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

38

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50 Abstract

51

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

72

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

74 **Introduction**

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

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

91 Evaluation of AES impact has usually focused on birds (Kleijn, Berendse, Smit, & Gilissen, 2001,
 92 Kleijn et al., 2006; Marshall, West, & Kleijn, 2006) and vegetation (Critchley, Walker, Pywell, &
 93 Stevenson, 2007) mainly because they are the main targets of AES as arthropods are often neglected
 94 in biodiversity conservation policies (e.g., Cardoso, Erwin, Borges, & New, 2011). Nevertheless,
 95 some studies also dealt with arthropods- mainly bees and grasshoppers (Kleijn, Berendse, Smit, &
 96 Gilissen, 2001; Knop, Kleijn, Herzog, & Schmid, 2005), and found positive effects of AES. Despite

97 their recognised indicator value in agricultural landscapes, predator arthropods like spiders and
 98 carabid beetles remain relatively less studied in the context of AES compared to other taxa.

99 Flooding is a key driver of intertidal and riparian ecosystems, and particularly of arthropod
 100 communities (Desender & Maelfait, 1999) and vegetation (Violle et al., 2011). Arthropod
 101 communities of European rivers are likely to use a ‘risk strategy’ to survive in this naturally
 102 disturbed habitat. The strategy consists of a suite of life history traits such as high productivity (‘r-
 103 strategy’), high capacity for dispersion, and active recolonisation from areas that have been
 104 sheltered from flooding (Zulka, 1994). Vertical emigration to uplands or higher vegetation is also
 105 expected to increase recolonisation success (Adis & Junk, 2002). A few terrestrial species also
 106 withstand short to prolonged (up to several weeks) periods of submersion (e.g., insects: Hoback &
 107 Stanley, 2001, spiders: Pétillon et al., 2009). Conversely, flood events can be seen as a way to
 108 colonise new habitats and exchange individuals between distant populations (Lambeets et al.,
 109 2010), possibly enhancing among-site diversity in the long term. In the short-term, flood events
 110 strongly reduce local diversity. Floodplains are generally characterized by a low percentage of
 111 stenotopic species (Lafage, Papin, Secondi, Canard, & Pétillon, 2015). Specialist species with
 112 adaptations to flooding are found in more regularly flooded habitats like gravel banks (Lambeets,
 113 Vandegheuchte, Maelfait, & Bonte, 2008) or salt marshes (Pétillon, Potier, Carpentier & Garbutt,
 114 2014).

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

118 To test this hypothesis, we evaluated the role of AES and flooding in explaining α and β diversities,
 119 abundances (biomass for plants), species rarity and assemblage composition of two non-target
 120 groups (spiders and carabids) and vegetation in the flooded meadows of the Loire River (France).
 121 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).

125

126 **Material and methods**

127 *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, Dziok, 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, Jackknife1, Jackknife2 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 (β_t) and nestedness (β_n)- following Baselga (2010) and using the betapart R package (Baselga & Orme

2012). 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 & Pétilion, 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 than 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 α -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 realised to compare means of response variables depending on significant factors by GLM.

To identify the variables significantly influencing arthropod and plant β -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).

217 Results

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

230 Spider β -diversity was 0.97, corresponding to $\beta_t = 0.95$ and $\beta_n = 0.02$. Carabid β -diversity was
 231 0.95, corresponding to $\beta_t = 0.92$ and $\beta_n = 0.03$. Plant β -diversity was 0.96, corresponding to $\beta_t =$
 232 0.95 $\beta_n = 0.01$. β_n of the three groups was thus considered negligible and was not included in
 233 further analyses.

234 Repeated ANOVAs revealed no significant effect of AES, site, or of the interaction between AES
 235 and site on estimated α -diversity and abundance of spiders and carabids, or on plant productivity
 236 and α -diversity (Table 2). A significant difference was found for plant rarity (Table 2), the number
 237 of rare plants being higher in sites under AES. No significant difference was found between
 238 assemblages of sites under AES vs. sites not under AES for spiders ($R=0.011$, $P=0.365$), carabids
 239 ($R=0.008$, $P=0.347$) 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 α and β -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 α -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 β -diversity was significantly influenced by fertiliser amount and cutting-date (Table 3 and Fig. 3D and 3E). Spider mean β -diversity increased with increasing fertiliser amount, with the mean β -diversity being maximal with 60 kg/ha and free fertilisation. An opposite response was

found for the cutting-date: mean β -diversity was lower with later cutting dates and was maximal in fields not under AES.

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

Plant α -diversity was significantly influenced by moisture (Table 3). Plant α -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 β -diversity (Table 3) but no significant effect of fertiliser amount and cutting-date were found when comparing mean β -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).

