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Relative importance of management and natural flooding on spider, carabid and plant assemblages in extensively used grasslands along the Loire

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Abstract

In Europe, agri-environment schemes (AES) have been implemented to counteract the effects of agricultural intensification. Studies investigating the role of management improvement induced by AES are quite numerous, but rarely take into account the effect of natural perturbations such as flooding, although severe disturbances are well known to shape community structure. Here we investigated the relative importance of management improvement and flooding to explain community parameters of two dominant arthropod groups and vegetation in alluvial meadows. Sampling took place in 2013, using suction samplers for arthropods and phytosociological relevés for vegetation, in 83 meadows distributed along 200 km of the Loire Valley (France). Pair-matched approach (by R-ANOVA) was used to assess overall effects of AES whereas a gradient analysis (GLM) was carried out to assess the impact of AES prescriptions (fertilisation and cutting-date) together with indirect (long-term) and direct (short-term) effects of flooding. No significant effect of AES was found on arthropod and plant assemblages, abundance/productivity or diversity (both $\alpha$ and $\beta$), but the number of rare plant species was higher in sites under AES. Prescriptions had little impact on most response variables considered; the only significant impact being the positive effect of high-amounts of fertilisers on spider $\alpha$- and $\beta$- diversities. Conversely, systematic long-term effects of flooding were found on all response variables of spiders, carabids and plants, underlining the key role of this factor in alluvial meadows. Our study demonstrates that maintaining or enhancing hydrological functioning of ecosystems is even more important than regulating both the cutting-dates and the low input of fertilisers for conservation purposes in flooded, already naturally nutrient rich, meadows.

Keywords: Coleoptera Carabidae, Araneae, stochastic disturbance, cutting-date, fertilizers.
Introduction

Over the last decades, agricultural intensification has accelerated adverse effects on wildlife (Millennium Ecosystem Assessment 2005). In Europe, agri-environment schemes (AES) have been implemented to counteract these effects by providing financial incentive for farmers to adopt extensive agricultural practices. Farmers involved in AES preferentially engage fields which are less suitable for intensive farming (Kleijn & van Zuijlen, 2004), explaining why semi-natural grasslands are especially targeted by AES.

Investments in AES were substantial, with for example 34.9 billion Euros provided for 2007-2013 programmes (COM, 2008). They currently cover 21% of all farmlands in the 27 EU countries. Despite these high financial inputs, AES seem to have contrasting successes (Kleijn et al., 2006), depending on the AES type and the model studied. For example, AES are recognised to have positive effects on birds in the UK (Brereton, Warren, Roy, & Stewart, 2007) and on pollinators in Switzerland (Albrecht, Duelli, Muller, Kleijn, & Schmid, 2007). However, AES also prove damaging when poorly designed or when targeting single taxon (Konvicka et al., 2007). Results on plant diversity are usually reported to be positive (e.g., Kleijn, Berendse, Smit, & Gilissen, 2001; Critchley, Walker, Pywell, & Stevenson, 2007). Monitoring and evaluating these schemes is imperative to improve their efficiency and maximize the conservation outcomes.

Evaluation of AES impact has usually focused on birds (Kleijn, Berendse, Smit, & Gilissen, 2001, Kleijn et al., 2006; Marshall, West, & Kleijn, 2006) and vegetation (Critchley, Walker, Pywell, & Stevenson, 2007) mainly because they are the main targets of AES as arthropods are often neglected in biodiversity conservation policies (e.g., Cardoso, Erwin, Borges, & New, 2011). Nevertheless, some studies also dealt with arthropods- mainly bees and grasshoppers (Kleijn, Berendse, Smit, & Gilissen, 2001; Knop, Kleijn, Herzog, & Schmid, 2005), and found positive effects of AES. Despite
their recognised indicator value in agricultural landscapes, predator arthropods like spiders and
carabid beetles remain relatively less studied in the context of AES compared to other taxa.

