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Ruben van de Walle, François Massol, Martijn L Vandegehuchte, Dries Bonte. The functional composition of dune nematode communities is structured by both biogeographic region and the local marram grass environment. *European Journal of Soil Biology*, 2023, 117, pp.103511. 10.1016/j.ejsobi.2023.103511 . hal-04273874

HAL Id: hal-04273874

<https://hal.science/hal-04273874v1>

Submitted on 7 Nov 2023

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1 The functional composition of dune nematode communities is
2 structured by both biogeographic region and the local marram grass
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19

20 Abstract

21 Nematodes are involved in many important ecosystem functions such as nutrient cycling and plant
22 growth. Nematode communities are thought to be structured at regional scales mainly by abiotic soil
23 characteristics and climatic drivers and at local scales by habitat heterogeneity and biotic
24 interactions. Blond dunes are dominated by marram grass (*Calamagrostis arenaria*), the key dune-
25 forming plant species in Western Europe. Consequently, nematode food webs are mainly associated
26 with marram grass in these coastal areas.

27 We investigated the relative importance of regional biogeographic factors and local biotic drivers,
28 such as the vegetation's spatial structure and the occurrence of an invasive plant species, in
29 determining the functional diversity of belowground nematode communities inhabiting the roots of
30 marram grass and surrounding soil in coastal dune areas.

31 We found that nematode functional group abundances mainly differed among biogeographic
32 regions, but that abundances could not be linked to plant-associated parameters, such as plant
33 vitality or abundance. Additionally, the abundances of different functional groups seemed to be
34 positively associated within both rhizosphere and bulk soil, an effect that could be the result of
35 ecological filtering or facilitative interactions.

36 Nematode pressure has been assumed to be an important driver of marram grass degeneration
37 under ceasing sand dynamics. We here show that variation in nematode functional group
38 composition is only weakly related to these local changes in plant vigour, but that large-scale
39 patterns in nematode communities may explain regional variation in marram dynamics in coastal
40 dunes.

41

42 **Key words:** soil biota, coastal dunes, feeding guilds, co-occurrence, JSDM

43 Introduction

44 Nematodes are the most abundant animals on the planet, occurring in all ecosystems [1]. Nematode
45 numbers and functional group composition are affected by abiotic factors at different spatial scales.
46 At global scales, total nematode and functional group abundances of soil nematodes were shown to
47 be mainly affected by regional soil characteristics such as soil organic carbon content or soil acidity
48 [2–4]. Climatic drivers, such as precipitation and mean annual temperature, also affect nematode
49 abundances, albeit not as importantly as soil characteristics [2–4].

50 Because nematodes are poor dispersers [1], the current view is that environmental heterogeneity at
51 smaller scales is a more important driver of soil nematode community structure. Nevertheless,
52 passive dispersal seems to enable nematodes to disperse over longer distances [5,6]. Soil disturbance
53 and environmental heterogeneity are examples of small-scale phenomena commonly linked to
54 nematode abundances [3,7,8]. Disturbed soils mainly host opportunistic bacterivorous nematodes,
55 and are poor in predatory and omnivorous species [7,9,10]. An increase in potential niches due to
56 environmental heterogeneity also increases nematode species diversity [8,11,12].

57 The abundance and functional diversity of soil biota is not only driven by abiotic factors. Biotic
58 interactions among nematodes and between nematodes and other taxa, especially host plants, can
59 furthermore influence nematode abundances. The characteristics of the vegetation (plants species
60 composition) will affect the nature and amount of resources available to the food web via root
61 exudates, root turnover, leaf litter return, and water use [7,13]. Moreover, plants can defend
62 themselves against herbivory either directly, e.g., via production of chemical compounds [14], or
63 indirectly, e.g., by attracting natural predators of their pests [15,16]. Apart from host plants, invasive
64 plant species can also drastically alter nematode abundances [17,18], for instance, via altering the
65 native plant community [18] or by acidification of the soil [19].

66 One host plant species from which the soil nematode community is already well described is marram
67 grass (*Calamagrostis arenaria* (L.) Roth, formerly *Ammophila arenaria*). This plant received much

68 attention due to its key role in the process of dune formation in Western Europe [20], which is driven
69 by the interaction between vegetation development and aeolian dynamics, the movement of sand by
70 wind. Marram grass not only tolerates high levels of sand burial, it even needs sand burial to survive
71 and it thrives best at intermediate burial rates of about 30 cm of sand per growing season [21]. If
72 sand dynamics cease, marram grass slowly decays and is outcompeted by later successional plant
73 species [22]. This phenomenon was already observed more than fifty years ago and coined ‘the
74 *Ammophila* problem’ [23]. Marram grass is able to overcome this problem by capturing sand, which
75 in turn positively affects its growth and sand accumulation capacity, causing a positive feedback loop.
76 The reduction in marram grass performance is thought to be caused by the biological component of
77 the soil, in particular the root-feeding nematodes [22,24–27; see 27 for a review].

78 At the regional scale, dune soil characteristics depend strongly on the biogeographic history of the
79 area, which is tightly linked with large-scale differences in soil pH, nutrient concentrations and
80 climate variables [28–30]. Variation in soil characteristics in dune areas within Western Europe is
81 mainly linked with acidity and nutrient concentrations. For example, the Belgian coast consists of
82 lime-rich sand [28], while others are completely decalcified and thus more acidic, such as the
83 Northern part of the Dutch coast [29]. More acidic soils are known to harbour lower nematode
84 numbers [31]. At a local scale, the constant sand burial can be seen as a form of (natural) soil
85 disturbance. If marram grass occurs in a patchy distribution, its sand-trapping efficiency is optimal
86 [27,32,33], and therefore the associated nematode abundances (especially those of predatory and
87 omnivorous nematodes) are expected to be lower.

