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ORIGINAL RESEARCH

Non-native vegetation encroachment drives trophic turnover in island nematodes

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Abstract

Nematodes are important components of terrestrial ecosystems. There is currently limited understanding of how soil nematode communities are altered by non-native vegetation encroachment. The spatial turnover of nematode communities was studied on Ascension Island in the South Atlantic: an isolated and degraded volcanic island of sparse native vegetation. Many non-native plants were introduced in the mid-1800's, and non-native shrubs have more recently spread across the lowlands. Ascension's elevation gradient represented a unique space-for-time proxy for non-native vegetation colonisation of a relatively barren landscape. Nematodes were collected at 0, 200, 400, 600 and 800 m elevations along three transects and their community composition linked to Landsat-derived vegetation cover and moisture over the 2000–2023 period. Although taxonomic turnover was elevation independent, both nematode abundance and richness increased with elevation. The moist and densely-vegetated mountain top was dominated by plant-root parasites, less dense mid-elevations by omnivores, dry and sparsely-vegetated lowlands by fungivores, and the moist littoral habitat by predators. Landsat analysis predicted that the relative abundance of root parasitic nematodes on Ascension increased by 23% with spreading non-native vegetation over 24 years. While taxonomic turnover in nematode composition may be resultant solely of historic species introductions, trophic turnover is spatially structured and likely follows non-native vegetation encroachment closely. Root parasitic nematodes may be spreading rapidly with non-native vegetation, especially on oceanic islands. The abundance of such nematodes in soil could become an unanticipated hinderance in the restoration of invaded habitat – potentially requiring management long after non-native vegetation is cleared.

Keywords Ecological restoration · Elevation gradients · Invasive species · Nematodes · Non-native vegetation · Root parasites · Spatial turnover · Trophic ecology.

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Extended author information available on the last page of the article

Introduction

Nematodes (phylum: Nematoda) are highly diverse both taxonomically (Blaxter 2016; Hodda 2011) and functionally (Cheng et al. 2021; Peralta et al. 2020; Tong et al. 2010; Vandegehuchte et al. 2015; Xiong et al. 2020). They are found in most, if not all, terrestrial ecosystems: from deserts (Treonis et al. 2022; Vandegehuchte et al. 2015) to Antarctic islands (Raymond and Wharton 2013). Historically, nematodes have been frequently utilised as bioindicators of substrate health (Neher 2001), particularly in agricultural systems (Neher 2010; Wilschut and Geisen 2021). However, nematodes are important components of both natural and modified ecosystems (Yeates et al. 2008) and recent research has highlighted their global significance in shaping plant communities and habitat restoration processes (Lazarova et al. 2021; Dutta and Phani 2023), whilst also having the ability to cause ecological damage where they have been introduced (Hockland et al. 2024).

Soil nematodes can influence plant growth. Certain species can increase plant growth through movement and activation of beneficial microbes, enhancement of nutrient cycling, and predation of pests (Hodda et al. 2009). Other nematode species can reduce plant growth by driving negative plant-soil feedbacks, transmitting infections and directly damaging roots (Topalović and Geisen 2023; Wilschut and Geisen 2021); root-parasitic nematodes in particular, can facilitate such negative processes (Dutta and Phani 2023). In return, vegetation can influence soil nematode communities. Colonisation by non-native plants can alter nematode community structure (Xiao et al. 2013), however, impacts vary between nematode trophic groups (Peralta et al. 2020) and habitats (Čerevková et al. 2019). Nematodes are therefore important in human-modified landscapes (Dutta and Phani 2023) – encroaching non-native vegetation modifies nematode communities, which may impact native plant species.

There is currently limited knowledge of the mechanisms by which nematode communities and non-native vegetation interact, especially in modified landscapes (Wilschut and Geisen 2021). Shifts in nematode communities can be strongly associated with water availability (Cheng et al. 2021; Sohlenius and Wasilewska 1984; Treonis et al. 2022; Xiong et al. 2020); Nematodes are largely aquatic or semi-aquatic, existing in terrestrial systems within tiny water pockets (Neher 2010). Abundance and richness of nematodes have been observed to increase with moisture in native habitat (Treonis et al. 2022; Xiong et al. 2020), although shifts are dependent upon trophic groups (Cheng et al. 2021) and can be slow (on the scale of years; Vandegehuchte et al. 2015). Moisture can also drive trophic turnover in nematodes (Tong et al. 2010; Xiong et al. 2020). Non-native vegetation encroachment can influence soil moisture through increased plant matter deposition (Kuebbing et al. 2014; Thaxton et al. 2012) and it could thus be expected that encroachment would indirectly impact nematode diversity and trophic turnover.

Soil communities of nematodes may be important in active habitat restoration, whereby non-native vegetation is manually removed and native vegetation replanted. Biotic and abiotic restoration of soil is a key factor in such habitat management (Heneghan et al. 2008) although it may be overlooked, or only considered passively. Decline in nematode taxonomic and trophic diversity caused by habitat degradation can be long-lasting (Coffey and Otfinowski 2019). Previous studies have found that proportions of root-parasitic nematodes are highest in habitats where vegetation has recently been introduced or planted (Otfinowski and Coffey 2020), which can result in reduced ecosystem functioning and plant health (Wang et al. 2022). In addition, nematode communities may not transition back towards “natural" states over time, even following replanting of native vegetation (Kardol et al. 2005). This suggests that nematode communities in restored soil and vegetation may be negatively impacted both in short-term establishment and in long-term resilience, both of which need to be addressed for the successful restoration of ecological communities (Suding 2011). Further research is required to understand spatiotemporal shifts in nematode communities, particularly regarding shifts in root-parasite assemblages that result from non-native vegetation encroachment. The presence of invasive non-native vegetation is widespread on oceanic islands (Barton and Fortunel 2023) where it can impact native species ecology (Chin et al. 2024) affect community composition and cause extinctions to occur. It seems highly likely then that nematode communities on oceanic islands have been altered by shifts in vegetation communities caused by the spread of invasive non-native plants.

Nematodes are also abundant on islands (Santos and Venekey 2018) however many island nematode species may be undescribed (de Jesús-Navarrete 2007). One example is Ascension Island in the South Atlantic, which is a volcanic landmass with low native species diversity (Ashmole and Ashmole 2000; Duffey 1964) but many introduced species (Chin et al. 2024; Sharp and Tawatao 2023; Sherwood et al., 2023), however, the nematode diversity of Ascension has not been studied. It seems likely though that nematode communities will comprise of non-native species introduced alongside plants and soil during an 1850's effort to make Ascension more habitable for humans (Ashmole and Ashmole 2000). The ecology of the non-native vegetation of Ascension is in a state of flux and often hampers the active restoration of sites for endemic plant species (Lambdon et al. 2009, 2024).