Flooding is a key driver of intertidal and riparian ecosystems, and particularly of arthropod
communities (Desender & Maelfait, 1999) and vegetation (Violle et al., 2011). Arthropod
communities of European rivers are likely to use a ‘risk strategy’ to survive in this naturally
disturbed habitat. The strategy consists of a suite of life history traits such as high productivity (‘r-
strategy’), high capacity for dispersion, and active recolonisation from areas that have been
sheltered from flooding (Zulka, 1994). Vertical emigration to uplands or higher vegetation is also
expected to increase recolonisation success (Adis & Junk, 2002). A few terrestrial species also
withstand short to prolonged (up to several weeks) periods of submersion (e.g., insects: Hoback &
Stanley, 2001, spiders: Pétillon et al., 2009). Conversely, flood events can be seen as a way to
colonise new habitats and exchange individuals between distant populations (Lambeets et al.,
2010), possibly enhancing among-site diversity in the long term. In the short-term, flood events
strongly reduce local diversity. Floodplains are generally characterized by a low percentage of
stenotopic species (Lafage, Papin, Secondi, Canard, & Pétillon, 2015). Specialist species with
adaptations to flooding are found in more regularly flooded habitats like gravel banks (Lambeets,
Vandegehuchte, Maelfait, & Bonte, 2008) or salt marshes (Pétillon, Potier, Carpentier & Garbutt,
2014).

No study has assessed the relative effects of AES vs. stochastic disturbances induced by flooding in
such ecosystems, yet their expected effects on biodiversity are potentially opposite. Consequently,
no or few effects of AES in shaping arthropod and plant assemblages are expected in floodplains.

To test this hypothesis, we evaluated the role of AES and flooding in explaining α and β diversities,
abundances (biomass for plants), species rarity and assemblage composition of two non-target
groups (spiders and carabids) and vegetation in the flooded meadows of the Loire River (France).

For spiders and carabids, analyses of rarity were not performed because of the lack of proper...
national or regional statuses of rarity (the English classification cannot be applied here: Pétillon, Courtial, Canard, & Ysnel, 2007), and also because the number of stenotopic and/or rare species is low in these habitats (Lafage, Papin, Secondi, Canard, & Pétillon, 2015).

Material and methods

Study area and sampling design

The study area covered 200 km of the Loire Valley (France: Fig. 1). Land is mainly covered by hay meadows with an extensive hedgerow network. Meadows are usually cut in early or mid-summer with second-crop grazing. The amount of fertilisers is generally low as regular winter and spring floods bring a large amount of organic matter into the system. Pesticides are seldom used. Thus, the management intensity is rather low. The study site included four AES zones with various prescriptions regarding cutting-dates and fertilizers. Cutting-dates were between June 5th to July 20th, within four defined classes: free (not under AES), before June 20th, between June 20th and July 1st, after July 1st. Fertiliser prescriptions were 0, 30 or 60 N unit/ha. A 'free' class was added for sites not under AES. Almost all meadows are flooded during winter for about 3 months, but in 2012 and 2013, the study sites were also flooded during spring for 5 to 22 days. Spring-flood had not occurred since 2004 in the Loire Valley.

Carabids, spiders and plants were sampled in 83 hay meadows. To reduce the variance between fields, a paired-matched approach was used to test the impact of AES (see statistical analysis section). Paired sites (with and without AES contract) were chosen with same vegetation types and flooding regime. Distance between sites belonging to a pair was inferior to 1 km. Table 1 summarizes the number of sites per treatment and moisture level. Site size ranged from 1.3 ha to 265.3 ha (mean = 34.7 ± 50.3 SD ha).
Carabids and spiders were sampled using suction sampling (a standard technique providing quantitative data, i.e. abundance of individuals, on arthropods: Brook, Woodcock, Sinka, and Vanbergen, 2008). Each site was sampled once during June 2015 before the first cutting date- given the strong impact of cutting on spiders and carabids (e.g., Lafage & Pétillon 2014). Suction sampling was realised using a 12.5 cm diameter intake placed on the ground. At each sampling site, 5 samples (10 x 15 s suctions) were taken (total area: 0.12 m²/sample). Samples were stored in 70% alcohol and taken to the laboratory for sorting and identification to species level.

At each site, plants were sampled once during spring 2013 (from June 1st 2013 to July 10th 2013, before the first cutting date). Sampling followed the Braun-Blanquet (1928) method. One phytosociological relevé per sampling site was made in a 16 m² plot. Vegetation biomass was approximated using a vegetation index derived from MODIS satellite imagery: the Enhanced Vegetation Index (EVI: Lafage, Secondi, Georges, Bouzillé, & Pétillon, 2014) measured during 16 days by LP DAAC (product MOD13Q1).