88 While marram grass is the dominant plant species in many European coastal dunes, the invasive herb
89 *Senecio inaequidens* D.C. is expanding its range into European coastal dunes [34]. Plants of the
90 *Senecio* family are well-known for their production of pyrrolizidine alkaloids as defence mechanism
91 against herbivory [14,35], with *S. jacobaea* even shown to protect surrounding plants via
92 associational resistance [36]. What the long-term effects of the colonization of coastal dunes by *S.*

93 *inaequidens* will be is largely unknown [34]. However, giving its potent chemical defenses, effects of
94 *S. inaequidens* invasion on dune soil food webs are plausible.

95 As marram grass seems to mainly rely on a combination of sand overtopping and associations with
96 microorganisms to escape root-feeding nematodes [26,37], small-scale biotic interactions are
97 omnipresent in marram dunes. Interspecific competition among nematodes has been shown to
98 alleviate average declines in marram grass fitness under lab conditions [38]. However, addition of the
99 same species did not influence plant performance in a more natural environment [25]. Facilitating
100 interactions between nematodes received far less attention; nevertheless it has been established in
101 some lab experiments [39–42].

102 We investigated the relative importance of regional biogeographic factors, associated with soil
103 characteristics and climate, and two local biotic drivers: marram grass spatial structure and *Senecio*
104 *inaequidens* occurrence, in determining the functional structure of belowground nematode
105 communities inhabiting the roots of marram grass and the surrounding soil in coastal dune areas in
106 Western Europe. We hypothesised that (1) at regional scales, nematode functional abundance is
107 lower in the regions with more acidic coastal dunes. (2) An increasing cover of marram grass
108 positively influences abundances of nematodes found in the roots, while (3) nematode abundances
109 would increase with clustering of the host plant as a consequence of the less efficient sand-capture
110 of these configurations. (4) The fungivorous and bacterivorous nematodes are expected to be more
111 abundant in soil from underneath less vital marram grass tussocks due to the presence of
112 decomposing organic matter and fungus growth, while plant-feeding nematodes are expected to
113 increase in abundance with marram grass vitality. (5) Since *Senecio* species are known to produce
114 chemical compounds, we expect a decline in all, but especially root-feeding, nematode functional
115 group abundances when *S. inaequidens* is present in the vicinity.

116 Material & Methods

117 **Study area**

118 Our study was conducted in the North of France, Belgium, the Netherlands and the United Kingdom.
119 Respectively, 124, 39, 19, 30 samples were taken along 19 different transects parallel to the coast
120 line in these countries. The transects were located within the first 100 m from the seaward side of
121 marram-dominated, yellow dunes (Natura 2000 habitat 2120, CORINE biotope 16.21). The number of
122 samples per transect depended on the length of the dune transect, with an average of 11 samples
123 per transect (min 4; max 31). Individual sampling locations were separated by at least 20 m.

124 We subdivided our study area into five distinct biogeographical districts (Fig. 1), which differ all in
125 climate and soil characteristics because of their geological history [30]. In general, these differences
126 are inherently correlated with a gradient from South to North, with lime richness and mean annual
127 temperature declining from the Boulonnais to the Flemish, Renodunal and Wadden district [28–30].
128 The temperature in the UK region is similar to regions situated on the same latitude, but the sandy
129 sediments have a higher acidity compared to the French and Belgian dunes, and in general a more
130 species-poor biodiversity compared to continental dunes.

131

132 **Data collection**

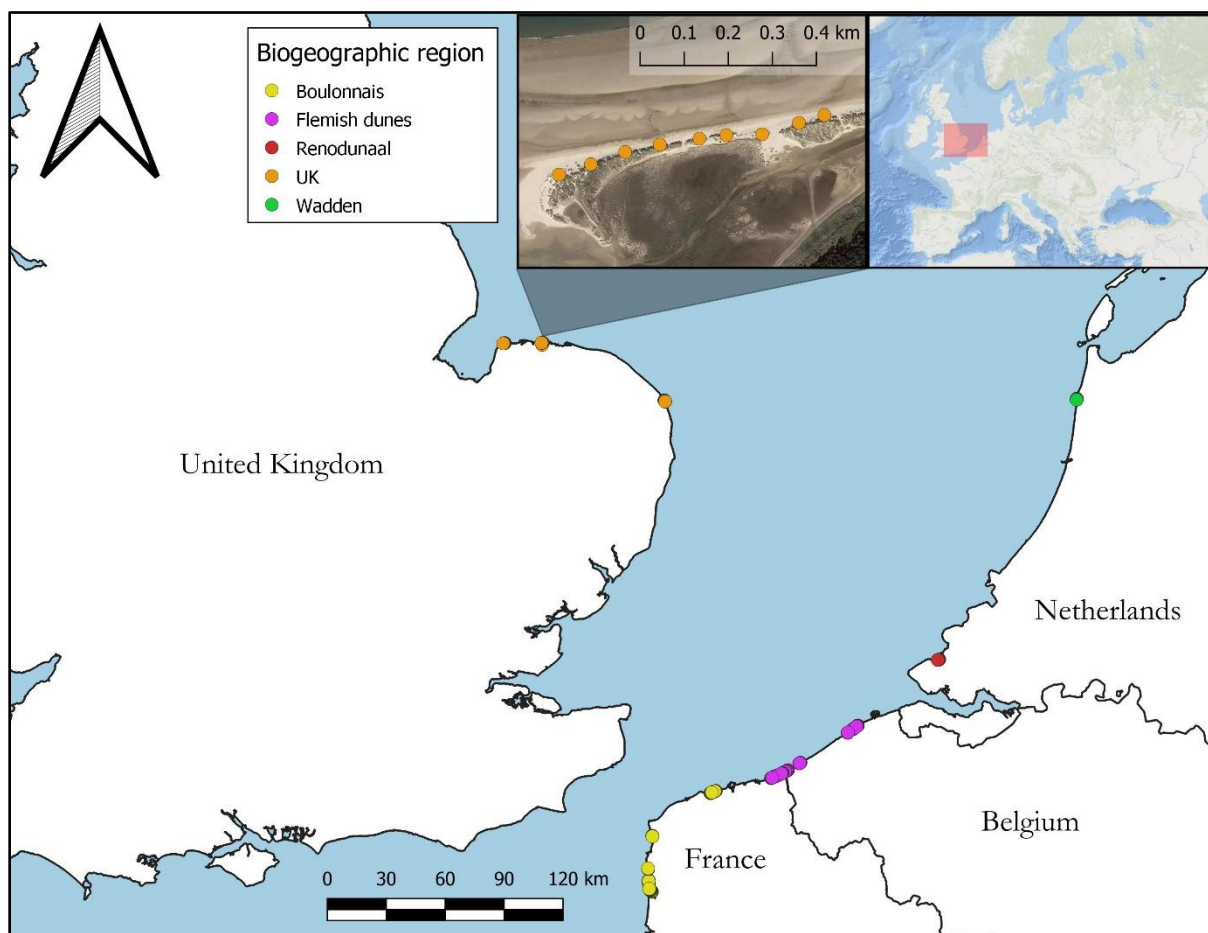
133 Each sampling location had a central marram grass tussock from which soil and root samples were
134 taken at the minimum depth at which live marram grass roots were found during the summer of
135 2018 or 2019. Samples were stored in the field in a box containing cooling elements to slow down
136 nematode metabolism, consequently lowering mortality. In the lab, samples were stored in the
137 fridge until processing for the same reason. Nematodes were extracted from roots and sand
138 separately, using 2 +/- 0.5 and 20 +/- 1 g fresh material respectively, via the Baermann Funnel
139 extraction method [43]. This method ensures that only the active fraction of the nematode soil
140 community is quantified. Roots and soil were sieved (2.0 mm mesh) and roots were gently washed
141 before the extractions. 15 mL water was collected every 24 h for three consecutive days. Finding

