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1 Vole disturbances and plant community diversity in a productive hay

2 meadow

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11 Abstract

12 It is recognized that disturbances by fossorial small mammals are important factors determining plant
13 community diversity, especially in grasslands. However, although information about the effects of
14 disturbances by fossorial small mammals on species richness are starting to accumulate, we know
15 little about the impact of these disturbances on the functional and phylogenetic facets of plant
16 community diversity in grasslands.

17 In a study site located in the French Jura Mountains, we compared taxonomic, functional and
18 phylogenetic diversity of plant communities in areas highly disturbed by montane water vole (*Arvicola*
19 *terrestris*) with areas lowly disturbed by this small mammal. In accordance with previous studies, we
20 found that species richness was higher in highly disturbed communities. Indeed, competitive species
21 unable to withstand disturbances were less abundant in disturbed communities, allowing species less
22 adapted to competition for light to survive. Because these species have different trait values in
23 comparison to strong competitors, functional richness was also higher in highly disturbed communities.
24 Results were similar for phylogenetic richness, maybe due to the fact that the used metric was not
25 independent from species richness. Although species composition differed between highly and lowly
26 disturbed communities, functional composition was very similar. Thereby, the studied disturbances
27 were probably not strong enough to affect plant community functioning. Rao functional diversity and
28 functional evenness were not different between both community types. Interestingly, phylogenetic
29 evenness was lower in highly disturbed areas, supporting the idea that disturbances might select for
30 disturbance tolerance traits that are phylogenetically conserved.

31 Though correlational, our results suggest that water vole disturbances may modify multiple facets of
32 plant community diversity, while ecosystem functioning is maintained across disturbance levels.

33 Further research is needed to understand causal mechanisms in this system and the ecological
34 repercussions of small mammal disturbances more broadly.

36 1. Introduction

37 Fossorial small mammals provide valuable ecosystem services in many grassland ecosystems
38 throughout the world (Delibes-Mateos *et al.* 2011; Davidson *et al.* 2012). In particular, fossorial small
39 mammals are important in structuring plant assemblages in grasslands. Many studies have highlighted
40 that their presence increases plant species richness in grasslands (Martinsen *et al.* 1990; Kotliar *et al.*
41 1999; Fahnestock and Detling 2002; Bagchi *et al.* 2006; Questad and Foster 2007), especially through
42 the creation of a mosaic of micro-habitats at the community level (Collins 1989; Canals and Sebastià
43 2000; Yoshihara *et al.* 2009). Martinsen *et al.* (1990) and Hobbs *et al.* (2007) highlighted that the cover
44 of competitive species is lower in plant communities where small mammals are presents.
45 Consequently, subordinate and annual species are present at higher abundances (Martinsen *et al.*
46 1990; Questad and Foster 2007; Yoshihara *et al.* 2009).

47 Small mammals can affect plant communities via engineering interactions and non-engineering
48 interactions such as trophic effects (Sanders *et al.* 2014). In particular, soil disturbances by fossorial
49 small mammals when they create their burrows are important in shaping vegetation assemblages.
50 Indeed, it is recognized that disturbances affect plant species diversity and community composition
51 (White 1979) by creating niche or colonization opportunities through released resources and impaired
52 relationships between species (Huston 1994; Grime 2001; Platt and Connell 2003). Disturbances by
53 ecosystem engineers act also as a major source of heterogeneity in many ecosystems (Jones *et al.*
54 1997; Davidson *et al.* 2012), which is an important driver of species diversity (Huston 1994; Tilman
55 1999). Earth tumuli (i.e. the mounds of earth raised at the entrance of the burrows of fossorial small
56 mammals) damage the existing vegetation when they are created, allowing light to reach lower
57 vegetation layers. Thereby, competition for light is reduced near earth tumuli, permitting species less
58 adapted to competition for light to survive (Seifan *et al.* 2010) and seedlings to grow faster (Martinsen
59 *et al.* 1990). Moreover, changes in soil properties following soil disturbances by fossorial small

60 mammals can improve germination success of certain plant species (Fahenstock *et al.* 2003; Mallen-
61 Cooper *et al.* 2019). Indeed, it has been shown that activities of small mammals may also indirectly
62 impact plant species distribution through effects on circulation and release of soil nutrients (Gervais *et*
63 *al.* 2010; Yurkewycz *et al.* 2014; Risch *et al.* 2015) and on distribution of soil micro-organisms
64 (Aguilera *et al.* 2016). Herbivorous small mammals preferentially consume geophyte species (Hobbs
65 *et al.* 2007), legume species (Kopp 1988; Lantová and Lanta 2009) or grass biomass when easily
66 available (Stenseth *et al.* 1977) while granivorous small mammals preferentially consume seeds of
67 large-seeded species (Stenseth *et al.* 1977). Herbivory by small mammals negatively affects the
68 consumed species (Korell *et al.* 2017) but may increase plant diversity by suppressing dominant
69 species (Prugh and Brashares 2012). However, some authors pointed out that small mammals allow
70 active seed dispersal and increase the germination success of some plant species through
71 endozoochory (Soriguer 1986; Dellafiore *et al.* 2009). Even if engineering interactions (*i.e.*
72 disturbances during the creation of the burrows) seem to have stronger effects on plant community
73 than non-engineering interactions (Prugh and Brashares 2012), both engineering and non-engineering
74 effects are likely to affect plant communities in different ways (Sanders *et al.* 2014) and have to be
75 considered.