Statistical analysis

Spatial autocorrelation, tested using Moran's I, was low enough (see Appendix A, table 1) to be neglected (Gerisch, Dziock, Schanowski, Ilg, & Henle, 2012). Spatial patterns in response variables were also researched using Moran’s eigenvector maps (MEM) following Borcard, Gillet, and Legendre (2011), but they were not significant (see Appendix A, table 2).

Arthropod α-diversities were estimated for each sampling site using the average of four non-parametric estimators based on species incidence: Chao1, Jacknife1, Jacknife2 and Bootstrap (Carvalho et al. 2012). β-diversity was estimated through a dissimilarity matrix (corresponding to Sørensen pair-wise dissimilarity) partitioned into its two components -species turnover (βt) and nestedness (βn)- following Baselga (2010) and using the betapart R package (Baselga & Orme...
Vegetation diversity was estimated by the classical Shannon index. Plant rarity was estimated using the number of plants red-listed at either national or regional scale per sample. As no red list exists for spiders and carabids in France, analyses on arthropod rarity were not performed.

A paired-sample approach (with or without AES) was used to test the overall AES effect on abundance/productivity, α-diversity, β-diversity and rarity (plants) of arthropods and plants.

Repeated analyses of variance (R-ANOVA) with site as the within-subjects factor (e.g., Varet, Burel, Lafage & Pétillon, 2013) and AES presence/absence as a fixed factor were performed between paired sites presenting similar abiotic conditions (see similar designs in previous studies on AES efficiency: Knop, Kleijn, Herzog, & Schmid, 2005; Kleijn et al. 2006; Scheper et al. 2013).

To test for differences in spider, carabid and plant assemblages between sites under AES and sites not under AES, analyses of variance (ANOSIM) were performed.

To test for differences in β-diversities among groups (i.e., between sites under AES and not under AES), multiple-site dissimilarity matrices were computed using the betapart package for R (Baselga & Orme 2012) and the Simpson dissimilarity index. We then performed a re-sampling procedure in the β-diversity matrix (50 pairs of sites were randomly sampled 50 times) to perform multiple comparison tests.

To investigate arthropod and plant responses to management and flooding, drivers of species assemblages were investigated using constrained analysis. The choice between redundancy analysis (RDA) and constrained correspondence analysis (CCA) was made according to the axis length of a detrended correspondence analysis (DCA). Abundances of all species (for arthropods) and Braun-Blanquet coefficients of abundance (for plants) were the response variables. The cutting-date (four classes), fertiliser input (three levels), a variable describing whether or not the site had been flooded during spring 2013 (i.e., binary variable for short-term effects of flooding), and a moisture gradient (i.e., discrete variable for long-term effects of flooding) were predictors. Five moisture classes were...
defined from low (1) to very high (5) according to the mean Ellenberg indicator value (Ellenberg et al., 1992) of each vegetation type (defined by a Two-Way Indicator Species Analysis). Class 1 corresponded to sites with mean Ellenberg value lower the 5 (mean=4.6), class 2 to sites with 5<Ellenberg value< 6 (mean=5.4), class 3 to sites with 6<Ellenberg value<7 (mean=6.4), class 4 to sites with 7<Ellenberg value<8 (mean=7.5) and class 5 to sites with Ellenberg value higher than 8 (mean=8.3). Monte Carlo tests with 999 permutations were carried out to test the significance of the selected environmental factors and constrained analyses axes.

Responses of arthropod and plant $\alpha$-diversities, and abundances and vegetation productivity to both the cutting-date (four classes) and fertiliser input (three levels) were tested using Generalised Linear Models (GLMs) with gaussian distribution and a stepwise model selection by AIC (Akaike, 1974). Flooding (i.e., binary variable for short-term effects of flooding) and moisture (five classes) variables were also included. As flooding was expected to influence both the effects of the cutting-date and of fertiliser amounts, interactions between those variables were also included. The same GLM were applied to explain plant rarity. Pairwise-t-test were relaisised to compare means of response variables depending on significant factors by GLM.