142 fresh roots was difficult for some sampling locations, resulting in a relatively large difference in the
143 amount of roots used for the extraction. To account for this discrepancy, the number of nematodes
144 per gram dry sand/roots was determined by drying separate portions of substrates in an oven at 70°C
145 for 24h to obtain relative moisture contents, which were consecutively used to calculate dry weights
146 of the portion of the samples used for the extraction. The whole roots were cut up and mixed prior
147 to separating the portions for the extraction and the water content determination. Nematodes were
148 fixed and stored in 5% hot formalin (60-70°C). The vials were sealed with parafilm until they were
149 counted. While counting, nematodes were classified into functional groups, using an inverse
150 microscope (10x40 or 10x100 magnitude), based on characteristics of their mouth apparatus,
151 pharynx, and cuticle. These functional groups differ in their feeding habits: plant feeders, bacterial
152 feeders, fungal feeders, omnivores and carnivores [44]. A sixth “Unknown” class was used for
153 nematodes too damaged to classify. When nematodes were very abundant, classification was done
154 until 200 nematodes were counted and numbers were then extrapolated based on the area of the
155 counting dish.

156 The following variables were used as explanatory variables in the analysis: The proportion of marram
157 grass and its spatial configuration, the vitality of the tussock, the biogeographical district (as
158 described above), and the presence-absence of *Senecio inaequidens*.

159 Within a 10 m radius around each central marram grass tussock, marram grass cover (P , expressed as
160 proportion) and spatial auto-correlation (Moran's I ; Moran 1950, Bivand and Wong 2018) were
161 calculated from vegetation maps of the coastal dune areas [27]. Moran's I is negative when the
162 marram grass is regularly distributed in the landscape. If marram grass is randomly distributed, the
163 parameter is close to 0, and it is positive when the marram grass occurs in clusters. As pointed out by
164 Bonte et al. (2021), marram grass distribution is almost always clustered and rarely random. The
165 sample locations were chosen so that they maximised the variety of surrounding marram grass
166 configurations within one dune transect.

167 Furthermore, small-scale environmental heterogeneity is mainly linked with marram grass vitality in
168 our study: vital tussocks provide mainly fresh plant material while less vital tussocks provide a
169 mixture of both alive and dead plant material. To include this parameter in our analysis, each
170 marram grass tussock was given a vitality score (integer value ranging from 0 to 4) based on the
171 estimated % of green leaves visible in the tussock on a photograph. Finally, occurrence
172 (presence/absence) of *Senecio inaequidens* was mapped within a 5 m radius around the central
173 marram grass tussock.



174
175 **Figure 1:** Geographic scope of the study. Transects are indicated and coloured per biogeographical district. The left inset
176 shows an example of the sampling unit locations (orange dots) within the indicated transect (Holkham, UK; satellite image:
177 © 2023 Google). Figure made with QGIS v3.2.3-Bonn [47].