As a result of the historic introduction of ungulates and the planting of non-native vegetation on Ascension (Ashmole and Ashmole 2000) the abundance of native plants has been severely reduced (Duffey 1964; Lambdon et al. 2009). The elevational gradient suggested by Studer (see Duffey 1964) now represents a unique co-gradient in near-entirely non-native vegetation cover (Lambdon et al. 2024). Soil nematode communities have been shown to be spatially structured along elevational gradients elsewhere (Afzal et al. 2021; Dong et al. 2017; Semeraro et al. 2022), although the Ascension gradient is unique in that the biotic variable potentially explaining ecological change (non-native vegetation) is relatively unconfounded (for example, by native vegetation). This means that the effects of non-native vegetation on soil nematodes are both quantifiable and directly relatable to other ecosystems. The peak of Ascension's central "Green Mountain" is 859 m elevation, which is considerably lower than sites from other purely-elevational studies (Afzal et al. 2021; Dong et al. 2017; Semeraro et al. 2022) and thus there is comparatively lesser abiotic impact of microclimate change. Non-native vegetation in the upper elevations is comparatively stable in composition (P. Ashmole and Ashmole 2000) and thus even very slow shifts in nematode community composition (Coffey and Otfinowski 2019; Vandegehuchte et al. 2015) could be expected to have manifested in those areas. Non-native vegetation in the middle and lower elevations was introduced around the same time but has been slower and more dynamic in its land area colonisation (P. Ashmole and Ashmole 2000). Although plant identity has been linked to presence of some root parasites, studies have found moisture (Xiong et al. 2020) and microbial community (Wang et al. 2022) to be more important determinants of nematode composition. Furthermore, Ascension's landscapes are near-entirely dominated by non-native vegetation (Lambdon et al. 2024) and so only negligible native species interactions could be expected. Elevation on Ascension is therefore a convenient linear space-for-time dimension along which to study non-native vegetation and nematode dynamics in a relatively controlled and changing landscape. The simplicity of Ascension's ecosystem render it an ideal location for assessing turnover in nematode composition through non-native vegetation encroachment given comparatively limited present-day influence by native plants.

Three main effects were tested, that (1) non-native vegetation cover and moisture would drive turnover in nematode composition on Ascension, (2) trophic traits of nematodes would be more dominant determinants of community structure than taxonomy, and (3) root-parasitic nematodes would increase in relative abundance with increasing non-native vegetation encroachment and length of establishment. The aim was to identify the broad vegetation associations of nematode trophic groups in a heavily-modified landscape, with the intention of predicting how nematode community composition shifts through time with vegetation invasion.

Methods

Sampling and processing nematodes

Nematode samples were taken at 11 points across Ascension during August 2023 (Fig. 1a). Points were positioned along three linear transects extending approximately north, south and west and meeting close to the central peak of "Green Mountain" – the highest wettest and most vegetated habitat on Ascension. Individual points were positioned at 0 m (one only – North transect), 200 m, 400 m, 600 m and 800 m elevation (one only – meeting point for all transects). The 0 m point comprised a location of shell sand and rocks on the boundary of the intertidal zone that was saturated with sea water. Points at 200 m largely comprised coarse, gravelly substrate with sparse woody shrubs including Mexican thorn *Prosopis juliflora* (Sw.) DC. and common guava *Psidium guajava* L. Points at 400 m comprised finer substrate with dense woody plants including Bermuda pine *Juniperus bermudiana* L. and denser common guava. Points at 600 m comprised better-developed organic soil with a mixture of coniferous and deciduous trees and leafy vegetation. The central 800 m point was within near-entirely non-native cloud forest with slow-draining, well-developed organic soil. A complete list of sample points with plant species is included in the Supplementary Material (S1).

Nematode substrate samples were collected by hand with a trowel. Samples of 200 g were collected to a maximum depth of approximately 20 cm, and thus contained nematodes inhabiting the surface and upper substrate. Entire samples were temporarily stored open in a cool space with moist kitchen towels for less than 48 h to preserve the live nematodes. They were closed and transported via flight to the nematology laboratory at Fera Science Ltd., where nematodes were immediately extracted using the Whitehead tray technique (EPPO 2013) for 48 h to separate live, motile nematodes from the substrate. Motile nematodes were isolated by washing through three 53 µm sieves, collected in boiling tubes, sealed using parafilm and stored at 5 °C (Cammies et al. 2023). Following extraction, individual nematodes were taxonomically identified and quantified using a Leica M50 stereomicroscope (Leica microsystems, Wetzlar, Germany). Specimens were heat relaxed in water at 65 °C and fixed in a small volume of single strength TAF fixative (7 ml formalin equivalent to 40% formaldehyde, 2 ml triethanolamine, 91 ml distilled water; Southey 1986) on a glass microscope slide, sealed with paraffin wax and nail varnish. Nematodes were studied using