76 Since the early 1970s, subsequent to the specialization of agriculture in dairy production in the French
77 Jura Mountains, almost all the utilized agricultural area has been converted into permanent
78 grasslands, resulting in an increase of montane water vole (*Arvicola terrestris*) densities (Giraudoux *et*
79 *al.* 1997). Montane water voles are herbivorous small mammals feeding on plant roots. They find roots
80 by tunneling underground at approximately 20 cm depth (Delattre and Giraudoux 2009). Thus, their
81 foraging activities have engineering effects on soils. Cyclic outbreaks of montane water vole
82 populations (200 to 1000 individuals per hectare) occur every 5 to 8 years (Berthier *et al.* 2014) and do
83 considerable damage on vegetation (Delattre and Giraudoux 2009), resulting in an important loss of

84 forage production (Quéré *et al.* 1999; Schouwey *et al.* 2014). Many studies have been conducted to
85 understand the determinism of these outbreaks (Giraudoux *et al.* 1997; Morilhat *et al.* 2007; Morilhat *et*
86 *al.* 2008) and to limit their intensity (Couval and Truchetet 2014; Foltête *et al.* 2016). However, the
87 impact of montane water vole disturbances on plant diversity and composition in grassland
88 ecosystems have not been assessed yet. In the French Jura mountains, montane water vole density is
89 positively correlated with their disturbance activity (Giraudoux *et al.* 1995). Thus, it is not possible to
90 separate the engineering from the trophic effects of montane water vole on plant diversity and
91 composition. Thereby, the next mentions of disturbances by montane water voles will refer to both
92 engineering and trophic effects.

93 Although the effects of disturbances by small mammals on species richness are well documented, the
94 functional and phylogenetic facets of plant diversity have been taken into account in very few studies.
95 As taxonomic, functional and phylogenetic diversity have been acknowledged to be complementary
96 aspects of community structure, responding differently to environmental changes (Cadotte *et al.* 2013;
97 Pavoine *et al.* 2013), the objective of this work was to investigate the effects of disturbances by
98 montane water voles on different facets of grassland plant alpha diversity and composition in the
99 French Jura Mountains. To do so, we selected a site disturbed by montane water voles at the
100 beginning of the study year and compared plant communities in areas highly vs. lowly disturbed by
101 montane water voles. Richness and evenness were evaluated for both taxonomic, functional and
102 phylogenetic facets of community diversity. We also evaluated taxonomic diversity using the inverse
103 Simpson index and functional and phylogenetic diversity through Rao quadratic diversity with Jost
104 correction. As it corresponds to a generalization of the inverse Simpson index (Jost 2007; de Bello *et*
105 *al.* 2010), it allows for direct comparison of the taxonomic, functional, and phylogenetic facets of
106 community diversity. Moreover, we also considered species composition and functional composition

107 through plant life forms (*i.e.* forbs, legumes and grasses), CSR strategies (Pierce *et al.* 2017) and
108 community weighted means of functional traits.

109 We expected plant taxonomic, functional and phylogenetic diversity metrics to be higher in highly
110 disturbed areas because of the creation of niche opportunities through reduction of resource
111 competition, mainly for light. We hypothesized light availability to be principally altered in comparison
112 to soil resources because the study was conducted in a productive hay meadow fertilized once a year
113 for forage production. Thus, the reduction of competition for light through disturbances by montane
114 water voles would allow the colonization by species less adapted to light competition. We expected the
115 cover of ruderal species to be higher in highly disturbed areas, because these species are favored by
116 disturbances (Pierce *et al.* 2017). At the opposite, the cover of competitive species was expected to be
117 lower because these species do not tolerate disturbances (Pierce *et al.* 2017). Moreover, the cover of
118 legume species was also expected to be lower in highly disturbed areas because they are
119 preferentially consumed by montane water voles (Kopp 1988). However, we supposed that
120 competitive and legume species would still be present along with those that colonized highly disturbed
121 areas, therefore leading to higher plant taxonomic, functional and phylogenetic diversity in highly
122 disturbed areas.

123 2. Material and methods

124 2.1. Study site and sampling design

125 The study site is located in the central part of the French Jura Mountains (La Planée, 6°15'42" E,
126 46°49'36" N) at 975 m a.s.l. Climate is nemoral with a strong suboceanic influence. The mean annual
127 temperature is 6.6°C and the mean annual precipitation is 1187 mm (<http://www.meteofrance.com>).

