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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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40

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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: Pétilion 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, & Pétilion, 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 (Pétilion, 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

122 national or regional statuses of rarity (the English classification cannot be applied here: Pétilion,
123 Courtial, Canard, & Ysnel, 2007), and also because the number of stenotopic and/or rare species is
124 low in these habitats (Lafage, Papin, Secondi, Canard, & Pétilion, 2015).

125

126 **Material and methods**

127 *Study area and sampling design*

128 The study area covered 200 km of the Loire Valley (France: Fig. 1). Land is mainly covered by hay
129 meadows with an extensive hedgerow network. Meadows are usually cut in early or mid-summer
130 with second-crop grazing. The amount of fertilisers is generally low as regular winter and spring
131 floods bring a large amount of organic matter into the system. Pesticides are seldom used. Thus, the
132 management intensity is rather low. The study site included four AES zones with various
133 prescriptions regarding cutting-dates and fertilizers. Cutting-dates were between June 5th to July
134 20th, within four defined classes: free (not under AES), before June 20th, between June 20th and
135 July 1st, after July 1st. Fertiliser prescriptions were 0, 30 or 60 N unit/ha. A 'free' class was added
136 for sites not under AES. Almost all meadows are flooded during winter for about 3 months, but in
137 2012 and 2013, the study sites were also flooded during spring for 5 to 22 days. Spring-flood had
138 not occurred since 2004 in the Loire Valley.

139 Carabids, spiders and plants were sampled in 83 hay meadows. To reduce the variance between
140 fields, a paired-matched approach was used to test the impact of AES (see statistical analysis
141 section). Paired sites (with and without AES contract) were chosen with same vegetation types and
142 flooding regime. Distance between sites belonging to a pair was inferior to 1 km. Table 1
143 summarizes the number of sites per treatment and moisture level. Site size ranged from 1.3 ha to
144 265.3 ha (mean = 34.7 ± 50.3 SD ha).

145 Carabids and spiders were sampled using suction sampling (a standard technique providing
146 quantitative data, i.e. abundance of individuals, on arthropods: Brook, Woodcock, Sinka, and
147 Vanbergen, 2008). Each site was sampled once during June 2015 before the first cutting date- given
148 the strong impact of cutting on spiders and carabids (e.g., Lafage & Pétillon 2014). Suction
149 sampling was realised using a 12.5 cm diameter intake placed on the ground. At each sampling site,
150 5 samples (10 x 15 s suction) were taken (total area: 0.12 m²/sample). Samples were stored in 70%
151 alcohol and taken to the laboratory for sorting and identification to species level.

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

158

159 *Statistical analysis*

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

164 Arthropod α -diversities were estimated for each sampling site using the average of four non-
165 parametric estimators based on species incidence: Chao1, Jackknife1, Jackknife2 and Bootstrap
166 (Carvalho et al. 2012). β -diversity was estimated through a dissimilarity matrix (corresponding to
167 Sørensen pair-wise dissimilarity) partitioned into its two components -species turnover (β_t) and
168 nestedness (β_n)- following Baselga (2010) and using the betapart R package (Baselga & Orme

169 2012). Vegetation diversity was estimated by the classical Shannon index. Plant rarity was
170 estimated using the number of plants red-listed at either national or regional scale per sample. As no
171 red list exists for spiders and carabids in France, analyses on arthropod rarity were not performed.

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

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

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

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

185 To investigate arthropod and plant responses to management and flooding, drivers of species
186 assemblages were investigated using constrained analysis. The choice between redundancy analysis
187 (RDA) and constrained correspondence analysis (CCA) was made according to the axis length of a
188 detrended correspondence analysis (DCA). Abundances of all species (for arthropods) and Braun-
189 Blanquet coefficients of abundance (for plants) were the response variables. The cutting-date (four
190 classes), fertiliser input (three levels), a variable describing whether or not the site had been flooded
191 during spring 2013 (i.e., binary variable for short-term effects of flooding), and a moisture gradient
192 (i.e., discrete variable for long-term effects of flooding) were predictors. Five moisture classes were

193 defined from low (1) to very high (5) according to the mean Ellenberg indicator value (Ellenberg et
194 al., 1992) of each vegetation type (defined by a Two-Way Indicator Species Analysis). Class 1
195 corresponded to sites with mean Ellenberg value lower than 5 (mean=4.6), class 2 to sites with
196 $5 < \text{Ellenberg value} < 6$ (mean=5.4), class 3 to sites with $6 < \text{Ellenberg value} < 7$ (mean=6.4), class 4 to
197 sites with $7 < \text{Ellenberg value} < 8$ (mean=7.5) and class 5 to sites with Ellenberg value higher than 8
198 (mean=8.3). Monte Carlo tests with 999 permutations were carried out to test the significance of
199 the selected environmental factors and constrained analyses axes.

