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1 **Title:** Agriculture erases climate constraints on soil nematode communities across
2 large spatial scales

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6 **Running title:** Agriculture erases constraints on nematodes

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22

23 **Keywords:** land conversion; environmental gradient; beta diversity; functional traits;

24 phylogenetic diversity; soil biodiversity; soil nematodes; biotic homogenization

25

26 **Paper type:** Primary Research Article

27

28 **Abstract**

29 Anthropogenic conversion of natural to agricultural land reduces aboveground
30 biodiversity. Yet the overall consequences of land-use changes on belowground
31 biodiversity at large scales remain insufficiently explored. Furthermore, the effects of
32 conversion on different organism groups are usually determined at the taxonomic level,
33 while an integrated investigation that includes functional and phylogenetic levels is rare
34 and absent for belowground organisms. Here, we studied the Earth's most abundant
35 metazoa – nematodes – to examine the effects of conversion from natural to
36 agricultural habitats on soil biodiversity across a large spatial scale. To this aim, we
37 investigated the diversity and composition of nematode communities at the taxonomic,
38 functional, and phylogenetic level in 16 assemblage pairs (32 sites in total with 16 in
39 each habitat type) in mainland China. While the overall alpha and beta diversity did not
40 differ between natural and agricultural systems, all three alpha diversity facets
41 decreased with latitude in natural habitats. Both alpha and beta diversity levels were
42 driven by climatic differences in natural habitats, while none of the diversity levels
43 changed in agricultural systems. This indicates that land conversion affects soil
44 biodiversity in a geographically dependent manner and that agriculture could erase
45 climatic constraints on soil biodiversity at such a scale. Additionally, the functional
46 composition of nematode communities was more dissimilar in agricultural than in
47 natural habitats, while the phylogenetic composition was more similar, indicating that
48 changes among different biodiversity facets are asynchronous. Our study deepens the

49 understanding of land-use effects on soil nematode diversity across large spatial scales.

50 Moreover, the detected asynchrony of taxonomic, functional, and phylogenetic

51 diversity highlights the necessity to monitor multiple facets of soil biodiversity in

52 ecological studies such as those investigating environmental changes.

53

54

55 **Introduction**

56 To meet increasing food demands, a large number of natural systems is being converted
57 to agricultural ecosystems at a global scale (Tilman, Balzer, Hill, & Befort, 2011).
58 Conversion of natural to agricultural ecosystems was shown to reduce the biodiversity
59 of insects, plants, birds, and mammals at both local and regional scales, and to
60 homogenize biological communities across space (Flynn et al., 2009; Gossner et al.,
61 2016; Karp et al., 2012; Ponisio, M'Gonigle, & Kremen, 2016; Solar et al., 2015).
62 Ultimately, these losses might negatively affect ecosystem services and human
63 well-being (Díaz, Fargione, Chapin, & Tilman, 2006). To efficiently conserve
64 biological diversity and maintain ecosystem functions, it is crucial to monitor diversity
65 changes and investigate the underlying processes relating to land-use changes.

66 As an essential component of global biodiversity, soil biota (including animals and
67 microbes) contribute to the provisioning of several ecosystem services (Bardgett & van
68 der Putten, 2014; van den Hoogen et al., 2019; Wardle et al., 2004). Nematodes are
69 among the most diverse, abundant, and widespread metazoa on Earth. Being distributed
70 in multiple trophic levels in the soil food web, nematodes participate in diverse
71 ecological processes like the decomposition of organic material and the mineralization
72 of nutrients in soils (Bongers & Ferris, 1999; Yeates, 2003). Nematodes respond
73 quickly and in a taxon-specific manner to environmental changes, and as a result, they
74 are valuable bioindicators (Bongers & Ferris, 1999; Chen, Daniell, Neilson,
75 O'Flaherty, & Griffiths, 2010; Yeates, 2003). For instance, opportunistic nematodes

76 with a short generation time, small body size, and/or high fecundity – often
77 bacterivores – respond positively to disturbance, while taxa with a longer generation
78 time, larger body size, and/or lower fecundity – often omnivores and predators – are
79 sensitive to disturbance (Bongers & Ferris, 1999; Ferris, Bongers, & de Goede, 2001;
80 Liu, Guo, Ran, Whalen, & Li, 2015). This suggests that functional composition might
81 change following land conversion regardless of taxonomic changes. Numerous studies
82 have assessed the effects of land-use intensification on soil biodiversity with a focus on
83 nematodes in agricultural habitats at local and regional scales (Freckman & Ettema,
84 1993; Neher, 2010; Postma-Blaauw, de Goede, Bloem, Faber, & Brussaard, 2010).
85 Nevertheless, the large-scale patterns and processes determining nematode diversity
86 have only been investigated in a few studies to date (Decaëns, 2010; Nielsen et al.,
87 2014; Wu, Ayres, Bardgett, Wall, & Garey, 2011). This prevents us from fully
88 understanding how nematode communities are structured according to different
89 land-use types. Moreover, these studies mostly focus on a particular facet of diversity
90 (e.g., species richness), which might undermine other important changes induced by
91 land conversion (e.g., changes in functional or phylogenetic composition) that affect
92 soil nematodes.

93 Diversity is a key measurement describing communities, which can be defined in
94 different ways. Alpha diversity refers to the diversity in a specific area (generally at a
95 local scale) and can be defined as taxonomic (TD), functional (FD), and phylogenetic
96 diversity (PD). Each of these biodiversity facets provides distinct information about the

97 impacts of different abiotic and biotic factors on biodiversity across time and space,
98 thereby enabling better predictions of potential consequences of biodiversity change
99 (Jarzyna & Jetz, 2016). For example, TD can inform whether and how taxonomic
100 diversity (e.g., taxon richness) changes in response to the gains or losses of taxa. FD
101 describes the functional differences among taxa in a community, which can be used to
102 examine whether a community can maintain its functions under environmental changes
103 (Petchey & Gaston, 2002). PD incorporates the phylogenetic difference between taxa,
104 which is useful for evaluating the potential features of taxa to adapt in changing
105 environments, as it is based on evolutionary relationships between taxa (Faith, 1992;
106 Winter, Devictor, & Schweiger, 2013). Compared to TD, both FD and PD have only
107 recently been included in soil nematode research (Li et al., 2014; Mulder & Maas,
108 2017), despite that they might help in understanding potential consequences of land
109 conversion.

