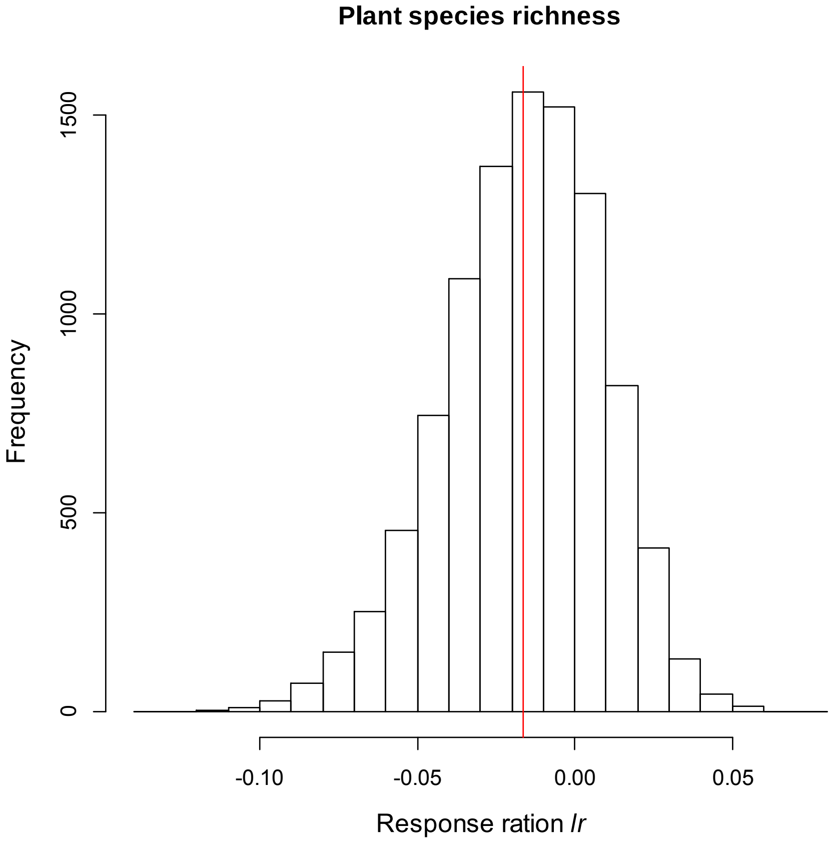


Figure 1. Histogram of the 10’000 boostraps (samples with replacement) for plant species richness, including all postponing schedule. Number of study included = 35. Mean effect size (*lr*) = -0.017 (red line on the figure), median = -0.015, and 95% CI = -0.070 – 0.028.

When including only the studies with an early cut in spring (before July 1) associated with a delayed cut in summer (July to September), mean *lr* became significantly positive (mean *lr* = 0.050 with 95% CI 0.010 – 0.091, Fig. 2). When including only the studies with all other combinations of early and delayed cuts (spring to fall, early summer to late summer and summer to fall, but excluding one early spring to late spring study (Cop et al. 2009)), mean *lr* became significantly negative (mean *lr* = 0.092 with 95% CI -0.190 – -0.026, Fig. 3).

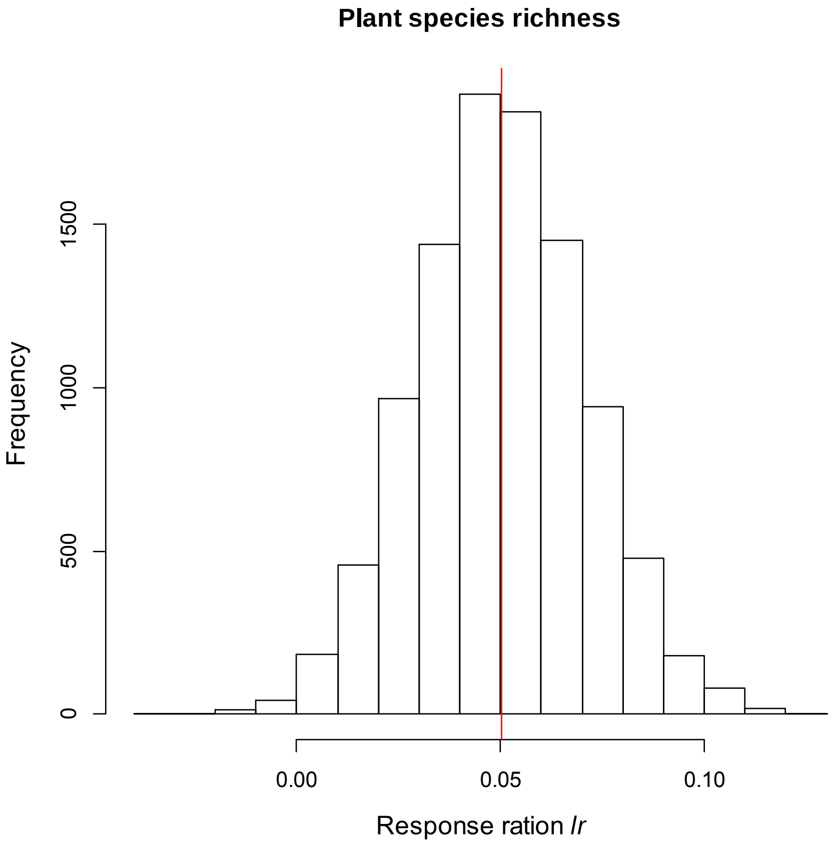


Figure 2. Histogram of the 10’000 boostraps (samples with replacement) for plant species richness, including only studies with an early cut in spring (May or June) associated with a delayed cut in summer (July to September). Number of study included = 19. Mean effect size (*lr*) = 0.050 (red line on the figure), median = 0.050, and 95% CI = 0.010 – 0.091.

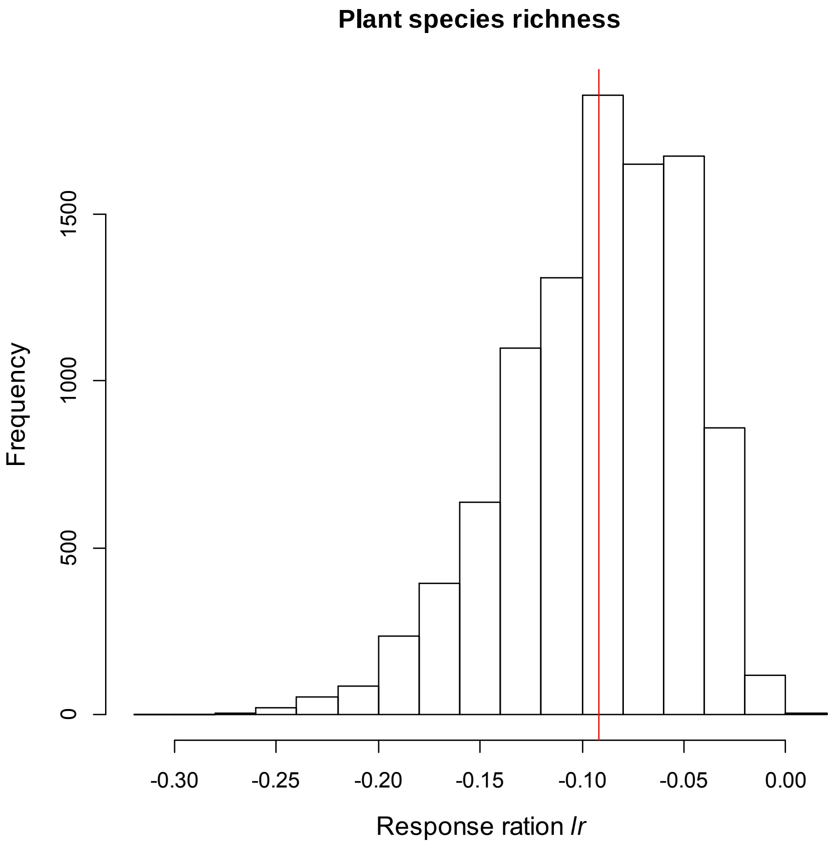


Figure 3. Histogram of the 10’000 boostraps (samples with replacement) for plant species richness, including only studies with spring to fall delayed cuts, early summer to late summer delayed cuts, and summer to fall delayed cuts (excluding spring to summer cuts). Number of study included = 15. Mean effect size (*lr*) = 0.092 (red line on the figure), median = -0.087, and 95% CI = -0.190 – -0.026.

Effects on invertebrate species richness

A significant positive effect of delaying the first mowing date on invertebrate species richness was found (mean *lr* = 0.222 with 95% CI 0.010 – 0.486, Fig. 4).

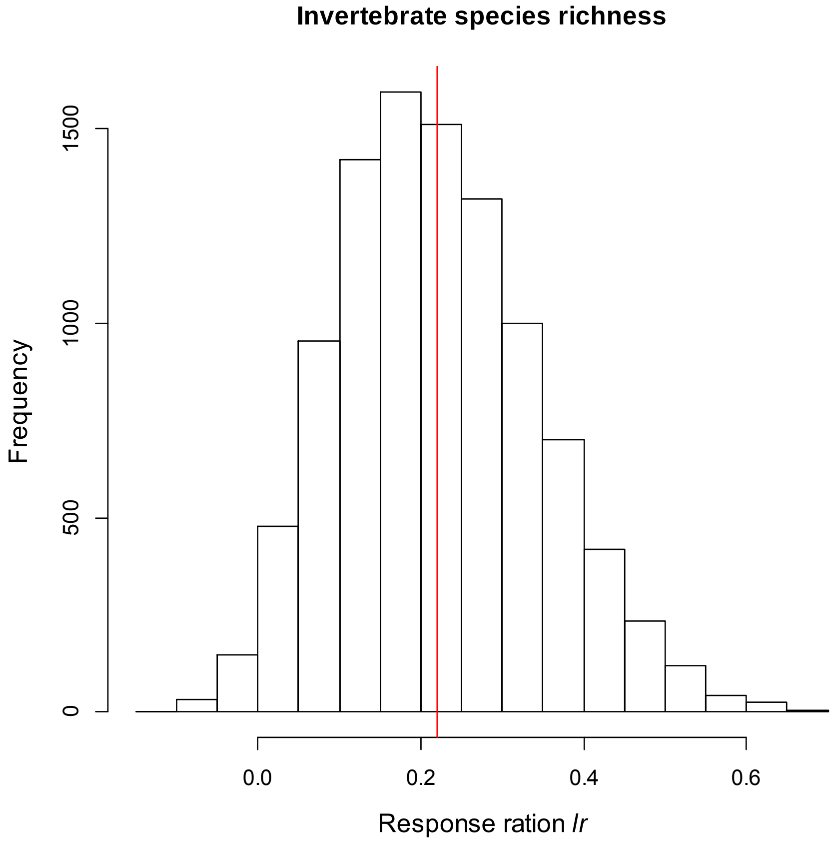


Figure 4. Histogram of the 10’000 boostraps (samples with replacement) for invertebrate species richness. Number of study included = 10. Mean effect size (*lr*) = 0.222 (red line on the figure), median = 0.216, and 95% CI = 0.010 – 0.486.

Effects on invertebrate abundance

No significant effect of delaying the first mowing date on invertebrate abundance was found (mean *lr* = 0.072 with 95% CI -0.352 – 0.446, Fig. 5). For comparison with the weighted meta-analysis, excluding Morris's studies from the analysis also led to significant positive effect of delaying the first mowing date on invertebrate abundance (mean *lr* = 0.352 with 95% CI 0.082 – 0.582, Fig. 6).

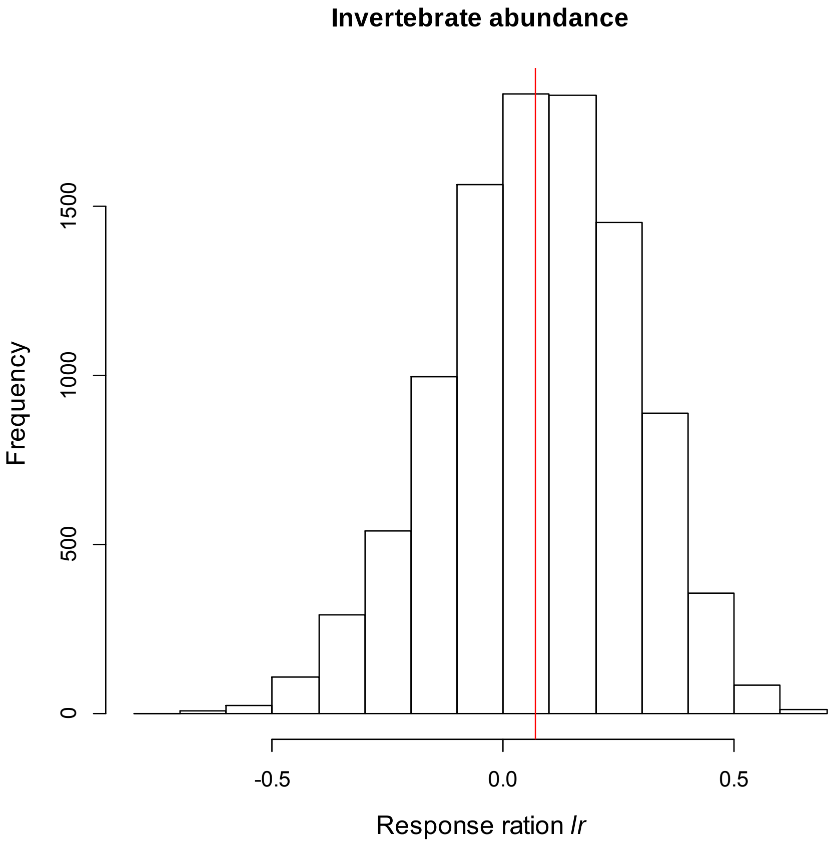


Figure 5. Histogram of the 10'000 boostraps (samples with replacement) for invertebrate abundance. Number of study included = 10. Mean effect size (*lr*) = 0.072 (red line on the figure), median = 0.082, and 95% CI = -0.352 – 0.446.

Additional file 4: Tables with details on selected null, univariate and multivariate models

		Test for Heterogeneity											95% CI	
Model	**AIC**	**Q**	**df**	**P-value**	**I^2 in %**	**Tau^2**	**R^2 in %***	**Parameter**	**Estimate****	**SE**	**Z-value**	**P-value**	**Lower b.**	**Upper b.**
For plant species richness														
Null	63.66	56.88	25	<0.001	54.01	0.2055		Intercept	0.017	0.130	0.134	0.894	-0.237	0.271
Years	71.09	55.22	24	<0.001	54.01	0.2042	0.63	Intercept	-0.094	0.181	-0.518	0.604	-0.448	0.261
								Years	0.016	0.018	0.878	0.380	-0.019	0.051
Cut_1	66.51	43.12	24	0.010	54.01	0.1324	35.57	Intercept	2.582	0.904	2.856	**0.004**	0.811	4.354
								Cut_1	-0.015	0.005	-2.878	**0.004**	-0.025	-0.005
Cut_2	71.90	49.77	24	0.002	54.01	0.1806	12.12	Intercept	1.507	0.837	1.800	0.072	-0.134	3.147
								Cut_2	-0.007	0.004	-1.805	0.071	-0.013	0.001
Time_lapse	74.75	56.78	24	<0.001	54.01	0.2280	0.00	Intercept	0.036	0.297	0.122	0.903	-0.546	0.618
								Time_lapse	0.000	0.004	-0.057	0.955	-0.009	0.008
Habitat	64.38	52.34	23	<0.001	54.01	0.2016	1.90	Intercept	0.526	0.502	1.048	0.295	-0.458	1.510
								meso	-0.667	0.526	-1.269	0.205	-1.698	0.363
								wet	-0.221	0.563	-0.393	0.695	-1.325	0.883
Veget_size	71.54	56.86	24	<0.001	54.01	0.2222	0.00	Intercept	0.022	0.142	0.152	0.880	-0.256	0.299
								Veget_size	-0.001	0.021	-0.028	0.978	-0.042	0.041
Cut_1 + Cut_2	77.51	41.71	23	0.010	54.01	0.1407	31.53	Intercept	2.805	0.993	2.823	**0.005**	0.858	4.752
								Cut_1	-0.013	0.006	-2.213	**0.027**	-0.025	-0.002
								Cut_2	-0.002	0.004	-0.546	0.585	-0.010	0.005
Cut_1 x Cut_2	95.11	41.57	22	0.007	54.01	0.1586	22.82	Intercept	-0.311	6.138	-0.051	0.960	-12.341	11.719
								Cut_1	0.005	0.036	0.134	0.894	-0.066	0.075
								Cut_2	0.011	0.025	0.430	0.667	-0.039	0.061
								Cut_1:Cut_2	0.000	0.000	-0.518	0.605	0.000	0.000

Continued

		Test for Heterogeneity											95% CI	
Model	**AIC**	**Q**	**df**	**P-value**	**I^2 in %**	**Tau^2**	**R^2 in %***	**Parameter**	**Estimate****	**SE**	**Z-value**	**P-value**	**Lower b.**	**Upper b.**
For invertebrate species richness														
Null	24.63	14.97	8	0.060	34.67	0.1126		Intercept	0.511	0.195	2.622	**0.009**	0.129	0.893
Cut_1	33.90	14.35	7	0.045	34.67	0.2178	0.00	Intercept	-0.420	1.434	-0.293	0.770	-3.231	2.391
								Cut_1	0.006	0.009	0.644	0.519	-0.012	0.024
Cut_2	31.62	13.76	7	0.056	34.67	0.1906	0.00	Intercept	-3.761	4.189	-0.898	0.369	-11.971	4.450
								Cut_2	0.021	0.021	1.018	0.309	-0.019	0.061
Cut_1 + Cut_2	38.65	12.90	6	0.045	34.67	0.2198	0.00	Intercept	-9.053	8.062	-1.123	0.261	-24.853	6.747
								Cut_1	-0.018	0.024	-0.761	0.447	-0.066	0.029
								Cut_2	0.061	0.056	1.088	0.277	-0.049	0.170
Years***	25.04	11.59	5	0.041	58.59	0.3320	14.52	intrcpt	-0.241	0.568	-0.424	0.672	-1.354	0.873
								year	0.154	0.117	1.322	0.186	-0.074	0.382
Null	35.96	31.04	8	<0.001	87.12	1.3291		Intercept	-0.053	0.427	-0.125	0.901	-0.889	0.783
Cut_1	43.01	24.85	7	0.001	87.12	1.4365	0.00	Intercept	-2.969	2.864	-1.037	0.300	-8.583	2.644
								Cut_1	0.019	0.019	1.025	0.305	-0.018	0.056
Cut_2	40.92	24.55	7	0.001	87.12	1.3819	0.00	Intercept	-10.980	9.774	-1.123	0.261	-30.137	8.178
								Cut_2	0.054	0.049	1.118	0.264	-0.041	0.149
Cut_1 + Cut_2	22.76	2.47	6	0.871	87.12	0.0000	100	Intercept	-811.179	171.128	-4.740	**<0.001**	-1146.582	-475.775
								Cut_1	-2.129	0.453	-4.699	**<0.001**	-3.017	-1.241
								Cut_2	5.607	1.185	4.730	**<0.001**	3.284	7.930

Model abbreviations Years = study duration in years
Cut_1 = ordinal day of the date of the early cut
Cut_2 = ordinal day of the date of the delayed cut
Time_lapse = number of days between the early and the delayed cuts
Habitat = meadow type (dry, meso or wet)
Veget_size = size of the vegetation relevé (in m^2)

* R^2 in %, is the proportion of variance explained by the covariates (Borenstein et al. 2009)
** Weighted meta-regression, based on the Hedges'*d* effect size
*** This model is without the study of Valtonen et al. (2006), thus AIC value cannot be compared with the other models

Additional file 5: Articles excluded after full text filtering

	Inclusion filtering			Further exclusion because of			
#	Title	Abstract	Full text	duplication	unsuitable data for a MA	Reason for exclusion	References
1	yes	yes	yes		x	No delay mowing treatment (number of cut not equal)	[1]
2	yes	yes	yes	x		Same experiment as Bobbink and Willems (1991)	[2]
3	yes	yes	yes		x	Confounding factors (gap creation and fertilization)	[3]
4	yes	yes	yes		x	Observational study with confounding factors (e.g. fertilizer application)	[4]
5	yes	yes	yes	x		Same experiment as Köhler et al. 2005	[5]
6	yes	yes	yes	x		Same data in Morris 1979 and Morris 1981	[6]
7	yes	yes	yes	x		Subsamples of the data of Morris 1981	[7]
8	yes	yes	yes	x		Subsamples of the data of Morris and Rispin 1987	[8]
9	yes	yes	yes	x		Subsamples of the data of Morris 1981	[9]
10	yes	yes	yes	x		Same experiment as Köhler et al. 2005	[10]
11	yes	yes	yes		x	Regarding vegetation; 1998-2000 all plots were cut on July 21	[11]
12	yes	yes	yes		x	Management intensity correlated with mowing date	[12]
1	yes	yes	no			No delay mowing treatment	[13]
2	yes	yes	no			No delay mowing treatment	[14]
3	yes	yes	no			No delay mowing treatment	[15]
4	yes	yes	no			No data on delaying mowing	[16]
5	yes	yes	no			Confounding factors, and no data on mowing dates	[17]

6	yes	yes	no	No delay mowing treatment	[18]
7	yes	yes	no	Not in Europe (South Africa)	[19]
8	yes	yes	no	Confounding factors (management intensity), and no data on mowing dates	[20]
9	yes	yes	no	No data on delaying mowing	[21]
10	yes	yes	no	Not in Europe (South Africa)	[22]
11	yes	yes	no	Summer and winter cut not every year	[23]
12	yes	yes	no	No data on delaying mowing	[24]
13	yes	yes	no	No delay mowing treatment (study on cutting frequencies)	[25]
14	yes	yes	no	On the success of establishment of sown species	[26]
15	yes	yes	no	No delay mowing treatment	[27]
16	yes	yes	no	No delay mowing treatment	[28]
17	yes	yes	no	Models based on the phenology of the birds, no experiment	[29]
18	yes	yes	no	Only mown meadows vs pastures	[30]
19	yes	yes	no	On mowing frequency, and no data on mowing dates	[31]
20	yes	yes	no	2 years after cessation of management treatments	[32]
21	yes	yes	no	No data on delaying mowing	[33]
22	yes	yes	no	Based on the phenology, no data	[34]
23	yes	yes	no	Winter cuts, not on delaying mowing	[35]

References

[1] Baines M, Hambler C, Johnson PJ, Macdonald DW, Smith H. The effects of arable field margin management on the abundance and species richness of Araneae (spiders). Ecography. 1998;21:74-86.

[2] Bobbink R, During H, Schreurs J, Willems J, Zielman R. Effects of selective clipping and mowing time on species diversity in chalk grassland. Folia geobot phytotax. 1987;22:363-76.

[3] Burke MJW, Grime JP. An Experimental Study of Plant Community Invasibility. Ecology. 1996;77:776-90.

[4] Critchley CNR, Fowbert JA, Wright B. Dynamics of species-rich upland hay meadows over 15 years and their relation with agricultural management practices. Applied Vegetation Science. 2007;10:307-14.

[5] Jeschke M, Kiehl K, Pfadenhauer J, Gigon A. Long-term effects of former management on the diversity of vascular plants, mosses and lichens in a calcareous grassland. Botanica Helvetica. 2008;118:95-109.

[6] Morris MG, Lakhani KH. Responses of Grassland Invertebrates to Management by Cutting. I. Species Diversity of Hemiptera. Journal of Applied Ecology. 1979;16:77-98.

[7] Morris MG, Plant R. Responses of Grassland Invertebrates to Management by Cutting. V. Changes in Hemiptera Following Cessation of Management. Journal of Applied Ecology. 1983;20:157-77.

[8] Morris MG, Rispin WE. A beetle fauna of oolitic limestone grassland, and the responses of species to conservation management by different cutting régimes. Biological Conservation. 1988;43:87-105.

[9] Morris MG. Resoneses of Grassland Invertebrates to Mangement by Cutting: IV Positive Responses of Auchenorhyncha. Journal of Applied Ecology. 1981;18:763-71.

[10] Ryser P, Langenauer R, Gigon A. Species Richness and Vegetation Structure in a Limestone Grassland after 15 Years Management with Six Biomass Removal Regimes. Folia Geobotanica & Phytotaxonomica. 1995;30:157-67.

[11] Smith RS, Shiel RS, Millward D, Corkhill P, Sanderson RA. Soil seed banks and the effects of meadow management on vegetation change in a 10-year meadow field trial. Journal of Applied Ecology. 2002;39:279-93.

[12] Verhulst J, Kleijn D, Berendse F. Direct and indirect effects of the most widely implemented Dutch agri-environment schemes on breeding waders. Journal of Applied Ecology. 2007;44:70-80.

[13] Amiaud B, Touzard B. The relationships between soil seed bank, aboveground vegetation and disturbances in old embanked marshlands of Western France. Flora - Morphology, Distribution, Functional Ecology of Plants. 2004;199:25-35.

[14] Baba W. Changes in the structure and floristic composition of the limestone grasslands after cutting trees and shrubs and mowing. Acta Societatis Botanicorum Poloniae. 2003;72:61.9.

[15] Baba W. The species composition and dynamics in well-preserved and restored calcareous xerothermic grasslands (South Poland). Biologia. 2004;59:447-56.

[16] Berlin GAI, Linusson A-C, Olsson EGA. Vegetation changes in semi-natural meadows with unchanged management in southern Sweden, 1965–1990. Acta Oecologica. 2000;21:125-38.

[17] Bollinger EK. Successional changes and habitat selection in hayfield bird communities. The Auk. 1995;112:720-30.

[18] Calvo L, Alonso I, Marcos E, De Luis E. Effects of cutting and nitrogen deposition on biodiversity in Cantabrian heathlands. Applied Vegetation Science. 2007;10:43-52.

[19] Chambers BQ, Samways MJ. Grasshopper response to a 40-year experimental burning and mowing regime, with recommendations for invertebrate conservation management. Biodiversity & Conservation. 1998;7:985-1012.

[20] Cauwer B, Reheul D. Impact of land use on vegetation composition, diversity and potentially invasive, nitrophilous clonal species in a wetland region in Flanders. Agron Sustain Dev. 2009;29:277-85.

[21] Dölle M, Schmidt W. The relationship between soil seed bank, above-ground vegetation and disturbance intensity on old-field successional permanent plots. Applied Vegetation Science. 2009;12:415-28.

[22] Fynn RWS, Morris CD, Edwards TJ. Effect of Burning and Mowing on Grass and Forb Diversity in a Long-Term Grassland Experiment. Applied Vegetation Science. 2004;7:1-10.

[23] Güsewell S, Buttler A, Klötzli F. Short-Term and Long-Term Effects of Mowing on the Vegetation of Two Calcareous Fens. Journal of Vegetation Science. 1998;9:861-72.

[24] Helden AJ, Leather SR. Biodiversity on urban roundabouts—Hemiptera, management and the species–area relationship. Basic and Applied Ecology. 2004;5:367-77.

[25] Kramberger B, Kaligaric M. Semi-natural grasslands: the effects of cutting frequency on long-term changes of floristic composition. Polish Journal of Ecology. 2008;56:33.

[26] Lawson CS, Ford MA, Mitchley J. The influence of seed addition and cutting regime on the success of grassland restoration on former arable land. Applied Vegetation Science. 2004;7:259-66.

[27] Le Duc MG, Pakeman RJ, Marrs RH. A restoration experiment on moorland infested by Pteridium aquilinum: Plant species responses. Agriculture, Ecosystems & Environment. 2007;119:53-9.

[28] MacDougall AS, Turkington R. Does the type of disturbance matter when restoring disturbance-dependent grasslands? Restoration Ecology. 2007;15:263-72.

[29] Nocera JJ, Parsons GJ, Milton GR, Fredeen AH. Compatibility of delayed cutting regime with bird breeding and hay nutritional quality. Agriculture Ecosystems & Environment. 2005;107:245-53.

[30] Saarinen K, Jantunen J. Grassland butterfly fauna under traditional animal husbandry: Contrasts in diversity in mown meadows and grazed pastures. Biodiversity and Conservation. 2005;14:3201-13.

[31] Saarinen K, Valtonen A, Jantunen J, Saarnio S. Butterflies and diurnal moths along road verges: Does road type affect diversity and abundance? Biological Conservation. 2005;123:403-12.

[32] Smith RS, Shiel RS, Bardgett RD, Millward D, Corkhill P, Rolph G, et al. Soil microbial community, fertility, vegetation and diversity as targets in the restoration management of a meadow grassland. Journal of Applied Ecology. 2003;40:51-64.

[33] Vanderpoorten A, Delescaille L-M, Jacquemart A-L. The bryophyte layer in a calcareous grassland after a decade of contrasting mowing regimes. Biological Conservation. 2004;117:11-8.

[34] Walter T, Schneider K, Gonseth Y. The mowing date of ecological compensation areas: influence on the fauna. Agrarforschung. 2007;14:114-9.

[35] Whittingham MJ, Devereux CL. Changing grass height alters foraging site selection by wintering farmland birds. Basic and Applied Ecology. 2008;9:779-88.

3

Delaying mowing and leaving uncut refuges boosts orthopterans in extensively managed meadows: Evidence drawn from field-scale experimentation

Delaying mowing and leaving uncut refuges boosts orthopterans in extensively managed meadows: Evidence drawn from field-scale experimentation

Pierrick Buri[a], Raphaël Arlettaz[a,b], Jean-Yves Humbert[a]

[a] Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland
[b] Swiss Ornithological Institute, Valais Field Station, Rue du Rhône 11, CH-1950 Sion, Switzerland

Manuscript:
In press in *Agriculture, Ecosystem and Environment*
on 5 September 2013

3.1 Abstract

Semi-natural grasslands are widely recognized for their high ecological value. They often count among the most species-rich habitats, especially in traditional cultural landscapes. Maintaining and/or restoring them is a top priority, but nevertheless represents a real conservation challenge, especially regarding their invertebrate assemblages. The main goal of this study was to experimentally investigate the influence of four different mowing regimes on orthopteran communities and populations: (1) control meadow (C-meadow): mowing regime according to the Swiss regulations for extensively managed meadows declared as ecological compensation areas, i.e. first cut not before 15 June; (2) first cut not before 15 July (delayed treatment, D-meadow); (3) first cut not before 15 June and second cut not earlier than 8 weeks from the first cut (8W-meadow); (4) refuges left uncut on 10-20% of the meadow area (R-meadow). Data were collected two years after the introduction of these mowing treatments. Orthopteran densities from spring to early summer were five times higher in D-meadows, compared to C-meadows. In R-meadows, densities were, on average, twice as high as in C-meadows, while mean species richness was 23% higher in R-meadows than in C-meadows. Provided that farmers were given the appropriate financial incentives, the D- and R-meadow regimes could be relatively easy to implement within agri-environment schemes. Such meadows could deliver substantial benefits for functional biodiversity, including sustenance to many secondary consumers dependent on field invertebrates as staple food.

Keywords: Biodiversity; Bush cricket; Conservation; Cutting; Grasshopper; Haying

3.2 Introduction

Extensively managed grasslands are among the most species-rich habitats of the Palaearctic, typifying its characteristic cultural landscapes. These low input grasslands are considered of high natural value, inhabited as they are by many threatened plant and animal taxa (Veen et al., 2009). Biodiversity-rich grasslands have suffered dramatically from the green revolution: they have been systematically converted into arable lands, improved (i.e. intensified), or simply abandoned (Poschlod and WallisDeVries, 2002; Torok et al., 2011). Grassland intensification interventions include an increase of fertilizer input, application of pesticides, and reseeding, all of which results in increased grass production, enabling earlier and more frequent cuts, or higher grazing intensity. Concurrently, mechanization improved, field sizes expanded, and farming practices temporally and spatially simplified the matrix, leading to a massive homogenization of the agricultural landscape (Robinson and Sutherland, 2002). Most changes linked to farming intensification negatively impact grassland biodiversity, by eliminating plant, invertebrate and vertebrate populations (e.g. Wilson et al., 1999; Vickery et al., 2001; Marini et al., 2008; Wesche et al., 2012). To counteract this, many European countries have implemented targeted grassland agri-environment schemes (AES). Despite these incentives for more environmentally friendly management practices, such as reduced, or no fertilizer application, these conservation schemes have so far had only limited success (e.g. Kleijn et al., 2006; Knop et al., 2006; Aviron et al., 2009).

Mowing is a common practice in extensively managed grasslands and is considered to be one of the most efficient management options to fulfil the needs of the field flora (Grime, 2001; Schaffers, 2002). Thus, it is not surprising that the influence of mowing on plant communities has been intensively studied by conservation biologists and restoration ecologists (e.g. Bakker et al., 2002; Cop et al., 2009; Torok et al., 2011; Valko et al., 2012). In comparison, the influence of mowing on field invertebrates as received relatively little research attention (Littlewood et al., 2012). It is only recently that the impact of the regime and technique of mowing on invertebrates has been properly quantified (Humbert et al., 2009; Humbert et al., 2012b).

In 2010, we launched an ambitious research programme with a double objective: 1) to better appraise the influence of different mowing regimes on invertebrates, and 2) to propose management measures that can be easily implemented by farmers. A multidisciplinary group of experts was created at the beginning of the programme, which included, among others, representatives of local and national environment and agriculture offices. This early collaboration was intended to overcome the conventional gap that exists between science, policy and practice, by building, from the outset, a catalogue of pragmatic evidence-based management measures for effective public actions (Sutherland et al., 2004; Arlettaz et al., 2010; Braunisch et al., 2012; Caudron et al., 2012). The research programme took place on the Swiss Plateau in extensively managed meadows, declared as ecological compensation areas (ECA) by the Swiss AES (Swiss Federal Council, 1998). We focused on ECA meadows because they currently are, among the Swiss lowland grasslands, those that harbour the less impoverished biodiversity.

Orthopterans were selected as a model taxon because they are key components of food chains within grasslands; principally herbivores, they represent an important food source for many predators, such as insectivorous vertebrates (Arlettaz et al., 1997; Wilson et al., 1999; Baur et al., 2006). In addition, orthopterans are considered to be good indicators of grassland ecosystem health as they readily respond to management intensification, which negatively affects species richness and population density (Van Wingerden et al., 1992; Marini et al., 2008).