128 The study site covers approximately 4 ha used for forage production and is not grazed by cattle.

129 According to the farmer, management practices on the study site did not change during the last 5

130 years. The vegetation is fertilized once a year (precise information about the nutrient input were not
131 communicated but it doesn't exceed $120 \text{ kg N ha}^{-1} \text{ yr}^{-1}$), mowed twice a year (in late spring and
132 middle summer) and belongs to the *Trisetum flavescens*–*Polygonum bistorta* Braun-Blanquet & Tüxen
133 ex Marschall 1947 (mountain mesic hay meadows). The study was carried out 18 months after a high
134 density phase of a montane water vole population cycle, during the decrease period.

135 We divided the study site into contiguous sampling units of 100 m^2 ($10 \text{ m} \times 10 \text{ m}$) arranged in a cell
136 grid. To avoid potential edge effects, units located at the border of the study site were excluded. Thus,
137 we obtained a grid of 312 units. During the last week of April 2018, we counted the number of earth
138 tumuli made by montane water voles in each of the 312 units, which has been identified to be
139 positively correlated with their density and disturbance activity (Giraudoux *et al.* 1995). The number of
140 tumuli in a distinct unit ranged from 3 to 53 (mean = 25). According to Giraudoux *et al.* (1995), in units
141 of 25 m^2 , the number of tumuli is significantly positively correlated with water vole abundance for a
142 number higher than 10. Thus, we defined units with more than 40 tumuli as "high density units" (HDU,
143 $n = 37$) and units with less than 20 tumuli as "low density units" (LDU, $n = 135$). Searching for the most
144 contrasted situations, we paired a HDU with an adjacent LDU. In order to limit spatial autocorrelation,
145 each pair had to be separated from the others by at least two units (20 m). As a result, we obtained 16
146 different pairs.

147 The vegetation was sampled during the last week of May 2018 in a plot of 16 m^2 ($4 \text{ m} \times 4 \text{ m}$) located
148 at the center of each selected unit. Total surface covered by plants was significantly different in plots
149 located in HDU ($94.7\% \pm 1.6\%$) in comparison to plots located in LDU ($100\% \pm 0\%$) ($P = 0.004$ using a
150 Wilcoxon-Mann-Whitney paired test). All encountered vascular plant species were listed and their
151 cover estimated using the Braun-Blanquet scale (r, +, 1, 2, 3, 4, 5). We converted these codes into
152 absolute percentage cover (van der Maarel 1979) and adjusted them to relative percentage cover by

153 summing to 100% for each plot (Appendix A). Based on these calculated values, we computed
154 different diversity metrics for the 32 plots.

155 *2.2. Diversity metrics and functional composition*

156 To account for the complementary facets of community diversity, we computed taxonomic, functional
157 and phylogenetic alpha diversities at the plot level (Devictor *et al.* 2010; Cadotte *et al.* 2013; Dainese
158 *et al.* 2015). All metrics computations were done under R v 3.4.2 (<http://www.R-project.org>). Species
159 richness (N0) and inverse Simpson diversity (N2) were computed to evaluate taxonomic diversity,
160 using respectively the `specnumber()` and `diversity()` functions from the `vegan` package (Oksanen *et al.*
161 2018). These metrics are based on Rényi general entropy and expressed as species number
162 equivalents (Hill 1973). Pielou evenness (J1) was also computed according to Jost (2010).

163 To compute functional diversity, we selected four functional traits: specific leaf area (SLA), leaf
164 nitrogen content per dry mass (LNC), leaf dry matter content (LDMC) and maximum plant height (MH).
165 These traits were chosen as they are commonly used in functional ecology of grasslands (Louault *et al.*
166 2005; Ansquer *et al.* 2009; Garnier and Navas 2012; Lososová *et al.* 2016; Mauchamp *et al.*,
167 2016). Maximum plant height is a morphological trait conditioning plant competitive ability (Tilman
168 1988; Westoby *et al.* 2002). LNC, SLA and LDMC provide information about plant growing strategy as
169 they are linked to resource acquisition or conservation (Garnier *et al.* 2004). These functional traits
170 were extracted from two databases: TRY database for LNC and MH (Kattge *et al.* 2011) and LEDA
171 Traitbase for SLA and LDMC (Kleyer *et al.* 2008). From a standardized Euclidean distance matrix, we
172 computed multi-trait Rao quadratic diversity (RaoFD) weighted by the relative percentage cover of
173 each individual plant species. To do so, we used the `Rao()` function provided in de Bello *et al.* (2010).
174 We also calculated multidimensional functional diversity indices: functional richness (FRic) and
175 functional evenness (FEve) (Villéger *et al.* 2008; Laliberté and Legendre 2010) using the `dbFD()`
176 function from the `FD` package (Laliberté *et al.* 2014). Species with missing trait values were excluded

177 from the calculations (7 species out of 56). Thereby, functional metrics were sometimes computed with
178 a bit less than 90% of the sum of relative percentage cover (at least 87%).