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

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

212

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

216

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%), *Bathyphantes 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 -

240 diversity of sites under vs. not under AES for spiders ($\chi^2=49$, $P=0.473$), carabids ($\chi^2=45.60$,
241 $P=0.555$) or plants ($\chi^2=46.74$, $P=0.625$).

242 CCA on spider assemblages was significant ($F=1.61$, $P=0.048$) and explained 55.5% of the total
243 variance, with the first three axes of the CCA being significant (respectively $P=0.005$; $P=0.020$ and
244 $P=0.020$). Axis 1 and 3 were associated with moisture index and axis 2 with cutting date but the
245 only variable significantly explaining spider species composition was moisture ($F=1.67$, $P=0.050$)
246 (Fig. 2).

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

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

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

261 Spider β -diversity was significantly influenced by fertiliser amount and cutting-date (Table 3 and
262 Fig. 3D and 3E). Spider mean β -diversity increased with increasing fertiliser amount, with the
263 mean β -diversity being maximal with 60 kg/ha and free fertilisation. An opposite response was
11

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

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

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

271 Plant α -diversity was significantly influenced by moisture (Table 3). Plant α -diversity of sites with a
272 high moisture level (Class 5) was significantly lower than those with a lower moisture level (class
273 1: Fig. 3H). Plant biomass (EVI) was significantly and positively impacted by moisture. Higher EVI
274 was found in moister sites, although differences among means were not significant. Fertiliser
275 amount, cutting-date, flooding, and moisture all had a significant effect on plant β -diversity (Table
276 3) but no significant effect of fertiliser amount and cutting-date were found when comparing mean
277 β -diversity between classes (Fig. 3I, 3J). Plant rarity was significantly impacted by moisture, with a
278 higher number of rare plants in moister sites (Table 3 and Fig. 3K).

279

280 Discussion

281 Overall, our results demonstrated no significant impact of AES on α -diversity, β -diversity,
282 abundance / biomass and assemblages of the three groups studied in flooded meadows. A positive
283 effect was still found on rare plants. The absence of differences between meadows with vs.
284 meadows without AES is in accordance with some previous studies in non-flooded habitats that
285 focussed on spiders (Knop, Kleijn, Herzog, & Schmid, 2005; Marshall, West, & Kleijn, 2006),
286 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), Pétilion, Georges, Canard, Lefevre, Bakker and
301 Ysnel (2008) and Lafage, Maugenest, Bouzillé, and Pétilion (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 & Pétilion 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

312 with medium or low nitrogen inputs. This is in accordance with studies suggesting a “bottom-up”
313 control of arthropod diversity (Siemann, 1998; Patrick, Fraser, & Kershner, 2008) mediated by plant
314 and consumer biomass (Borer, Seabloom, & Tilman, 2012). Nevertheless, these findings are still
315 being discussed as, for example, Haddad, Haarstad, and Tilman (2000) found insect diversity to be
316 negatively influenced by long-term fertiliser input. The lack of fertilisation effects on spider and
317 carabid abundances could be explained by a threshold effect. Fertiliser inputs remained low, even in
318 fields not under AES contract, compared to the large quantities of organic matter introduced in the
319 system by winter floods (Junk & Wantzen, 2004). Consequently, the fertiliser levels might remain
320 too low to initiate a trophic cascade which is confirmed by the absence of impact of fertilisers on
321 plant biomass and α -diversity (see below).