178

179 **Statistics**

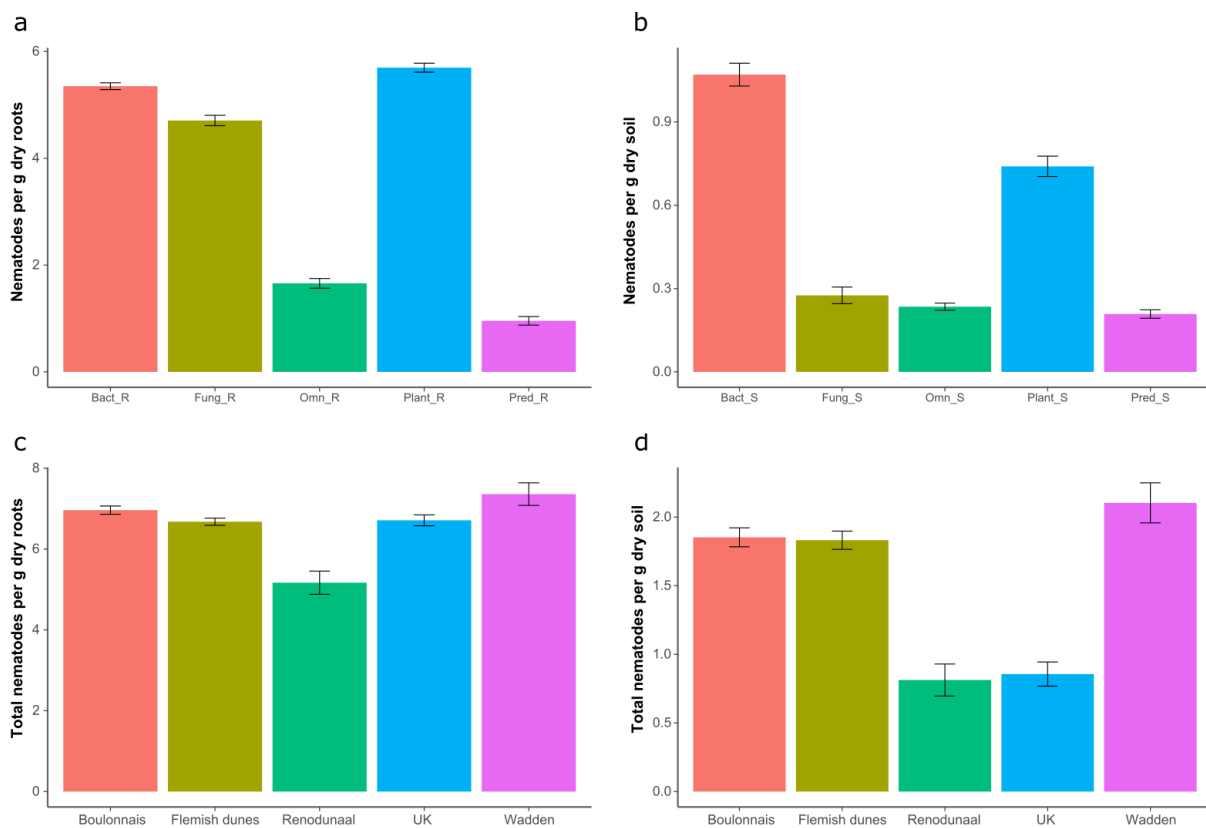
180 The nematode data were analysed using the HMSC framework, according to the methods described
181 by Ovaskainen & Abrego (2020). For this multivariate analysis, the functional group data (abundance
182 per g of dry root or soil) for both the soil and root sample for each marram grass tussock were (log +
183 1)-transformed. The proportion of marram grass and its spatial configuration, the vitality of the
184 tussock, the biogeographical district and the presence-absence of *S. inaequidens* were used as
185 explanatory variables. To test for a quadratic effect of the proportion of marram grass (P) and the
186 vitality (V) of tussocks, four JSDBMs were fitted with either P and/or V as a quadratic term or not.
187 Among those, the 'best' model was selected using the Widely-Applicable Information Criterion
188 (WAIC; Watanabe 2010, Ovaskainen and Abrego 2020). The random effect structure was
189 implemented to account for the spatial context of our study. A large, regional-scale random effect
190 was modelled on the transect level to correct for possible dependency of data within transects. A
191 local-scale random effect was modelled on the marram grass tussock level. This enables us to infer
192 residual associations between feeding guilds after accounting for the effects of the explanatory
193 variables [48]. Partitioning of the explained variance between all fixed and random effects was used
194 to discern the importance of the different parameters for functional group abundances. The F-
195 statistic of the fixed effects was manually calculated in order to account for the varying degrees of
196 freedom when comparing relative importance of the effects. For all models described above, the
197 posterior distribution was sampled with three Markov chain Monte Carlo (MCMC) chains. HMSC
198 specifically uses blocked Gibbs sampling [50]. Each chain ran 150 000 iterations, with a burn-in period
199 of 50 000 samples and thinning factor of 100. Each chain ran for 1000 posterior samples per chain for
200 a total of 3000 posterior samples.

201 R Statistical Software version 4.0.4 [51] was used for all data analyses. Moran's I of marram grass
202 surrounding the central tussock was calculated using the "moran.test" function from the "spdep"
203 package [46]. The HMSC was performed using the R package "Hmsc" [52]. Trace plots,
204 autocorrelation plots and posterior densities were made and calculated using the 'mcmcplots'
205 package [53].

206 The code is available on GitHub [https://github.com/Ruben-VDW/Marram_nematodes].

207 Results

208 Total nematode counts varied from 29 to 6800 individuals per gram of dry roots or 0.1 to 92
209 individuals per gram of dry bulk soil, with means (median) of 1236 (890) and 6 (4.4) respectively.
210 Bacterivorous and plant-feeding nematodes reached, on average, the highest abundances in both the
211 root and soil samples compared to omnivores and predators, while fungal feeders reached densities
212 close to bacterial feeders in the root samples only (see Fig. 2a and 2b). Total nematode abundances
213 were lowest in the Renodunal district, followed by the UK, for both the root and soil portions of the
214 samples (see Fig. 2c and 2d).