279

280 Discussion

Overall, our results demonstrated no significant impact of AES on α -diversity, β -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;

287 Marshall, West, & Kleijn, 2006). However, the existence of different levels in AES prescriptions
 288 could potentially lower the impact of the most binding AES. Furthermore, meadows not under AES
 289 remain rather extensively managed. It is thus possible that AES prescriptions do not constitute a
 290 sufficient change in practices to have a detectable impact. The positive impact of AES
 291 contractualisation on protected plants might not be a consequence of a change in farmers' practices.
 292 Indeed, farmers preferentially engage in AES fields which are less suitable for intensive farming
 293 (Kleijn & van Zuijlen, 2004). In our case, fields with higher moisture levels are preferentially
 294 engaged because soil bearing does not allow early cutting-dates. In the Loire Valley, most of the
 295 protected plants are hygrophilous and are thus located in the engaged fields. In a large-scale study,
 296 Kleijn et al. (2006) found no impact of AES on rare arthropods and plants, except for a positive one
 297 on plant rarity in two countries. Our results are partly in opposition but, like in Kleijn et al. (2006),
 298 the low number of rare species encountered prevents reliable estimates of AES impacts.
 299 Spider assemblages and α -diversity were significantly influenced by moisture which is in
 300 accordance with Desender and Maelfait (1999), Pétillon, Georges, Canard, Lefeuvre, Bakker and
 301 Ysnel (2008) and Lafage, Maugenest, Bouzillé, and Pétillon (2015). Cutting-date only influenced
 302 spider β -diversity. Cutting-date has recently been shown to have little impact on spider α -diversity
 303 and abundance, but a significant impact on traits (Lafage & Pétillon 2014), suggesting a potential
 304 impact on β -diversity in accordance with our results.
 305 We found spider β -diversity to decrease when cutting-dates were delayed. That could be explained
 306 by the fact that the engaged farmers have to cut their fields in a very narrow time-frame in order to
 307 maximise the nutritional value of hays (that decreases over time: Nocera, Parsons, Milton, &
 308 Fredeen, 2005). In fields not under AES, the diversity of cutting dates would oppositely increase the
 309 β -diversity of spiders.
 310 As opposed to the biodiversity-productivity theory (Grime, 1973), sites fertilised with 60 kg/ha
 311 nitrogen supported highest spider α -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)

337 and slightly inferior than recommended by Brook, Woodcock, Sinka, and Vanbergen (2008) for
 338 beetles (54,8x15,6s recommended vs 5x10x15s performed) with similar sampling area. We can thus
 339 consider that our results were not biased by the sampling technique, and that the dominance of
 340 small aerial dispersers was a consequence of an environmental filter, here the stochasticity due to
 341 flooding (Zulka 1994).

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

352 Regarding AES prescriptions, cutting-date significantly influenced β -diversity and plant
 353 assemblages. Late cutting dates are indeed well known to induce vegetation modifications by
 354 favouring annual plant species; maximum plant α -diversity being usually observed for late cutting-
 355 dates (mid-June to mid-July) in European grasslands (e.g. Critchley, Walker, Pywell, & Stevenson,
 356 2007).

357 Fertilisation level had a significant impact only on plant β -diversity, which is in accordance with
 358 Klimek et al. (2008) who found plant species β -diversity being influenced, at a local scale, by
 359 fertilisation input. A significant reduction of α -diversity and a biomass increase are usually observed
 360 even for low levels of fertilizers (e.g., Plantureux, Peeters, & Mccracken, 2005). Nevertheless, in
 361 flooded grasslands, no effect of fertilisation on plant diversity was reported under 90 kg/ha/yr

362 (Bonis, Dausse, Dia, & Bouhnik-le Coz, 2008). Thus, the fertilisation level permitted in sites under
 363 AES and effectively used in sites not under AES, may be too low to allow a detection of their
 364 impact.
 365 Our results suggest that flooding might be a stronger driver of vegetation and arthropod
 366 assemblages than differences in cutting dates or low fertilizer inputs. The impact of flooding and
 367 management practices seems to vary with organism mobility (Adis & Junk, 2002). Indeed, we
 368 found plants to be the organisms that are the most sensitive to perturbations induced by flooding,
 369 and also to variations in management practices. Conversely, carabid assemblages, mainly composed
 370 of highly mobile small species, were only influenced by flooding.
 371 Our results further suggest that the regulation of cutting dates and low input fertilisers of grasslands
 372 has few, if any, effects on arthropods and plants compared to those induced by a prolonged flooding.
 373 Conservation actions in such ecosystems might have to focus on maintaining and/or enhancing
 374 hydrological functioning in order to rewild those ecosystems (Merckx & Pereira, 2014).
 375 Nevertheless, because natural meadows are in constant regression by conversion to intensive
 376 agriculture (Millennium Ecosystem Assessment 2005), AES can yet be considered an efficient way
 377 of maintaining an endangered habitat, despite their limited efficiency in flooded systems.