179 To summarize the functional composition of each plot, we calculated the relative percentage cover of
180 the usual agronomic plant-life forms (*i.e.* grasses, legumes and forbs) by summing the relative
181 percentage cover of the corresponding species. We also computed community-weighted means for
182 the four functional traits and community-weighted means of CSR strategies, using the values given by
183 Pierce *et al.* (2017).

184 To compute phylogenetic diversity, we constructed a phylogenetic tree composed of the vascular plant
185 species identified in the 32 plots. To build this phylogenetic tree, we followed the same procedure
186 presented in many studies in the French Jura Mountains (Perronne *et al.* 2014; Mauchamp *et al.* 2014;
187 Gillet *et al.* 2016; Mauchamp *et al.* 2016). From GenBank database (Benson *et al.* 2006), we extracted
188 the sequences of two genes encoding chloroplast proteins (*rbcL* and *matK*) for each species. Their
189 complementarity allows to have a good resolution of the phylogenetic tree (Hilu *et al.* 2003). Species
190 not yet sequenced for the selected genes were replaced by their closest available relative (2 species
191 out of 56), according to the APG III classification (APG 2009). We first aligned the sequences using
192 ClustalX 2.1 software (Larkin *et al.* 2007) and then adjusted them manually for both genes. Following
193 the Bayesian Monte Carlo Markov Chain (MCMC) approach under BEAST 1.8.4 software (Drummond
194 and Rambaut 2007), we performed a combined analysis of these two gene datasets. We used
195 MrModeltest2 software (v. 2.0, Evolutionary Biology Center, Uppsala University, SE) to select the
196 model of nucleotides substitution that best fitted the data according to Akaike's information criterion.
197 The retained model was the general time reversible model (GTR), with among-site substitution rate
198 heterogeneity described by a gamma distribution (Yang 1994). Following the APG III phylogeny (APG
199 2009), several family relationships were constrained in BEAST in order to calibrate the rates of
200 molecular evolution of each lineage for angiosperms clades (Bell *et al.* 2005). For branch length

201 calculation, we used an uncorrelated relaxed molecular clock that takes into account evolutionary
202 heterogeneity between lineages (Drummond *et al.* 2006). The ultrametric tree topology was saved in a
203 newick format. To compute phylogenetic diversity (RaoPD), we used Rao quadratic entropy weighted
204 by the ultrametric distances of the phylogenetic tree. To do so, we used the Rao() function provided in
205 de Bello *et al.* (2010). We computed the Faith's PD index (Faith 1992; Tucker *et al.* 2017) to assess
206 phylogenetic richness (PRic), using the pd() function from the picante package (Kembel *et al.* 2019).
207 Phylogenetic evenness (PEve) was calculated using the pse() function (Helmus *et al.* 2007) from the
208 picante package (Kembel *et al.* 2019).

209 *2.3. Statistical analyses*

210 We first tested for differences in average species composition between HDU and LDU applying a
211 PerMANOVA (Anderson and Walsh 2013) on the Bray-Curtiss dissimilarity matrix of the 32 vegetation
212 plots. To do so, we used the adonis() function from the vegan package (Oksanen *et al.* 2018) setting
213 5000 permutations. Because each plot in a HDU was paired with an adjacent plot in a LDU,
214 permutations were constrained within each pair of plots. A nonmetric multidimensional scaling (NMDS)
215 on the Bray-Curtis dissimilarity matrix of the 32 vegetation plots was then performed (Borcard *et al.*
216 2018). We used the vegdist() functions from the vegan package (Oksanen *et al.* 2018) to compute the
217 dissimilarity matrix and the ggplot() function from the ggplot2 package (Wickham *et al.* 2019) to
218 differentiate vegetation plots made in HDU and LDU. We also drew ellipses at 95% confidence level
219 around these two groups to visualize whether their species composition was related or different. Then,
220 we used the betadisper() function from the vegan package (Oksanen *et al.* 2018) to compare the
221 amount of variation in species composition within HDU and LDU.

222 To assess if some species were associated with HDU or LDU, we used the phi coefficient of
223 association (De Cáceres and Legendre 2009), a measure of species fidelity. Applied to species cover
224 data, this index is the Pearson correlation computed between a quantitative vector (*i.e.*, the vector

225 containing the species cover values in the vegetation plots) and a binary vector (*i.e.*, “1” for vegetation
226 plots belonging to the target group, HDU for example, and “0” for vegetation plots belonging to the
227 other group). We performed the computation using the `multipatt()` function from the `indicspecies`
228 package (De Cáceres and Legendre 2009) setting 5000 permutations.

229 We tested for differences in diversity metrics, cover of grasses, legumes and forbs and community-
230 weighted means of CSR strategies between the two plots groups. To do so, we used Wilcoxon-Mann-
231 Whitney paired tests.