The aim of this paper was to study how the different investigated mowing regimes affect orthopteran species richness and population sizes. The standard regulation for lowland ECA meadows stipulates a first cut not before 15 June. This practice is the most widely implemented AES option throughout Switzerland, covering 6.3% of the agricultural area (OFAG, 2012); it served as a control baseline in our experiments. It must be clear, however, that this measure is already considered to be an active management strategy aimed at promoting biodiversity in farmland. The following three management treatments were derived from the basic prescriptions of these control meadows. The first experimental mowing treatment stipulated delaying the first cut by one month. While the influence of delayed mowing on field invertebrates has been shown to be neutral or positive (reviewed in Humbert et al. (2012b)), its effects have never been specifically investigated on orthopterans. Predictions are thus not so easy to formulate. On the one hand, delaying mowing from 15 June to 15 July might have positive effects because it might give time to some orthopterans to reproduce before any mowing intervention. On the other hand, a summer cut may negatively impact the demography of larger organisms (including orthopterans) that typically have a longer developmental stage, i.e. a later phenology, compared to smaller organisms (Humbert et al., 2010b). The second experimental treatment limited the number of cuts to two per year, with a minimum of eight weeks in between. It has been established that reducing or limiting the number of cuts per year favours invertebrates (Helden and Leather, 2004; Marini et al., 2008), although it remains unclear if limiting the number of cuts to two provides better biodiversity outcomes than mowing regimes with non-prescribed number and frequency of cuts. The third experimental mowing treatment stipulated that each time the meadow was mown, an uncut grass area had to be left as a refuge. We hypothesized that this treatment would have a pronounced positive effect through basically two mechanisms: first, leaving uncut areas mitigate the directly negative mechanical impact of the harvesting process (Humbert et al., 2012a); second, uncut grass will enhance orthopteran fitness by providing continuity of shelter and food resources, which suddenly disappears over the area of the meadow which has been mown (Gardiner and Hassall, 2009).

The present study addresses these different issues through field-scale experiments, in which treatments consisted in specific targeted mowing regimes by farmers, with a given treatment being randomly attributed to a meadow. The major advantage of such an experimental approach, over a traditional correlational study, is that it better accounts for confounding factors, such as the influence of surrounding landscape features or the fact that AES are systematically applied in more marginal, i.e. less optimal agricultural land, thereby enabling firm, evidence-based recommendations to be drawn for meadowland management.

3.3 Material and methods

3.3.1 Study sites

In 2010, 48 extensively managed hay meadows, registered as ECA since at least 2004 were selected in 12 study regions (with 4 meadows per region) across the Swiss Plateau (in the cantons of Vaud, Fribourg, Neuchâtel, Bern, Aargau and Basel-Landschaft; see Appendix A for exact coordinates). The meadows were situated between 390 and 833 m altitude. The four meadows in a single region were all located within 3.5 km radius, but were separated by a minimal distance of 440 m. The regions themselves were at least 5 km distant from each other (border to border). The average size of a meadow was 0.8 ha (range: 0.3 – 1.7 ha).

3.3.2 Experimental design

A randomized block design was adopted, where different management regimes were applied within each region, the latter representing the blocks, such that treatment replicates were across the regions, thus ensuring data independence. Within each region, the following management patterns (with abbreviations), consisting of different mowing regimes, were randomly assigned to the four meadows:

(1) Extensively managed meadow with first cut not before 15 June, but with no restriction on the number and frequency of subsequent cuts (standards for ECA meadows according to Swiss regulations). These meadows constitute our baseline and are henceforth called control meadows (C-meadows) although they actually represented a specific management targeting biodiversity.

(2) Extensively managed meadow with first cut not before 15 July, with again no restriction on the number and frequency of subsequent cuts (D-meadow, with D for delayed).

(3) Extensively managed meadow with a maximum of two cuts per year and at least 8 weeks between the cuts, with first cut not before 15 June (8W-meadow, with 8W for eight weeks).

(4) Extensively managed meadow with a rotational uncut refuge on 10–20% of the meadow area, meaning that a corresponding proportion of the area

is left uncut each time the meadow is mown, with the location of the refuge being changed from time to time to avoid vegetation succession; otherwise first cut not before 15 June (R-meadows, with R for refuge).

Other management constraints included no fertilizer or pesticide application as well as grazing allowed only between 1 September and 30 November as specified in the present ECA regulations (Swiss Federal Council, 1998). The experiment started in spring 2010, with the random assignment of the different mowing regimes to the meadows; orthopterans were sampled in 2012.

3.3.3 Orthopteran sampling

The density of orthopterans (number of individuals per m^2) was measured using a biocenometer made of a net fastened around a strong circular wire so as to provide a total capture area of exactly 1 m^2. This technique is equivalent to the 1 m^2 box quadrat approved sampling methodology described by Badenhausser e*t al*. (2009), except that our device was circular. The biocenometer was thrown into the field, and all trapped orthopterans belonging to the super families Tettigonioidea and Acridoidea (juveniles and adults) were recorded visually.

Orthopteran density was measured five times between 20 May and 17 August: twice before any mowing intervention; once at the end of June – beginning of July, when C-meadows, 8W-meadows and R-meadows had been mown, but not D-meadows; and twice after 25 July when all meadows had been mown at least once. Sampling took place on sunny days between 9 am and 6 pm. In each meadow, 16 x 1 m^2 samples were regularly taken across the meadow, along 2-4 (depending on meadow shape) parallel transects at a distance of 10 m, but excluding a 10 m buffer zone around the meadow border in order to minimize edge effects (Knop et al., 2006). In R-meadows, during the last three sampling sessions, eight extra samples were taken from the uncut area of a meadow, in addition to the 16 samples collected in the mown area outside the refuges.

The mean orthopteran density per meadow was calculated over the 16 samples. However, the initial developmental stages (< 1 cm body length) were not included in the datasets because the detectability of early nymphs may vary between cut and uncut meadows. Adult orthopterans were identified to species level while juveniles (nymphs) were simply classified into their sub-order (Caelifera or Ensifera). In order to obtain a full picture of orthopteran species richness, two persons proficient at orthopteran identification carried out a 15 min qualitative visual and acoustic survey in each meadow during the three summer sampling sessions (3rd, 4th and 5th session). Species richness was then calculated as the addition of species found with the biocenometer and during the visual surveys.

3.3.4 Statistical analysis

Effects of mowing regimes were analyzed with generalized linear mixed models. Response variables were orthopteran density and species richness; they were analyzed with either Poisson (density) or Gaussian (species richness) error distribution. Fixed effects were the four mowing regimes (C, D, 8W and R) and, when necessary, the sampling sessions, while regions (12 spatial replicates) were considered as a random effect.

Density analyses were performed with three linear models, using three seasonal datasets that regrouped sampling sessions (first model: sessions 1 and 2; second model; session 3; third model: sessions 4 and 5). In order to better appraise the influence of the mowing regime on the reproductive segment of the orthopteran populations, the same statistical analyses were then performed on adult density only, i.e. discarding nymphs. As species from the suborder Ensifera are, on average, larger than species from the suborder Caelifera, and given that these two suborders differ in terms of mobility and ecology (Reinhardt et al., 2005), separate models on each suborder were run. We also investigated variation in species-specific responses, but only focusing on the most abundant ones. Finally, linear models were run with data from R-meadows only, testing whether, within these meadows, density in the uncut refuges differed from density in the cut area.

In order to asses to which extent mowing regimes differed in their effects, planned orthogonal comparisons were additionally conducted by removing the control, or the control and D-treatment from the dataset. Model assumptions were checked and met for each analysis. All statistics were performed using R version 2.15.3 (R Core Team, 2013).

3.4 Results

3.4.1 Mowing regimes

C-meadows (control) and 8W-meadows (8 weeks treatment) had very similar management regimes: they were both cut on average 1.9 ± 0.5 (mean 2010-2012 ± standard deviation) times per year, with the first cut occurring on average on 22 June, and the second cut (if present) taking place at the end of August (see Table 1 for all cutting dates per year per treatment). R-meadows (refuge treatment) were cut on average 2.1 (± 0.4) times per year, with the first cut occurring on average on 21 June and the second cut on 19 August. D-meadows (delayed treatment) were cut on average 1.6 (± 0.6) times a year, with the first cut occurring on average on 23 July and the second cut on 13 September. In spring 2012, one D-meadow was unfortunately lost through conversion into a gravel-pit extraction site.

3.4.2 Orthopteran density

Mean orthopteran densities varied from 0.6 to 16 individuals per m^2 and were clearly influenced by mowing regimes (Fig. 1a). Before mowing (first and second sampling sessions), mean orthopteran density was significantly higher in D-meadows (mean ± standard error, SE, = 11.93 ± 3.34) and R-meadows (4.86 ± 1.10) than in C-meadows (2.33 ± 0.6) and 8W-meadows (3.30 ± 0.75; all $P <$ 0.001, except for R-meadows vs 8W-meadows $P =$ 0.002; see Table 2a for detailed model outputs). There were also significantly more orthopterans in D-meadows than in R-meadows ($P <$ 0.001), while 8W-meadows and C-meadows did not differ from each other ($P =$ 0.086). During the third sampling session (i.e. after all meadows except D-meadows had been cut), orthopteran density was significantly higher in D-meadows (14.38 ± 3.20) compared to C-meadows (1.63 ± 0.76; $P <$ 0.001), whereas densities in 8W-meadows (1.43 ± 0.39), R-meadows (1.80 ± 0.37) and C-meadows did not differ from each other. During the fourth and fifth sampling sessions, i.e. after all meadows had been cut, there were significantly fewer orthopterans per m^2 in D-meadows (0.89 ± 0.15) than in C-meadows (2.51 ± 0.66; $P <$ 0.001), whilst densities in 8W-meadows (1.99 ± 0.42), R-meadows (2.31 ± 0.44) and C-meadows did not differ from each other (Table 2a).

When restricting the analysis to adult orthopterans, too few adult specimens were available from the first and second sampling sessions for any statistical testing (Fig 1b). During the third sampling session, there were significantly more adults in D-meadows (3.56 ± 1.97) than in C-meadows (0.19 ± 0.08; $P < 0.001$; Table 2b). Densities in 8W-meadows (0.24 ± 0.08), R-meadows (0.30 ± 0.10) and C-meadows did not differ. During the last two sampling sessions, there were significantly fewer adults per m^2 in the D-meadows (0.61 ± 0.12) compared to C-meadows (1.20 ± 0.56; $P = 0.015$). Densities in 8W-meadows (1.04 ± 0.36), R-meadows (1.29 ± 0.31) and C-meadows did not differ.

Analyses on Caelifera and Caelifera adults only (Fig. 1c and 1d; Table 2c and 2d) showed exactly the same responses as overall orthopterans, i.e. the same statistical differences between regimes appeared. Analyses on Ensifera and Ensifera adults only (Fig. 1e and 1f; Table 2e and 2f) showed responses that were broadly the same, but not all comparisons were significant (at $P = 0.05$ level). For example, no differences were found among regimes in sessions four and five. Note that Ensifera were at relatively low densities compared to Caelifera, which limited power in the analyses of the former taxon.

The even more restricted analyses of species-specific responses to mowing regimes retained the following seven dominant species (number of meadows out of 47 harbouring the species): *Chorthippus parallelus* (47), *Chorthippus biguttulus* (46), *Metrioptera roeselii* (41), *Mecostethus parapleurus* (28), *Tettigonia viridissima* (25), *Chorthippus brunneus* (23), *Gomphocerippus rufus* (15). Analyses were limited to sampling sessions three, four and five; because nymphs recorded in sampling sessions one and two were not identified to species level. Species-specific responses showed the same trends as with all orthopterans pooled, but significant differences were detected only for *C. parallelus:* during the third sampling session, the density in D-meadows was significantly higher than in C-meadows, 8W-meadows and R-meadows ($P < 0.001$ for all tests).

After the first cut (samples from the third, fourth and fifth sessions), densities of orthopterans differed between uncut and cut areas within R-meadows (Fig. 2a). While density inside uncut grass refuges (9.44 ± 3.00) was significantly higher compared to density outside them (1.80 ± 0.38; $P < 0.001$, Table 3a) during the third sampling session, the difference vanished during the fourth sampling session (mean ± SE density inside and outside refuge was 4.83 ± 1.24 and 3.11 ± 0.69, respectively), reappearing only during the fifth sampling session, with density inside uncut grass refuges being higher (2.68 ± 0.68) than outside refuges (1.11 ± 0.34; *P* = 0.012; Table 3a). The same significant differences appeared when analysing Caelifera only, but no differences were detected when analysing Ensifera only (Fig. 2b and 2c; Table 3b and 3c).

3.4.3 Orthopteran species richness

Overall, 22 orthopteran species were recorded, of which six are red listed (Appendix A). Average (± SE) number of species per meadow was 6.38 ± 0.26 (Fig. 3). There were significantly more species in R-meadows (7.42 ± 0.56) than in C-meadows (5.75 ± 0.49; *P* = 0.018) and D-meadows (6.00 ± 0.50; *P* = 0.048), but not than in 8W-meadows (6.33 ± 0.47; *P* = 0.142; Table 4a). Species richness in C-meadows, D-meadows and 8W-meadows did not differ significantly. Additional analyses on species richness of Caelifera and Ensifera separated showed similar trends, but significant differences were detected only for Ensifera with more species in R-meadows (2.67 ± 0.43) than in C-meadows (1.58 ± 0.23; P =0.022; Table 4b and 4c; figures not shown).

3.5 Discussion

This study shows that relatively slight changes in grassland management practices, such as delaying mowing or leaving uncut grass refuges, can make a significant difference for biodiversity. Compared to our control meadows (C-meadows; first cut not before 15 June, no grass refuge left), orthopteran density in the spring and early summer two years after the introduction of these alternative management measures were, on average, five times higher in meadows in which mowing was delayed by a month (D-meadows), and twice as high in meadows where an uncut refuge was maintained during mowing operations (R-meadows). Furthermore, we were able to show that, after just two years of this targeted management, leaving uncut grass refuges also promotes species richness among orthopterans. Delaying mowing, or leaving small patches of the grassland area uncut does not require extra work by farmers and would thus be readily implementable in extant agri-environment schemes (AES). The different experimental mowing regimes were readily implemented by the farmers, suggesting that these could be well-accepted measures providing financial compensation were made available for the reduction in hay production and nutritive value (Cop et al., 2009).

These findings provide clear advice not only for improving biodiversity in extensively managed meadows or field margins under AES (e.g. Kleijn et al., 2006; Badenhausser and Cordeau, 2012), but also for the management of high natural value grasslands beyond AES, buffer zones of wetland nature reserves, river and canal embankments, and road verges (Noordijk et al., 2009; Veen et al., 2009). By providing additional resources to upper trophic levels, all these measures will contribute to re-instating integral, functional food chains within modern agro-ecosystems.

3.5.1 Impact of mowing regimes on orthopteran density

A first major outcome of our experimental manipulation of mowing regimes is the demonstration of a so-called "cumulative" effect, namely that measures implemented in 2010 and 2011 had carried-over effects discernable in 2012. In fact, we observed tremendously increased densities of orthopterans on the first two sampling sessions in 2012, i.e. in spring prior to any mowing operation. A five times higher orthopteran density in spring 2012 in D-meadows, compared to baseline control C-meadows, means that massively increased egg production took place the previous year, due either to a larger number of reproducers and/or to a higher individual reproductive success (Grant et al., 1993). Definitely, delaying the first possible cut until 15 July (D-meadows) allowed many more orthopterans to reach adulthood and to reproduce, thanks to both continuous food supply and no mortality induced by the mowing operation itself before the first cut (68-82% mortality according to Humbert et al., 2010a). In fact, in D-meadows during the third sampling session (ca 4 July) there were 3.6 adults orthopteran per m^2 which is more than what was recorded at any other time of the season, and more than in any other mowing regimes. Delaying the first cut to 15 July in turn led to delaying the second cut to mid-September, when reproduction is over for most orthopterans (Baur et al., 2006), while it additionally contributed to fewer mean number of cuts per year in that treatment. The positive effect of the uncut grass refuge principally results from the same mechanisms as for delaying mowing. An earlier experiment has established that leaving 10% of the area of a meadow uncut can reduce orthopteran mortality by 30-35% (Humbert et al., 2012a).

Later in the season (at the fourth and fifth sampling sessions), when all mowing operations are finished, any observed differences among mowing regimes mirror the combined immediate and cumulative effects of the various mowing patterns. D-meadows had significantly lower densities than the other mowing regimes, which contrasts with the mass densities they harboured until mid summer, but values in all regimes were extremely low compared to the situation from spring to midsummer. This dramatic decrease to a few orthopterans per m^2 we observed confirms the overall severe negative impact of mowing on orthopterans (Humbert et al., 2010a).

Within R-meadows, orthopteran density remained spatially heterogeneous for a while after the first cut. If a high density in the uncut refuge just after mowing is not surprising (Müller and Bosshard, 2010; Humbert et al., 2012a), a discernable effect until two weeks (ca 4 July) after mowing was reported for the first time. Uncut refuges thus not only enable orthopterans to avoid being mechanically eliminated by mowing, but they also provide shelter and food resources until the re-colonisation of the mown fraction of the meadow is again possible (see also Gardiner et al., 2002).

A second important outcome is that both suborders, Caelifera and Ensifera, responded in the same way to the mowing regimes, i.e. they were both more abundant in the D- and R-treatments, and inside the uncut refuge area, showing that even if they have some different ecological requirements, these management measures can favour both suborders. Data were limited regarding species-specific conclusions, and only *C. parallelus* was sufficiently abundant and widespread to detect a positive effect of D-treatment on its population. Nevertheless, the impact of mowing regime on orthopteran density depends on the identity and environmental requirements of the dominant species, which were in this study mainly generalists (Reinhardt et al., 2005).

Finally, the observation that orthopteran communities and population sizes did not differ between the 8W-meadows and the C-meadows is due to unexpectedly very similar mowing practices in these two regimes: actually, the average number of weeks between the first and second cut was 9.7 weeks in 8W-meadows and 9.4 weeks in C-meadows, demonstrating that such a mowing prescription is meaningless.

3.5.2 Impact of mowing regimes on orthopteran species richness

There were, on average, 23% more species (n = 7.4) in R-meadows compared to C-meadows (n = 5.8), while the other two treatments did not increase species numbers. Knop *et al*. (2006) already found significantly more orthopteran species in Swiss extensively managed ECA hay meadows compared to conventionally managed, improved meadows. Here we demonstrate that, among extensively managed ECA hay meadows, species richness can be further increased if uncut grass refuges are left uncut when mowing. Leaving uncut areas increases local-scale habitat and sward heterogeneity, offering a broad palette of ecological niches that boost invertebrate diversity including orthopterans (Guido and Gianelle, 2001). Ensifera benefitted more than Caelifera from the measure (see also Braschler et al., 2009), which is easily explained by a general preference of the former for denser, more structured habitats (Baur et al., 2006).

3.5.3 Conclusions and management recommendations

This study provides strong evidence that, among extensively managed hay meadows, delaying the first mowing date from early to mid summer boosts orthopteran density, while leaving uncut grass refuges is an efficient measure favouring orthopteran species diversity and abundance. While landscape factors must be considered in agri-environmental conservation planning for most components of farmland biodiversity, this research suggests that specific conservation and restoration action for orthopterans inhabiting meadowland can be achieved by simple measures implemented at the field scale (see also Poniatowski and Fartmann, 2010).

We recognize that these outcomes are not totally new. Delayed, and in particular partial or rotational mowing have already been recommended, not only for orthopterans (e.g. Guido and Gianelle, 2001; Marini et al., 2008; Braschler et al., 2009; Gardiner and Hassall, 2009; Müller and Bosshard, 2010; Humbert et al., 2012a), but also for several other grassland invertebrates that are sensitive to mechanized mowing, such as butterflies (both larvae and adults), bees and spiders (e.g. Buri et al. 2013 in prep; Baines et al., 1998; Dover et al., 2010; Humbert et al., 2010b; Cizek et al., 2012). This study, however, is the first that actually proves positive, immediate and cumulative (over three years) effects of such measures on an essential component of grassland food chains. Although it remains to be experimentally established to what extent other taxa of the upper trophic levels benefit from these measures, it is likely that an increased abundance of orthopterans will have positive effects on agro-ecosystem functioning and food web integrity given that this taxon constitutes a staple commodity for a great variety of insectivorous predators (e.g. Arlettaz et al., 1997; Vickery et al., 2001; Kovacs-Hostyanszki et al., 2011). We also stress that the exact responses of orthopterans to the different mowing regimes might depend on the weather conditions of the previous and current years which, in turn, influence the phenological development of the species (Thorens, 1993; Gardiner and Hassall, 2009). In Switzerland, 2011 was the hottest year since the climatic records began in 1864, and it was also rather dry. Spring 2012 was relatively hot and sunny too, which may have advanced orthopteran development, while June and July were cooler and wetter than usual.

Based on our principal findings, we formulate the following recommendations for improving agri-environmental measures, within the Swiss scheme and beyond. A fraction of extensively managed meadows should have their earliest possible mowing date postponed until mid summer (ca 15 July), while another fraction of these extensive meadows should maintain, including over winter, an uncut grass refuge on typically 10-20% of the grassland area (see also Schmidt et al., 2008). If implemented in concert across the matrix, these two measures are likely to produce additional positive effects through the increase of spatial habitat heterogeneity at the landscape scale (Benton et al., 2003). We believe that these rather simple measures could pave the way toward more efficient AES and sustainable agricultural management in the future.

Acknowledgements

We thank our colleagues at the Division of Conservation Biology and the members of the accompanying group for valuable inputs, logistical support, and field assistance, with a special credit to Laura Bruppacher and Nadia Bianco.

Thanks to the farmers who collaborated in this project, allowing us to work in their fields and applying the management we prescribed. We are grateful to the Swiss National Science Foundation (grant no. 31003A_125398/1 to R. Arlettaz), the Federal Office for the Environment, and several Swiss cantons (Aargau, Bern, Basel-Landschaft, Fribourg, Graubünden, Neuchâtel and Vaud) for their financial support. Many thanks to Markus Fischer and Jérôme Pellet for co-initiating this project, and to Aliki Buhayer who assisted with the English.

3.6 References

Arlettaz, R., Perrin, N., Hausser, J., 1997. Trophic resource partitioning and competition between the two sibling bat species *Myotis myotis* and *Myotis blythii*. J. Anim. Ecol. 66, 897-911.

Arlettaz, R., Schaub, M., Fournier, J., Reichlin, T.S., Sierro, A., Watson, J.E.M., Braunisch, V., 2010. From publications to public actions: when conservation biologists bridge the gap between research and implementation. Bioscience 60, 835-842.

Aviron, S., Nitsch, H., Jeanneret, P., Buholzer, S., Luka, H., Pfiffner, L., Pozzi, S., Schupbach, B., Walter, T., Herzog, F., 2009. Ecological cross compliance promotes farmland biodiversity in Switzerland. Front. Ecol. Environ. 7, 247-252.

Badenhausser, I., Amouroux, P., Lerin, J., Bretagnolle, V., 2009. Acridid (Orthoptera: Acrididae) abundance in Western European Grasslands: sampling methodology and temporal fluctuations. J. Appl. Entomol. 133, 720-732.

Badenhausser, I., Cordeau, S., 2012. Sown grass strip-A stable habitat for grasshoppers (Orthoptera: Acrididae) in dynamic agricultural landscapes. Agr. Ecosyst. Environ. 159, 105-111.

Baines, M., Hambler, C., Johnson, P.J., Macdonald, D.W., Smith, H., 1998. The effects of arable field margin management on the abundance and species richness of Araneae (spiders). Ecography 21, 74-86.

Bakker, J.P., Elzinga, J.A., de Vries, Y., 2002. Effects of long-term cutting in a grassland system: perspectives for restoration of plant communities on nutrient-poor soils. Appl. Veg. Sci. 5, 107-120.

Baur, B., Baur, H., Roesti, C., Roesti, D., Thorens, P., 2006. Sauterelles, Grillons et Criquets de Suisse. Haupt, Bern, CH.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol. Evol. 18, 182-188.

Braschler, B., Marini, L., Thommen, G.H., Baur, B., 2009. Effects of small-scale grassland fragmentation and frequent mowing on population density and species diversity of orthopterans: a long-term study. Ecol. Entomol. 34, 321-329.

Braunisch, V., Home, R., Pellet, J., Arlettaz, R., 2012. Conservation science relevant to action: a research agenda identified and prioritized by practitioners. Biol. Conserv. 153, 201-210.

Caudron, A., Vigier, L., Champigneulle, A., 2012. Developing collaborative research to improve effectiveness in biodiversity conservation practice. J. Appl. Ecol. 49, 753-757.

Cizek, O., Zamecnik, J., Tropek, R., Kocarek, P., Konvicka, M., 2012. Diversification of mowing regime increases arthropods diversity in species-poor cultural hay meadows. J. Insect Conserv. 16, 215–226.

Cop, J., Vidrih, M., Hacin, J., 2009. Influence of cutting regime and fertilizer application on the botanical composition, yield and nutritive value of herbage of wet grasslands in Central Europe. Grass Forage Sci 64, 454-465.

Dover, J.W., Rescia, A., Fungariño, S., Fairburn, J., Carey, P., Lunt, P., Dennis, R.L.H., Dover, C.J., 2010. Can hay harvesting detrimentally affect adult butterfly abundance? J. Insect Conserv. 14, 413-418.

Gardiner, T., Pye, M., Field, R., Hill, J., 2002. The influence of sward height and vegetation composition in determining the habitat preferences of three Chorthippus species (Orthoptera: Acrididae) in Chelmsford, Essex, UK. J. Orthoptera Res. 11, 207-213.

Gardiner, T., Hassall, M., 2009. Does microclimate affect grasshopper populations after cutting of hay in improved grassland? J. Insect Conserv. 13, 97-102.

Grant, A., Hassall, M., Willott, S.J., 1993. An alternative theory of grasshopper life-cycles. Oikos 66, 263-268.

Grime, J.P., 2001. Plant Strategies, Vegetation Processes, and Ecosystem Properties. John Wiley, Chichester, UK.

Guido, M., Gianelle, D., 2001. Distribution patterns of four Orthoptera species in relation to microhabitat heterogeneity in an ecotonal area. Acta Oecol. 22, 175-185.

Helden, A.J., Leather, S.R., 2004. Biodiversity on urban roundabouts-Hemiptera, management and the species-area relationship. Basic Appl. Ecol. 5, 367-377.

Humbert, J.-Y., Ghazoul, J., Walter, T., 2009. Meadow harvesting techniques and their impacts on field fauna. Agr. Ecosyst. Environ. 130, 1-8.

Humbert, J.-Y., Ghazoul, J., Richner, N., Walter, T., 2010a. Hay harvesting causes high orthopteran mortality. Agr. Ecosyst. Environ. 139, 522–527.

Humbert, J.-Y., Ghazoul, J., Sauter, G.J., Walter, T., 2010b. Impact of different meadow mowing techniques on field invertebrates. J. Appl. Entomol. 134, 592–599.

Humbert, J.-Y., Ghazoul, J., Richner, N., Walter, T., 2012a. Uncut grass refuges mitigate the impact of mechanical meadow harvesting on orthopterans. Biol. Conserv. 152, 96–101.

Humbert, J.-Y., Pellet, J., Buri, P., Arlettaz, R., 2012b. Does delaying the first mowing date benefit biodiversity in meadowland? Environmental Evidence 1, 1-9.

Kleijn, D., Baquero, R.A., Clough, Y., Diaz, M., De Esteban, J., Fernandez, F., Gabriel, D., Herzog, F., Holzschuh, A., Johl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M., Yela, J.L., 2006. Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecol. Lett. 9, 243-254.

Knop, E., Kleijn, D., Herzog, F., Schmid, B., 2006. Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. J. Appl. Ecol. 43, 120-127.

Kovacs-Hostyanszki, A., Korosi, A., Orci, K.M., Batary, P., Baldi, A., 2011. Set-aside promotes insect and plant diversity in a Central European country. Agr. Ecosyst. Environ. 141, 296-301.

Littlewood, N.A., Stewart, A.J., Woodcock, B.A., 2012. Science into practice – how can fundamental science contribute to better management of grasslands for invertebrates? Insect Conserv. Diver. 5, 1-8.

Marini, L., Fontana, P., Scotton, M., Klimek, S., 2008. Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps. J. Appl. Ecol. 45, 361-370.

Müller, M., Bosshard, A., 2010. Altgrasstreifen fördern Heuschrecken in Ökowiesen - Eine Möglichkeit zur Strukturverbesserung im Mähgrünland. Nat.schutz Landsch.plan. 42, 212-217.

Noordijk, J., Delille, K., Schaffers, A.P., Sykora, K.V., 2009. Optimizing grassland management for flower-visiting insects in roadside verges. Biol. Conserv. 142, 2097-2103.

OFAG, 2012. Rapport agricole 2012. OFAG, Bern.

Poniatowski, D., Fartmann, T., 2010. What determines the distribution of a flightless bush-cricket (*Metrioptera brachyptera*) in a fragmented landscape? J. Insect Conserv. 14, 637-645.

Poschlod, P., WallisDeVries, M.F., 2002. The historical and socioeconomic perspective of calcareous grasslands - lessons from the distant and recent past. Biol. Conserv. 104, 361-376.

R Core Team, 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reinhardt, K., Kohler, G., Maas, S., Detzel, P., 2005. Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. Ecography 28, 593-602.

Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. J. Appl. Ecol. 39, 157-176.

Schaffers, A.P., 2002. Soil, biomass, and management of semi-natural vegetation - Part II. Factors controlling species diversity. Plant Ecol. 158, 247-268.

Schmidt, M.H., Rocker, S., Hanafi, J., Gigon, A., 2008. Rotational fallows as overwintering habitat for grassland arthropods: the case of spiders in fen meadows. Biodiversity Conserv. 17, 3003-3012.

Sutherland, W.J., Pullin, A.S., Dolman, P.M., Knight, T.M., 2004. The need for evidence-based conservation. Trends Ecol. Evol. 19, 305-308.

Swiss Federal Council, 1998. Ordonnance sur les paiements directs versés dans l’agriculture. RS 910.13.

Thorens, P., 1993. Effets de la fauche sur une population du Criquet *Chorthippus mollis* (Charp.) (Orthoptera, Acrididae) dans une prairie du pied sud du Jura suisse. Bull. Soc. Ent. Suisse 66, 173-182.

Torok, P., Vida, E., Deak, B., Lengyel, S., Tothmeresz, B., 2011. Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. Biodiversity Conserv. 20, 2311-2332.

Valko, O., Torok, P., Matus, G., Tothmeresz, B., 2012. Is regular mowing the most appropriate and cost-effective management maintaining diversity and biomass of target forbs in mountain hay meadows? Flora 207, 303-309.

Van Wingerden, W.K.R.E., van Kreveld, A.R., Bongers, W., 1992. Analysis of species composition and abundance of grasshoppers (Orth. Acrididae) in natural and fertilized grasslands. J. Appl. Entomol. 113, 138-152.

Veen, P., Jefferson, R., de Smidt, J., van der Straaten, J., 2009. Grasslands in Europe of High Nature Value. KNNV Publishing, Zeist, the Netherlands.

Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J., Brown, V.K., 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J. Appl. Ecol. 38, 647-664.

Wesche, K., Krause, B., Culmsee, H., Leuschner, C., 2012. Fifty years of change in Central European grassland vegetation: Large losses in species richness and animal-pollinated plants. Biol. Conserv. 150, 76-85.

Wilson, J.D., Morris, A.J., Arroyo, B.E., Clark, S.C., Bradbury, R.B., 1999. A review of the abundance and diversity of invertebrate and plant foods of granivorous birds in northern Europe in relation to agricultural change. Agr. Ecosyst. Environ. 75, 13-30.

Table 1. Summary of the mowing regimes. Mean ± standard deviation (and number of meadows) of the ordinal day the first and second cut occurred in 2010, 2011 and 2012. Not all meadows were cut a second time.

	2010		2011		2012	
Treatment	1st cut	2n cut	1st cut	2n cut	1st cut	2n cut
Control	174.5 ± 5.4 (12)	239.4 ± 11.4 (9)	174.2 ± 2.8 (12)	242.5 ± 19.4 (8)	171.0 ± 4.7 (12)	235.7 ± 23.9 (12)
Delayed	200.0 ± 7.0 (12)	248.3 ± 20.3 (7)	209.3 ± 10.4 (12)	278.0 ± 34.6 (6)	204.9 ± 9.2 (11)	243.3 ± 19.3 (5)
Refuge	172.5 ± 2.8 (12)	234.4 ± 17.1 (12)	171.6 ± 3.3 (12)	233.5 ± 19.6 (12)	173.3 ± 9.7 (12)	225.1 ± 12.8 (11)
8W	172.3 ± 2.0 (12)	243.6 ± 19.7 (11)	175.6 ± 11.8 (12)	240.0 ± 14.6 (9)	174.9 ± 13.1 (12)	243.4 ± 21.2 (12)

Table 2. Effect of mowing regimes on orthopteran densities (individuals m^{-2}). Table refers to, and follows the same layout as Fig. 1. Density analyses were performed with generalized linear mixed models, using three seasonal datasets that regrouped sampling sessions (first model: sessions 1 and 2; second model; session 3; third model: sessions 4 and 5). Parameter estimates (differences between expected mean densities on log scale) are given for the paired regime comparisons and significant contrasts are highlighted in bold. Abbreviations are: (C) C-meadows: control meadows with first cut not before 15 June; (D) D-meadows: mowing delayed by a month, i.e. after 15 July; (8W) 8W-meadows: as C-meadows, but minimum of 8 weeks between first and second cut; (R) R-meadows: as C-meadows, but uncut refuge left over 10-20% of meadow area.

