Spatial structure and soil properties shape local community structure of plant-parasitic nematodes in cultivated olive trees in southern Spain

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ABSTRACT

Numerous studies have documented the distribution of plant and animal communities with respect to spatial structure; however, relatively little is known about the involvement of spatial structures in the diversity of soil organisms such as plant-parasitic nematodes (PPN). Host plants such as olive trees are of particular interest because they host a large number of PPN and have a high economic and cultural importance. In this study, we investigated how different aspects of the environment (i.e. the factors soil, above-ground environment, and agricultural management) and spatial structure shaped the variation of species composition (expressed as beta diversity) and species richness of plant-parasitic nematodes infesting the soil rhizosphere in 376 commercial olive orchards in the south of Spain. We used variation partitioning to assess the relative importance of the unique and shared contributions of the factors describing the environment and spatial structure. To identify sites and species of particular interest, we partitioned beta diversity into local and species contributions.

Contrary to our expectation that soil and agricultural management would largely determine the community structure of PPN, more than two-thirds of the variation remained unexplained. Spatial structure and soil were the most important factors shaping species richness and beta diversity. Surprisingly, the effects of agricultural management on species richness were lower than expected, and null [or nonexistent, or nonsignificant] on beta diversity. We found relatively high levels of shared contributions of the different factors, especially in combination with spatial structure, indicating the presence of spatial gradients of the variables describing the environmental factors.

Species contributions to beta diversity (SCBD) were positively correlated with nematode prevalence and density range; thus, SCBD could be related to the niche

position as reported in other ecosystems. Local contributions to beta diversity (LCBD) were mainly related with habitat filtering mechanisms (e.g. soil physiochemical and agronomic management predictors), suggesting a relationship between nematode total biomass and ecological gradients. Overall, we revealed novel insights into the spatial structure of PPN communities and showed that its beta diversity is less structured by spatial and environmental factors compared to other organism types.

Keywords:
below-ground ecosystems
soil nematodes
ecological uniqueness
beta diversity
variation partitioning
olive tree

1. Introduction

The diversity of soil organisms is enormous, with thousands of species often occurring within a single square metre, a single gram of soil may contain a diverse range of nematodes, protozoa, earthworms, mites, molluscs, arthropods, and arachnids among other soil fauna (Bardgett, 2005). However, while ecologists, long fascinated by aboveground habitats (Bardgett and van der Putten, 2014), currently apply the emerging focus on spatial structures in the distribution of plant and animal communities (beta diversity; Soininen, 2016), relatively few studies have investigated such spatial structures in communities of soil organism.

Nematodes are the most diverse metazoan taxa on Earth with approximately one million species (Bardgett and van der Putten, 2014). Indeed, a recent study revealed that the total biomass of nematodes inhabiting soils across the world is about 0.3 gigatonnes (van den Hoogen et al., 2019). They are the most common and diverse multicellular terrestrial animals, and are found in all soil environments (Ferris et al., 2001). Nematodes occupy all consumer trophic levels within the soil food web, which allows them to play a central role in numerous soil functions, such as transferring energy among members of ecological networks (Ferris et al., 2001). Nematodes are frequently associated with other organisms including plants, fungi, bacteria, micro-arthropods and other nematodes. Over 4,000 nematodes species have been identified as plant feeding or plant-parasitic nematodes (PPN) (Gaugler and Bilgrami, 2004).

Although 0.4% of the nematode species richness is identified as PPN, only a small group of these are of economic importance because of the direct damage that they cause or because they act as virus vectors (Nicol et al., 2011). An important example for this is the olive tree (*Olea europaea* L.), both in wild and cultivated forms, that serves as a host to a wide diversity of PPN, including endoparasitic and ectoparasitic species

(Castillo et al., 2010; Ali et al., 2014). Recent studies have shown an exceptional diversity and prevalence of ectoparasitic PPN belonging to the family Longidoridae that infest the rhizosphere and can reduce growth in both natural (Freckman and Virginia, 1989) and agricultural ecosystems (Castillo et al., 2010).

Although studies on nematode ecology are numerous, relatively little attention has been paid to the different ecological factors that control spatial variation in species richness and community composition (i.e., beta diversity) of PPN. Traditionally, the host plants are considered the most important driver of PPN populations (Norton, 1989; Neher, 2010), with soil abiotic variables determining the distribution of PPN in natural (Freckman and Virginia, 1989) and agricultural ecosystems (Duyck et al., 2012). Studies of multiple gradients in the above-ground environment (e.g. climatic and topographic variables) as drivers of PPN patterns at the regional scale have shown contrasting results that make generalisations difficult (Duyck et al., 2012; Palomares-Rius et al., 2015).

Pure spatial structure, a spatial component that is independent of the measured environmental variables (Borcard et al., 1992),is an important factor driving beta diversity in plant communities (Hubbell, 2001; De Cáceres et al., 2012; Amici et al., 2013; Baldeck et al., 2013a) and in other major organisms (Soininen, 2016). However, it is not clear whether such effects occur in PPN. For example spatial structure may result from limited dispersal, while PPN can be dispersed via the movement of farm machinery, seeds, and animals or by water runoff and air movement (Castillo et al., 2010; Neher, 2010). Agronomic practices may reduce the distribution and/or the diversity of the nematode community, such as when herbicides application under the tree canopy reduces the soil nematode community in comparison to that in untreated areas (Sánchez-Moreno et al., 2009). In plant communities, though, a considerable

proportion of variation in species composition (and species richness) remains unexplained by the variables that describe pure spatial structure and the environment (Baldeck et al., 2013b). Therefore we expect that a similar result might be true for PPN, although we expect that soil and agricultural management factors may strongly determine PPN community structure (Neher, 2010).

The variation of species composition among sites (i.e. beta diversity) (Whittaker, 1960; Anderson et al., 2011) can be partitioned in two different ways to obtain additional information (Legendre and De Cáceres, 2013). First, beta diversity can be partitioned into the contribution of single sites (local contributions to beta diversity; LCBD) that allows us to assess the ecological uniqueness of sites in terms of community composition. The LCBD patterns might be influenced by environmental conditions and/or general characteristics of the PPN community as previously described for other organisms and ecosystems (Heino and Grönroos, 2017). High LCBD values might indicate sites with exceptional species composition (combinations of rare species), degraded sites, or sites with particular ecological conditions (Legendre and Gauthier, 2014). Second, beta diversity can be partitioned into the contribution of individual species (species contributions to beta diversity, SCBD) allowing us to assess the relative importance of each species in affecting beta diversity (Legendre and De Cáceres, 2013). SCBD may indicate species of particular importance for beta diversity and could be associated with special species characteristics (e.g. occupancy, abundance and niche) (Heino and Grönroos, 2017).

The aim of the present study was to assess the relative contribution of different factors in controlling the spatial variation in species composition and species richness of PPN communities among sites. Our analysis included the factors (1) above-ground environment (climate and topography), (2) soil, (3) agricultural management, and (4)

134 spatial structure, that is any non-random spatial organisation in the distribution of
135 communities (Peres-Neto and Legendre, 2010). As outlined above, we hypothesize that
136 the two factors soil and agricultural management will strongly determine spatial
137 variation in species composition and species richness of PPN (Neher, 2010), and that a
138 considerable proportion of the spatial variation will remain unexplained. To test our
139 hypotheses, we used a wide range of potential predictors in describing each of these
140 four factors. This allowed us to assess the role of each of these components and its
141 shared contributions in explaining the spatial variation of PPN communities.

142 More specifically, to assess the relative importance of these factors, we proceeded
143 as follows: (i) we applied redundancy analyses including a forward selection procedure
144 to select the explanatory variables representing the ecological factors that govern spatial
145 variation in species richness and composition (Blanchet et al., 2008); and in a second
146 step (ii) we applied variation partitioning (Borcard et al., 1992; Legendre and Legendre,
147 2012a) to assess the unique and shared contributions of the different environmental
148 factors and spatial structure in explaining the spatial variation of PPN species richness
149 and composition. In addition, we assessed local and species contributions to beta
150 diversity (LCBD and SCBD, respectively) to identify their particular importance and
151 potential drivers.