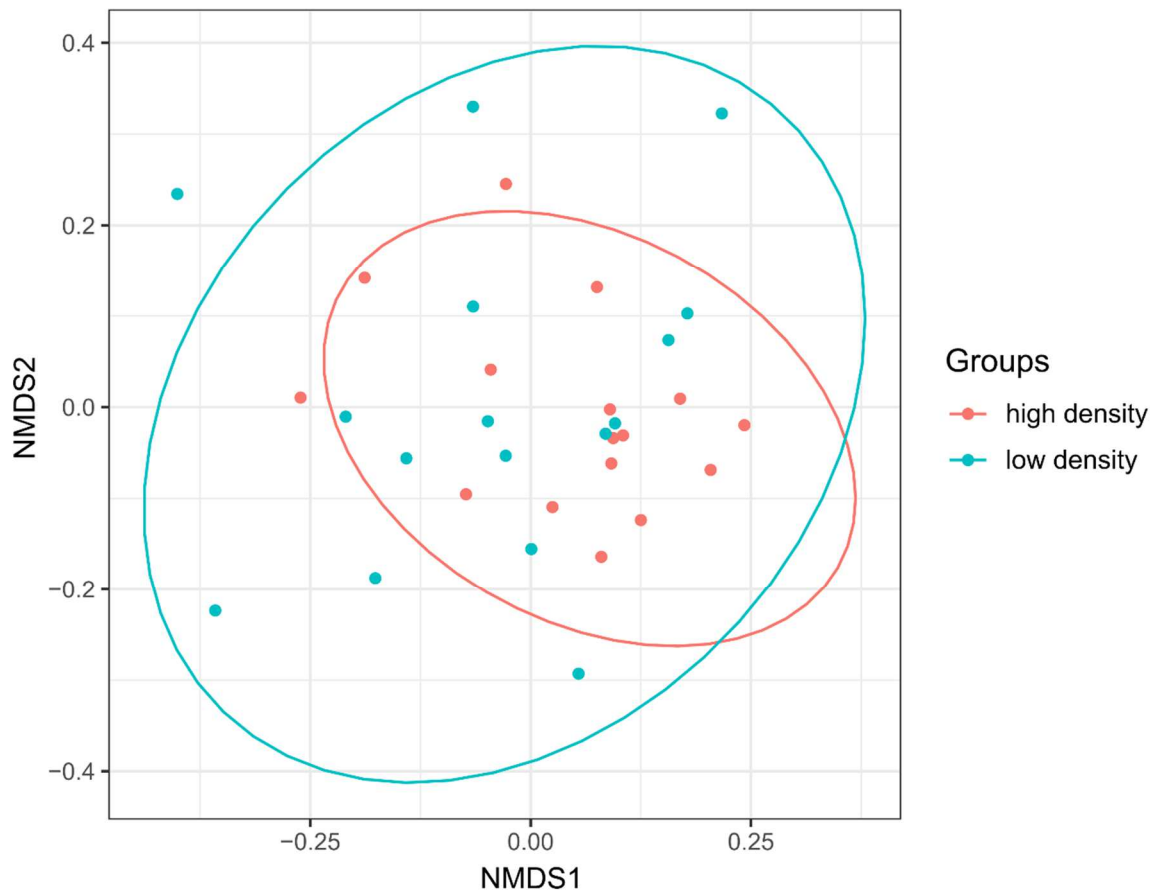
232 We finally tested for differences in average functional composition between HDU and LDU applying a
233 PerMANOVA (Anderson and Walsh 2013) on community-weighted means of functional traits (SLA,
234 LNC, LDMC and MH). Because the selected quantitative functional traits were expressed in different
235 units, we computed a Euclidean distance matrix on the scaled data. To perform the PerMANOVA, we
236 used the `adonis()` function from the `vegan` package (Oksanen *et al.* 2018) setting 5000 permutations.
237 Permutations were constrained within each pair of plots.

238 All analyses were performed under R v 3.6.2 (<http://www.R-project.org>).

239 3. Results

240 3.1. *Plant community composition*

241 Results of the PerMANOVA on species relative cover ($R^2 = 0.064$, $P = 0.007$) revealed that plant
242 communities located in LDU and HDU were different. However, differences were not very large. As
243 evidenced by NMDS (Fig. 1), HDU vegetation plots were more closely related than LDU vegetation
244 plots, which were more scattered (average distance to centroid was 0.28 for HDU and 0.34 for LDU).



245

246 Fig. 1: Nonmetric multidimensional scaling of the Bray-Curtis dissimilarity matrix of the 32 vegetation
 247 plots. Vegetation plots located in “high density units” are displayed in red. Vegetation plots located in
 248 “low density units” are displayed in blue. The confidence level for ellipses is 95%.

