

Article (refereed) - postprint

Andriuzzi, Walter S.; Keith, Aidan M.; Bardgett, Richard D.; van der Wal, René. 2013. **Soil nematode assemblage responds weakly to grazer exclusion on a nutrient-rich seabird island.**

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[10.1016/j.ejsobi.2013.05.009](https://doi.org/10.1016/j.ejsobi.2013.05.009)

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1 *Short communication*

2 **Soil nematode assemblage responds weakly to grazer exclusion on a**
3 **nutrient-rich seabird island**

4

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16

17 **Abstract**

18 The effects of aboveground herbivores on plant-soil interactions are highly context dependent
19 and a key underlying factor controlling this is thought to be nutrient availability. Here, we
20 tested whether the effects of vertebrate grazing on the soil food web varied with nutrient
21 availability and hypothesised that soil food web structure would be driven more by the
22 exclusion of vertebrate grazers than by nutrient enrichment. An 8-year long grazer exclusion
23 experiment was performed in grasslands on a small Scottish island near soil nutrient-
24 enriching seabird colonies at the coast and in less fertile conditions inland. We investigated
25 the trophic structure of the soil nematode assemblage as a proxy for soil food web structure.
26 Across all eight study sites the bacterial energy channel was predominant over the fungal

27 channel. Grazer exclusion strongly enhanced plant biomass accumulation and although this
28 tended to be associated with a somewhat lower abundance of bacterial-feeders, this effect was
29 non-significant and surprisingly weak given the observed changes aboveground. Indeed, plant
30 species identity, diversity and dominance were, just as any other vegetation descriptor, weak
31 predictors of nematode trophic structure. Instead, site specific conditions were important,
32 despite the small island area and apparently homogenous sampling conditions.

33

34 **Keywords**

35 Soil food web; Nematode feeding groups; Grazing; Trophic structure; Aboveground-
36 Belowground interaction; Exclosure

37

38 *Introduction*

39 Effects of aboveground primary consumers on the soil food web are context-dependent [1].
40 Herbivores may either promote plant species that produce recalcitrant litter and enhance the
41 fungal energy channel [2], or benefit plants that produce easily decomposable detritus,
42 thereby promoting the bacterial energy channel [3]. This may have important implications for
43 ecosystem functioning, e.g. the response of soil processes to drought [4-5]. Comparison of
44 studies across different ecosystems suggests that the direction of change in soil webs
45 resulting from aboveground grazing may be depend on the fertility of the ecosystem [1]; this
46 hypothesis, however, has rarely been tested.

47 Long-term exclosures have been used to investigate the effects of herbivores on plant-
48 soil linkages in field conditions [6-7], and by sampling such systems repeatedly in time, both
49 short and long term effects of herbivore removal can be studied. This could reveal trends and
50 mechanisms that are otherwise difficult to detect, either early on in a short term experiment or
51 later through comparing an advantage stage to a control. For instance, effects of a plant

52 species on soil can persist years after that species has been replaced, i.e. a plant legacy effect
53 [8]. Herbivores can change the plant species composition of an ecosystem and therefore
54 induce such legacies. Longer term experiments that focus on the interactions between
55 herbivores, plants and soil in different environmental conditions are needed to progress from
56 context-dependent generalisations to context-specific predictions.

57 Here we report on an herbivore exclusion study at sites with contrasting levels of
58 nutrient enrichment to test whether nutrient availability regulates the effects of aboveground
59 herbivory on the soil food web. In particular, we studied the effects of vertebrate herbivores
60 and natural nutrient enrichment on the soil nematode trophic structure on the Isle of May, a
61 small (1.5 × 0.5 km) seabird island in the Firth of Forth, eastern Scotland, UK (56°11'9" N,
62 2°33'27" W). Because the coastal areas of the island receive greatest nutrient inputs from
63 seabird colonies [9], inland and coastal sites were used to represent low and high levels of
64 nutrient enrichment, respectively. Exclosures (n=8) were compared to neighbouring plots that
65 were intensively grazed by rabbits (*Oryctolagus cuniculus*). The main hypothesis was that
66 removal of grazers would override seabird nutrient enrichment in driving the soil food web
67 structure given the profound effect of rabbits on the island's vegetation. We also expected the
68 relative abundance of bacterial-feeders to be greater in grazed areas than in the exclosures,
69 due to a combination of increased rhizodeposition and input of labile organic compounds
70 through faeces and urine, and that such a difference would be weaker at coastal sites as a
71 consequence of greater nutrient availability. While shorter term effects (i.e. over three years
72 following grazing exclusion) of grazing exclusion on the nematode community have been
73 previously reported [10], here we report longer term (eight years) effects. Furthermore, we
74 investigated whether quantitative and qualitative changes in vegetation could explain patterns
75 in nematode trophic structure.