152 We selected the olive growing area of southern Spain as study area because of its
153 high agriculture and socio-economic importance and because of the extensive
154 distribution of cultivated olive trees in this region (Infante-Amate, 2012; MAGRAMA,
155 2016). Additionally, our study area includes a wide range of ecological gradients
156 including climate, soil, and topographical components (Ortega et al., 2016), as well as a
157 large variety of agronomic management practices covering the diversity of cropping

158 systems (from traditional to high-density and super-intensive orchards) (REDIAM,
159 2016).
160
161 **2. Materials and methods**
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163 *2.1. Study area, soil-sampling design*
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165 The study was conducted in Andalusia, southern Spain, and covered an area of
166 approximately 90,000 km^2 (extent: 35.9377º to 38.7289º; -1.6272º to -7.5226º) (Fig. 1).
167 Andalusia is a geomorphologically heterogeneous area characterised by high mountain
168 ranges surrounded by extensive lowlands of alluvial origin with elevation ranging
169 between 0 and 3,479 m above sea level (Sierra Nevada). The south of Spain is
170 characterized by a Mediterranean climate which also receives influences from the
171 Atlantic Ocean. Mean annual temperatures is 16ºC, and mean annual rainfall is 350 mm,
172 showing strong seasonality (REDIAM, 2016).

173 In Andalusia, olive cultivation covers more than 1.6 million ha and accounts for
174 19% of the total surface area of the region (MAGRAMA, 2016). Based on a
175 classification of olive growing areas into biological zones (70 homogeneous areas based
176 on environmental and agricultural similarities such as climatic conditions, orography,
177 cultivars, hydrology and landscape; REDIAM, 2016), a total of 376 commercial olive
178 orchards were selected for the present study (Fig. 1). The number of orchards sampled
179 was proportional to the surface occupied by each biological zone (e.g. we conducted a
180 representative sampling) and arbitrarily selected in each zone. Permission to sample was
181 granted by the landowners.

182 Soil samples were collected between 2013 and 2016 during the spring season, when
183 soil environmental conditions are favourable for biological nematode activity (Norton,
184 1978). In each commercial olive orchard, soil samples were taken from four, or five,
185 georeferenced olive trees that were arbitrarily chosen. Soil samples were collected with
186 a hoe discarding the upper 5cm soil profile, from 5 to 50cm depth using a pick in close
187 vicinity to the active olive tree roots. For each orchard, the soil sample was separated
188 into two portions, one for nematode identification and the other for the measurement of
189 soil variables. We ensured that the roots from plants other than olive were not included
190 in the sample. All individual samples were mixed together to obtain a single sample for
191 each orchard before nematode extraction and measurement of physiochemical variables.

192 Nematodes were extracted separately from two 250cm^3 subsamples of soil using
193 the magnesium sulphate centrifugal-flotation method (Coolen, 1979; Castillo et al.,
194 2010), then re-mixed for the diagnostic and identification of nematodes from 500 cm^3 of
195 soil. Nematodes were identified at the species level using an integrative approach
196 combining molecular and morphological techniques to obtain efficient and accurate
197 identification (Archidona-Yuste et al., 2016). For the estimation of beta diversity,
198 relative total biomass for each species present was determined and derived from the
199 abundance and nematode size among species. For each orchard, nematode abundance
200 was calculated as the total number of PPN per 500 cm^3 of soil and at least 100
201 nematodes were arbitrarily selected and identified. For samples containing less than 100
202 nematodes, all individuals were identified. Nematode individual fresh biomass was
203 calculated according to an adjusted Andrássy´s (1986) formula, wherein relative
204 biomass (µg) = L x D^2 * 1,600,000^{-1}; where L is nematode body length (in µm), and D
205 is nematode maximum body width (in µm). Nematode size was obtained using the
206 "Nematode-Plant Expert Information System" (Nemaplex;

207 http://nemaplex.ucdavis.edu/) and the original descriptions of nematode species.
208 Additionally, for each orchard we determined the number of nematode species found.
209
210 *2.2. Explanatory variables*
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212 To meet our objectives, we measured a wide range of explanatory variables derived
213 from our hypotheses. These variables were grouped into four sets related to the factors
214 environment, soil, agronomic management, and spatial structure (Appendix A1,
215 Supplementary Information Table S1.1). The set of environmental variables included
216 climate and topographical variables; the set of soil variables included physiochemical,
217 textural, and edaphic properties; and the set of agronomic management variables was
218 represented by plant variables and the orchard management system. All explanatory
219 variables were recorded as continuous data (except for categorical phytoclimatic areas)
220 in raster layers from which individual values for each olive orchard were extracted
221 using the raster to point tool in QGIS (QGIS_Development_Team, 2016).
222 The environmental data set comprised 27 broad range abiotic variables including
223 bioclimatic predictors (BIOCLIM) based on temperature and precipitation (Nix, 1986),
224 explanatory variables related to topography such as aspect and slope, global solar
225 radiation (GR), annual average olive tree potential evapotranspiration (PET), a
226 standardised drought index (DI), and a categorical variable related to phytoclimatic
227 areas (CA). A description of each variable is given in Supporting Information Appendix
228 A. The topographical attributes were measured in the commercial olive orchards was
229 the mean of the values derived for each of four, or five, olive trees: slope with values
230 from 0.01 to 41.5º, and aspect, with values from 0.06 to 359.8º. Aspect refers to the
231 direction that a slope faces. Temperature and precipitation data were obtained from the

232 Environmental Information Network of Andalusia (REDIAM) for the period 1970-2016
233 at 100 m ground resolution (REDIAM, 2016), from which 19 bioclimatic variables were
234 derived using the R package dismo (Hijmans et al., 2016). GIS-derived topographical
235 variables included the continuous variables slope, aspect and the SAGA wetness index
236 (SWI). Each of these variables was derived in QGIS using a digital elevation model
237 (DEM) obtained from the Spanish National Geographic Institute at a 5 m ground
238 resolution (NGI, 2016). Slope and aspect variables were calculated from the DEM based
239 on the second-degree polynomial adjustment method using the library morphometry of
240 the open source GIS SAGA (Conrad et al., 2015). SWI, which predicts potential areas
241 with relatively higher soil moisture, was computed from elevation DEM using the
242 hydrology module in SAGA (Boehner and Selige, 2006). Since aspect is a circular
243 variable measured in degrees, aspect was transformed into a categorical variable with
244 six categories (i.e. northeast, east, southeast, southwest, west, and northwest) (Legendre
245 et al., 2009).

246 The second set of variables comprised soil physiochemical variables, texture and
247 edaphic type. Explanatory variables related to soil physiochemical variables comprised
248 12 variables including cation exchange capacity (CEC), Ca, Mg, exchangeable K, Na,
249 carbonate content (CO3), extractable P, soil organic matter (SOM), total organic carbon
250 (Corg) and nitrogen (Norg), C:N ratio, and pH (KCl). The edaphic type was obtained
251 from REDIAM by extracting information from each sampling point (Supporting
252 Information Table S1.3; (REDIAM, 2016). To avoid collinearity among texture
253 variables, soil texture from the 376 commercial olive orchards sampled was categorised
254 into 12 texture classes according to the USDA soil texture classification (Appendix A1,
255 Supporting Information Table S1.4). This analysis was performed using the package
256 soiltexture using the R software (Moeys, 2015). Soil texture was estimated by the

257 relative amounts of sand, clay and silt according to soil texture Bouyoucos method
258 (FAO, 1980), which values ranging 1.3-90.5%, 3.5-64.1% and 3.7-71.3%, respectively.

259 The third set of variables, agronomic management, included variables that were
260 related to either plant or orchard management. For the first subset, we used the age of
261 the olive tree plantation and the olive tree cultivars. The second subset comprised seven
262 categorical variables (olive plant density, irrigation pattern and system, source of
263 irrigation water, agronomic practices below the olive tree canopy and in the alley
264 between trees, and type of vegetation cover in the alley). Plant density data was
265 categorised into three classes, traditional, intensive and super high-density olive
266 orchards, based on Rallo et al. (2013). The landowner provided age and cultivar
267 information, which ranged from approximately 2 to 100 years and 21 cultivars. Further
268 details are provided in Appendix A1 (Table S1.5).

