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Impact of land use and management practices on soil nematode communities of Machair, a low-input calcareous ecosystem of conservation importance

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HIGHLIGHTS

- Land use and season were the main drivers of nematode communities from Machair soils.
- Functionally, nematode communities from grassland were distinct.
- Bacterial-feeding nematodes dominated all land uses.

GRAPHICAL ABSTRACT

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ABSTRACT

Machair is a vulnerable low-lying coastal ecosystem with internationally recognised conservation importance. It is characterised by wind-blown calcareous shell-sand soils that support a patchwork of low-input land-use types including species rich grasslands and small-scale arable production. In contrast to numerous above-ground studies, few below-ground studies have been made on the Machair. Thus, a knowledge gap exists, and no baseline data is available to determine the impact, if any, of fundamental changes in Machair land management practices such as a move from traditional rotational to permanent grazing, and increased use of inorganic fertiliser. To address this knowledge deficit, we assessed the impact of different agronomic management practices (cropped, fallow and grasslands) on the structure of soil nematode communities over a two-year period along a geographically limited north-south gradient of coastal Machair of the Outer Hebrides archipelago. Land use followed by season were the main drivers of nematode communities from Machair soils. Functionally, nematode communities from grassland were typically distinct from cropped or fallow communities driven primarily by differential contributions to the overall nematode community by the dominant bacterial-feeding nematodes. Temporally, nematode communities sampled in spring and autumn were distinct.

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1. Introduction

Threats to soil function and biodiversity as a direct consequence of intensive agricultural production are well recognised (Banwart, 2011; Powlson et al., 2011; Gardi et al., 2013; Gibbs and Salmon, 2014; Tsiafouli et al., 2015; Geisen et al., 2019), compounded by a changing climate (Hoegh-Guldberg et al., 2018) and a diminishing land resource for production (Lambin and Meyfroidt, 2011). The dynamic nature of low-lying coastal regions drives further vulnerability to coastal agricultural soils due to water (Elliott et al., 2014; Young et al., 2014; Gracia et al., 2018) and wind (Young et al., 2015) mediated erosion. Machair is one such vulnerable low-lying coastal low-input grassland system with internationally recognised conservation importance (EU Habitats Directive Annex I, EU Council Directive 92/43/EEC). Land coverage of Machair extends globally to approximately 25,000 ha and is geographically restricted to the western coasts of Scotland and Ireland (Angus and Dargie, 2002; Maddock, 2008). Areas of Machair are characterised as having wind-blown calcareous shell-sand soils that underpin a multifunctional landscape typically with dunes immediately on the coast and to the interior a mosaic of low-input species-rich grasslands, wetlands and the so-called “blacklands” where Machair meets peatland (Hansom and Angus, 2005). There is a close cultural connection between Machair and local communities who have historically managed the land since Mesolithic times (Edwards et al., 2005) through subsistence-like farming (Gilbertson et al., 1996) and in the modern era, crofting, a system of tenanted landholding unique to Scotland (Crofting Commission, 2019). This traditional crofting method delivers a patchwork of low-input rotational arable production combined with (semi-) permanent grassland (Crawford, 1990; Vink et al., 2014). As soil management impacts the community composition of the soil biota with concomitant effects on delivery of ecosystem services that the biota mediates (De Vries, 2013), a move away from traditional agronomic management practices has raised concerns on the potential impact on the fragile Machair ecosystem and in particular biodiversity (Pakeman et al., 2012 and references therein).

In sharp contrast to numerous studies on the impact of changing Machair management on above-ground vegetation diversity (e.g. Owen et al., 2000; Pakeman et al., 2012; Lewis et al., 2014; Pakeman et al., 2017b, 2017a), pollinators (Redpath-Downing et al., 2013) and birds (Fuller et al., 2010; Calladine et al., 2014; Hancock et al., 2016), though the latter may be confounded by the increasing presence of hedgehogs (Calladine et al., 2017), there are few studies on below-ground taxa.

