

Temperature-based bioclimatic parameters can predict nematode metabolic footprints

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Abstract Nematode metabolic footprints (MFs) refer to the lifetime amount of metabolized carbon per individual, indicating a connection to soil food web functions and eventually to processes supporting ecosystem services. Estimating and managing these at a convenient scale requires information upscaling from the soil sample to the landscape level. We explore the feasibility of predicting nematode MFs from temperature-based bioclimatic parameters across a landscape. We assume that temperature effects are reflected in MFs, since temperature variations determine life processes ranging from enzyme activities to community structure. We use microclimate data recorded for 1 year from sites differing by orientation, altitude and vegetation cover. At the same sites we estimate MFs for each nematode trophic group. Our models show that bioclimatic parameters, specifically those accounting for temporal variations in temperature and extremities, predict most of the variation in nematode MFs. Higher fungivorous and lower bacterivorous nematode MFs are predicted for sites with high seasonality and low isothermality (sites of low vegetation, mostly at low altitudes), indicating differences in the relative contribution of the corresponding food web channels to the metabolism of carbon across the landscape. Higher plant-parasitic MFs were predicted for sites with high seasonality. The fitted models provide

realistic predictions of unknown cases within the range of the predictor's values, allowing for the interpolation of MFs within the sampled region. We conclude that upscaling of the bioindication potential of nematode communities is feasible and can provide new perspectives not only in the field of soil ecology but other research areas as well.

Keywords Altitude · Multivariate linear modeling · Mosses · Soil communities · Upscaling

Introduction

Soil organisms are important for maintaining soil functionality and regulating processes that support ecosystem services, like nutrient and water retention, carbon storage and pest resistance (Wall et al. 2012; Mulder et al. 2011), while the diversity and the composition of soil communities determine ecosystem multifunctionality (Wagg et al. 2014). Among soil animals, nematodes (Nematoda) occur in high diversity and density in every soil and sediment type (Treonis and Wall 2005; Wu et al. 2011). This group of animals is very diverse in terms of trophic preferences (omnivorous, predatory, bacterivorous, fungivorous and herbivorous), life history strategies, and sensitivity to disturbance (Bongers and Bongers 1998; Yeates et al. 1993). Nematodes are involved at several trophic levels in the soil food web (Ferris 2010a; Mulder et al. 2011; Moore and de Ruiter 2012) and significantly contribute to soil nutrient turnover (Savin et al. 2001; Ferris et al. 2004). Thus, nematodes are among the most preferred bioindicators of soil condition (Bongers and Ferris 1999; Zhao and Neher 2013).

A number of nematode community indices, e.g., the maturity and plant-parasitic index (Bongers 1990); the

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structural, enrichment and channel index (Ferris et al. 2001), have been developed and successfully applied to monitor land use changes, management effects, environmental disturbance and pollution (Tsiafouli et al. 2007; Salamun et al. 2012; Vonk et al. 2013). Neher et al. (1995, 1998, 2012) tested nematode community indices across spatial scales, quantified their linkage to ecosystem function and suggested the use of nematode community indices for large-scale (regional and/or national) soil monitoring programs.

These indices, although useful for assessing the functioning of the soil food web, cannot provide information on the magnitude of soil functions (Ferris 2010b). Based on the recognition that carbon is the common currency of ecosystem energetics determining food web size and activity, Ferris (2010b) introduced the metabolic footprint (MF) concept. It refers to carbon utilization by nematodes, as a functional index that provides metrics for the magnitudes of the ecosystem functions and services. With the MFs, nematode biomass and metabolism are given a greater value than abundance as measures of importance in ecological studies, as is also done in other studies (e.g., Zhao and Neher 2014). There are two components accounted for in the estimation of MFs: the production component based on the amount of carbon used for growth and reproduction and the respiration component based on the carbon used for metabolic activity. The MFs of the different nematode trophic groups, such as the MF of herbivores, bacterivores and fungivores, indicate the amount of carbon and energy entering the soil food web through the three major channels.

Nematode MFs have been used in few studies until now. For example, they were found to be able to differentiate soil food webs among non-tillage and conventional-tillage systems (Zhang et al. 2012). MFs in young, mid- and old-aged forests were able to indicate how resource export from or entry into the soil food web is processed during forest development (Zhang et al. 2015). Rodríguez-Martín et al. (2014) found that nematode MFs showed accurate sensitivity to soil physicochemical changes caused by metal pollution, while they proved to be significant in studying spatial relationships with soil factors. The nematode MFs analysis by Ferris et al. (2012) showed that, compared to compost additions, treatments that were cover cropped annually not only affected organisms at the entry level of the food web (bacterivorous nematodes) but that resources were transferred to higher trophic levels (predatory nematodes) which in turn increased the top-down pressure on plant-parasitic nematodes. The MF analysis focusing on function (i.e., utilization of carbon) rather than community composition appears to be a promising tool for soil ecology but more work is needed to evaluate its capacity in adding complementary knowledge regarding the functioning of the soil food web.

Like any other nematode community index, MFs are estimated at scales relevant to nematode body sizes, normally from soil cores with a diameter not exceeding 10 cm. Since the effort and expertise needed to evaluate a sample are high, a normal sampling is accordingly limited to a few samples per study and to local scales. This limits the applicability of the indices since the functional significance of biodiversity may appear at the landscape scale, where exchanges occur among local ecosystems (Swift et al. 2004; Tschardt et al. 2005; Culman et al. 2010). Moreover for mitigating climate change effects, it is important to understand how landscape characteristics affect biodiversity patterns and ecological processes at local but also at landscape scales (Tschardt et al. 2012). Hence, for issues related to biodiversity in soil and soil communities it is important to find methods to upscale information from the local to the landscape scale.

In this work we consider the feasibility of predicting nematode MF variation from temperature-based bioclimatic parameters. Temperature is considered a major determinant for life processes ranging from enzyme activities to individual metabolism, growth and sex determination, individual fitness, population growth rates and distribution, community and food web structures, as well as species interactions (O'Connor et al. 2009; Petchey et al. 2010; Kallimanis 2010; Garcia-Pichel et al. 2013; Dell et al. 2011; Romo and Tylianakis 2013). In this respect, coarse-resolution average background climate estimates based on global weather models are often used to predict geographic ranges of species (Araujo and Peterson 2012). In terrestrial systems, however, local variation in topography and vegetation cover can generate large ground and near-surface temperature differences over short distances (Lenoir et al. 2013), and this local variation might have more pronounced effects on organisms than the average climate of a region (Suggitt et al. 2011; Gillingham et al. 2012; Hagen et al. 2012). This holds specifically for sessile organisms and animals with limited mobility (like soil inhabitants), for which temperature can have an effect at a scale relevant to organism size and dispersal range (Bennie et al. 2008; Gillingham et al. 2012). From a number of laboratory and field studies it is known that nematodes and nematode communities sharply respond to temperature as the latter affects nematode activity, feeding rates, and community structure (Anderson and Coleman 1982; Bakonyi et al. 2007; Ekschmitt et al. 2003; Nielsen et al. 2014). So, we hypothesize that the effect of temperature will be expressed accordingly in nematode MFs.

