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Vole disturbances and plant community diversity in a productive hay meadow

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Abstract

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

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

Though correlational, our results suggest that water vole disturbances may modify multiple facets of plant community diversity, while ecosystem functioning is maintained across disturbance levels. Further research is needed to understand causal mechanisms in this system and the ecological repercussions of small mammal disturbances more broadly.

Key-words: small mammals; grasslands; diversity metrics; disturbances; Jura Mountains

1. Introduction

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

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

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

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

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

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

2. Material and methods

2.1. Study site and sampling design

The study site is located in the central part of the French Jura Mountains (La Planée, 6°15’42’’ E, 46°49’36’’ N) at 975 m a.s.l. Climate is nemoral with a strong suboceanic influence. The mean annual temperature is 6.6°C and the mean annual precipitation is 1187 mm (http://www.meteofrance.com). The study site covers approximately 4 ha used for forage production and is not grazed by cattle. 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 kg N ha^{-1} yr^{-1}), mowed twice a year (in late spring and
132 middle summer) and belongs to the *Triseto flavescentis–Polygonion bistortae* 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 m × 10 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 m × 4 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% ± 1.6%) in comparison to plots located in LDU (100% ± 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*
166 *al*. 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

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

2.3. Statistical analyses

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

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

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

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

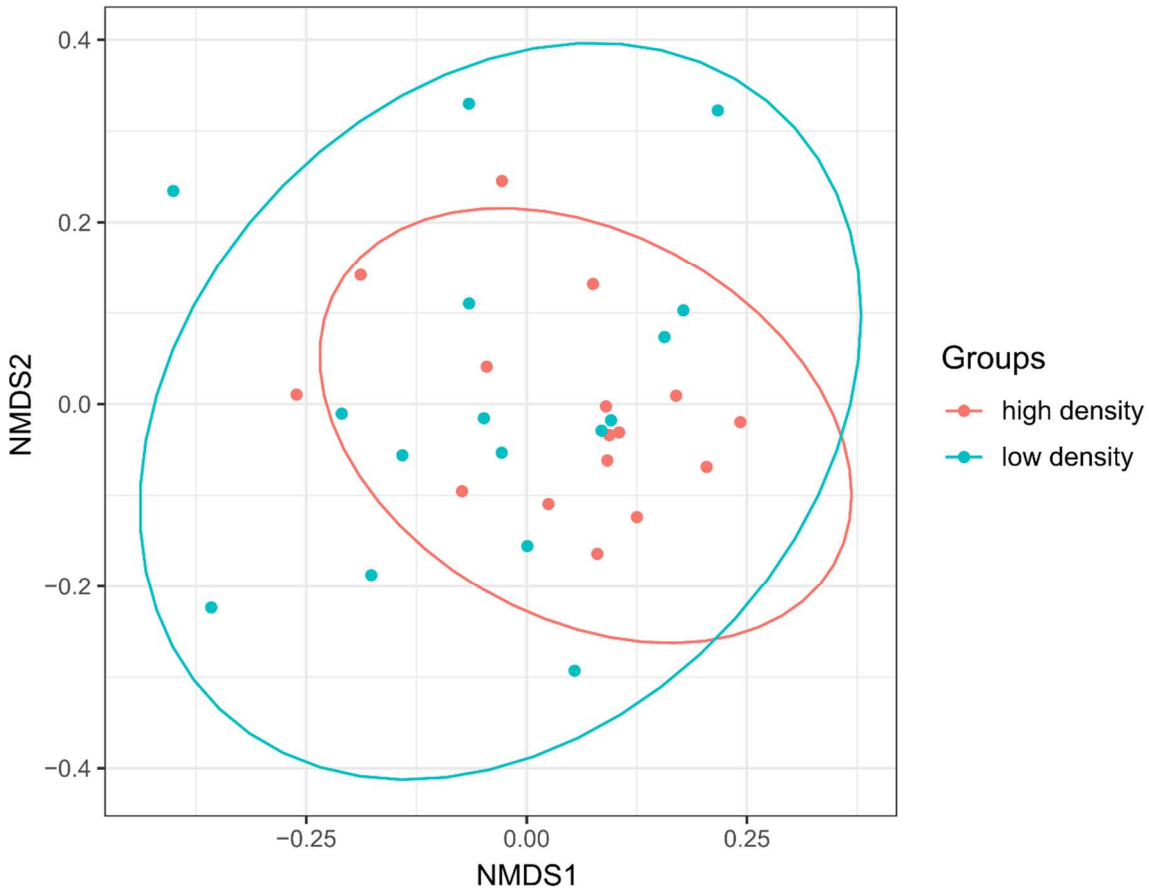
We finally tested for differences in average functional composition between HDU and LDU applying a PermANOVA (Anderson and Walsh 2013) on community-weighted means of functional traits (SLA, LNC, LDMC and MH). Because the selected quantitative functional traits were expressed in different units, we computed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

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

3. Results

3.1. Plant community composition

Results of the PermANOVA on species relative cover ($R^2 = 0.064$, $P = 0.007$) revealed that plant communities located in LDU and HDU were different. However, differences were not very large. As evidenced by NMDS (Fig. 1), HDU vegetation plots were more closely related than LDU vegetation 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.

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

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

3.2. Plant community diversity and functional composition

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

Table 2: Results of the paired Wilcoxon-Mann-Whitney rank tests comparing community descriptors between vegetation plots located in "low density units" and "high density units". *V* is the value of the 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	*V*	*P*
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 richnness	**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

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

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

4.1. Differences in plant community composition

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

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

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

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

In grasslands, the creation of disturbances allows weaker competitors for light to survive in the community (Rajaniemi 2002), which can explain that short species such as *Veronica chamaedrys, Cerastium fontanum, Alchemilla monticola*, *Bellis perennis* and *Ajuga reptans* were associated with 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

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

5. Conclusion

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