Those few studies on below-ground taxa have mostly been biogeographic and/or taxonomic reports (Morton Boyd, 1957; Boag et al., 1997; Brown et al., 1997; Reavy et al., 2015; Boag and Neilson, 2019). To date there has been a paucity of ecological studies focussing on soil taxa on the Machair. However, Morton Boyd (1958) reported results of a temporal study of earthworms associated with cattle grazing on the Machair of Tiree, part of the Inner Hebrides archipelago. More recently, Vink et al. (2014) assessed the temporal and land use effects on soil bacterial community structure from a range of Machair habitats throughout the Outer Hebrides archipelago. Orr et al. (2020) included Machair soil in their study of *Pasteuria*, endospore forming bacteria that are considered natural antagonists to soilborne nematodes.

Due to their inherent contribution to soil processes and ecosystem function (Bardgett and van der Putten, 2014) it has been suggested that biological indicators and specifically soil biota could be used as a proxy measure to assess the impact on soil of environmental change such as land management (Wardle et al., 2004). Nematodes are numerically one of the most abundant metazoan phyla (Van den Hoogen et al., 2019, 2020), their contribution to soil processes (for example, Sackett et al., 2010; Paterson et al., 2011; Ferris et al., 2012; Gebremikael et al., 2016) are important to the effective functioning of soils and in addition they have shown significant potential as indicators of soil quality (Neher, 2001; Neilson et al., 2009; Pulleman et al., 2012). Furthermore,

there is good evidence that nematode phenotype (“biodiversity”) is linked to function (Ettema, 1998; Bardgett et al., 1999) and their diversity and short generation time supports nematodes as indicators of changing soil conditions (Ritz and Trudgill, 1999). This is consistent with Ritz et al. (2009) who assessed nearly two hundred candidate biological indicators of which twenty-one, including nematodes, were ranked as having potential for deployment for environmental monitoring.

Whilst nematode abundance and community composition are known to vary temporally under various management systems including managed grassland (Cheng and Grewal, 2009; Viketoft et al., 2011; Chen et al., 2014), arable (Jiang et al., 2013), alpine meadow (Wu et al., 2017) and agroforestry (Arosa et al., 2016), there is a knowledge gap with regard to low-input traditional systems such as Machair. Here we explore the impact, if any, of different agronomic management practice (cropped, fallow and grasslands) on the structure of soil nematode communities along a geographically limited (0.27°, representing <60 km) north-south gradient of coastal Machair.

As antecedent land use (Griffiths et al., 2002) and agricultural practices are known to drive the diversity and structure of nematode communities (for example, Meng et al., 2006; Culman et al., 2010; Griffiths et al., 2012; Postma-Blaauw et al., 2010, 2012; Tsiafouli et al., 2015) we hypothesise that land use would be the primary driver of nematode community structure in Machair soils.

2. Materials and methods

2.1. Sampling locations and information

Ten locations (see Table 1 in Vink et al., 2014) within the so-called Machair area (Anon, 1999) were initially selected for sampling in spring (April/May), summer (July) and autumn (October) of 2007 (Year 1) with four of these locations re-sampled during the same months in 2008 (Year 2, see Table 1 in Vink et al., 2014). Across years 1 and 2, three fields each of three land uses (cropped, fallow and grassland) were sampled, with each field randomly split into three nominally equal-sized replicated zones, thus generating nine sampling points per location (total samples collected: Year 1, $n = 270$; Year 2, $n = 108$). Vink et al. (2014) reports the main soil texture (Fraserburgh soil association, Hudson et al., 1982) associated with each sampled location. The ten sampling locations were distributed across four adjoining islands in a north-south gradient of the Outer Hebrides archipelago as follows: North Uist ($n = 4$), Benbecula ($n = 1$), Baleshare ($n = 1$), and South Uist ($n = 5$).

Long term (30 year) average weather data for the nearest meteorological station (South Uist Range) are: mean air temperature of 9.2 °C; total annual rainfall 1194 mm, 203 rain days of ≥ 1 mm and 19 days of air frost (UK Met Office, 2018).