249 The fidelity analysis showed that some species were associated with LDU or HDU (Table 1, see
 250 Appendix B for non-significant results). Larger phi values (close to 1) indicate a greater degree of joint
 251 fidelity between the species and the considered group. As these values were rather low, they indicated
 252 a low degree of joint fidelity. *Anthriscus sylvestris* and *Geranium sylvaticum*, two competitive forbs,
 253 were associated with LDU. At the opposite, the short species *Veronica chamaedrys*, *Cerastium*
 254 *fontanum*, *Alchemilla monticola*, *Bellis perennis* and *Ajuga reptans*, as well as *Achillea millefolium* and
 255 *Vicia cracca*, were associated with HDU.

256 Table 1: Degree of joint fidelity (ϕ) of the species associated with one group (“low density units” or
 257 “high density units”) obtained after 5000 permutations. Only significant results are displayed.

	ϕ	P
Species associated with low density units		
<i>Anthriscus sylvestris</i>	0.449	0.009
<i>Geranium sylvaticum</i>	0.318	0.031
Species associated with high density units		
<i>Vicia cracca</i>	0.430	0.014
<i>Veronica chamaedrys</i>	0.414	0.005
<i>Cerastium fontanum</i>	0.390	0.016
<i>Alchemilla monticola</i>	0.356	< 0.001
<i>Bellis perennis</i>	0.339	0.045
<i>Achillea millefolium</i>	0.338	0.002
<i>Ajuga reptans</i>	0.285	< 0.001

258

259 3.2. Plant community diversity and functional composition

260 According to Wilcoxon-Mann-Whitney paired tests (Table 2), plant communities sampled in HDU
 261 generally showed higher species richness (N0), functional richness (FRic), phylogenetic richness
 262 (PRic) and relative cover of grass species (grass). On the other side, plant communities sampled in
 263 LDU generally showed higher phylogenetic evenness (PEve), relative cover of forbs (forb) and
 264 competitive species (straC). Moreover, Rao phylogenetic diversity (RaoPD) showed $P = 0.074$ and
 265 tended to be higher in communities sampled in LDU. Results of the PerMANOVA on community-
 266 weighted mean trait values ($R^2 = 0.043$, $P = 0.144$) revealed that plant communities located in LDU
 267 were not functionally different from plant communities located in HDU.

268 Table 2: Results of the paired Wilcoxon-Mann-Whitney rank tests comparing community descriptors
 269 between vegetation plots located in “low density units” and “high density units”. V is the value of the
 270 paired Wilcoxon-Mann-Whitney rank test and P the P -value. Group means and standard errors are

271 presented for each community descriptors for plots located in “low density units” and “high density
 272 units”.

		Low density units	High density units	<i>V</i>	<i>P</i>
Taxonomic diversity					
N0	Species richness	21 ± 2	26 ± 1	91	0.002
J1	Pielou evenness	0.69 ± 0.01	0.66 ± 0.02	41	0.175
N2	Inverse Simpson diversity	6.15 ± 0.34	6.43 ± 0.44	78	0.632
Functional diversity					
FRic	Functional richness	7 ± 1	11 ± 1	126	0.001
FEve	Functional evenness	0.39 ± 0.03	0.43 ± 0.02	94	0.193
RaoFD	Rao functional diversity	1.29 ± 0.01	1.30 ± 0.01	78	0.632
Phylogenetic diversity					
PRic	Phylogenetic richness	1342 ± 26	1492 ± 39	117	0.009
PEve	Phylogenetic evenness	0.63 ± 0.03	0.55 ± 0.04	26	0.029
RaoPD	Rao phylogenetic diversity	3.17 ± 0.17	2.83 ± 0.21	33	0.074
Community-weighted means of CSR strategies					
straC	Competitive ability	44.2 ± 1.0	40.4 ± 1.0	27	0.034
straS	Stress tolerance	14.3 ± 0.8	16.0 ± 0.9	90	0.274
straR	Disturbance tolerance	41.5 ± 0.8	43.6 ± 1.0	92	0.231
Plant-life forms					
grass	Relative cover of grasses	57.3 ± 3.7	67.2 ± 3.7	115	0.013
forb	Relative cover of forbs	37.6 ± 3.7	28.6 ± 3.6	27	0.034
legume	Relative cover of legumes	5.1 ± 1.1	4.1 ± 0.9	54	0.495

273

274 4. Discussion

275 According to the results of this study, we discuss several possible ecological processes that may
 276 explain our observations. As previously mentioned, the density of montane water voles is positively
 277 correlated with their disturbance activities (Giraudoux *et al.* 1995). Thus, we discuss the disturbances
 278 by montane water voles as including both engineering and non-engineering (trophic) interactions. The
 279 expression of the disturbances by fossorial small mammals is linked to their behavior and population
 280 dynamics. Here, the study has been carried out 18 months after a high-density phase of a montane
 281 water vole population cycle, during the decrease period. However, in the French Jura Mountains, we

282 do not know whether montane water voles select the place where they create their burrows under the
283 influence of specific environmental factors, or if this selection is random. Thereby, the results of our
284 study may suggest causal effects of vole disturbances on plant communities, but they should be
285 interpreted in light of area selection being a potentially confounding variable.