76 ***Materials and methods***

77 The study was carried out at four sites located near seabird colonies (coastal sites),
78 subject to high deposition of ammonia-derived N [9-10] and another four approximately 100
79 m from the colonies (inland sites) subject to lower levels of nutrient supply. Each site was
80 composed of a 5×5 m enclosure which effectively kept out rabbits since its erection in April
81 2003, and an adjacent designated control area of the same size grazed by rabbits. In June
82 2011, two grass-dominated plots (50×50 cm), one in the enclosure and the other in the
83 control, were randomly located at each site. In each plot, the litter layer was removed and
84 three soil turves (4×4 cm, 10 cm deep) were collected with a knife and pooled to obtain a
85 single composite sample from which to extract nematodes and measure soil moisture, salinity
86 and $\text{pH}_{\text{H}_2\text{O}}$. For each plot we also measured the depth of the litter layer (average of three
87 measurements), plant species % cover and vegetation height, and counted the number of
88 rabbit droppings (as indication of grazing intensity). Nematodes were extracted as in [10] and
89 specimens were counted to estimate density. In each sample, 100 random specimens were
90 attributed to one of the following feeding groups: bacterial-feeders, fungal-feeders, plant-
91 feeders, omnivores, and predators [11]. The relative abundance of different feeding groups
92 were used to calculate Trophic Diversity ($1/\sum p_i^2$, where p_i is the proportion of the i th feeding
93 group [12]), and Nematode Channel Ratio ($B/(B+F)$, where B and F are the proportions of
94 bacterial- and fungal-feeders [13]). Plant species data were used to calculate the Shannon-
95 Wiener index of diversity ($-\sum [p_i \ln(p_i)]$, where p_i is the frequency of the i th species) and the
96 Berger-Parker index of dominance (N_{max}/N , where N_{max} and N are the abundance of the
97 dominant species and of all species, respectively).

98 The effects of grazing (fence vs. no fence), location (coastal vs. inland) and their
99 interaction on vegetation height, litter layer depth, plant diversity, nematode density,
100 Nematode Channel Ratio, and Trophic Diversity were investigated with linear models. To
101 determine the extent of between-site variability, site was also used as predictor in separate

102 models. To explore differences in feeding group relative abundances across all sample
103 locations, non-metric multidimensional scaling (NMDS) was performed on a matrix of Bray-
104 Curtis dissimilarities based on feeding group proportions. PERMANOVA [14] was carried
105 out on the Bray-Curtis matrix to determine the extent to which grazing, location and site
106 explained variance in feeding group proportions. Co-Correspondence analysis [15] with plant
107 species as predictors and nematode feeding groups as response variable was also performed.
108 All statistical analyses were performed in R [16] (packages *vegan* [17], *cocorresp* [18] and
109 *nlme* [19]). Model distributional assumptions and homogeneity were checked by plotting
110 standardised residuals against fitted values and producing normal quantile-quantile plots. In
111 the linear models Nematode Channel Ratio was transformed as $\log(x+1)$ to improve
112 normality; residual variance was allowed to differ among levels of a factor when needed to
113 improve homogeneity. Feeding group densities and plant species cover were log-transformed
114 (as $\ln(x+1)$) to reduce skewedness for Co-Correspondence analysis. Data are expressed as
115 mean \pm standard error.

116 ***Results and discussion***

117 A summary of the biotic and abiotic data is provided in Table 1. We found that the
118 fences had effectively excluded rabbits, as no droppings were found in exclosures. Vegetation
119 height was dramatically affected by grazer exclusion ($F_{1,12} = 476.87$, $p < 0.0001$), being 14 \times
120 taller inside the fences along with a 3 \times deeper litter layer than in the controls ($F_{1,12} = 116.45$,
121 $p < 0.0001$). Grazing exclusion led to a less diverse and even grassland community at both
122 coastal and inland sites: the Shannon-Wiener index was higher in the controls than in the
123 exclosures (0.89 ± 0.08 vs. 0.43 ± 0.10 , $F_{1,12} = 11.07$, $p = 0.006$), while the reverse was found
124 for the Berger-Parker index (0.43 ± 0.04 vs. 0.59 ± 0.04 , $F_{1,12} = 7.60$, $p = 0.02$).