Sampled sites were under a typical rotation of two-year cropped followed by two-year fallow (for details see Vink et al., 2014). Briefly, cropped areas comprised a mixture of mostly rye (*Secale cereale* L.) and small oats (*Avena strigosa* Schreb.) grown from locally produced seeds. Fallow sites were previously cropped but left to recover for two years. Grassland sites were those typically located in areas unsuitable for cropping. Grazing occurred in all areas but due to township regulations, especially on the Uist Machair, occurred during the post-harvest and pre-ploughing periods in cropped areas with livestock typically removed from unfenced areas by early May. Fertilisation was typically a mixture of mineral fertiliser and composted seaweed applied a short time prior to ploughing and sowing in spring.

2.2. Abiotic measurements

For each sampling time point, ammonium-N, dissolved organic carbon, nitrate-N, pH and phosphorous were measured from collected soil samples as outlined in Vink et al. (2014). Similarly, soil moisture content

for the Year 1 samples was determined as described by Vink et al. (2014). However, for Year 2, *in situ* moisture readings were taken, using a ML2x Theta moisture probe and HH2 moisture meter (Delta-T devices, Cambridge, UK) inserted into the soil next to each core, to relate the soil moisture content more directly with the cores.

2.3. Nematode sampling and extraction and DNA extraction

To mitigate known large within field variation of nematode distribution (Marshall et al., 1998; Yeates and Bongers, 1999), composite soil samples were taken using a grass plot sampler (Eijkelkamp, Giesbeek, The Netherlands) each consisting of approximately 20 random cores ($\varnothing$ 2.3 cm) to a depth of 10 cm. As the Outer Hebrides is geographically remote with limited facilities, samples were stored outside at ambient temperature for a maximum of 10 days until return to the laboratory where they were stored at 4 °C until further processing.

Nematodes were extracted from 200 g soil (*sensu* Wiesel et al., 2015) from each replicate soil sample using the modified Baermann funnel extraction method of Brown and Boag (1988) and after 48 h collected in 2 ml of water. After settling for 2 h, water volume was carefully reduced to approximately 0.5 ml using a modified pipette tip connected to a vacuum pump. Thereafter, nematode samples were freeze-dried for 72 h. Nematode DNA was extracted using a Purelink 96 Genomic DNA kit (Invitrogen, Paisley, UK) according to the instructions listed by the manufacturer.

2.4. Community analysis by T-RFLP

The T-RFLP protocol described by Donn et al. (2012) was used, with the following minor modifications applied: amplification of nematode DNA included 1 mM dNTPs, 0.4 mg ml⁻¹ BSA; an annealing temperature of 51 °C for 30 s per cycle; and 0.25 µl GeneScan™ 1200 LIZ® Size Standard (Life Technologies, Grand Island, NY, USA) added to the digested products prior to analysis. Post run analysis of terminal restriction fragments (T-RFs) between 50 and 1000 base pairs (bp) were sorted according to length and assigned to 2 bp width bins (Deng et al., 2010) using Genemapper software (Applied Biosystems, Foster City, USA). Where possible identified T-RFs were assigned taxonomy as outlined by Donn et al. (2012) and separated into nematode functional groups depending upon their feeding strategies (Yeates et al., 1993; Ferris et al., 2001). In addition to the identified T-RFs listed by Neilson et al. (2020) an additional T-RF identified as the herbivorous genus *Longidorus* was included in this study.

2.5. Data analysis

Peak area in each bin was calculated using a cubic spline algorithm with a fluorescence detection threshold of 50 units within each sample and Hellinger transformed (Blackwood et al., 2003). Thereafter, data were visually inspected to check for mis-assigned T-RFs and the relative peak areas of adjacent mis-assigned T-RFs combined. Any major T-RF whose relative abundance had a strong relationship with total fluorescence was excluded from the analysis as they were considered PCR artefacts. Furthermore, T-RFs with a relative abundance of <1% of the total in any given sample were regarded as background fluorescence and removed. All T-RFs < 120 bp in length were excluded from analysis as they occurred predominantly in negative controls and samples with low total fluorescence and thus were considered PCR artefacts. Relative T-RF peak areas were recalculated following removal of artefactual peaks.