110 In contrast to these alpha diversity measurements focusing on single site metrics,
111 beta diversity compares the community composition among sites and provides
112 complementary information about taxon turnover (McGill, Dornelas, Gotelli, &
113 Magurran, 2015). For instance, it is possible to investigate whether the original
114 community distinctiveness is lost (i.e., increased community similarity) under
115 environmental changes by assessing changes in taxonomic (β TD), functional (β FD), or
116 phylogenetic beta diversity (β PD) (Graham & Fine, 2008; Swenson, 2011; Whittaker,
117 1972). In other words, it allows us to decipher the difference between current similarity

118 (e.g., community similarity after land conversion) and initial similarity (e.g.,
119 community similarity before land conversion). Understanding these changes is
120 important for monitoring and maintaining diversity and ecosystem functions in
121 response to future land-use change (Mori, Isbell, & Seidl, 2018; Socolar, Gilroy,
122 Kunin, & Edwards, 2016). To date, the generally negative effects (diversity loss and
123 biotic homogenization) of land-use intensification on biodiversity have been
124 documented across taxonomic (Gossner et al., 2016; Karp et al., 2012; Solar et al.,
125 2015), functional (Devictor et al., 2008; Flynn et al., 2009; Karp et al., 2012), and
126 phylogenetic facets of diversity (Frishkoff et al., 2014; Nowakowski, Frishkoff,
127 Thompson, Smith, & Todd, 2018; Sol, Bartomeus, González-Lagos, & Pavoine, 2017).
128 However, most of these studies focus on aboveground organisms, including insects,
129 plants, birds, and mammals (Flynn et al., 2009; Gossner et al., 2016; Karp et al., 2012;
130 Ponisio et al., 2016; Solar et al., 2015). To our knowledge, no study to date has assessed
131 the effects of land conversion on both alpha and beta diversity of soil fauna (e.g.,
132 nematodes) in terms of taxonomic, functional, and phylogenetic aspects.

133 To determine the effects of habitat conversion (from natural habitats to agriculture)
134 on soil biodiversity at a large spatial scale, we obtained soil samples from 32 paired
135 sites across mainland China from different climatic conditions. We then calculated the
136 taxonomic, functional, and phylogenetic diversity of nematode communities using
137 incidence-based data (i.e., any nematode taxon in a community with a population size
138 greater than zero is treated as presence; otherwise absence) at both alpha and beta

139 diversity levels. We used incidence-based data to avoid the intractable nematode
140 population dynamics that are mediated by local microhabitats (Paul, 2015) and to be
141 comparable with diversity patterns in aboveground animal groups for which
142 presence-absence data are widely used for analyzing large-scale patterns (Flynn et al.,
143 2009). We also examined the potential drivers (e.g., climatic and soil parameters)
144 associated with these biodiversity patterns. We hypothesized that 1) land conversion
145 reduces the TD of soil nematodes and promotes the homogenization of nematode
146 communities (decrease in β TD), since homogeneous agricultural landscapes have been
147 shown to support lower diverse communities (Flynn et al., 2009; Gossner et al., 2016;
148 Karp et al., 2012); 2) agricultural activities do not affect the FD and β FD of nematode
149 communities because of a high functional redundancy among nematode taxa (Bongers
150 & Bongers, 1998; Ferris et al., 2001); and 3) PD and β PD show similar changes to FD
151 and β FD, because taxa with similar functional traits may share a similar evolutionary
152 history (Blomberg & Garland, 2002).

153

154 **Materials and methods**

155 *Soil sampling and nematode identification*

156 Consistent with previous studies, we used a space-for-time substitution approach to
157 examine the effects of land-use changes on soil biodiversity (Karp et al., 2012; Pickett,
158 1989). Briefly, we obtained soil samples from 16 pairs of agricultural fields with a
159 nearby natural habitat and covering a broad spatial range in mainland China (Fig. S1).

160 Here, we focused our site selection on agricultural fields in upland double-cropping
161 areas, as they represent more than 60% of arable upland systems and provides food for
162 nearly 50% of the Chinese population (Li et al., 2017; Li et al., 2019). Yet the broad
163 patterns and processes of soil diversity (e.g., nematode diversity) in these soil systems
164 are still unclear. Furthermore, as arable upland systems are sensitive to environmental
165 changes at a global level (Montgomery, 2007), understanding the distribution of soil
166 biota and their response to environmental changes (e.g., land conversion) is essential to
167 optimize further soil management. From these systems, we standardized our site
168 selection by focusing on maize planting areas. Maize is the most commonly grown
169 second crop in annual rotations, and it covers a large area of mainland China (Meng,
170 Hu, Shi, & Zhang, 2006). We selected the field sites by maximizing the geographical
171 gradient, avoiding large and industrialized cities with high levels of additional
172 anthropogenic disturbance, and considering the accessibility and affordability of
173 sampling sites. This conservative selection yielded 16 highly comparable sites, which
174 had been in place for at least 20 years (induced by the reduction of cropping areas in the
175 Grain for Green Project in 1999). These agricultural sites are located in flat areas and
176 are managed conventionally. Low agricultural income combined with limited
177 manpower for land management results in the reduced application of fertilizers,
178 pesticides, and other inputs. Despite the lack of detailed information on agricultural
179 practices, the measured soil properties mentioned below could reflect the effects of
180 these practices on soil. Correspondingly, we defined the nearby natural communities as

181 those that were largely unaffected by agricultural activity, mainly shrublands and
182 woodlands near the agricultural fields (Fig. S2). Within each site, three plots (about 20
183 m²), situated at least 100 m from each other, were randomly selected. After removing
184 litter, roots, and rocks, five soil cores with a diameter of 3.5 cm and a depth of 0-10 cm
185 were randomly collected and mixed for each plot. In total, 96 soil samples were
186 collected from August to October 2016 during the maize harvest to minimize the
187 effects of agricultural management, including fertilization, tillage, and pesticide
188 application. Nematodes were extracted from 100 g fresh soil using a modified
189 Baermann method followed by sugar centrifugal flotation (Liu et al., 2008). This
190 method has the advantage of obtaining comprehensive information on the whole
191 nematode community, while being less labor-consuming than traditional Baermann
192 funnel and centrifugation methods (Liu et al., 2008). After counting the total number of
193 nematodes, about 150 randomly chosen individuals from each soil sample were
194 identified to genus with a light microscope (Olympus, Japan) at 400x magnification
195 (Bongers & Bongers, 1998; Liu et al., 2015), which result in a total of about 14,400
196 individuals identified. All plots were measured separately, and values were averaged to
197 represent site conditions of natural and agricultural habitats separately.