215

216 **Figure 2:** The log-transformed $[\ln(\text{abundance} + 1)]$ number of nematodes found per functional group in (a) the roots and (b)
217 the soil. Error bars represent standard errors. Functional groups are indicated as follows: Bact: bacterivore nematodes,
218 Fung: fungivore nematodes, Omn: omnivore nematodes, Plant: root-feeding nematodes, Pred: predatory nematodes; the
219 last letter of the code indicates the substrate used for the extraction (R = roots, S = soil). The total number of nematodes
220 found in (c) the roots and (d) the soil per biogeographical district. For c & d, barplots are based on 74 samples for the
221 Boulonnais, 89 samples for the Flemish dunes, 10 for the Renodunal district, 30 for the UK and 9 for the Wadden district.

222

223 MCMC convergence and model selection

224 Convergence of the HMSC models was good for all four models. Trace plots of the iterations showed
 225 an irregular pattern with similar running means for all chains. Furthermore, the potential scale
 226 reduction factors were all below the 1.1 threshold for all models. Based on WAIC, no clear best
 227 model could be discriminated, thus the least complex model was chosen for further analysis (also
 228 lowest WAIC, see table 1).

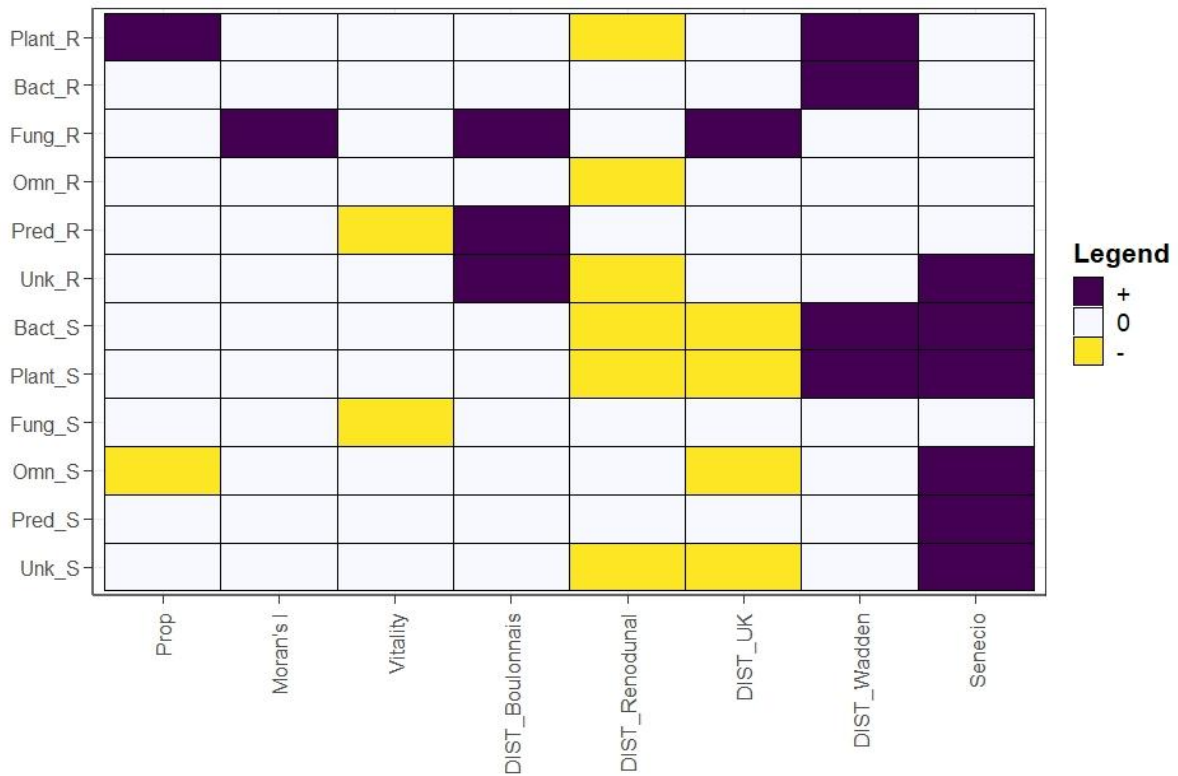
229 *Table 1: Summary measures of model fit and model selection. For R2 and RMSE the mean is given over all species with the*
 230 *interquartile range between parenthesis. CV stands for cross-validation.*

| Model | Structure | R | R (CV) | RMSE | RMSE (CV) | WAIC |
|-------|-----------------------------------|---------------|---------------|---------------|---------------|----------|
| 1 | P + Vit | 0.545 (0.244) | 0.109 (0.131) | 0.494 (0.307) | 0.711 (0.590) | 25.87953 |
| 2 | P ² + Vit | 0.548 (0.251) | 0.090 (0.164) | 0.492 (0.610) | 0.769 (0.788) | 25.99523 |
| 3 | P + Vit ² | 0.550 (0.249) | 0.081 (0.139) | 0.490 (0.611) | 0.771 (0.745) | 25.96141 |
| 4 | P ² + Vit ² | 0.528 (0.343) | 0.075 (0.091) | 0.465 (0.544) | 0.777 (0.717) | 27.21449 |

231

232 Responses to environmental variables

233 When describing the relationship between the environmental variables and the different functional
 234 groups, we focussed only on effects with at least 95% posterior probability (Fig. 3). The proportion of
 235 marram grass in the near vicinity was only positively correlated with the abundance of plant-feeding
 236 nematodes found in the roots, while it was negatively correlated with the abundance of omnivores
 237 found in the bulk soil. The spatial configuration of marram grass only affected the abundance of
 238 fungivorous nematodes found in the rhizosphere. Fewer predatory and fungivorous nematodes were
 239 found in the bulk soil of more vital marram grass tussocks. The biogeographical regions clearly
 240 affected the root and soil nematode functional abundances, with generally more nematodes found in
 241 the Boulonnais and the Wadden district, and fewer nematodes in the Renodunal district and in the
 242 UK. Finally, the presence of *Senecio* positively influenced all nematode abundances found in the bulk
 243 soil, except fungivore nematode abundance.