T-RF relative abundance data was analysed with principal component analysis (PCA) using a sum of squares and products matrix (Genstat version 14, VSN International, Hemel Hempstead, UK). Two different data sets were analysed, the first using data from Year 1 only and the second comprising the four sampling locations sampled in both Years 1 and 2. To ascertain whether there was a relationship

between nematode PCA or feeding (functional) group (*sensu* Yeates et al., 1993) data with abiotic measurements, Pearson's correlation coefficient was calculated using SPSS Statistics 17.0 (SPSS Inc., Chicago, USA) for all combinations and considered significant when $p < 0.05$.

To determine the effect of temporal and geographic variability in nematode communities under the different land uses, PCA scores from the first three axes and relative abundances of the main T-RFs and functional groups were analysed using Residual Maximum Likelihood (REML) in GenStat. Residual plots were produced for each axis for confirmation that assumptions of normality had been met (Payne et al., 2012). The fixed model used was either: Land use $\times$ Season $\times$ Year $\times$ Location for the Year 1 data or Land use $\times$ Season $\times$ Year $\times$ Location for the combined Years 1 and 2 data, with Replicate as a random effect. All factors were analysed for main effects and two-way interactions. Predicted means and corresponding standard errors were calculated for all significant effects with an averaging of all available combinations present.

To ascertain whether relationships existed between vegetation (see Vink et al., 2014) and/or abiotic factors in Year 1 spring and all sample points in Year 2 (see Vink et al., 2014 for an explanation), Pearson's correlation coefficients were calculated with the first three principal components of the nematode community and functional group data (SPSS v.17.0, SPSS Inc., Chicago, USA) and, as previously, considered significant when $p < 0.05$. Pearson's correlation coefficient is sensitive to outliers, which can have a large effect on the line of best fit and the Pearson correlation coefficient. Thus, we initially assessed the number and magnitude of outliers in the dataset and once that threshold was passed, we applied the Shapiro-Wilk test of normality to our data.

3. Results

3.1. Impact of land use and season on nematode community structure (Year 1)

The first three axes of the PCA captured c. 70% (PCA 1 48.1%, PCA 2, 13.1% and PCA 3, 8.6%) of the variation in the Year 1 dataset. Land use was the key determinant of nematode communities sampled in Year 1 (Fig. 1) with grassland separating from cropped and fallow in PCA1 ($p < 0.001$) and cropped separating from grassland and fallow in PCA2 ($p < 0.001$). A strong seasonal effect existed (Fig. 2) with samples collected in spring distinct from those collected in summer and autumn in PCA1 ($p < 0.001$) and autumn samples distinct from spring and summer in PCA2 ($p < 0.01$). Interactive effects existed for land use $\times$ location (Fig. 3) with land use the driver in PCA1 ($p < 0.001$) and grassland separating from the other land uses and location in PCA2 ($p < 0.001$) manifested through distinct nematode communities at WG (fallow, grassland), BL (fallow) and BS (cropped).

Abundance of bacterivorous nematodes increased ($p < 0.001$) from cropped through fallow to grassland (Fig. 4A). In contrast, fewer predators ($p < 0.001$) were recorded in grasslands than either fallow or

Fig. 1. Land use effects on nematode community composition for Year 1 samples (all 10 locations). Mean PCA scores and standard errors are shown.

Table 1

PCA scores of the 2007 nematode samples. Mean PCA scores, standard errors in parentheses and significance levels are shown for the main effects; for interactive effects only significance levels are shown; n.s. = not significant; location codes as described in Fig. 3.