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387

388 "Appendix A. Supplementary data

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

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390 **References**

- 391 Adis J., & Junk, W. J. (2002). Terrestrial invertebrates inhabiting lowland river floodplains of
 392 Central Amazonia and Central Europe: a review. *Freshwater Biology* 47, 711–731.
- 393 Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on*
 394 *Automatic Control*, 19, 716–723.
- 395 Albrecht, M., Duelli, P., Muller, C., Kleijn, D., & Schmid, B. (2007). The Swiss agri-environment
 396 scheme enhances pollinator diversity and plant reproductive success in nearby intensively
 397 managed farmland. *Journal of Applied Ecology*, 44, 813–822.
- 398 Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global*
 399 *Ecology and Biogeography*, 19, 134–143.
- 400 Baselga, A., & Orme, C.D.L. (2012). betapart: an R package for the study of beta diversity. *Methods*
 401 *in Ecology Evolution*, 3, 808–812.
- 402 Bonis, A., Dausse, A., Dia, A., & Bouhnik-le Coz, M. (2008). Fertilisation et qualité de l'eau en
 403 prairies naturelles humides (marais de l'Ouest). *Fourage*, 196, 485–489.
- 404 Borcard, D., Gillet, F., & Legendre, P. (2011). *Numerical ecology with R*. Springer, New York.
- 405 Borer, E. T., Seabloom, E. W., & Tilman, D. (2012). Plant diversity controls arthropod biomass and
 406 temporal stability. *Ecology Letters*, 15, 1457–1464. <http://doi.org/10.1111/ele.12006>
- 407 Braun-Blanquet, J. (1928). Pflanzensoziologie. Grundzüge der Vegetationskunde. *Springer, Wien,*
 408 *AT*.
- 409 Brereton, T. M., Warren, M. S., Roy, D. B., & Stewart, K. (2007). The changing status of the
 410 Chalkhill Blue butterfly *Polyommatus coridon* in the UK: the impacts of conservation policies
 411 and environmental factors. *Journal of Insect Conservation*, 12, 629–638.
- 412 Brook, A. J., Woodcock, B. A., Sinka, M., & Vanbergen, A.J. (2008). Experimental verification of
 413 suction sampler capture efficiency in grasslands of differing vegetation height and structure.
 414 *Journal of Applied Ecology*, 45, 1357–1363.

- 415 Cardoso, P., Erwin, T. L., Borges, P. A. V., & New, T. R. (2011). The seven impediments in
 416 invertebrate conservation and how to overcome them. *Biological Conservation*, 144, 2647–
 417 2655.
- 418 Carvalho, J. C., Cardoso P., Crespo, L. C., Henriques, S., Carvalho, R., & Gomes, P. (2012).
 419 Determinants of spider species richness in coastal dunes along a gradient of mediterraneity.
 420 *Insect Conservation and Diversity*, 5, 127–137.
- 421 COM (2008). *Rural development in the European Union: Statistical and economic information*.
 422 Brussels.
- 423 Critchley, C. N. R., Walker, K. J., Pywell, R. F., & Stevenson, M. J. (2007). The contribution of
 424 English agri-environment schemes to botanical diversity in arable field margins, in: *Aspects of*
 425 *Applied Biology*. pp. 293–300.
- 426 Desender, K., & Maelfait, J. P. (1999). Diversity and conservation of terrestrial arthropods in tidal
 427 marshes along the River Schelde: a gradient analysis. *Biological Conservation*, 87, 221–229.
- 428 Duffey, E. (1974). Comparative sampling methods for grassland spiders. *Bulletin of the British*
 429 *Arachnological Society*, 3, 34–37.
- 430 Dwire, K. A., Kauffman, J. B., Brookshire, E. N. J., & Baham, J. E. (2004). Plant biomass and
 431 species composition along an environmental gradient in montane riparian meadows.
 432 *Oecologia*, 139, 309–17. <http://doi.org/10.1007/s00442-004-1498-2>
- 433 Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., & Paulißen, D. (1992). Zeigerwerte
 434 von Pflanzen in Mitteleuropa, 2nd ed. *Scripta Geobotanica*, 18, 1–258.
- 435 Gerisch, M., Dziöck, F., Schanowski, A., Ilg, C., & Henle, K. (2012). Community resilience
 436 following extreme disturbances: the response of ground beetles to a severe summer flood in a
 437 central European lowland stream. *River Research and Applications*, 28, 81–92.
- 438 Grime, J. P. (1973). Control of species density in herbaceous vegetation. *Journal of Environmental*
 439 *Management*, 1, 151–167.