125 Nematode density was not significantly affected by grazing or location (Table 1).
126 Nematode Trophic Diversity was not affected by grazing, but was higher at inland ($2.88 \pm$

127 0.19) than coastal sites (2.27 ± 0.13 ; $F_{1,13} = 7.06$, $p = 0.02$). Nematode Channel Ratio
128 appeared highest in grazed conditions (Exclosure: 0.76 ± 0.04 , Control: 0.82 ± 0.02), but this
129 response was not significant ($F_{1,12} = 2.55$, $p = 0.13$), and there was no difference in this
130 measure between coastal and inland sites ($F_{1,12} = 1.81$, $p = 0.20$). The hypothesis that
131 differences in Nematode Channel Ratio between control and exclosures would be weaker at
132 coastal than inland sites was not supported, as the interaction of grazing and location was also
133 non-significant ($F_{1,12} = 0.04$, $p = 0.83$). The Nematode Channel Ratio was always greater than
134 0.5, pointing to a dominance of the bacterial energy channel across all grassland sites.

135 No clear differences in nematode trophic structure among treatments were detected by
136 NMDS, although PERMANOVA indicated a different nematode trophic structure between
137 coastal and inland samples ($F_{1,14} = 3.83$, $p = 0.03$), but not between grazed and exclosure
138 samples ($F_{1,14} = 0.59$, $p = 0.61$). Co-Correspondence analysis confirmed that plant species did
139 not explain patterns in the nematode assemblage (first axis 10.41% fit, $p = 0.58$, 9999
140 permutations), and neither Shannon-Wiener index nor Berger-Parker index had detectable
141 effects on Trophic Diversity or Nematode Channel Ratio. Therefore, the trophic structure of
142 the nematode community was little affected by differences in the vegetation aboveground,
143 despite dramatic effects of grazer exclusion on vegetation height and litter layer depth (Table
144 1). Instead, between-site variation was important, with significant effects on nematode
145 density ($F_{1,7} = 4.08$, $p = 0.03$), Trophic Diversity ($F_{1,7} = 5.70$, $p = 0.01$) and the Nematode
146 Channel Ratio ($F_{1,7} = 32.22$, $p < 0.001$).

147 Overall, the hypothesis that the Nematode Channel Ratio would be higher in the
148 grazed plots relative to those in exclosures was not supported by the data. This may reflect a
149 weak below-ground effect of grazing, as also found by Wright et al. in the first three years of
150 the experiment [10]. Although several studies have shown increases in bacterial-feeding
151 nematodes under grazed conditions [3, 20], the opposite effect has also been reported [2, 21].

152 The lack of effect in our study, however, is surprising given the large effects of rabbits on
153 plant growth (vegetation height) and biomass accumulation (litter layer depth). An
154 explanation could be that our sample size (n=8 exclosures) was too small to overcome the
155 spatial heterogeneity characterising nematode assemblages [22] and, in fact, site was the main
156 factor that explained patterns in nematode trophic structure. The occurrence of such small-
157 scale spatial variability was unexpected, because the island is relatively small, all study sites
158 were ecological replicates in that they were all placed in one plant community, and all sample
159 plots were grass-dominated. However, the absence of a grazer exclusion effect is more likely
160 to be genuine than an artefact of our study design, as no such effect was detected even when
161 controlling for between-site variability. It is also possible that grazing effects occurred in the
162 litter layer (here not sampled) but failed to extend to the soil underneath.

163 Vegetation data did not significantly explain variance in nematode trophic structure.
164 Plant identity has been shown to be an important determinant of the soil nematode
165 community [23-24], but our sites were rather homogeneous in plant species composition. All
166 samples were dominated by the same grass species (Table 1). Therefore, litter quality - a
167 well-known driver of soil food web structure [1] - may not have differed much between
168 treatments. Litter quantity, however, was considerably greater in non-grazed plots, but did not
169 explain variance in nematode trophic structure in the soil below the litter layer. Shifts in
170 species composition that could not be detected by the chosen level of identification might
171 however have occurred.