The aim of this study is to explore whether it is feasible to predict nematode MFs across entire landscapes from potentially available landscape-level microclimate data. Specifically, we explore the potential power of temperature-based bioclimatic parameters to predict nematode MFs, and raise the following questions:

1. How do MFs of various nematode trophic groups vary with varying bioclimatic parameters, and which of these parameters are the most important to predict the observed variation of MFs?
2. To what extent do models predicting MF variations predict yet unknown cases, allowing for the interpolation of MFs within the sampled region?

Materials and methods

Study area and sampling design

The study area is located on Mt Holomontas on the slopes around the Vigla peak (40°25'42.1", 23°9'55.89"), Chalkidiki, Greece (see also Bhusal et al. 2014). In Fig. 1 an ombrothermic diagram from a meteorological station near by the study area is provided. The climate of the region is transient from Mediterranean to temperate and is characterized by hot and relatively dry summers and mild winters. The minimum, mean and maximum temperatures are 2.2, 11.4 and 22.1 °C, respectively, while annual precipitation is, on average, 752 mm.

For temperature monitoring and sampling we selected ten sites at three orientations (east, north and south), two altitudes (high and low) and two types of vegetation cover, namely forest cover (forested) and low vegetation without tree cover (open). Of the 12 possible combinations of orientation, altitude and cover we used ten because of a failure in temperature monitoring at the two south-low sites. A three-letter code is used to describe the sites, denoting the orientation [east (E), north (N), south (S)], the altitude [high (H), low (L)], and the cover [open (O), forested (F)], respectively; EHF for example is the code for the east-high-forested site. The vegetation of the area is a Mediterranean oak (*Quercus pubescens*) forest except for the east-low sites where the vegetation is an evergreen shrub dominated by *Quercus coccifera*.

Samples were taken in January 2010 at three microhabitats per site, namely soil (SL), soil mosses (SM), and rock mosses (RM) (three replicate plots per microhabitat). The minimum distance among replicate plots was 30 m except for the SHO site where the minimum distance was 15 m because of the small surface area and the elongated shape of that site. For the soil microhabitat, samples were taken at 15-cm depth, with a corer 5 cm in diameter. For the moss microhabitats, pieces of about 20 × 20 cm² in area were separated and cut from the moss carpet. In the case of small moss patches on rocks a number of neighboring patches were collected to get a total area of about 400 cm². In all cases the dominant moss species *Hypnum cupressiforme* Hedw. (Sabovljevic et al. 2008) was sampled. Mosses of this species formed almost continuous carpets inside the forest but in the open areas carpets were highly fragmented.

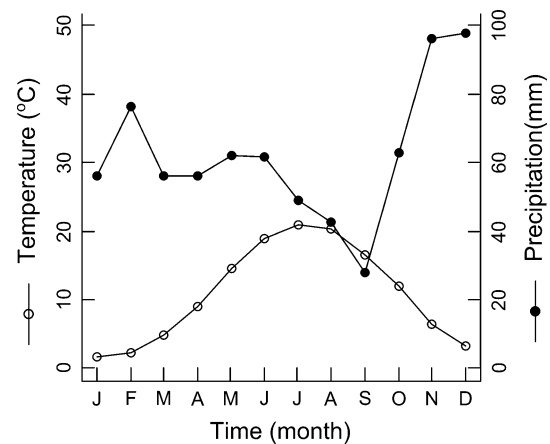


Fig. 1 Ombrothermic diagram of the study area. Data from the meteorological station of Mt Holomontas, Chalkidiki (850 m a.s.l.) for 1974 to 2000

Extraction and identification of nematodes

Soil samples were gently mixed by hand and soil aggregates were broken. Nematodes were extracted from a 150-ml subsample by Cobb's sieving and decanting method, as proposed by S'Jacob and Van Benzooijen (1984). Mosses were gently cut into pieces by hand and for extraction a total of 150 ml was placed into a modified Baermann funnel (Ruess 1995). After collection in water, nematodes were counted alive under the stereoscope, heat killed, and fixed with 4 % formaldehyde. From each sample, 150 randomly selected nematodes were identified under the microscope to genus level, by the identification key of Bongers (1994). Specimens were further allocated to life history strategies (*c-p* values) and trophic groups after Bongers (1990) and Yeates et al. (1993), respectively.

The size and biomass (fresh weight) of each selected specimen was estimated from microscopic images (taken by a Nikon-DS-Fi-L2 camera) using a software tool we especially developed for this purpose (Sgardelis et al. 2009). This tool detects the nematode body edges and estimates the medial axis (skeleton) of the body. The body volume is estimated by summing the volumes of small segments defined across the medial axis that is assumed to be circular in cross section, tapering across both ends. In total 101 equally spaced points across the medial axis were used to define 100 segments. At each point *i* the radius (*R_i*) of the circle representing the cross section of the body was estimated as the length of the line between the medial axis and the body edge, perpendicular to the medial axis. Each segment defined between two points *i* and *i + h* is considered a cone frustum and its volume (*V_i*) is given by $V_i = 0.333 h\pi (R_i^2 + R_i R_{i+h} + R_{i+h}^2)$ where *R_i* and *R_{i+h}* are the radii of the frustum bases. The fresh weight (biomass) of the nematode

was then calculated by adding the volumes of all the segments and multiplying the sum by 1.084, the average specific gravity of nematodes as given by Andr assy (1956).

Metabolic footprints

MFs were calculated according to Ferris (2010b). The MF of nematodes as an index of carbon utilization is the sum of the lifetime amount of carbon partitioned into growth, egg production and respiration. Analytically, $MF = 0.1 W m^{-1} + 0.273 W^{0.75}$, where W is the fresh weight of the individual and m is the c - p value of the taxon it belongs to. For more details regarding the estimation method and the coefficient values see Ferris (2010b). The MFs per trophic group were eventually calculated by summing the MFs of individuals belonging to the given trophic group and serve as indicators of the amount of carbon and energy entering the soil food web through the relevant channels. MFs in each site were estimated per microhabitat and the average values of the three replicates per site and microhabitat were finally used for data analysis.