198

199 *Soil and climate attributes*

200 After drying and sieving soil samples, we measured several key soil physicochemical
201 properties for all samples. Soil organic carbon (SOC; g/kg) and total nitrogen (TN;

202 g/kg) were analyzed using a C/N analyzer (Elementar Co., Germany) (Nielsen et al.,
203 2014; Wu et al., 2011). Soil pH was measured using a soil water suspension (1:2.5
204 weight/volume) with a pH meter (Hanna, Italy) (Delgado-Baquerizo et al., 2018).
205 Percentages of clay, silt, and sand were estimated after sieving by granulometric
206 analysis (Gee & Or, 2002). For each site, we also extracted four climate variables, i.e.,
207 the mean values of annual temperature (°C), annual precipitation (mm), temperature
208 seasonality, and precipitation seasonality, from WorldClim
209 (<http://www.worldclim.org/>) at a resolution of 30 arc-second (approximately 1 km at
210 the equator). All these variables have been documented as potential determinants of the
211 diversity and composition of above- and belowground organisms (Decaëns, 2010;
212 Hawkins et al., 2003; Nielsen et al., 2014; Wu et al., 2011).

213

214 *Functional traits*

215 We used three trait categories to describe the functional characterization of the
216 nematodes: 1) diet: bacterivore, fungivore, herbivore, omnivore, and predator (Neher,
217 Peck, Rawlings, & Campbell, 1995; Yeates, Bongers, de Goede, Freckman, &
218 Georgieva, 1993); 2) *c-p* value (colonizer-persister): ranges from 1 to 5, representing
219 the position of the taxon on a *r-K* spectrum, with higher *c-p* groups being more
220 susceptible to environmental disturbance and change (Bongers & Bongers, 1998;
221 Bongers & Ferris, 1999); and 3) body mass (µg): the mass averaged across species in a
222 given genus. These traits are critical for nematodes to perform a variety of functions

223 (e.g., soil nutrient cycling) within ecosystems, since taxa with different functional traits
224 may respond to local resources and environmental stressors differently (Bongers &
225 Bongers, 1998; Ferris, 2010; Yeates, 2003). Although other indices such as structure
226 index and metabolic footprint (Ferris, 2010; Ferris et al., 2001) can be used to describe
227 the physiological and ecological characteristics of nematodes, these are mainly
228 calculated from the abovementioned traits using empirical formulas. For this reason,
229 they were not considered in this study. We obtained these traits from the database of
230 Nematode Ecophysiological Parameter (<http://nemaplex.ucdavis.edu>). The
231 associations between these functional traits and the abovementioned environmental
232 variables were assessed with fourth-corner analysis for natural and agricultural habitats
233 separately. The fourth-corner method analyzes the associations through the link of
234 three matrices of environmental data, presence-absence data, and taxon trait data (Dray
235 & Legendre, 2008; Legendre, Galzin, & Harmelin-Vivien, 1997). A sequential
236 approach with models 2 and 4 and 999 permutations was used to evaluate the
237 significance of these associations (Dray & Legendre, 2008).

238

239 *Phylogeny*

240 Unlike many aboveground taxa, the genetic analysis of soil fauna is still at its infancy.
241 Despite the availability of a substantial amount of gene sequences (e.g., 18S rRNA) for
242 soil nematodes, which can infer their phylogenetic relationships, PD for soil nematodes
243 has been infrequently used to date (Floyd, Abebe, Papert, & Blaxter, 2002; Geisen et

244 al., 2018). Thus, we acknowledge that more studies using PD are required to confirm
245 the ecological relevance of this metric. Here, we built a phylogenetic tree of all genera
246 identified in the current study from the Open Tree of Life (OTL) using the *rotl* R
247 package v.3.0.4 (Michonneau, Brown, & Winter, 2016). As the most comprehensive
248 tree of life, OTL assembles both the global reference taxonomy and the database of
249 published phylogenies mapped to this taxonomy, which provides up-to-date
250 phylogenetic information for fundamental biodiversity research and relevant
251 applications (Hinchliff et al., 2015). Because the branch lengths of these nematodes are
252 unknown, they were computed based on Grafen's method (Grafen, 1989) after
253 resolving multichotomies using the *ape* package v.5.2 (Paradis, Claude, & Strimmer,
254 2004), whereby each node is given a branch length equal to the number of descendant
255 tips minus one (Fig. S3).

256

257 *Alpha and beta diversity index*

258 Many different metrics can be used to measure FD, each with different advantages and
259 disadvantages (Mouchet, Villéger, Mason, & Mouillot, 2010; Petchey & Gaston, 2002;
260 Schleuter, Daufresne, Massol, & Argillier, 2010; Villéger, Mason, & Mouillot, 2008).
261 To be comparable with the PD metrics, which are generally calculated on phylogenetic
262 trees, we adopted a dendrogram-based approach to measure FD. To create a trait
263 dendrogram, we calculated a distance matrix (functional dissimilarity) by using the
264 functional traits to compute the distances between taxon pairs, while Gower's distance

265 was used to measure the interspecific dissimilarity, because some traits are qualitative.
266 The matrix was then constructed into a hierarchical dendrogram using an unweighted
267 pair group method with arithmetic mean clustering method (Jarzyna & Jetz, 2017;
268 Podani & Schmera, 2006) (Fig. S4). Body mass was log-transformed before building
269 the functional tree.