286 Moreover, the total percentage of the surface covered by plants was significantly lower in plots located
287 in HDU in comparison to plots located in LDU. Despite the fact that cover differences were rather small
288 between each pair of plots (approximately 5%), diversity metrics may have been underestimated in
289 HDU because the cover was lower.

290 *4.1. Differences in plant community composition*

291 By altering species interactions, disturbances by small mammals can affect plant communities via
292 engineering interactions and non-engineering interactions such as trophic effects (Sanders *et al.*
293 2014). The comparison of plant communities in areas highly disturbed by montane water voles with
294 plant communities in lowly disturbed ones revealed differences in plant community composition.

295 Differences in plant community composition concerned only a restricted number of species. Only a
296 small set of species was associated with lowly or highly disturbed communities. Contrary to our
297 expectation, the cover of legume species was not lower in highly disturbed plant communities.
298 Moreover, *Taraxacum officinale* and *Trifolium pratense* were not associated with lowly disturbed plant
299 communities although they are known to be preferentially consumed by montane water voles (Kopp
300 1988). Forage quality has been shown to have a positive effect on prairie vole habitat selection (Lin *et*
301 *al.* 2006). Thereby, it might be possible that *Taraxacum officinale* and *Trifolium pratense* were more
302 abundant in areas that were highly disturbed by montane water voles. Because these species were
303 preferentially consumed, their cover could have been decreased before the field work, resulting in an
304 absence of association with lowly or highly disturbed communities. Contrary to our expectations and to

305 findings of other studies (Questad and Foster 2007; Yoshihara *et al.* 2009), the relative cover of
306 ruderal species was not significantly higher in highly disturbed plant communities. The fact that earth
307 tumuli might be quickly colonized by the neighbouring vegetation (Sebastià and Puig 2008), not
308 allowing exogenous ruderal species to colonize the study site, could explain these results.

309 In plant communities highly disturbed by montane water voles, the relative percentage cover of
310 competitive species was lower, probably because these species are not able to withstand
311 disturbances (Grime 1974; Grime 1977; Grime and Pierce 2012). *Anthriscus sylvestris* and *Geranium*
312 *sylvaticum*, two competitive species, seemed to be affected by disturbances. In the study region, these
313 species are commonly found in forest-edge communities and advanced stages of ecological
314 succession in hay meadows (Ferrez *et al.* 2011). Disturbances are known to shift back the stage of
315 succession (Huston 1994; Chesson and Huntly 1997), which could explain why these species
316 presented lower relative cover in highly disturbed plant communities. It is also possible that *Anthriscus*
317 *sylvestris* and *Geranium sylvaticum* were consumed by water voles, thus being less abundant in highly
318 disturbed areas. As these two dominant forbs seemed to be strongly affected by disturbances in our
319 study site, the relative percent cover of forbs was lower in plant communities highly disturbed by
320 montane water voles, contrary to the results of other studies (Martinsen *et al.* 1990; Questad and
321 Foster 2007; Yoshihara *et al.* 2009). Moreover, in our study site, the relative percent cover of grass
322 species was greater in highly disturbed plant communities although it did not concern some species in
323 particular, suggesting that grass species predominate in the fast recovery of vegetation (Rogers *et al.*
324 2001).

325 In grasslands, the creation of disturbances allows weaker competitors for light to survive in the
326 community (Rajaniemi 2002), which can explain that short species such as *Veronica chamaedrys*,
327 *Cerastium fontanum*, *Alchemilla monticola*, *Bellis perennis* and *Ajuga reptans* were associated with
328 highly disturbed plant communities. Indeed, earth tumuli created by montane water voles may provide

329 colonization opportunities for species less competitive for light, as it has been shown to be the case for
330 molehills (Seifan *et al.* 2010). Moreover, the regression of competitive species probably caused by soil
331 disturbances and trophic interactions could also have allowed the development of short species at
332 higher abundance. However, we were able to find these results because we were working in a
333 productive site with a high plant canopy. It is expected that, in less productive sites with a low plant
334 canopy, limitation of light competition by disturbances by montane water voles should be less
335 important. *Achillea millefolium* was also associated with highly disturbed plant communities, which is
336 not surprising considering the fact that this species is typical of intensively grazed grasslands and well
337 adapted to soil disturbances (Sebastià and Puig 2008).