269 The fourth set included explanatory variables related to spatial structure. Spatial
270 predictors were computed across the locations of the 376 commercial olive orchard
271 using the distance-based Moran's eigenvector map (dbMEM) analysis (Borcard and
272 Legendre, 2002; Borcard et al., 2004; Dray et al., 2006). The spatial dbMEM
273 eigenvectors were obtained by computing a matrix of geographical distances among the
274 sites that were then truncated based on a distance threshold (Borcard and Legendre,
275 2002). A Principal Coordinates Analysis (PCoA) was performed using the truncated
276 (geographical) distance matrix, resulting in orthogonal variables of spatial structure with
277 high and low eigenvalues corresponding to broader and finer spatial scales, respectively.
278 In addition to the spatial eigenfunctions, this approach permits the computation and
279 testing of Moran`s I coefficients associated with all dbMEMs, thereby allowing a pre-
280 selection of eigenfunctions with positive and significant spatial autocorrelation (Dray et

al., 2006). A total of 101 MEM eigenvectors with positive correlation were retained with a truncation distance of 26,953 m. The dbMEM analysis was performed using the dbmem function implemented in the adespatial package (Dray et al., 2019) as described by Dray et al. (2006).

For each diversity index, we mapped the fitted site scores of the final selected eigenvectors to discriminate among broad-, medium-, and fine-scale spatial patterns (Borcard et al., 2018). In order to interpret the spatial variation, we performed linear regression models using the most influent spatial variables and the selected explanatory variables in both diversity indexes (Borcard et al., 2018).

2.3. Statistical analyses

Data analyses included the following four steps: calculation of observed beta-diversity, selection of explanatory variables, variation partitioning, and determination of the contribution of locations (LCBD) and species (SCBD) to beta diversity, as well as their relationships with explanatory variables and the prevalence of PPN. All statistical analyses were performed using the R v. 3.5.1 freeware (R_Core_Team, 2018).

Prior to the statistical analysis we transformed the biomass - site matrix data of the PPN using a Hellinger transformation (Rao, 1995) that is recommended when the data matrix contains zeros, extreme values, and double absences of species per site (Legendre and Gallagher, 2001) as occurred in our study.

2.3.1. Beta diversity computation

Total beta diversity was estimated as the total variance of the transformed abundance-biomass community data table following the methodology described by Legendre et al. (2005). This approach allows for partitioning beta diversity into the sum of the contributions of individual species (SCBD) and into the sum of the contribution of individual sampling sites (LCBD) (Legendre and De Cáceres, 2013). LCBD values, which sum to 1, were tested for significance by the random distribution of species among sampling sites as null hypothesis (using 999 random permutations and preserving species abundance data) (Legendre and De Cáceres, 2013). We mapped the spatial variation of LCBD values among sampling sites. Beta diversity and its local and species contributions were computed using the beta.div function implemented in the *adespatial* software package (Dray et al., 2019).

Species richness and community composition maps were produced to summarise the spatial variation in the study area (Baldeck et al., 2013b). This approach involved a non-metric multidimensional scaling (NMDS) ordination analysis on the biomass-abundance matrix data using the Bray-Curtis dissimilarity index with three dimensions and 100 random stars as arguments to obtain a low value of stress statistic index. Then, scores from the three axes were translated to an RGB colour following the methodology described by several authors (Thessler et al., 2005; Baldeck et al., 2013b). Sampling sites with more similar species composition were represented by more similar colour patterns, which were then interpreted by the prevalence level of PPN (rare and common species) regarding the ordination axes of species scores from the NMDS analysis. The NMDS ordination analysis was computed using the metaMDS function found in the *vegan* software package (Oksanen et al., 2019).

2.3.2. Selection of explanatory variables

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331 The selection of explanatory variables included the following three steps: (i) a
332 forward selection procedure using all explanatory variables from each data-set, (ii) a
333 collinearity test based on the values of the variance inflation factor (VIF), and (iii) a
334 second forward selection procedure using the selected and non-correlated variables in
335 each data-set to be used in the variation partitioning analysis.
336 As suggested by Borcard et al., (2018), we used first a forward selection procedure
337 using all explanatory variables in each data set (i.e., factor) before checking for
338 multicollinearity. This is because collinearity may affect (i.e. exclude) one or more
339 important variables that structure the PPN community spatial structure patterns we are
340 interested in (Borcard et al., 2018). In a second step we conducted a redundancy
341 analysis (RDA) on the remaining variables in each data-set, and the result object of the
342 RDA was subsequently tested for collinearity (Borcard et al., 2018). To minimise
343 collinearity effects, we used the VIF method that iteratively excludes numeric covariates
344 within each variable set that show VIF values > 10 as suggested by Montgomery and
345 Peck (1992). Finally, a second forward selection procedure was performed for each set
346 of explanatory variables to retain only those variables that were significantly correlated
347 with species richness (or community composition). For this step, categorical variables
348 were transformed as dummy variables. Overall, we used a modified forward selection
349 method (Blanchet et al., 2008) based on a permutation procedure with two stopping
350 criteria (using 9999 random permutations) combined into one that was evaluated
351 simultaneously; that is, variables were added to the selection set until it exceeded the
352 critical p value (alpha threshold = 0.05), or the final model adjusted R^2 value did not
353 exceed that of the global model, which was performed using the *packfor* package
354 software (Dray, 2011).

355

356 *2.3.3. Variation partitioning*

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358 Variation partitioning (Borcard et al., 1992; Peres-Neto et al., 2006) was based on
359 redundancy analysis for community composition of PPN (i.e., beta diversity) and on
360 multiple linear regression for species richness. This allowed us to quantify the relative
361 contribution (unique and joint fractions) of the four sets of explanatory variables to the
362 total variation of beta diversity and species richness (Borcard et al., 1992; Peres-Neto et
363 al., 2006). For easier comparison among analyses, we expressed the variance explained
364 by unique and joint proportions in terms of the fractions of the total explained variance.
365 The significance of the unique and overall fractions (i.e. unique + joint fraction) was
366 tested by partial redundancy analysis (partial RDA) using 999 random permutations
367 (Borcard et al., 2018). Variation partitioning analysis was performed using the varpart
368 function implemented in the *vegan* software package (Oksanen et al., 2019).

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370 *2.3.4. LCBD and SCBD explanatory variables*

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372 Following the methodology described by Heino and Grönroos (2017), we used a
373 combination of multivariate methods to examine the variation in local (LCBD) and
374 species (SCBD) contributions to beta diversity. First, we performed multiple regression
375 to determine the drivers that correlate with LCBD and SCBD using community metrics
376 and species traits, respectively, as predictors. SCBD patterns were tested with the
377 following species traits: density range (e.g. range between maximum and minimum
378 abundance of each identified nematode species expressed as nematodes per 500 cm^3 of
379 soil) and prevalence (e.g. the ratio between the number of sites in which each nematode

380 species was detected and the total number of sites expressed as a percentage). The
381 variation of the LCBD index was tested with community metrics related to each
382 commercial olive orchard including total nematode abundance-biomass e.g. the total
383 nematode biomass detected (µg/500cm^3)], total nematode abundance-numeric [e.g. the
384 total number of nematode specimens (nematodes/500cm^3)], and species richness.
385 Additional details regarding the species and community metrics used as predictors can
386 be found in the accompanying DATA in BRIEF article. For the relationship among
387 LCBD and SCBD and explanatory variables from each sampling site, we used a partial
388 linear regression based on the methodology described by Legendre and Gauthier (2014).

389 Patterns in LCBD could also be influenced by environmental predictors; therefore,
390 this index was tested with ecological predictors related to the factors aboveground
391 environment, soil, and agronomic management. To estimate the proportion of variation
392 of the dependent variable that could be assigned solely to one set of predictors, having
393 considered the effect of the other factor, we used partial linear regression (Legendre and
394 Legendre, 2012a). This analysis was performed by controlling the effects of the spatial
395 component of LCBD using dbMEM (i.e., the principal coordinates of neighbour
396 matrices) as variables, thereby determining the effect that could be exclusively
397 attributed to the ecological variables at each sampling site. We used all explanatory
398 variables included in the factors aboveground environment, soil, and agronomic
399 management together as ecological predictors. Then, we selected the most influential
400 variables that determined the LCBD patterns by forward selection using the same
401 criteria as described above (i.e. double stopping and 9999 random permutations)
402 (Blanchet et al., 2008).