Temperature monitoring

Thermochron DS1922L temperature logger iButtons (Maxim Integrated Products, Sunnyvale, CA) were used for recording temperature. These sensors were sufficiently small to reflect ground temperature as averaged across a range of no more than a few centimeters. One iButton per site was set at a depth of 1–2 cm into the soil. We considered this depth as representative of upper soil but also moss temperatures. The iButtons were programmed to record temperatures every 90 min and left operating in the field from August 2009 to October 2010. Eventually, a total of 5840 records for the period from 1 September 2009 to 30 September 2010 were used. The temperature monitoring program in the area was a part of a more extensive project conducted in the frame of the European Scales project (EU Seventh Framework Programme).

Temperature-based bioclimatic parameters

From the temperature data series, temperature-based bioclimatic parameters including the annual mean temperature, minimum temperature of the coldest month, maximum temperature of warmest month, mean diurnal range, temperature annual range, isothermality and seasonality were estimated. Isothermality is defined as the ratio of the mean diurnal range over the annual temperature range. Seasonality is the coefficient of variation of mean monthly temperatures. Furthermore, a number of parameters accounting for the percentage of records among the 5840, where temperature was within certain limits, were also estimated. Among

many such parameters, the most important for MF prediction proved to be $p_{t < 5}$, $p_{t < 10}$, $p_{t > 20}$ and $p_{10 < t < 20}$, which refer to the proportion of records with $t < 5$ °C, $t < 10$ °C, $t > 20$ °C and 10 °C $< t < 20$ °C, respectively.

Data analysis

The response of nematode MFs was analyzed for each microhabitat separately, since temperature estimates were available per site and not per microhabitat. We used multivariate approaches to MF analysis. More specifically, we used the multivariate linear modeling approach of Warton et al. (2012) to: (1) assess the significance of altitude, orientation, and cover and their interactions as factors imposing variation on nematode MFs; and (2) produce linear models predicting MF variation from the variation of temperature-based bioclimatic parameters across sites. The option to shrink the correlation matrix was used to account for possible correlations among the MFs of different trophic groups (Warton et al. 2012).

For the first case, linear modeling was used as an alternative to distance-based methods like permutational multivariate ANOVA. According to Warton et al. (2012), distance-based methods may confound location and dispersion effects due to the strong mean–variance relationships that frequently characterize ecological data. Model selection in this case was based on Akaike information criterion sum minimization.

For modeling the effects of temperature-based bioclimatic parameters on MFs the response multivariate data used were the log-transformed MF values. The raw, the log-transformed and the squared values of the bioclimatic variables were used as predictors. The transformations allowed us to fit functions of the form $Y = a_0 + a_1X + a_2X^2$ or $Y = a_0 + a_1X + a_2\ln(X)$ to account for possible hump-shaped responses (Y) to temperature-based bioclimatic variables (X). The former function (quadratic) has an extreme value at $X = -a_1/a_2$ that is at a maximum when $a_2 < 0$, and is symmetric around that extreme. The latter has an extreme at $X = -a_2/a_1$ when $a_1a_2 < 0$. The extreme is a maximum if $a_2 > 0$. The function is not symmetric; the extreme is closer to the smaller root of the function.

To select the best combination of predictors first the number of terms (N) to be used for the construction of the model formulas ($N = 2, 3$ or 4) was set. For each given number of terms all possible combinations of available predictors (including transformations) that could serve as potential models were constructed. Eventually, the model providing the lowest prediction error (prediction error sum of squares; PRESS) under a leave-one-out cross-validation procedure (Aitkin et al. 2009) was selected (model A). To simulate the situation of upscaling the local estimates of MFs to the landscape level we excluded one site per time

and the remaining nine were used for model building. The excluded site was not used at any step of the model selection and calibration procedure. The models were fitted to the remaining nine sites using leave-one-out cross-validation for model selection. The model selected (model B) was the one minimizing the prediction error sum of squares (PRESS) and its significance was evaluated by the likelihood ratio (LR) test. The model selected was calibrated using the set of the nine available sites and used to predict the excluded one. Eventually, two different predictions for each MF were made for each site: (a) the prediction by model A (calibrated with all sites included), and (b) the prediction of the model B (calibrated with all other sites except the one to be predicted). Note that for the latter case the models selected can vary in their formulation according to the site excluded.

For the implementation of the linear modeling of multivariate data we used the `manylm` function of the `mvabund` package (Wang et al. 2012) in R (R Development Core Team 2013). The model goodness of fit and the significance of each predictor were assessed using the summary and anova methods provided for the multivariate linear models, accounting for the correlation between response variables for valid multivariate inference. Summary statistics were based on the LR estimated from 1000 residual resampling iterations. Hooper's R^2 , a generalization of the univariate R^2 , was used as indicative of the proportion of variance of the multivariate response variables captured by the model (the predictor variables). It is worth noting that the multivariate modeling approach we used fits the same linear formula to model the response of different MFs to bioclimatic variables or factors. We plotted multivariate data as recommended by Warton (2008).

Results

Temperature variations and bioclimatic parameters

There were considerable temperature differences among sites according to altitude and vegetation cover type (Fig. 2). The sites differentiated mostly on the basis of the maximum rather than the minimum temperatures and the differences were more pronounced during spring and summer and especially between covered and open sites. Forest cover reduced the diurnal variation and kept the soil cool during summer and rather warm during winter. The differences by altitude were more pronounced among the open sites (Fig. 2). There were significant differences in bioclimatic parameters by cover type ($P = 0.044$) but not by altitude. The bioclimatic parameters (Fig. 3) that differed significantly by cover were $p_{t > 20}$ ($P = 0.037$, higher in open sites), seasonality ($P = 0.047$, higher in open sites) and $p_{10 < t < 22}$ ($P = 0.021$, higher in forested sites).