270 For alpha diversity, TD was assessed using the number of genera within a
271 community. FD and PD were respectively measured as the sum of the total branch
272 lengths of the functional and phylogenetic trees connecting all genera in a community
273 (Faith's index) (Faith, 1992; Petchey & Gaston, 2002). To assess whether the chosen
274 sample size for nematode identification (i.e., 150 individuals per sample) will affect the
275 measurements of multifaceted diversity, we rarefied 150 individuals from each site for
276 999 times to obtain the expected values of TD, FD, and PD. Thereafter, we calculated
277 the correlations between the observed values and the medians of these expected values.
278 Extremely high correlation coefficients were found for all three diversity metrics (all r
279 > 0.89 , all $p < 0.001$; Table S1). This indicates that the identification of 150 individuals
280 is a good representation of the total nematode community composition. For beta
281 diversity, the Sørensen's index was used to calculate the β TD for each paired
282 assemblage (Baselga, 2010). PhyloSor index, a derivative of Sørensen's index, which
283 considers both shared and total branch lengths between communities, was used to
284 calculate β FD and β PD (Bryant et al., 2008).

285

286 *Significance of changes and congruence between facets*

287 The differences in the taxonomic, functional, and phylogenetic diversities (alpha
288 diversity) between natural and agricultural communities were tested using the
289 Wilcoxon signed-rank test. Analysis of similarities (ANOSIM) with 999 permutations
290 was used to test whether taxonomic, functional, and phylogenetic community
291 compositions (beta diversity) differed between natural and agricultural sites (Clarke,
292 1993). The dissimilarities between communities were visualized with nonmetric
293 multidimensional scaling. Pearson's correlation coefficients were used to measure the
294 correlations between TD, FD, and PD. Correlations in β TD, β FD, and β PD were
295 examined using the Mantel tests based on 999 permutations (Goslee & Urban, 2007).

296 To assess the congruence between changes in taxonomic, functional, and phylogenetic
297 aspects at both alpha or beta diversity levels, we used a permutation procedure with 999
298 iterations to test the difference in slopes between the regression line of any two changes
299 and the 1:1 line. In addition, we disentangled the cross-associations of changes in
300 taxonomic, functional, and phylogenetic diversity ($[\text{agricultural diversity} - \text{natural}$
301 $\text{diversity}] / \text{natural diversity}$) or similarity ($\text{agricultural similarity} - \text{natural similarity}$)
302 into different scenarios to gain a better understanding of the underlying processes of
303 biodiversity changes (Fig. 1) (Baiser & Lockwood, 2011; Jarzyna & Jetz, 2017). For
304 example, a larger increase in TD compared to the increase in FD (or PD) could come
305 from a gain in functionally (or phylogenetically) redundant taxa (Fig. 1a, region II);
306 while a larger increase in FD (or PD) could be explained by a gain in functionally (or

307 phylogenetically) distinct taxa (Fig. 1a, region I) (Jarzyna & Jetz, 2017). A similar
308 magnitude of increase for both taxonomic and functional (or phylogenetic) similarities
309 indicates that taxa contribute equally to traits diversity (or evolutionary history) (Fig.
310 1b, region I) (Baiser & Lockwood, 2011).

311

312 *Assessing the drivers of diversity and composition*

313 To identify the potential drivers of the multiple facets of soil nematode diversity, we
314 used different approaches for alpha and beta diversity metrics. For alpha diversity, we
315 used univariate linear regression analysis to test the effect of latitude as well as the
316 climate and soil predictors on TD, FD, and PD. Spatial autocorrelation (i.e., proximate
317 sites show similar values than distant sites) could bias our modeling results, because the
318 residuals of the statistical models might not be independent from each other (Dormann
319 et al., 2007). Thus, we tested spatial autocorrelation in the residuals of these models
320 using Moran's I statistic (999 permutations) (Bivand, Pebesma, & Gomez-Rubio,
321 2013). If spatial autocorrelation was found, then the spatial simultaneous
322 autoregressive error model (SAR), which treats the autocorrelation by incorporating
323 spatial dependence into the error term, was used to investigate the effect of the given
324 variable on diversity (Dormann et al., 2007). A spatial distance weights matrix based on
325 the minimum distance linking each site to at least one other site was used to define the
326 spatial dependence. Due to the high levels of multicollinearity among these climate or

327 soil variables (Fig. S5), and the small sample size, we did not conduct further multiple
328 linear regression models to examine the effects of climate and soil together.

329 To evaluate the effects of spatial distance, climate, and soil conditions on β TD,
330 β FD, and β PD, we first calculated the climate and soil differences between sites using
331 Euclidean distance on all the principal components obtained from the principal
332 component analyses (PCA) for the climate and soil variables separately (Fig. S6).
333 Spatial distance (km) was calculated based on the coordinates of the sampling sites.
334 Multiple regression on distance matrices (MRM) was used to examine the relationships
335 between the predictor matrices (spatial distance, climate, and soil differences) and three
336 beta diversity metrics (β TD, β FD, and β PD) (Lichstein, 2007). The significance of all
337 regression coefficients was determined using a permutation test ($n = 999$).

338 Unlike climate condition and spatial location, which were almost consistent for a
339 matched pair of natural and agricultural habitats, differences in soil abiotic parameters
340 within each pair may be larger than the difference between isolated pairs. However, we
341 found that all soil attributes were not significantly different between paired natural and
342 agricultural habitats (Table S2). Each attribute in both habitats generally showed
343 similar trends with latitude (except for SOC, which exhibited a significant latitudinal
344 trend in natural but not agricultural soils) (Fig. S7). Thus, for each soil attribute, we
345 used the mean value of the two habitats to represent the condition of the site pair. In
346 addition, another PCA was conducted for these mean soil variables (Fig. S6), and the
347 Euclidean distances on the transformed principal component axes were used to

348 represent the soil differences between site pairs. We then adopted the MRM models
349 with 999 permutations to assess the effects of initial similarity (similarity in natural
350 habitats), spatial distance, as well as climate and soil differences on the changes in
351 taxonomic, functional, and phylogenetic similarity. All analyses were conducted using
352 R 3.3.0 (R Core Team, 2016).