403

3. Results

3.1. Beta diversity of PPN

In the soil samples the soil samples of the 376 commercial olive orchards 128 PPN species from 13 families were identified. The total number of PPN in each olive orchard ranged from 7 (site O031) to 19,796 (site O333) nematode specimens per 500 cm^3 of soil, and the species prevalence ranged from 0.3% (several nematodes species detected only at one sampling site) to 72.6% (*Merlinius brevidens*). Migratory ectoparasite PPN such as *Helicotylenchus oleae* and *Ogma rhombosquamatum* showed the highest abundance (19,720 and 9,800 nematodes per 500-cm^3 of soil, respectively). Rare (usually having low prevalence) sedentary endoparasitic PPN species such as *Meloidogyne javanica* were also detected at high abundance in many of the samples (i.e. 10,000 nematodes per 500-cm^3 of soil).

Overall, species richness showed high heterogeneity among the 376 sampling sites (Fig. 2a). This resulted in a remarkable variation in community patterns, as visualised by the beta diversity map (Fig. 2b). The grey sites on this map comprise generally common PPN species (high prevalence) such as migratory ectoparasitic PPN, whereas sites with a prevalence of rare species are shown by the radial gradient thorough the RGB colour spectrum (Fig. 2b).

3.2. Selection of explanatory variables

Overall, the total number of variables that were significantly related to the spatial pattern variation of PPN communities was higher for beta diversity (15) than for species richness (10). Approximately 10% of the variation in beta diversity was explained by the four sets of variables, with soil and spatial variables, accounting for 5% each, explaining that variation almost entirely (Table 1; Table S2.3 in Appendix A2). In contrast, approximately 30% of the variation in species richness was explained by the four sets of variables, with spatial variables accounting for 18% and soil and agronomic management accounting for 12% each (Table 1; Table S2.3 in Appendix A2).

Thirteen spatial variables (i.e., distance-based Moran´s eigenvector maps; dbMEM) were retained to represent spatial structure for community composition and eight for species richness (Table 1; Appendix A2). The most significant spatial variable detected for beta diversity was associated with an eigenvector representing a fine-scale structure (MEM26; R^2 *adj* = 0.0075); Table S2.1). The spatial variable MEM2 was also included in the model, but it also had a negligible influence (R^2 *adj* = 0.0068). In contrast, the spatial variation of species richness was primarily determined by eigenvectors modelling broad- and medium-scale structures (particularly MEM2; Table S2.2). Maps of significant spatial community patterns, MEMs, were included as Supplementary data (Appendix A3).

Soil physiochemical variables were the most influential soil variables for beta diversity and variation in species richness, followed by soil texture and edaphic type. Beta diversity was affected by chemical variables such as Ca, pH (KCl), Na, and total organic N (Table 1; Appendix A2, Supplementary Table S2.1), whereas variation in species richness was affected only by the two physiochemical variables Na and extractable P. Soil extractable P accounted for 7% of the variation in species richness

451 (Table 1; Appendix A2, Supplementary Table S2.2). Soil texture and edaphic type were
452 also important but with a lower effect than that of the physiochemical variables (Table
453 1; Appendix A2, Supplementary Tables S2.1 and S2.2).

454 Variables quantifying the factor aboveground environment explained only a low
455 proportion of beta diversity (3%) and variation in species richness (7%), with variables
456 closely related to climate being the most important ones (Table 1; Table S2.3 in
457 Appendix A2). The most important predictors within the environmental data set for beta
458 diversity were those describing temperature variability such as the mean temperature of
459 the wettest quarter (i.e. quarterly indices are based on running 3-month intervals)
460 (BIO8) and isothermality (BIO3), and the variation of species richness was related to
461 the precipitation of the wettest quarter (BIO16) and the rainfall deficit factor (RD). Both
462 metrics were also influenced by the phytoclimatic type.

463 Agronomic management accounted for 12% of the variation in species richness,
464 with only 2% allocated to beta diversity (Table 1; Table S2.3 in Appendix A2). Only six
465 management predictors accounted for that variation, with the irrigation class being the
466 most important for beta diversity, and the age of the olive trees important for both
467 metrics. The presence or absence of soil-vegetation cover affected both beta diversity
468 (in the case of below canopy) and species richness (in the case of in the alley). Both
469 metrics were also influenced by the olive tree cultivar.

470

471 *3.3. Variation partitioning*

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473 Variation partitioning analysis revealed a high amount of unexplained variance of
474 PPN community composition and species richness. Approximately 10% of the variation

475 of community composition and 30% of species richness patterns were explained by all
476 four factors together (Table 1; Supplementary Table S2.3). Overall, we found a large
477 contribution of the unique fractions of the different sets of variables that represented
478 more than half of the total contribution of each predictor set (i.e. unique + joint
479 components). The contribution of the joint fractions of the different sets of variables
480 was close to 40% of the total contribution of each predictor set. In addition, the relative
481 (but not absolute) variance explained by the different sets of environmental variables
482 and their joint effects were relatively similar between beta diversity and species richness
483 (Fig. 3).

484 Most of the variation of PPN community metrics (e.g. beta diversity and species
485 richness) was spatially structured and the spatial variables explained 5.1% and 18.5% of
486 the variation in species composition and species richness, respectively, including unique
487 and joint fractions (Table 1; Table S2.3). For species richness the pure space component
488 [d] explained 7.9% (approximately 27% of the total variance explained); however, it
489 showed a lower unique contribution for beta diversity (2.3%). The soil variables
490 explained 12.5% of the variation in species richness and 5.3% of species composition,
491 being the most important factor for beta diversity and the third important factor for
492 species richness. The unique (non-spatial) contribution of soil variables [b] explained
493 2.9% of the variation of species composition and 3.5% of the variation of species
494 composition. Although the pure soil component explained 3.5% of the variation of
495 species richness, this had no significant effect. The pure environment component [a] had
496 no effect on species richness and showed a low explanatory contribution for beta
497 diversity because the environmental variables tended to be spatially structured and
498 related to patterns of the soil data set (Fig. 3; Appendix A2). Finally, agronomic
499 management variables explained 12% of the variation in species richness, but only

500 2.53% of species composition. The pure agronomic management component [c] had the
501 second highest effect on species richness with 4.8%; however, it had a negligible effect
502 on beta diversity.
503
504 *3.4. Species and local contributions to beta diversity*
505
506 Species contributions (SCBD) ranged from almost zero to 17%. Overall, migratory
507 ectoparasitic PPN species including *Helicotylenchus digonicus* (SCBD = 0.1711), *H.*
508 *vulgaris* (SCBD = 0.1164), *Xiphinema pachtaicum* (SCBD = 0.091476), and *H. oleae*
509 (SCBD = 0.0792) showed the highest distribution heterogeneity in our study (DATA IN
510 BRIEF). However, the majority of the remaining taxa were more homogeneously
511 distributed (SCBD < 0.002). SCBD was significantly related with nematode prevalence
512 and density range (Table 2).

513 Local contributions (LCBD) exhibited a heterogeneity pattern across space (Fig.
514 2c). Permutation test identified 27 orchard units with significant LCBD values. A
515 simple linear regression model showed that LCBD was not significantly linearly related
516 to the PPN community metrics such as species richness and total nematode abundance
517 in each olive orchard (Table 2). Therefore, large LCBD values may indicate sites that
518 have rare species combinations or may occur due to the ecological requirements of
519 specific species. Partial linear regression and subsequent forward selection procedures
520 (Legendre and Gauthier, 2014) revealed that soil characteristics appeared to be more
521 important at explaining LCBD (Table 3). The contribution of agronomic management
522 characteristics was relatively moderate and additional environmental variables had only
523 a marginal influence on LCBD.
524

4. Discussion

4.1. The role of stochasticity on PPN community patterns

Variation partitioning has been used to assess the relative effect of deterministic and stochastic processes in plant communities (Svenning et al., 2004; Legendre et al., 2009; Amici et al., 2013; Baldeck et al., 2013a; Punchi-Manage et al., 2014), amphibians (Luiz et al., 2016), and below-ground communities (Dumbrell et al., 2009). For example, Baldeck et al. (2013a) found that 26% to 68% of the spatial variation in species composition remained unexplained in 25-50 ha plots of tropical forests, and Amici et al. (2013) found similar figures (28% to 58%) in Mediterranean forests. We found an even more prominent role of unexplained variation in structuring PPN communities, reaching 90% in species composition and 70% in species richness (Table 1). The lack of information about the relative importance of stochastic and deterministic processes on the spatial distribution of soil biota is notable. Nonetheless, the large faction of unexplained variation found here is consistent with results of a recent study based on the overall community of soil nematodes in agricultural and natural ecosystems (Quist et al., 2019). Frequent disturbance of soils in agricultural systems might explain the relative low contribution of deterministic processes (Ferrenberg et al., 2013), as opposed to the natural system where the spatial variation of nematode communities is more dominated by deterministic rather than stochastic processes (Moroenyane et al., 2016). The large proportion of unexplained variation may also be due to the omission of exploratory variables and mechanisms such as species interactions (De Cáceres et al., 2012). Additional factors influencing the relative importance of different mechanisms on beta diversity may be the scale of the study as