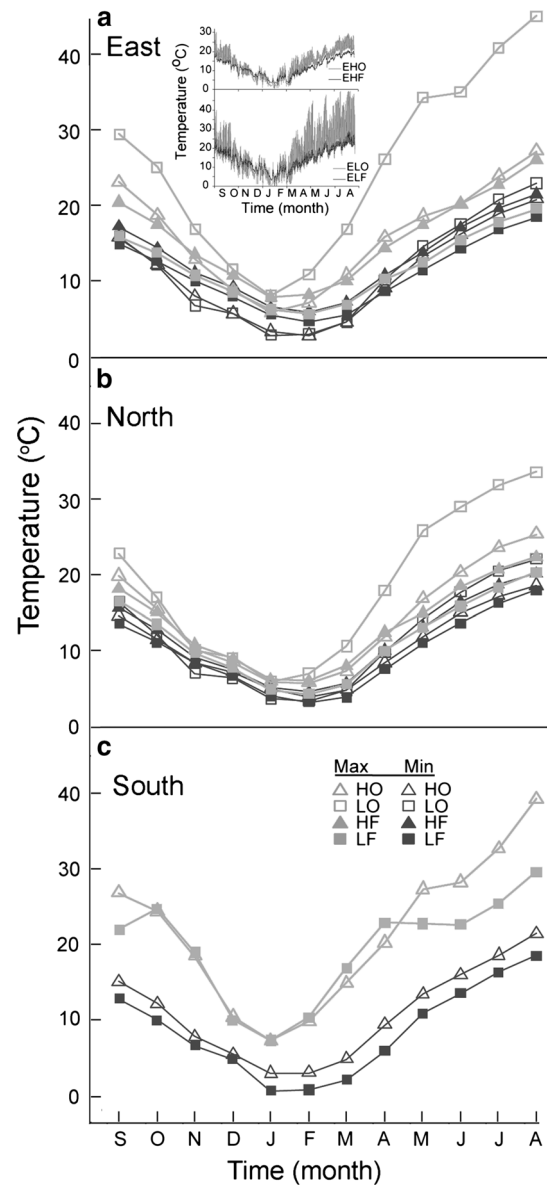


Fig. 2 Mean monthly minimum and maximum temperatures at the slopes around the peak of Vigla (Greece); **a** east, **b** north, and **c** south orientation. **a** *Inset* example of the resulting time-series from temperature recording at the east orientation. Grey symbols, lines max temperatures; black symbols, lines min temperatures. HO High altitude-open site, LO low altitude-open site, HF high altitude-forested site, LF low altitude-forested site

Nematode MFs

Variation by site

There were significant variations in MFs by microhabitat (Fig. 4a) with bacterivorous MF (BMF), non-parasitic herbivorous MF (NMF), plant-parasitic MF (PMF) and predatory nematode MF (PrMF) showing significantly higher values in soil than in mosses ($P < 0.001$ in all cases).

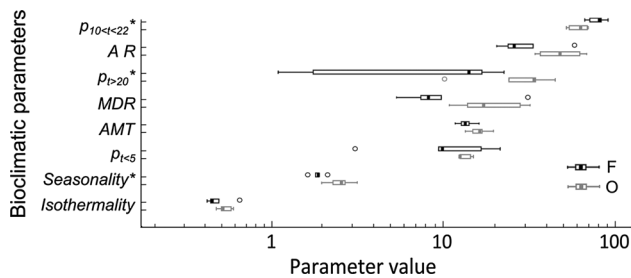


Fig. 3 Bioclimatic parameter values for the F and O sites. Parameters are ordered on the y-axis according to their mean value. *Boxes* Mean \pm SD, *whiskers* extend to 1.5 times the interquartile range from the box, *circles* extreme values. *Asterisks* indicate significant differences ($P < 0.05$) between F (black) and O (grey). Note *log scale*. *AR* annual range, *MDR* mean diurnal range, *AMT* annual mean temperature, $p_{t < 5}$ percentage of temperature records with $t < 5$ °C, $p_{t > 20}$ percentage of temperature records with $t > 20$ °C, $p_{10 < t < 22}$ percentage of temperature records with 10 °C $< t < 22$ °C; for other abbreviations, see Fig. 2

Significant interactions between microhabitat and cover were detected for soil (Fig. 4b) regarding fungivorous MF (FMF) ($P = 0.014$, higher values in the open sites) and PrMF ($P = 0.041$, higher values in the forested sites), while the interaction of microhabitat and altitude was significant regarding soil mosses (Fig. 4c), with PrMF showing significantly higher values in the high altitudes ($P = 0.01$).

Effects of bioclimatic variables on MFs

The coefficients and summary statistics of the multivariate linear models are presented in Table 1. In almost all cases the fitted terms were statistically significant ($P < 0.05$). In soil (Table 1) temperature seasonality was a significant term. Positive coefficients were obtained for FMF and PMF indicating an increase of FMF and PMF values with increasing seasonality. For all other MFs the coefficients were negative. Regarding isothermality, coefficients were positive for BMF and PrMF but negative for all the other MFs. Finally, increasing $p_{10 < t < 22}$ had a positive effect only for the PrMF. Seasonality and $p_{10 < t < 22}$ were also used as predictors for rock mosses (Table 1) and affected MFs of the different trophic groups in a similar way as for soil, although in rock mosses increased $p_{10 < t < 22}$ had a positive effect not only on the PrMF but also on OMF. The fitted model was, however, much more complicated as it included $p_{t < 5}$ and the logarithm of $p_{t < 5}$. Isothermality and its logarithm along with $p_{t > 20}$ were the terms used to predict soil moss MFs (Table 1). The model coefficients indicate that increasing $p_{t > 20}$ had a positive effect on FMF and NMF and a negative effect for all other MFs. The effects of isothermality on the different MFs for different values of $p_{t > 20}$ are shown in Fig. 5. The responses were unimodal and, with the exception of the NMF, the extreme was a