322 As expected, carabids were only influenced by spring floods and moisture, for β -diversity and
323 abundance respectively. Carabids have been shown to recover less rapidly than spiders after spring
324 floods (Lafage, Papin, Secondi, Canard, & Pétillon, 2015), especially regarding species
325 composition, which could explain the impact of spring floods on carabid β -diversity. Gerisch et al.
326 (2012) demonstrated that carabid β -diversity remains high after important flooding events,
327 indicating persistent shifts in species assemblages. Gerisch et al. (2012) and Lafage, Papin,
328 Secondi, Canard, and Pétillon (2015) finally show massive decreases in carabid abundance after
329 spring floods. This dominance of small species could first be attributed to a sampling effect,
330 although suction sampling is usually recommended to quickly obtain a representative sample of
331 epigeic arthropod communities (e.g. Duffey 1974). In fact, Mommertz, Schauer, Kösters, Lang, and
332 Filser (1996) considered it an inefficient way to sample large arthropods (such as Carabidae and
333 Lycosidae). However, Brook, Woodcock, Sinka, and Vanbergen (2008) considered suction sampling
334 an efficient technique to sample arthropods, including Carabidae, pending a sufficient sampling
335 effort. Here we performed sampling duration and replication higher than recommended by Brook,
336 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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380

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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."

Accepted Manuscript

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541 **Figure caption**

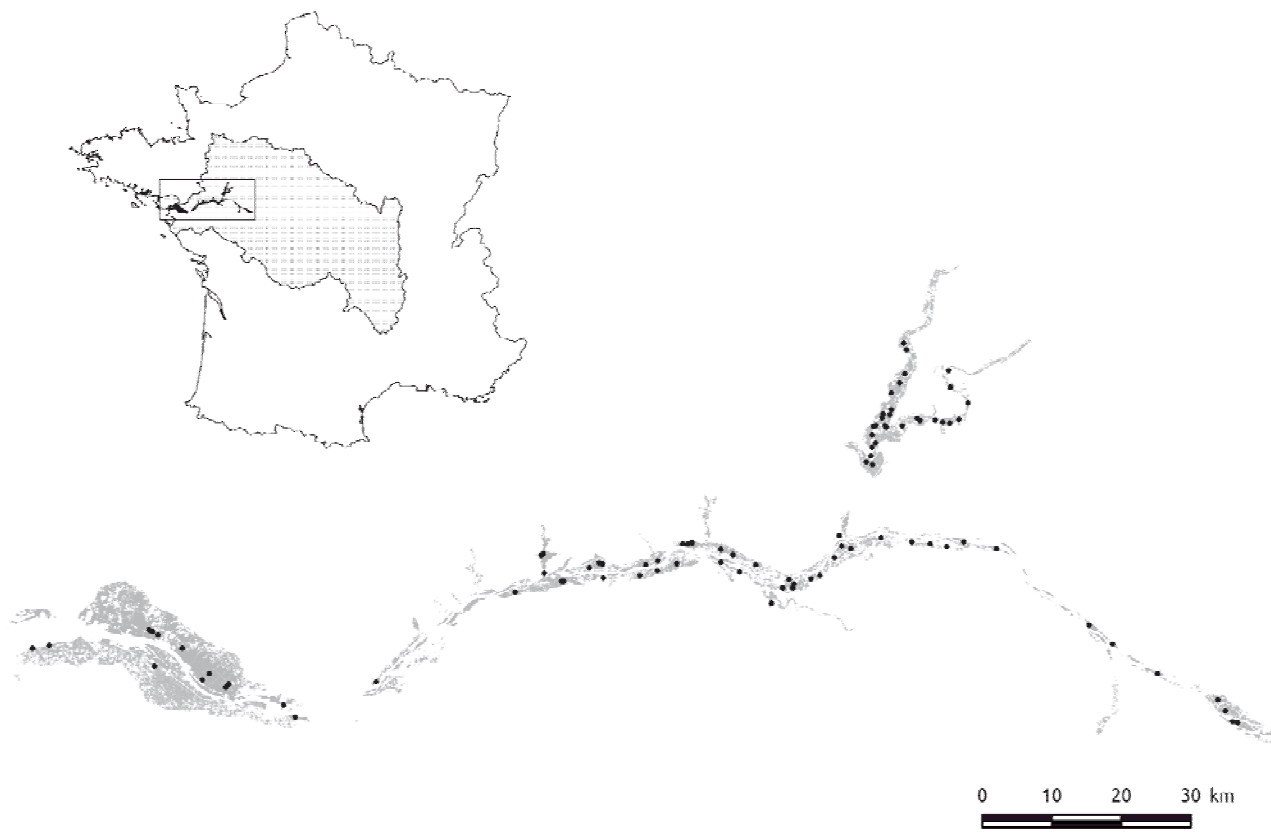
542 **Fig. 1.** Location of the study sites in the Loire watershed (France). Grey surfaces indicate meadows
 543 and black dots correspond to the sampled meadows.