To identify the variables significantly influencing arthropod and plant $\beta$-diversities, similarity matrices corresponding to species turnover were regressed against environmental variables using the Canonical Analysis of Principal Coordinates (CAP) implemented in the vegan package for R (Oksanen et al. 2013). The model included the same explanatory variables as previous GLMs.

Statistical analyses were performed using R software (R Development Core team 2013) with vegan (Oksanen et al., 2013), MASS (Venables & Ripley 2002) and PCNM packages (Legendre, Borcard, Blanchet, & Dray, 2013).
Results

A total of 6,036 spiders belonging to 97 species (see Appendix A, Table 3 for a detailed list of species), 383 carabids (see Appendix A, Table 4 for a detailed list of species) belonging to 43 species, and 150 plant species (see Appendix A, Table 5 for a detailed list of species), 3 of them being red-listed, were sampled. Spider and carabid assemblages were dominated by small aerial dispersers: 78% of spiders were Linyphiidae and 78% of carabids were small winged species. Spider assemblages were dominated by six linyphiid species *Tenuiphantes tenuis* (29.4% of individuals), *Meioneta rurestris* (7.0%), *Erigone dentipalplis* (4.8%), *Bathyphantes gracilis* (4.8%), *Oedothorax fuscus* (4.4%) and *Meioneta mollis* (4.2%). Carabid assemblages were dominated by two harpaline species (*Acupalpus exiguus*: 51.0% and *Syntomus obscuroguttatus*: 15.4%) and one bembidiine species (*Bembidion biguttatus*: 7.8%). Plant assemblages were more balanced with ten species cumulatively covering 35%, with a frequency ranging from 6.1% (*Lolium perenne*) to 2.3% (*Plantago lanceolata*).

Spider β-diversity was 0.97, corresponding to βₜ = 0.95 and βₙ = 0.02. Carabid β-diversity was 0.95, corresponding to βₜ = 0.92 and βₙ = 0.03. Plant β-diversity was 0.96, corresponding to βₜ = 0.95 βₙ = 0.01. βₙ of the three groups was thus considered negligible and was not included in further analyses.

Repeated ANOVAs revealed no significant effect of AES, site, or of the interaction between AES and site on estimated α-diversity and abundance of spiders and carabids, or on plant productivity and α-diversity (Table 2). A significant difference was found for plant rarity (Table 2), the number of rare plants being higher in sites under AES. No significant difference was found between assemblages of sites under AES vs. sites not under AES for spiders (R=0.011, P=0.365), carabids (R=0.008, P=0.347) or plants (R=-0.039, P=0.879). No significant difference was found between β-
diversity of sites under vs. not under AES for spiders ($\chi^2=49, P=0.473$), carabids ($\chi^2=45.60, P=0.555$) or plants ($\chi^2=46.74, P=0.625$).

CCA on spider assemblages was significant ($F=1.61, P=0.048$) and explained 55.5% of the total variance, with the first three axes of the CCA being significant (respectively $P=0.005$; $P=0.020$ and $P=0.020$). Axis 1 and 3 were associated with moisture index and axis 2 with cutting date but the only variable significantly explaining spider species composition was moisture ($F=1.67, P=0.050$) (Fig. 2).

RDA on carabid assemblages was not significant ($F=0.98, P=0.430$). RDA on plant assemblages was significant ($F=1.58, P=0.005$) and explained 66.3% of the total variance, with the first three axes of the RDA being significant (respectively $P=0.005$; $P=0.015$ and $P=0.005$). Cutting-date, occurrence of a spring flood in 2013 and moisture were the three variables significantly explaining species assemblages (respectively $F=1.99, P=0.010$; $F=1.64, P=0.010$; $F=2.89, P=0.010$).

In the GLMs performed on spider, carabid and plant $\alpha$ and $\beta$-diversities, abundance, and rarity, no interaction between flooding and prescriptions (i.e., fertiliser amount and cutting-date) were found, indicating that the impact of prescriptions, if any, was not influenced by flooding (Table 3).

Spider estimated $\alpha$-diversity was significantly influenced by fertiliser amount and moisture (Table 3). Sites under AES with 60 kg/ha nitrogen had higher estimated spider species richness (Fig. 3A). Sites with low moisture level (classes 1 and 3, i.e. with less frequent floods) presented higher estimated spider species richness than sites with very high moisture level (class 5) (Fig. 3B). Spider abundance was significantly affected by fertilisation but post-hoc tests were not significant (Table 3 and Fig. 3C).