Model (sampling sess.) and comparison	**(a) All**			**(b) Adults only**		
	Estimate	*SE*	*P(>|z|)*	*Estimate*	*SE*	*P(>|z|)*
Model 1 (sess. 1 & 2)						
D vs. C	1.547	0.141	**<0.001**	-	-	-
8W vs. C	0.288	0.168	0.086	-	-	-
R vs. C	0.719	0.155	**<0.001**	-	-	-
8W vs. D	-1.270	0.126	**<0.001**	-	-	-
R vs. D	-0.839	0.108	**<0.001**	-	-	-
R vs. 8W	0.431	0.142	**0.002**	-	-	-
Model 2 (sess. 3)						
D vs. C	2.178	0.243	**<0.001**	2.984	0.703	**<0.001**
8W vs. C	-0.130	0.332	0.696	0.267	0.901	0.767
R vs. C	0.103	0.313	0.741	0.477	0.863	0.581
8W vs. D	-2.320	0.258	**<0.001**	-2.733	0.625	**<0.001**
R vs. D	-2.087	0.233	**<0.001**	-2.522	0.569	**<0.001**
R vs. 8W	0.233	0.326	0.474	0.210	0.785	0.789
Model 3 (sess. 4 & 5)						
D vs. C	-1.104	0.268	**<0.001**	-0.804	0.332	**0.015**
8W vs. C	-0.228	0.197	0.248	-0.160	0.266	0.546
R vs. C	-0.139	0.193	0.471	-0.037	0.257	0.887
8W vs. D	0.852	0.277	**0.002**	0.618	0.337	0.067
R vs. D	0.940	0.274	**0.001**	0.742	0.331	**0.025**
R vs. 8W	0.089	0.205	0.664	0.124	0.268	0.644

Continued

(continued)

	(c) Caelifera only			**(d) Caelifera adults only**		
	Estimate	*SE*	*P(>|z|)*	*Estimate*	*SE*	*P(>|z|)*
Model 1 (sess. 1 & 2)						
D vs. C	1.603	0.154	**<0.001**	-	-	-
8W vs. C	0.359	0.181	0.058	-	-	-
R vs. C	0.789	0.168	**<0.001**	-	-	-
8W vs. D	-1.255	0.134	**<0.001**	-	-	-
R vs. D	-0.826	0.115	**<0.001**	-	-	-
R vs. 8W	0.430	0.150	**0.004**	-	-	-
Model 2 (sess. 3)						
D vs. C	2.125	0.246	**<0.001**	2.906	0.738	**0.000**
8W vs. C	-0.151	0.337	0.653	0.141	0.972	0.885
R vs. C	0.102	0.316	0.746	0.455	0.909	0.617
8W vs. D	-2.289	0.264	**<0.001**	-2.782	0.697	**0.000**
R vs. D	-2.035	0.236	**<0.001**	-2.468	0.605	**<0.001**
R vs. 8W	0.254	0.331	0.443	0.314	0.854	0.713
Model 3 (sess. 4 & 5)						
D vs. C	-1.128	0.272	**<0.001**	-0.834	0.339	**0.014**
8W vs. C	-0.216	0.198	0.275	-0.139	0.268	0.605
R vs. C	-0.157	0.195	0.419	-0.066	0.263	0.802
8W vs. D	0.888	0.281	**0.002**	0.669	0.344	0.052
R vs. D	0.947	0.279	**0.001**	0.742	0.340	**0.029**
R vs. 8W	0.059	0.206	0.775	0.073	0.272	0.789

	(e) Ensifera only			**(f) Ensifera adults only**		
	Estimate	*SE*	*P(>|z|)*	*Estimate*	*SE*	*P(>|z|)*
Model 1 (sess. 1 & 2)						
D vs. C	1.237	0.360	**0.001**	-	-	-
8W vs. C	-0.163	0.464	0.725	-	-	-
R vs. C	0.273	0.417	0.513	-	-	-
8W vs. D	-1.405	0.385	**<0.001**	-	-	-
R vs. D	-0.969	0.327	**0.003**	-	-	-
R vs. 8W	0.436	0.432	0.314	-	-	-
Model 2 (sess. 3)						
D vs. C	3.476	1.660	0.036	3.582	2.344	0.127
8W vs. C	0.606	2.030	0.765	1.099	2.667	0.680
R vs. C	0.154	2.225	0.945	0.693	2.829	0.806
8W vs. D	-2.870	1.243	**0.021**	-2.483	1.393	0.075
R vs. D	-3.322	1.541	**0.031**	-2.888	1.682	0.086
R vs. 8W	-0.452	1.934	0.815	-0.406	2.108	0.848
Model 3 (sess. 4 & 5)						
D vs. C	0.000	1.670	1.000	0.000	1.670	1.000
8W vs. C	-2.485	4.163	0.551	-2.485	4.163	0.551
R vs. C	0.734	1.405	0.601	0.734	1.405	0.601
8W vs. D	-2.485	4.178	0.552	-2.485	4.178	0.552
R vs. D	0.734	1.447	0.612	0.734	1.447	0.612
R vs. 8W	3.219	4.079	0.430	3.219	4.079	0.430

Table 3. Paired comparisons of orthopteran densities (individuals m^{-2}) inside vs. outside (area of the meadow submitted to mowing) the uncut refuge within R-meadows after the initiation of mowing operations (sampling sessions 3-5). Table refers to, and follows the same layout as Fig. 2. Density analyses were performed with generalized linear mixed models on each sampling session separately. Parameter estimates (differences between expected mean densities on log scale) are given for the paired comparisons and significant contrasts are highlighted in bold.

Suborder(s), and sampling sess.	*Estimate*	*SE*	*P(>|z|)*
(a) All			
Session 3	1.656	0.235	**<0.001**
Session 4	0.350	0.222	0.116
Session 5	0.867	0.346	**0.012**
(b) Caelifera only			
Session 3	1.609	0.239	**<0.001**
Session 4	0.368	0.226	0.103
Session 5	0.860	0.349	**0.014**
(c) Ensifera only			
Session 3	2.825	1.556	0.070
Session 4	-0.270	1.368	0.844
Session 5	1.163	2.708	0.668

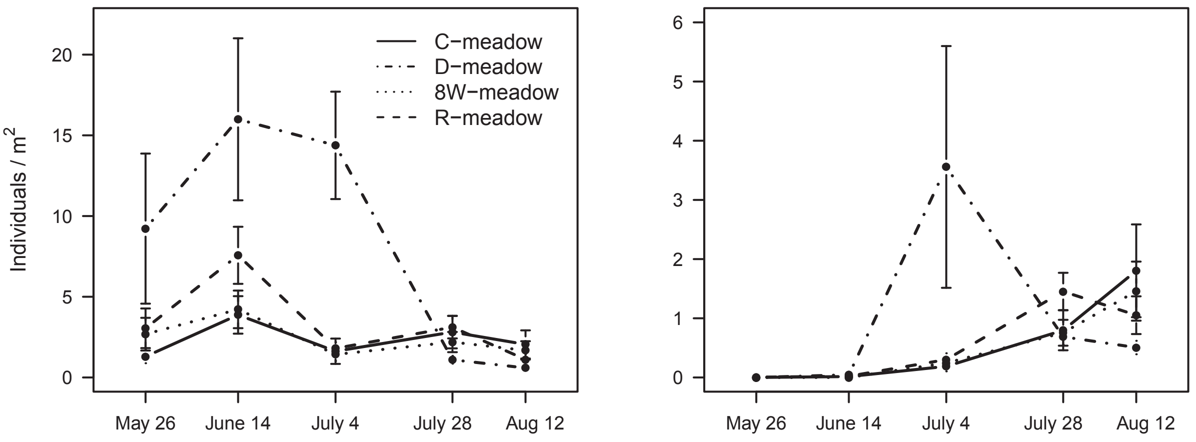
Table 4. Orthopteran species richness in relation to mowing regime. Table shows results for all orthopteran species (including both Caelifera and Ensifera), Caelifera species, and Ensifera species only. Data were analysed with linear mixed models, p-values and 95% confidence intervals (CI) were computed with 1 million Markov chain Monte Carlo (MCMC) iterations. MCMC mean parameter estimates (differences between expected mean densities) are given for the paired regimes comparisons and significant contrasts are highlighted in bold. For abbreviations, see legend of Table 2.

Suborder(s) and comparison	MCMC mean	Lower 95% CI	Upper 95% CI	MCMC *P*-value
(a) All				
D vs. C	0.242	-1.147	1.642	0.727
8W vs. C	0.584	-0.798	1.930	0.391
R vs. C	1.667	0.301	3.026	**0.018**
8W vs. D	0.334	-1.074	1.761	0.633
R vs. D	1.409	0.026	2.802	**0.048**
R vs. 8W	1.085	-0.407	2.554	0.142
(b) Caelifera				
D vs. C	0.017	-0.913	0.891	0.975
8W vs. C	0.166	-0.720	1.056	0.724
R vs. C	0.585	-0.296	1.493	0.191
8W vs. D	0.152	-0.783	1.056	0.749
R vs. D	0.567	-0.325	1.518	0.209
R vs. 8W	0.412	-0.535	1.379	0.377
(c) Ensifera				
D vs. C	0.235	-0.682	1.198	0.618
8W vs. C	0.416	-0.509	1.347	0.369
R vs. C	1.086	0.199	2.061	**0.022**
8W vs. D	0.175	-0.815	1.235	0.735
R vs. D	0.846	-0.137	1.922	0.102
R vs. 8W	0.667	-0.366	1.660	0.192

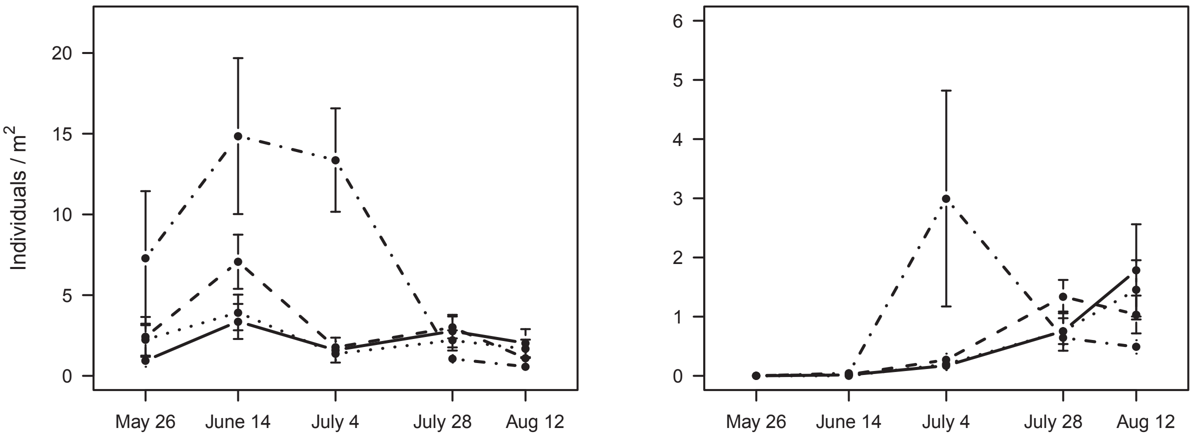
Figure 1. Seasonal (May-August 2012) density (mean ± standard error) of orthopterans in response to the four different mowing regimes. Each sampling session is represented by a single date that corresponds to the average of the 4-12 days needed to complete the session. The figure is divided in six parts according to orthopteran suborder(s) and developmental stage: (a) all individuals (nymphs and adults of both Caelifera and Ensifera); (b) adults only; (c) Caelifera only; (d) Caelifera adults only; (e) Ensifera only; (f) Ensifera adults only. C-meadows: control meadows (first cut not before 15 June); D-meadows: mowing delayed by a month, i.e. after 15 July; 8W-meadows (as C-meadows, but minimum of 8 weeks between first and second cut); R-meadows: as C-meadows, but uncut refuge left over 10-20% of meadow area. See Table 2 for statistical analyses.

Figure 1.

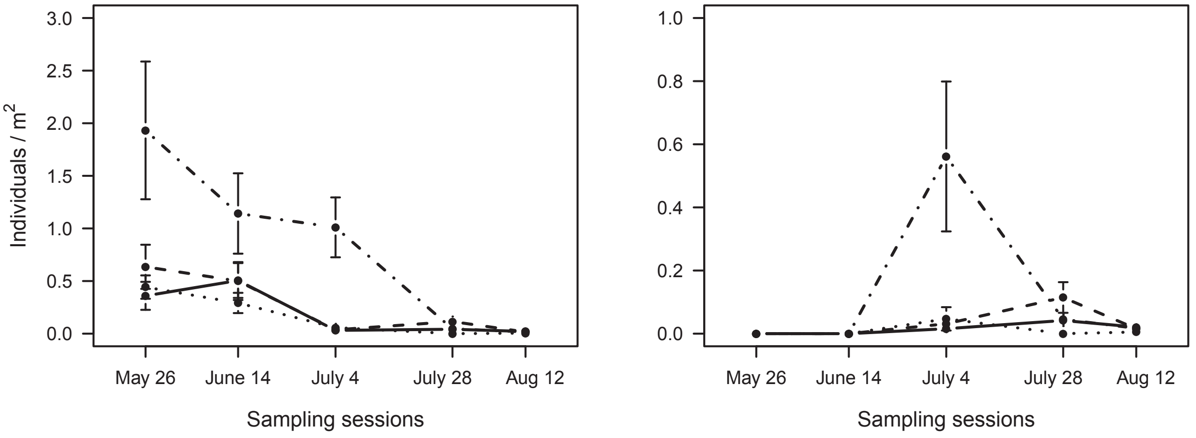
(a) **All** (b) **Adults only**



(c) **Caelifera only** (d) **Caelifera adults only**



(e) **Ensifera only** (f) **Ensifera adults only**



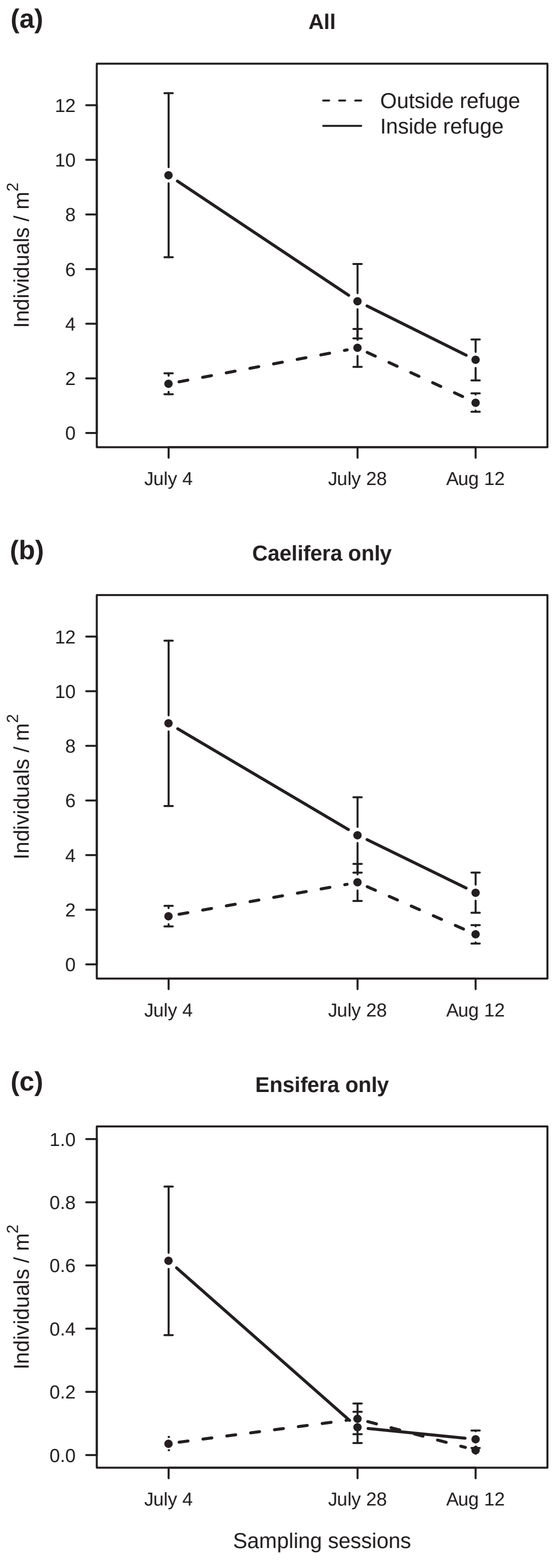


Figure 2. Seasonal density (mean ± standard error) of orthopterans within R-meadows after the initiation of mowing operations (sampling sessions 3-5). Shown are the densities inside and outside (area of the meadow submitted to mowing) the uncut refuge. See Table 3 for statistical analyses.

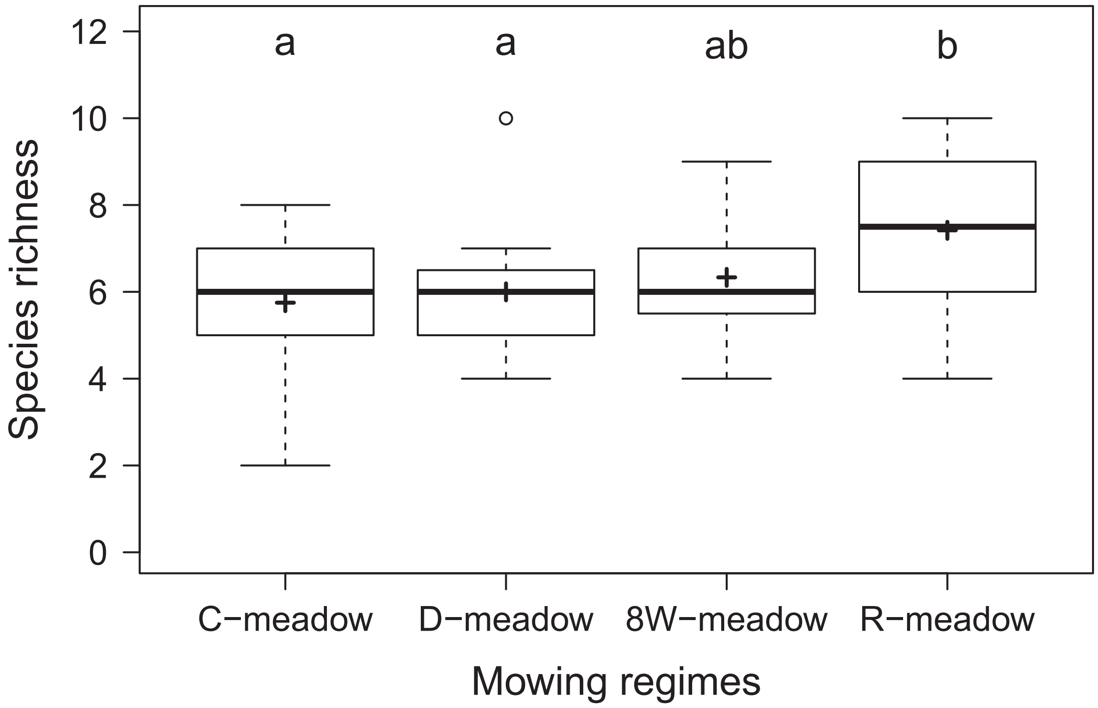


Figure 3. Orthopteran species richness with respect to mowing regime (median: bold line; mean: cross; first and third quartiles: box borders; interquartile distance multiplied by 1.5: whiskers; and open circles: outliers). Different letters indicate significant differences among regimes at an alpha rejection level of 0.05. For abbreviations, see legend of Fig. 1, for statistical analyses see Table 4a.

Appendix A. List of the different orthopteran species collected at the different study sites.

Cantons: AG = Aargau, BE = Bern, BL = Basel-Landschaft, FR= Fribourg, NE = Neuchâtel and VD = Vaud.
Coordinates according to both the Swiss grid system and the World Geodetic decimal System (WGS 84).
Species occurrence indicated by a cross.
NA: meadow missing from the final sample due to land-use conversion.

Canton	Region	Mowing treatment	Swiss grid X	Swiss grid Y	WGS84_X	WGS84_Y	Elevation [m.a.s.l.]	*Phaneroptera falcata*	*Meconema meridionale*	*Ruspolia nitidula*	*Tettigonia viridissima*	*Tettigonia cantans*	*platycleis albopunctata albopunctata*	*Metrioptera bicolor*	*Metrioptera roeselii*	*Pholidoptera griseoaptera*	*Mecostethus parapleurus*	*Chrysocraon dispar*	*Euthynteria brachyptera*	*Omocestus viridulus*	*Stenobothrus lineatus*	*Gomphocerippus rufus*	*Stauroderus scalaris*	*Chorthippus albomarginatus*	*Chorthippus biguttulus*	*Chorthippus brunneus*	*Chorthippus dorsatus*	*Chorthippus parallelus*	*Euchorthippus declivus*
AG	Lupfig	C-meadow	655871	255464	8.17942	47.44759	429								X		X								X		X	X	
AG	Lupfig	D-meadow	656488	254973	8.18753	47.44312	421				X				X		X								X		X	X	
AG	Lupfig	8W-meado	656968	254806	8.19388	47.44158	431				X				X		X					X			X		X	X	
AG	Lupfig	R-meadow	658689	255134	8.21673	47.44438	390								X		X								X	X	X	X	
BE	Belp	C-meadow	605487	192366	7.51062	46.88239	581				X				X		X					X			X			X	
BE	Belp	D-meadow	602699	195929	7.47407	46.91446	541								X										X	X		X	
BE	Belp	8W-meado	605869	193107	7.51564	46.88905	520								X									X	X			X	
BE	Belp	R-meadow	605992	193887	7.51727	46.89607	515								X		X								X			X	
BE	Grossaffoltern	C-meadow	595281	212666	7.37652	47.06500	510				X				X									X	X			X	
BE	Grossaffoltern	D-meadow	595164	213838	7.37496	47.07554	516								X		X							X	X	X		X	
BE	Grossaffoltern	8W-meado	592103	214070	7.33466	47.07760	516	X			X				X										X	X		X	
BE	Grossaffoltern	R-meadow	593100	212533	7.34781	47.06378	519				X				X		X							X	X	X	X	X	
BE	Hindelbank	C-meadow	612352	209751	7.60116	47.03868	568								X		X								X			X	
BE	Hindelbank	D-meadow	608715	211818	7.55334	47.05733	515				X				X							X			X	X		X	
BE	Hindelbank	8W-meado	608282	208143	7.54758	47.02428	589								X									X	X			X	
BE	Hindelbank	R-meadow	609796	208848	7.56751	47.03060	553									X	X					X			X	X	X	X	
BE	Huttwil	C-meadow	628558	215769	7.81477	47.09231	712					X			X		X			X	X			X				X	
BE	Huttwil	D-meadow	631454	217636	7.85304	47.10897	708				X				X		X								X			X	
BE	Huttwil	8W-meado	630859	216684	7.84513	47.10044	735					X			X			X		X				X	X			X	
BE	Huttwil	R-meadow	629144	217791	7.82261	47.11047	640					X			X		X					X			X			X	
BE	Wohlen	C-meadow	595389	205416	7.37801	46.99978	615				X						X								X	X		X	

BE	Wohlen	D-meadow	598952	205162	7.42486	46.99751	574				X													X	X			X	
BE	Wohlen	8W-meado	598193	203540	7.41489	46.98292	585				X				X	X	X								X			X	
BE	Wohlen	R-meadow	596265	202101	7.38956	46.96997	541	X			X				X	X	X								X	X		X	
BL	Diegten	C-meadow	628587	252768	7.81750	47.42509	481				X		X		X		X				X	X			X			X	
BL	Diegten	D-meadow	629724	254270	7.83267	47.43855	621								X		X				X			X	X		X	X	
BL	Diegten	8W-meado	628895	252035	7.82153	47.41849	558				X				X		X				X				X			X	
BL	Diegten	R-meadow	628554	251603	7.81699	47.41462	488				X		X	X	X		X				X				X	X		X	
FR	Cousset	C-meadow	565063	185881	6.98079	46.82316	482								X	X	X					X			X	X		X	
FR	Cousset	D-meadow	564488	185974	6.97325	46.82397	466				X											X			X	X		X	
FR	Cousset	8W-meado	564697	185486	6.97602	46.81959	481								X							X			X	X		X	
FR	Cousset	R-meadow	566709	186749	7.00230	46.83105	530				X				X	X	X				X			X	X	X		X	
NE	Coffrane	C-meadow	556126	205774	6.86176	47.00157	784																		X			X	
NE	Coffrane	D-meadow	555484	205770	6.85332	47.00149	790	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
NE	Coffrane	8W-meado	555499	206934	6.85340	47.01196	833				X			X	X	X			X		X		X		X			X	
NE	Coffrane	R-meadow	555200	206511	6.84951	47.00814	826				X				X				X		X		X		X			X	
VD	Avenches	C-meadow	567193	197127	7.00789	46.92443	550	X	X								X					X			X	X	X	X	
VD	Avenches	D-meadow	570876	198726	7.05615	46.93898	444		X	X	X				X	X	X					X			X	X		X	
VD	Avenches	8W-meado	571156	199189	7.05980	46.94316	479	X		X	X		X		X		X							X	X	X		X	
VD	Avenches	R-meadow	566771	196996	7.00236	46.92323	547	X							X		X					X			X	X		X	
VD	Nyon	C-meadow	506251	141110	6.21926	46.41479	466								X							X	X		X	X		X	
VD	Nyon	D-meadow	504394	137098	6.19594	46.37844	434			X	X				X		X								X	X		X	
VD	Nyon	8W-meado	503625	137146	6.18594	46.37876	451								X		X					X			X	X		X	
VD	Nyon	R-meadow	508935	140280	6.25433	46.40769	415			X	X		X	X	X								X		X	X		X	X
VD	Orbe	C-meadow	528474	173673	6.50323	46.71043	568				X				X						X		X		X			X	
VD	Orbe	D-meadow	527588	172614	6.49181	46.70081	612								X						X		X		X			X	X
VD	Orbe	8W-meado	526781	172298	6.48131	46.69787	649								X	X					X	X	X		X	X		X	X
VD	Orbe	R-meadow	528116	174457	6.49843	46.71744	560				X				X						X				X			X	

Red listed species in Switzerland:

Species	Status
Phaneroptera falcata	VU
Ruspolia nitidula	NT
Platycleis albopunctata	NT
Metripotera bicolor	VU
Chrysochraon dispar	NT
Euchorthippus declivus	VU

LC = Least Consern

VU = Vulnerable

4

Promoting pollinating insects in intensive agricultural matrices: field-scale experimental manipulation of hay-meadow mowing regimes and its effects on bees

Promoting pollinating insects in intensive agricultural matrices: field-scale experimental manipulation of hay-meadow mowing regimes and its effects on bees

Pierrick Buri[1], Jean-Yves Humbert[1], Raphaël Arlettaz[1,2]

[1] Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland

[2] Swiss Ornithological Institute, Valais Field Station, Rue du Rhône 11, CH-1950 Sion, Switzerland

Manuscript:
Submitted to *PLoS ONE*

4.1 Abstract

Bees are a key component of biodiversity as they ensure a crucial ecosystem service: pollination. This ecosystem service is nowadays threatened, because bees suffer from agricultural intensification. Yet, bees rarely benefit from the measures established to promote biodiversity in farmland, such as agri-environment schemes (AES). We experimentally tested if the spatio-temporal modification of mowing regimes within extensively managed hay meadows, a widespread AES, can promote bees. We applied a randomized block design, replicated 12 times across the Swiss lowlands, that consisted of three different mowing treatments: 1) first cut not before June 15 (conventional regime for meadows within Swiss AES); 2) first cut not before 15 June, as treatment 1 but with 15% of area left uncut serving as a refuge; 3) first cut not before 15 July. Bees were collected with pan traps, twice during the vegetation season (before and after mowing). Wild bee abundance and species richness significantly increased in meadows where uncut refuges were left, in comparison to meadows without refuges: there was both an immediate (within year) and cumulative (from one year to the following) positive effect of the uncut refuge treatment. An immediate positive effect of delayed mowing was also evidenced in both wild bees and honey bees. Conventional AES could easily accommodate such a simple management prescription that promotes farmland biodiversity and is likely to enhance pollination services.

Keywords: bowl trap; bumblebees; solitary bees; ecological compensation areas; honey bees; postponed mowing

4.2 Introduction

Animal pollination is an essential ecosystem service, without which more than 80% of flowering plants could not properly set seeds [1] and many important food products would become difficult to grow [2]. Despite its key role, pollination is nowadays threatened by numerous factors [3]. For example, managed honey bees *Apis mellifera* are impacted by a global colony loss, which has recently decimated up to 53% of European colonies [3,4]. Alternative pollinators that are not directly managed by humans, like wild bees, are also threatened by habitat loss, landscape fragmentation, use of agro-chemicals, and general degradation of ecological resources [5,6]. This phenomenon is referred to as the "pollination crisis" [7], but see [8]. The pollination role of wild bees in food production has long been debated, but recent studies indicate it might be much more important than previously thought [9,10]. The situation for pollinators is likely to worsen in the future due to the rising demand for food production that will inevitably lead to further agricultural intensification, which will in turn translate into even more demand for, and pressure on pollination [10,11].

The intensification of farming practices has been the main process eroding biodiversity in low-input farmland, which was the typical cultivated landscape across Europe until World War II [12-14]. Intensification is achieved via the application of fertilizers and pesticides, and through a growing reliance on heavy machinery that necessitates radical landscape simplification [15]. In order to counter this negative impact of agricultural intensification on biodiversity, agri-environment schemes (AES) were established in the early 1990's throughout Europe in order to encourage farmers to adopt more environmental friendly farming practices [16]. AES primarily aim at protecting and restoring farmland biodiversity, thus securing or even enhancing several ecosystem services, including pollination. Some AES like the sown wildflower strips and areas were specifically designed to promote pollinating insects, but their temporary based management misses the restoration of semi-natural habitats [17]. In comparison, extensively managed (low-input) grasslands established under AES regulations are widespread [16], usually harbouring more wild bees than high-intensity grasslands [18,19]. However, several studies have established that these AES have only a moderate positive impact on overall biodiversity and bees

[20]. This calls for the development of more appropriate management practices that can favour biodiversity, including pollinating insects [21].

The main aim of this study was to test whether and how slight modifications of mowing regimes may improve wild bee biodiversity in extensively managed hay meadows, a widespread AES scheme [22]. These altered management regimes had to be easily implementable by farmers to ensure their potential future uptake; they consisted of 1) not mowing a fraction of the meadow so as to leave an uncut area as refuge that is expected to boost wild bee biodiversity by continuously providing them with food resources, essentially nectar and pollen, during the entire season; 2) delaying by one month the first cut in order to provide undisturbed meadows with flowers and other crucial resources during the whole peak of natural wild bee activity. These two experimental treatments were compared with the Swiss AES serving as 'control'; the ecological compensation areas (ECA). Standard management for hay meadows complying with ECA regulations are: first cut not before 15 June and; with no uncut refuge left behind. These treatments were applied at the field scale, two years in a row (2010 and 2011), in order to test for both immediate (within season) and cumulative (from one year to the following) effects. For this purpose, wild bees were collected twice in 2011: firstly in June, before the onset of any mowing intervention in all meadows; secondly beginning of July, when meadows with uncut refuges and control meadows were mown, but not meadows with delayed mowing regimes. To our knowledge, this study is the first attempt to manipulate mowing regimes at the field scale to test whether such simple measures can promote bee diversity. Although drawn from the Swiss context, the resulting recommendations have far-reaching implications for the establishment of AES across Europe if not beyond. They will contribute to de development and implementation of pollinator-friendly management practices and could potentially complement wild-flower strips [23]. They are also timely given the current intention of the European Union to frame a more biodiversity-friendly common agricultural policy [23]. In order to avoid jeopardizing essential components of biodiversity such as the guilds of natural pollinators, innovative farming practices have to be developed. We also take the opportunity to investigate and provide new data about the effectiveness our sampling method.

4.3 Material and methods

4.3.1 Ethic statement

Farmers that participated to this project were informed about, and approved, the studies before they started.

4.3.2 Study sites

We selected 36 extensively managed hay meadows registered as ECA across the Swiss Plateau (lowlands between the Jura and the Alps) in 2010 (see Appendix S1 and S2). The Swiss Plateau can be characterized mainly as a simple landscape where non-crop habitats are still present, but constitute usually only 1–20 % of the matrix [14]. The ECA retained for our experiments had to be registered since latest 2004 (range: 1993–2004) and had to have a minimal area of 0.3 ha (range: 0.3–1.7 ha). The meadows were situated between 390 and 833 m altitude. They were clustered in 12 study areas (our geographic replicates) distant from each other by ≥ 5 km, each area containing three meadows that were more than 400 m distant (range: 440– 6170 m) but that were enclosed within a radius of 3.5 km.

We had first to assess the different land covers as these could be important covariates that should be accounted for in our analysis. Land covers were extracted from the Vector 25 data base of the Swiss Federal Office of Topography [24], using QGIS [25] and SpatiaLite [26] software. Land covers [proportion of forest, settlements, water bodies (including rivers), special crops (vineyards and orchards), and gravel pits] were quantified around each meadow within different nested concentric radii ranging from 250 to 3000 m, with steps of 250 m. A principal component analysis (PCA) was then conducted on land covers to draw synthetic information about the various landscape contexts at the different geographic replicates [27,28]. The PCA was performed with land cover values averaged across these radii, this to avoid auto-correlation [28-30]. We retained only PCA axes that had a proportion of variance superior to a broken-stick model with heuristic for principal component selection [31], with the function *PCAsignificance* of the package BiodiversityR [32]. Then the coefficients of the Pearson product-moment correlation (eigenvectors) of the retained axes were used to select important land covers with 0.5 as cutting of value.

4.3.3 Study design

A randomized block design was adopted [33], where the three mowing regimes (our two experimental treatments and a control) were applied once each within each study area. Hence, each area represented a geographic replicate (*n* = 12), i.e. an experimental block in the design, which allowed achieving data independency. The following treatments and control were randomly assigned to the three meadows within each area. We start with the control, because it represents the standard management that today prevails among extensively managed hay meadows within the ECA (ecological compensation areas) measures of the Swiss AES: 1) control meadow (abbreviated C, C-meadow): managed according to the Swiss regulations for ECA extensive hay meadows, i.e. first cut not before 15 June; 2) refuge treatment (R, R-meadow): same as C, but at each cut 10 to 20% of the meadow area were left uncut; 3) delayed mowing (D, D-meadow): same as C, but first possible cut not before 15 July (one month later than C). All other management aspects (such as non-application of fertilizers and pesticides or minimal duration of 6 years) abided by the present regulation [34]. Each farmer was interviewed about mowing dates and related management issues using a standardized questionnaire.