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: *Leptyphantès 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.

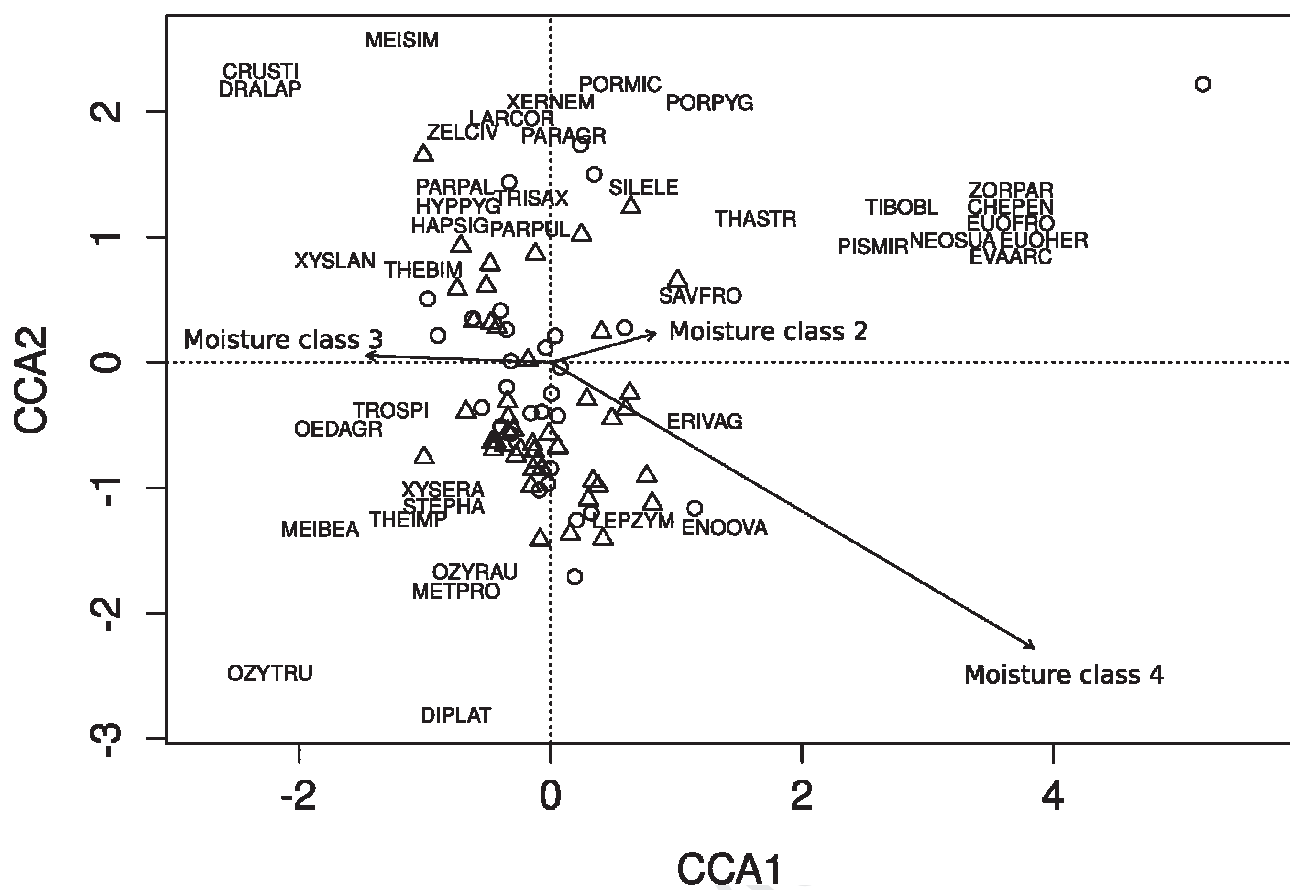


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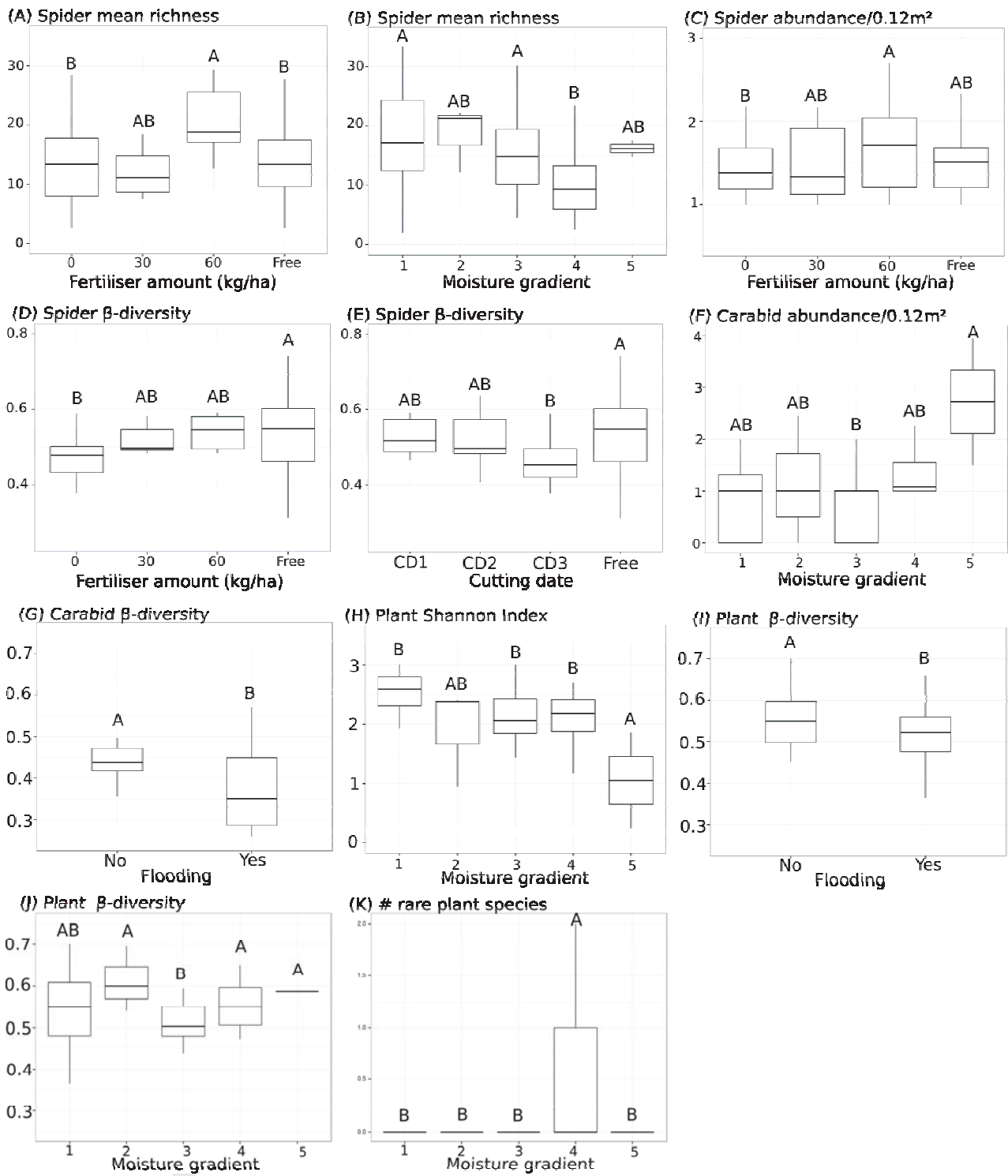
573 Figure 1. Lafage and Pétilon, 2015

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576 Figure 2 : Lafage and Pétilion, 2015



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578 Figure 3 : Lafage and Pétilon, 2015

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580 Table 1. Number of sites per class. Contract : whether or not sites are under AES contract ;
 581 Fertilisers : classes of fertiliser input allowed in kg/Ha ; Cutting date : classes of cutting dates (Free:
 582 not under AES, CD1: before 20th June, CD2: between 20th June and CD3: 1st July, after 1st July.);
 583 Flooding: whether or not site has been flooded during summer 2013; Moisture: classes of Ellenberg
 584 indicator value for moisture from low (1) to very high (5).

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	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

589 Table 2. Per site means \pm s.e. of response variables for fields under AES or not (Free), with F and P
 590 values for fixed factor (contract), within-subject factor (site) and their interaction (R-ANOVA).

591 Abundance: total number of individuals per 0.12m². Estimated species richness: average of four
 592 non-parametric estimators based on species incidence: Chao1, Jackknife1, Jackknife2 and Bootstrap.

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		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	0.00	1.8	0.18	0.68	0.41
				9	9	7	4	3	7

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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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