353

354 **Results**

355 *Alpha diversity and associated drivers*

356 In total, we collected 86,365 individuals in 67 nematode genera from all the samples.
357 The mean number of genera was 30.0 ± 1.7 (mean \pm SE) in natural habitats, which was
358 not significantly higher than the mean number of $28.1 (\pm 1.9)$ in agricultural habitats
359 (Wilcoxon signed-rank test $p = 0.452$). There were also no significant differences
360 between natural and agricultural habitats in FD (2.4 ± 0.1 versus 2.2 ± 0.1) and PD (6.9
361 ± 0.3 versus 6.7 ± 0.3) (Wilcoxon signed-rank test $p = 0.105$ and 0.782 , respectively),
362 neither in the variance among natural versus agricultural habitats (Levene's test, $p >$
363 0.05 for all alpha diversity metrics). We also found that TD, FD, and PD were
364 positively correlated with each other in both natural and agricultural habitats (Pearson r
365 > 0.90 ; all $p < 0.001$; Table S3). Furthermore, the results of the fourth-corner analysis
366 suggested that the functional traits (i.e., diet and $c-p$ value) mainly vary along
367 environmental gradients in natural systems (Fig. S8).

368 The latitudinal trends of these diversity indices varied between natural and
369 agricultural habitats (Fig. 2). All diversity metrics declined with increasing latitude in
370 natural habitats (Pearson $r = -0.64, -0.70,$ and -0.59 for TD, FD, and PD, respectively; p
371 < 0.01 for TD and FD, $p < 0.05$ for PD), but remained constant in agricultural habitats
372 (Pearson r : TD: 0.15; FD: 0.12; PD: 0.00; all $p > 0.05$; Fig. 2). In natural habitats, the
373 univariate linear regression models showed that all three facets of diversity were
374 positively associated with annual mean temperature (Pearson r : TD: 0.75; FD: 0.77;
375 PD: 0.60; $p < 0.001$ for TD and FD, $p < 0.05$ for PD) but negatively correlated with
376 temperature variation (Pearson r : TD: -0.65; FD: -0.65; PD: -0.60; $p < 0.01$ for TD and
377 FD, $p < 0.05$ for PD). FD and PD were negatively affected by soil pH (Pearson $r = -0.56$
378 and -0.58 , respectively; all $p < 0.05$) but with TD marginally affected (Pearson $r =$
379 -0.49 ; $p = 0.054$) in natural habitats (Table S4). However, no significant determinants
380 were observed in agricultural habitats (Table S4). Moran's I statistics showed no spatial
381 autocorrelation in the residuals of the linear regression models for most variables,
382 except for precipitation seasonality as well as clay and sand content for TD and FD in
383 natural soils (Table S4). However, further SAR models suggested that these variables
384 were not supported when the spatial autocorrelation was accounted for (Table S4).

385

386 *Beta diversity and associated drivers*

387 The taxonomic, functional, and phylogenetic structures of nematode communities were
388 not different between natural and agricultural habitats (ANOSIM's R : β TD: 0.026;

389 β FD: 0.057; β PD:0.034; all $p > 0.05$; Fig. 3). β TD, β FD, and β PD were positively
390 correlated with each other in both natural and agricultural habitats (Mantel $r > 0.58$; all
391 $p < 0.001$; Table S5).

392 The outputs of the MRM models demonstrate that the spatial distance and
393 differences in soil attributes had no effects on β TD, β FD, and β PD for the two habitat
394 types (Table 1). Climatic differences on the nematode community structure were only
395 observed in natural habitats, and a greater difference in climate conditions could induce
396 a higher dissimilarity in taxonomic, functional, and phylogenetic compositions (Table
397 1).

398

399 *Changes in community similarity and drivers of change*

400 We found that there were no significant changes in taxonomic similarity (Wilcoxon
401 signed-rank test $p = 0.862$; Fig. S9a), while the functional community composition was
402 more dissimilar (differentiation; Wilcoxon signed-rank test $p < 0.001$; Fig. S9b). The
403 phylogenetic composition was more similar in agricultural sites (homogenization;
404 Wilcoxon signed-rank test $p = 0.001$; Fig. S9c).

405 We found that the initial community similarity was the most important predictor of
406 changes in similarity, while communities with a higher initial similarity were less likely
407 to become more taxonomically, functionally, or phylogenetically similar after habitat
408 conversion (Table S6 and Fig. S10). However, spatial distance, climate, and soil
409 differences had no effects on the changes for all similarities. More than 55.0% of the

410 variation was explained by full models, which included all the predictors of both the
411 changes in taxonomic and phylogenetic similarities, while a relatively small proportion
412 of the variation in the changes of functional similarity was accounted for (35.4%; Table
413 S6).

414

415 *Congruence among changes in taxonomic, functional, and phylogenetic diversity*

416 Although the three facets of diversity were highly correlated with each other at both the
417 alpha and beta diversity levels (Tables S3 and S5), the changes in these facets were not
418 congruent. A large change in TD was generally associated with a small change in both
419 FD and PD (slopes significantly less than 1; Fig. 4a-c). Among the seven sites that
420 experienced increases in TD, most experienced smaller increases in FD (4) and PD (7).
421 Of the nine sites that showed decreases in TD, declines were smaller for FD (6) and PD
422 (7). In addition, comparison between changes in FD and PD showed that FD changed
423 faster than PD. Similarly, we found relatively larger changes in taxonomic similarity
424 than changes in functional or phylogenetic similarity, and in functional than in
425 phylogenetic similarity among the assemblage pairs (slopes significantly less than 1;
426 Fig. 4d-f).

427

428 **Discussion**

429 Our study confirms that land-use conversion from natural to agricultural habitats
430 affects the composition of soil biodiversity, as shown here for nematodes, in multiple

431 diversity facets. Specifically, we found that functional community composition became
432 more dissimilar in agricultural than in natural habitats, while phylogenetic composition
433 became more similar. Unlike other studies, which found a loss of TD, FD, or PD in
434 agricultural compared to natural habitats (Flynn et al., 2009; Frishkoff et al., 2014), we
435 did not find such a pattern for soil nematodes. Thus, the hypotheses were not
436 completely supported by our results, as the patterns and determinants of nematode
437 diversity and composition differed between natural and agricultural soils and among
438 diversity facets. Overall, unlike in natural habitats, the diversity and composition of soil
439 nematodes in agricultural habitats did not vary with climate and soil conditions.