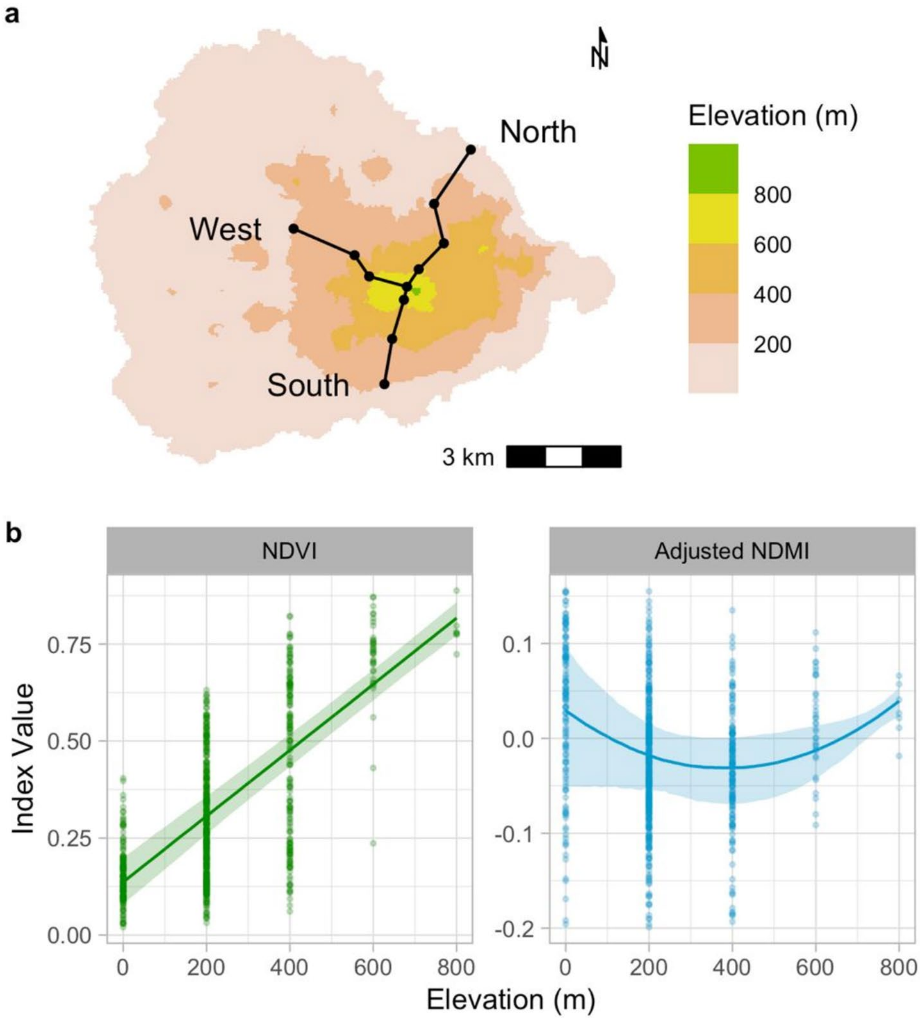

Fig. 1 Nematode sampling points and satellite-derived environmental variables on Ascension Island, South Atlantic. **a**. Locations of sampling points along three elevational transects: North, South and West. **b**. Normalized Difference Vegetation Index (NDVI) and adjusted Normalized Difference Moisture Index (NDMI) values extracted for five elevation bands of ± 10 m on Ascension for the year 2023. Model lines are 95% confidence intervals are derived from bootstrapped linear regression estimates

a high-power compound microscope (Zeiss Axio Imager 2, ZEISS, Germany) utilizing differential interference phase contrast (DIC) and image analysis software. Nematodes were grouped into five trophic groups according to their taxonomic identification (Bongers and Bongers 1998), namely: bacterivores, fungivores, omnivores, predators and root parasites.

Data analysis

Unless otherwise specified, all data analysis and manipulation was conducted in *R version 4.3.1* (R Core Team 2023). Plots were generated using the *ggplot2* (Wickham 2016) and *corrplot* (Wei and Simko 2021) packages.

Deriving vegetation information from satellite imagery

The dominant woody plant species were recorded (S1) but all measures of vegetation used in the analysis were derived from Landsat-7, -8 and –9 satellite imagery (courtesy of the US Geological Survey), and sampling sites chosen that were dominated by a range of non-native plant species, to best minimize species-specific affects. Google Earth Engine (Gorelick et al. 2017) was utilised to retrieve Landsat imagery of Ascension for lowest cloud cover in each of the years 2000–2024 (25 total). Many early Landsat images were incomplete, and the missing and clouded portions of each annually-selected image were masked. Repeated measurements were assembled ($n \geq 3$) for >98% of the island area (median count per-pixel = 16). Normalized Difference Moisture Index (NDMI) and Normalized Difference Vegetation Index (NDVI) were calculated from the raw satellite imagery bands:

$$NDMI = \frac{NIR - SWIR}{NIR + SWIR}$$

$$NDVI = \frac{NIR - Red}{NIR + Red}$$

where *NIR* is Near InfraRed, *SWIR* is Short-Wave InfraRed, and *Red* is the red wavelength band. Both indices scale naturally from – 1 to 1. NDMI is a measure of the moisture held within plant leaves, however it scales closely also with soil moisture (Cahyono et al. 2022). NDVI is an approximation of vegetation cover. Both NDMI and NDVI were resampled to 200 m resolution by median pixel value. Values of $NDVI < 0$ were adjusted to 0 because values – 1 to 0 are indicative of no vegetation cover.

NDMI and NDVI were separately modelled through time to control for seasonal fluctuation and recording error in values. Each individual 200 × 200 m pixel was taken in turn and fitted a linear regression predicting NDMI or NDVI from year. The response was logit transformed before model fitting – NDMI was first scaled from 0 to 1 and back-transformed in later predictions. Where the gradient of that regression was significant ($P < 0.05$), it was predicted that the index changed across the 2000–2024 time period. Where the gradient was insignificant, the mean pixel value was assigned to all years. Modelling change at pixel-scale was advantageous in that it avoided the inherent statistical complication of combined spatial and temporal autocorrelation between pixels and across time. All spatial differences in vegetation growth related to biotic and abiotic factors such as substrate geology, non-random grazing by feral donkeys and uneven rainfall and substrate moisture were accounted for.

Elevational trends in NDMI and NDVI in the year of nematode collection (2023) were examined by extracting values within ± 10 m elevation of the 0 m, 200 m, 400 m, 600 m and 800 m contours. NDMI and NDVI were strongly positively correlated (Pearson’s rho = 0.75,

$P < 0.001$). To validly use the two indices in predictive models of nematode community composition, NDMI was adjusted to be independent of NDVI by fitting a linear regression predicting the former from the latter and utilizing the residual values as "adjusted NDMI". There were naturally great numbers of values for lower elevations, a bootstrap-equivalent approach was used in order to fit parameter estimates with equal weighting attributed to each elevation band. 10,000 linear regressions predicting adjusted NDMI/NDVI from elevation to subsets of values were fitted, sampling 7 values from each elevation band (total $= 35$; $> 5.38 \times 10^{44}$ possible combinations). Final gradient estimates were derived from quantiles of the 10,000 fitted parameters. In terms of vegetation ecology, this adjusted NDMI represents the additional or lacking "expected" plant moisture within a given area relative to the vegetation cover there. NDMI alone is less informative in that regard as the index is inherently linked to vegetation cover – a high NDMI value could indicate either high vegetation cover or high vegetation moisture, whereas a high adjusted NDMI value could indicate only the latter.