338 *4.2. Differences in plant community diversity*

339 In accordance with previous studies (Martinsen *et al.* 1990; Kotliar *et al.* 1999; Fahnestock and Detling
340 2002; Bagchi *et al.* 2006; Questad and Foster 2007), we observed that plant communities highly
341 disturbed by montane water voles presented higher species richness. Indeed, herbivory by water voles
342 may increase species richness by impacting dominant species (Prugh and Brashares 2012), thus
343 allowing more species to coexist. Moreover, in accordance to the observed differences in plant
344 community composition, this could also be explained by the fact that soil disturbances by montane
345 water voles play an important role in enhancing species richness by providing sites with altered
346 resource availability and reduced competition for light (Seifan *et al.* 2010). Because species less
347 adapted to strong light competition are shorter and present different functional traits in comparison to
348 strong competitors (Ansquer *et al.* 2009; Garnier and Navas 2012), a greater functional richness was
349 also observed in highly disturbed communities

350 Interestingly, we observed no differences in Rao functional diversity and functional evenness between
351 highly and lowly disturbed plant communities. Moreover, as revealed by the PermANOVA on
352 community-weighted mean trait values, functional composition was not different between the two

353 community types. These results support the idea that disturbances by montane water voles, which
354 occurred in our study site before the field work, may not be strong enough to affect community
355 functioning. This also highlights the strong resilience of the studied plant communities. Indeed,
356 permanent grassland vegetation is known to recover relatively quickly from disturbances by small
357 mammals (Quéré *et al.* 1999; Sebastià and Puig 2008). However, since our functional analyses relied
358 on four functional traits, it was important to consider phylogenetic diversity, which summarizes the trait
359 space within a community (Srivastava *et al.* 2012; Winter *et al.* 2013). Results showed that
360 phylogenetic richness was greater in plant communities highly disturbed by montane water voles.
361 However, this was likely due to the fact that phylogenetic richness is not independent from species
362 richness (Faith 1992). At the opposite, phylogenetic evenness was lower in plant communities highly
363 disturbed by montane water voles, suggesting that disturbances might select for disturbance tolerance
364 traits which could be phylogenetically conserved (Dinnage 2009). Indeed, some studies have shown
365 that disturbance increases average relatedness among species (Warwick and Clarke 1998; Verdu and
366 Pausas 2007). Because of reduced competition, disturbed plant communities might be more strongly
367 influenced by environmental filtering of niche traits (Dinnage 2009), allowing only closely related
368 species to become dominant.

369 The limitation of light competition through the creation of gaps in the plant canopy (likely as a result of
370 both herbivory and vegetation destruction during the burrow creation) seems to be the main process
371 affecting plant diversity in highly disturbed plant communities. However, like it was the case for other
372 small mammals (Fahnestock *et al.* 2003; Verdú *et al.* 2009), the seedling recruitment of species
373 associated with highly disturbed communities could also have been improved by soil disturbances and
374 endozoochory. It has been shown by various authors (Kalisz and Davis 1992; Huntly and Reichman
375 1994; Whitford and Kay 1999; Questad and Foster 2007; Mallen-Cooper *et al.* 2019) that disturbances
376 by small mammals might increase soil nutrient input, suggesting that plants located in disturbed areas

377 grow on more fertile soils. However, as plant species associated with highly disturbed communities
378 were mainly short species, it is likely that disturbances principally altered light availability in
379 comparison to the distribution of soil resources. Moreover, changes in soil resources should have
380 been detected by a difference in functional composition because the functional traits used in this study
381 are linked to resource acquisition and conservation (Garnier *et al.* 2004).

382 5. Conclusion

383 Our results suggest that disturbances by montane water voles may modify plant community diversity
384 and composition in the grasslands of the French Jura Mountains. In our study site, like disturbances
385 induced by many other fossorial small mammals, disturbances by montane water voles probably
386 increased species richness and functional richness mainly through the reduction of light competition,
387 allowing weaker competitors for light to occur. However, according to our set of traits, it seems that
388 such disturbances were not strong enough to modify Rao functional diversity, functional evenness and
389 functional composition. Nevertheless, disturbed communities were more dominated by closely related
390 species and thus presented a lower phylogenetic evenness. Montane water voles, perceived as pests
391 and targeted for control in the French Jura Mountains, are likely to play an important role in shaping
392 plant community diversity in permanent grasslands. Indeed, causal effects established in other studies
393 suggest that the results here are also causal. However, pre-disturbance differences in soil structure
394 and in plant community composition within our study site could have influenced our results. Such
395 differences probably influenced area selection by voles, which is thereby a potential confounding
396 variable in our study. Moreover, the observed differences in plant community diversity and composition
397 may also be linked to the past-history of the study site. Thus, further studies aiming at understanding
398 the role of montane water voles on the long-term functioning of grassland ecosystems have to be
399 conducted. Longitudinal monitoring of plots over population cycles of montane water vole, recording
400 jointly plant community, soil properties and small mammal population dynamics, should be a priority.

401 Such monitoring would allow to disentangle the results of area selection by montane water voles from
402 the effects of their disturbances on plant community diversity and composition. Moreover, manipulative
403 experiments should also be conducted to establish causal mechanisms.

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