- 440 Hoback, W. W., & Stanley D. W. (2001). Insects in hypoxia. *Journal of Insect Physiology* 47, 533–
441 542.
- 442 Junk, W. J., & Wantzen, M. (2004). The flood pulse concept: new aspects, approaches and
443 applications - an update. In *Second International Symposium on the Management of Large*
444 *Rivers for Fisheries* (pp. 117–140). Food and Agriculture Organization and Mekong River
445 Commission, FAO Regional Office for Asia and the Pacific.
- 446 Kleijn, D., Baquero, R. A., Clough, Y., Díaz, M., De Esteban, J., Fernández, F., Gabriel, D., Herzog,
447 F., Holzschuh, A., Jöhl, R., Knop, E., Kruess, A., Marshall, E. J. P., Steffan-Dewenter, I.,
448 Tscharnkte, T., Verhulst, J., West, T. M., & Yela, J. L. (2006). Mixed biodiversity benefits of
449 agri-environment schemes in five European countries. *Ecological Letters*, 9, 243–54;
450 discussion 254–7.
- 451 Kleijn, D., Berendse, F., Smit, R., & Gilissen, N. (2001). Agri-environment schemes do not
452 effectively protect biodiversity in Dutch agricultural landscapes. *Nature*, 413, 723–725.
- 453 Kleijn, D., & van Zuijlen, G. J. C. (2004). The conservation effects of meadow bird agreements on
454 farmland in Zeeland, the Netherlands, in the period 1989–1995. *Biological Conservation*, 117,
455 443–45.
- 456 Klimek, S., Marini, L., Hofmann, M., & Isselstein, J. (2008). Additive partitioning of plant diversity
457 with respect to grassland management regime, fertilisation and abiotic factors. *Basic and*
458 *Applied Ecology*, 9, 626–634.
- 459 Knop, E., Kleijn, D., Herzog, F., & Schmid, B. (2005). Effectiveness of the Swiss agri-environment
460 scheme in promoting biodiversity. *Journal of Applied Ecology*, 43, 120–127.
- 461 Konvicka, M., Benes, J., Cizek, O., Kopecek, F., Konvicka, O., & Vitaz, L. (2007). How too much
462 care kills species: Grassland reserves, agri-environmental schemes and extinction of *Colias*
463 *myrmidone* (Lepidoptera: Pieridae) from its former stronghold. *Journal of Insect Conservation*,
464 12, 519–525.
- 465 Lafage, D., & Pétilon, J. (2014). Impact of cutting date on carabids and spiders in a wet meadow.
466 *Agriculture, Ecosystems & Environment*, 185, 1–8.

- 467 Lafage, D., Maugenest, S., Bouzillé, J.-B., & Pétillon, J. (2015). Disentangling the influence of
 468 local and landscape factors on alpha and beta diversities: opposite response of plants and
 469 ground-dwelling arthropods in wet meadows. *Ecological Research*, 30, 1025–1035.
- 470 Lafage, D., Papin, C., Secondi, J., Canard, A., & Pétillon, J. (2015). Short term recolonisation by
 471 arthropod after a spring flood, with a focus on spiders and carabids. *Ecohydrology*, 8, 1584-
 472 1599. doi: 10.1002/eco.1606
- 473 Lafage, D., Secondi, J., Georges, A., Bouzillé, J.-B., & Pétillon, J. (2014). Satellite-derived
 474 vegetation indices as surrogate of species richness and abundance of ground beetles in
 475 temperate floodplains. *Insect Conservation and Diversity*, 7, 327–333.
- 476 Lambeets, K., Breyne, P., & Bonte, D. (2010). Spatial genetic variation of a riparian wolf spider
 477 *Pardosa agricola* (Thorell, 1856) on lowland river banks: The importance of functional
 478 connectivity in linear spatial systems. *Biological Conservation*, 143, 660–668.
- 479 Lambeets, K., Vandegehuchte, M. L., Maelfait, J.-P., & Bonte, D. (2008). Understanding the impact
 480 of flooding on trait-displacements and shifts in assemblage structure of predatory arthropods
 481 on river banks. *Journal of Animal Ecology*, 77, 1162–74. doi:10.1111/j.1365-
 482 2656.2008.01443.x
- 483 Legendre, P., Borcard, D., Blanchet, F. G., & Dray, S. (2013). *PCNM: MEM spatial eigenfunction*
 484 *and principal coordinate analyses*.
- 485 Marshall, E. J. P., West, T. M., & Kleijn, D. (2006). Impacts of an agri-environment field margin
 486 prescription on the flora and fauna of arable farmland in different landscapes. *Agriculture,*
 487 *Ecosystems & Environment*, 113, 36–44.
- 488 Merckx, T., & Pereira, H. M. (2014). Reshaping agri-environmental subsidies: From marginal
 489 farming to large-scale rewilging. *Basic and Applied Ecology*, 16, 95-103.
- 490 Millennium Ecosystem Assessment (2005). *Ecosystems and Human Well-Being: Biodiversity*
 491 *Synthesis*. Washington DC.

- 492 Mommertz, S., Schauer, C., Kösters, N., Lang, A., & Filser, J. (1996). A comparison of D-Vac
 493 suction, fenced and unfenced pitfall trap sampling of epigeal arthropods in agro- ecosystems.
 494 *Annales Zoologici Fennici*, 33, 117–124.
- 495 Nocera, J. J., Parsons, G. J., Milton, G. R., & Fredeen, A. H. (2005). Compatibility of delayed
 496 cutting regime with bird breeding and hay nutritional quality. *Agriculture, Ecosystems &*
 497 *Environment*, 107(2-3), 245–253. doi:10.1016/j.agee.2004.11.001
- 498 Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O’Hara, R. B., Simpson, G. L.,
 499 Solymos, P., Henry, M. H., Wagner, S., & Wagner H. (2013). *vegan: Community Ecology*
 500 *Package*.
- 501 Patrick, L. B., Fraser, L. H., & Kershner, M. W. (2008). “Brown” World Invertebrates Contradict
 502 “Green” World Biodiversity Theory. *Research Letters in Ecology*, 2008, 1–4.
- 503 Pétillon, J., Courtial, C., Canard, A., & Ysnel, F. (2007). First assessment of spider rarity in Western
 504 France. *Revista Ibérica de Arachnologia*, 15, 106-113.
- 505 Pétillon J., Georges A., Canard A., Lefeuvre J.-C., Bakker J. P., & Ysnel, F. (2008) Influence of
 506 abiotic factors on spider and ground beetles communities in different salt-marsh systems. *Basic*
 507 *and Applied Ecology*, 9, 743-751.
- 508 Pétillon, J., Montaigne, W., & David, R. (2009). Hypoxic coma as a strategy to survive inundation
 509 in a salt-marsh inhabiting spider. *Biology Letters*, 5, 442–445.
- 510 Pétillon J., Potier, S., Carpentier, A., & Garbutt, A. (2014). Evaluating the success of managed
 511 realignment for the restoration of salt marshes: lessons from invertebrate communities.
 512 *Ecological Engineering*, 69, 70-75.
- 513 Plantureux, S., Peeters, A., & Mccracken, D. (2005). Biodiversity in intensive grasslands: Effect of
 514 management, improvement and challenges. *Agronomy Research*, 3, 153–164.
- 515 R Development Core team (2013) *R: A Language and Environment for Statistical Computing*.