Quantifying spatial shifts in nematode abundance and taxonomic diversity

The overall trend in nematode taxonomic diversity was examined, both along the elevation gradient and between transects. The total abundance and richness of nematodes per site was calculated from the fresh soil samples, and predicted both from elevation via Poisson Generalized Linear Models (GLMs) with log link function. The mean Bray-Curtis dissimilarity in taxon presence/absence was calculated, both between transects (North, South and West; without the 0 m and 800 m elevation sites) and separately between elevation bands (0 m, 200 m, 400 m, 600 m and 800 m). Significance of those spatial turnover measures was assessed via randomization. For between-transect dissimilarity, species were mixed between sites of the same elevation band and the Bray-Curtis index recalculated 10,000 times. For between-elevation dissimilarity, species were mixed between sites of the same transect and Bray-Curtis indices recalculated in the same fashion. "True" dissimilarity was considered significant where that value was greater than 95% of randomized values.

Linking non-native plant traits with elevation and nematode composition

To test whether functional traits of present non-native plant species impacted nematode communities beyond vegetation cover and moisture, data was accessed from the TRY plant trait database (Kattge et al. 2020). The species-specific data was collated for all variables where at least five of the plant species dominating one of our sampling points (S1) was represented. The subset plant traits relating to individuals of species were ecosystem rooting depth, plant height, leaf area, dry leaf mass, leaf nitrogen content, leaf nitrogen/phosphorous ratio, leaf phosphorous content, specific leaf area and wood density. Subset traits relating to sites occupied by the relative plant species were actual evapotranspiration, fractional absorption of photosynthetically active radiation, gross primary productivity, leaf area index, maximum green vegetation fraction, annual sum of potential evapotranspiration, NDVI, net primary productivity, Priestley-Taylor evapotranspiration, soil bulk density, soil carbon and nitrogen per ground area, soil pH, plant-available water of root zone, soil profile available water, soil wilting point and wetness of sample areas (S4), After assigning those variable values to sampling points, Spearman's rank correlation coefficient was calculated with elevation (over only the 200–800 m elevations where vascular plants were present), nematode abundance and nematode richness.

Quantifying elevational turnover in nematode trophic groups

Initial detection of spatial segregation between nematode trophic groups was achieved by calculating Spearman's correlation between both abundance and richness of the five trophic groups. Due to the overall strong correlation between total nematode abundance/richness and elevation (described in Results), it was misinformative to test the significance of those correlations against a value of 0. Inter-group correlations were instead tested against the hypothesis that they were lesser than expected by chance (even if that correlation was >0). This was achieved, again, by randomization. True correlations between trophic group abundance and richness were calculated, and subsequently mixed values between samples and recalculated Spearman's rho 10,000 times. Correlations were considered significantly lesser at the $P<0.05$, $P<0.01$ or $P<0.001$ significance levels where 95%, 99% or 99.9% of randomized values were greater than the true correlation value.

The effects of NDVI and adjusted NDMI were next examined, and elevation on the relative proportions of nematode trophic groups. Taking each group in turn, logistic regressions were fitted predicting whether each collected individual nematode belonged to that group (coded as 1) or not (coded as 0). Data points were weighted such that the elevation bands contributed equally to the model fit. Two models for each trophic group were fitted. Parameters were selected via AIC from the following candidate terms: NDVI, NDVI^2 and adjusted NDMI. NDVI^2 was tested to detect potential peaks in the index for nematode trophic groups. In addition, the pairwise interaction between NDVI was tested and adjusted NDMI to detect whether vegetation-related trends were moisture dependent. Interactions between NDVI^2 and adjusted NDMI were not tested as this combination over-fitted models and could not be reasonably linked to ecological theory. NDVI^2 was not included as a predictor for fungivores as inclusion led to unresolvable model instability, perhaps resulting from limited data for that group. Separately, the relative proportion of nematode trophic groups was predicted from elevation using logistic regression and the same weighting as previously applied. For these secondary models, parameters were selected via AIC from only elevation and elevation^2.

Predicting co-encroachment of root parasites with non-native vegetation

In order to quantify the potential spatial expansion in root parasitic nematodes over time, the link between pixel vegetation cover and relative abundance of nematodes was quantified before extrapolating pre-pixel nematode abundance across time. Only NDVI was used, in place of NDMI or adjusted NDMI, as it was the only variable that was selected in prior models as being of significance to root parasitic nematodes (described in Results). A GLM predicting root parasitic abundance was fitted from NDVI in the year 2000, and additive increased in NDVI 2000–2023 (2023 was the year of nematode collection). The additive NDVI increase term was included to account for potential lag in the colonisation of vegetated land by nematodes. A quasipoisson error distribution was used to account for overdispersion in the response, and a log link function. Then, using the previously generated per-year maps of Ascension NDVI, the per-pixel relative abundance of root parasitic nematodes was estimated for the years 2000 and 2023. No extrapolation outside of the bounds of the modelled explanatory variables was performed (values greater than 0.81 for year-2000 NDVI, and values greater than 0.53 for NDVI increase) – in occasional cases where pixel values were greater ($<1\%$ of values), the maximum value in the model explanatory variables was predicted.

Results

Nematodes were detected at all but one of the sampling points: elevation 200 m on the northern transect. A total of just 415 individual nematodes were isolated from samples, with 45 taxa identified (S3). Of those taxa, eight species were identified, and the remaining 37 taxa were identified to genus ($n=27$), subfamily ($n=2$) or family ($n=8$). Dagger nematodes were the most abundant root-parasitic group ($n=93$), belonging to the species *Xiphinema diffusum* Lamberti & Bleve-Zacheo 1979 and *Xiphinema krugi* Lordello 1955. Spiral nematodes of the genus *Helicotylenchus* ($n=40$) were the next most abundant. Root parasites, including *Xiphinema* and *Helicotylenchus*, comprised 41% of all individual nematodes isolated. Most other trophic groups were relatively balanced in total abundance: 16% were bacterivores, 18% were omnivores and 19% were predatory. Fungivores were least represented, comprising just 6% of the total individuals.

Vegetation indices shifted significantly along the elevational gradient (Fig. 1b). NDVI increased at a rate of 0.051 units per 100 m elevation increase (bootstrap-derived 95% CI=0.043–0.061) while adjusted NDMI peaked at highest and lowest elevation (elevation term: median = -0.030, 95% CI = -0.063-0.010; elevation^2 term: median$=3.97\times10^{-5}$, 95% CI$=0.0835\text{-}7.42\times10^{-5}$). There was also only one trait reported from the TRY database (Kattge et al. 2020) that correlated significantly with elevation (200–800 m): plant-available water of root zone, which correlated negatively ($P<0.05$; S4). This suggested that realized plant moisture and soil moisture were lowest in Ascension's inland lowlands, around 200–400 m elevation. Vegetation moisture relative to vegetation cover was highest at the coast and at the mountain peak, while overall vegetation cover increased linearly with elevation. No additional significant elevational trends were detected ($P>0.05$) in TRY data on physical plant traits (e.g. rooting depth, plant height), leaf nutrients (e.g. nitrogen and phosphorous content), physiological rates (e.g. evapotranspiration, primary productivity), soil traits (e.g. density, soil carbon and nitrogen, pH) or factors relating to remote sensing of vegetation cover (e.g. maximum green vegetation fraction, NDVI; S4). Therefore, while plant composition transitioned from mixed non-native forest at the mountaintop to sparse Mexican thorn and guava shrub in the lowlands, no directional shifts in plant functional traits were detected.