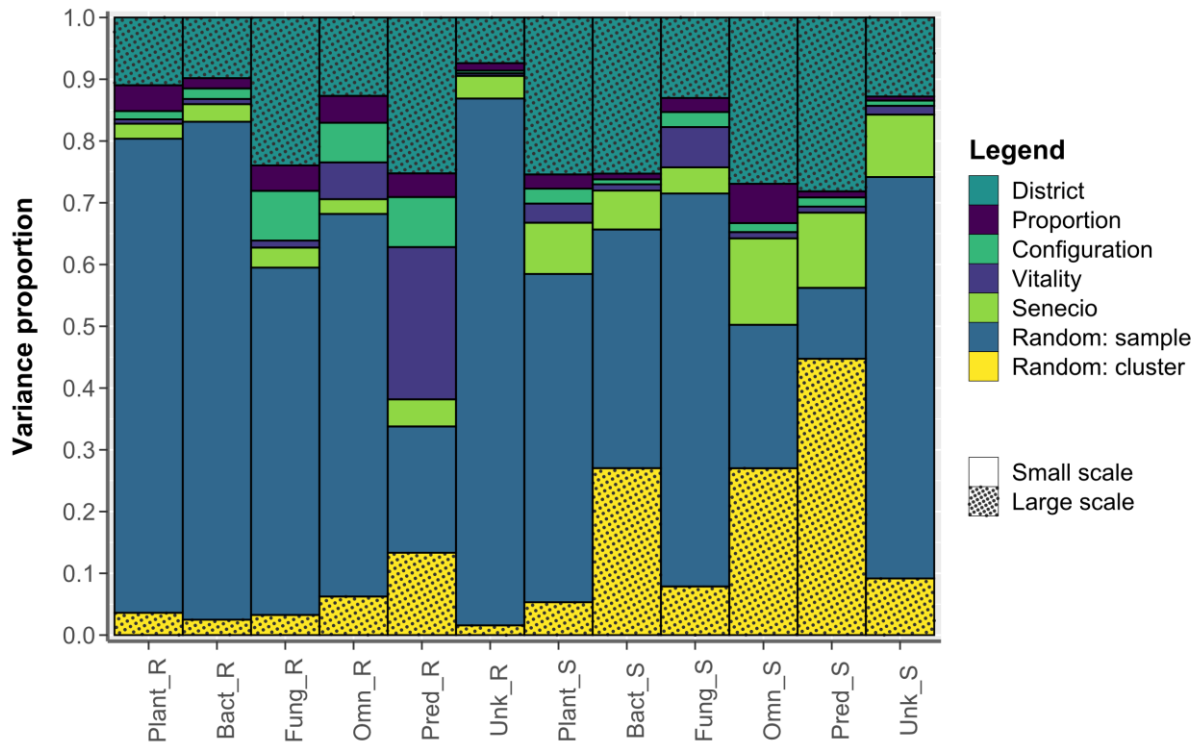


245

246 **Figure 3:** The responses (β 's) of the species to the environmental variables. Responses that are positive with at least 95%
 247 posterior probability are shown in purple and responses that are negative with at least 95% posterior probability are shown
 248 in yellow. Functional groups are indicated on the y-axis, codes as in Fig. 2.

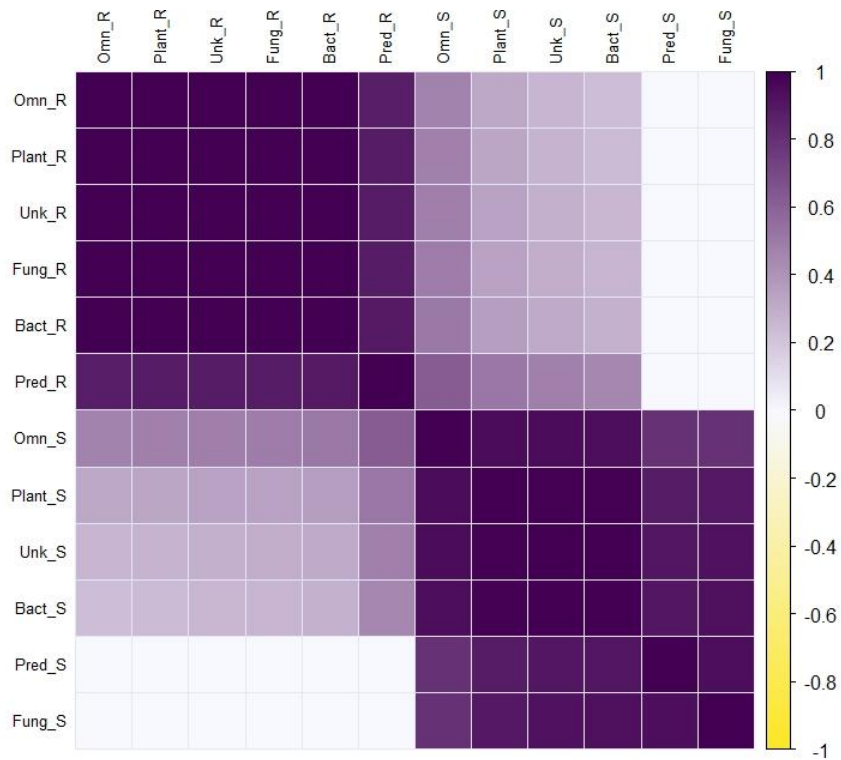
249 Variance partitioning over the fixed effects showed that the explained variation (median) can be
 250 attributed for 18.9% ($F_{4,192} = 13.8$) to large-scale and for 15.6% ($F_{4,192} = 11.4$) to small-scale
 251 environmental variables. Among the environmental variables, the explained variation was distributed
 252 as follows: the different biogeographical districts explained 18.5 % ($F_{4,192} = 13.5$), the presence of *S.*
 253 *inaequidens* 4.3 % ($F_{1,192} = 12.5$), the proportional cover of marram grass 2.3 % ($F_{1,192} = 6.73$), marram
 254 grass spatial configuration 1.6 ($F_{1,192} = 4.68$) % and marram grass vitality 1.1 % ($F_{1,192} = 3.22$) (Fig. 4).
 255 Finally, the random effect on transect unit scale covered 7.1%, while the residual variance on sample
 256 level scale was 59.1%. Most variation is thus associated with single samples, demonstrating that
 257 either other unmeasured effects or stochasticity are driving most of the variation in the local
 258 nematode functional group composition. From the residual association matrix (Fig. 5), it is very clear
 259 that different nematode functional groups extracted from the roots are highly positively associated