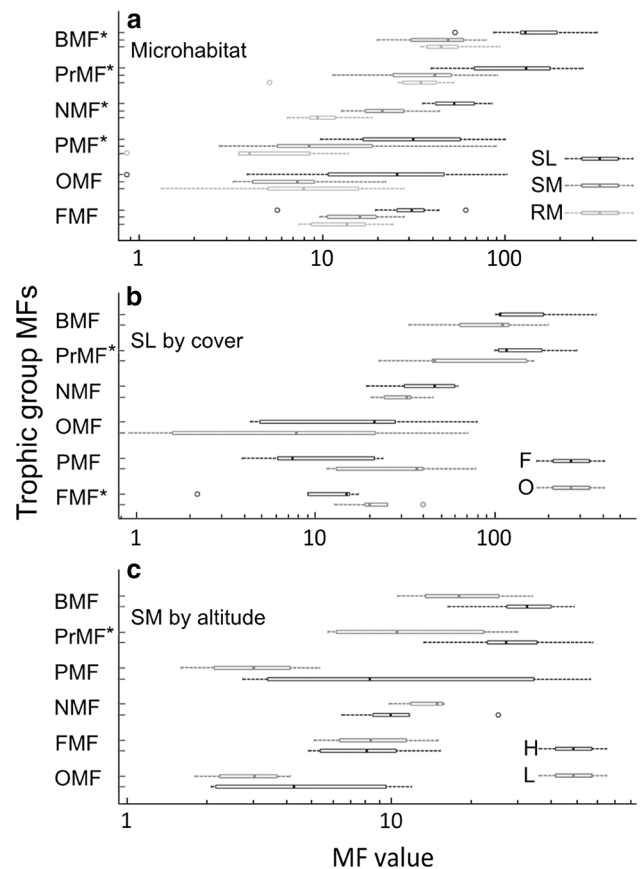


Fig. 4 Values of metabolic footprints (MFs) of the different nematode trophic groups. *Plots* refer to the overall significant effects (Hooper's $R^2 = 0.64$) of **a** microhabitat ($P < 0.001$), **b** the significant effects of microhabitat (soil) by cover ($P = 0.015$) interaction, and **c** microhabitat (soil mosses) by altitude ($P = 0.046$) interaction. Univariate tests: $P < 0.001$ for MFs of bacterivorous (BMF), non-parasitic herbivorous (NMF; root hair-feeders), and predatory nematodes (PrMF); $P = 0.015$ for fungivorous nematodes (FMF); and $P = 0.009$ for plant-parasitic (PMF) nematodes. *Boxes* Mean \pm SD, *whiskers* extend to 1.5 times the interquartile range from the box, *circles* extreme values. *Asterisks* Significant differences ($P < 0.05$) between values for each specific case. Note *log scale* used in plots. *SL* Soil, *SM* soil moss, *RM* rock moss, *OMF* omnivorous MF; for other abbreviations, see Fig. 2

maximum. The relative contribution of $p_{t > 20}$ was high in the cases of the PMF and the BMF and low in the cases of FMF and NMF.

Prediction of yet unseen cases

The predictors (bioclimatic variables plus cover type) used per site and microhabitat for the prediction of unseen cases are listed in Table 2. For predicting MFs in the soil microhabitat, seasonality was used in all ten predictive models, $p_{10 < t < 22}$ was used in seven, annual range in four (three referring to open sites), and mean diurnal range in three models. Although cover type was included as a factor in the

Table 1 Coefficients and summary statistics of the multivariate linear models predicting nematode metabolic footprints (MFs) of the different trophic groups from temperature-based bioclimate parameters at all available sites for model selection and calibration

Micro-habitat	Variable	Coefficients						Summary statistics	
		BMF	FMF	NMF	PMF	OMF	PrMF	LR	Significance
Soil		Hooper's $R^2 = 0.59$, LR = 67.66, $P = 0.003$							
	Intercept	25.84	6.71	16.80	17.68	48.41	7.65	30.3	0.020
	Seasonal.	-2.70	0.44	-0.82	0.72	-3.50	-1.64	32.4	0.015
	ln (isotherm.)	2.53	-0.69	-0.97	-1.97	-5.26	0.38	29.2	0.015
	ln ($p_{10 < t < 22}$)	-3.37	-1.62	-3.30	-4.82	-11.08	0.10	28.3	0.029
Soil mosses		Hooper's $R^2 = 0.61$, LR = 61.46, $P = 0.011$							
	Intercept	24.26	13.99	-24.52	56.83	24.50	36.67	28.2	0.039
	$p_{t > 20}$	-0.06	0.01	0.01	-0.12	-0.03	-0.05	41.8	0.007
	Isotherm.	-24.06	-15.64	30.59	-65.08	-28.91	-41.96	26.6	0.049
	ln (isotherm.)	11.86	7.20	-14.59	29.55	12.64	17.88	27.6	0.041
Rock mosses		Hooper's $R^2 = 0.73$, LR = 64.32, $P = 0.049$							
	Intercept	16.69	8.15	17.84	13.14	-40.10	-8.11	31.9	0.037
	$p_{t < 5}$	0.21	0.08	0.00	-0.08	-0.16	-0.38	31.7	0.038
	ln ($p_{t < 5}$)	-1.25	-0.96	-0.57	0.25	2.75	4.26	36.7	0.023
	ln ($p_{10 < t < 22}$)	-2.85	-1.48	-3.60	-2.87	8.17	1.22	29.6	0.048
	ln (seasonal.)	-2.87	0.08	-2.09	-1.59	5.13	-0.45	28.7	0.056

Summary statistics are based on likelihood ratio (LR) with 1000 residual resampling iterations

BMF Bacterivorous MF, FMF fungivorous MF, NMF non-parasitic herbivores MF, PMF plant-parasitic MF, OMF omnivorous MF, PrMF predatory nematode MF, Seasonal. seasonality, Isotherm. isothermality, $p_{t < 5}$ percentage of temperature records with $t < 5$ °C, $p_{t > 20}$ percentage of temperature records with $t > 20$ °C, $p_{10 < t < 22}$ percentage of temperature records with 10 °C $< t < 22$ °C

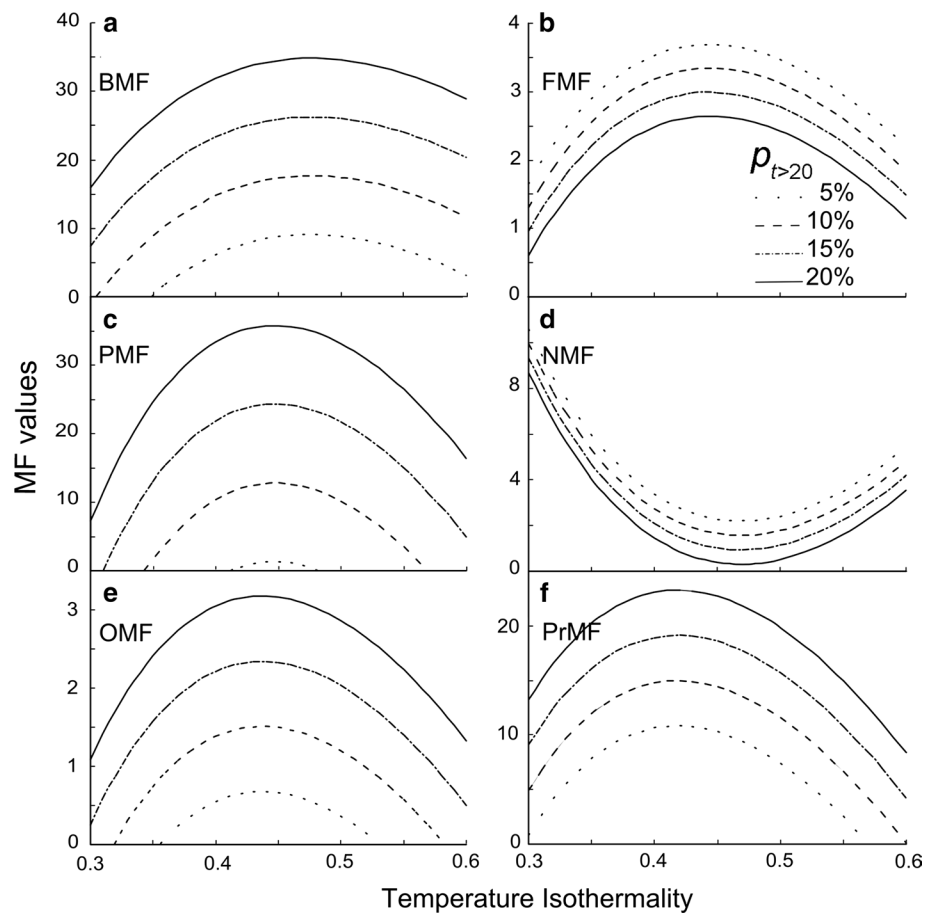
list of possible predictors, it never appeared as a term in a selected model. Apparently, the effects of cover type on the soil MFs were effectively captured by the bioclimatic parameters. Cover type was, however, used frequently (in six out of ten models) for the soil moss MFs prediction along with annual mean temperature, $p_{t > 20}$ and $p_{t < 5}$. For rock mosses, $p_{t < 5}$ was used in all models, $p_{t > 20}$ in six and $p_{10 < t < 20}$ in three. In most cases the models were significant. Non-significant models were obtained in the case of rock mosses, especially when an open site was excluded.