Factor		PCA 1 (46.9%)	PCA 2 (13.1%)	PCA 3 (8.6%)
Land use	Cropped	0.058 (0.017)	-0.056 (0.009)	0.018 (0.007)
	Fallow	0.054 (0.018)	-0.018 (0.009)	0.005 (0.008)
	Grassland	-0.121 (0.017)	0.044 (0.009)	-0.017 (0.007)
	Significance	p < 0.001	p < 0.001	p < 0.01
Season	Spring	0.051 (0.017)	-0.014 (0.009)	-0.032 (0.007)
	Summer	-0.040 (0.017)	-0.011 (0.009)	-0.014 (0.008)
	Autumn	-0.020 (0.017)	0.029 (0.009)	0.049 (0.007)
	Significance	p < 0.001	p < 0.01	p < 0.001
Location	BL	0.002 (0.032)	-0.015 (0.016)	-0.012 (0.013)
	BR	-0.038 (0.032)	-0.026 (0.016)	0.005 (0.013)
	BS	0.045 (0.032)	0.043 (0.016)	-0.022 (0.013)
	CC	0.051 (0.032)	-0.023 (0.016)	0.076 (0.013)
	DD	-0.065 (0.032)	-0.006 (0.016)	-0.007 (0.013)
	KD	-0.037 (0.032)	-0.025 (0.016)	-0.061 (0.013)
	LC	0.035 (0.032)	-0.004 (0.016)	0.029 (0.014)
	PG	-0.047 (0.032)	-0.029 (0.016)	-0.012 (0.013)
	SG	-0.065 (0.032)	-0.025 (0.016)	0.027 (0.013)
	WG	0.080 (0.031)	0.123 (0.015)	-0.002 (0.013)
	Significance	p < 0.01	p < 0.001	p < 0.001
Land use × Season		n.s.	n.s.	n.s.
Land use × Location		p < 0.001	p < 0.001	n.s.
Season × Location		n.s.	n.s.	p < 0.001
Land use × Season × Location		n.s.	n.s.	n.s.

Statistically significant values are highlighted in bold.

Fig. 2. Temporal effects on nematode community composition for Year 1 samples (all 10 locations). Mean PCA scores and standard errors are shown.

cropped (Fig. 4A). Overall, both carnivores ($p < 0.001$) and omnivores ($p < 0.001$) decreased in abundance throughout the growing season (Fig. 4B) whereas abundance of bacterivores slightly increased ($p < 0.05$, Fig. 4B). Bacterivores were the dominant functional group across all sampled sites (Fig. 5). Except for fungivores (data not shown) location to a varying extent impacted the relative abundance (Fig. 5) of bacterivores ($p < 0.05$), predators ($p < 0.01$), omnivores ($p < 0.001$) and herbivores ($p < 0.001$).

3.2. Impact of land use and season on nematode community structure (Years 1 and 2)

As with Year 1, land use was a driver of nematode communities in both PCA1 (46.2%, $p < 0.001$) and PCA2 (13.5%, $p < 0.001$) for the sites sampled in both years with grassland being distinct from both fallow and cropped in PCA1 and cropped separated from fallow and grassland (Table 2). Only autumn of Year 2 imparted a seasonal effect on nematode communities ($p < 0.001$). Of the four sites sampled in both years, the nematode communities from CC differed slightly ($p < 0.05$) to the

Fig. 3. Interactive effect of location and land use on Year 1 nematode communities by land use, (a) cropped, (b) fallow and (c) grassland. Means and standard errors are shown. Location codes: BL, Baleshare; BR, Balranard; BS, Kildonan; CC, Clachan Sands; DD, Drimsdale; KD, Bornish; LC, Lionacleit; PG, Paiblesgarry; SG, Stilligarry; WG, West Gerinish.

other sites in PCA1 whereas those from BL were distinct ($p < 0.001$) in PCA2 (Table 2).

Year separated along both PCA1 ($p < 0.001$) and PCA2 ($p < 0.05$). Although season by itself had a limited effect on nematode communities, there was a strong interactive effect with year (PCA1, $p < 0.05$; PCA2, $p < 0.001$) driven by nematode communities sampled in spring and autumn 2008 compared to the other samples (Fig. 6). Significant interactive effects between year and location occurred in PCA2 ($p < 0.01$) and

Fig. 4. Effects of A) land use and B) season on functional grouping of nematodes (see Table 1 for p values) from 2007 (all 10 sites).

PCA3 ($p < 0.05$) but not in PCA1. In PCA2 this was due to distinct nematode communities from CC and BL (Years 1 and 2) and in PCA3 from PG (2008) and CC (2007) (Fig. 7).