Spider $\beta$-diversity was significantly influenced by fertiliser amount and cutting-date (Table 3 and Fig. 3D and 3E). Spider mean $\beta$-diversity increased with increasing fertiliser amount, with the mean $\beta$-diversity being maximal with 60 kg/ha and free fertilisation. An opposite response was
found for the cutting-date: mean $\beta$-diversity was lower with later cutting dates and was maximal in fields not under AES.

Carabid estimated $\alpha$-diversity was not influenced by predictive variables. Carabid abundance was significantly influenced by moisture (Table 3), with higher carabid abundances in sites presenting very high moisture level (class 5) (Fig. 3F).

Carabid $\beta$-diversity was significantly influenced by the occurrence of a flooding in spring 2013, with the mean $\beta$-diversity being higher in fields that were not flooded during spring 2013 (Fig. 3G).

Plant $\alpha$-diversity was significantly influenced by moisture (Table 3). Plant $\alpha$-diversity of sites with a high moisture level (Class 5) was significantly lower than those with a lower moisture level (class 1: Fig. 3H). Plant biomass (EVI) was significantly and positively impacted by moisture. Higher EVI was found in moister sites, although differences among means were not significant. Fertiliser amount, cutting-date, flooding, and moisture all had a significant effect on plant $\beta$-diversity (Table 3) but no significant effect of fertiliser amount and cutting-date were found when comparing mean $\beta$-diversity between classes (Fig. 3I, 3J). Plant rarity was significantly impacted by moisture, with a higher number of rare plants in moister sites (Table 3 and Fig. 3K).

Discussion

Overall, our results demonstrated no significant impact of AES on $\alpha$-diversity, $\beta$-diversity, abundance / biomass and assemblages of the three groups studied in flooded meadows. A positive effect was still found on rare plants. The absence of differences between meadows with vs. meadows without AES is in accordance with some previous studies in non-flooded habitats that focussed on spiders (Knop, Kleijn, Herzog, & Schmid, 2005; Marshall, West, & Kleijn, 2006), carabids (Marshall, West, & Kleijn, 2006) and plants (Kleijn, Berendse, Smit, & Gilissen, 2001);
However, the existence of different levels in AES prescriptions could potentially lower the impact of the most binding AES. Furthermore, meadows not under AES remain rather extensively managed. It is thus possible that AES prescriptions do not constitute a sufficient change in practices to have a detectable impact. The positive impact of AES contractualisation on protected plants might not be a consequence of a change in farmers’ practices. Indeed, farmers preferentially engage in AES fields which are less suitable for intensive farming (Kleijn & van Zuijlen, 2004). In our case, fields with higher moisture levels are preferentially engaged because soil bearing does not allow early cutting-dates. In the Loire Valley, most of the protected plants are hygrophilous and are thus located in the engaged fields. In a large-scale study, Kleijn et al. (2006) found no impact of AES on rare arthropods and plants, except for a positive one on plant rarity in two countries. Our results are partly in opposition but, like in Kleijn et al. (2006), the low number of rare species encountered prevents reliable estimates of AES impacts.

Spider assemblages and $\alpha$-diversity were significantly influenced by moisture which is in accordance with Desender and Maelfait (1999), Pétillon, Georges, Canard, Lefeuvre, Bakker and Ysnel (2008) and Lafage, Maugenest, Bouzillé, and Pétillon (2015). Cutting-date only influenced spider $\beta$-diversity. Cutting-date has recently been shown to have little impact on spider $\alpha$-diversity and abundance, but a significant impact on traits (Lafage & Pétillon 2014), suggesting a potential impact on $\beta$-diversity in accordance with our results.

We found spider $\beta$-diversity to decrease when cutting-dates were delayed. That could be explained by the fact that the engaged farmers have to cut their fields in a very narrow time-frame in order to maximise the nutritional value of hays (that decreases over time: Nocera, Parsons, Milton, & Fredeen, 2005). In fields not under AES, the diversity of cutting dates would oppositely increase the $\beta$-diversity of spiders.