440 Agriculture is associated with lower diversities at low-latitude sites but with higher
441 diversities at high-latitude sites compared to nearby natural habitats, resulting in no
442 changes in overall alpha diversities. Since high diversity is often created by many rare
443 and specialist taxa (Magurran & Henderson, 2003; Mouillot et al., 2013) that are
444 sensitive to environmental changes (Davies, Margules, & Lawrence, 2004), we suggest
445 that agricultural practices might lead to losses of these taxa in low-latitude sites.

446 However, in contrast to low-latitude sites, the human-mediated dispersal of generalist
447 taxa might increase the richness in high-latitude sites, because agricultural landscapes
448 could be susceptible to species introduction when the biotic resistance is low (e.g., with
449 low initial richness) (Early et al., 2016; Levine, Adler, & Yelenik, 2004). As the
450 negative effects of agriculture on nematode communities are linked to warmer climates
451 in low-latitude regions, nematode biodiversity might be increasingly lost under climate

452 warming in agricultural soils. Nevertheless, the general hypothesis that land conversion
453 would reduce nematode diversity is not supported here, as the effect of land conversion
454 is latitude-dependent.

455 Changes in TD were generally larger than changes in FD or PD, indicating that
456 most of the lost/gained genera did not have unique functional roles or distinct
457 phylogenetic distributions. Therefore, a profound level of functional and phylogenetic
458 redundancy seems to be present in nematode assemblages, while the situation of larger
459 changes in FD than in PD suggested that the functional and phylogenetic redundancies
460 are not equivalent. We also detected an asynchrony of changes in taxonomic,
461 functional, and phylogenetic similarity, which supports previous findings that changes
462 in taxonomic composition provide limited information on ecosystem functioning and
463 evolutionary history (Baiser & Lockwood, 2011; Jarzyna & Jetz, 2017; Villéger,
464 Grenouillet, & Brosse, 2013). The asynchronous changes between TD and FD in alpha
465 diversity suggest that nematode communities experienced losses of functionally
466 redundant taxa. Additionally, the decreases in both taxonomic and functional similarity
467 could be due to the gains of different nematode genera with different traits and/or the
468 losses of the same genera with similar traits. Therefore, the detected functional
469 differentiation would mostly be caused by the losses of the same functionally redundant
470 genera. Thus, unlike what we have hypothesized (i.e., agriculture would not affect the
471 FD and β FD of nematode communities due to functional redundancy among nematode
472 taxa), the functional redundancy does not eliminate the effect of land conversion on FD

473 and β FD. Similarly, gains and losses of phylogenetically redundant genera after land
474 conversion in combination with the increases in both taxonomic and phylogenetic
475 similarity indicate that the gains of the same phylogenetically redundant genera would
476 mostly contribute to phylogenetic homogenization of soil nematode communities.
477 Therefore, these different responses between functional and phylogenetic composition
478 of nematode communities do not support the hypothesis that PD and β PD show similar
479 changes to FD and β FD.

480 A higher annual mean temperature or less temperature variation is associated with
481 higher TD, FD, and PD in natural habitats. The crucial role played by temperature on
482 alpha diversity was documented across a wide range of taxonomic groups (Hawkins et
483 al., 2003), likely explained by differences in energy supply with high energy
484 availability enabling higher numbers of co-existing taxa (Currie, 1991; Hawkins et al.,
485 2003). We found sites with more similar climates that have similar nematode
486 compositions in natural habitats. This finding is also supported across various
487 taxonomic groups, including plants, birds, mammals, and soil organisms at large scales
488 (Nielsen et al., 2014; Qian, Badgley, & Fox, 2009; Qian & Ricklefs, 2007; Tedersoo et
489 al., 2014; Veech & Crist, 2007; Wang et al., 2017). Unlike other studies that point out
490 the important role of soil properties (e.g., SOC, TN and pH) on soil fauna (Decaëns,
491 2010; Wu et al., 2011), we found a limited effect of any of the measured soil properties
492 on the diversity of soil nematodes (only pH was negatively associated with FD and PD
493 in natural habitats, indicating an environmental selection by pH on nematode functional

494 and phylogenetic composition). The weak impact of soil properties on nematode
495 communities may largely be explained by two reasons: 1) we used a large spatial scale
496 (ranging from 22°N to 40°N with a distance of over 2,600 km), at which taxon
497 distribution may mainly be determined by macroclimate (Currie, 1991; Hawkins et al.,
498 2003); and 2) the resolution of nematodes to genus level might overlook patterns and
499 drivers only present at higher taxonomic resolution as commonly obtained through
500 molecular sequencing tools for soil microorganisms (Delgado-Baquerizo et al., 2018;
501 Tedersoo et al., 2014). Furthermore, we did not observe any effect of spatial distance on
502 the composition of soil nematodes. This could be because environmental similarity
503 (e.g., climate similarity) prompts greater taxon turnover directly (Nekola & White,
504 1999; Soininen, McDonald, & Hillebrand, 2007), while changes in community
505 similarity at distances are slow among passively dispersed organisms (including
506 nematodes) at large scales (Bahram et al., 2016; Finlay, 2002; Soininen et al., 2007).

507 A few limitations should be considered in this study. First, we identified
508 nematodes at the genus level, whereas subtle differences among species might provide
509 diversity information at a higher resolution. Species-level resolution is not possible in
510 larger-scale ecological studies using morphological identification (Geisen et al., 2018).
511 Nevertheless, we expect that higher taxonomic resolution data, potentially obtained
512 through developments in molecular approaches, will show similar results as found
513 here, largely because the functional and phylogenetic relationships among the new
514 units could be generally conserved at the genus or even family level (Geisen et al.,

515 2018). Indeed, this higher resolution might strengthen our findings (i.e., different
516 diversity patterns in natural and agricultural habitats, and asynchronous changes among
517 multiple facets of diversity). Similar to other large-scale soil animal-centered studies
518 (Nielsen et al., 2014; Wu et al., 2011), logistic constraints along the gradient of 2,600
519 km across China and our conservative site selection of comparable natural and
520 agricultural sites reduced the sample size. We thus suggest that future studies should be
521 conducted to evaluate our findings. Although the differences in vegetation composition
522 and structure (especially among the natural sites) were not considered in this study, a
523 recent study suggested that vegetation was not the main determinant of nematode
524 communities at a global level (van den Hoogen et al., 2019). We focus our analysis on
525 three functional traits that describe habitat preference and food acquisition of soil
526 nematodes, because additional traits including morphological, physiological, and
527 ecological traits are lacking for most nematodes (Bongers & Bongers, 1998; Bongers &
528 Ferris, 1999; Ferris et al., 2001; Yeates et al., 1993), while the documented
529 characteristics (e.g., *c-p* value, body size) may vary among individuals and populations
530 in response to local environmental conditions (Liu et al., 2015; Zhao & Neher, 2013).
531 However, in comparison to other soil organisms, nematodes can all reliably be
532 classified into trophic feeding groups with different functional traits. Therefore, this
533 study provides unique functional information on soil biodiversity.