260 with each other, and that the same holds true for nematodes extracted from soil. Several weaker
 261 positive associations were found among nematode functional groups from bulk and rhizosphere soil.



262
 263 **Figure 4:** Variance partitioning of the explained variation among the random and fixed effects in the HMSC model. The two
 264 random effects are based on the residual variation. *Functional groups are indicated on the x-axis, codes as in Fig. 2.*

265



266

267

268

Figure 5: Residual species association matrix that shows species pairs with a positive (purple) or negative (yellow) association. Associations are only shown if the association had at least 95 % probability. Functional group-codes as in Fig. 2.

269 Discussion

270 Compared to other terrestrial biomes, we found coastal dune areas to be characterised by
271 intermediate nematode abundances in the bulk soil with an average total of 6 nematodes per gram
272 of soil, as expected [2,54]. With an average of 1200 nematodes per gram of roots, nematode
273 abundances found in marram grass roots and rhizosphere were on the higher end, but still within
274 expectations [55,56].

275 The biogeographical districts differed significantly in terms of nematode abundances, with the lowest
276 abundances in general found in the Renodunal district, while the UK had low nematode counts in
277 bulk soil samples only. The differences between the districts could be related to complex changes in
278 climate and soil characteristics [2,4] or to unmeasured marram grass properties (defensive
279 mechanisms or nutrient composition) possibly covarying with climate or soil characteristics.
280 However, the ameliorating effect of the sea dampens climatic variability [57] while dune ecosystems
281 are homogeneously resource-poor [58]. Thus, neither climate nor soil nutrients are likely to explain
282 these results. We consequently expect these differences in nematode numbers to be mainly
283 explained by a difference in soil acidity [31]. However, none of these parameters were measured
284 because of this known association with biogeographical region. Hence, any speculation on the actual
285 cause should be done with caution. The variance partitioning clearly indicated that this large-scale
286 factor greatly influenced nematode functional group abundances. Such a relationship was already
287 known for other groups, i.e., plants and spiders [30,59], and is here confirmed for soil nematodes.

288 As expected, more plant-feeding nematodes were found in marram grass roots when more marram
289 grass was present in the near vicinity, probably because of more available resources in the form of
290 marram grass roots. Additionally, this may partly be explained by the low plant diversity in marram
291 grass-dominated dunes, where marram grass forms large quasi-monocultures, while diverse plant
292 communities have been shown to decrease belowground herbivore loads [60]. Other functional
293 groups were not correlated with the proportion of marram grass, except for the number of
294 omnivores found in the bulk soil, which declined when there was more marram grass present.

295 Assuming omnivorous nematodes are mainly affected by resource availability [61], our results
296 seemed to indicate that these nematodes are able to find more food in bare sand. Omnivorous
297 nematode species are indeed able to live in bare sand, albeit together with bacterivorous and
298 fungivorous nematodes potentially serving as food source [62]. Next to other nematodes,
299 omnivorous nematodes are known to feed on numerous soil microbes ranging from algal filaments
300 to protists, supplemented with fungal hyphae and bacteria when their primary food sources are
301 unavailable [7]. Increased competition for nutrients of these soil microbes with marram grass roots
302 could decrease their numbers, consequently explaining the decrease in omnivorous nematode
303 abundance when marram grass cover is higher.

304 We hypothesised nematode abundances to increase with an increasing clustering of marram grass
305 because of the lower sand-capture efficiency [27,33,63] and because the captured sand is thought to
306 be largely free of nematodes. This was only true for fungivorous nematodes residing in the
307 rhizosphere, while no correlations were found for other nematode functional groups. These results
308 confirm that fungivorous nematodes are sensitive to disturbances of different origins, but thrive
309 under more stable conditions [7]. The mechanism behind this process is most likely linked to the
310 development of fungi. Fresh wind-blown sand from the beach probably only contains low amounts of
311 fungi [64]. When sand accretion slows down, development of fungi around marram grass roots can
312 be assumed to increase, while fungal development is minimal in bulk soil because it is probably not
313 suitable for most hyphae formation [13]. Hence, fungivore nematode abundance only increased in
314 the rhizosphere. The lack of correlations between other nematode groups and the spatial clustering
315 of marram grass could point towards a relatively quick colonization of marram grass roots by soil
316 nematodes after initial formation, confirming observations of other field studies [55].