4.3.4 Wild bees sampling

In 2011, plastic bowl traps (13 cm in diameter and 12.5 cm deep) were used to sample wild bees (Hymenoptera: Apoidea) applying the following protocol: three bowl traps (blue, white and yellow) were fixed on a wooden pole just above the grass vegetation layer [35]. They were operated at daylight (8:00 –19:00) during only one day in order to avoid local population depletion [36]. Three such poles equipped with three bowl traps were placed at the apexes of a virtual isosceles triangle (base: 14 m; sides: 10 m) randomly placed inside the meadow, within at least 10 m from meadow edges so as to reduce margin effects [18]. Meadows were sampled twice, a first time between 23 May and 14 June, i.e. before the onset of mowing in any treatment and control meadows (hereafter referred to as the 'June' samples) and a second time between 2 July and 12 July, i.e. before the first mowing of D-meadows but when C-meadows and R-meadows were regrowing (hereafter 'July' samples). Samplings took place on sunny, non-windy days with ambient temperature ≥ 15°C [35]. All the meadows within a given area were sampled simultaneously (Supporting information Appendix S2 for exact dates). Samples were stored individually in plastic bags and frozen at -20°C. Before sorting them, defrozen samples were washed, bees pinned and dried [37]. Bees were identified according to identification keys for Central Europe [38-44].

4.3.5 Data analysis

Data were analysed with generalized linear mixed models (GLMMs) using the *lmer* function from the *lme4* package for R [45]. Wild bees consisted of the so-called "solitary bees" and of bumblebees pooled together. Fixed effects were the mowing treatments and the land covers selected in the previous part. The latter were added in the models, progressively increasing model complexity, following a bidirectional stepwise procedure [46,47]. Areas (our geographic replicates) were designated as a random effect. Response variables were pooled for each meadow and resulted in: wild bee abundance; species richness and; diversity (Shannon-Wiener index). The former two variables were analysed fitting a Poisson error distribution and the latter one fitted a normal error distribution. Data of the two sampling periods (June and July) were first analysed pooled together, then separately, this in order to better appraise underlying patterns. Planned orthogonal comparisons were done to identify significant differences between the treatments. In addition, we also investigated in a similar way the effects of these mowing regimes on the abundance of honey bees given that feral honey bee colonies apparently do not occur in Switzerland [48] and the efficiveness of the different colours of our traps. All the analyses were performed with statistical software R version 2.15.0 [49].

4.4 Results

We collected a total of 1’620 wild bees (Appendix S2) and 281 honey bees. Cryptic, sibling species of bumblebees that were difficult to identify were grouped within their respective taxonomic groups, mostly subgenera (*Bombus* sensu stricto, *Megabombus* and *Thoracobombus* [43]). Cryptic, sibling species of solitary bees were grouped within the following categories: *Halictus simplex* group (*Halictus simplex*; *H. eurygnathus* and *H. langobardicus* and *Andrena ovatula* group *(Andrena ovatula* and *A. albofasciata*). Altogether, we could identify 62 wild bee species (9 bumblebee and 56 solitary bee species; full species list in supporting information Appendix S3).

4.4.1 Bowl trap efficiency

Yellow bowl traps were generally more efficient (greater number of captures of wild bees) than white traps which were themselves more attractive than the blue ones. These differences were significant when the June and July samples were pooled, and when the June data was considered separately. In July, however, yellow and white traps did not differ in efficiency between each other though they were still more attractive than the blue traps (detailed analysis in supporting information Appendix S4).

4.4.2 Management and land cover

Our study meadows were mown, on average (±SD), 1.92 times (0.56) and 1.81 times (0.49) in 2010 and 2011, respectively, with a minimum number of cuts of one and a maximum of three. There was no significant difference in the yearly number of cuts between 2010 and 2011. In 2011, the first cut took place between 15 June and 26 June in C– and R–meadows, and between 15 July and 15 August in D–meadows (exact dates are provided in the appendix S5). In R-meadows, uncut grass refuges covered, on average, 15% of the meadow area.

Regarding the PCA on landscape covers, only the first component fulfilled the broken-stick criteria (73.41% of variance explained vs 45.66% expected). The following land covers were identified as significant based on their eigenvalues (Pearson product-moment correlation) and retained for subsequent analyses: forest (-0.511); special crops (0.566) and water bodies (0.515).

4.4.3 Effect of mowing treatments on wild bees

In the analyses performed with data from June and July pooled together, the mean abundance (±SE) of wild bees was 53.16 (±14.15) in R-meadows (refuge) and was significantly higher compared to C-meadows (control, 39.08 ±8.9; Fig. 1a and Table 1). Abundance in D-meadows (delayed mowing) was only marginally higher than in C-meadows. Finally, significantly fewer individuals were found in D-meadows compared to R-meadows ($Z = 3.677$, $P < 0.001$). The land covers retained in this first model were forest and water bodies with both a negative effect on wild bee abundance; in contrast, special crops had a positive effect. Species richness did not show any significant difference among the mowing regimes with the June and July samples pooled (Fig. 2a and Table 2). Neither did we find any difference for the Shannon-Wiener index of diversity for pooled data.

In June, the abundance of wild bees in R-meadows was, on average, 22.17 (± 5.05), i.e. significantly higher than in C-meadows (11.08 ± 2.44) and D-meadows (8.75 ± 2.60; $Z = 2.101$, $P = 0.035$; Fig. 1b). Abundance in D-meadows was also marginally lower than in C-meadows. Only special crops were retained as a significant land cover in this model, with a positive effect. Species richness in R-meadows was 7.25 (± 1.15), significantly higher than in both C-meadows (4.92 ± 0.80; Table 2) and D-meadows (3.67 ± 0.58; Z = 3.664, $P <$ 0.001; Fig. 2b). Special crops coverage had again a positive effect on species richness. In contrast, we detected no significant effect on the Shannon-Wiener index of diversity.

In July, the mean abundance of wild bees collected in D-meadows was 34.00 (± 8.78) individuals, i.e. significantly higher than in C-meadows (28.00 ± 8.17; Fig 1c). The abundance in R-meadows (31 ± 10.07) was also higher than in C-meadows ($Z = 2.472$, $P = 0.\ 0013$). Forest ($Z = 2.319$, $P = 0.\ 021$) and water bodies ($Z = -4.021$, $P < 0.001$) were the only land covers retained by the model; both had a significant negative effect. Neither species richness nor the Shannon-Wiener index of diversity showed any significant difference among mowing regimes.

When the data of June and July were pooled, honey bee abundance was, on average, 9.91 ± 2.49 in D-meadows, i.e. significantly higher than the abundance recorded in C-meadows (6.5 ± 1.08; GLMM with Poisson; $Z = 2.894$, $P = 0.0038$) and R-meadows (6.83 ± 1.38, Z = 0.316, $P = 0.75$). In June, no significant difference was found, while in July honey bee abundance was significantly higher in D-meadows (6.83 ± 2.05) compared with C-meadows (3.67 ± 0.88; $Z = 3.323$, $P <0.001$) and R-meadows (3.08 ± 0.91; $Z = 3.221$, $P = 0.00128$).

4.5 Discussion

This study shows that leaving 10-20% of the area of an extensive meadow uncut when mowing (R-meadows) is overall beneficial for wild bee populations, more so than delaying the date of mowing by one month (D-meadows). There were variations in the observed pattern according to whether we consider immediate (within the same season) or cumulative (from one year to the following) effects. Regarding cumulative effects [samples collected in June in the year following (i.e. year_{t+1}) the year of first application (year_t) of the different management treatments, but before any mowing event in year_{t+1}], positive effects were evidenced for both wild bee abundance and species richness. The average wild bee abundance was double so high in R-meadows compared to C-meadows, and even 2.4 times higher than in D-meadows that had the lowest values (Fig. 1b). Species richness was, on average, 1.75 and 1.4 higher in R-meadows compared to D-meadows and C-meadows, respectively (Fig. 2b). Immediate effects showed a reversed pattern, but only regarding wild bee abundance, with D-meadows harbouring, on average, 1.2 and 1.1 times more individuals than C- meadows and R-meadows, respectively; this is not very surprising given that D-meadows were not yet mown at the second sampling session. Concerning, honey bee population size estimates, we could not evidence a cumulative effect, while immediate effects showed that D-meadows supported ca. 1.8 and 2.3 times greater abundances than C-meadows and R-meadows, respectively.

The positive cumulative effect of the refuge treatment (R) on wild bee abundance indicates that populations could build up thanks to the grass refuge installed the year before. This demonstrates that uncut grass refuges have a positive impact on these pollinating insects beyond the season they are applied in. This cumulative effect is crucial for the maintenance of pollination services because pollination efficiency is based on the redundancy principle, which emphasizes the importance of pollinator abundance above species richness [7,50,51]. Our results further confirm that wild bees can react extremely rapidly to changes in management practices: this first analysis stems from just one year of field experimentation (June 2010 – July 2011). Such a rapid positive reaction is consistent with the responses of bumblebees to modifications in grazing management [52] and manipulation of the cutting management of flower patches [27]. Similar responses were also observed in other taxa, such as orthopterans [53], spiders [54] and the only other pollinator taxon studied, butterflies [55]. Finally, the absence of a similar effect in honey bees in the present study can be due to the fact that these Hymoneptera depend neither on the structures nor on the food resources offered by the refuges for building their colonies, while they furthermore profit from artificial feeding at the hives (feral honey bees are extremely rare in Switzerland [48]). The continuation of our experiments during the coming years will allow assessing whether cumulative effects may further grow with additional years of implementation of the treatments.

Regarding immediate effects, delayed mowing (D-meadows) appeared to be more efficient than the creation of an uncut refuge (R-meadows) for increasing abundance of both wild and honey bees. Yet, the magnitude of these positive effects was strikingly lower than the cumulative effects obtained with the refuge treatment. Furthermore, this effect reflects the fact that D-meadows were not yet mown at the time of the second sampling session, contrary to R-meadows and C-meadows that were already regrowing after the first cut. These D-meadows were thus the main sources of nectar and pollen left in the agricultural matrix at that time of the year, which corresponds to the peak of hymenopteran pollinator activity [27], thus typically generating some short-term spatio-temporal concentration [56]. This hypothesis of a temporary concentration effect is further supported by the lower wild bee abundance and species richness in D-meadows compared to C- and R-meadows in June: for many species that firstly depend on vegetation with a late phenology, mowing around mid-July could still be too early. Notwithstanding the fact that bowl trapping is not the most efficient method to capture honey bees [35,57], their concentration in D-meadows in July highlights the need for valuable flowering patches at this time of the year. Maintaining uncut meadows in the middle of the summer could indeed provide them with precious floral resources between the massive spring blossoming of both natural flowers and some crops (mainly oilseed rape *Brassica napus*) and other crops with a later phenology, e.g. sunflowers *Helianthus annuus* [58].

Improvement of species richness was only detected as a cumulative effect (June samples) and occurred furthermore only in R-meadows, but not in D-meadows. This result is in accordance with the outcome of the main study on Hymenoptera retrieved in the meta-analysis on delaying mowing done by

Humbert et al. [59]. To the contrary of the main trend for arthropods, no effect of postponing mowing could be evidenced for bumblebee species richness [60].

Surprisingly, the effect of our mowing treatments did not affect species diversity (Shannon-Wiener index). An explanation could be that the relative population sizes of different sympatric wild bee species do not vary in relation to the number of co-occurring species [61], which would lead to little spatial variation in the index. Moreover, although R-meadows harboured, on average, more species than C-meadows and D-meadows in June, there was no new species specifically profiting from the refuge that appeared in the samples. Actually, among the 62 different species captured, only twelve occurred in more than seven of the 12 study areas (Appendix S4). This high level of spatial differentiation in bee communities, i.e. apparent high level of functional redundancy, was particularly striking within bee genera having similar ecological requirements, such as *Lasioglossum* and *Halictus* [6].

Land covers have an important influence on bees that are relatively mobile organisms [28-30]. The major land covers selected through the PCA were forest, water bodies and special land managements. The two first ones had the most part of time a negative influence, because they represent less suitable habitats for bees. Thus a high proportion of such features in the surroundings have a negative influence. Special land management had a positive influence in spring. This could be due to the kind of crops present in this land cover, especially orchards that are reputed to be major nectar sources.

Concerning the difference observed between the colours of the traps, the conclusion of the effectiveness of the yellow is in accordance with the literature [35]. Interestingly, other colours, especially white, can be as effective and more representative of the plant flowering community and thus illustrates the complementarity of the different colours for this traps.

4.6 Management recommendations and conclusions

This study constitutes to our knowledge the first attempt to experimentally test, moreover at real field-scale, the effects of different grassland management regimes in hay meadowland on wild bee communities and population sizes. It demonstrates that creating uncut refuges on a relatively small fraction of a hay meadow can quickly and efficiently promote pollinating insects such as wild bees during the following year, which is likely to enhance an essential ecosystem service. Although it remains to be established whether the inter-annual positive effects we observed further cumulate beyond one year, this measure represents a promising agri-environmental option, especially given that its simplicity of implementation might ensure a quick up-take by farmers, of course providing that financial incentives exist. In contrast, delaying mowing seems to have comparatively much smaller positive effects on bees as it simply leads to a temporary concentration of bees on the few patches with flowering plants that remain in farmland matrices that otherwise become hostile for pollinators after late spring mowing operations. Uncut refuges could enter the toolkit for promoting pollinators within farmland, similar to, for instance, wildflower sown margins [27].

Another advantage of the uncut refuge option, over the delayed mowing option, is that it does not affect hay production to the same extent, given that only a fraction of the meadow remains unmown. The hay extracted from the non-refuge area would furthermore be of overall better quality because the timing of mowing operations can take place earlier than in D-meadows, i.e. closer to the period of forage quality peak. A systematic implementation of this measure within extensive hay meadows across the agricultural matrix might efficiently boost wild bee populations and communities. We may furthermore expect that the overall impact of a network of such refugial structures reaches beyond the sum of the local effects, due to opportunities for reconstituting functional meta-populations and integral communities, this especially given the short flight radius of numerous pollinators [29,30]. This simple measure could also easily be integrated in extant AES which – given the extension of grassland AES [20,22] – would theoretically lead to widespread improvement of pollination services in agriculture. Finally, the fact that this measure is already suggested as a voluntary enrolment for farmers in such schemes will enhance the probability of its uptake.[62,63]. Future research must investigate whether extra positive cumulative effects will, in the mid and long run, add to the short-term effects observed in this study. It must also establish whether other plant and animal taxa benefit from uncut refuges, and whether combining this measure with delayed mowing on, for instance, another small fraction of the same meadow might multiply the benefits for biodiversity, especially pollinating insects.

Acknowledgments

We thank Markus Fischer and Jérôme Pellet for their input in proposal preparation. We are grateful to Sabine Oertli for the identification of solitary bees, Christophe Praz for advice with sampling design, Nastassja Rieder and Franck Gandiaga for general assistance. We also thank Vincent Dietemann for fruitful discussions about honey bees. Special thanks go to all the farmers who participated in this project. This project was done with the technical support of the Federal Office of Environment, and the following cantonal offices of environment and/or agriculture: Bern, Vaud, Basel-Landschaft, Aargau, Neuchâtel, Fribourg, Valais and Graubünden. We also express our gratitude to all the members of the project accompanying group for their strong support and to the anonymous reviewers for their helpful comments.

4.7 References

1. Bawa KS (1990) Plant-pollinator interactions in Tropical rain forests. Annual Review of Ecology and Systematics 21: 399-422.
2. Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, et al. (2007) Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B 274: 303-313.
3. Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O, et al. (2010) Global pollinator declines: trends, impacts and drivers. Trends in Ecology & Evolution 25: 345-353.
4. Carreck N, Neumann P (2010) Honey bee colony losses. Journal of Apicultural Research 49: 1-1.
5. Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, et al. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313: 351-354.
6. Winfree R, Aguilar R, Vàzquez DP, Lebuhn G, Aizen MA (2009) A meta-analysis of bees’ responses to anthropogenic disturbance. Ecology 90: 2068-2076.
7. Steffan-Dewenter I, Potts SG, Packer L (2005) Pollinator diversity and crop pollination services are at risk. Trends in ecology & evolution 20: 651-652.

8. Ghazoul J (2005) Buzziness as usual? Questioning the global pollination crisis. Trends in ecology & evolution 20: 367-373.
9. Aizen MA, Garibaldi LA, Cunningham SA, Klein A-M (2009) How much does agriculture depend on pollinators? Lessons from long-term trends in crop production. Annals of Botany 103: 1579-1588.
10. Breeze TD, Bailey AP, Balcombe KG, Potts SG (2011) Pollination services in the UK: How important are honeybees? Agriculture, Ecosystems & Environment 142: 137-143.
11. Diekötter T, Kadoya T, Peter F, Wolters V, Jauker F (2010) Oilseed rape crops distort plant-pollinator interactions. Journal of Applied Ecology 47: 209-214.
12. Bignal EM, McCrackent DI (1996) Low-intensity farming systems in the conservation of the countryside. Journal of Applied Ecology 33: 413-424.
13. Hendrickx F, Maelfait J-P, Van Wingerden W, Schweiger O, Speelmans M, et al. (2007) How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. Journal of Applied Ecology 44: 340-351.
14. Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. Ecology Letters 8: 857-874.
15. Warren J, Lawson CS, Blecher K (2008) The Agri-Environment. Cambridge, United Kingdom. 1-232 p.
16. Kleijn D, Sutherland WJ (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity ? Journal of Applied Ecology 40: 947-969.
17. Haaland C, Naisbit RE, Bersier L-F (2011) Sown wildflower strips for insect conservation: a review. Insect Conservation and Diversity 4: 60-80.
18. Knop E, Kleijn D, Herzog F, Schmid B (2006) Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. Journal of Applied Ecology 43: 120-127.
19. Albrecht M, Duelli P, Müller C, Kleijn D, Schmid B (2007) The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. Journal of Applied Ecology: 813-822.

20. Kleijn D, Baquero Ra, Clough Y, Díaz M, De Esteban J, et al. (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. Ecology letters 9: 243-254; discussion 254-247.
21. Littlewood NA, Stewart AJA, Woodcock BA (2012) Science into practice - how can fundamental science contribute to better management of grasslands for invertebrates? Insect Conservation and Diversity 5: 1-8.
22. FOAG (2012) Rapport Agricole 2011. Bern: Federal Office of Agriculture. 1-284 p.
23. Hart K, Baldock D (2011) Greening the CAP: Delivering environmental outcomes through pillar one. http://www.ieep.eu/assets/831/Greening_Pillar_1_IEEP_Thinkpiece_-_Final.pdf
24. Swisstopo (2012) Vector 25. Federal Office of Topography, Wabern, Switzerland.
25. Quantum GIS Development Team (2012) *QGIS*. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project.
26. Furieri A (2008) SpatiaLite - A complete spatial DBMS in a nutshell. http://www.gaia447gis.it/gaia-sins/
27. Pywell RF, Meek WR, Hulmes L, Hulmes S, James KL, et al. (2011) Management to enhance pollen and nectar resources for bumblebees and butterflies within intensively farmed landscapes. Journal of Insect Conservation 15: 853-864.
28. Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharntke T, et al. (2002) Scale-dependant effects of landscape context on three pollinator guilds. Ecologgy 83: 1421-1432.
29. Gathmann A, Tscharntke T (2002) Foraging ranges of solitary bees. Journal of Animal Ecology 71: 757-764.
30. Kohler F, Verhulst J, Van Klink R, Kleijn D (2007) At what spatial scale do high-quality habitats enhance the diversity of forbs and pollinators in intensively farmed landscapes? Journal of Applied Ecology 45: 753-762.
31. Peres-Neto PR, Jackson Da, Somers KM (2005) How many principal components? stopping rules for determining the number of non-trivial axes revisited. Computational Statistics & Data Analysis 49: 974-997.

32. Kindt R, Coe R (2005) Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. In: (ICRAF) WAC, editor. Nairobi.
33. Gotelli NJ, Ellison AM (2004) A Primer of Ecological Statistics. Sunderland, USA: Sinauer Associates Incorporated. 1-479 p.
34. Swiss Federal Council (1998) Verordnung über die Direktzahlungen an die Landwirtschaft. 93013. pp. 229-265.
35. Westphal C, Bommarco R, Carré G, Lamborn E, Morison N, et al. (2008) Measuring bee diversity in different European habitats and biogeographical regions. Ecological Monogrpahs 78: 653-671.
36. Russell KN, Ikerd H, Droege S (2005) The potential conservation value of unmowed powerline strips for native bees. Biological Conservation 124: 133-148.
37. Droege S, Tepedino VJ, Lebuhn G, Link W, Minckley RL, et al. (2010) Spatial patterns of bee captures in North American bowl trapping surveys. Insect Conservation and Diversity 3: 15-23.
38. Amiet F (1996) Apidae 1. Teil. Allgemeiner Teil, Gattungsschlüssel, die Gattungen Apis, Bombus und Psithyrus. Neuchatêl, Switzerland: Centre Suisse de Cartogrpahie de la Faune. 1-98 p.
39. Amiet F, Herrmann M, Müller A, Neumeyer R (2001) Apidae 3. Halictus, Lasioglossum. Neuchatêl, Switzerland: Centre Suisse de Cartogrpahie de la Faune. 1-208 p.
40. Amiet F, Herrmann M, Müller A, Neumeyer R (2004) Apidae 4. Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia, Stelis: Centre Suisse de Cartogrpahie de la Faune. 1-273 p.
41. Amiet F, Herrmann M, Müller A, Neumeyer R (2007) Apidae 5. Ammobates, Ammobatoides, Anthophora, Biastes, Ceratina, Dasypoda, Epeoloides, Epeolus, Eucera, Macropis, Melecta, Melitta, Nomada, Pasites, Tetralonia, Thyreus, Xylocopa: Centre Suisse de Cartogrpahie de la Faune. 1-356 p.
42. Amiet F, Neumeyer R (1999) Apidae 2. Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha. Neuchatêl, Switzerland: Centre Suisse de Cartogrpahie de la Faune. 1-219 p.
43. Rasmont P, Terzo M (2010) Catalogue et clé des sous-genres et espèces du genre Bombus de Belgique et du nord de la France (Hymenoptera ,

Apoidea) par Catalogue des sous-genre et espèces du genre Bombus (Apidae , Apinae , Bombini). Mons, Belgium. 1-28 p.

44. Schmid-Egger C, Scheuchl E (1997) Illustrierte Bestimmungstabellen der Wildbienen Deutschlands und Österreichs, Band III : Andrenidae. 1-180 p.
45. Bates D, Maechler M, Bolker B (2012) Package 'lme4'.
46. Johnson JB, Omland KS (2004) Model selection in ecology and evolution. Trends in ecology & evolution 19: 101-108.
47. Pywell RF, Warman EA, Hulmes L, Hulmes S, Nuttall P, et al. (2006) Effectiveness of new agri-environment schemes in providing foraging resources for bumblebees in intensively farmed landscapes. Biological Conservation 129: 192-206.
48. Jaffé R, Dietemann V, Allsopp MH, Costa C, Crewe RM, et al. (2010) Estimating the density of honeybee colonies across their natural range to fill the gap in pollinator decline censuses. Conservation biology 24: 583-593.
49. R Development Core Team (2012) R: A Language and Environment for Statistical Computing. 2.15.0 ed. Vienna, Austria: R Foundation for Statistical Computing.
50. Fontaine C, Collin CL, Dajoz I (2008) Generalist foraging of pollinators: diet expansion at high density. Journal of Ecology 96: 1002-1010.
51. Memmott J, Waser NM, Price MV (2004) Tolerance of pollination networks to species extinctions. Proceedings of the Royal Society B 271: 2605-2611.
52. Carvell C, Meek WR, Pywell RF, Goulson D, Nowakowski M (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. Journal of Applied Ecology 44: 29-40.
53. Humbert J-Y, Ghazoul J, Richner N, Walter T (2012) Uncut grass refuges mitigate the impact of mechanical meadow harvesting on orthopterans. Biological Conservation 152: 96-101.
54. Schmidt MH, Rocker S, Hanafi J, Gigon A (2008) Rotational fallows as overwintering habitat for grassland arthropods: the case of spiders in fen meadows. Biodiversity and Conservation 17: 3003-3012.
55. Valtonen A, Saarinen K, Jantunen J (2006) Effect of different mowing regimes on butterflies and diurnal moths on road verges. Animal Biodiversity and Conservation 29: 133-148.

56. Veddeler D, Klein A-M, Tscharntke T (2006) Contrasting responses of bee communities to coffee flowering at different spatial scales. Oikos 112: 594-601.
57. Roulston TaH, Smith SA, Brewster AL (2007) A Comparison of Pan Trap and Intensive Net Sampling Techniques for Documenting a Bee (Hymenoptera : Apiformes) Fauna. Journal of the Kansas Entomological Society 80: 179-181.
58. Decourtye A, Mader E, Desneux N (2010) Landscape enhancement of floral resources for honey bees in agro-ecosystems. Apidologie 41: 264-277.
59. Humbert J-Y, Pellet J, Buri P, Arlettaz R (2012) Does delaying the first mowing date benefit biodiversity in meadowland? A meta-analysis. Environmental Evidence: 1-9.
60. Potts SG, Woodcock BA, Roberts SPM, Tscheulin T, Pilgrim ES, et al. (2009) Enhancing pollinator biodiversity in intensive grasslands. Journal of Applied Ecology 46: 369-379.
61. Burel F, Baudry J, Butet A, Le Coeur D, Dubs F, et al. (1998) Comparative biodiversity along a gradient of agricultural landscapes. Acta Oecologica 19: 47-60.
62. Anonymous (2009) Bewirtschaftungsverträge Naturnahe Landwirtschaft Richtlinien. Aargau, Switzerland: Departement Bau Verkehr und Umwelt. 1-50 p.
63. OAN (2009) Projets de mise en réseau selon l'ordonnance sur la qualité écologique Directives cantonales l'ordonnance sur la préservation des bases naturelles de la vie et des paysages (OPBNP). Bern, Switzerland: Office de l'agriculture et de la nature du canton de Berne. 1-17 p.

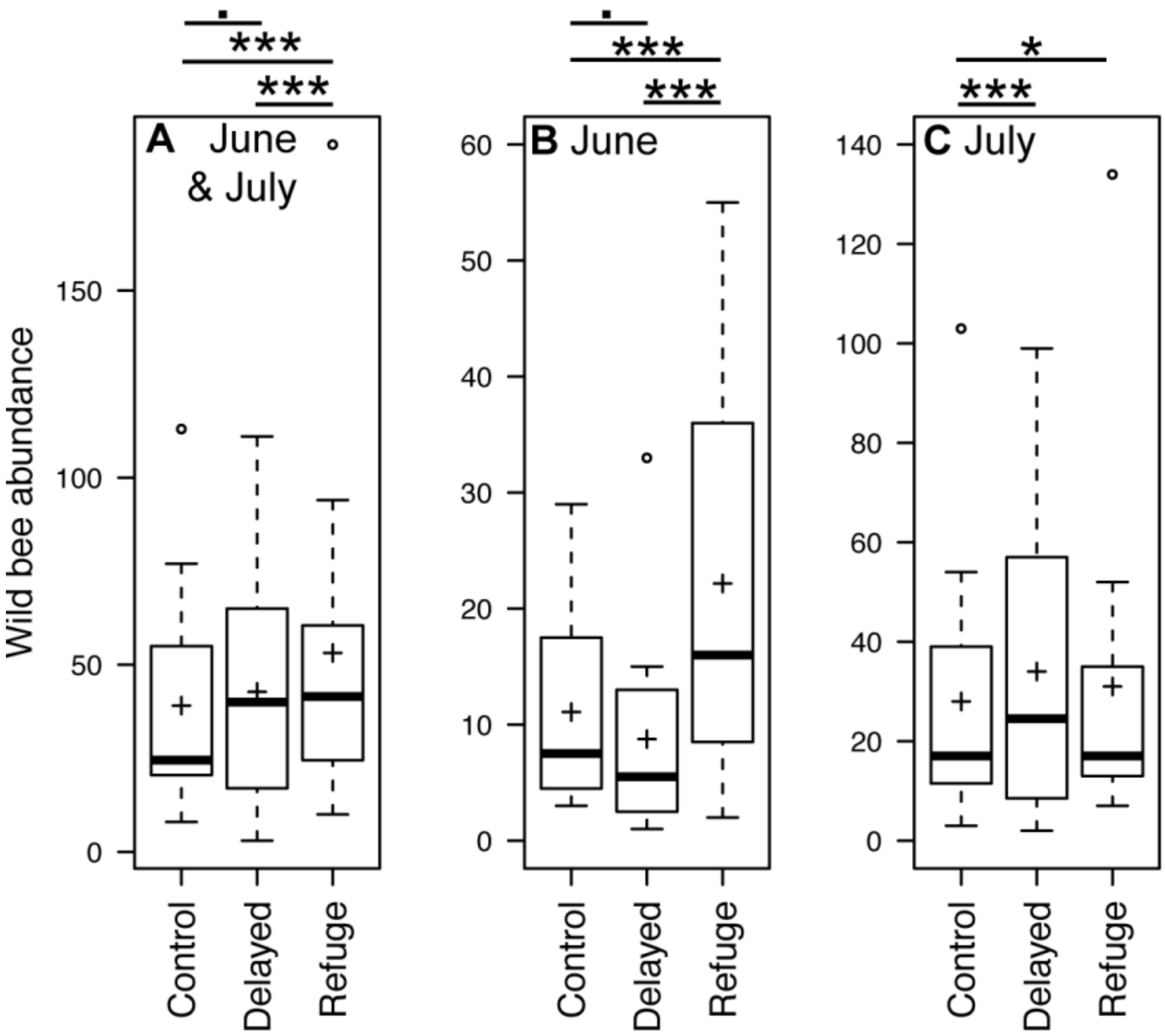


Figure1. Abundance of wild bees. Number of individuals captured according to the different mowing treatments in: a) June and July (pooled data); b) June only; and c) July only. Bold transversal bars represent medians; + the means; box boundaries the first and last quartiles; whiskers the inter-quartile distance multiplied by 1.5; and open dots the outliers. Significance codes of statistical tests: · marginally significant results (0.1 < *P* < 0.05); * significant results, *P* < 0.05; *** highly significant results, *P* < 0.001.

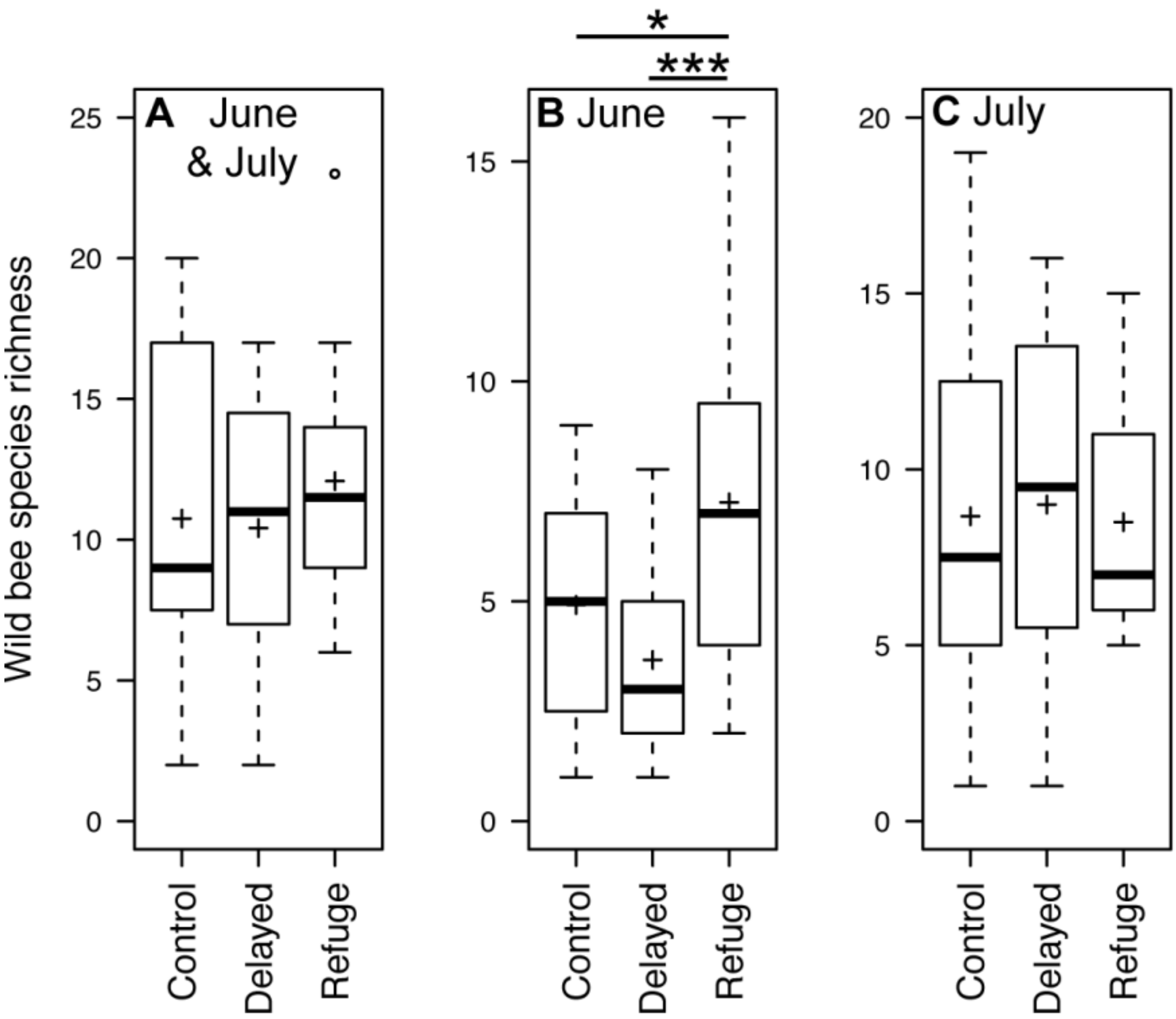


Figure 2. Species richness of wild bees. Number of species captured according to the different mowing treatments in: a) June and July (pooled data); b) June only; and c) July only. Symbols as in Fig. 1

Table 1. **Abundance of wild bees**. GLMM outputs on the abundance of the wild bees recorded according to the different managements and the most important land covers. Analyses presented are the pooled data (June and July added); the June sampling session and; the sampling of July. Significant contrasts are highlighted in bold.

	Total		**June**		**July**	
Parameters	***Z*-value**	***P*-value**	***Z*-value**	***P*-value**	***Z*-value**	***P*-value**
Delayed	1.713	0.086	-1.927	0.054	3.594	**< 0.001**
Refuge	4.036	**< 0.001**	5.487	**< 0.001**	2.472	**0. 001**
Forest	-2.843	**0.005**	-	-	-2.319	**0. 021**
Water bodies	-2.683	**0.007**	-	-	-4.021	**< 0.001**
Special crops	2.669	**0.008**	2.044	**0.041**	-	-

Table 2. **Species richness of wild bees** GLMM outputs on the species richness of the wild bees recorded according to the different managements and the most important land covers. Analyses are presented in the same way as Table 1.