As opposed to the biodiversity-productivity theory (Grime, 1973), sites fertilised with 60 kg/ha nitrogen supported highest spider $\alpha$-diversity. Sites not under AES were also not different from sites.
with medium or low nitrogen inputs. This is in accordance with studies suggesting a “bottom-up”
control of arthropod diversity (Siemann, 1998; Patrick, Fraser, & Kershner, 2008) mediated by plant
and consumer biomass (Borer, Seabloom, & Tilman, 2012). Nevertheless, these findings are still
being discussed as, for example, Haddad, Haarstad, and Tilman (2000) found insect diversity to be
negatively influenced by long-term fertiliser input. The lack of fertilisation effects on spider and
carabid abundances could be explained by a threshold effect. Fertiliser inputs remained low, even in
fields not under AES contract, compared to the large quantities of organic matter introduced in the
system by winter floods (Junk & Wantzen, 2004). Consequently, the fertiliser levels might remain
too low to initiate a trophic cascade which is confirmed by the absence of impact of fertilisers on
plant biomass and α-diversity (see below).

As expected, carabids were only influenced by spring floods and moisture, for β-diversity and
abundance respectively. Carabids have been shown to recover less rapidly than spiders after spring
floods (Lafage, Papin, Secondi, Canard, & Pétillon, 2015), especially regarding species
composition, which could explain the impact of spring floods on carabid β-diversity. Gerisch et al.
(2012) demonstrated that carabid β-diversity remains high after important flooding events,
indicating persistent shifts in species assemblages. Gerisch et al. (2012) and Lafage, Papin,
Secondi, Canard, and Pétillon (2015) finally show massive decreases in carabid abundance after
spring floods. This dominance of small species could first be attributed to a sampling effect,
although suction sampling is usually recommended to quickly obtain a representative sample of
epigeic arthropod communities (e.g. Duffey 1974). In fact, Mommertz, Schauer, Kösters, Lang, and
Filser (1996) considered it an inefficient way to sample large arthropods (such as Carabidae and
Lycosidae). However, Brook, Woodcock, Sinka, and Vanbergen (2008) considered suction sampling
an efficient technique to sample arthropods, including Carabidae, pending a sufficient sampling
effort. Here we performed sampling duration and replication higher than recommended by Brook,
Woodcock, Sinka, and Vanbergen (2008) for spiders (16x2s recommended vs 5x10x15s performed)
and slightly inferior than recommended by Brook, Woodcock, Sinka, and Vanbergen (2008) for beetles (54.8x15.6s recommended vs 5x10x15s performed) with similar sampling area. We can thus consider that our results were not biased by the sampling technique, and that the dominance of small aerial dispersers was a consequence of an environmental filter, here the stochasticity due to flooding (Zulka 1994).

Plant $\alpha$-diversity, $\beta$-diversity, biomass and assemblages were systematically influenced by flooding (i.e., moisture and occurrence of spring floods) because of both its large spatial extent (including both AES and non-AES meadows) and its duration (here several months). These results are in accordance with previous studies. The central role of moisture in shaping plant communities has indeed been demonstrated by many authors (e.g., Dwire, Kauffman, Brookshire, & Baham, 2004; Wassen, Peeters, & Olde Venterink, 2002; Zelnik & Čarni, 2008). Moisture’s role on plant diversity has also been demonstrated. For example, Zelnik and Čarni (2008) found plant $\alpha$ and $\beta$-diversities to be strongly and negatively influenced by moisture in wetlands. Plant rarity was also positively affected by moisture, which is not surprising as most plant species protected in the area are hygrophilous or meso-hydrophilous species.

Regarding AES prescriptions, cutting-date significantly influenced $\beta$-diversity and plant assemblages. Late cutting dates are indeed well known to induce vegetation modifications by favouring annual plant species; maximum plant $\alpha$-diversity being usually observed for late cutting-dates (mid-June to mid-July) in European grasslands (e.g. Critchley, Walker, Pywell, & Stevenson, 2007).