Shifts in vegetation cover and moisture were accompanied by elevational increases in nematodes (Fig. 2a). Total nematode abundance was greatest at highest elevation with a small increase at the coastal point also (elevation term: Z = -9.00, $P<0.001$; elevation^2 term: $Z=12.94$, $P<0.001$). Nematode taxonomic richness increased with elevation (elevation term: $Z=5.77$, $P<0.001$). Neither abundance nor richness of nematodes correlated significantly with traits of the plants species dominating individual sampling points ($P>0.05$), as reported from TRY (S4). Mean Bray-Curtis dissimilarity was greater than expected by

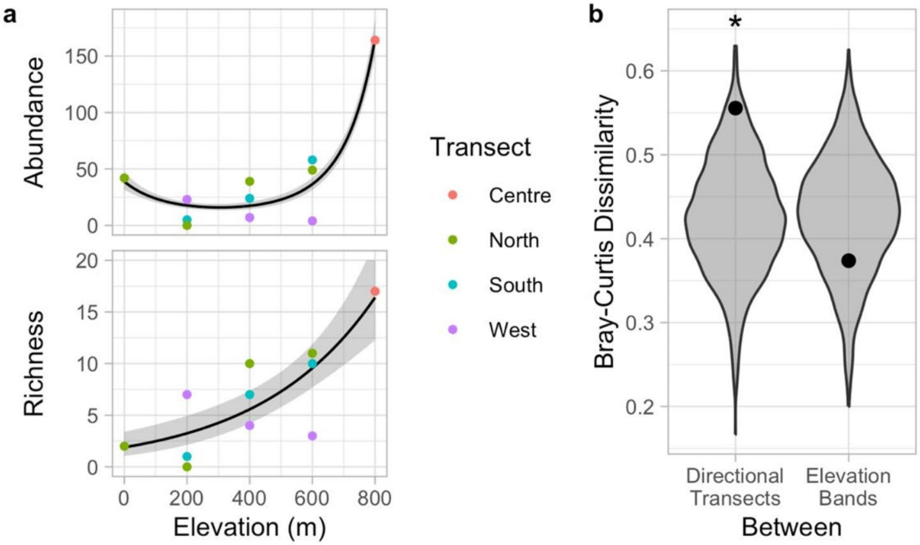

Fig. 2 Summary of nematode taxonomic community structure on Ascension Island in 2023. **a**. Nematode total abundance and species richness from each sampling site on three transects meeting at the Centre (peak of the central mountain). Grey bands represent 95% confidence intervals derived from standard errors. **b**. Spatial turnover in nematode taxonomic composition. True mean values of Bray-Curtis dissimilarity are indicated by black points. Distributions of randomized Bray-Curtis values expected through chance are represented by violin plots. True Bray-Curtis values greater than 95% of randomized values ($P<0.05$) are indicated by *

chance between directional transects (index=0.56, $P<0.05$) but not between elevation bands (index=0.37, $P>0.05$; Fig. 2b).

Spatial correlations in both abundance and richness of nematode trophic groups were overall positive due to the strong elevational increase in nematodes (Fig. 3). No trophic groups were more positively correlated in either abundance or richness than expected ($P>0.05$). All of the trophic groups were more negatively correlated in abundance with at least two other groups than expected ($P<0.05$). Fungivores were correlated more negatively than expected with all other trophic groups in both abundance ($P<0.05$) and richness ($P<0.05$). None of the other trophic groups were more negatively correlated in richness than expected ($P>0.05$).

Vegetation indices showed significant differences in proportion of nematode trophic groups across the elevation gradient (Fig. 4a). Bacterivores were negatively associated with NDVI ($Z = -4.43$, $P<0.001$) and adjusted NDMI ($Z = -5.10$, $P<0.001$), and positively associated with the interaction between NDVI and adjusted NDMI ($Z=4.46$, $P<0.001$). Fungivores were associated with neither NDVI ($Z=1.29$, $P>0.05$) nor adjusted NDMI alone ($Z=0.59$, $P>0.05$) but were associated with their interaction ($Z = -3.17$, $P<0.01$). Omnivores exhibited a polynomial relationship with NDVI (NDVI term: $Z=3.95$, $P<0.001$; $NDVI^2$ term: $Z = -4.35$, $P<0.001$) but also increased in proportion with adjusted NDMI ($Z=1.98$, $P<0.05$). Proportion of predatory nematodes was increased by NDVI ($Z=2.14$, $P<0.05$), adjusted NDMI ($Z=5.47$, $P<0.001$) and reduced by the interaction between the two ($Z = -4.76$, $P<0.001$). Predators reached a relative plateau at high NDVI (NDVI term:

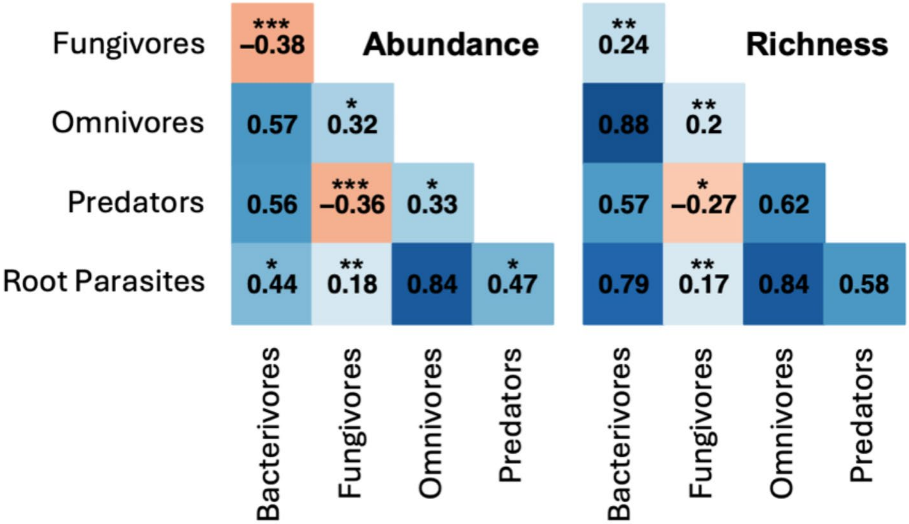

Fig. 3 Spearman's correlation in occurrence of nematode trophic groups. Positive correlations are represented by blue and negative by red. None of the trophic groups were more positively correlated than expected (assessed via randomization). Significance at the $P<0.05$, $P<0.01$ and $P<0.001$ levels are indicated by *, ** and *** respectively