550 well as the spatial configuration and strength of ecological gradients used (Smith and
551 Lundholm, 2010).
552
553 *4.2. Spatial structure of PPN community patterns*
554

555 A recent meta-analysis by Soininen (2016) regarding major organism types and
556 ecosystems showed that a mean of 11% of the variation in community composition was
557 uniquely explained by spatial variables. However, the unique contribution of spatial
558 variables observed in our study was somewhat lower for both beta diversity and species
559 richness, with the spatial descriptors explaining a larger fraction of the variation in
560 species richness than in beta diversity.

561 We found a significant influence of broad-scale structures on the spatial variation of
562 species richness, where the most influent spatial variables (MEM2) (Table 1; Appendix
563 A2, Supplementary Table S2.2; Appendix A3). Overall, spatial patterns of soil
564 communities likely reflect the outcome and interplay of multiple community processes,
565 In particular, the broad-scale trend in species richness could indicate spatial richness
566 gradients or 'hotspots' of species richness that in many cases can be explained by
567 habitat filtering processes (Legendre and Legendre, 2012b). In fact, we found a
568 significant influence of the soil edaphic type and climatic type explaining the broad-
569 scaled spatial variation (MEM2) on the variation of PPN species richness ($P < 0.001$;
570 Appendix A3). Thus, habitat richness in PPN may be delimited by spatial homogeneity
571 at regional scale sustained through soil environment patterns (i.e. soil edaphic type) and
572 climate conditions (i.e. climate type area) but not by local environment gradients

573 (Nielsen et al., 2014; Godefroid et al., 2017). A similar pattern has been shown for other
574 soil organism such as collembolan (Widenfalk et al., 2016).

575 In contrast, spatial analysis showed that the overall variation of community
576 composition was mostly associated with fine-scale variation (MEM26) in combination
577 with broad-scale variation (MEM2) (Table 1; Appendix A2, Supplementary Table S2.1;
578 Appendix A3). However, the rather low influence of both these spatial variables (1.4%
579 of the variation) agrees with the large spatial heterogeneity (Fig. 2) and the important
580 role of stochasticity for beta diversity found here, and also previously reported for soil
581 nematodes (Quist et al., 2019). The fine-scale relationships (MEM26) were dominated
582 by local environmental gradients in combination with regional gradients. This does not
583 suggest a clear habitat pattern (Appendix 3) for beta diversity, which may rather be
584 influenced by small-scale environmental microhabitats (Nielsen et al., 2014).

585 Overall, the total contribution of the joint fractions detected by spatial variables in
586 both diversity indexes was higher than that of the total unique fractions (Fig. 3;
587 Appendix A2, Supplementary Table S2.3). Therefore, PPN communities showed
588 moderate levels of spatial structure caused by pure spatial structure and spatial gradients
589 in explanatory variables as discussed above. The pure spatial component might
590 represent the role of dispersal limitation of PPN within the soil ecosystem (De Cáceres
591 et al., 2012). Although the three-dimensional movement of soil nematodes is difficult to
592 assess, we can expect that they will actively move rather short distances due to their
593 small body size (Gaugler and Bilgrami, 2004). Movements over larger distances are
594 passive, and probably mostly due to agricultural activities (e.g. farm machinery, plant
595 propagation material, or seeds) (Castillo et al., 2010).

596

4.3. Role of soil on PPN community patterns

Our study highlights the influence of soil drivers in structuring PPN communities. The unique contribution of soil was significant only for beta diversity but not for spatial variation of species richness. Thus, gradients in soil properties induced changes in the variation of PPN biomass and therefore, producing "habitat filtering" that reflected assemblage patterns of PPN communities largely independent of the above-ground environmental gradients (in climate and topography) as also suggested soil organisms in general (Ettema and Wardle, 2002). However, the effect of soil variables on the variation of species richness was spatially structured and/or shared with other explanatory variables describing above-ground environment (e.g. climate, topography or agronomic management), given the large relative contribution (unique and joint fractions) of soil to species richness (12.5%) compared to beta diversity (5.3%).

Overall, soil chemical gradients showed the strongest influence on the distribution of PPN communities among the soil properties (Table 1), especially for Ca, pH, Na availability or extractable P in the case of species richness (Appendix A. Supplementary data, Tables S2.1 and S2.2). The significant and strong influence of Ca on beta diversity may result from its negative effect on PPN densities as a driver on the abundance of nematodes (and therefore on nematode biomass), although the possible underlying mechanisms are not as clear for the overall community of PPN as those suggested by Wallace et al. (1993). In contrast to beta diversity, the variation of species richness was strongly influenced by the availability of P (Appendix A. Supplementary data, Table S1.); suggesting that this variable could play a key role in community patterns of PPN infesting soils of olive orchards. Although P availability has been identified as a determinant of PPN abundance (Norton, 1978), other studies have revealed filtering

622 effects by P gradients on the size of soil nematodes (Mulder, 2010). Specifically, the
623 variability of P concentration could structure PPN assemblages based on nematodes
624 presence to the entire community depending on the size of the PPN species (Gaugler
625 and Bilgrami, 2004).
626
627 *4.4. Role of the environment on PPN community patterns*
628
629 Overall, the variance explained by the unique contribution of environmental
630 climatic and topographic variables [a] was relatively small compared to that explained
631 by the other sets of variables, highlighting that in comparison to similar approaches in
632 above-ground ecosystems these variables did not influence species richness (Fig. 3;
633 Appendix A2). For example, studies on tropical forest (Baldeck et al., 2013a) and
634 amphibian species (Luiz et al., 2016), found that a higher portion of species
635 composition variation was mainly explained by topographical and geomorphical
636 variables, respectively. The relatively low contribution of environmental effects on PPN
637 communities may be partly attributed to the scale at which the present study was carried
638 out. For instance, Nielsen et al. (2014) found that climate was strongly related with
639 nematode assemblages at global scales but not with local diversity descriptors. The
640 negligible effect of topography may also be influenced by scale in relation to the range
641 of the elevation gradient (Dong et al., 2017).
642
643 *4.5. Role of agronomic management practices on PPN community patterns*
644
645 Population dynamics of PPN in olive agroecosystems respond rapidly to
646 agricultural management practices (Sánchez-Moreno et al., 2009; Palomares-Rius et al.,

2015; Ali et al., 2017), yet our study unexpectedly indicated a negligible effect of the pure management component [c] on beta diversity (Fig. 3; Appendix A2, Supplementary Table S2.1). Previous information is limited as earlier studies have not included spatial descriptors which would allow the effect of management practices to be related to spatially structured (Vleminckx et al., 2017). Furthermore, the majority of those studies were not based on beta diversity approaches but on alpha or gamma diversity descriptors, which could show different trends.

The variation in species richness was associated with the pure management component (Fig. 3; Appendix A2, Supplementary Table S2.2) and was related to the age of the olive tree plantation and absence of soil-vegetation cover below the canopy, with the irrigation pattern in the orchard as the most important predictor for beta diversity (Table 1; Appendix A2, Supplementary Table S2.2). These results tend to agree with previous studies showing changes in nematode community patterns related to forest stand ages (Zhang et al., 2015). That is, if conditions are suitable, more nematode species will accumulate over longer periods of time, indicated by olive trees age. Additionally, larger canopies of older trees and optimum soil moisture may improve the soil environmental conditions, influencing PPN diversity as suggested in other types of ecosystems for overall above- and below-ground organisms (Caldeira et al., 2014). The soil-vegetation cover was also important for structuring the patterns of PPN communities for species richness (Table 1; Appendix A2, Supplementary Table S2.3). The influence on species richness caused by natural herbaceous plants composing the soil cover below the tree canopy supports that plant species affect the relative selection of PPN at the species level (Palomares-Rius et al., 2015).