Fertilisation level had a significant impact only on plant $\beta$-diversity, which is in accordance with Klimek et al. (2008) who found plant species $\beta$-diversity being influenced, at a local scale, by fertilisation input. A significant reduction of $\alpha$-diversity and a biomass increase are usually observed even for low levels of fertilizers (e.g., Plantureux, Peeters, & Mccracken, 2005). Nevertheless, in flooded grasslands, no effect of fertilisation on plant diversity was reported under 90 kg/ha/yr.
(Bonis, Dausse, Dia, & Bouhnik-le Coz, 2008). Thus, the fertilisation level permitted in sites under AES and effectively used in sites not under AES, may be too low to allow a detection of their impact.

Our results suggest that flooding might be a stronger driver of vegetation and arthropod assemblages than differences in cutting dates or low fertilizer inputs. The impact of flooding and management practices seems to vary with organism mobility (Adis & Junk, 2002). Indeed, we found plants to be the organisms that are the most sensitive to perturbations induced by flooding, and also to variations in management practices. Conversely, carabid assemblages, mainly composed of highly mobile small species, were only influenced by flooding.

Our results further suggest that the regulation of cutting dates and low input fertilisers of grasslands has few, if any, effects on arthropods and plants compared to those induced by a prolonged flooding. Conservation actions in such ecosystems might have to focus on maintaining and/or enhancing hydrological functioning in order to rewild those ecosystems (Merckx & Pereira, 2014). Nevertheless, because natural meadows are in constant regression by conversion to intensive agriculture (Millennium Ecosystem Assessment 2005), AES can yet be considered an efficient way of maintaining an endangered habitat, despite their limited efficiency in flooded systems.

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"Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at XXXXX."
References


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Figure caption

Fig. 1. Location of the study sites in the Loire watershed (France). Grey surfaces indicate meadows and black dots correspond to the sampled meadows.


Fig. 3. Variations in mean response variables depending on significant factors by GLM (different successive letters indicate significant differences in means according to Tukey’s post-hoc tests with Bonferroni correction). (A) Mean estimated spider richness by fertiliser class (Free: not under AES). (B) Mean estimated spider richness by moisture gradient (1 to 5: increasing moisture gradient). (C) Spider abundance per 0.12m² by fertiliser class. (D): Spider mean β-diversity by...
fertiliser class. (E) Spider mean $\beta$-diversity by cutting date (Free: not under AES, CD1: before 20th June, CD2: between 20th June and 1st July, CD3: after 1st July). (F) Carabid abundance by moisture gradient. (G) Carabid mean $\beta$-diversity by flooding (Yes: sites flooded during summer 2013, No: sites not flooded). (H) Plant Shannon Index by moisture gradient. (I) Plant mean $\beta$-diversity by flooding. (J) Plant mean $\beta$-diversity by moisture gradient. (K) Number of rare plant species by moisture gradient. The horizontal bar in box-plots indicates the median, the ends of the boxes indicate the interquartile range, and the whiskers indicate the 10th and 90th quantiles.
Figure 1. Lafage and Pétillon, 2015
Figure 2: Lafage and Pétillon, 2015
Figure 3: Lafage and Pétillon, 2015
Table 1. Number of sites per class. Contract: whether or not sites are under AES contract; Fertilisers: classes of fertiliser input allowed in kg/Ha; Cutting date: classes of cutting dates (Free: not under AES, CD1: before 20th June, CD2: between 20th June and CD3: 1st July, after 1st July); Flooding: whether or not site has been flooded during summer 2013; Moisture: classes of Ellenberg indicator value for moisture from low (1) to very high (5).

<table>
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<tr>
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<td>15</td>
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<td>4</td>
<td>27</td>
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<td>5</td>
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Table 2. Per site means ± s.e. of response variables for fields under AES or not (Free), with F and P values for fixed factor (contract), within-subject factor (site) and their interaction (R-ANOVA).

Abundance: total number of individuals per 0.12m². Estimated species richness: average of four non-parametric estimators based on species incidence: Chao1, Jacknife1, Jacknife2 and Bootstrap.