$Z=2.61$, $P<0.01$; NDVI^2 term: $Z=-2.33$, $P<0.05$). In dry conditions (low adjusted NDMI), it was predicted that bacterivores would dominate low vegetation cover (low NDVI), and fungivores and root parasites would dominate high vegetation cover areas (high NDVI). In contrast, under moist vegetation conditions (high adjusted NDMI) predators would dominate low vegetation cover, omnivores would dominate moderate vegetation cover, and root parasites would still dominate high vegetation (Fig. 4a).

The relationships between nematode groups and vegetation appeared to drive elevational turnover in trophic group (Fig. 4b). Most trophic groups exhibited a polynomial association with elevation: bacterivores (elevation term: $Z=2.53$, $P<0.05$; elevation^2 term: $Z=-2.97$, $P<0.01$), fungivores (elevation term: $Z=4.24$, $P<0.001$; elevation^2 term: $Z=-4.42$, $P<0.001$), omnivores (elevation term: $Z=5.50$, $P<0.001$; elevation^2 term: $Z=-5.62$, $P<0.001$) and predators (elevation term: $Z=-8.98$, $P<0.001$; elevation^2 term: $Z=7.30$, $P<0.001$). Proportion of root parasites increased without polynomial function (elevation term: $Z=9.41$, $P<0.001$). It was predicted that in 2023 elevations below approximately 170 m were dominated by predatory nematodes, elevations 170–330 m were dominated by fungivores, elevations 330–560 m were dominated by omnivores and elevations greater than around 560 m were dominated by root parasites. Bacterivores were present across elevations.

Relative abundance of root parasites was related to both long-established (year 2000) NDVI and increasing NDVI (additive change since year 2000). The effect of recent NDVI increase (estimate: 12.10, $t_8=3.59$, $P<0.01$) was lesser than the effect of year 2000 NDVI (estimate: 16.14, $t_8=4.85$, $P<0.01$), indicating a lag in the colonisation of recently-vegetated land by nematodes. Island areas where year 2023 NDVI>~0.7 were most abundant with root-parasitic nematodes (Fig. 5a). NDVI was estimated to have increased across

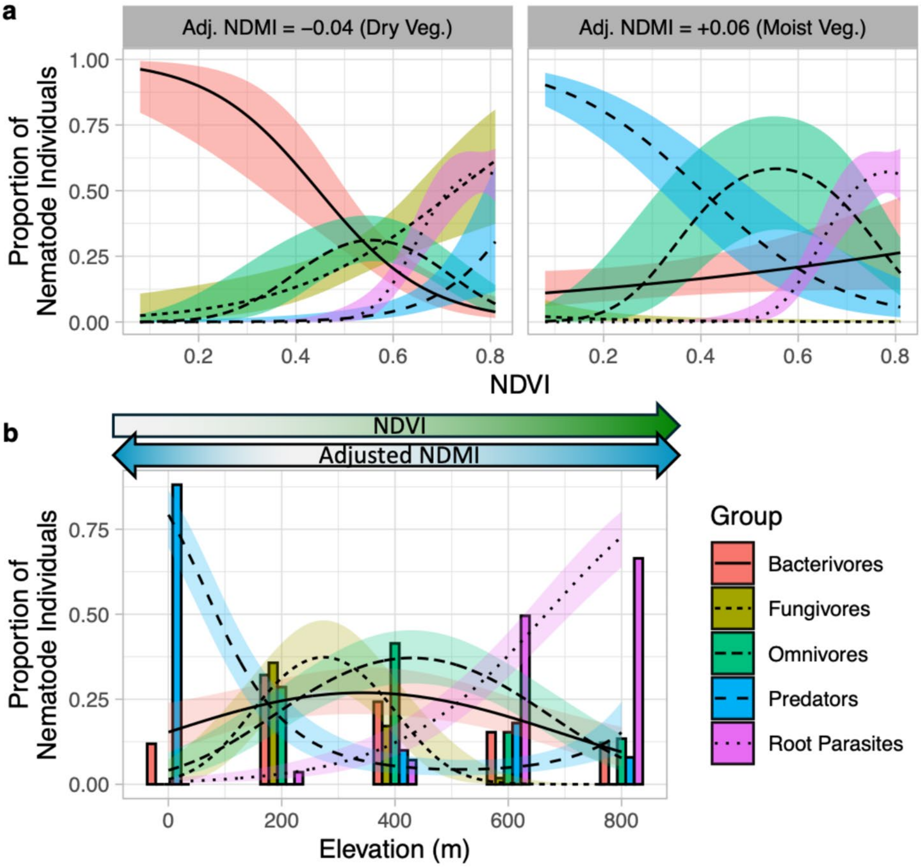

Fig. 4 Turnover in nematode trophic composition. **a**. Modelled relationships (separate logistic regressions) between trophic groups and Normalized Difference Vegetation Index (NDVI) and Normalized Difference Moisture Index (NDMI; adjusted to be independent of NDVI). Representative adjusted NDMI values are the 10% and 90% quantiles of measured values. Coloured bands indicated 95% confidence intervals derived from standard errors. **b**. Elevational turnover in nematode trophic groups. Coloured bars represent observed proportions of nematodes. Lines and 95% confidence intervals represent individual logistic regressions

Ascension in the 2000–2024 period (Fig. 5b). Per-pixel values increased by median 0.19 units in NDVI. The year-2024 land area where NDVI < 0.1 (corresponding to barren areas of rock or sand) was just 7% of equivalent year-2000 area (>14x absolute change). The rate of change in dense vegetation area was comparatively lower - the year-2024 land area where NDVI > 0.7 (corresponding to dense vegetation) was 215% of equivalent year-2000 area (>2x absolute change). Extrapolating from island-scale increases in NDVI, we estimated that abundance of root parasite nematodes increased by 23% between 2000 and 2023 (Fig. 5c).