	Total		**June**		**July**	
Parameters	***Z*-value**	***P*-value**	***Z*-value**	***P*-value**	***Z*-value**	***P*-value**
Delayed	-0.251	0.802	1.490	0.1363	0.274	0.784
Refuge	0.965	0.335	2.044	**0.036**	-0.139	0.889
Forest	-	-	-	-	-	-
Water bodies	-	-	-	-	-	-
Special crops	-	-	2.044	0.041	-	-

Appendix 1. Location of the study sites (Buri_samples_sites.kmz , electronic file for google earth software)

Supporting information S2

Table S2. Location of all study sites (n = 36 in total), indicating Swiss canton (VD = Vaud; FR = Fribourg; NE = Neuchâtel; BE = Bern; BL = Basel-Landschaft; AG = Aargau), sampling date, mowing regime, geographic coordinates (decimal WGS84 system, location of the randomly selected point for sampling), and number of arthropods caught during the two sampling periods in June and July. Plant communities were classified according to a Bray-Curtis dissimilarity matrix and where MG4= well drained mesotrophic grassland with Alopecurus pratensis; MG1= mesotrophic grassland with Arrenatherum elatius; CG3 = calcicolous grassland with Bromus erectus and; ND = non-defined former highly intensive grasslanddescribed according to Rodwell (1992),

				Coordinates		June						July						Sp. Nb		
Canton	Region	Sampling dates	Mowing regime	E	N	Solitary bees	Bumblebees	Honey bees	Coleoptera	Diptera	Others	Solitary bees	Bumblebees	Honey bees	Coleoptera	Diptera	Others	Solitary bees	Bumblebees	Meadow type
VD	Nyon	29.05.11-02.07.11	Control	6.2193	46.41479	28	1	0	299	52	4	45	3	1	12	161	14	14	3	MG1
		29.05.11-02.07.11	Delayed	6.1959	46.37844	14	0	2	116	11	17	50	4	14	4	20	14	13	2	MG1
		29.05.11-02.07.11	Refuge	6.2543	46.40769	39	3	1	159	103	237	50	2	3	6	126	8	11	2	CG3
	Orbe	28.05.11-02.07.11	Control	6.5032	46.71043	17	4	2	4	129	6	29	1	6	5	103	38	13	4	CG3
		28.05.11-02.07.11	Delayed	6.4918	46.70081	10	2	10	26	135	9	93	6	24	21	94	13	11	3	CG3
		28.05.11-02.07.11	Refuge	6.4984	46.71744	21	18	8	36	343	3	24	8	11	16	122	17	15	8	CG3
	Avenches	23.05.11-05.07.11	Control	7.0079	46.92443	10	0	0	16	59	4	100	3	3	9	67	17	14	3	MG1
		23.05.11-05.07.11	Delayed	7.0562	46.93898	6	2	3	7	34	7	55	7	2	13	26	17	13	4	MG1
		23.05.11-05.07.11	Refuge	7.0598	46.94316	54	1	0	11	35	3	130	4	4	5	97	16	14	3	MG1
FR	Cousset	24.05.11-03.07.11	Control	6.9808	46.82316	5	0	2	22	81	10	51	3	2	33	156	9	18	2	CG3
		24.05.11-03.07.11	Delayed	6.9733	46.82397	1	1	3	13	32	22	55	5	2	35	65	8	13	2	CG4
		24.05.11-03.07.11	Refuge	7.0023	46.83105	8	3	0	17	92	8	35	3	5	22	145	9	12	3	MG4
NE	Coffrane	12.06.11-12.07.11	Control	6.8618	47.00157	13	3	0	99	62	2	2	5	4	24	109	20	3	4	MG1
		12.06.11-12.07.11	Delayed	6.8533	47.00149	3	2	7	148	61	3	19	4	3	26	42	22	10	2	MG1
		12.06.11-12.07.11	Refuge	6.8495	47.00814	15	6	10	407	143	10	11	2	4	32	129	17	8	4	MG1
BE	Wohlen	04.06.11-05.07.11	Control	7.378	46.99978	3	1	5	37	123	5	7	2	9	105	101	5	2	2	MG4
		04.06.11-05.07.11	Delayed	7.4249	46.99751	14	1	2	95	421	2	3	0	3	19	67	2	4	1	ND
		04.06.11-05.07.11	Refuge	7.3896	46.96997	10	1	5	76	90	6	13	0	4	24	184	2	10	1	MG1
	Grossaff*	12.06.11-06.07.11	Control	7.3765	47.065	18	1	8	1542	167	6	16	1	0	9	348	6	6	2	ND
		12.06.11-06.07.11	Delayed	7.375	47.07554	33	0	3	332	34	1	21	5	4	15	44	3	10	2	MG4
		12.06.11-06.07.11	Refuge	7.3478	47.06378	31	2	6	129	96	3	14	2	0	5	169	12	9	3	MG4
	Belp	23.05.11-05.07.11	Control	7.5106	46.88239	3	0	2	17	107	3	16	1	0	8	157	12	9	1	ND
		23.05.11-05.07.11	Delayed	7.4741	46.91446	4	0	3	13	32	22	43	5	0	3	75	11	8	2	MG1

		23.05.11-05.07.11	Refuge	7.5173	46.89607	2	0	3	21	77	2	12	1	2	6	88	2	7	1	MG1
	Hindelbank	07.06.11-05.07.11	Control	7.6012	47.03868	4	0	7	26	56	4	14	4	2	42	54	1	7	1	MG4
		07.06.11-05.07.11	Delayed	7.5533	47.05733	2	0	2	149	16	2	2	2	2	21	30	5	4	2	ND
		07.06.11-05.07.11	Refuge	7.5675	47.0306	1	2	1	13	39	3	5	2	3	29	119	1	4	3	ND
	Huttwil	14.06.11-11.07.11	Control	7.8148	47.09231	5	0	3	772	47	6	3	0	4	0	233	8	2	0	ND
		14.06.11-11.07.11	Delayed	7.853	47.10897	0	1	1	296	36	6	1	1	6	9	105	1	1	1	ND
		14.06.11-11.07.11	Refuge	7.8226	47.11047	10	0	0	46	141	4	11	4	7	5	181	3	9	2	ND
BL	Diegten	30.05.11-09.07.11	Control	7.8175	47.42509	5	0	5	15	43	8	13	3	4	12	415	18	6	2	CG3
		30.05.11-09.07.11	Delayed	7.8327	47.43855	3	0	0	10	23	30	9	4	8	12	100	10	8	1	MG1
		30.05.11-09.07.11	Refuge	7.817	47.41462	29	3	3	32	89	5	16	2	2	5	146	19	8	2	CG3
AG	Lupfig	07.06.11-11.07.11	Control	8.1794	47.44759	11	1	0	239	58	4	10	4	9	19	119	17	8	3	MG4
		07.06.11-11.07.11	Delayed	8.1875	47.44312	4	2	1	686	8	9	7	7	14	6	123	11	5	3	MG4
		07.06.11-11.07.11	Refuge	8.2167	47.44438	6	1	2	511	66	1	19	2	0	0	177	3	4	2	MG4
Total						442	62	110	6437	3141	477	1004	112	171	617	4497	391			

Grossaff* = Grossaffoltern

Reference

Rodwell, J.S. (1992) British Plant Communities. Vol. 3. Grasslands and Montane Communities. Cambridge University Press, Cambridge, UK.

Supporting information S3

Table S3. Number of individuals of bee species captured in June and July within the 12 geographic replicates (3 sites per replicates)

Species	Avenches	Belp	Coffrane	Cousset	Diegten	Grossaff.*	Hindel.*	Huttwil	Lupfig	Nyon	Orbe	Wohlen
Apis mellifera (honey bees)	12	10	27	14	21	21	17	21	26	21	61	28
Bombus barbutellus	1	0	0	0	0	0	0	0	0	0	3	0
Megabombus group	2	1	1	5	0	0	1	0	0	2	5	1
Bombus lapidarius	3	0	4	0	1	3	0	0	6	2	8	1
Thoracobombus group	1	2	3	1	3	1	3	0	2	2	4	2
Bombus pratorum	0	0	0	0	0	0	0	2	0	0	0	0
Bombus ruderarius	0	0	0	0	0	0	0	0	0	0	3	0
Bombus rupestris	0	0	1	0	0	0	0	0	0	0	2	0
Bombus sylvestris	0	0	0	0	0	0	1	0	0	0	2	0
Bombus sensus stricto	10	4	13	9	8	7	5	4	9	7	12	1
Andrena alfkenella	0	1	0	0	0	0	0	0	0	0	1	0
Andrena cf.trimmerana	0	0	0	0	0	0	0	0	0	1	0	0
Andrena chrysosceles	0	1	0	0	1	0	0	0	0	0	0	0
Andrena curvungula	0	0	3	0	0	0	0	0	0	0	0	0
Andrena dorsata	0	0	0	0	1	0	2	0	0	4	0	0
Andrena flavipes	4	1	1	1	0	0	0	0	1	1	0	1
Andrena fulvata	0	0	0	0	0	0	0	0	0	0	1	0
Andrena humilis	0	0	0	1	0	0	0	0	0	0	2	0
Andrena minutula	0	0	0	0	1	0	0	0	0	1	1	0
Andrena ovatula group	0	0	0	1	0	0	1	0	0	0	0	0
Chelostoma campanularum	0	2	0	0	0	0	0	0	0	0	0	0
Chelostoma rapunculi	0	0	0	0	0	0	0	1	0	0	0	0
Eucera longicornis	0	0	0	0	0	0	0	1	0	0	0	0
Halictus confusus	0	0	0	0	0	0	0	0	0	1	0	0
Halictus maculatus	1	6	1	0	0	0	0	0	0	2	1	0
Halictus rubicundus	0	0	0	2	0	3	0	1	0	0	4	0
Halictus scabiosae	6	0	1	10	0	2	0	0	2	1	1	2
Halictus subauratus	1	0	0	0	0	0	0	0	0	0	0	0
Halictus tumulorum	4	7	6	18	12	6	2	1	22	32	8	1
Halictus.simplex group	8	16	7	13	14	11	0	0	4	33	63	8
Hylaeus annularis	0	0	0	0	0	1	0	0	0	0	1	0
Hylaeus confusus	0	0	0	0	0	1	1	0	0	0	0	0
Hylaeus kahri	0	1	0	0	0	0	2	0	0	0	0	1

Hylaeus punctulatissimus	0	1	0	0	0	0	0	0	0	0	0	0
Hylaeus sinatus	0	0	0	0	1	0	0	0	0	0	0	0
Lasioglossum aeratum	0	0	0	0	0	0	0	0	0	0	2	0
Lasioglossum calceatum	6	4	7	39	4	4	1	8	1	12	58	0
Lasioglossum convexiusculum	1	0	0	0	0	0	0	0	0	0	0	0
Lasioglossum fulvicorne	0	0	2	1	0	0	0	1	0	0	5	0
Lasioglossum glabriusculum	0	0	0	0	3	0	0	0	7	8	0	0
Lasioglossum griseolum	0	0	0	0	0	0	0	0	0	3	0	0
Lasioglossum laticeps	57	0	10	4	0	0	0	0	1	21	13	4
Lasioglossum lativentre	3	0	2	2	0	0	0	0	1	0	0	0
Lasioglossum leucopus	0	0	0	0	0	1	0	0	0	0	0	0
Lasioglossum leucozonium	0	1	2	2	0	5	1	0	1	1	8	0
Lasioglossum lineare	15	0	0	1	0	0	0	0	0	5	1	0
Lasioglossum lucidulum	2	0	0	0	0	0	0	0	0	0	0	0
Lasioglossum malachurum	197	23	0	20	5	19	1	0	3	64	11	3
Lasioglossum morio	10	0	2	3	2	0	0	1	0	4	0	2
Lasioglossum nigripes	2	3	0	0	0	0	1	2	0	0	0	0
Lasioglossum pauxillum	20	1	2	6	24	9	0	0	3	21	4	2
Lasioglossum politum	5	0	0	4	0	0	0	0	0	0	0	0
Lasioglossum punctatissimum	1	0	0	4	0	0	0	0	0	0	0	0
Lasioglossum villosulum	4	0	0	3	0	0	0	0	0	2	5	0
Lasioglossum zonulum	2	11	16	15	5	69	16	12	9	3	1	22
Megachile circumcincta	0	0	0	0	0	0	0	0	0	1	0	0
Megachile ericetorum	1	1	0	0	0	0	0	0	0	0	0	0
Melitta leporina	0	0	0	1	0	1	0	0	0	0	2	0
Osmia adunca	0	0	0	0	0	0	0	0	0	0	0	1
Panurgus calcaratus	0	0	0	0	0	0	0	2	0	0	0	0
Sphecodes ephippius	0	0	0	1	0	0	0	0	0	0	0	0
Xylocopa valga	0	0	0	0	0	0	0	0	0	1	0	0
Xylocopa violacea	1	0	0	0	0	0	0	0	0	0	0	0
unidentified	4	0	1	3	2	1	0	0	2	4	1	3

*
Grossaff. = Grossaffoltern
Hindel. = Hindelbank

Supporting information S4: Study of the effects of different colours of bowl traps

Data analysis

The attractiveness for wild bees of different colours of bowl traps were first analysed with standard GLMMs: abundance and species richness of captured wild bees served as response variables, bowl colours (yellow, white or blue) and experimental treatmentsas fixed effects, and sites as a random factor. Secondly, species-specific preferences were investigated using a model-based analysis of multivariate abundance, using the function *manyglm()* from the package *mvabund* (Wang *et al.* 2012). Multivariate abundance data analyses were performed only on species that were present in at least eight sampling areas so as to ensure sufficient statistical power and scientifically sound inferences. Data of the two sampling periods (June, July) were first pooled and then analysed separately.

Results

In the pooled analyses, the abundance observed (average ± SE) in yellow bowl traps was (20.58 ± 4.96) higher than in blue traps (8.42 ± 2.54; GLMM with Poisson; $Z = -13.091$, $P < 0.001$) and white traps (16.00 ± 4.18; $Z = -4.519$, $P < 0.001$); white traps were in turn more efficient than blue traps ($Z = 9.050$, $P < 0.001$). In June, yellow traps collected, on average, a higher number (7.64 ± 2.46) than blue traps (2.41 ± 0.77; $Z = -9.285$, $P < 0.001$) and white traps (3.95 ± 1.10; $Z = -6.315$, $P < 0.001$). In July, the abundances recorded in yellow (12.95 ± 3.68) and white (12.06 ± 3.75) traps were not different ($Z = -1.103$, $P = 0.27$), but blue traps (6.00 ± 2.01) caught significantly fewer wild bees than the two other colours; $Z = -9.365$, $P < 0.001$).

Species-specific preferences were then investigated in the more widespread species (present in ≥ 8 areas, out of 12). Twelve wild bee species met that criterion, with 8 showing significant differences regarding colour preference. Yellow traps caught more specimens than blue traps. White was in four species as successful as yellow (*Bombus sensus stricto* group, *Halictus tumulorum*, *Lasioglossum calceatum* and *Lasioglossum puaxillum*); it was even significantly more attractive than the other two colours in the *Halictus simplex* group (Table

S3). Analyses carried out with separate seasonal datasets (June, July) showed the same patterns as with the pooled data; they are therefore not presented here.

Discussion

Overall (June and July pooled), wild bees were mostly attracted by yellow traps, followed by white traps, and finally blue traps. In June, similar preferences were observed as with pooled seasonal samples. However, in July, no significant difference between yellow and white traps could be detected, though both were more efficient than the blue ones. This result shows that attractiveness of bowl traps can vary among species and according to season. It confirms the recommendations of Westphal et al. (2008) of using the three (yellow, blue and white) colours in parallel.

Despite this recommendation several studies have used only one or two colours (e.g. Tuell, Ascher, & Isaacs 2009; Krewenka *et al.* 2011). In our case, white traps were as successful in July as the yellow ones, probably because more flowers with white corolla were blooming at that time of the year (P. Buri, personal observations). Notwithstanding the fact that yellow remains the most attractive colour for measuring general bee abundance, this does not apply to all wild bee species, which calls for systematically using traps of different colorations. Four species were equally attracted by the yellow and white traps, while the *Halictus simplex* group was even more linked to white traps (Table S3). Regarding blue traps, they seemed quite unattractive in our experiment, although five individuals of four different species were caught only in blue traps (one *Bombus sylvestris*, one *Halictus confusus*, two *Chelostoma campanularum*, and one *Eucera longicornis*). We recognize that this pattern could emerge randomly, but cannot exclude the possibility that these species would have been missed if no blue traps were set.

Table S4. Bowl traps colour attractiveness. Species or species groups included in the multivariate analysis, with indication of the total number of individuals trapped, the number of replicates that harboured the species or species group, bowl trap colour preference with respective *P*-values. For more details, see Fig. S3 that provides information about bee abundance vs bowl trap colours for each species or species group. Significant differences in bold.

Species or species group	**Number of individuals**	**Number of replicates**	**Bowl trap colour preference**	***P*-value (adjusted)**
Halictus simplex group	177	10	white > blue = yellow	**0.001**
Halictus tumulorum	118	12	yellow = white > blue	**0.001**
Lasioglossum calceatum	144	11	white > blue	**0.001**
Lasioglossum malachurum	346	10	yellow > white > blue	**0.001**
Lasioglossum zonulum	181	12	yellow > white > blue	**0.001**
Lasioglossum pauxillum	91	10	white > blue	**0.002**
Bombus sensus stricto	89	12	yellow > white = blue	**0.029**
Halictus scabiosae	25	8	yellow = white = blue	0.111
Bombus lapidarius	28	8	yellow = white = blue	0.285
Lasioglossum leucozonium	21	8	yellow = white = blue	0.285
Bombus hortorum	18	8	yellow = white = blue	0.859
Bombus pascuorum	24	11	yellow = white = blue	0.859

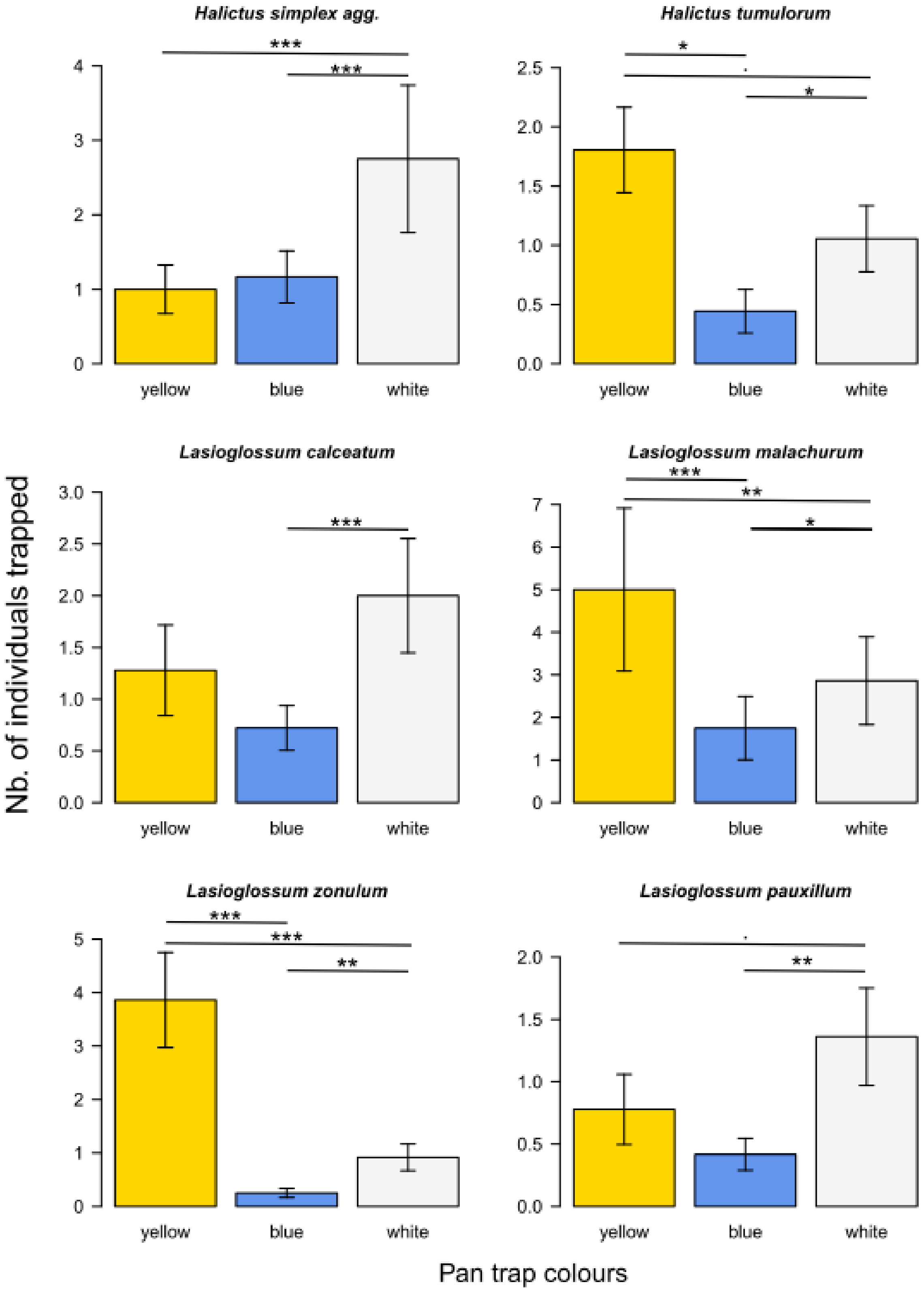
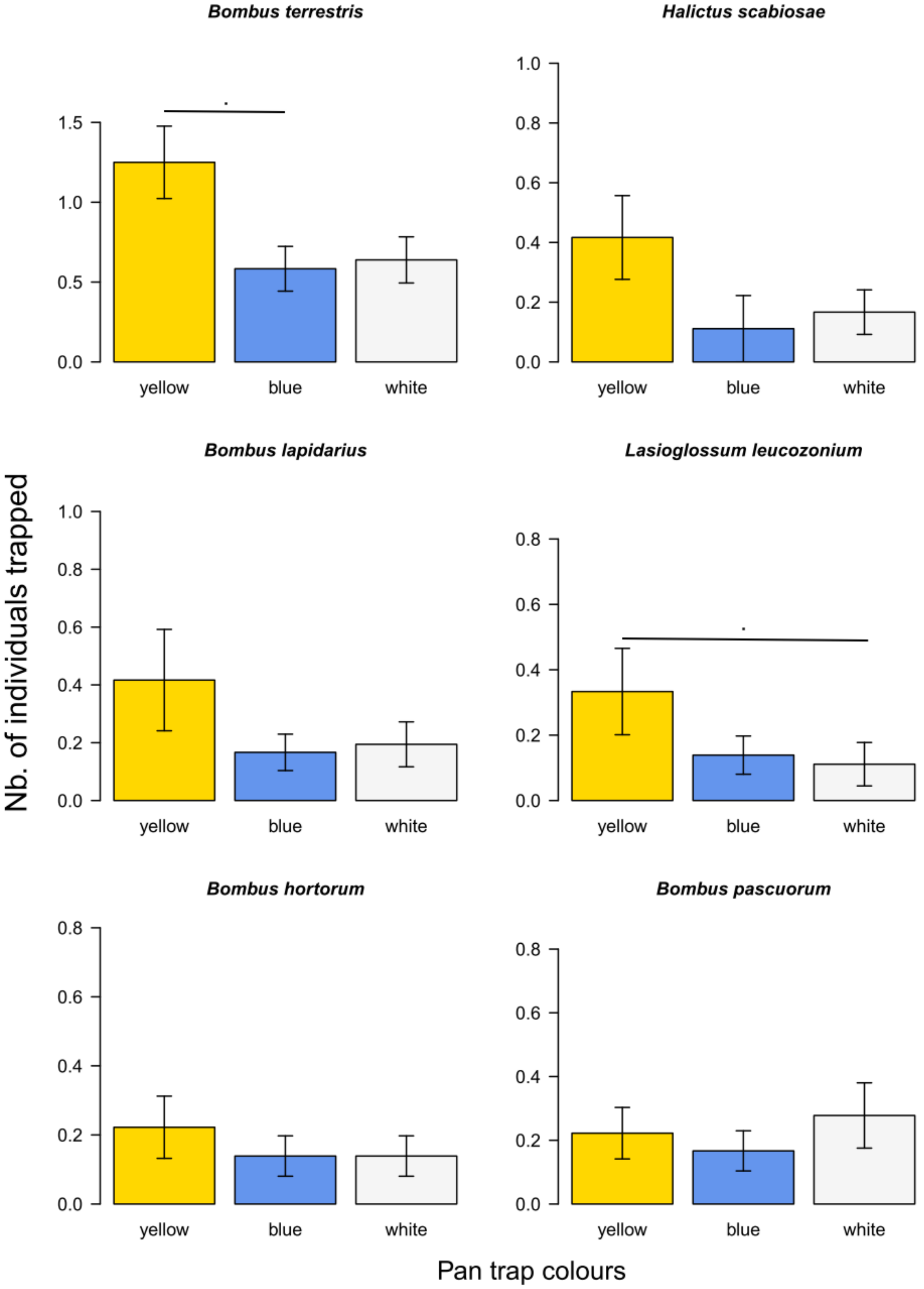


Figure S2. Mean (±SE) number of wild bees trapped with respect to bowl trap colour. Significance codes of statistical tests: · marginally significant results (0.1 < *P* < 0.05); * significant results, *P* < 0.5;** very significant results, 0.01 <.*P* < 0.001; *** highly significant results, *P* < 0.001.


Bombus terrestris
1.5
1.0
0.5
0.0
.
yellow
blue
white
Halictus scabiosae
1.0
0.8
0.6
0.4
0.2
0.0
yellow
blue
white
Bombus lapidarius
1.0
0.8
0.6
0.4
0.2
0.0
yellow
blue
white
Lasioglossum leucozonium
0.8
0.6
0.4
0.2
0.0
.
yellow
blue
white
Bombus hortorum
0.8
0.6
0.4
0.2
0.0
yellow
blue
white
Bombus pascuorum
0.8
0.6
0.4
0.2
0.0
yellow
blue
white
Nb. of individuals trapped
Pan trap colours

References

Krewenka, K.M., Holzschuh, A., Tscharntke, T. & Dormann, C.F. (2011) Landscape elements as potential barriers and corridors for bees, wasps and parasitoids. *Biological Conservation,* **144,** 1816-1825.

Tuell, J.K., Ascher, J.S. & Isaacs, R. (2009) Wild Bees (Hymenoptera : Apoidea : Anthophila) of the Michigan Highbush Blueberry Agroecosystem. *Conservation Biology and Biodiversity,* **102,** 275-287

Supporting information S5

Table S5. Mowing date collected with a standardized survey in 2011. All the meadows were cut at least one and maximum three time.

Canton	Region	Mowing regime	1st cut	2nd cut	3rd cut	Nb cuts
VD	Nyon	Control	25.06.11	30.09.11	-	2
	Nyon	Delayed	15.08.11	-	-	1
	Nyon	refuge	23.06.11	27.09.11	-	2
	Orbe	Control	19.06.11	-	-	1
	Orbe	Delayed	17.07.11	-	-	1
	Orbe	refuge	20.06.11	22.08.11	-	2
	Avenches	Control	23.06.11	07.09.11	-	2
	Avenches	Delayed	09.08.11	30.11.11	-	2
	Avenches	refuge	17.06.11	23.08.11	-	2
BE	Hindelbank	Control	24.06.11	09.08.11	-	2
	Hindelbank	Delayed	29.07.11	03.11.11	-	2
	Hindelbank	refuge	24.06.11	09.08.11	-	2
	Wohlen	Control	19.06.11	22.08.11	27.09.11	3
	Wohlen	Delayed	30.07.11	-	-	1
	Wohlen	refuge	20.06.11	10.08.11	-	2
	Coffrane	Control	18.06.11	20.09.11	-	2
	Coffrane	Delayed	16.07.11	20.09.11	-	2
	Coffrane	refuge	18.06.11	20.09.11	-	2
	Belp	Control	25.06.11	-	-	1
	Belp	Delayed	30.07.11	02.09.11	-	2
	Belp	refuge	24.06.11	10.08.11	-	2
	Grossaffoltern	Control	24.06.11	10.08.11	-	2
	Grossaffoltern	Delayed	31.07.11	20.09.11	-	2
	Grossaffoltern	refuge	20.06.11	19.08.11	-	2
	Huttwil	Control	26.06.11	-	-	1
	Huttwil	Delayed	16.07.11	-	-	1
	Huttwil	refuge	20.06.11	11.08.11	-	2
FR	Cousset	Control	24.06.11	19.08.11	-	2
	Cousset	Delayed	15.07.11	13.09.11	-	2
	Cousset	refuge	15.06.11	01.08.11	-	2
BL	Diegten	Control	24.06.11	14.09.11	-	2
	Diegten	Delayed	08.08.11	-	-	1
	Diegten	refuge	19.06.11	30.07.11	-	2
AG	Lupfig	Control	24.06.11	18.08.11	-	2
	Lupfig	Delayed	30.07.11	-	-	1
	Lupfig	refuge	25.06.11	14.09.11	-	2

5

Field-scale experimental manipulation of alternative mowing regimes in extensively managed grasslands: effects on biodiversity and novel management recommendations

Field-scale experimental manipulation of alternative mowing regimes in extensively managed grasslands: effects on biodiversity and novel management recommendations

Pierrick Buri[1,*], Marzena Stanka[2], Izabela Hajdamowicz[2], Eléonore Tran[1], Martin H. Entling[3], Jean-Yves Humbert[1], Raphaël Arlettaz[1,4]

[1] Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland

[2] Siedlce University of Natural Sciences and Humanities, Department of Zoology, Prusa 12, 08-110 Siedlce, Poland

[3] University of Koblenz-Landau, Institute for Environmental Sciences, Fortstrasse 7, D-76829 Landau/Pfalz, Germany

[4] Swiss Ornithological Institute, Valais Field Station, Rue du Rhône 11, CH-1950 Sion, Switzerland

Manuscript:
In preparation

5.1 Abstract

1. Biodiversity-rich farmland habitats such as semi-natural grasslands have been severely impacted by agricultural intensification. As a remedy, agri-environment schemes (AES) have been introduced, yet these AES could neither halt nor revert the trend towards conversion of grasslands into other land uses, nor maintain low intensity management in most remaining grasslands.
2. This study investigated, at the field scale and through a randomized experimental block design, the effects of four alternative mowing regimes on the biodiversity of extensively-managed meadows, with the idea to offer more efficient management options within AES prescriptions. The alternative regimes we tested were;1) mowing regime according to the Swiss AES prescriptions for extensively managed hay meadows, i.e. first cut not before 15 June (control meadows, hereafter C-meadows); 2) first cut not before 15 July (delayed treatment, D-meadows); 3) first cut not before 15 June and second cut not earlier than 8 weeks after the first cut (8W-meadows); 4) refuge left uncut on 10-20% of the meadow area (R-meadows). During three years, leaf- and planthoppers (Auchenorrhyncha) and plant-dwelling spiders (Araneae) were collected before and after mowing with suction samplers, while ground-dwelling Araneae were collected with pitfall traps during the third year.
3. After three years, the density of Auchenorrhyncha and Araneae were significantly higher in D-meadows than in all other mowing regimes. Densities were also significantly higher in 8W-meadows compared to C- and R-meadows for both taxa, but differences were tiny. In contrast, no effect of the R-treatment was detected. A cumulative effect (from the second to the third year) was detected within the D-treatment, but only for spiders. Species richness and diversity (Shannon-Wiener index) were not affected by any of the mowing regimes applied.
4. *Synthesis and applications*. Maintaining and restoring semi-natural grasslands is not only a major worldwide, but also one of the most heavily subsidized conservation operations, especially in European cultural landscapes. Along with a few previous experiments, the present study demonstrates that delaying grass mowing and, to a lesser extent, leaving

an uncut refuge in a mown meadow, would improve the effectiveness, and thus return on investment, of current AES.

Keywords
Ecological compensation areas, leafhoppers, pitfall traps, Planthoppers, suction sampling, spiders

5.2 Introduction

Traditional farming practices have been creating some of the biodiversity richest semi-natural habitats of the Palaearctic. Yet, in the second half of the 20th century, due to an increasing demand on commodities and other agricultural products such as biofuels, these practices have been progressively replaced by more intensive management in a massive effort to rationalize production. These novel agricultural practices consist of various chemical applications, including mineral fertilizers, heavy mechanisation, increase in field sizes, as well as shifts from mixed farming to highly specialized, monocultural systems (Warren, Lawson & Blecher 2008). Consequences are a strong spatial and temporal homogeneization of the farming practices, uniformisation of the agricultural landscape, with dramatic losses of semi-natural habitats, which have led to a collapse of farmland biodiversity (Bignal & McCrackent 1996; Benton, Vickery & Wilson 2003; Tscharntke *et al.* 2005).

To lessen the negative consequences of farming intensification, many countries established agri-environment schemes (AES) in the early 1990's. The main objective of AES is to preserve or even to restore biodiversity (Kleijn & Sutherland 2003). However, despite the accumulated knowledge on numerous farmland taxa, such as birds (Guerrero *et al.* 2012), plants (Critchley, Burke & Stevens 2003) and various arthropod groups (Kleijn *et al.* 2006), the first evaluations of AES provided evidence for only weak benefits for biodiversity (Kleijn *et al.* 2006; Aviron *et al.* 2009; Whittingham 2011), questioning these measures and calling for the development of more adapted AES options that could actually benefit biodiversity (Batáry *et al.* 2011).