- 516 Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S. G., Rundlöf, M., Smith, H. G., & Kleijn, D.
 517 (2013). Environmental factors driving the effectiveness of European agri-environmental
 518 measures in mitigating pollinator loss – a meta-analysis. *Ecology Letters*, 16, 912–920.
- 519 Siemann, E. (1998). Experimental tests of effects of plant productivity and diversity on grassland
 520 arthropod diversity. *Ecology*, 79, 2057–2070
- 521 Varet, M., Burel, F., Lafage, D., & Pétillon, J. (2013). Age-dependent colonisation of urban
 522 habitats : a diachronic approach using carabid beetles and spiders. *Animal Biology*, 63, 257–
 523 269.
- 524 Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S*, Fourth. ed. Springer,
 525 New York.
- 526 Violle, C., Bonis, A., Plantegenest, M., Cudennec, C., Damgaard, C., Marion, B., Le Cœur, D., &
 527 Bouzillé, J.-B. (2011) Plant functional traits capture species richness variations along a
 528 flooding gradient. *Oikos*, 120, 389–398.
- 529 Wassen, M. J., Peeters, W. H. M., & Olde Venterink, H. (2002). Patterns in vegetation, hydrology
 530 and nutrient availability in an undisturbed river floodplain in Poland. *Plant Ecology*, 165, 27–
 531 43.
- 532 Zelnik, I., & Čarni, A. (2008). Distribution of plant communities, ecological strategy types and
 533 diversity along a moisture gradient. *Community Ecology*, 9, 1–9.
 534 <http://doi.org/10.1556/ComEc.9.2008.1.1>
- 535 Zulka, K. P. (1994). Carabids in a Central Europe floodplain: species distribution and survival
 536 during inundations. In K. Desender et al. (Ed.), *Carabid Beetles: Ecology and Evolution*.
 537 Kluwer Academic Publishers, Netherlands.

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541 **Figure caption**

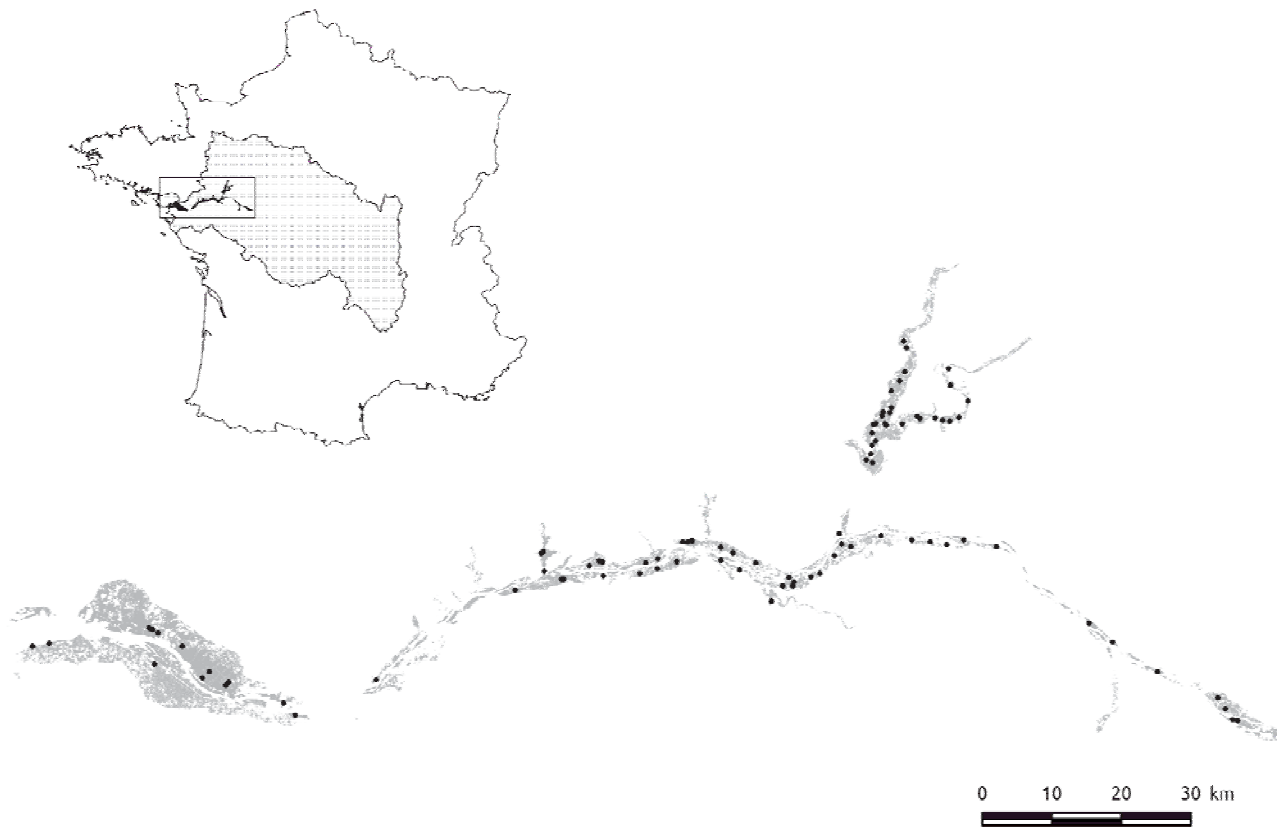
542 **Fig. 1.** Location of the study sites in the Loire watershed (France). Grey surfaces indicate meadows
543 and black dots correspond to the sampled meadows.