The importance of year on nematode communities also translated to functional groups with impacts on bacterivores ($F_{1,169} = 39.9$, $p < 0.001$), fungivores ($F_{1,169} = 7.7$, $p < 0.01$), omnivores ($F_{1,169} = 26.2$, $p < 0.001$) and herbivores ($F_{1,169} = 26.4$, $p < 0.001$) but there was no effect on predators. Across all locations in both years, similar to the Year 1 sampling, land use was a driver of bacterivores and carnivores ($p < 0.001$) with bacterivores again increasing from cropped to grassland, though carnivores had a different pattern with an increased abundance in fallow and least abundant in grassland. In addition,

Table 2

PCA of 2007 and 2008 nematode samples. Mean PCA scores, standard errors in parentheses and significance levels are shown for the main effects; for interactive effects only significance levels are shown; n.s. = not significant; location codes as described in Fig. 3.

Factor		PCA 1 (46.2%)	PCA 2 (13.5%)	PCA 3 (11.2%)
Land use	Cropped	0.065 (0.021)	−0.051 (0.010)	−0.027 (0.010)
	Fallow	0.022 (0.020)	0.005 (0.009)	0.004 (0.009)
	Grassland	−0.092 (0.021)	0.040 (0.010)	0.021 (0.010)
	Significance	$p < 0.001$	$p < 0.001$	$p < 0.001$
Season	Spring	−0.033 (0.010)	−0.033 (0.010)	0.017 (0.010)
	Summer	−0.025 (0.009)	−0.025 (0.009)	−0.026 (0.010)
	Autumn	−0.056 (0.010)	0.056 (0.010)	0.011 (0.010)
	Significance	n.s.	$p < 0.001$	$p < 0.001$
Location	BL	−0.001 (0.025)	0.049 (0.011)	0.001 (0.012)
	CC	0.037 (0.024)	−0.016 (0.011)	−0.054 (0.011)
	DD	−0.049 (0.024)	−0.008 (0.011)	0.015 (0.011)
	PG	−0.006 (0.024)	−0.014 (0.011)	0.040 (0.011)
	Significance	$p < 0.05$	$p < 0.001$	$p < 0.001$
Year	2007	−0.059 (0.017)	0.011 (0.008)	−0.024 (0.008)
	2008	0.052 (0.017)	−0.012 (0.008)	0.026 (0.008)
	Significance	$p < 0.001$	$p < 0.05$	$p < 0.001$
Land use × Season		n.s.	$p < 0.001$	n.s.
Land use × Year		$p < 0.01$	n.s.	n.s.
Season × Year		$p < 0.05$	$p < 0.001$	$p < 0.001$
Land use × Location		n.s.	n.s.	n.s.
Season × Location		n.s.	n.s.	$p < 0.001$
Year × Location		n.s.	$p < 0.01$	$p < 0.05$
Land use × Season × Location		n.s.	n.s.	n.s.

Statistically significant values are highlighted in bold.

there was a decrease ($p < 0.001$) in herbivores from cropped to grassland (Fig. 8A). As with Year 1, abundance of bacterivores increased ($p < 0.001$) throughout the growing season, whereas omnivores ($p < 0.05$) and herbivores ($p < 0.01$) decreased (Fig. 8B).

3.3. Interactions between abiotic factors, vegetation and nematode community structure

For Year 1 spring data, once outliers ($n = 3$ under each land use) were removed there was no overall relationship between vegetation and nematode communities (data not shown). Considering nematode functional group and land use, a positive relationship existed for bacterial feeding nematodes ($r = 0.23$, $p < 0.01$) and a negative relationship for both herbivores ($r = 0.22$, $p < 0.01$) and omnivores ($r = 0.42$, $p < 0.001$) with vegetation from cropped areas but not for fallow or grassland.

Few correlations existed between nematode communities and abiotic factors: soil moisture and nematode communities (PCA2) for all three land use types (cropped, $r = 0.20$, $p < 0.01$; fallow, $r = 0.47$,

Fig. 5. Mean relative abundance of nematode functional groups at each sampled location in Year 1. Error bars represent standard errors and location codes as listed in Fig. 3.

Fig. 6. Temporal effects (season and year) on nematode community composition for Year 1 and 2 samples (4 locations). Mean PCA scores and standard errors are shown.