<table>
<thead>
<tr>
<th></th>
<th>AES Mean ± s.e.</th>
<th>Free Mean ± s.e.</th>
<th>Contract F</th>
<th>Free P</th>
<th>Site F</th>
<th>Free P</th>
<th>AES Interaction F</th>
<th>Free P</th>
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<tbody>
<tr>
<td><strong>Spiders</strong></td>
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<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abundance</td>
<td>2.24 ± 1.84</td>
<td>1.83 ± 1.19</td>
<td>0.96</td>
<td>0.338</td>
<td>2.12</td>
<td>0.158</td>
<td>0.04</td>
<td>0.838</td>
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<tr>
<td>Estimated species richness</td>
<td>14.74 ± 7.14</td>
<td>10.50 ± 3.97</td>
<td>3.98</td>
<td>0.060</td>
<td>0.24</td>
<td>0.630</td>
<td>0.143</td>
<td>0.709</td>
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<td><strong>Carabids</strong></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Abundance</td>
<td>1.02 ± 1.01</td>
<td>1.64 ± 1.47</td>
<td>1.53</td>
<td>0.228</td>
<td>0.06</td>
<td>0.804</td>
<td>0.05</td>
<td>0.833</td>
</tr>
<tr>
<td>Estimated species richness</td>
<td>2.08 ± 2.40</td>
<td>3.45 ± 3.46</td>
<td>1.13</td>
<td>0.298</td>
<td>2.47</td>
<td>0.129</td>
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<td>0.760</td>
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<td><strong>Plants</strong></td>
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<td></td>
</tr>
<tr>
<td>Shannon Index</td>
<td>2.15 ± 0.42</td>
<td>2.24 ± 0.37</td>
<td>0.19</td>
<td>0.667</td>
<td>2.08</td>
<td>0.162</td>
<td>0.02</td>
<td>0.883</td>
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<tr>
<td>EVI</td>
<td>5366 ± 1187</td>
<td>5135 ± 1097</td>
<td>0.31</td>
<td>0.594</td>
<td>0.29</td>
<td>0.594</td>
<td>1.43</td>
<td>0.243</td>
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<tr>
<td>Rarity</td>
<td>4.73 ± 2.81</td>
<td>2.06 ± 1.98</td>
<td>9</td>
<td>9</td>
<td>7</td>
<td>4</td>
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</table>
Table 3. GLM selected by stepwise procedure for spider, carabid and plant abundance / biomass (approximated by EVI index), estimated richness ($\alpha$-diversity), $\beta$-diversity, and rarity (for plants only).

<table>
<thead>
<tr>
<th>Group</th>
<th>Response</th>
<th>Estimated species richness ($\alpha$-diversity)</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spiders</td>
<td>Fertilisers</td>
<td>4.28</td>
<td>0.008</td>
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<tr>
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<td>Moisture</td>
<td>4.45</td>
<td>0.003</td>
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<tr>
<td></td>
<td>F x VT</td>
<td>1.92</td>
<td>0.101</td>
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<tr>
<td>Abundance</td>
<td>Fertilisers</td>
<td>3.33</td>
<td>0.024</td>
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<td>Moisture</td>
<td>1.75</td>
<td>0.150</td>
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<tr>
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<td>F x VT</td>
<td>1.99</td>
<td>0.090</td>
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<tr>
<td>$\beta$-diversity</td>
<td>Fertilisers</td>
<td>1.59</td>
<td>0.020</td>
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<tr>
<td></td>
<td>Cutting date</td>
<td>1.69</td>
<td>0.020</td>
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</tbody>
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<table>
<thead>
<tr>
<th>Group</th>
<th>Response</th>
<th>Estimated species richness ($\alpha$-diversity)</th>
<th>F</th>
<th>P</th>
</tr>
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<tbody>
<tr>
<td>Carabids</td>
<td>Fertilisers</td>
<td>1.16</td>
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<td>$\beta$-diversity</td>
<td>Flooding</td>
<td>1.03</td>
<td>0.010</td>
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<tr>
<td>Plants</td>
<td>Shannon Index (α-diversity)</td>
<td>Cutting date</td>
<td>0.03</td>
<td>0.993</td>
</tr>
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<tr>
<td></td>
<td>Fertilisers</td>
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<td>Moisture</td>
<td>7.47</td>
<td>&lt;0.001</td>
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<tr>
<td>EVI</td>
<td>Cutting date</td>
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<td>0.993</td>
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<tr>
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<td>Fertilisers</td>
<td>1.21</td>
<td>0.303</td>
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<td>Moisture</td>
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<td>2.35</td>
<td>0.010</td>
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