4.6. Contrast between species richness and species composition

672

673 Our study revealed substantial differences between the effects of overall
674 environmental variables on beta diversity and on spatial variation in species richness.
675 First, the variation explained in species richness was higher than that of beta diversity,
676 which is contrary to the general pattern detected in above-ground systems where it was
677 similar or showed the opposite trend (Legendre et al., 2009; Punchi-Manage et al.,
678 2014). Habitat gradients influencing nematode abundance are exceptionally
679 heterogeneous in soil ecosystems which are strongly dominated by stochasticity. Thus,
680 different numbers of species among sampling points may be more influenced by soil
681 heterogeneity, whereas neutral processes may strongly influence nematode abundance.
682 Second, whereas the pure management component had a negligible effect on beta
683 diversity, it influenced the variation of species richness. This is not surprising because
684 some of the PPN genera or specific species groups have shown particular sensitivity to
685 agronomic practices (Sánchez-Moreno et al., 2009; Palomares-Rius et al., 2012;2015).
686 For instance, agricultural practices such as vegetation cover and irrigation causes a
687 notable effect on the diversity of root-knot nematodes (*Meloidogyne* spp.) spatial
688 structure in commercial olive tree orchards (Archidona-Yuste et al., 2018).

689

690 *4.7. Ecological uniqueness of sites and species contributions to overall beta*
691 *diversity of PPN*

692

693 The species contributions to beta diversity (SCBD) was positively correlated with
694 nematode occupancy, that is, nematode prevalence and density range (R^2 = 57%; Table
695 2). Thus, SCBD could be related to niche position (Heino and Grönroos, 2017). This
696 relationship would also allow the dominant PPN species that showed the largest

abundance variation among sites to be used as suitable indicators of fluctuations of specific environmental properties in agroecosystems (Heino and Grönroos, 2017). We found that the PPN species with the highest SCBD index belonged to the genera *Helicotylenchus* and *Xiphinema* (DATA IN BRIEF), which have been characterised as having wide distributions and high prevalence as well as large abundance (Archidona-Yuste et al., 2016; Palomares-Rius et al., 2018). In addition, the fact that most of these species are migratory ectoparasities and yet are also characterised as "persister" nematodes make them suitable indicators to predict fluctuations of soil ecological properties or stable habitats (Bongers, 1990).

We expected that the local contributions to beta diversity (LCBD) would be associated primarily with species richness and nematode abundance (Heino and Grönroos, 2017), however, this was not the case. We found, instead, that LCBD was positively related to total nematode biomass at each site, although this relationship was weak (adjusted R^2 = 0.02; Table 2). Sites with significant values (highest LCBD index) showed communities composed of rare species (Fig. 2b, c) as reported by Legendre and De Cáceres (2013). Most of the sampling sites with large and significant LCBD values were mainly grouped into separate geographical areas (Fig. 2c). The highest and significant LCBD values were mainly found in olive orchards located in the western middle area and close to the downstream course of the Guadalquivir River (Fig. 2c). However significant LCBD values were also observed in the south-east area, characterised by a semi-arid climate and is markedly different from the rest of the study area (Rodrigo et al., 2012). These geographically-related differences may suggest that habitat filtering mechanisms underlie some of the variation of LCBD (Table 3), while the role of stochasticity in driving LCBD was also prominent, as was seen in beta diversity and species richness (Table 3).

722 Overall, soil variables, particularly soil texture, pH and soil type, showed the
723 strongest influence on the variation of LCBD. Nonetheless, some variables describing
724 management, such as olive tree age and cultivars, were also important. These findings
725 agree with previous results and hypotheses regarding the filtering effect of agronomic
726 practices on PPN community composition in agroecosystems, especially in olive
727 orchards (Palomares-Rius et al., 2015; Sánchez-Moreno et al., 2015). Futures studies
728 based on spatial-temporal variation in LCBD (Legendre and Gauthier, 2014) may reveal
729 novel insights as to the influence of different agronomic practices on PPN community
730 assemblages.
731
732 **5. Conclusion**
733
734 Although numerous studies have documented the distribution of plant and animal
735 communities with respect to spatial structure (Soininen, 2016), relative little attention
736 has been paid to the involvement of spatial structure in the diversity of soil organisms.
737 We found that PPN communities in olive orchards showed moderate levels of spatial
738 correlation in the variation in species composition and species richness, as indicated by
739 the fractions of beta diversity and species richness variation explained by spatial
740 descriptors. Soil was the following most influential factor driving communities of PPN.
741 Agronomic management practices, however, showed less influence than expected. We
742 found that more than two thirds of the variation remained unexplained, which contrasts
743 with common expectations that soil and management would primarily determine PPN
744 community variation among sites. Future studies should examine whether PPN
745 associated with wild forms of olive trees show more spatial structure in beta diversity
746 than that found here in the olive orchards. Our findings revealed novel insights

747 regarding the spatial variation diversity and distribution of PPN infesting soils from
748 agricultural ecosystems, and showed that their beta diversity was less structured by the
749 factors space and environment compared to other organism types such as plants or
750 amphibian.
751

752 **Acknowledgements**

753 This research was supported by grant AGL2012-37521 from Ministerio de Economía y
754 Competitividad of Spain, grant 219262 ArimNET-ERANET FP7 2012-2015 Project
755 PESTOLIVE and grant P12AGR 1486 Consejería de Economía, Innvovación y Ciencia
756 of the Junta de Andalucía, and Union Europea, Fondo Europeo de Desarrollo regional,
757 'Una manera de hacer Europa'. A. Archidona-Yuste was a recipient of research contract
758 BES-2013063495 from Ministerio de Economía y Competitividad, Spain; and at present
759 is a recipient of Humboldt Research Fellowship for Postdoctoral Researchers at
760 Helmholtz Centre for Environmental Research-UFZ, Leipzig, Germany. The authors
761 thank J. Martín-Barbarroja, C. Cantalapiedra-Navarrete and G. León Ropero (IAS-
762 CSIC) for the excellent technical assistance, H.F. Rapoport (IAS-CSIC) for her
763 exhaustive final review of the manuscript and suggestions for improving the English
764 style, and four anonymous reviewers for comments that greatly improved the
765 manuscript.
766

767 **Appendix A. Supplementary data**

768 Supplementary data associated with this article can be found, in the online version, at
769 https://doi.org/xxxxxxxxxxxxxx/.
770

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1024

1025

1026 **Table 1**

1027 Explanatory variables significantly related to the spatial variation of community composition

1028 and species richness of plant-parasitic nematodes (PPN).

Variable	Community composition	Species richness
A) Environment		
BIO3	X	-
BIO8	X	-
BIO16	-	X
BIO18	X	-
Aspect	Southeast	-
Rainfall deficit	-	X
Climatic areas	7, 8	5
B) Soil		
Ca	X	-
Na	X	X
Norg	X	-
Pext	-	X
pH (KCl)	X	-
Soil Texture	SaClLo, SaLo	SaClLo
Soil edaphic unit	3, 44, 49, 52, 56	37, 47
C) Agronomic management		
Cultivar	"Arberquina", "Manzanilla Serrana", "Lechín"	"Manzanilla Sevilla"
Age	X	X
Irrigation	Irrigated	-
Canopy	-	Nothing
Alley	Vegetative cover	-
D) Spatial patterns		
MEM variables	26, 2, 6, 1, 16, 19, 14, 31, 7, 23, 25, 44, 3	2, 14, 10, 6, 90, 51, 42, 9

Summary	% variation explained (unique, total)	% variation explained (unique, total)
Unique fractions		
Env	0.7, 2.9	-, 6.6
Soil	2.9, 5.3	3.4, 12.5
Mana	0.5, 2.5	4.8, 12.5
Spa	2.3, 5.1	8.0, 15.5
Joint fractions		
Env_Soil	0.2	0.1
Soil_Mana	0.6	2.8
Env_Mana	0.1	-
Env_Spa	0.9	3.1
Soil_Spa	0.5	2.1
Mana_Spa	0.3	0.4

Env_Soil_Spa	0.5	0.9
Env_Soil_Mana	0.2	0.2
Soil_Mana_Spa	0.3	1.4
Env_Mana_Spa	0.2	1.1
Env_Soil_Mana_Spa	0.1	1.4
Total	**10.3**	**29.7**
Unexplained	**89.7**	**70.3**

1029

1030 Notes: Significant explanatory variables are indicated by X. For categorical variables
1031 (Appendix A1), selected predictors are indicated by each significant variable. Spatial patterns
1032 are described by MEM variables (see Materials and Methods), indicating only the significant
1033 MEM variables for community composition and species richness.