The predictions are shown in Fig. 6a–c. The best predictions were obtained for soil mosses and the worst for rock mosses. As expected, the predictions based on the full data set including all sites were more accurate, apart from the case of soil mosses (Fig. 6b). In many cases the models overestimated MFs for sites where the observed MF values were considerably lower than the mean and underestimated those from sites where the observed values were much higher than the mean. In general, the fitted models were able to capture the major trends of variations in MFs among sites. In many cases, if the model calibrated by all sites overestimates or underestimates a MF value, so does the model predicting that value when the relevant site is excluded. This, however, did not hold in all cases, so it was not possible to make an estimation of the prediction error on the basis of the relevant error obtained by the calibration set.

Discussion

Our results show that temperature and temperature-based bioclimatic parameters exert strong variation among neighboring sites with a different type of cover, and that this local variation is expressed as variation in nematode MFs. The variation by cover is comparable or higher to variations among sites located at different altitudes and orientations for both the bioclimatic parameters and the nematode MFs. This supports arguments (Suggitt et al. 2011; Gillingham et al. 2012) that high resolution temperature maps incorporating local topography and vegetation structure are essential for accessing climate and climate change effects on biota in ways that can inform conservation. In our models, temperature-based bioclimatic parameters alone predict most of the variation in nematode MFs. This is in accordance with the finding of Gillingham et al. (2012) that at local scales, high-resolution temperature variables can be better predictors of species distributions than habitat features. But at a finer scale (within sites) nematode MFs vary by microhabitat (soil, soil mosses and rock mosses) as also observed for the nematode community structure (Bhusal et al. 2014), reflecting the effects of the different type and dynamics of resources. The higher values of predatory, bacterivorous and fungivorous nematode MFs in soil indicate that soil (per unit volume) is richer in resources available

Fig. 5 Effects of isothermality on MFs for different levels of $p_{t>20}$. BMF (a), FMF (b), PMF (c), NMF (d), OMF (e), PrMF (f). Different lines show the 5, 10, 15 and 20 % levels of $p_{t>20}$. For abbreviations, see Figs. 3 and 4



to nematodes than mosses. This also means that the magnitude (sensu Ferris et al. 2010a, b) of the bacterial and fungal energy pathways is higher in soil than in mosses.

Among bioclimatic parameters the most important predictors of nematode MFs are those accounting for temperature variations at various time scales like seasonality, isothermality and parameters indicative of extremities like $p_{t < 5}$ and $p_{t > 20}$, while mean annual temperature has been used in only a few cases. It is generally accepted that for a range of biotic processes temperature variations and extremities are more influential than their averages (East-erling et al. 2000; Thompson et al. 2013), given that the averages are within certain limits. However, the relative importance of bioclimatic parameters differed according to microhabitat. Seasonality is the most important predictor of MFs in soil while $p_{t < 5}$ and $p_{t > 20}$ are especially important for rock mosses.

We included vegetation cover type as a predictor in our models, assuming that the variation of MFs between cover types can only partly be attributed to microclimatic differences. Other factors like resource quality and quantity imposed by differences in litter production, litter quality and temporal patterns in litter fall (Hodson et al. 2014; Cesarz et al. 2013) would have a major effect in shaping

nematode communities and eventually MFs in soil. We further assumed that mosses would better reflect temperature effects across vegetation cover types because they are epiphytes, forming their own substrate (Lindo and Gonzalez 2010), which is not much affected by litter inputs. Though, contrary to our initial assumptions, beyond the implied effect of cover on bioclimatic parameters, cover type per se is not a significant predictor of MFs in soil, but it is a significant predictor for MFs in soil mosses. One possible explanation for this, initially unexpected result, is the fact that there are major differences in the extent and fragmentation of the soil moss carpet between forested and open sites. The degree of fragmentation of the moss carpet, and thus its vulnerability to desiccation, is probably controlled by microclimatic conditions which indirectly affect biota by changing turnover rates of dead moss parts and thus enrichment with nutrients (Lindo and Gonzalez 2010). The extent of the moss carpet, on the other hand, can directly affect population sizes and the structure of nematodes communities, effects that cannot be attributed directly to microclimate conditions but to area-isolation-population size relationships (Gonzalez 2000). For rock mosses, cover is not included in the list of predictors; moss carpet fragmentation and extent in this case are mostly due to the substrate

Table 2 Multivariate linear model formulas used to predict nematode MFs in soil, soil moss and rock moss microhabitats at sites not used for variable selection and calibration