544 **Fig. 2.** CCA on spider species. Sites under AES are represented by triangles and sites not under
545 AES by circles. Only species most contributing to axes are represented. (CHEPEN:
546 *Cheiracanthium pennyi*, CRUSTI: *Crustulina sticta*, DIPLAT: *Diplocephalus latifrons*, DRALAP:
547 *Drassodes lapidosus*, ENOOVA: *Enoplognatha ovata*, EUOFRO: *Euophrys frontalis*, EUOHER:
548 *Euophrys herbigrada*, EVAARC: *Evarcha arcuata*, ERIVAG: *Erigone vagans*, HAPSIG:
549 *Haplodrassus signifer*, HYPPYG: *Hypsosinga pygmaea*, LARCOR: *Larinioides cornutus*,
550 LEPZYM: *Leptyphantus zimmermanni*, MEIBEA: *Meioneta beata*, MEISIM: *Meioneta*
551 *simplicitarsis*, METPRO: *Metopobactrus prominulus*, NEOSUA: *Neottiura suaveolens*, OEDAGR:
552 *Oedothorax agrestis*, OZYRAU: *Ozyptila rauda*, OZYTRU: *Ozyptila trux*, PARAGR: *Pardosa*
553 *agrestis*, PARPAL: *Pardosa palustris*, PISMIR: *Pisaura mirabilis*, PORMIC: *Porrhomma*
554 *microphthalmum*, PORPYG: *Porrhomma pygmaeum*, SAVFRO: *Savignia frontata*, SILELE:
555 *Silometopus elegans*, STEPHA: *Steatoda phalerata*, THASTRE: *Thanatus striatus*, THEBIM:
556 *Theridion bimaculatum*, THEIMP: *Theridion impressum*, TIBOBL: *Tibelus oblongus*, TRISAX:
557 *Trichoncus saxicola*, TROSPI: *Trochosa spinipalpis*, XERNEM: *Xerolycosa nemoralis*, XYSERR:
558 *Xysticus erraticus*, ZELCIV: *Zelotes civicus*, ZORPAR: *Zora parallela*.

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560 **Fig. 3.** Variations in mean response variables depending on significant factors by GLM (different
561 successive letters indicate significant differences in means according to Tukey's post-hoc tests with
562 Bonferroni correction). (A) Mean estimated spider richness by fertiliser class (Free: not under
563 AES). (B) Mean estimated spider richness by moisture gradient (1 to 5: increasing moisture
564 gradient). (C) Spider abundance per 0.12m² by fertiliser class. (D): Spider mean β -diversity by

565 fertiliser class. (E) Spider mean β -diversity by cutting date (Free: not under AES, CD1: before 20th
566 June, CD2: between 20th June and 1st July, CD3: after 1st July). (F) Carabid abundance by
567 moisture gradient. (G) Carabid mean β -diversity by flooding (Yes: sites flooded during summer
568 2013, No: sites not flooded). (H) Plant Shannon Index by moisture gradient. (I) Plant mean β -
569 diversity by flooding. (J) Plant mean β -diversity by moisture gradient. (K) Number of rare plant
570 species by moisture gradient. The horizontal bar in box-plots indicates the median, the ends of the
571 boxes indicate the interquartile range, and the whiskers indicate the 10th and 90th quantiles.