$p < 0.001$; grassland, $r = 0.42$, $p < 0.001$), in Year 1 spring (Fig. 9A). A similar relationship was reflected in summer of Year 2 (Fig. 9B) but only with grassland ($r = 0.35$, $p < 0.05$) and fallow ($r = 0.53$, $p < 0.01$). Of the other abiotic measures, only dissolved organic carbon (DOC) in fallow ($r = 0.29$, $p < 0.01$) and grassland ($r = 0.31$, $p < 0.01$) yielded significant relationships.

Analysis of the relationship between the various nematode functional groups and abiotic factors showed several significant relationships in 2008 but none in 2007. However, no clear pattern was evident; carnivorous nematodes were positively ($r = 0.70$, $p < 0.001$) and herbivores negatively ($r = 0.41$, $p < 0.05$) related to soil moisture content but only at fallow sites in summer 2008. Whereas a positive bacterivore ($r = 0.60$, $p < 0.01$) and a negative plant-feeder ($r = 0.35$, $p < 0.05$) relationship with $\text{NH}_4\text{-N}$ was noted in summer 2008 in grassland.

4. Discussion

Data generated in this study provides a baseline for future monitoring of the impact of fundamental changes in Machair land use and management practices such as a move from rotational to permanent grazing (Love, 2009), introduction of block rather than strip cultivation (Angus, 2009), increased use of inorganic fertiliser (Owen et al., 2000; Angus, 2009) and use of deep ploughing (Owen et al., 2000). Except for a taxonomic study on the plant parasitic nematode species *Longidorus vineicola* (Boag and Brown, 1987), this is the first study on soil nematode communities from the low-input Machair ecosystem and on below-ground taxa in general, though earthworms (Morton Boyd, 1957; Boag et al., 1997), soil-borne viruses (Reavy et al., 2015), bacteria (Vink et al., 2014) and invasive planarians (Boag and Neilson, 2019) have been previously studied.

Fig. 7. Effect of year and location on the nematode communities of the 2007 and 2008 sampling in PCA 2 and 3 (4 locations). Mean PCA scores and standard errors are shown. Location codes as listed in Fig. 3.

Fig. 8. Effects of A) land use and B) season on functional grouping of nematodes (see Table 2 for p values) for the 4 sites sampled in both 2007 and 2008.

In this study, land use followed by season were the main drivers of nematode communities from Machair soils. The only comparable study on Machair soil biota (Vink et al., 2014) reported that soil compartment (rhizosphere vs bulk soil) was the primary determinant of microbial community composition. However, soil compartment was not assessed in this study as the amount of rhizosphere soil adhering to plant roots was insufficient (Wiesel et al., 2015) to enable a robust nematode extraction from samples.

In Year 1, as per our hypothesis, Machair land use was the main driver of the functional composition of nematode communities with those from grassland typically distinct from cropped or fallow communities consistent with the pattern reported for microbial communities from the same sites (Vink et al., 2014). These differences were mainly due to a higher relative abundance of bacterial feeding nematodes and contrasting lower relative abundance of predatory nematodes in grassland compared to the other land use types studied. Across all land use types, bacterial feeding nematodes dominated, consistent with a global review of nematode communities from pasture, cropped, forest and natural sites (Yeates, 2003) and assessment of functional diversity across terrestrial ecosystems (Sechi et al., 2019). Furthermore, a recent global scale biogeographic assessment of nematodes noted that bacterivorous nematodes was the most prevalent and abundant nematode functional group across a range of diverse biomes (Van den Hoogen et al., 2019, 2020). Land use as a driver of nematode community composition from field samples in this study aligned with that reported for a controlled pot experiment studying four agricultural soils in the context of nematode recolonization post defaunation (Griffiths et al., 2002).