534 Overall, this study sheds light on the ecological patterns and processes that
535 determine soil nematode diversity under land-use changes. This will help us to

536 understand and mitigate the effects of agriculture on belowground biodiversity by
537 considering the interactions of land-use and environmental gradients, with the aim to
538 maintain and enhance soil biodiversity and ultimately ecosystem functioning in soil.

539

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552

553 **Data accessibility**

554 The raw data used in this study are available in the data repository Zenodo
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556

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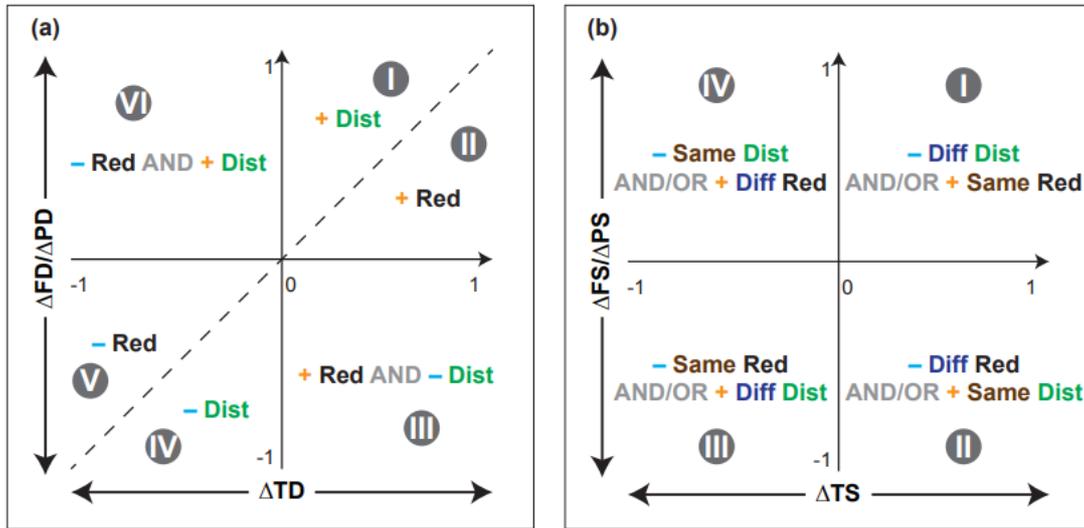
796

797 **Table 1. Results of the MRM models testing the effects of spatial distance as well**
798 **as climatic and soil condition on taxonomic (β TD), functional (β FD), or**
799 **phylogenetic (β PD) beta diversity in natural and agricultural habitats. The**
800 **significance shown in parentheses was calculated based on 999 permutations for each**
801 **predictor, with the significant predictors being shown in bold ($p < 0.05$).**

| | | Spatial distance | Climate condition | Soil condition | R^2 |
|---------------------|-----------------------------|-----------------------------|------------------------------|---------------------------|-------------------------|
| Natural | βTD | 0.000(0.303) | 0.036(0.020) | 0.009(0.468) | 0.161 |
| | βFD | 0.000(0.387) | 0.024(0.004) | -0.003(0.611) | 0.194 |
| | βPD | 0.000(0.401) | 0.022(0.039) | 0.001(0.892) | 0.095 |
| Agricultural | βTD | 0.000(0.488) | 0.005(0.555) | 0.007(0.474) | 0.017 |
| | βFD | 0.000(0.507) | 0.000(0.993) | -0.002(0.767) | 0.013 |
| | βPD | 0.000(0.095) | -0.003(0.715) | 0.004(0.595) | 0.050 |

802

803 **Figure captions**



804

805 **Figure 1. Conceptual diagram of the relationship between changes in taxonomic**

806 **diversity (ΔTD) and changes in functional (ΔFD) or phylogenetic diversity (ΔPD)**

807 **(a), and the relationship between changes in taxonomic similarity (ΔTS) and**

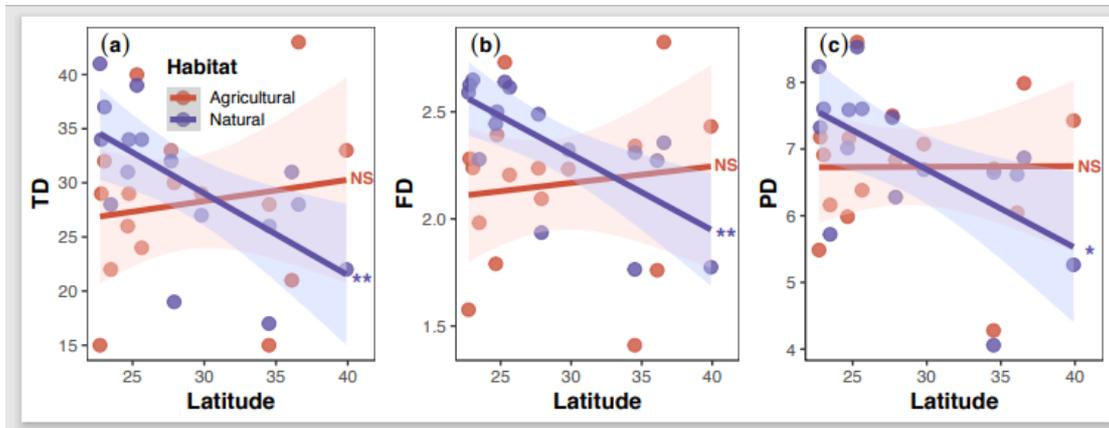
808 **changes in functional (ΔFS) or phylogenetic similarity (ΔPS) (b). + and - indicate**