1034

Table 2

Results of the regression analysis to explain the species contributions to beta diversity (SCBD) and the local contributions to beta diversity (LCBD) by PPN community indices.

	Estimate	SE	t value	*P value*		R^2	R^2_{adj}
A) SCBD[1]							
(Intercept)	2.3 e-04	1.4 e-03	0.17	0.87			
Density range[2] (nem/500 cm^3)	2.5 e-06	5.6 e-07	4.5	1.6 e-05	***		
Prevalence (%) [3]	1.2e-03	1.2 e-04	10.3	< 2 e-16	***		
Model				< 2 e-16	***	0.58	0.57
B) LCBD[4]							
(Intercept)	2.7 e-03	1.9 e-04	14.1	< 2 e-06	***		
Total nematode biomass (µg/500cm^3)	2.5 e-05	8.7 e-06	2.9	0.004	**		
Total nematode Abundance (nem/500cm^3)	-6.0 e-06	4.3 e-06	-1.4	0.16			
Species richness	-1.3 e-04	1.1 e-04	-1.2	0.23			
Model				0.01		0.03	0.02

[1] Result from the linear regression model analysis based on Hellinger transformed abundance data form each PPN species.

[2] Density range index includes minimum and maximum density (nematodes/500 cm^3) detected for each PPN species.

[3] Prevalence was calculated by dividing the number of samples in which PPN species was detected by the total number of samples and expressed as a percentage.

[4] Results from the linear regression model based on Hellinger transformed abundance data from each site.

1049 **Table 3**
1050 Results of the forward selection procedure of ecological predictors in explaining
1051 variation of LCBD (local contributions to beta diversity) of plant-parasitic nematodes
1052 (PPN).
1053

	LCBD		
Ecological predictors 1, 2,3,4	R^2	$R^2_{adj\ cum}$	*P value*
Soil texture			
LoSa (loamy sand)	0.0552994	0.0527734	< 0.0001
pH (KCl)	0.0251797	0.0755487	0.0018
Soil edaphic unit			
I Re Lc Be	0.0133137	0.0864847	0.0129
Age of olive orchards	0.0150989	0.0993963	0.0119
Cultivar of olive orchards			
"Gordal"	0.0121414	0.1092668	0.0212
Soil edaphic unit			
Bv Vc Bk Rc	0.0119632	0.1190115	0.0225
Bk Bg Rc	0.0116259	0.1284646	0.0224
Cultivar of olive orchards			
"Lechín Granada"	0.0096819	0.1359829	0.0383
Climatic areas			
Sub-humid Atlantic Mediterranean	0.0098059	0.1436692	0.0367
Soil texture			
Sa (sand)	0.0096629	0.1512507	0.0382

1054
1055 [1] We used as ecological predictors the explanatory variables included in the
1056 environment, soil, and agronomic management data sets as whole.
1057 [2] Order of explanatory variables is based on the R^2 values.
1058 [3] See Supporting Information Appendix A for details of explanatory variables.
1059 [4] Forward selection procedure was performed by controlling the effects of spatial
1060 component from the LCBD patterns using the dbMEM variables as predictor set using
1061 partial linear regression with the indications described by Legendre and Gauthier, 2014.

1062 For more details, see Materials and Methods section.

Figure legends

Fig. 1. Map of Andalusia (Southern Spain) showing the olive growing area including the location of the sampled commercial olive orchards (376 sampling sites) and the Guadalquivir River and tributaries.

Fig. 2. Maps of diversity indices used in the analysis. (a) Species richness, ranging from 2 (cyan) to 14 (dark blue). (b) Beta diversity map. Similar colours indicate similar species composition based on Bray-Curtis dissimilarity. (c) LCBD values map. LCBD values ranging from 0.0012 (small circles) to 0.0044 (large circles). Nonsignificant sites are indicated by black circles, and significant sites ($P < 0.005$) are indicated by red circles. In all maps the River Guadalquivir is indicated by a blue line.

Fig. 3. Variation partitioning to explain the variation in community composition and species richness of plant-parasitic nematodes (PPN) based on variables describing the environment (Env), soil (Soil), agronomic management (Mana) and spatial patterns (Spa). The PPN infest soils from cultivated olive trees in Andalusia (Southern Spain). The relative proportion of variation explained by Env, Soil, Mana and Spa, split into unique and joint fractions (Env_Soil_Mana represent the joint fraction of environment, soil and agronomic management variables) is show as a Venn diagram. The proportions of individual fractions sum to 100%. For clarity, the fractions with less than 1.5% of relative variance explained are not shown. Levels of significance: $P < 0.001$ (***), $P < 0.01$ (**), $P < 0.05$ (*), and no mark (no significant).

Figure_1
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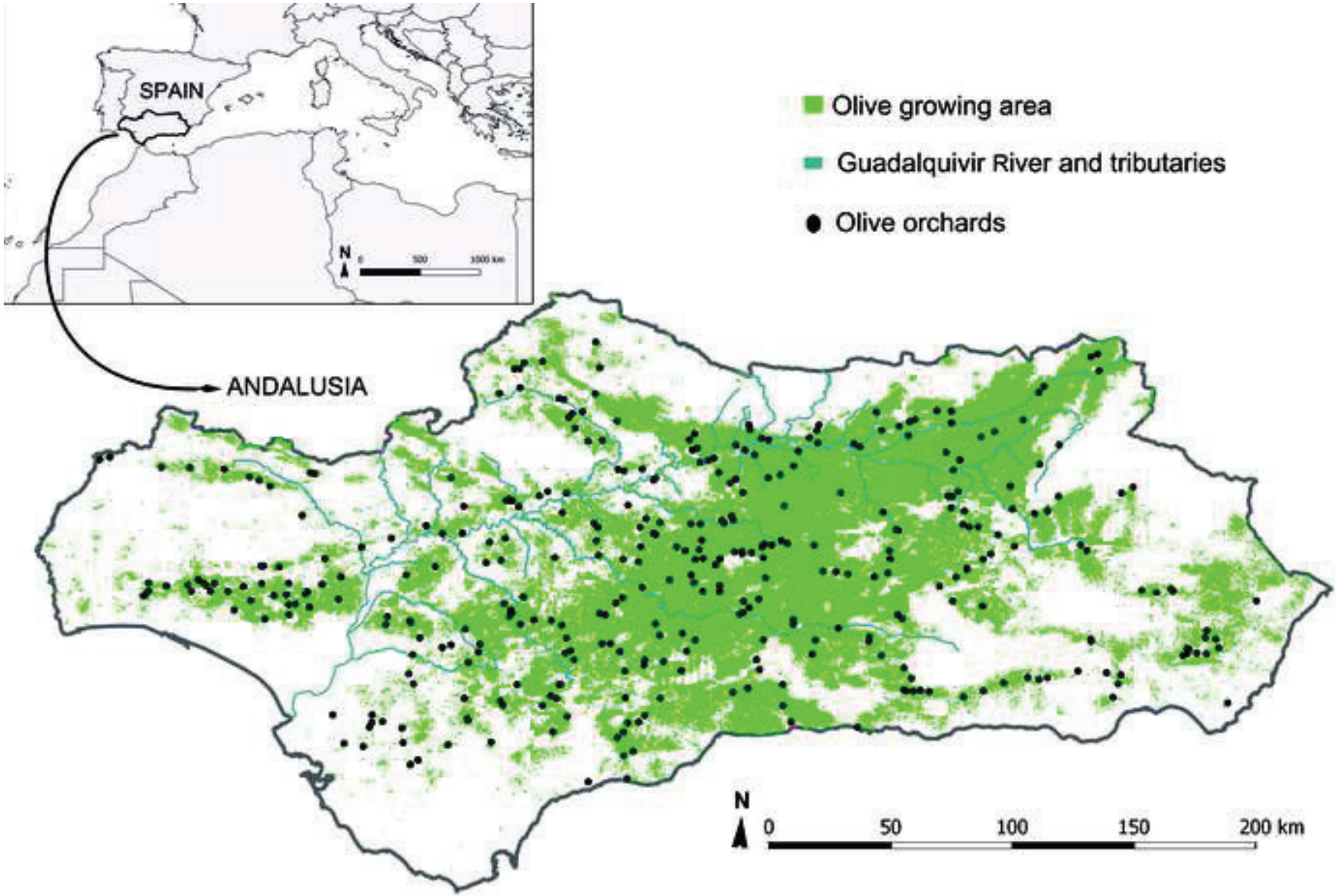