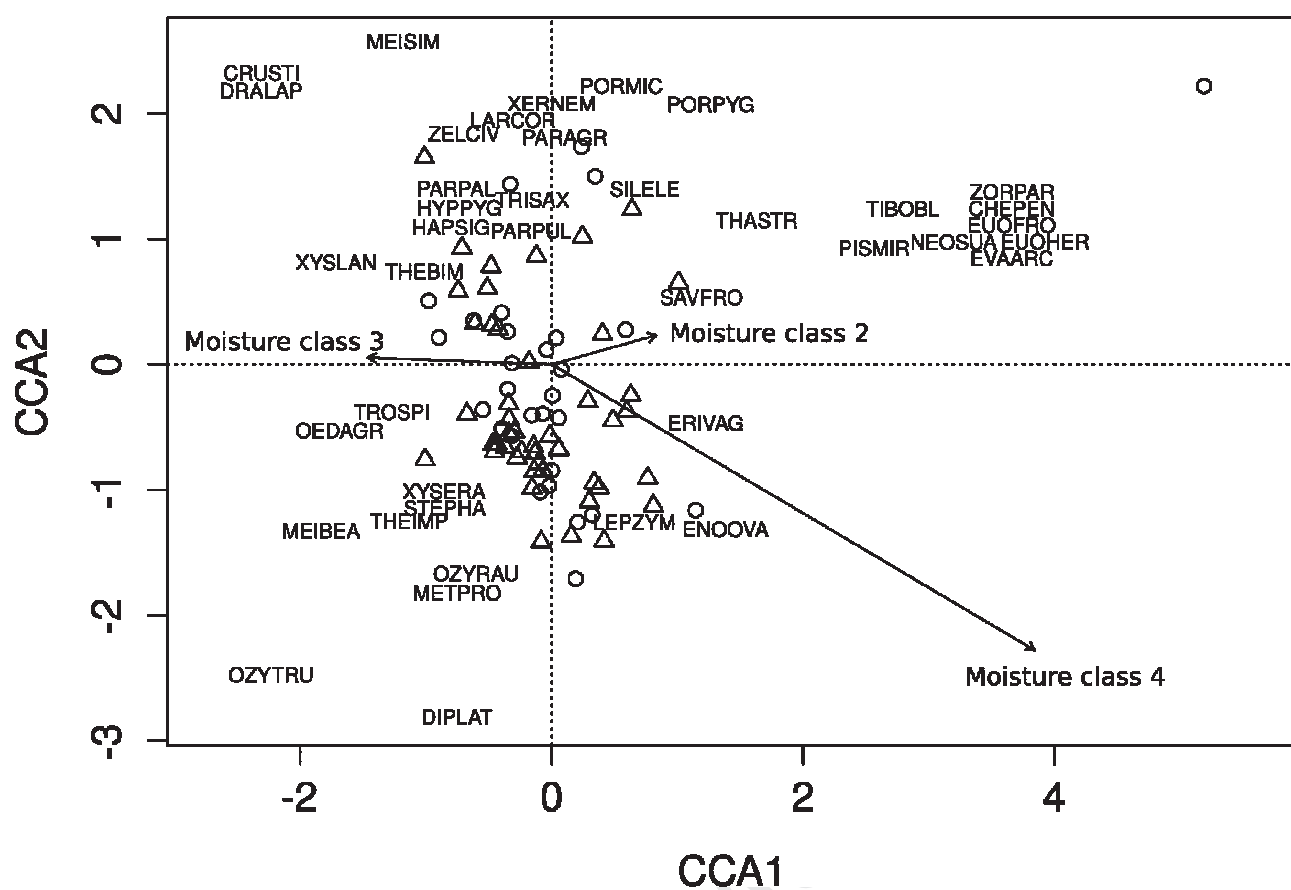


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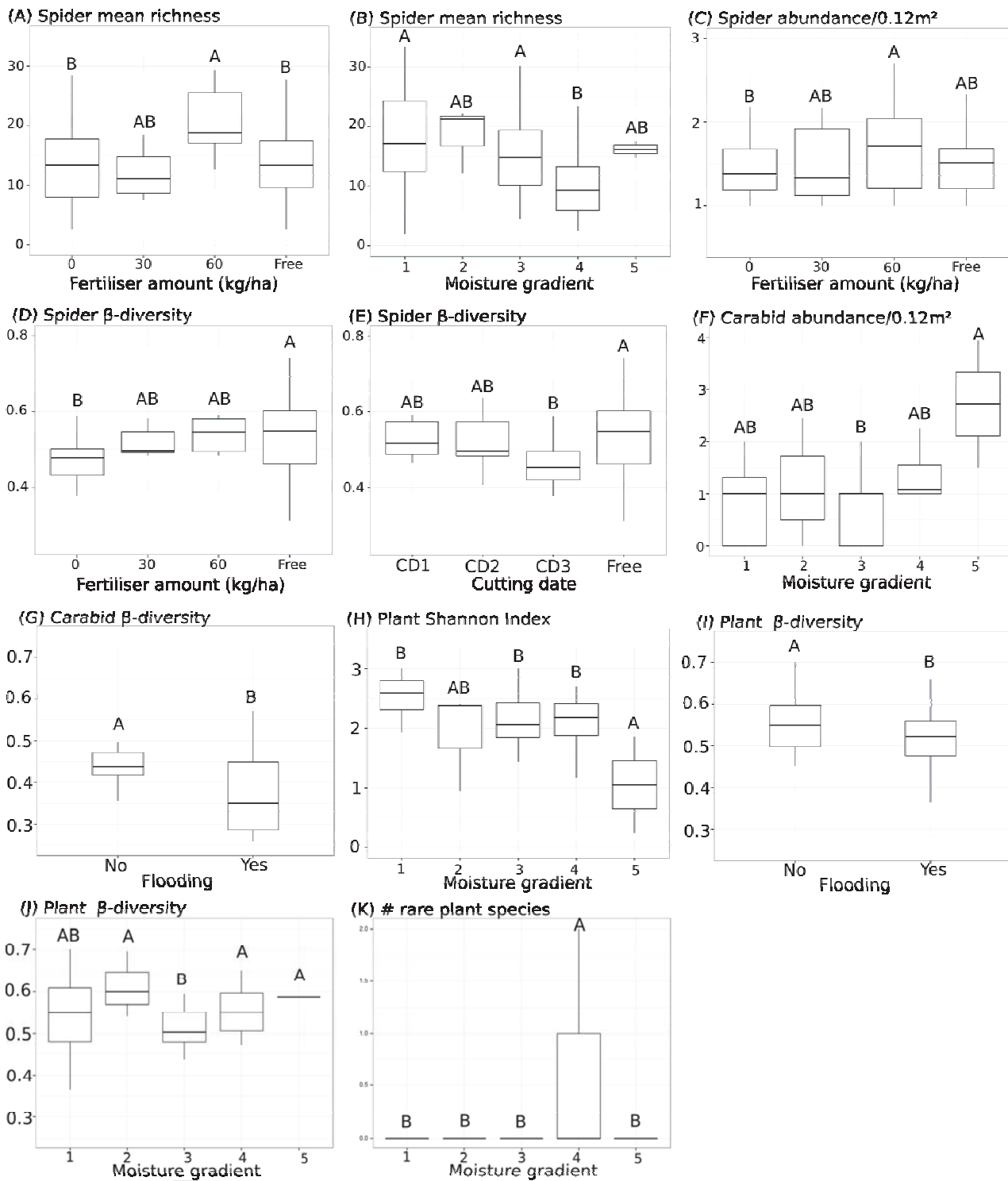
573 Figure 1. Lafage and Pétillon, 2015

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576 Figure 2 : Lafage and Pétillion, 2015



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578 Figure 3 : Lafage and Pétillon, 2015

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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).

	classe	#sites
Contract	Yes	42
	No	41
Fertilisers	0	15
	30	17
	60	10
	Free	41
Cutting date	CD1	12
	CD2	14
	CD3	16
	Free	41
Flooding	No	33
	Yes	50
Moisture	1	16
	2	15
	3	28
	4	27
	5	6

Table 2. Per site means \pm 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, Jackknife1, Jackknife2 and Bootstrap.

		AES	Free	Contract		Site		Interaction	
		Mean \pm s.e.	Mean \pm s.e.	F	P	F	P	F	P
Spiders	Abundance	2.24 \pm 1.84	1.83 \pm 1.19	0.96	0.338	2.12	0.158	0.04	0.838
	Estimated species richness	14.74 \pm 7.14	10.50 \pm 3.97	3.98	0.060	0.24	0.630	0.143	0.709
Carabids	Abundance	1.02 \pm 1.01	1.64 \pm 1.47	1.53	0.228	0.06	0.804	0.05	0.833
	Estimated species richness	2.08 \pm 2.40	3.45 \pm 3.46	1.13	0.298	2.47	0.129	0.10	0.760
Plants	Shannon Index	2.15 \pm 0.42	2.24 \pm 0.37	0.19	0.667	2.08	0.162	0.02	0.883