The main aim of this study was to test different alternative management measures relatively compatible with current prescriptions for extensively managed hay meadows, one of the most widespread type of AES, with the idea improve the effectiveness of these schemes (Kleijn & Sutherland 2003; FOAG 2012). Biodiversity in semi-natural meadows is vanishing because of the intensification of farming practices, notably through a massive application of fertilizers, which dramatically increase grazing capacity and/or hay yield. As a result, meadows are nowadays mown much earlier in the season and more frequently than in the past (Čop, Vidrih & Hacin 2009). Assisted by new efficient machinery, mowing operations can be undertaken within a short time window, which leads to some spatio-temporal homogeneization of both agricultural management interventions and landscape configuration, with the associated severe impacts upon biodiversity (Humbert, Ghazoul & Walter 2009). Therefore, this study aims not only at promoting meadowland management beneficial to biodiversity but also at prescribing pragmatic, uncomplicated options within AES that would ensure their uptake by farmers. The alternative mowing regimes tested consisted thus of: 1) delaying by a month the first authorized grass cut in extensively-managed meadows, this in order to provide valuable food sources and still undisturbed, dense grassy habitats at a time when most of the agricultural matrix has become void of grass structures (Humbert *et al.* 2012b); 2) limiting the number of cuts to two per year, with a minimum of 8 weeks in-between, so as to reduce disturbance frequency, the mowing rate being detrimental to biodiversity, such as bugs (Insecta: Hemiptera) or slugs (Mollusca: Gastropoda; Helden & Leather 2004; Blake *et al.* 2011; Everwand, Scherber & Tscharntke 2013); and 3) not mowing a fraction of the meadow, i.e. leaving uncut refuges that can provide field-scale continuity of food resources and shelters across the cultivated matrix (Humbert *et al.* 2012a). These experimental treatments were compared with meadows complying with Swiss AES prescriptions for extensively managed meadows, serving as control. Treatments were applied during three years (2010-2012) in order to evaluate direct, short-term effects (before vs after the cut) and cumulative effects (from one year to another).

Two groups of arthropods that well characterize grasslands were selected as bioindicators: Auchenorrhyncha (Insecta: Hemiptera) and Araneae (Chelicerata: Arachnida). The former taxon is exclusively feeding on plant sap, constituting an important part of the invertebrate herbivore community of grasslands. Increased spatio-temporal heterogeneity in grass management could secure a broader palette of undisturbed plant species, i.e. of ecological niches, for these arthropods (Nickel 2003; Biedermann *et al.* 2005). Araneae are a key component of farmland biodiversity: as predators, they provide an essential ecosystem service, namely pest control (Nyffeler & Benz 1987). Unlike Auchenorrhyncha, Araneae are mostly not linked to particular host plant species, but essentially depend on vegetation structure. This is true for both plant-dwelling and ground-dwelling Araneae although these two subgroups might respond differently to the different mowing treatments we applied experimentally (Bell, Wheater & Cullen 2001).

The association of the present results with the outcomes of our previous experiments on wild bees and orthopterans (Buri, Humbert & Arlettaz, in review and in press, respectively) provides a rather comprehensive appraisal of the effectiveness of four different alternative mowing regimes (see above). This helps setting the stage for new prescriptions that may enhance the overall effectiveness of AES, given that extensively managed grasslands remain one of the most widespread AES options. Such recommendations are furthermore particularly relevant to the debate about "greening" agricultural policies, both within the European Union and beyond (Hart & Baldock 2011).

5.3 Materials and Methods

5.3.1 Study sites

In 2010, 48 extensively managed hay meadows registered as ecological compensation areas (ECA) within the Swiss AES were selected across the Swiss Plateau (see Appendix 1; exact site coordinates in Appendix 2). The Swiss Plateau can be characterized as a simple landscape where non-crop habitats make up only 1–20 % of the landscape matrix depending on the region (Tscharntke *et al.* 2005). Meadows retained for the experiments had to be registered as ECA since at least 2004 (range: 1993–2004) and had to have a minimal size of 0.3 ha (range: 0.3–1.7 ha). Meadows were situated between 390 and 833 m altitude and were dispersed among 12 study areas distant from each other by ≥ 5 km. Each area contained four meadows (one per treatment, see below) that were distant of at least 400 m (range: 440 – 6170 m) but that were enclosed within a radius of 3.5 km.

5.3.2 Study design

A fully randomized block design was adopted, where four different management treatments were applied within each study area, the latter representing the blocks, such that treatment replicates were across the regions, thus ensuring data independence. Within each region, the following management treatments (with abbreviations), consisting of different mowing regimes, were randomly assigned to the four meadows:

1) Extensively managed meadow (typically declared as ecological compensation area within the Swiss AES): first cut not before 15 June, but without further restrictions concerning the number and frequency of subsequent cuts. These meadows constitute our control meadows (C-meadows).
2) Extensively managed meadow with first cut not before 15 July, with no restriction on the number and frequency of subsequent cuts (D-meadow, with D for delayed).
3) Extensively managed meadow with a maximum of two cuts per year and at least 8 weeks between the cuts, with first cut not before 15 June (8W-meadow, with 8W for eight weeks).
4) Extensively managed meadow with a rotational uncut refuge on 10–20% of the meadow area, meaning that a corresponding proportion of the area was left uncut each time the meadow was mown, with the location of the refuge changing from a cut to another to avoid vegetation succession; otherwise first cut not before 15 June (R-meadows, with R for refuge).

Other restrictions (such as no fertilizer or pesticide application, as well as grazing allowed only between 1 September and 30 November) were kept as specified in the present ECA regulations (Swiss Federal Council 1998). The experiment started in spring 2010 with the random assignment of the different mowing treatments to the meadows and first implementation.

5.3.3 Sampling methods

In 2010, 2011 and 2012, Auchenorrhyncha and plant-dwelling Araneae were collected with a suction sampler (Stihl SH86; Stihl, Waiblingen, Germany). The device has an air flow rate of 770 m^3 h^{-1} and an air suction velocity of 85 m s^{-1}. This method is recognized as being efficient to collect the two above-mentioned taxonomic groups (Sanders & Entling 2011). Samples were vacuumed from inside a circular metallic enclosure of 0.51 m diameter (0.2 m^2) that prevented arthropods to escape (Hossain, Gurr & Wratten 1999), thus allowing density estimates (Bergthaler & Rėlys 2002). Samples were collected twice a year: a first time before any mowing action occurred, i.e. between end of May and mid-June (hereafter called June samples); and a second time around the beginning of July, after all meadows but D-meadows had been mown (hereafter called July samples; for exact date of collection see Appendix 2). Five 0.2 m^2 (circular enclosure) samples were taken per visit and meadow, within a 20 x 20 m virtual square randomly placed in the meadow, thus covering a total sampled area of 1 m^2. After collection, samples were transferred into plastic bags and stored in a deep freezer (-20° C) before being categorized to main taxonomic groups and counted. However, adult individuals collected in 2012 were identified to a finer resolution, i.e. to species level, based on classical identification keys (Biedermann and Niedringhaus (2009) for Auchenorrhyncha; Nentwig *et al.* (2013) for Araneae).

In 2012, for a better assessment of spider communities, pitfall traps were additionally used for collecting ground-dwelling Araneae. Traps were installed twice during one week without interruption, a first time before and a second time after mowing, i.e. in parallel to the two suction samplings (June and July). Three traps were set within the same 20 x 20 m virtual square as used for suction sampling, at each angle of a 11 m side virtual equilateral triangle. Traps were simple plastic cups (9 cm in diameter, 15 cm deep; Lange, Gossner & Weisser 2011) covered with a solid transparent plastic shield (12 x 12 cm) nailed to the ground at 3 cm above its surface (Buchholz *et al.* 2010). Traps were filled with 100 ml of ethylene glycol mixed with water (1:3) to which we added 50 mg of sodium-dodecyl sulphate to reduce surface tension (Jud & Schmidt-Entling 2008). Collected Araneae were kept in 70% ethanol. The content of one randomly chosen trap per meadow was identified according to an identification key (Nentwig *et al.* 2013).

5.3.4 Statistical analyses

Density, species richness and diversity (Shannon-Wiener index) of Auchenorrhyncha and Araneae were analysed via generalized linear mixed models (GLMM) with mowing treatments as a main fixed effect. Species richness and diversity were pooled over the two seasonal samples of 2012 during the investigation. The lists of Aranea species collected with either the pitfalls or the suction sampler were merged for the analysis. In contrast, density data were pooled per meadow, with period of sampling (June vs July) and year (2010, 2011 and 2012) as co-variables. Other co-variables that could influence Auchenorrhyncha and Araneae communities were selected beforehand with a non-metric multidimensional scaling analysis (NMDS): elevation, slope, mean ambient temperature, registration duration as ECA, meadow size (ha), growth period, and proportion of different land covers within a 250 m radius (forest; gravel pits; special crops – vineyards plus orchards; settlements; water bodies). Land covers were extracted from the Vector 25 data base of the Swiss Federal Office of Topography (Swisstopo), using QGIS (Quantum GIS, 2013) and SpatiaLite (Furieri 2008) software. Plant species richness of the meadows was also included for Auchenorrhyncha. Empirical p-values of the NMDS factors were calculated with 999 permutations and we retained only significant factors (p-values ≤ 0.05; Carré *et al.* 2009). A model selection procedure based on the AICc ranking was then performed to identify the model with the best fit (Sugiura 1978; see Appendix 4). Density data had to be log transformed for the Auchenorrhyncha and square rooted transformed for the Araneae in order to achieve normal distribution of the residuals. Density and diversity data were analysed with a normal error distribution while a Poisson error distribution was applied to species richness. Interaction between treatments and year were tested and removed if not significant. To further appraise underlying patterns, density at each session was additionally analysed separately (generating 6 different models per taxon) with GLMMs having mowing treatment as a fixed effect. All analyses were performed with the statistical software R version 3.0.1 (R Core Team, 2013).

5.4 Results

A total of 25’330 Auchenorrhyncha were collected in 2010, 2011 and 2012. From the 2012 sample (identification to species level), we retrieved 53 species out of 7’600 individuals (Appendix 3). A total of 9’789 Araneae were collected via suction sampling in 2010-2012. In 2012, 71 species of Araneae could be identified and sorted out of 3’613 individuals collected via suction sampling while 52 species were identified from 2’529 spiders collected with pitfall traps. In total we recognized 94 species of Araneae species, i.e. 29 species were collected with both sampling methods.

5.4.1 Mowing regimes

C-meadows (control) and 8W-meadows (8 weeks treatment) eventually showed comparable management: they were both cut, on average (mean for 2010-2012 ± standard deviation), 1.9 ± 0.5 times a year, with the first cut occurring on average on 22 June, and the second cut (if present) taking place at the end of August. R-meadows (refuge treatment) were cut (except the refuge of course), on average, 2.1 (± 0.4) times a year, with the first cut occurring, on average, on 21 June and the second cut on 19 August. D-meadows (delayed treatment) were cut, on average, 1.6 (± 0.6) times a year, with the first cut taking place, on average, on 23 July and the second cut on 13 September. In spring 2012, one D-meadow was unfortunately lost through unexpected conversion into a gravel pit, while one 8W-meadow had to be removed from the analyses because its management was too close to that of a D-meadow.

5.4.2 Auchenorrhyncha

Elevation and ambient temperature were removed from the NMDS analysis of Auchenorrhyncha as they correlated with other variables. The NMDS retained the following co-variables: plant species richness (NMDS1 = 0.988; NMDS2 = 0.0155; r^2 = 0.121; P = 0.047); registration duration as ECA (NMDS1 = -0.941; NMDS2 = -0.337; r^2 = 0.132; P = 0.049) and forest (NMDS1 = -0.369; NMDS2 = 0.929; r^2 = 0.309; P = 0.001).

Auchenorrhyncha density (number of individuals per m^2) significantly differed across years (Fig. 1a and Table 1): mean (± SE) was 57.49 (± 5.47) in 2010, 129.90 (± 14.13) in 2011 and 80.85 (± 7.17) in 2012. Overall, i.e. when data were pooled across treatments, Auchenorrhyncha density was higher in June, i.e. before mowing (101.45 ± 8.71) than in July, i.e. after mowing (77.09 ± 7.67). Density was above all significantly affected by the mowing treatment, being higher in D-meadows (138.69 ± 14.8) and 8W-meadows (72.02 ± 6.33) than in C-meadows (69.15 ± 10.90) and R-meadows (66.82 ± 6.82), this again when the two samples from a year were pooled. The model with the lowest AICc included no additional co-variable.

When the sampling sessions of June were analysed for each year in three different models (Table 2), the treatments did not differ, with the noticeable exception of the average (± SE) of R-meadows in June 2010 (87.83 ± 20.94) that was higher than the density of C-meadows (52.75 ± 12.60). Concerning the three analyses done one each sampling sessions of July, samples from D-meadows harboured the three years, higher densities (145.98 ± 18.17) than C-meadows (42.28 ± 5.96), R-meadows (42.39 ± 5.10) and 8W-meadows (79.63 ± 19.47).

The analysis of the high taxonomic resolution data collected in 2012 showed that neither species richness (mean ± SE per meadow: 12.38 ± 0.48) nor diversity (Shannon-Wiener index: 1.74 ± 0.07) differed significantly between mowing treatments and season (June vs July; Fig. 2a and Table 1).

5.4.3 Araneae

As for Auchenorrhyncha, elevation and ambient temperature were removed by the NMDS procedure as they correlated with other variables. The duration of registration of a meadow as an ECA within the Swiss AES was the unique co-variable retained by NMDS (NMDS1 = 0.849; NMDS2 = -0.529; $r^2 = 0.323$; $P = 0.001$).

The average (± SE) density of plant-dwelling Araneae (suction sampling) differed between years [23.30 (± 2.27) in 2010; 42.00 (± 2.38) in 2011; 38.44 (± 2.62) in 2012]. Overall, i.e. when data were pooled across treatments, plant-dwelling Araneae reached higher densities, on average, in July (43.83 ± 2.38) than in June (25.27 ± 1.42). D-meadows (46.77 ± 3.54) and 8W-meadows (37.11 ± 1.75) harboured significantly higher densities than C-meadows (29.07 ± 2.68) and R-meadows (25.87 ± 2.41), again when the two seasonal samples were pooled. The model with the lowest AICc included no additional co-variable.

When the sampling sessions of June were analysed in three separate models, i.e. before any mowing operations (Table 2), no contrast was observed between the treatments, with the noticeable exception that density was, on average (± SE), then higher in D-meadows (35.82 ± 5.43) in June 2012 than in C-meadows (18.83 ± 3.17). Concerning the three analyses done on each sampling sessions of July, density was higher the three years in D-meadows (65.43 ± 4.9) than in C-meadows (35.81 ± 4.26), R-meadows (31.41 ± 4.11) and 8W-meadows (42.77 ± 3.66).

The analysis of the high taxonomic resolution data collected in 2012 (data from suction sampling and pitfall trapping pooled together) showed that neither species richness (mean ± SE per meadow: 15.11 ± 0.61) nor diversity

(Shannon-Wiener index: 1.77 ± 0.06 differed significantly between mowing treatments and season (June vs July) (Fig. 2a and Table 1).

5.5 Discussion

European AES (including Swiss ECA) have so far delivered only moderate benefits for farmland biodiversity, including grassland invertebrate communities and abundances (Kleijn *et al.* 2006; Aviron *et al.* 2009). Our results show that delaying the first possible mowing date of extensively managed meadows by a month (here from 15 June to 15 July) boosts Auchenorrhyncha and Araneae densities. A similar trend was observed for species richness although the pattern is not significant. These results corroborate our previous experimental findings that showed five times higher orthopteran densities occurred in meadows with delayed mowing compared to early mown meadows (Buri, Humbert & Arlettaz in press) and are in line with a recent systematic review on the effects of delay mowing on plant and invertebrate communities and populations (Humbert *et al.* 2012b). If our experiments provide clear guidance for improving the effectiveness of AES, they might also be influential for a more biodiversity-friendly management of other grassy habitats such as wetland nature reserves, stream and canal banks, and road verges (Noordijk *et al.* 2009; Veen *et al.* 2009; Hoste-Danyłow, Romanowski & Żmihorski 2010)

5.5.1 Impact of mowing regimes on Auchenorrhyncha

Overall, i.e. when the two seasonal samples from a year were pooled, leafhopper and planthopper density was, on average, about twice higher in meadows with grass cut delayed to 15 July (D-meadows) than the other treatments. Auchenorrhyncha densities severely dropped between June (before any meadows were mown) and July (when all meadows but D-meadows had been mown), supporting the view that mowing has a direct negative impact on this taxon (Humbert, Ghazoul & Walter 2009). This strong positive effect of postponing mowing operations (in July, density was ca doubled in D-meadows compared to in C-meadows) might thus be due both to less direct mortality caused by machinery during, or habitat suppression after the mowing process, and a lower level of total disturbance induced by less frequent detrimental mowing operations. In effect, the mean number of cuts per year was 1.6 in D-meadows vs 1.9 in C-meadows.

Meadows with limited cut frequency (8W-meadows; first cut not before 15 June with at maximum two cuts a year and at least eight weeks in between) were significantly higher compared to both control meadows (C-meadows; first cut not before 15 June and no limitation on the number and date of subsequent cuts) and meadows harbouring uncut refuges (R-meadows; first cut not before 15 June with 10-20% of the area left uncut as refuge at any mowing event), but the measured effect was just 3%. However, the fact that a less pronounced effect was observed within 8W-meadows, despite that their management converged with that of C-meadows, is intriguing. This discrepancy might be due to the size difference observed between C- and 8W-meadows. Larger meadows usually harbour more stable Auchenorrhyncha communities and therefore could influence the results we obtained (Rösch *et al.* 2013). This unexpected phenomenon occurred by chance during the randomization of our treatments, where larger meadows were selected for 8W-meadows. Although statistically significant, this result does not support strong biological conclusions because the observed relative difference in Auchenorrhyncha density between 8W and C-meadows was less than 3% while it was doubled between C and D-meadows (Martínez-Abraín 2008). Interestingly, July densities were ca 66% higher in R-meadows than in C-meadows, pointing to a possible cumulated, carry-over effect of that specific treatment from the first to the second year, but the interannual variation seems to have blurred any underlying pattern due to the dramatic drop in densities in all situations in 2012.

In contrast to density, species richness and diversity did not at all differ between mowing regimes. Auchenorrhyncha are known to readily react to disturbance (Biedermann *et al.* (2005) and the species identified in this study are all typical of early-succession habitats, meaning that the recurrence of mowing operations in our four treatments would not be compatible with community diversification. The mechanism behind this pattern might be comparable to other taxa, such as Hymenoptera, Diptera or Lepidoptera that use hebaceaous plants as hosts for egg laying and larval development (Rothenwöhrer, Scherber & Tscharntke 2013). Auchenorrhyncha lay their eggs directly on plants; they are hence systematically eliminated by hay removal (Nickel 2003). The intensive management that once prevailed in all our experimental meadows might also explain this pattern: past fertilization might have modified the availability of nutrients in the sap and thus promoted only a few generalist species (Prestidge 1982). Three years of survey, despite a current absence of fertilization, might in addition not be sufficient to capture community changes (Mountford, Lakhani & Holland 1996). Finally, Auchenorrhyncha are suffering from landscape homogeneization and fragmentation, which might compromise community recovery within restored grasslands (Schuch, Wesche & Schaefer 2012).

5.5.2 Impact of mowing regimes on Araneae

The patterns found for spiders roughly showed a similar trend to Auchenorrhyncha, although the contrast due to the effect of mowing treatment was less pronounced while the year effect differed. Overall densities in D-meadows and 8W-meadows were, on average, 20-50% higher than in C-, 8W- and R-meadows, with the higher density in D-meadows mainly driven by the July samples. These results corroborate the principal findings reviewed in Nyffeler (2000): undisturbed grasslands generally harbour 10-50% larger densities of spiders than mown meadows. As for plant- and leafhoppers, the pattern observed in July also demonstrates the beneficial effect of keeping a large fraction of the matrix unmown until rather later in the season: D-meadows exhibited, on average, ca twice higher densities than C-meadows and R-meadows, and ca 40% higher densities than 8W-meadows. The outcome of the refuge treatment also suggests that leaving a small fraction of the area unmown does not provide substantial benefits. Finally, the almost twice higher density detected in June 2012 in D-meadows compared to C-meadows is indicative of cumulative effects (i.e. carry-over effects from 2010 to 2012) of that mowing treatment that appears most effective for boosting plant- and leafhoppers. Note here that the dry and warm weather conditions of 2011 might have accentuated the pattern in the following year (MétéoSuisse 2012).

In terms of species richness and diversity, there was no significant difference between any of the mowing treatments. This supports the former view of Knop et al. (2006) and suggests that our experimental extensification might have been too shallow to elicit any diversification of spider communities, at least in the mid term as carry-over effects were already suspected for this taxon. Araneae appear to be so sensitive to mechanical disturbance (Cattin *et al.* 2003) that only very delayed mowing regimes, fully compatible with the late phenology of most spider populations, might well be the sole solution (Baines *et al.* 1998). Similar advantages of late mowing operations have been established for other taxonomic groups such as orthopterans (Buri, Humbert & Arlettaz in press), but not all organisms benefit from this measure (Humbert *et al.* 2012b). The situation of spiders might be comparable to that of plant- and leafhoppers, with communities inhabiting our study sites comprising mostly generalist species. Although plant- and ground-dwelling Araneae have different ecological requirements, the majority of studies has focused on the latter (Schmidt *et al.* 2005; Schmidt *et al.* 2008; Cizek *et al.* 2011), with the exception of studies on the effects of field margins among cropland on plant-dwelling Araneae (Blake *et al.* 2013). The present study provides thus valuable additional information for the restoration of Araneae in grasslands.

5.5.3 Conclusions and management recommendations

Although Auchenorrhyncha and Araneae belong to two different trophic levels, both responded similarly to our experimental mowing regimes: densities were systematically higher in D-meadows than in C- and R-meadows. There also tended to be higher densities in 8W-meadows than in C- and R-meadows, but with relatively much smaller effect sizes. A mid-term cumulative positive effect of that delayed mowing treatment over the years was also evidenced for Araneae. This, in line with previous experimental evidence (Buri, Humbert & Arlettaz in press), tends to confirm that delayed mowing would promptly enhance conditions for overall meadowland biodiversity. Although benefits for species richness could not be demonstrated, increases in population densities are likely to elicit cascading effects along the food chain, contributing to reinstate more integral communities and ecosystem functionalities (e.g. Arlettaz *et al.* 2010).

AES have been launched to conserve and restore biodiversity in farmland, yet these highly subsidized schemes delivered only moderate benefits for grassland wildlife up to date. This calls for serious improvements of these schemes (Kleijn *et al.* 2006). Despite the fact that our experiments were carried out in the somehow singular farming context of Switzerland, our results have clear management implications beyond its border. Delaying the first possible grass cut by a month (here typically till 15 July, which would roughly correspond to the average situation in temperate central Europe) appears to be one top solution. If this is not an option locally, leaving uncut grass refuges on a fraction of a mown meadow might be another, although less beneficial alternative measure (Everwand, Scherber & Tscharntke 2013; Buri, Humbert & Arlettaz in press; Buri, Humbert & Arlettaz submitted). These two options would probably further benefit from being applied in concert, as two alternative, mutually complementary measures. However, further research is needed to experimentally test whether the conjunction of these management options in space and time, and longer durations of their application, further boosts conditions for biodiversity. For now, it seems that reinstating spatio-temporal heterogeneity within agricultural matrices is a key for the preservation and restoration of its biological diversity in the long run (Benton, Vickery & Wilson 2003; Batáry *et al.* 2011).

Acknowledgements

We are grateful to Gernot Kunz for the identification of Auchenorrhyncha, Eva Knop for advice on the sampling design, Hans Bärlocher, Mauricio Benincore, Franck Gandiaga and all the students of our Division for assistance. We also thank the community Ecology group, University of Bern, for general support. Special thanks go to all the farmers who participated in this project. This project was supported by a Swiss National Science Foundation Grant to R.A. (No. 31003A_125398/1), the Federal Office of Environment, the Federal Office of Agriculture and the following cantonal offices for the environment and/or agriculture: Bern, Vaud, Basel-Landschaft, Aargau, Neuchâtel, Fribourg, Valais and Graubünden. Many thanks go to Markus Fischer and Jérôme Pellet for their contribution in the project proposal. We also express our gratitude to all the members of the project accompanying group.

5.6 References

Arlettaz, R., Krähenbühl, M., Almasi, B., Roulin, A. & Schaub, M. (2010) Wildflower areas within revitalized agricultural matrices boost small mammal populations but not breeding Barn Owls. *Journal of Ornithology,* **151,** 553-564.

Aviron, S., Nitsch, H., Jeanneret, P., Buholzer, S., Luka, H., Pfiffner, L., Pozzi, S., Schüpbach, B., Walter, T. & Herzog, F. (2009) Ecological Cross Compliance

Promotes Farmland Biodiversity in Switzerland. *Frontiers in Ecology and the Environment,* **7,** 247-252.

Baines, M., Hambler, C., Johnson, P.J., Macdonald, D.W. & Smith, H. (1998) The effects of arable field margin management on the abundance and species richness of Araneae (spiders). *Ecography,* **21,** 74-86.

Batáry, P., Báldi, A., Kleijn, D. & Tscharntke, T. (2011) Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proceedings of the Royal Society B: Biological Sciences,* **278,** 1894-1902.

Bell, J.R., Wheater, C.P. & Cullen, W.R. (2001) The implications of grassland and heathland management for the conservation of spider communities: a review. *Journal of Zoology,* **255,** 377-387.

Benton, T.G., Vickery, J.a. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution,* **18,** 182-188.

Bergthaler, G.J. & Rėlys, V. (2002) Suction sampling in alpine habitats: experiences and suggestions. *European Arachnology 2000* (eds S. Toft & N. Scharff), pp. 291-297. Aarhus University Press, Aarhus.

Biedermann, R., Achtziger, R., Nickel, H. & Stewart, A.J.A. (2005) Conservation of Grassland Leafhoppers: A Brief Review. *Journal of Insect Conservation,* **9,** 229-243.

Biedermann, R. & Niedringhaus, R. (2009) *The Plant- and Leafhoppers of Germany - Identification key to all species*. Scheeßel, Germany.

Bignal, E.M. & McCrackent, D.I. (1996) Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology,* **33,** 413-424.

Blake, R.J., Woodcock, B.A., Ramsay, A.J., Pilgrim, E.S., Brown, V.K., Tallowin, J.R. & Potts, S.G. (2011) Novel margin management to enhance Auchenorrhyncha biodiversity in intensive grasslands. *Agriculture, Ecosystems & Environment,* **140,** 506-513.

Blake, R.J., Woodcock, B.A., Westbury, D.B., Sutton, P. & Potts, S.G. (2013) Novel management to enhance spider biodiversity in existing grass buffer strips. *Agricultural and Forest Entomology,* **15,** 77-85.

Buchholz, S., Jess, A.M., Hertenstein, F. & Schirmel, J. (2010) Effect of the colour of pitfall traps on their capture efficiency of carabid beetles (Coleoptera: Carabidae), spiders (Araneae) and other arthropods. *European Journal of Entomology,* **107,** 277-280.

Buri, P., Humbert, J.Y. & Arlettaz, R. (in press) Delaying mowing and leaving uncut refuges boost orthopterans in extensively managed meadows: evidence drawn from real field-scale experimentation. *Agriculture, Ecosystems and Environment*.

Buri, P., Humbert, J.Y. & Arlettaz, R. (submitted) Promoting pollinating insects in intensive agricultural matrices: field-scale experimental manipulation of hay-meadow mowing regimes and its effects on bees. *PLoS ONE*.

Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., Krewenka, K., Potts, S.G., Roberts, S.P.M., Rodet, G., Settele, J., Steffan-Dewenter, I., Szentgyörgyi, H., Tscheulin, T., Westphal, C., Woyciechowski, M. & Vaissière, B.E. (2009) Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agriculture, Ecosystems and Environment,* **133,** 40-47.

Cattin, M.-F., Blandenier, G., Banašek-Richter , C. & Bersier, L.-F. (2003) The impact of mowing as a management strategy for wet meadows on spider (Araneae) communities. *Biological Conservation,* **113,** 179-188.

Cizek, O., Zamecnik, J., Tropek, R., Kocarek, P. & Konvicka, M. (2011) Diversification of mowing regime increases arthropods diversity in species-poor cultural hay meadows. *Journal of Insect Conservation,* **16,** 215-226.

Čop, J., Vidrih, M. & Hacin, J. (2009) Influence of cutting regime and fertilizer application on the botanical composition, yield and nutritive value of herbage of wet grasslands in Central Europe. *Grass and Forage Science,* **64,** 454-465.

Swiss Federal Council (1998) Verordnung über die Direktzahlungen an die Landwirtschaft. *930.13*, pp. 229-265. Bundesrat.

Critchley, C.N.R., Burke, M.J.W. & Stevens, D.P. (2003) Conservation of lowland semi-natural grasslands in the UK: a review of botanical monitoring results from agri-environment schemes. *Biological Conservation,* **115,** 263-278.

Everwand, G., Scherber, C. & Tscharntke, T. (2013) Slug responses to grassland cutting and fertilizer application under plant functional group removal. *Acta Oecologica,* **48,** 62-68.

FOAG (2012) Rapport Agricole 2011. pp. 1-284. Federal Office of Agriculture, Bern.

Furieri, A. (2008) SpatiaLite - A complete spatial DBMS in a nutshell.

Guerrero, I., Morales, M.B., Oñate, J.J., Geiger, F., Berendse, F., Snoo, G.d., Eggers, S., Pärt, T., Bengtsson, J. & Clement, L.W. (2012) Response of ground-nesting farmland birds to agricultural intensification across Europe: Landscape and field level management factors. *Biological Conservation,* **152,** 74-80.

Hart, K. & Baldock, D. (2011) Greening the CAP: Delivering environmental outcomes through pillar one.

Helden, A.J. & Leather, S.R. (2004) Biodiversity on urban roundabouts—Hemiptera, management and the species–area relationship. *Basic and Applied Ecology,* **5,** 367-377.

Hossain, Z., Gurr, G.M. & Wratten, S.D. (1999) Capture efficiency of insect natural enemies from tall and short vegetation using vacuum sampling. *Annals of Applied Biology,* **135,** 463-467.

Hoste-Danyłow, A., Romanowski, J. & Żmihorski, M. (2010) Effects of management on invertebrates and birds in extensively used grassland of Poland. *Agriculture, Ecosystems & Environment,* **139,** 129-133.

Humbert, J.-Y., Ghazoul, J., Richner, N. & Walter, T. (2012a) Uncut grass refuges mitigate the impact of mechanical meadow harvesting on orthopterans. *Biological Conservation,* **152,** 96-101.

Humbert, J.-Y., Pellet, J., Buri, P. & Arlettaz, R. (2012b) Does delaying the first mowing date benefit biodiversity in meadowland? A meta-analysis. *Environmental Evidence***,** 1-9.

Humbert, J.Y., Ghazoul, J. & Walter, T. (2009) Meadow harvesting techniques and their impacts on field fauna. *Agriculture, Ecosystems and Environment,* **130,** 1-8.

Jud, P. & Schmidt-Entling, M.H. (2008) Fluid type, dilution, and bitter agent influence spider preservation in pitfall traps. *Entomologia Experimentalis et Applicata,* **129,** 356-359.

Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M. & Yela, J.L. (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters,* **9,** 243-254.

Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology,* **40,** 947-969.

Lange, M., Gossner, M.M. & Weisser, W.W. (2011) Effect of pitfall trap type and diameter on vertebrate by-catches and ground beetle (Coleoptera: Carabidae) and spider (Araneae) sampling. *Methods in Ecology and Evolution,* **2,** 185-190.

Martínez-Abraín, A. (2008) Statistical significance and biological relevance: A call for a more cautious interpretation of results in ecology. *Acta Oecologica,* **34,** 9-11.

MétéoSuisse (2012) Bulletin climatologique année 2011. pp. 13. Federal Department of Home Affairs FDHA, national weather services, Genève.

Mountford, J.O., Lakhani, K.H. & Holland, R.J. (1996) Reversion of vegetation following the cessation of fertilizer application. *Journal of Vegetation Science,* **7,** 219-228.

Nentwig, W., Blick, T., Gloor, D., Hänggi, A. & Kropf, C. (2013) araneae, sipders of Europe.

Nickel, H. (2003) *The Leafhoppers and Planthoppers of Germany (Hemiptera, Auchenorrhyncha): Patterns and strategies in a highly diverse group of phytophagous insects*. Pensoft.

Noordijk, J., Delille, K., Schaffers, A.P. & Sýkora, K.V. (2009) Optimizing grassland management for flower-visiting insects in roadside verges. *Biological Conservation,* **142,** 2097-2103.

Nyffeler, M. (2000) Ecological impact of spider predation : a critical assessment of Bristowe' s and Turnbull' s estimates. *Bulletin of the British Arachnological Society,* **11,** 367-373.

Nyffeler, M. & Benz, G. (1987) Spiders in natural pest control: A review1. *Journal of Applied Entomology,* **103,** 321-339.

Prestidge, R.A. (1982) The influence of nitrogenous fertilizer on the grassland Auchenorrhyncha (Homoptera). *Journal of Applied Ecology,* **19,** 735-749.

Quantum GIS Developement Team (2013) QGIS. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project.

R CoreTeam (2013) R: A language and environment for statistical computing. Vienna, Austria.

Rösch, V., Tscharntke, T., Scherber, C. & Batáry, P. (2013) Landscape composition, connectivity and fragment size drive effects of grassland fragmentation on insect communities. *Journal of Applied Ecology,* **50,** 387-394.

Rothenwöhrer, C., Scherber, C. & Tscharntke, T. (2013) Grassland management for stem-boring insects: Abandoning small patches is better than reducing overall intensity. *Agriculture, Ecosystems & Environment,* **167,** 38-42.

Sanders, D. & Entling, M.H. (2011) Large variation of suction sampling efficiency depending on arthropod groups, species traits and habitat properties. *Entomologia Experimentalis et Applicata,* **138,** 234-243.

Schmidt, M.H., Lefebvre, G., Poulin, B. & Tscharntke, T. (2005) Reed cutting affects arthropod communities, potentially reducing food for passerine birds. *Biological Conservation,* **121,** 157-166.

Schmidt, M.H., Thies, C., Nentwig, W. & Tscharntke, T. (2008) Contrasting responses of arable spiders to the landscape matrix at different spatial scales. *Journal of Biogeography,* **35,** 157-166.

Schuch, S., Wesche, K. & Schaefer, M. (2012) Long-term decline in the abundance of leafhoppers and planthoppers (Auchenorrhyncha) in Central European protected dry grasslands. *Biological Conservation,* **149,** 75-83.

Sugiura, N. (1978) Further analysis of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics: Theory and Methods,* **7,** 13-26.

Swisstopo Vector 25. (Federal Office of Topography. Swisstopo). Wabern, Switzerland.

Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity - ecosystem service management. *Ecology Letters,* **8,** 857-874.

Veen, P., Jefferson, R., Smidt, J.d. & Straaten, J.v.d. (2009) *Grasslands in Europe of high nature value.* KNNV Publishing, Zeist, the Netherlands.

Warren, J., Lawson, C.S. & Blecher, K. (2008) *The Agri-Environment*. Cambridge, United Kingdom.

Whittingham, M.J. (2011) The future of agri-environment schemes: biodiversity gains and ecosystem service delivery? *Journal of Applied Ecology,* **48,** 509-513.

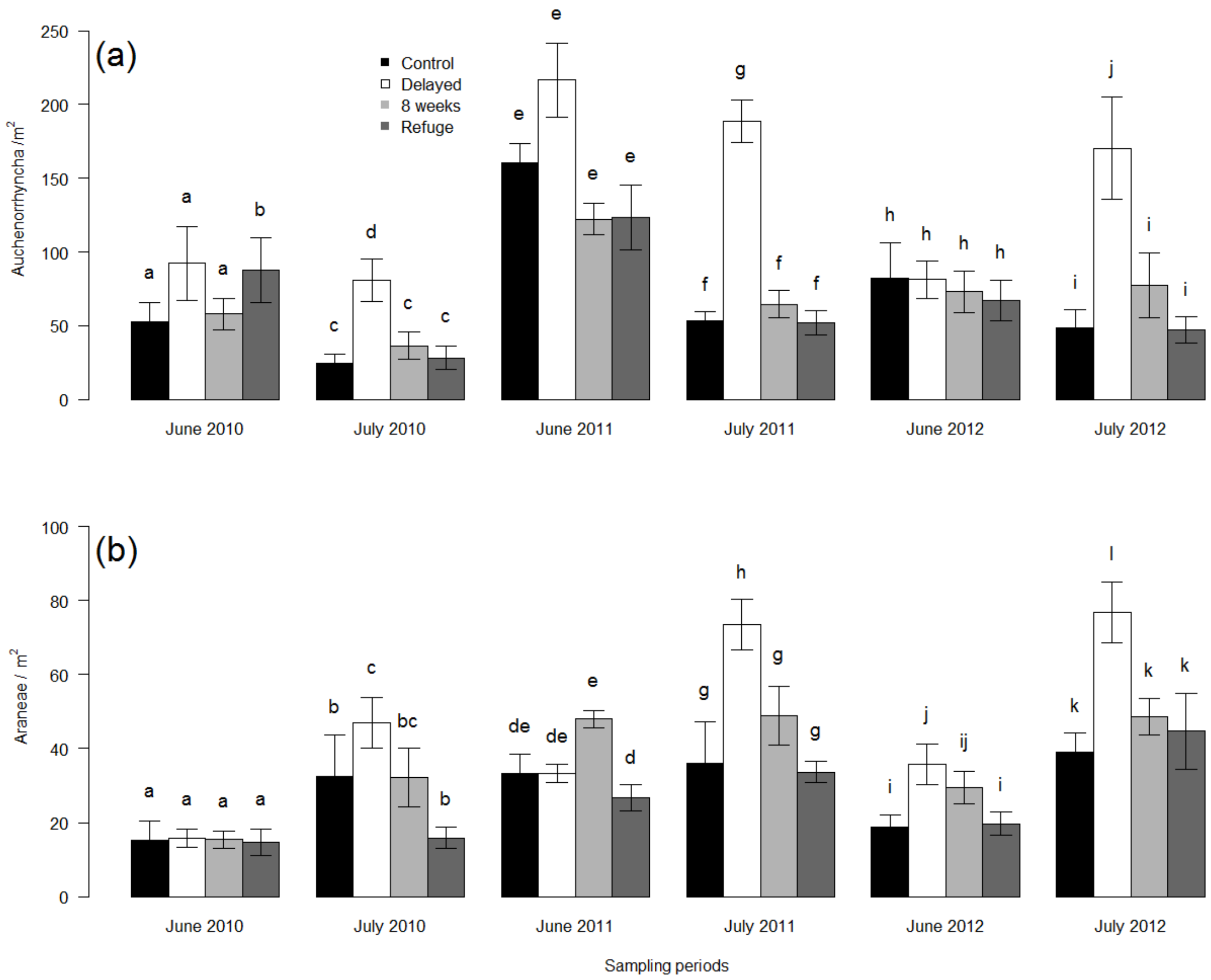


Figure 1. Mean yearly density (individuals per m^2) of (a) Auchenorrhyncha and (b) Araneae with respect to mowing treatment. Error bars represent standard errors of the mean. Significant differences ($p < 0.05$) are indicated by different letters

Figure 2.

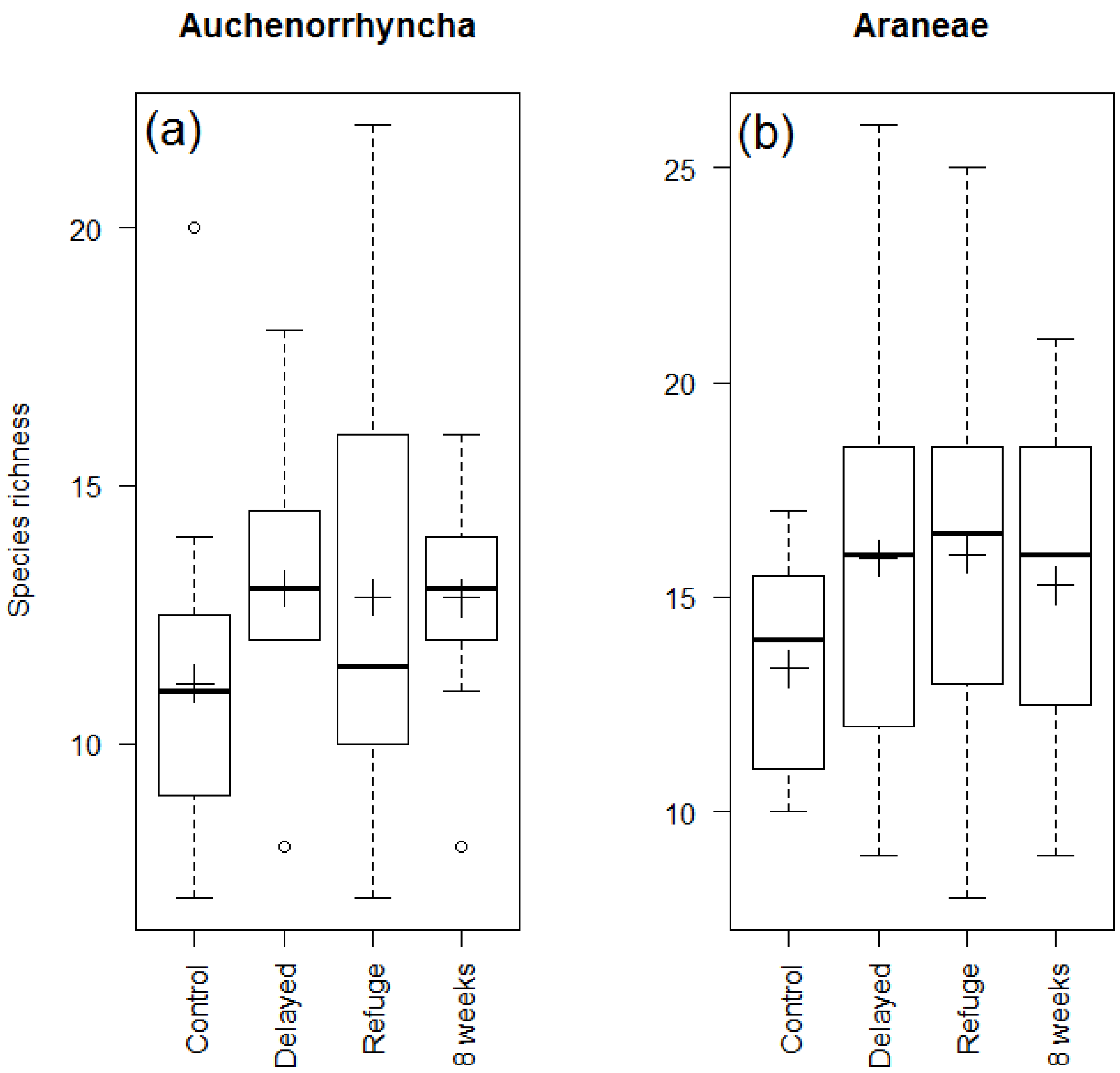


Figure 2. Species richness of (a) Auchenorrhyncha and (b) Araneae with respect to mowing treatment. Bold transversal bars represent medians, crosses the means, box boundaries the first and last quartiles, whiskers the inter-quartile distance multiplied by 1.5, and open dots the outliers

Table 1. Overall effects (data pooled across seasons and years) of different mowing treatments, season and year on density, species richness and diversity (Shannon-Wiener index) of Auchenorrhyncha and Araneae. Auchenorrhyncha metrics were estimated from suction sampling data. Araneae density and Shannon-Wiener diversity index were calculated from the data collected with suction sampling, while spider species richness combines suction sampling and pitfall trapping. Significant p-values are highlighted in bold.

		Density			Species richness			Shannon Wiener index		
	Treatment	Estimate	t	*P*	Estimate	z	Pr(>|z|)	Estimate	t	*P*
Auchenorrhyncha	delayed	0.8728	6.572	**0.0001**	0.15429	1.281	0.2	-0.1098	-0.574	0.5534
	refuge	0.0910	0.688	0.5180	0.13911	1.177	0.239	0.0353	0.185	0.8580
	8 weeks	0.3504	2.659	**0.0088**	0.11944	1.006	0.315	0.1567	0.820	0.4204
	Period	0.4038	4.318	**0.0001**	-	-	-	-	-	-
	Year 2011	0.7305	6.387	**0.0001**	-	-	-	-	-	-
	Year 2012	0.4032	3.525	**0.0004**	-	-	-	-	-	-
Araneae	delayed	0.5643	5.229	**0.0001**	0.1926	1.752	0.0798	0.0309	0.214	0.8370
	refuge	-0.1021	-0.950	0.3386	0.1823	1.701	0.0889	0.2408	1.706	0.0934
	8 weeks	0.3187	2.976	**0.0024**	0.1229	1.109	0.2675	0.1008	0.698	0.5096
	Period	0.52645	6.926	**0.0001**	-	-	-	-	-	-
	Year 2011	-0.52645	8.335	**0.0001**	-	-	-	-	-	-
	Year 2012	0.66966	7.205	**0.0001**	-	-	-	-	-	-

Table 2. Specific effects (seasons and years separated, thus 6 different models) of mowing treatment on density of Auchenorrhyncha and Araneae. Significant p-values are highlighted in bold.

		Auchenorrhyncha						Araneae					
		June			July			June			July		
Year	Treatment	Estimate	t	*P*	Estimate	t	*P*	Estimate	t	*P*	Estimate	t	*P*
2010	delayed	0.4673	1.989	0.0924	1.2126	4.053	**0.0001**	0.30635	0.701	0.5308	0.7741	2.527	**0.03**
	refuge	0.5811	2.474	**0.0406**	-0.1047	-0.35	0.7364	0.01297	0.03	0.9922	-0.3264	-1.066	0.3368
	8 weeks	0.3054	1.3	0.272	0.2144	0.717	0.4718	0.28099	0.643	0.5586	0.0347	0.113	0.9212
2011	delayed	0.5615	1.729	0.0984	1.3737	4.035	**0.0014**	0.0596	0.097	0.931	2.5852	4.856	**0.0001**
	refuge	0.1619	0.489	0.6518	-0.2011	-0.591	0.5886	-0.6339	-1.014	0.2968	-0.2085	-0.392	0.7278
	8 weeks	0.2714	0.835	0.4226	0.5582	1.64	0.1378	0.87591	1.329	0.171	0.8184	1.404	0.235
2012	delayed	0.4142	0.431	0.6778	1.3908	5.293	**0.0002**	1.6256	3.322	**0.0042**	2.6494	4.315	**0.0006**
	refuge	-0.3252	-0.347	0.7692	0.0476	0.186	0.8664	0.1536	0.322	0.767	0.1689	0.282	0.805
	8 weeks	-0.1148	-0.123	0.9266	0.4332	1.544	0.138	1.0058	2.109	0.059	0.6798	1.136	0.2928

Appendix 1. Location of the study sites (Buri_samples_sites.kmz , electronic file for google earth software)

Appendix 2. Table S1. Main summary of the data obtained with the suction samplers for the Auchenorrhyncha and the spiders. Sampling dates are indicated in the Day/Month system and coordinates in the WGS 84 geodesic system.

			Sampling dates			Coordinates	
Canton	Region	Mowing regime	2010	2011	2012	E	N
VD	Nyon	Control	06.06 / 11.07	29.5 / 01.07	01.06 / 12.07	6.21926	46.41479
	Nyon	Delayed	06.06 / 11.07	29.5 / 01.07	01.06 / 12.07	6.19594	46.37844
	Nyon	8 Weeks	06.06 / 11.07	29.5 / 01.07	01.06 / 12.07	6.18594	46.37876
	Nyon	Refuge	06.06 / 11.07	29.5 / 01.07	01.06 / 12.07	6.25433	46.40769
	Orbe	Control	06.06 / 10.07	26.5 / 01.07	01.06 / 12.07	6.50323	46.71043
	Orbe	Delayed	06.06 / 10.07	26.5 / 01.07	01.06 / 12.07	6.49181	46.70081
	Orbe	8 Weeks	06.06 / 10.07	26.5 / 01.07	01.06 / 12.07	6.48131	46.69787
	Orbe	Refuge	10.06 / 10.07	26.5 / 01.07	01.06 / 12.07	6.49843	46.71744
	Avenches	Control	07.06 / 10.7	17.05 / 12.07	01.06 / 11.07	7.00789	46.92443
	Avenches	Delayed	07.06 / 09.07	17.05 / 12.07	01.06 / 11.07	7.05615	46.93898
	Avenches	8 Weeks	07.06 / 10.7	17.05 / 12.07	01.06 / 11.07	7.00236	46.92323
	Avenches	Refuge	07.06 / 09.07	17.05 / 12.07	01.06 / 11.07	7.0598	46.94316
FR	Cousset	Control	07.06 / 09.07	17.05 / 12.07	01.06 / 11.07	6.98079	46.82316
	Cousset	Delayed	07.06 / 09.07	17.05 / 12.07	01.06 / 11.07	6.97325	46.82397
	Cousset	8 Weeks	07.06 / 09.07	17.05 / 12.07	01.06 / 11.07	6.97602	46.81959
	Cousset	Refuge	07.06 / 09.07	17.05 / 12.07	01.06 / 11.07	7.0023	46.83105
NE	Coffrane	Control	10.06 / 12.07	19.05 / 12.07	02.06 / 17.07	6.86176	47.00157
	Coffrane	Delayed	10.06 / 12.07	19.05 / 12.07	NA	6.85332	47.00149
	Coffrane	8 Weeks	10.06 / 12.07	19.05 / 12.07	02.06 / 17.07	6.8534	47.01196
	Coffrane	Refuge	10.06 / 12.07	19.05 / 12.07	02.06 / 17.07	6.84951	47.00814
BE	Wohlen	Control	04.06 / 06.07	20.05 / 04.07	02.06 / 04.07	7.37801	46.99978
	Wohlen	Delayed	04.06 / 06.08	20.05 / 04.07	02.06 / 04.07	7.42486	46.99751
	Wohlen	8 Weeks	04.06 / 06.09	20.05 / 04.07	02.06 / 04.07	7.41489	46.98292
	Wohlen	Refuge	04.06 / 06.10	20.05 / 04.07	02.06 / 04.07	7.38956	46.96997
	Grossaffoltern	Control	04.06 / 14.07	19.05 / 12.07	02.06 / 05.07	7.37652	47.065
	Grossaffoltern	Delayed	04.06 / 12.07	19.05 / 12.07	02.06 / 05.07	7.37496	47.07554
	Grossaffoltern	8 Weeks	04.06 / 14.07	19.05 / 12.07	02.06 / 05.07	7.33466	47.0776
	Grossaffoltern	Refuge	22.06 / 14.07	19.05 / 12.07	02.06 / 05.07	7.34781	47.06378
	Belp	Control	09.06 / 06.07	18.05 / 04.07	07.06 / 04.07	7.51062	46.88239
	Belp	Delayed	09.06 / 06.07	18.05 / 04.07	07.06 / 04.07	7.47407	46.91446
	Belp	8 Weeks	09.06 / 06.07	18.05 / 04.07	07.06 / 04.07	7.51564	46.88905
	Belp	Refuge	09.06 / 06.07	18.05 / 04.07	07.06 / 04.07	7.51727	46.89607
	Hindelbank	Control	11.06 / 14.07	21.05 / 04.07	14.6 / 10.07	7.60116	47.03868
	Hindelbank	Delayed	08.06 / 13.07	21.05 / 04.07	14.6 / 10.07	7.55334	47.05733
	Hindelbank	8 Weeks	08.06 / 14.07	21.05 / 04.07	14.6 / 10.07	7.54758	47.02428
	Hindelbank	Refuge	08.06 / 08.07	21.05 / 04.07	14.6 / 10.07	7.56751	47.0306
	Huttwil	Control	08.06 / 07.07	22.05 / 09.07	14.06 / 09.07	7.81477	47.09231
	Huttwil	Delayed	08.06 / 07.07	22.05 / 09.07	14.06 / 09.07	7.85304	47.10897
	Huttwil	8 Weeks	08.06 / 08.07	22.05 / 09.07	14.06 / 09.07	7.84513	47.10044
	Huttwil	Refuge	08.06 / 08.07	22.05 / 09.07	14.06 / 09.07	7.82261	47.11047
BL	Diegten	Control	09.06 / 08.07	21.05 / 06.07	09.06 /10.07	7.8175	47.42509
	Diegten	Delayed	09.06 / 08.07	21.05 / 06.07	09.06 /10.07	7.83267	47.43855
	Diegten	8 Weeks	09.06 / 08.07	21.05 / 06.07	09.06 /10.07	7.82153	47.41849
	Diegten	Refuge	09.06 / 08.07	21.05 / 06.07	09.06 /10.07	7.81699	47.41462
AG	Lupfig	Control	11.06 / 13.07	20.5 / 06.07	09.06 / 09.07	8.17942	47.44759
	Lupfig	Delayed	11.06 / 13.07	20.5 / 06.07	09.06 / 09.07	8.18753	47.44312
	Lupfig	8 Weeks	11.06 / 13.07	20.5 / 06.07	09.06 / 09.07	8.19388	47.44158
	Lupfig	Refuge	11.06 / 13.07	20.5 / 06.07	09.06 / 09.07	8.21673	47.44438

continued

(continued)

	Auchenorrhyncha abundance						Spiders abundance						Species number	
	June 2010	July 2010	June 2011	July 2011	June 2012	July 2012	June 2010	July 2010	June 2011	July 2011	June 2012	July 2012	Auchenorrhyncha	Spiders
	95	25	288	112	142	36	8	2	28	16	39	39	12	12
	68	57	221	66	101	75	19	22	33	32	40	70	13	13
	57	20	120	17	65	25	9	12	35	33	27	31	16	14
	77	5	25	0	38	57	2	9	3	3	8	21	10	6
	43	10	27	11	81	21	7	5	7	14	12	31	11	11
	22	51	160	109	84	243	10	54	43	80	41	81	13	13
	27	5	70	44	47	85	7	5	30	47	24	48	13	10
	176	66	173	29	95	61	14	13	10	37	14	61	11	11
	82	15	542	67	88	8	68	2	56	36	18	21	7	7
	251	208	281	238	170	201	38	53	40	68	20	64	17	12
	102	9	167	32	84	94	21	4	32	25	53	49	13	9
	250	4	306	62	198	34	15	4	23	27	15	26	22	9
	161	18	450	16	292	111	12	21	13	19	21	38	20	7
	207	46	207	89	106	49	12	15	12	46	32	101	12	12
	110	23	114	40	192	54	23	41	26	38	26	56	11	9
	180	82	141	80	62	86	38	30	36	58	46	108	17	13
	11	47	43	70	33	113	15	42	32	36	13	84	13	12
	24	41	55	87	NA	NA	21	31	19	59	NA	NA	NA	NA
	34	27	95	83	60	237	31	32	53	58	33	66	14	12
	43	28	98	72	42	98	8	30	43	45	33	101	16	17
	56	19	28	36	74	21	21	16	43	37	20	20	10	6
	12	67	228	243	99	344	12	91	13	122	51	132	8	8
	44	80	93	95	51	42	13	86	83	81	46	43	12	11
	58	23	86	73	57	24	10	14	37	33	23	20	11	11
	23	18	48	23	18	16	6	140	64	31	36	31	8	10
	44	61	193	124	57	92	16	66	38	88	52	69	13	7
	22	95	53	69	41	26	20	46	37	46	45	57	8	12
	33	14	84	18	42	19	35	21	31	27	17	20	9	8
	47	11	118	117	91	38	16	36	31	73	13	37	11	6
	76	88	97	213	69	114	15	23	15	52	24	56	18	10
	39	17	73	72	71	24	12	9	65	42	29	16	15	8
	34	8	61	36	54	30	7	3	10	19	18	20	12	5
	52	33	150	98	120	120	7	39	47	63	29	45	14	10
	201	110	835	529	81	350	8	55	46	113	67	74	13	12
	50	60	135	118	51	178	9	54	50	30	15	55	14	8
	74	15	68	99	58	80	4	26	19	47	10	31	13	3
	7	16	21	28	16	29	6	44	28	55	4	54	10	7
	20	44	21	206	16	197	12	65	60	103	18	100	8	4
	64	17	210	689	39	196	17	3	29	76	14	35	10	7
	49	28	144	76	63	27	23	20	34	54	18	36	10	6
	44	12	NA	11	11	40	14	12	NA	16	6	42	11	10
	118	81	135	159	27	37	10	30	42	35	5	34	12	9
	112	29	300	59	110	55	12	40	65	59	10	70	12	7
	47	6	NA	5	20	5	16	9	NA	26	15	13	7	11
	12	74	52	55	22	27	3	30	17	37	15	25	7	6
	63	116	166	202	84	172	17	59	39	83	44	64	15	5
	42	35	126	81	31	35	13	24	52	79	17	44	13	9
	33	59	171	74	78	43	5	12	47	28	19	79	16	15
Total	3496	2023	7279	4932	3531	4069	737	1500	1616	2332	1195	2418	53	71

Appendix 3. Table S1. List of the different species of Auchenorrhyncha and spiders identified in each study area. Presence are marked with a cross and absence by empty cells.

	Avenches	Belp	Coffrane	Cousset	Diegten	Grossaffoltern	Hindelbank	Huttwil	Lupfig	Nyon	Orbe	Wohlen
Auchenorrhyncha												
Acanthodelphax spinosa			X		X			X	X		X	X
Anaceratagallia ribauti		X	X	X	X	X	X		X	X	X	X
Anoscopus albifrons	X					X	X	X				
Anoscopus flavostriatus								X				
Anoscopus serratulae		X	X	X	X	X	X	X	X	X	X	X
Aphrodes bicincta	X	X	X	X	X			X	X	X	X	X
Aphrodes diminuta	X			X	X				X			X
Aphrophora alni	X			X	X		X			X		
Arthaldeus pascuellus		X				X	X	X	X	X		X
Balclutha punctata											X	
Chlorita paolii1												
Cicadella viridis	X			X			X					
Cicadula persimilis				X								
Deltocephalus pulicaris		X	X	X		X		X	X			X
Dicranotropis hamata	X	X	X	X	X	X	X	X	X	X		X
Ditropsis flavipes	X	X	X	X	X					X	X	
Emelyanoviana mollicula	X			X	X			X	X		X	
Empoasca decipiens	X											
Empoasca pteridis	X											
Errastunus oscellaris	X	X	X	X			X			X		
Eupelix cuspidata1	X		X									
Eupteryx atropunctata						X					X	
Eupteryx notata		X	X	X	X	X			X	X	X	X
Euscelis incisus		X	X	X	X	X	X	X	X	X	X	X
Evacanthus interruptus	X						X					
Graphocraerus ventralis			X		X		X				X	
Hardya tenuis		X		X	X		X		X	X	X	
Hyledelphax elegantula					X							X
Javesella dubia		X			X	X	X	X	X			
Javesella obscurella	X	X				X	X	X	X			X
Javesella pellucida		X	X	X	X	X	X	X	X	X	X	X
Laburrus cf impictifrons1	X	X							X			
Laodelphax striatella		X	X	X	X	X	X	X	X	X		
Lepyronia coleoptrata	X	X		X	X		X			X		X
Macrosteles cristatus	X	X					X		X			
Macrosteles laevis		X		X		X	X	X	X			X
Macrosteles sexnotatus				X				X				X
Megadelphax sordidula	X	X	X	X	X	X	X	X		X	X	X
Megophtalmus scanicus	X	X		X	X		X		X	X		X
Muellerianella fairmairei									X			
Neophilaeuns campestris										X	X	

	Avenches	Belp	Coffrane	Cousset	Diegten	Grossaffoltern	Hindelbank	Huttwil	Lupfig	Nyon	Orbe	Wohlen
Philaenus spumarius	X	X	X	X	X	X	X	X	X	X	X	X
Psammotettix confinis	X					X			X			
Psammotettix helvolus	X	X	X	X	X	X				X	X	
Recilia coronifer	X	X				X	X		X			
Ribautodelphax albostriata	X	X	X			X	X		X	X	X	X
Ribautodelphax angulosa	X	X	X	X		X	X	X	X	X	X	
Ribautodelphax imitans				X						X	X	
Streptanus aemulans	X	X					X		X	X	X	X
Streptanus sordidus		X					X	X				
Turrutus socialis		X	X	X			X	X				
Xanthodelphax stramineus						X			X			
Zyginidia scutellaris	X	X		X	X	X	X			X	X	
Spiders												
Aculepeira ceropegia	X		X							X		
Alopecosa cuneata										X	X	
Alopecosa pulverulenta	X	X	X	X	X		X	X	X		X	X
Araeoncus humilis	X	X		X		X		X	X	X	X	X
Arctosa leopardus	X	X				X	X	X				X
Arctosa lutetiana	X										X	X
Argenna subnigra			X		X					X	X	
Argiope bruennichi										X		
Asagena phalerata				X	X				X	X	X	
Atypus affinis				X								
Aulonia albimana			X		X				X			X
Bathyphantes gracilis	X									X		
Bathyphantes parvulus	X									X		
Cnephalocotes obscurus					X		X					
Collinsia inerrans						X						
Cryptachaea riparia	X									X		
Dictyna unicata	X										X	
Dicymbium nigrum		X	X		X	X	X	X	X	X	X	
Diplostyla concolor							X		X			
Drassyllus pusillus	X		X							X	X	
Enoplognatha elongata					X							
Enoplognatha thoracica		X	X		X				X		X	X
Erigone atra	X		X			X	X	X	X		X	X
Erigone dentipalpis		X	X	X	X	X	X	X	X	X	X	X
Euophrys thorelli	X										X	
Gongylidiellum latebricola							X					
Hania nava			X	X	X	X				X	X	
Haplodrassus signifer		X	X							X	X	
Heliophanus flavipes	X								X			
Histopona torpida				X								
Hypsosinga pygmaea											X	
Mangora acalypha		X		X	X		X				X	X

	Avenches	Belp	Coffrane	Cousset	Diegten	Grossaffoltern	Hindelbank	Huttwil	Lupfig	Nyon	Orbe	Wohlen
Meioneta affinis	X	X	X	X							X	X
Meioneta mollis										X		X
Meioneta rurestris		X	X	X	X	X	X		X	X	X	X
Meioneta saxatilis	X										X	X
Meioneta simplicitarsis			X							X	X	
Mermessus trilobatus	X	X	X	X	X	X	X	X	X	X	X	X
Micaria pulicaria	X		X							X		X
Micrargus subaequalis	X							X	X			
Microlinyphia pusilla	X				X	X			X	X	X	
Neoscona adianta					X							
Neottiura bimaculata		X					X					
Oedothorax apicatus		X	X	X		X	X			X		X
Oedothorax fuscus	X	X				X	X	X	X			X
Ozyptila claveata	X				X							
Ozyptila simplex				X	X					X	X	X
Pachygnatha clercki	X						X	X	X			
Pachygnatha degeeri	X	X	X	X	X	X	X	X	X	X	X	X
Paidiscura pallens	X		X									
Pardosa agrestis		X			X	X	X	X	X	X		X
Pardosa agricola	X										X	
Pardosa amentata		X	X		X	X	X					
Pardosa lugubris	X				X					X		X
Pardosa paludicola				X								
Pardosa palustris		X	X	X	X	X	X	X	X	X	X	X
Pardosa prativaga	X								X			
Pardosa proxima	X			X	X	X				X	X	
Pardosa pullata	X		X		X	X		X		X		
Pelecopsis parallela	X	X	X	X		X	X	X	X	X	X	X
Phlegra fasciata	X				X					X	X	
Phrurolithus festivus	X		X							X		
Phrurolithus minimusa	X									X		
Phrurolithus nigrinus					X							
Phylloneta impressa		X		X	X					X		
Pisaura mirabilis		X		X						X	X	
Pocadicnemis juncea	X					X						
Porrhomma microphthalmum				X				X			X	
Robertus arundineti			X									
Robertus neglectus						X						
Scotina palliardi					X							
Synageles venator		X										
Synema globosum												
Talavera aequipes	X		X							X		
Talavera aperta									X			
Tenuiphantes tenuis	X	X	X	X		X	X		X	X	X	X
Tetragnatha obtusa	X			X								
Tetragnatha pinicola			X	X			X					
Tiso vagans		X	X	X	X	X	X	X	X	X	X	X

	Avenches	Belp	Coffrane	Cousset	Diegten	Grossaffoltern	Hindelbank	Huttwil	Lupfig	Nyon	Orbe	Wohlen
Trichopterna cito										X		
Triychoncyboides simoni										X		
Trochosa ruricola		X	X	X	X	X	X	X	X	X	X	X
Trochosa terricola	X											X
Walckenaeria vigilax				X								
Xerolycosa miniata										X		
Xerolycosa nemoralis										X		
Xysticus acerbus				X					X			
Xysticus cristatus		X	X							X		
Xysticus kochi	X	X	X	X		X	X	X	X	X	X	X
Zelotes latreilli	X	X		X								
Zelotes lutentianus										X		
Zelotes praeficus	X			X	X						X	
Zelotes pusillus	X		X	X	X	X	X	X	X	X	X	X
Zodarion italicum	X		X							X		

Appendix 4. Selection of the different co-variables for the analyses of Auchenorrhyncha and spiders responses to different exprimental mowing regimes. Co-variables are: elevation, slope, mean temperature, registration duration as ECA, meadow size (ha), growth period, and in a radius of 250 m the proportion of different land covers: forest; gravel pits; special crops (vineyards plus orchards); settlements and; water bodies.

Auchenorryhncha

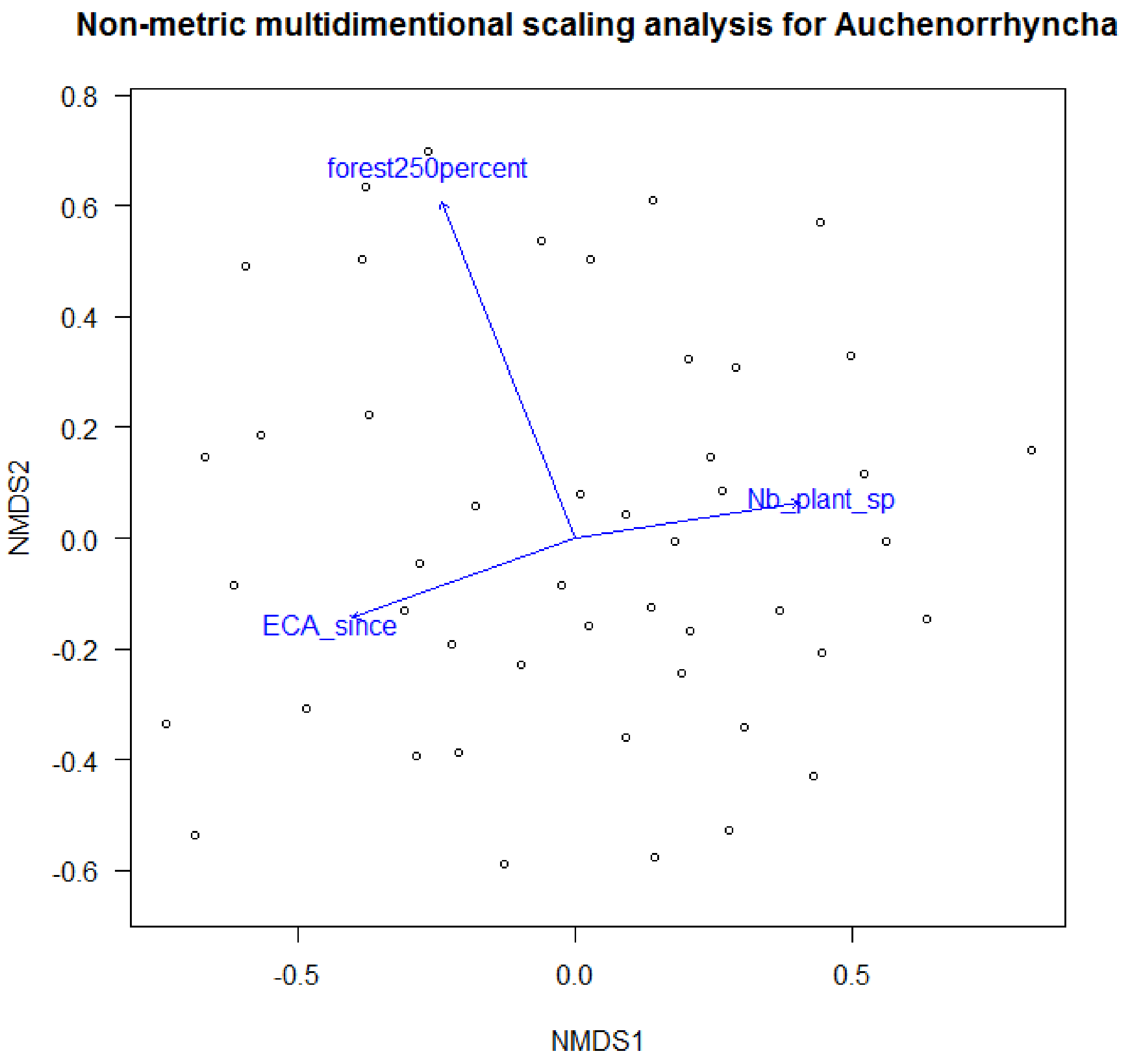


Figure S1. Graphical output of the two first axes of the non-metric multidimensional scaling for Auchenorrhyncha. The points represent the meadows and the arrows factor with a p-vlaue < 0.05. The length of the arrow represents the strength of the factor, based on the square root of the correlation coefficient r^2.