Whilst season within Year 1 was not the primary determinant of nematode community structure, communities sampled in spring and

Fig. 9. Relationship between PCA2 and soil moisture A) spring 2007 (10 locations) and B) summer 2008 (4 locations); square = cropped, diamond = fallow and triangle = grassland.

autumn were different in PCA1 and 3, respectively. Temporal variability in nematode communities from various habitats and vegetation types is well documented (for example, Cheng and Grewal, 2009; Viketoft et al., 2011; Jiang et al., 2013; Arosa et al., 2016; Wu et al., 2017). Annual variation was the dominant factor in Years 1 and 2 sampling, though land use remained highly significant. This is consistent with Boag et al. (1998) who reported large year to year variation in abundance of nematode functional groups across a range of habitats including arable and grasslands. In Year 2 the effect of land use was less pronounced than Year 1, but the same pattern of increasing bacterial feeders in grasslands and in autumn was present.

Although there were significant effects due to location, these were often due to one or more outlying values and difficult to ascribe to any specific land use or seasonal effect. Nematode communities can be highly variable at different scales (Marshall et al., 1998; Nielsen et al., 2010; Monroy et al., 2012) due to environmental and soil drivers (Boag and Yeates, 1998; Yeates and Bongers, 1999) or site history (based on a study of 30 grasslands, Monroy et al., 2012). As nematodes are considered sedentary organisms, dispersal limitation (Rasmussen et al., 2019) is likely to mitigate scale effects. However, at landscape scale c. 30% of the nematode community can be transported as a result of soil disaggregation and runoff during rainfall events and thus redistributed (Baxter et al., 2013; Gorman et al., 2018). Although scale probably played a role in this study, the sampled area extended for ca. 60 km (Vink et al., 2014), it had less obvious influence that the highly significant effects of land use, year and season.

Few clear relationships existed between nematode functional groups and either abiotic measures or vegetation. In cropped, but neither grassland nor fallow, the relative abundances of bacterivores,

herbivores and carnivores were significantly correlated with vegetation composition (PCA2 only, 13.1% variability represented). Soil moisture content was the main driver of PCA2 and significantly correlated with bacterivorous and herbivorous nematode abundance as well as microbial community composition (Vink et al., 2014), thus the relationship between those functional groups and vegetation could be indirect (Griffiths et al., 2003). However, previous studies have reported that to varying degrees vegetation composition and individual plants species (Yeates, 1999; de Deyn et al., 2004; Viketoft et al., 2005; Yergeau et al., 2010) affected nematode community composition, though more recent studies (Monroy et al., 2012; Rasmussen et al., 2019) have reported that neither vegetation composition nor plant genotype influence nematode community composition.

Notwithstanding that bacterial feeding nematodes are considered more prevalent in organic and low-input agricultural systems than conventionally managed fields (e.g. Berkelmans et al., 2003); generally low-input and organic agricultural systems, and especially unmanaged grasslands, are thought to have a fungal based food web with high abundance of fungivorous nematodes (Bardgett et al., 1999; Griffiths et al., 2007). Notable in this study was the low abundance of fungal feeding nematodes. This could be due to, for example, PCR bias in the amplification of DNA (Donn et al., 2008; Waeyenberge et al., 2019) or functional plasticity such as some Tylenchida primarily considered as plant-feeding nematodes (Yeates et al., 1993) have been shown to be fungivores (Okada et al., 2005). However, the results here are consistent with previous studies (using classical taxonomy) on coastal dune succession (Goralczyk, 1998; Wall et al., 2002; Pen-Mouratov et al., 2010; Liu et al., 2011) that reported fungal feeding nematodes only occurred in areas with a well-developed organic layer which within the Machair system typically is restricted to the “blacklands” and not sampled in this study.

This study has generated a baseline dataset of nematode communities from Machair soil across four islands that can in future be used as a comparator to assess the impact of future environmental or agronomic change. For the study sites investigated, land use and season were the primary drivers of the soil nematode communities. Nematode communities from grassland soils were distinct from those sampled from cropped or fallow soils driven by the contribution to the overall nematode community of bacterial-feeding nematodes.

CRedit authorship contribution statement

Stefanie N. Vink: Conceptualization, Investigation, Formal analysis, Writing - original draft. **Damian Bienkowski:** Writing - review & editing. **David M. Roberts:** Investigation, Writing - review & editing. **Tim J. Daniell:** Conceptualization, Writing - review & editing. **Roy Neilson:** Conceptualization, Writing - review & editing.

Declaration of competing interest

The authors have no competing interests to declare.

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