317 Less vital marram grass tussocks are characterized by increasingly more dead stems and leaf litter
318 deposition. This organic material, together with the high microbial biomass they support, provides
319 additional habitat and feeding opportunities for many soil nematode groups [2,12]. Because of this

320 increased resource availability, we expected a decrease in nematode abundances for all nematode
321 functional groups with increasing vitality, except for plant-feeding nematodes. Predatory and
322 fungivorous nematodes were found in larger quantities in respectively the rhizosphere and bulk soil
323 from less vital marram grass tussocks, hinting at the indirect importance of dead organic material for
324 these nematode functional groups [7]. Fungivorous nematodes benefit from an increase in fungi due
325 to the availability of decaying organic material while predators might profit from increased prey
326 abundances. On the other hand, predatory nematodes are shown to survive and reproduce better in
327 moist conditions [65,66], thus predators could benefit from increased water retention underneath
328 tussocks with more leaf litter. Since we did not observe a relationship between marram grass vitality
329 and bacterivorous and omnivorous nematode numbers, our results demonstrate that these
330 functional groups were able to persist, even when less resources such as dead plant material are
331 available. Note that marram grass vitality is based on the aboveground part of the marram grass
332 tussock. Including root vitality, which is shown to positively correlate with endoparasitic root-feeding
333 nematode numbers [56], could furthermore help clarify drivers of specific nematode functional
334 groups.

335 Contrary to our hypothesis, the presence of *Senecio inaequidens* had a positive rather than a
336 negative effect on the abundance of nematodes in bulk soil, except for fungivores nematodes. The
337 most likely explanation for these results is an increase in nutrient concentrations due to the presence
338 of *S. inaequidens* in soils with initially low resources [67], especially since nematodes are known to
339 positively react to increasing nutrient concentrations [62]. Furthermore, marram grass grew better in
340 sand harvested from underneath *S. inaequidens* compared to bare sand, which could also be
341 explained by a probable increase in nutrients [34]. These results indicated that chemical compounds,
342 like pyrrolizidine alkaloids, are not able to accumulate and negatively affect soil nematode
343 abundances in sandy environments. Alternatively, *Senecio* could negatively affect other organisms in
344 the soil, among which the natural enemies of nematodes, indirectly raising nematode numbers. If

345 nematodes facilitate decomposition of organic matter of *Senecio*, this interpretation could still
346 explain the improved marram grass growth in *Senecio*-altered soils [34].

347 The analysis of the residual covariance among nematode functional groups shows that abundances
348 of different functional groups tend to be positively associated within a given compartment
349 (rhizosphere or bulk soil), once the effects of local biotic and abiotic factors have been taken into
350 account. This effect is quite likely the result of ecological filtering by compartments: some roots will
351 harbour generally more nematodes of all functional groups while others will be symmetrically
352 impoverished of all functional groups because local conditions affect all groups in the same way. The
353 absence of negative covariances in our study also suggests that the extent of locally good or bad
354 conditions “seeps” to nearby compartments: if a root sample harbours a high abundance of
355 nematodes, it is very likely that the nearby bulk soil sample will also do so. This hints at the fact that
356 locally good/bad conditions occur at a scale larger than a single root or soil sample. It has been
357 shown that plant-feeding nematode activity can increase nutrient leakage from roots, which
358 consequently increases microbial populations, in turn providing food for bacterivore and fungivore
359 nematodes and even potentially their predators [68]. Marram grass-associated nematode functional
360 abundances are thus positively covarying in natural foredunes. These results are in line with a global
361 study done on the spatial structure of soil nematode functional groups [2]. We cannot claim that all
362 variables related to bottom-up structuring of nematode communities were included in the model,
363 yet we used variables that can be thought to substantially capture the most important drivers.
364 Variables such as root mass and leaf litter can be argued to correlate with marram grass vitality,
365 while nutrient concentrations are thought to be quite similar among coastal dunes [33]. Assuming
366 that the most important factors structuring nematode abundances were, at least indirectly, included
367 in the model, these results hint at the importance of studying the interactions between functional
368 nematode groups if we want to further develop our understanding of soil communities.

369 To conclude, our results indicate that local nematode functional group abundances are variable
370 among biogeographic regions. Within regions there is still much unexplained variation, caused by the
371 spatial clustering of nematode abundances. Hence, if nematode pressure is truly linked to the local
372 performance of marram grass in coastal dunes, this impact will be highly variable across space, which
373 would clarify why the *Ammophila* problem observed under constant conditions in the lab is still not
374 completely resolved in the field. Unravelling which factors and species interactions structure the
375 clustering at very small spatial scales could help shed light on this matter. In light of the recent
376 climate change, dunes are becoming more and more fixated by marram grass [69], which would lead
377 to an increase in plant-feeding nematodes according to our research. Since these abundances are
378 heterogeneous and highly spatially clustered, so would be their role and impact in dune development
379 and succession.

380 Acknowledgements

381 This research was conducted with financial support from the INTERREG 2 seas project ENDURE.

382 RVDW was funded by the University of Lille. DB was funded by BOF (grantnr: BOF/24J/2021/066). FM

383 would like to thank CNRS for general support.

384 We thank everyone who has assisted with the fieldwork: Paulien Vanhauwere, Laurian Van

385 Maldegem, Gillis Sanctobin, Noémie Van den Bon, Pieter Vantieghe and the Endure consortium. A

386 big extra thanks for Pieter Vantieghe for his help with the extraction of the nematodes. We thank

387 Hans Matheve for the construction of the vegetation maps and the consecutive calculations of the

388 marram grass spatial parameters (P & Moran's I).

389

390 **Author contributions**

391 RVDW and DB analysed the data. RVDW conducted the practical work and wrote the first draft of the

392 manuscript. All authors contributed substantially to interpretation of the results and revision of the

393 manuscript.

394

395 **Competing interests**

396 The authors declare that they have no known competing financial interests or personal relationships

397 that could have appeared to influence the work reported in this paper.

398

399 **Data availability**

400 The script and raw data are available via GitHub [<https://github.com/Ruben->

401 [VDW/Marram_nematodes](https://github.com/Ruben-VDW/Marram_nematodes)] and published on Zenodo [70].

402

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