172 Both univariate and multivariate analyses showed some differences in soil nematode
173 trophic structure between coastal and inland sites. This might be due to differences in soil
174 fertility induced by the seabirds, as the inland sites were not subject to the high levels of
175 guano and ammonia-derived N deposition that characterised coastal sites [9]. Seabirds
176 transfer nutrients from sea to land, often considerably enhancing soil fertility and primary

177 productivity of coastal areas and impacting on higher trophic levels where forming large
178 colonies [25-26]. However, the relative importance of differences in soil fertility in our study
179 is uncertain, as other factors might have been at play. For example, soil moisture was higher
180 at inland than coastal sites ($F_{1,6} = 6.85$, $p = 0.04$), but did not significantly explain variance of
181 any nematode response variable (not shown), and neither did other predictor variables.
182 Therefore, unmeasured factors, perhaps related to greater environmental stress on the plant-
183 soil system near the coast, might have partly driven the differences in the soil food web
184 associated with close proximity to coastal seabird colonies.

185 In conclusion, weak linkages between grazing and the trophic structure of soil
186 nematode assemblages were found on the Isle of May after eight years of herbivore
187 exclusion. In contrast with what was found in the first three years after erection of the
188 enclosures [10], proximity to seabird colonies was more important than grazer exclusion for
189 the overall trophic structure of the nematode community, despite strong effects of grazer
190 exclusion on plant height and litter build-up. No clear relationships between nematode
191 trophic structure and plant species were found. Notwithstanding apparent homogeneity in the
192 grass-dominated plots we sampled, important between-site differences in nematode density
193 and trophic structure were found, adding to the evidence of high spatial variability of
194 nematode assemblages.

195

196 **Acknowledgements**

197 We thank SNH for permission to conduct this research and invaluable logistical support,
198 David Pickett and Mark Newell for their help on the Isle of May, Dan Wright for
199 clarifications on the experimental design, Alex Douglas for statistical advice and two
200 anonymous reviewers for helpful comments on the manuscript.

201

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1 **Table 1.** Estimates (mean \pm SE, n=4) of abiotic and biological variables on the Isle of
 2 May, Scotland, in relation to distance from the main seabird cliffs (coastal or inland
 3 location) and grazing (exclosure or unfenced control)

	Inland Exclosure	Coastal Exclosure	Inland Control	Coastal Control
Environmental properties				
Moisture (%)	67.27 \pm 1.61	65.25 \pm 8.85	54.70 \pm 6.48	40.37 \pm 8.72
pH	4.88 \pm 0.36	5.15 \pm 0.50	5.31 \pm 0.52	5.56 \pm 0.03
Salinity (dS/m)	3.35 \pm 0.15	3.72 \pm 0.18	3.65 \pm 0.62	3.25 \pm 0.26
Vegetation height (cm)	24.65 \pm 1.81	26.30 \pm 1.19	1.80 \pm 0.14	1.72 \pm 0.07
Litter depth (cm)	7.75 \pm 0.25	8.87 \pm 0.72	2.25 \pm 0.59	3.50 \pm 0.29
Rabbit droppings	–	–	21.82 \pm 3.99	12.72 \pm 1.84
Soil nematodes				
Density (ind./cm²)	519.38 \pm 151.04	748.46 \pm 150.53	670.68 \pm 196.80	752.26 \pm 207.14
Bacterial-feeders (%)	38.50 \pm 6.12	60.50 \pm 7.92	49.00 \pm 4.56	59.75 \pm 3.350
Fungal feeders (%)	15.25 \pm 4.33	15.00 \pm 5.69	13.00 \pm 2.86	10.50 \pm 2.99
Plant feeders (%)	38.25 \pm 9.63	18.75 \pm 7.23	26.00 \pm 0.71	22.50 \pm 3.59
Omnivores (%)	5.25 \pm 2.06	1.75 \pm 0.63	6.00 \pm 4.06	3.00 \pm 0.71
Predators (%)	2.75 \pm 1.11	4.25 \pm 2.36	6.25 \pm 2.87	4.00 \pm 1.08
Plants species cover (%) †				
<i>Festuca rubra</i>	56.75 \pm 4.50	50.50 \pm 13.26	46.75 \pm 7.73	39.75 \pm 5.42
<i>Silene uniflora</i>	1.5 \pm 0.64	0.5 \pm 0.50	0.3 \pm 1.78	5.0 \pm 1.4719601
<i>Agrostis stolonifera</i>	5.00 \pm 1.87	27.50 \pm 15.16	16.00 \pm 2.97	23.75 \pm 4.66
<i>Holcus lanatus</i>	–	0.75 \pm 0.75	0.25 \pm 0.25	2.50 \pm 1.89
<i>Rumex acetosa</i>	1.00 \pm 1.00	1.00 \pm 1.00	1.50 \pm 0.64	1.00 \pm 1.00
<i>Potentilla erecta</i>	0.25 \pm 0.25	–	–	–

4 † Only species in more than 2 samples with 5% cover are shown

5