Site ^a	Soil	Soil mosses	Rock mosses
EHF	$\ln(I) + \ln(p_{10 < t < 22}) + S^2$ $R^2 = 0.63, P = 0.008$	$p_{t > 20} + \text{AMT}^2 + \text{cover}$ $R^2 = 0.63, P = 0.046$	$\ln(\text{AR}) + \ln(p_{t < 5}) + \ln(p_{t > 20})$ $R^2 = 0.56, P = 0.048$
EHO	$\ln(\text{AR}) + S + S^2$ $R^2 = 0.72, P = 0.003$	$I + \text{AR} + \text{cover}$ $R^2 = 0.62, P = 0.039$	$p_{t < 5} + \ln(p_{t < 5}) + \ln(p_{10 < t < 22})$ $R^2 = 0.59, P = 0.006$
ELF	$\text{AMT} + p_{t < 5} + \ln(S)$ $R^2 = 0.67, P = 0.012$	$p_{t > 20} + S + \ln(S)$ $R^2 = 0.66, P = 0.022$	$p_{t < 5} + \ln(S) + \ln(p_{10 < t < 22})$ $R^2 = 0.53, P = 0.159$
ELO	$\ln(\text{MDR}) + \ln(S) + \ln(p_{10 < t < 22})$ $R^2 = 0.64, P = 0.003$	$\text{AMT} + p_{t < 5} + \ln(\text{MDR})$ $R^2 = 0.66, P = 0.007$	$\ln(\text{MDR}) + p_{t < 5} + \ln(p_{t > 20})$ $R^2 = 0.44, P = 0.233$
NHF	$\ln(\text{AR}) + \ln(S) + \ln(p_{10 < t < 22})$ $R^2 = 0.59, P = 0.034$	$p_{t > 20} + \text{AMT}^2 + \text{cover}$ $R^2 = 0.63, P = 0.070$	$p_{t < 5} + p_{15 < t < 18} + \ln(p_{10 < t < 22})$ $R^2 = 0.59, P = 0.074$
NHO	$\text{AR} + \ln(S) + \ln(p_{10 < t < 22})$ $R^2 = 0.64, P = 0.029$	$\text{AMT} + \ln(\text{AMT}) + \text{cover}$ $R^2 = 0.64, P = 0.018$	$\ln(\text{MDR}) + p_{t < 5} + \ln(p_{t > 20})$ $R^2 = 0.42, P = 0.298$
NLF	$\ln(S) + \text{MDR}^2 + \ln(p_{10 < t < 22})$ $R^2 = 0.65, P = 0.018$	$\text{AMT} + \ln(\text{AMT}) + \text{cover}$ $R^2 = 0.57, P = 0.080$	$p_{t < 5} + \ln(p_{t < 5}) + \text{cover}$ $R^2 = 0.54, P = 0.026$
NLO	$\text{MDR} + \ln(\text{MDR}) + S$ $R^2 = 0.66, P = 0.028$	$S + \ln(p_{t < 5}) + \ln(p_{10 < t < 22})$ $R^2 = 0.64, P = 0.008$	$p_{t > 20} + \ln(I) + \ln(p_{t < 5})$ $R^2 = 0.57, P = 0.033$
SHF	$S + \ln(S) + \ln(p_{10 < t < 22})$ $R^2 = 0.68, P = 0.012$	$p_{t < 5} + p_{t > 20} + \ln(\text{MDR})$ $R^2 = 0.73, P = 0.001$	$p_{t < 5} + \ln(p_{t < 5}) + \ln(p_{t > 20})$ $R^2 = 0.59, P = 0.012$
SHO	$\text{AR} + \ln(S) + \ln(p_{10 < t < 22})$ $R^2 = 0.64, P = 0.016$	$p_{t > 20} + \text{AMT}^2 + \text{cover}$ $R^2 = 0.63, P = 0.080$	$\ln(\text{AR}) + \ln(p_{t < 5}) + \ln(p_{t > 20})$ $R^2 = 0.47, P = 0.162$

Hooper’s R^2 and model significance (P) based on the LR estimated from 1000 residual resampling iterations are provided for each model. The predictors were temperature-based bioclimatic parameters and cover type. The model formulas were with three terms and were fitted on log-transformed MFs

I Isothermality, S seasonality, AMT annual mean temperature, AR annual range, MDR mean diurnal range; for other abbreviations, see Table 1

^a Site is the site not used to build the model. Site codes are: east (E), north (N), south (S); altitude [high (H), low (L)]; and cover [open (O), forested (F)]

(rock) structure and in a way this is not so dependent on the position of the rock (within or beyond the forest cover).

Considering the MFs of the different trophic groups, the bacterivorous MFs dominated in all sites and microhabitat types over the MF of the other trophic groups. This suggests that in soil as well as in mosses the energy pathways are mostly bacterial dominated, which is in line with studies of Zhang et al. (2015), Ferris et al. (2012) and Rodríguez-Martín et al. (2014). On the other hand, as indicated by the small values of FMF, the metabolism of carbon through the fungal energy pathway is relatively small.

Bacterivorous and fungivorous nematode MFs show contrasting responses to bioclimatic parameters. In general higher values of fungivorous and lower values of bacterivorous nematode MFs are predicted for places with high seasonality, low isothermality and high $p_{t > 20}$, i.e., in open sites at low altitudes. This implies that the relative contribution of the corresponding food web channels to the metabolism of carbon can vary considerably across the landscape. Soil fungi are more tolerant than bacteria to temperatures that are above optimum (Barcenas-Moreno et al. 2009) and appear to increase their activity after a long-term increase of temperature, as indicated by fruit

body production (Gange et al. 2007). Organisms feeding on fungi are also more tolerant to elevated temperatures (Stamou and Sgardelis 1989; Maraun et al. 2007) and increase in abundance when moisture is not a limiting factor (Day et al. 2009; Kardol et al. 2010). In general organisms belonging to the fungal-based food web channel have been found to be more resistant and better able to adapt to climate change associated with drought (de Vries et al. 2012). Finally, it has been highlighted that fungi are important for the decomposition of terrestrial soil organic matter under the harsh environmental conditions of Mediterranean ecosystems, for which models predict even drier conditions in the future (Yuste et al. 2011).

The MFs of plant-parasitic nematodes increased with increasing temperature seasonality in soil in open sites at low altitudes. In such places the herbaceous vegetation is well developed with a variety of plant species and well-developed fine root systems offering more opportunities to plant-parasitic nematodes. As plant-parasitic nematodes show the most pronounced association with plant communities (Yeates and Bongers 1999), while bottom-up effects from plant communities are more important than other factors (e.g., predation) for plant-parasitic nematodes