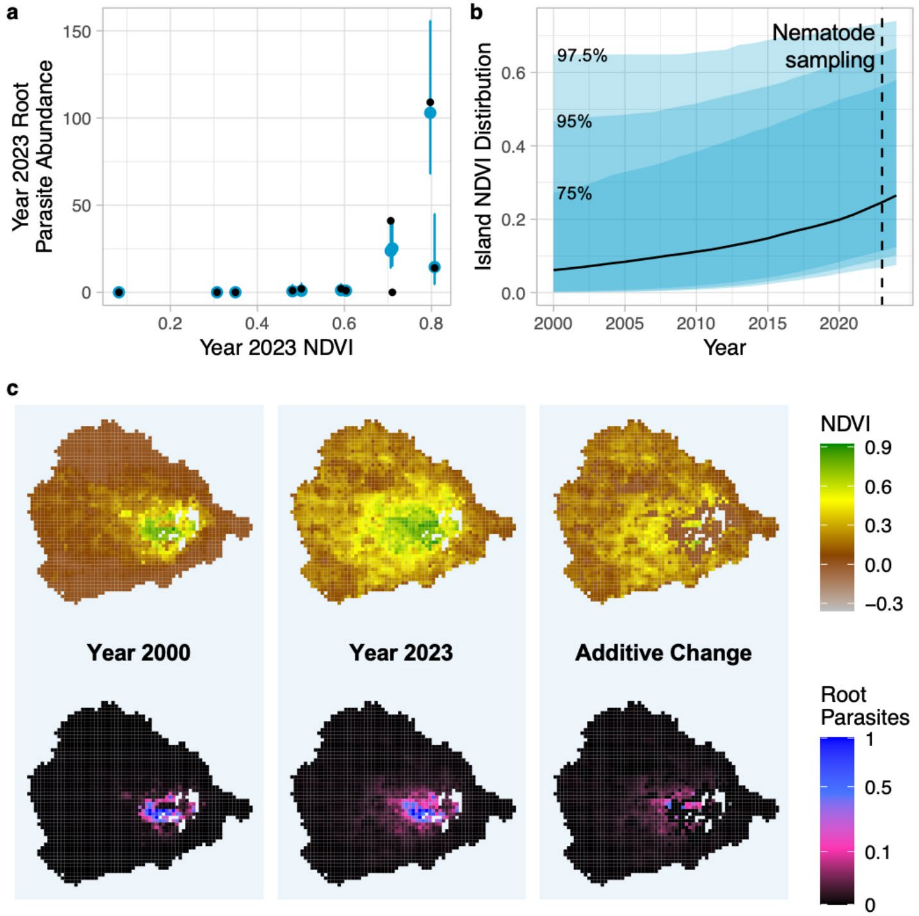

Fig. 5 Projected increase in root parasite abundance over the 2000–2023 time period. **a**. Quasipoisson GLM predicting root parasite abundance in the year 2023 from Normalized Difference Vegetation Index (NDVI) in 2000 and additive change in NDVI up until 2023. Blue points and vertical lines represent estimated medians and 95% confidence intervals respectively, and black points represent observed values. **b**. Increase in NDVI on Ascension Island over 2000–2024. Blue bands represent spatial quantiles in NDVI shifting over time. **c**. Outward expansion in NDVI and predicted relative root parasite abundance from the central Green Mountain. Empty pixels are those where there was insufficient data to assess NDVI change over the study period

Discussion

Our novel analysis of nematode community shift along an elevation and non-native vegetation co-gradient, on Ascension showed much of the nematode richness, and the majority of the comparatively limited number of individuals, belonged to species likely introduced to Ascension, either during the mass movement of vegetation in the 1850's (Ashmole and Ashmole 2000) or more recently. Many nematode individuals could not be identified to species using morphological characteristics, certain species are likely yet-undescribed taxa native to the island (de Jesús-Navarrete 2007). The nematode community exhibited clear trophic turnover that was closely linked with ongoing non-native vegetation encroachment on barren land.

A high proportion of the nematodes isolated were root parasites. Natively-barren islands have previously been reported as absent of root parasitic nematodes (Spaull 1973), presumably for the relative scarcity of vascular plants. Ascension's native habitats would likely be relatively lower in plant biomass compared to the modern dense mesquite and mountain forest habitats, for example (Ashmole and Ashmole 2000; Lambdon et al. 2024). However, dagger nematodes (of the widespread genus *Xiphinema*) and spiral nematodes (of similarly widespread *Helicotylenchus*) were relatively abundant. Both *Xiphenema* and *Helicotylenchus* species can be associated with spurges and grasses (Caveness 1967; Goodey and Goodey 1956; Siddiqui et al. 1973), such as would naturally be abundant in Ascension's lowlands but are now mostly absent (Ashmole and Ashmole 2000; Lambdon et al. 2009, 2024). However, both of those genera were found only at higher elevations, which would naturally be dominated by endemic ferns of the families Marattiaceae and Pteridaceae and are now dominated by translocated ornamental shrubs and trees (Ashmole and Ashmole 2000; Lambdon et al. 2009, 2024). While both *Xiphenema* and *Helicotylenchus* have previously been associated with certain fern families (Kaplan and Osborne 1986; Siddiqui et al. 1973), we can find no records of them parasitizing Marattiaceae or Pteridaceae fern species and many records of them parasitizing seeding ornamental families (Caveness 1967; Goodey and Goodey 1956; Siddiqui et al. 1973). We consider *Xiphenema* and *Helicotylenchus* nematodes to be non-native to Ascension, probably introduced in soil with intentionally translocated plants (Ashmole and Ashmole 2000). These nematodes are known to damage host plant root systems proportionally to their abundance, can act as virus vectors, and have wide host plant ranges (Cohn 1970; McElroy 1972). Whilst it is a possibility, there is no evidence to date that nematodes parasitize any of the present Ascension-endemic plants present – this may form the basis of future research on Ascension. Nonetheless, these nematodes are likely candidates as globally "invasive" species given their detrimental impacts on plant roots (Singh et al. 2013).