Table S1. Summary of the non-metric multidimensional scaling analysis for Auchenorrhyncha. NMDS 1 and NMDS 2 are the eigenvalues of the two first axes, r^2 the correlation coefficient of the variables and, Pr(>z) the p-values obtained after 999 permutations of the parameters. Significant p-values are highlighted in bold

	NMDS1	NMDS2	r^2	Pr(>r)
Elevation	-0.86929	-0.49430	0.0740	0.171
Slope	-0.99463	0.10345	0.1211	0.051
Registration duration as ECA	-0.94142	-0.33723	0.1317	**0.049**
Size (ha)	-0.78876	0.61470	0.0217	0.631
Growth period	0.38624	-0.92240	0.0378	0.443
Forest	-0.36917	0.92936	0.3093	**0.001**
Gravel pit	0.18136	-0.98342	0.0696	0.186
Special crops	0.97139	-0.23747	0.0244	0.605
settlement	0.74526	-0.66677	0.0693	0.228
Waterbodies	-0.94880	0.31587	0.0149	0.744
Nb plant species	0.98790	0.15511	0.1216	**0.047**

Table S2. Summary of the model selection for the Auchenorrhyncha. Parameters with a + were integreated in the respective models. The ΔAICc was obtained by substracting the AICc of the best model to the one presented on the respective line

Rank	Forest	Registration duration as ECA	Nb plants	AICc	ΔAICc
1	-	-	-	716.32	0
2	+	-	-	718.8	2.48
3	-	+	-	722.72	6.4
4	+	+	-	725.55	9.23
5	+	-	+	728.2	11.88
6	-	+	+	731	14.68
7	+	+	+	733.28	16.96

Araneae

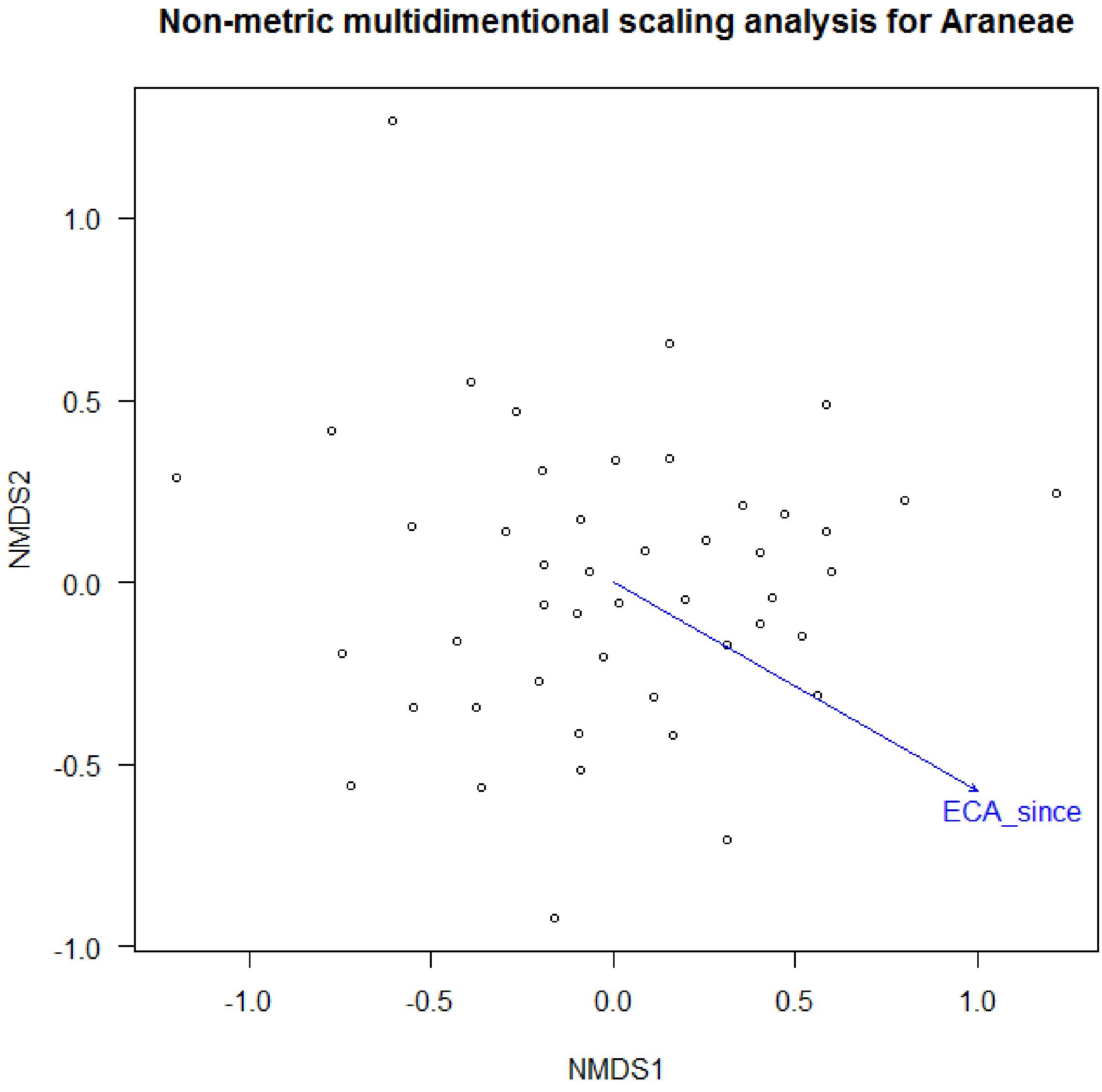


Figure S2. Graphical output of the two first axes of the non-metric multidimensional scaling for Spiders. Symbols are the same as in Figure 1.

Table S3. Summary of the non-metric multidimensional scaling analysis for Auchenorrhyncha. Columns are the same as in Table1.

	NMDS1	NMDS2	r^2	Pr(>r)
Elevation	0.999930	0.011792	0.0888	0.144
Slope	0.997443	0.071461	0.0785	0.184
Temp	-0.995868	-0.090811	0.0422	0.396
Registration duration as ECA	0.848579	-0.529069	0.3227	**0.001**
Size (ha)	0.273687	-0.961819	0.0083	0.842
Growth period	-0.621235	-0.783624	0.0305	0.497
Forest	0.704635	-0.709570	0.0999	0.102
Gravel pit	-0.866396	0.499357	0.0128	0.747
Special crops	-0.419191	-0.907898	0.0016	0.957
settlement	-0.141591	0.989925	0.0351	0.458
waterbodies	0.795994	0.605304	0.0109	0.778

Table S4. Summary of the model selection for the Auchenorrhyncha. Columns are the same as in Table 2

Rank	Registration duration as ECA	AICc	ΔAICc
1	-	602.22	0
2	+	608.75	6.53

6

General conclusion

The main goal of this PhD thesis was to test a set of alternative management measures that could improve the effectiveness of current AES among grasslands (Kleijn & Sutherland 2003). The ultimate goal is then to conserve and restore farmland biodiversity for future generations (European Communities 1985). Investigated management measures consisted of four different mowing regimes. In addition to have expected positive effects on biodiversity, these mowing regimes had to be straightforward, i.e. to be readily implementable by farmers. The mowing regimes were: i) delaying the first mowing date until 15 July; ii) limiting to two the number of cuts per year, with at least eight weeks in-between and; iii) leaving an uncut refuge on 10 – 20 % of a the meadow area at each cut, with the location of the refuge being changed from a cut to the next in order to avoid vegetation succession; iv) these treatments were compared to control meadows that were complying with management prescriptions for extensive ECA meadows (ecological compensation areas) within the Swiss AES.

From its onset, this PhD project was carried out within a collaborative framework, including among others: scientists (AGROSCOPE, UniBe), representatives of associations for agricultural development and rural affairs (AGRIDEA), representatives of cantonal and national offices for the environment and agriculture (Caudron, Vigier & Champigneulle 2012). This framework was used to link the themes and issues faced by conservation science and practice as well as to bridge the gap between research outputs and public actions (Arlettaz *et al.* 2010; Braunisch *et al.* 2012; Habel *et al.* 2013). It was intended to facilitate the future implementation of the management recommendations drawn from our results (Kleijn *et al.* 2006).

Measures were investigated at the field scale, which is the real scale for applying such management options, relying on a rigorous full block design experimental approach, with random allocation of the treatments to the different meadows. An advantage of the experimental approach when compared to mere observational and correlational studies, including quasi experiments, is the ability to disentangle the effects of the treatments from the effects of any potential confounding factors. For instance, a random treatment allocation to fields allows avoiding the *knowledge effect* (a typical sampling bias) that would typically lead the landowner to link a given treatment to a given field, based on his previous knowledge of the yield potential and phenology of that field, such as a systematic application of the most extensive management regime to the poorer productive circumstances. The experimental setup was replicated 12 times across Switzerland to be sure that the effects observed were not simply due to local conditions. This approach reinforces the strength of the outputs as such a replicated design reduces any risks that confounding factors would blur the underlying pattern. As a result, the evidence-based management recommendations drawn from this research are relevant not only to the whole Swiss plateau but even beyond the Swiss border. The fact that the landowners themselves were responsible for implementing the randomly allocated mowing regimes we had devised already constitutes a real-scale test of the applicability of these measures. The yearly standard interviews with the farmers allowed identifying any issues around the establishment of the selected management regimes, which is essential regarding the recommendations drawn from this study.

Notwithstanding the advantages provided by a fully controlled experimental approach, many points have to be considered. Such an experimental approach at the field scale generates substantial supplementary costs. It requires financial compensations for the farmers and high transportation expenses for travelling from the base to the study sites that were scattered across the Swiss plateau. This contrasts with, for instance, conventional common-garden experiments where treatments are typically applied in situ, even when replicated, which questions the capacity to extrapolate results. Though a greater number of alternative treatments can be tested simultaneously in common-garden experiments, spill-over effects might represent another source of uncertainty that is typically inexistent with our geographically replicated, field-scale experimental design (Hudewenz *et al.* 2012). However, an issue that is common to common garden and field scale experiments is the time needed by the organisms to react to experimental treatment, which might in part be linked to their ability to disperse (Woodcock *et al.* 2010).

Different groups were sampled to provide a better understanding of the effects of our measures on different guilds and / or trophic levels. Primary and secondary consumers were studied in chapter 4 (Auchenorrhyncha and Araneae), a taxon consisting of herbivores and insectivores in chapter 2 (orthopterans) and pollinators in chapter 3 (wild bees).

In the following sections, responses of the different group of organisms are summarized per mowing regime. A *management recommendations* section followed by a section that gives directions for future research close this general discussion.

6.1 Mowing delayed by a month (15 July)

A systematic review and meta-analysis was carried out about this widespread measure with the objective to draw a sound synthesis. The analysis shows that plant species richness could benefit from a delayed mowing if the mow is postponed from spring to summer. When the mow is further postponed, typically until autumn, damages are often recorded in plant communities that become less diverse. A benefit of postponing mowing was identified for arthropod species richness, whereas no effects on abundance could be detected. These conclusions, however, are based on a tiny evidence: only six studies on arthropods matched our inclusion criteria for the meta-analysis. Note also that several emblematic groups of arthropods characteristic of grasslands, such as orthopterans, were absent from the literature scrutinized.

Regarding the groups investigated in the other three chapters, a common pattern emerges: abundance and/or density of orthopterans, bees, Auchenorrhyncha and Araneae was higher in July in the delayed treatment, i.e. when the other types of meadow had been cut, confirming a strong negative direct effect of mowing on field invertebrates. A cumulative (from year $_{x}$ to year $_{x+1}$ or $_{X+2}$) positive effect could be evidenced only for Orthoptera and Araneae. These cumulated effects are most probably due to individuals that could reach adulthood between June and early July and thus could reproduce in favourable conditions, with demographic carry-over effects observed in the following year. Although wild bees directly benefitted from the presence of unmown meadows in the matrix, the data recorded in June 2011 showed a slight negative cumulative effect from the previous year on bee abundance. The presence in the matrix of meadows with abundant resources such as D-meadows could have generated a temporary concentration of this taxon (Veddeler, Klein & Tscharntke 2006). However, removal of these resources through mowing may have potentially reduced the reproductive capacity of wild bees, leading to the lower number of individuals observed in spring the following year.

In contrast, a positive direct effect of delaying mowing was demonstrated on honey bees although Swiss honey bees stem almost exclusively from managed hives (Jaffé *et al.* 2010). Agricultural intensification has reduced the number of cultivated crop species and led to the disappearance of semi-natural habitats, reducing the diet breadth of honey bees and thus directly threatening their survival (Nicolson & Human 2012). Consequently, they could benefit from the nectar resource provided by unmown meadows during early summer, especially nowadays that honey bees are experiencing dramatic population declines in the Northern Hemisphere (Carreck & Neumann 2010).

6.2 Two cuts a year, with eight weeks in-between

The result of the interviews with the farmers involved in this project evidenced that 8W- and C-meadows were actually managed in a very similar way. Only the results obtained with the Auchenorrhyncha and Araneae over three years yielded significant effects for this treatment. As discussed in chapter four, the observed densities were slightly higher than in controls, but the tiny effect size probably bears no biological meaning (Martínez-Abraín 2008). This management was recommended by some experts based on the time needed by ground-nesting birds to have a successful replacement clutch, when the first one was destroyed, typically by mowing (Müller *et al.* 2005). Such measures might still be profitable for meadow birds, but irrelevant for other taxa.

6.3 Uncut areas serving as refuges

Leaving uncut refuges had several positive effects on the investigated invertebrate populations. The second and third chapters evidenced a doubling of the abundance of orthopterans and wild bees in the following spring, pointing to a cumulative effect from one year to the next. Species richness was also higher in these treatments than in controls, this for both taxa. In orthopterans, it was mainly due to a higher number of species recorded, mainly bush crickets (Orthoptera: Tettigoniidae). The presence of some vertically heterogeneous herbaceous cover that could be generated by this management seems to benefit this taxon (Baur *et al.* 2006). Concerning bees, a positive effect was observed already after one year of implementation of our management, confirming that this taxon rapidly reacts to favourable management (Carvell *et al.* 2007). Such findings highlight the importance of grasslands as complement of wild flower strips for the conservation of wild bees in farmland (Öckinger & Smith 2007). They also provide a further illustration of the direct benefits of vegetation refuges (Humbert *et al.* 2012),

No effect of this management was detected for Auchenorrhyncha and Araneae. Although Auchenorrhyncha have a comparable niche as orthopterans, they differ in foraging and egg laying behaviour (Nickel 2003; Baur *et al.* 2006). While numerous species of orthopterans lay eggs in the soil, Auchenorrhyncha do it directly on their species-specific host plant. Grass removal has therefore a severe impact on Auchenorrhyncha and unmown refuges can only offer a very partial compensation for them. The recolonization of the meadow from an unmown refuge also depends on an organism's dispersal capacity. Maximum dispersal ranges are usually referred to in the literature (Bell, Wheater & Cullen 2001; Nickel 2003), while average dispersal range would certainly be more relevant and information about conditions promoting dispersal even more crucial. Therefore it is difficult to appreciate whether the size and interconnection of the refuges we created in our experiments actually match the basic spatial requirements of these two taxa.

6.4 Management recommendations

The taxa investigated reacted differently to our experimental mowing regimes, exemplifying the need for multiple and heterogeneous management options of grasslands for improving present day AES regulations. The hypothesis that biodiversity in farmland can be enhanced through reinstating more heterogeneous habitats is largely confirmed by our results, as least as regards grasslands (Benton, Vickery & Wilson 2003). The principal outcomes of the present research can be framed as take-home messages:

- **First cut not before 15 July** reduces the direct impact of mowing and is beneficial for several taxa as it provides suitable conditions for reproducing. This measure seems to be especially favourable for providing staple food resources for upper trophic levels, notably insectivorous predators.

- **Limiting the number of cuts to two** was unfortunately a management regime that was too close to the present Swiss AES regulation for extensively managed meadows, with thus little apparent benefits from this measure.
- **Uncut fraction of a meadow as a refuge** increases species richness, and population abundance and/or density in several taxa, but to a lesser extent than the delayed mowing regime. This measure appears thus mostly suitable when the objective is to increase species richness.

Notwithstanding that the alternative management measures investigated in this thesis were conceived mostly for extensively managed meadows within the Swiss AES, they have implications far beyond the Swiss border and for grassy habitats other than hay meadows. Temperate grasslands are widespread across Europe, constituting a great fraction of AES (Kleijn & Sutherland 2003). In this respect, the conclusions reached in this study might first bear some relevance for the on-going debate about greening the CAP at the EU level (Hart & Baldock 2011). Second, mown grasslands not included within AES such as road verges, grassy protected areas, banks of streams, canals and ditches could also benefit from the inputs of this project (Noordijk *et al.* 2009; Veen *et al.* 2009; Hoste-Danyłow, Romanowski & Żmihorski 2010).

The voluntary participation of the farmers involved in this project shows that at least some of them are ready to adapt their management when they are advised so and financially supported by cantonal and/or federal institutions (Anonymous 2009; OAN 2009; Whittingham 2011; McKenzie *et al.* 2013).

6.5 Further research

An extension of our experiments to other taxa could give a more comprehensive picture of the pros and cons of these alternative management regimes. Future candidate taxa would be butterflies and moths (Insecta: Lepidoptera) because they require different resources at different phases of their life-cycle, being thus particularly impacted by any changes in farmland habitat and farming practices (Cizek *et al.* 2011). Other taxa that provide crucial ecosystem services such as parasitoid wasps, which have the potential to limit the spread of agricultural pests, would also be worth investigating (Anderson *et al.* 2011). Assessing the effects of other mowing options, such as maintaining the uncut refuge during the entire year at the very same place, delaying mowing until August instead of July, or even combining these measures together would be another step forward, further testing conditions that might contribute to reinstate spatio-temporal heterogeneity within agro-ecosystems. Finally, the effect on upper trophic levels of these measures would deserve more consideration: the general, sometimes dramatic increase in biomass observed in D- and R-meadows, compared to controls, indicates in particular that insectivorous organisms might benefit from these boosted prey supplies (Benton *et al.* 2002), although remains the issue of the accessibility of that prey for insectivorous predators such as terrestrially foraging birds, which largely depends on the sward structure (Schaub *et al.* 2010).

6.6 References

Anderson, A., McCormack, S., Helden, A., Sheridan, H., Kinsella, A. & Purvis, G. (2011) The potential of parasitoid Hymenoptera as bioindicators of arthropod diversity in agricultural grasslands. *Journal of Applied Ecology*, **48,** 382-390.

Anonymous (2009) Bewirtschaftungsverträge Naturnahe Landwirtschaft Richtlinien. pp. 1-50. Departement Bau Verkehr und Umwelt, Aargau, Switzerland.

Arlettaz, R., Schaub, M., Fournier, J., Reichlin, T.S., Sierro, A., Watson, J.E.M. & Braunisch, V. (2010) From Publications to Public Actions: When Conservation Biologists Bridge the Gap between Research and Implementation. *BioScience*, **60,** 835-842.

Baur, B., Baur, H., Roesti, C., Roesti, D. & Thorens, P. (2006) *Sauterelles, Grillons et Criquets de Suisse*. Editions Haupt, Berne.

Bell, J.R., Wheater, C.P. & Cullen, W.R. (2001) The implications of grassland and heathland management for the conservation of spider communities: a review. *Journal of Zoology*, **255,** 377-387.

Benton, T.G., Bryant, D.M., Cole, L. & Crick, H.Q.P. (2002) Linking agricultural practice to insect and bird populations : a historical study over three decades. *Journal of Applied Ecology*, **39,** 673-687.

Benton, T.G., Vickery, J.a. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology & Evolution*, **18,** 182-188.

Braunisch, V., Home, R., Pellet, J. & Arlettaz, R. (2012) Conservation science relevant to action: A research agenda identified and prioritized by practitioners. *Biological Conservation*, **153,** 201-210.

Carreck, N. & Neumann, P. (2010) Honey bee colony losses. *Journal of Apicultural Research*, **49,** 1-1.

Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D. & Nowakowski, M. (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, **44,** 29-40.

Caudron, A., Vigier, L. & Champigneulle, A. (2012) Developing collaborative research to improve effectiveness in biodiversity conservation practice. *Journal of Applied Ecology*, **49,** 753-757.

Cizek, O., Zamecnik, J., Tropek, R., Kocarek, P. & Konvicka, M. (2011) Diversification of mowing regime increases arthropods diversity in species-poor cultural hay meadows. *Journal of Insect Conservation*, **16,** 215-226.

European Communities (1985) Perspectives for the Common Agricultural Policy. pp. 1-103. Brussel, Belgium.

Habel, J., Dengler, J., Janišová, M., Török, P., Wellstein, C. & Wiezik, M. (2013) European grassland ecosystems: threatened hotspots of biodiversity. *Biodiversity and Conservation*, **22,** 2131-2138.

Hart, K. & Baldock, D. (2011) Greening the CAP: Delivering environmental outcomes through pillar one.

Hoste-Danyłow, A., Romanowski, J. & Żmihorski, M. (2010) Effects of management on invertebrates and birds in extensively used grassland of Poland. *Agriculture, Ecosystems & Environment*, **139,** 129-133.

Hudewenz, A., Klein, A.-M., Scherber, C., Stanke, L., Tscharntke, T., Vogel, A., Weigelt, A., Weisser, W.W. & Ebeling, A. (2012) Herbivore and pollinator responses to grassland management intensity along experimental changes in plant species richness. *Biological Conservation*, **150,** 42-52.

Humbert, J.-Y., Ghazoul, J., Richner, N. & Walter, T. (2012) Uncut grass refuges mitigate the impact of mechanical meadow harvesting on orthopterans. *Biological Conservation*, **152,** 96-101.

Jaffé, R., Dietemann, V., Allsopp, M.H., Costa, C., Crewe, R.M., Dall'olio, R., De La Rúa, P., El-Niweiri, M.A., Fries, I., Kezic, N., Meusel, M.S., Paxton, R.J., Shaibi, T., Stolle, E. & Moritz, R.F.A. (2010) Estimating the density of honeybee colonies across their natural range to fill the gap in pollinator decline censuses. *Conservation Biology*, **24,** 583-593.

Kleijn, D., Baquero, R.A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog, F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E.J.P., Steffan-Dewenter, I., Tscharntke, T., Verhulst, J., West, T.M. & Yela, J.L. (2006) Mixed biodiversity benefits of agri-environment schemes in five European countries. *Ecology Letters*, **9,** 243-254.

Kleijn, D. & Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology*, **40,** 947-969.

Martínez-Abraín, A. (2008) Statistical significance and biological relevance: A call for a more cautious interpretation of results in ecology. *Acta Oecologica*, **34,** 9-11.

McKenzie, A.J., Emery, S.B., Franks, J.R. & Whittingham, M.J. (2013) Landscape-scale conservation: collaborative agri-environment schemes could benefit both biodiversity and ecosystem services, but will farmers be willing to participate? *Journal of Applied Ecology***,** n/a-n/a.

Müller, M., Spaar, R., Schifferli, L. & Jenni, L. (2005) Effects of changes in farming of subalpine meadows on a grassland bird, the whinchat (Saxicola rubetra). *Journal of Ornithology*, **146,** 14-23.

Nickel, H. (2003) *The Leafhoppers and Planthoppers of Germany (Hemiptera, Auchenorrhyncha): Patterns and strategies in a highly diverse group of phytophagous insects*. Pensoft.

Nicolson, S.W. & Human, H. (2012) Chemical composition of the 'low quality' pollen of sunflower (Helianthus annuus, Asteraceae). *Apidologie*, **44,** 144-152.

Noordijk, J., Delille, K., Schaffers, A.P. & Sýkora, K.V. (2009) Optimizing grassland management for flower-visiting insects in roadside verges. *Biological Conservation*, **142,** 2097-2103.

OAN (2009) Projets de mise en réseau selon l'ordonnance sur la qualité écologique Directives cantonales l'ordonnance sur la préservation des bases naturelles de la vie et des paysage (OPBNP). pp. 1-17. Office de l'agriculture et de la nature du canton de Berne, Bern, Switzerland.

Öckinger, E. & Smith, H.G. (2007) Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, **44,** 50-59.

Schaub, M., Martinez, N., Tagmann-Ioset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi, F., Zbinden, N., Jenni, L. & Arlettaz, R. (2010) Patches of Bare Ground as a Staple Commodity for Declining Ground-Foraging Insectivorous Farmland Birds. *PLoS ONE*, **5,** e13115 (13115 pages).

Veddeler, D., Klein, A.-M. & Tscharntke, T. (2006) Contrasting responses of bee communities to coffee flowering at different spatial scales. *Oikos*, **112,** 594-601.

Veen, P., Jefferson, R., Smidt, J.d. & Straaten, J.v.d. (2009) *Grasslands in Europe of high nature value.* KNNV Publishing, Zeist, the Netherlands.

Whittingham, M.J. (2011) The future of agri-environment schemes: biodiversity gains and ecosystem service delivery? *Journal of Applied Ecology*, **48,** 509-513.

Woodcock, B.A., Vogiatzakis, I.N., Westbury, D.B., Lawson, C.S., Edwards, A.R., Brook, A.J., Harris, S.J., Lock, K.A., Maczey, N., Masters, G., Brown, V.K. & Mortimer, S.R. (2010) The role of management and landscape context in the restoration of grassland phytophagous beetles. *Journal of Applied Ecology*, **47,** 366-376.

Acknowledgments

First of all, I would like to thank my two supervisors Raphaël Arlettaz and Jean-Yves Humbert for giving me the opportunity to do this exciting thesis. Thanks for your great support, your advice, your continued patience and the time you spent with me to make this project a reality.

I am grateful to Teja Tscharntke, Louis-Félix Bersier and Heinz Richner for accepting to be members of the evaluation committee of this thesis. I am also thankful to Markus Fischer and Jérôme Pellet for their contribution in the project proposal.

I would like to thank all the members of the project accompanying committee for their support and the interest they demonstrated regarding this thesis. This project would have not been possible without the technical and/or financial support of Swiss National Science Foundation (No. 31003A_125398/1), the Federal Office of Environment, the Federal Office of Agriculture and the following cantonal offices of environment and/or agriculture: Bern, Vaud, Basel-Landschaft, Aargau, Neuchâtel, Fribourg, Valais and Graubünden.

I express also my gratitude to Eva Knop, Martin H. Entling, Dirk Sanders and the other members of the Community Ecology Divison (Unibe) for their technical support. I am grateful to Jean-François Burri, Sabine Oertli, Gernot Kunz, Marzena Stanka and Izabela Hajdamowicz for their help with the identification of the samples collected.

I thank also Nadia Bianco, Laura Bruppacher, Franck Gandiaga, Franziska Hoffet, Denise Karp, Isabel Kühne, Nastassja Rieder, Tobias Schmid, Eléonore Tran, Judith Wunderlin, Stefan Zahnd and all the people who took an active part in the success of this thesis.

Thanks to the farmers who collaborated in this project, allowing us to work in their fields and applying the management we prescribed. Without their participation, none of experiments could have taken place.

My deepest gratitude gets to my family for the unfailing support, which allows me to focus on my thesis in good conditions.

Last but not least, I would like to thank all the people met inside and outside of academia who have done the time spent in Bern enjoyable and friendly.

Erklärung

gemäss Art. 28 Abs. 2 RSL 05

Name/Vorname:	**Buri Pierrick**
Matrikelnummer:	**03-403-490**
Studiengang:	**Phil.-nat. Ökologie und Evolution**
	Bachelor ☐ Master ☐ Dissertation ☐
Titel der Arbeit:	**Designing tomorrow's farmland: alternative mowing regimes for promoting biodiversity in extensively managed meadowland**
Leiter der Arbeit:	**Prof. Dr. R. Arlettaz** **Dr. Jean-Yves Humbert**

Ich erkläre hiermit, dass ich diese Arbeit selbständig verfasst und keine anderen als die angegebenen Quellen benutzt habe. Alle Stellen, die wörtlich oder sinngemäss aus Quellen entnommen wurden, habe ich als solche gekennzeichnet. Mir ist bekannt, dass andernfalls der Senat gemäss Artikel 36 Absatz 1 Buchstabe o des Gesetztes vom 5. September 1996 über die Universität zum Entzug des auf Grund dieser Arbeit verliehenen Titels berechtigt ist.

Bern, ……………………………………………

Ort/Datum

……………………………………………

Unterschrift

Curriculum Vitae

Name: Pierrick Buri

Address: La Tuilière B
CH - 1142 Pampigny

eMail: pierrick_buri@hotmail.ch

Date of birth: 22nd March 1983 (in Lausanne, Switzerland)

EDUCATION

2010-present University of Bern, Switzerland, Institute for Ecology and Evolution, Conservation Biology. PhD thesis: *Designing tomorrow's farmland: alternative mowing regimes for promoting biodiversity in extensively managed meadowland*

2007 – 2009 University of Lausanne, Master of Science in Biology, Evolution and Conservation Biology (BEC) at the Department of Ecology and Evolution, thesis: "Wood ant behavioural and chemical defences against predatory mites" at the Department of Ecology and Evolution, University of Lausanne, Switzerland; Supervisor: Dr Michel Chapuisat

2003 – 2007 University of Lausanne
Bachelor of Science in Biology

1999 – 2002 Gymnase de Morges
Maturité gymnasiale (Matura), Major: Biology and Chemistry

1994 – 1999 Secondary cycles
Beausobre School, Morges, Section Mathematics

1989 – 1994 First cycles
Apples – Bière School

Positions held

2009 **Internship**
Ecole d'ingénieurs de Lullier (GE), filière gestion de la Nature (University of applied technologies, canton of Geneva, Wildlife management Division), project of translocation out of the Canton of Geneva and monitoring of common hares in Haute-Savoie (74), France, supervised by Dr Claude Fischer

2009 **Field assistant**
Dr Luca Fumagalli (University of Lausanne) and Dr Jérome Pellet (A. Maibach Sàrl, Wildlife consulting firm), for the project "Detecting

hybridization between native Triturus cristatus and the introduced species T. carnifex in western Switzerland”

2008 – 2009 **Field assistant**
City of Lausanne (Switzerland) and A. Maibach Sàrl, Wildlife consulting firm, for the project “Suivi des migrations de batraciens dans le Jorat lausannois” (Amphibian migratory road survey in the Jorat woods)

List of publications

2012 Humbert J.-Y., Pellet J., **Buri P.,** Arlettaz R., 2012. Does delaying the first mowing date benefit biodiversity in meadowland? *Environmental Evidence* 1, 1-9.

2011 Pellissier L., Wassef J., Bilat J., Brazzola G., **Buri P.**, Colliard C., Fournier B., Hausser J., Yannic G., Perrin N., 2011. Adaptive colour polymorphism of *Acrida ungarica* H. (Orthoptera: Acrididae) in a spatially heterogeneous environment. *Acta Oecologica* 37(2), 93-98.

Reber A., Purcell J., Buechel S.D., **Buri P.**, Chapuisat M., 2011. The expression and impact of antifungal grooming in ants. *Journal of Evolutionary Biology* 24(5), 954-964.

Position held during civilian service

2011 **Lab technican**
Zoological Institute at the University of Basel, DNA amplification, sequencing and analyses of micro-satellites of Graylings (*Thymallus thymallus*). Supervised by Prof Dr Walter Salzburger

2010 **Assistant scientifique et à l’animation à la Maison de la Rivière**
Field assistant for the foundation *Maison de la Rivière*, electrofishing and to scalimetry, Supervised by Dr Jean-François Rubin

Prices and awards

2009 **Honorary Certificate**
from the school of Biology, University of Lausanne, for the participation beyond expectation in student activities as member of the committee of the Association of Biology Students (LAB)

2002 **Alexandre Yersin Price**
from the society of the” Vieux-Stelliens”, Switzerland, for the results obtained in fundamental sciences at the “Maturité fédérale”

Teaching experience

2011	**Teaching assistant for "Programming and Data Analysis with R"** University of Bern for students in 2nd year of Bachelor in Biology
2010-2013	**Teaching assistant for Field Practical Conservation Biology** University of Bern for students in 2nd and 3rd year of Bachelor in Biology
2007 – 2008	**Amphibian Field excursions** for sutdents in Bachelor of Biology, University of Lausanne
2008	**Teaching assistant for Botany practicals** for sutdents in 1st year of Bachelor in Biology and for students in 1st year of Bachelor in Pharmacology, University of Lausanne

---

Oral presentations

2013	**University of Siedlce** (Poland, seminar of the Institute of Natural Sciences) Buri P. Humbert J.-Y., Arlettaz R. Reaction of diverse taxa to changes in mowing regimes within extensively managed meadows after three years of experimentation
2012	**Symposium in ecology and evolution for doctoral students** (SeeDs, University of Bern, Switzerland) Buri P., Rieder N.R., Humbert J.-Y., Arlettaz R. Changes in mowing regimes within extensively managed meadows boost the abundance of wild bees (Hymenoptera: Apoidea)
	3rd European Conference of Conservation Biology (Glasgow, UK) Buri P. Rieder N.R., Humbert J.-Y., Arlettaz R. Changes in mowing regimes of extensively managed meadows boost the abundance of wild bees (Hymenoptera: Apoidea)
	13th Student conference in Conservation Sciences (University of Cambridge, UK) Buri P., Rieder N.R., Humbert J.-Y., Arlettaz R. When to mow a meadow? Impacts on wild bee pollinators
	Biology12 (University of Fribourg, Switzerland) Buri P., Rieder N.R., Humbert J.-Y., Arlettaz R. Temporal changes in mowing regimes of extensively managed meadows boost the abundance of wild bee pollinators (Hymenoptera: Apoidea)

Poster

2013	***Colloque Abeilles sous haute surveillance*** (Botanical Garden of Neuchâtel, Switzerland) Buri P. Humbert J.-Y., Arlettaz R. Promotion des pollinisateurs dans les prairies : différents régimes de fauches et leurs effets sur les abeilles