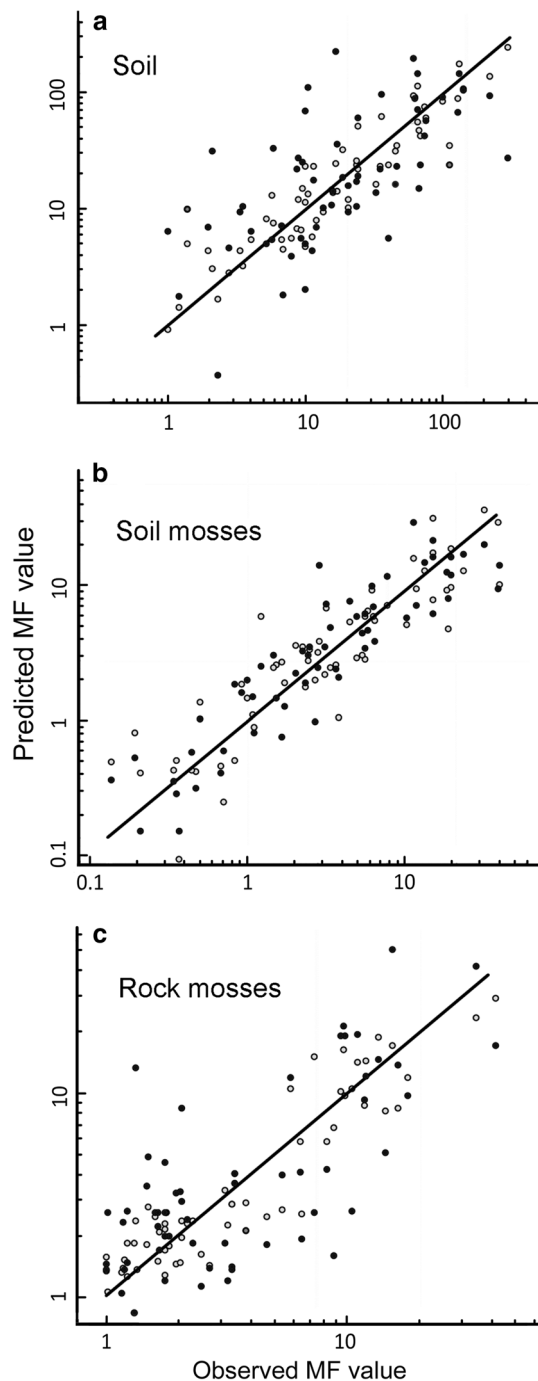


Fig. 6 Predicted vs. observed nematode MFs; MFs of the soil (a), soil moss (b) and rock moss microhabitat (c). Grey symbols refer to the prediction of models calibrated with all sites available and the black symbols to the prediction of models calibrated with the subset of sites remaining after the exclusion of the site to be predicted. Note log scale

(Zhang et al. 2015), the increase of PMF with seasonality apparently relates to changes in the population of plant-parasitic nematodes following seasonal changes in the root growth of their host plants. It should be noted that the study

of Thakur et al. (2014) highlights that temperature-induced shifts in soil nematode communities may cause changes in plant-soil feedback effects.

MFs are calculated based on the biomass of nematodes. Thus it is expected that bigger nematodes, like most of the predatory ones, will have relatively high MFs. On the other hand predatory nematodes represent the highest trophic level of the nematode community and their abundance is generally low, especially in disturbed environments (Bongers 1990; Wasilewska 1997). The MF of this group though, as depicted in our results (Fig. 3), shows that the contribution of predators to the metabolism of carbon is comparable to that of bacterivorous nematodes. This suggests that despite their abundance their contribution to the food web structure (Ferris et al. 2001; Ferris 2010a) as well as to carbon metabolism in soil is very significant. Contrary to the microbivorous and herbivorous trophic groups, the MFs of predatory nematodes in soil and rock mosses and also of omnivorous nematodes in rock mosses, increased with increasing $p_{10 < t < 22}$. This suggests that these groups are favored from temperatures which are within the typical temperature range of the region. Depending on the site the proportion of temperature records falling between 10 and 22 °C varies between 40 and 60 % of the total. The above temperature range corresponds mostly to the climate conditions of spring and autumn in the study region.

Within the range of bioclimatic parameter variations in the studied area, the observed responses of nematode MFs are in many cases linear, but hump-shaped responses are quite frequent (see Table 2). A hump-shaped response implies difficulties in forecasting direct effects of climate or climate change. The observed response can vary from an increase, decrease or no change at all according to the current situation and the magnitude of temperature change. Since hump-shaped biological responses to temperature (and other environmental variables) seem to be the rule rather than the exception for phenomena ranging from enzyme activity to population growth rates and equilibrium sizes (Rall et al. 2012), generalizations on the effects of temperature change should be treated with caution in this case.

As regards the prediction of unknown cases, the prediction errors are, as expected, higher than those of the model built using all available data, with the exception of soil moss MFs. Major over- or underestimations are mostly obtained for cases where the real values are well outside the range of the observed values (outliers) in the set of data used to build the models. This might mean that extremely low or high values of some nematode MFs are due to factors other than temperature effects. We also observe that selected models differ in formulation according to the excluded site. However, some bioclimatic parameters like seasonality in soil and $p_{t < 5}$ in rock mosses are used at a high frequency.

Since the prediction of unknown cases is a hard test for any model, we consider that our models performed well in this task given their rather simple formulation.

That nematode MFs variations among sites can be predicted from microclimate parameters alone does not imply that it is feasible to predict the long-term effects of climate shifts due to global climate change. What we consider feasible is the prediction of current nematode MFs across a landscape, given that a high resolution temperature map is available and the sampling for the estimation of MFs captures most of the microclimatic variation in the region. Despite many restrictions regarding the number of samples, the set of environmental predictors we used and our decision to use the same model formula for predicting MFs of all nematode trophic groups, the fitted models proved to be general enough to provide realistic predictions of new cases within the range of the predictor's values. This is important considering that such models can help to upscale the bioindication potential of nematode communities from the local to the landscape level in future studies.

Conclusion

Soil food web properties explain significant ecosystem functions which we use as ecosystem services (de Vries et al. 2013). Estimating or managing the functional performance of soil at scales that are important for maintaining ecosystem services, specifically under the threat of climate change, remain unresolved challenges. These challenges indicate that it is necessary to tackle obstacles connected to the spatial, temporal, biological and ecological complexity of soil in order to: (1) find representative indicators that are most informative about the functional performance of the entire soil food web; and (2) upscale this information from the sample-sized soil plot to the local, and further, to the landscape level. Regarding (1), nematodes and nematode community indices proved in the past successful at providing consistent information of the status of soil under different land uses and land use changes over a wide range of biogeographical regions and climate conditions, but have not been found to be sensitive to warming (Li et al. 2013). Nematode MFs, on the other hand, provide additional descriptive information on food web form and function and can detect quantitative differences between assemblages based on the magnitude of the MFs (Ferris 2010b). MF analysis introduces the orientation of biological functioning (i.e., utilization of carbon) into traditional community indices and deepens our understanding about ecosystem change, functions, and services. Moreover, MFs appeared to be sensitive to microclimate variations, as we showed in this study. Thus, the introduction of MF in soil studies enormously extends the utility of bioindication, allowing the evaluation of the joint effects of land use and climate on soil biological

activities. Regarding (2), in this work we show that it is feasible to predict nematode MFs using temperature-based bioclimatic parameters. This is a major step towards minimizing soil sampling effort and even gives the opportunity of preparing maps of soil functioning for entire regions given that high-resolution temperature maps are available. This, in turn, could provide new perspectives not only in the field of soil ecology but also in other research areas.

Author contribution statement D. R. B. conducted fieldwork and analyzed samples and data, M. A. T. and S. P. S. conceived the idea and wrote the manuscript, S. P. S. designed the fieldwork and developed the mathematical models.

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