Total nematode abundance and diversity was found to increase with elevation and vegetation cover. Previous studies reported opposing responses of nematode diversity to elevation (Afzal et al. 2021; Dong et al. 2017; Tong et al. 2010) and so it is proposed that elevational responses are tied mostly to site-specific habitat gradients – those were non-native vegetation cover and moisture in this study. It is accepted that the 800 m elevation gain in these study points probably also introduced some level of bias with, for example, a minor gradient in air temperature: 4.8 °C as estimated similar to Dong et al. (2017). However, soil temperatures can be more sensitive to vegetation cover than air temperatures (Yu et al. 2022). It is evident that the strong effects of vegetation (Čerevková et al. 2019; Peralta et al. 2020; Xiao et al. 2013) and moisture (Cheng et al. 2021; Sohlenius and Wasilewska 1984; Treonis et al. 2022; Xiong et al. 2020) on nematode communities out-weighed any variation in air temperature. Similarly, there was no evidence that non-native plant identity influenced soil nematode abundance or richness through trophic traits, although the plant data was from a global database (Kattge et al. 2020) and thus species-specific plant traits may have differed to some extent on Ascension. Nonetheless, the results of this study suggest that proportional non-native vegetation cover and moisture alone shaped nematode communities.

Spatial turnover in taxonomic diversity was linked mostly to transect instead of elevation band. This suggested that spatial taxonomic turnover in the Ascension nematode community was more so defined across two-dimensional space than elevation. High taxonomic turnover in nematodes has been observed in other heavily degraded landscapes (Wang et al. 2023) and is attributed to the directional turnover to non-random plant introductions. Ascension's non-native plants were widespread in their origin (S1), and translocated mostly via botanical gardens in the UK and South Africa (Ashmole and Ashmole 2000). It is considered that taxonomic turnover in nematodes was still mostly defined by the locations of historic plant and soil introductions, with which many non-native nematode species were likely also introduced. Trophic turnover was more actively structured across elevation by dynamic non-native vegetation in this degraded study system.

There was significant spatial segregation between nematode trophic groups which appeared to be resultant of spatiotemporal turnover. As in other studies, bacterivores were present across habitats (Spaull 1973), however increased to moderate proportions in the lowlands in response to aridity (Cheng et al. 2021). The comparatively low overall abundance of bacterivores may be attributed to low nutrient levels limiting bacterial growth (Jiang et al. 2018; Sohlenius and Wasilewska 1984), perhaps explained by the fact that nitrogen-fixing plants have been introduced only relatively recently. Predators dominated the lowest elevation, seemingly in association with moist algae and sparse ephemeral grasses. On Ascension, sandy coastlines are littered with animal protein sources including fish carcasses and green turtle *Chelonia mydas* L. nests. The results suggest that the moisture rather than the algae/vegetation presence was most important for predator nematodes. This was potentially important in facilitating the decomposition of animal protein by microbes and micro-invertebrates, on which certain predatory nematodes feed. Fungivores were more negatively correlated than expected in both abundance and diversity, presumably as this was the only group closely linked with sparse non-native vegetation in the lowlands. Fungivores have previously been associated with arid environments (Briar et al. 2012; Cheng et al. 2021), low soil nutrients (Jiang et al. 2018; Sohlenius and Wasilewska 1984), and exist at low abundance in barren landscapes (Spaull 1973) in accordance with these findings. In the mid elevations, omnivores dominated with increased moisture and intermediate vegetation cover. Omnivores are known to be more abundant in primitive (Spaull 1973) or undisturbed vegetation habitat, these habitats often have low nutrient input (Sieriebriennikov et al. 2014) which matches mid-elevation Ascension habitat. Omnivores were likely displaced at highest elevations by the root parasites, which according to feeding ecology must be well-adapted to high-density vegetation and nutrient-rich soils. These results validate prior knowledge regarding responses of nematode trophic groups in the context of a linear gradient in vegetation cover. It is predicted that the colonisation of dry, barren land by moist non-native vegetation would drive nematode composition from bacterivore dominance, to fungivores, omnivores and finally root parasites with increasing density. Similarly, it is predicted that colonisation by dry non-native vegetation would shift nematode composition towards a community dominated relatively equally by fungivores and root parasites.

On Ascension, one island of many where non-native vegetation is spreading rapidly, it was estimated that the relative abundance of root parasites increased moderately in the years 2000–2023. It was predicted that root parasites were abundant only where vegetation was dense (NDVI$>\sim$0.7), and non-native vegetation on Ascension appears to be more rapidly colonising new areas than becoming thicker in already-colonised places. This may be the result of more recently established non-native plants, including Mexican thorn and common guava, being able to rapidly colonize low-moisture lowland terrain where other introduced species were unable. Non-native vegetation will likely increase in density following this initial colonisation, and may also themselves modify substrates via deposition of moisture and nutrients (Kuebbing et al. 2014; Thaxton et al. 2012). This is concerning since areas of dense vegetation more than doubled in area over the years 2000–2024, and if current trends are maintained then those areas of particularly dense non-native vegetation will expand exponentially. Therefore, a large proportion of land may remain dominated by fungivores and omnivores in the short-term before non-native vegetation becomes sufficiently dense that root parasites increase in abundance. This turning point may occur soon on Ascension. The same may be true on other islands degraded by non-native vegetation, or may already be experiencing rapid shifts toward root parasite-dominated nematode communities.

There is novel threat to native island vegetation in that high abundances of root parasitic nematodes, native or non-native (Singh et al. 2013), may disrupt active restoration efforts (Lazarova et al. 2021). Modified nematode communities may not return to past composition following non-native vegetation clearance (Coffey and Otfinowski 2019; Kardol et al. 2005) and increased root parasite abundance may be detrimental to the later establishment and longevity of threatened and propagated plants (Dutta and Phani 2023; Topalović and Geisen 2023). Elevated root parasite density may be an emerging and unseen “curse” on the success of ecological restoration. Actual impact level will certainly be site- and species-specific, and depend heavily on whether root parasites are native or introduced with vegetation.

Nematodes will likely need to be managed during active habitat restoration efforts (Wilschut and Geisen 2021). Whilst it may be difficult or impossible to anticipate taxonomic turnover in heavily-degraded landscapes, it is concluded that non-native vegetation encroachment of barren landscapes inevitably lead to communities dominated by root parasites. The spatial structure of nematode communities are broadly predictable in relation to non-native vegetation cover and moisture, and may be incorporated into future decision-making. Further research should explore: (1) the potential detrimental impacts of altered nematode communities on native and threatened plant species, (2) the potential loss of ecological benefits from some trophic groups, and (3) methods of returning altered communities to natural states. These needs are especially pressing on oceanic islands, which are changing rapidly.

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Author contributions AS led study design and statistical analysis. AS and NT conceived the sampling design on Ascension. Nematode identification and functional diagnosis was led by MC, assisted by RL, and supervised by TP. AG contributed plant functional trait expertise and analyses. ML contributed remote sensing expertise and analyses. All Authors contributed to writing of this manuscript.

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Declarations

Competing interests The authors declare no competing interests.

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