809 gains and losses of taxa; Red and Dist indicate functionally or phylogenetically

810 redundant and distinct taxa; Same and Diff indicate same and different taxa,

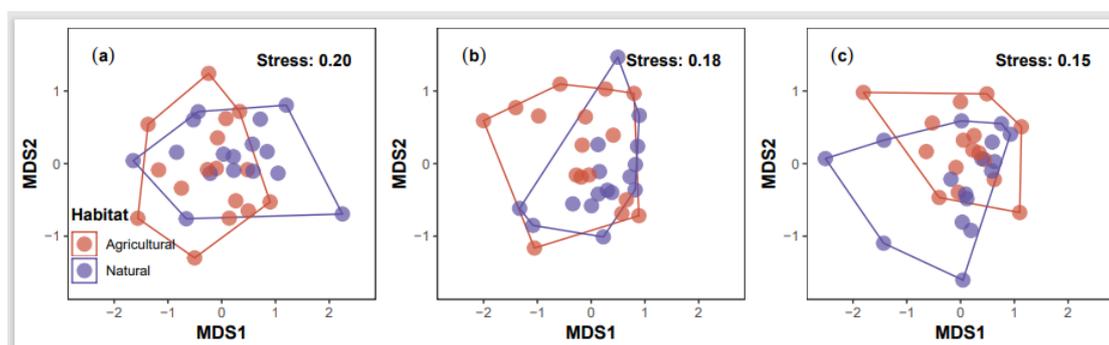
811 respectively. Panel (a) is adapted from Figure 1 in Jarzyna and Jetz (2017), and panel

812 (b) from Figure 1 in Baiser and Lockwood (2011).

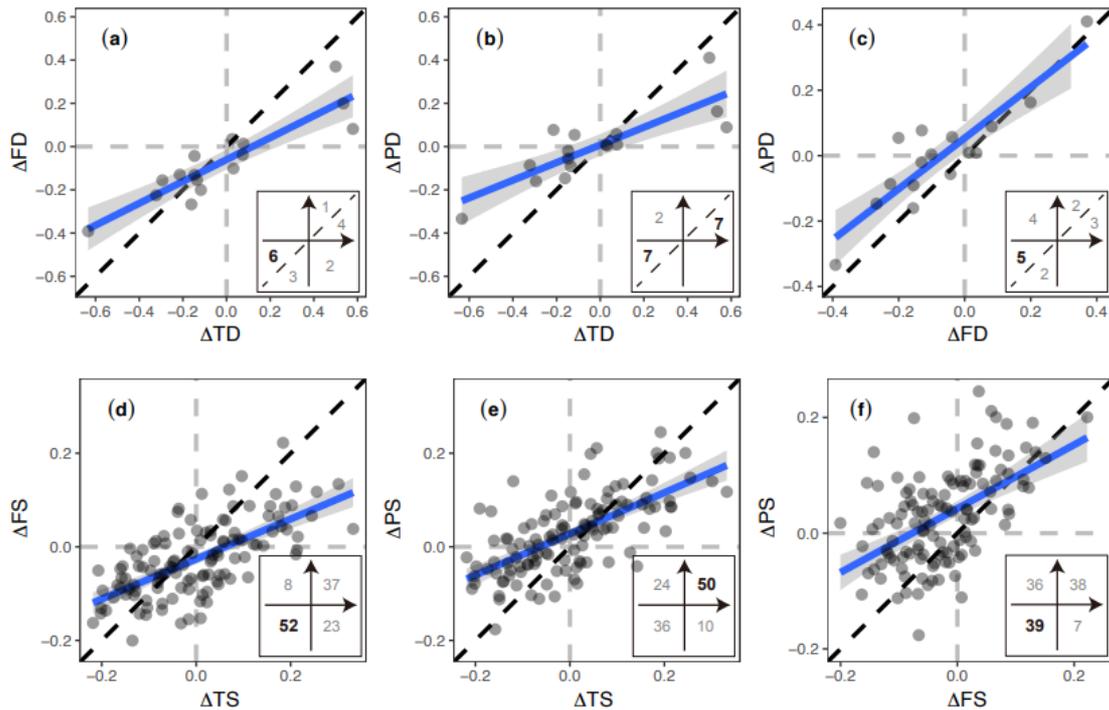


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814 **Figure 2. Patterns in the variation of taxonomic (a), functional (b), and**
 815 **phylogenetic (c) alpha diversity along latitude.** The colored lines depict linear
 816 relationships between diversity and latitude for natural and agricultural habitats. The
 817 significance of the slope of the regression line is indicated at the end of the line (* $p <$
 818 0.05 ; ** $p < 0.01$; NS, not significant). Significant models explain 41%, 49%, and 36%
 819 of the observed variation in TD, FD, and PD, respectively.



820
 821 **Figure 3. Nonmetric multidimensional scaling plots for the taxonomic (a),**
 822 **functional (b), and phylogenetic (c) composition of soil nematode communities in**
 823 **natural and agricultural habitats.** Sørensen's index was used to calculate taxonomic
 824 beta diversity, while PhyloSor index was used to calculate functional and phylogenetic
 825 beta diversity. Stress values indicate the goodness-of-fit measures for observations in
 826 nonmetric multidimensional scaling. Lower values correspond with a better model fit.



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828 **Figure 4. Relationships between changes in taxonomic, functional, and**

829 **phylogenetic diversity with the comparison between natural and agricultural**

830 **habitats based on alpha (a, b, and c) and beta diversity (d, e, and f). Changes in**

831 **alpha diversity were calculated as (agricultural diversity – natural diversity) / natural**

832 **diversity, and changes in similarity as (agricultural similarity – natural similarity). The**

833 **insets show the number of sites or site pairs within the different quadrants displayed in**

834 **Figure 1, with the largest value being shown in bold for each inset. Blue solid lines**

835 **indicate the slope of the relationship between any two kinds of changes. The dashed**

836 **lines indicate the 1:1 line. All the slopes are significantly different from 1 ($p < 0.05$).**

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