	EVI	5366 \pm 1187	5135 \pm 1097	0.31	0.594	0.29	0.594	1.43	0.243
	Rarity	4.73 \pm 2.81	2.06 \pm 1.98	7.9 9	0.00 9	1.8 7	0.18 4	0.68 3	0.41 7

603 Table 3. GLM selected by stepwise procedure for spider, carabid and plant abundance / biomass
 604 (approximated by EVI index), estimated richness (α -diversity), β -diversity, and rarity (for plants
 605 only).

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Group	Response	Variables kept	F	P
Spiders	Estimated species richness (α -diversity)	Fertilisers	4.28	0.008
		Moisture	4.45	0.003
		F x VT	1.92	0.101
	Abundance	Fertilisers	3.33	0.024
		Moisture	1.75	0.150
		F x VT	1.99	0.090
	β -diversity	Fertilisers	1.59	0.020
		Cutting date	1.69	0.020
Carabids	Estimated species richness (α -diversity)	-	-	-
	Abundance	Fertilisers	1.16	0.330
		Moisture	2.89	0.028
		F x VT	2.11	0.074
	β -diversity	Flooding	1.03	0.010

Plants	Shannon Index (α -diversity)	Cutting date	0.03	0.993
		Fertilisers	1.21	0.303
		Moisture	7.47	<0.001
	EVI	Cutting date	0.03	0.993
		Fertilisers	1.21	0.303
		Moisture	7.48	<0.001
	β -diversity	Fertilisers	1.99	0.010
		Cutting date	2.35	0.010
		Flooding	3.51	0.010
		Moisture	8.76	0.010
	Rarity	Moisture	5.23	0.025

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