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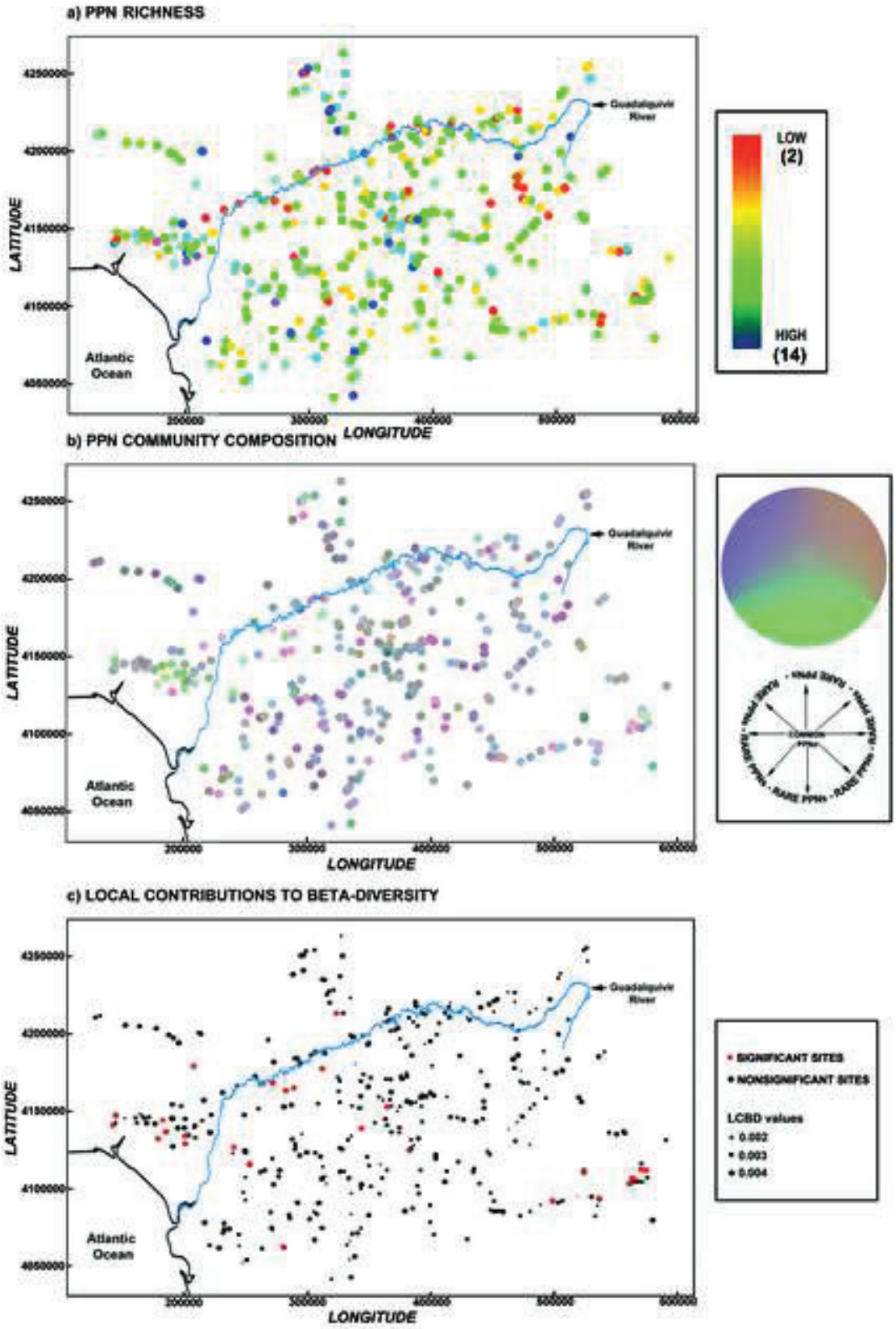

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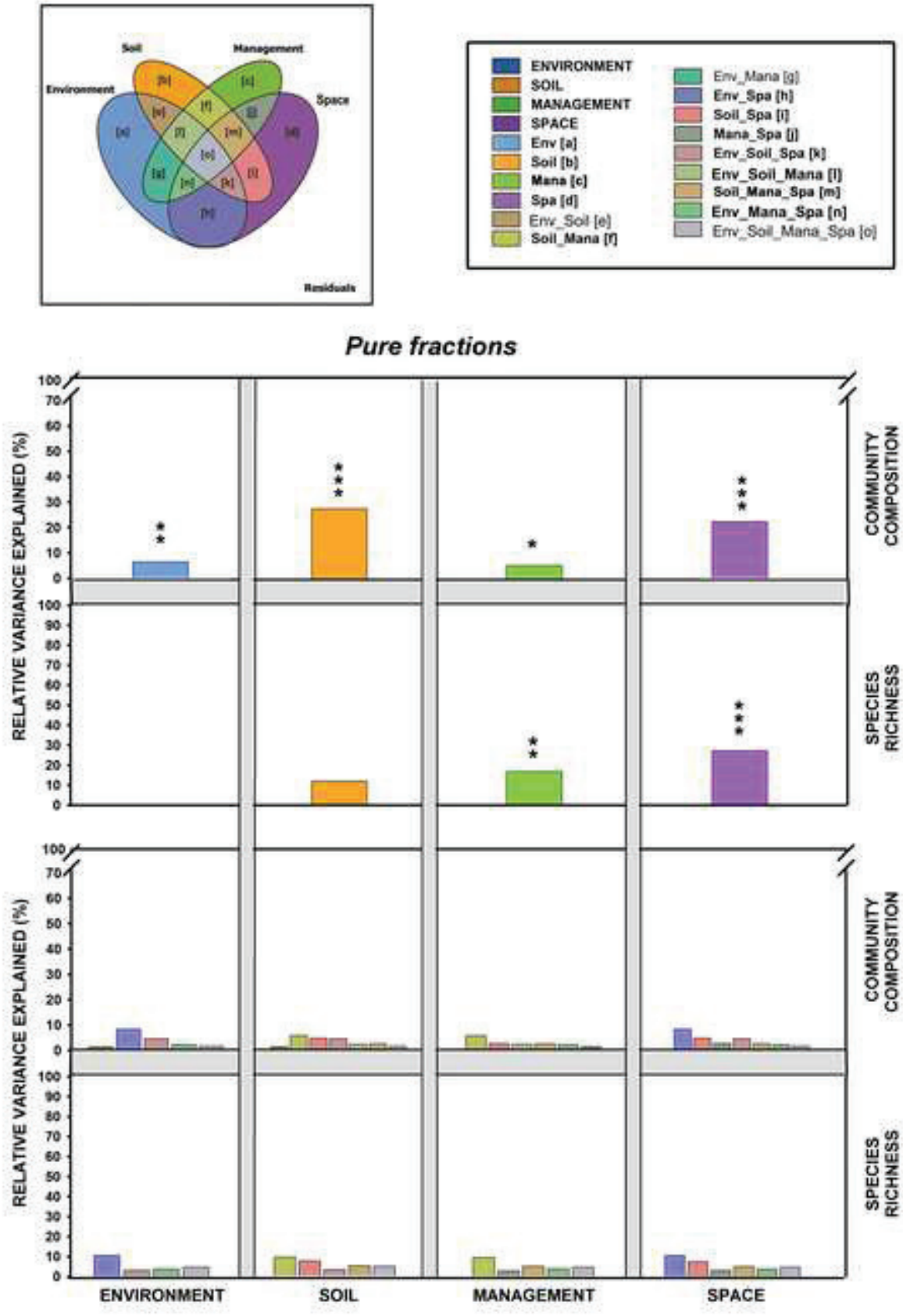

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