

High spatial turnover in springtails of the Cape Floristic Region

Running title: High spatial turnover in springtails

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10

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12

13 **ABSTRACT**

14

15 **Aim:** The extraordinary diversity of plants across the Cape Floristic Region is characterised
16 by considerable species turnover among sites. Phytophagous insects show similarly high
17 turnover, but their patterns are closely coupled to those of their hosts. If the mechanisms
18 underlying high plant turnover are not unique to plants, similar patterns of turnover should
19 also be seen in non-herbivorous arthropod groups. We tested this hypothesis using new data
20 for the Collembola fauna of the Fynbos biome.

21

22 **Location:** The south-western Cape, South Africa.

23

24 **Taxon:** Springtails (Hexapoda: Collembola)

25

26 **Methods:** We sampled springtails from six sites over two seasons. Species richness was
27 compared with expected values from other studies worldwide given the environmental
28 characteristics of the sites sampled. Nestedness and turnover components of beta diversity
29 were calculated and compared against beta diversity patterns of springtails across Europe.

30

31 **Results:** A total of 114 morphospecies from 14 families was collected. Species richness of
32 Fynbos sites ranged from 14 to 31 species, which was not significantly different to that
33 previously reported for non-Fynbos locations and generally within expectations given the
34 temperature, rainfall, and productive energy of each site. Beta diversity was high across all
35 pairwise comparisons of Fynbos sites and dominated by species replacement rather than
36 assemblage nestedness. Relative to the distance between sites, Fynbos assemblages, with a
37 median inter-site distance of 140 km, showed beta diversity substantially higher than in
38 European assemblages, which had a median inter-site distance of 1270 km.

39

40 **Main conclusions:** Alpha diversity of Fynbos Collembola assemblages is in keeping with
41 species richness expectations. By contrast, beta diversity is high given the small distances
42 among sites and is characterised predominantly by species turnover. These patterns of
43 unremarkable alpha diversity, but high turnover among sites are comparable to many Fynbos
44 plant groups. The mechanisms giving rise to high beta diversity of the plants may also have
45 led to high diversity in other taxa.

46

47 **KEYWORDS**

48 arthropods; belowground fauna; beta diversity; nestedness; species energy; soil diversity;
49 turnover

50 1 | INTRODUCTION

51 Despite a strong relationship between large-scale environmental variation and species
52 richness at global scales, some areas clearly stand out as extraordinarily diverse. One
53 of the most significant of these is the Cape Floristic Region (CFR), and specifically
54 the Fynbos Floristic Radiation at the south-western tip of Africa (Goldblatt, 1978;
55 Kreft & Jetz, 2007; Jiménez & Ricklefs, 2014; Linder & Verboom, 2015). Much has
56 therefore been done to document the region's exceptional botanical diversity and
57 understand the eco-evolutionary mechanisms underlying it (Cowling et al., 1996;
58 Linder, 2003; Barraclough, 2006, Hawkins, 2006; Rundel et al., 2016). Although
59 regional plant diversity is high, local (i.e. alpha) diversity is not exceptional compared
60 with similar habitats elsewhere. Rather, the high regional diversity is a consequence
61 of considerable turnover among local sites (Cowling et al., 1992; Cowling et al.,
62 1996; Cowling et al., 1998). Indeed, both spatial and temporal beta diversity is high in
63 the biome (Buerki et al., 2012). Several mechanisms are thought to underlie such
64 turnover, including limitations to gene flow (landscape barriers, pollinator and
65 phenological specialisations), and highly variable local geography and climate, but
66 long-term climatic stability, resulting in the extreme radiation of the Fynbos flora
67 (Linder, 1991, Linder, 2003; Dupont et al., 2011; Jiménez & Ricklefs, 2014; Cowling
68 et al., 2015; Linder & Verboom, 2015).

69 If mechanisms such as landscape variation and gene flow limitation are
70 responsible for the patterns in botanical diversity, they should also be manifest in the
71 diversity patterns of other taxa. Surprisingly few attempts have been made to
72 understand the relationships between local richness, turnover and regional richness of
73 animal groups in the Fynbos. To some extent, low vertebrate richness here relative to
74 other areas in Southern Africa (e.g. Huntley, 1989; Mokhatla et al., 2012; Perón &
75 Altwegg, 2015), may account for the paucity of studies. For other groups, however,
76 the situation is more complicated.

77 For arthropods, and notably the insects, the Fynbos was long thought to be low
78 in diversity generally (Johnson, 1992; Giliomee, 2003), though often without
79 considering the distinction between local and regional richness. Yet, in some
80 endophagous Fynbos insects, diversity is high (Wright & Samways, 2000). Indeed,
81 species richness on a par with other areas seems to be the general pattern for
82 phytophagous groups, with regional richness no lower than in other southern Africa
83 biomes (Procheş & Cowling, 2006). Despite a focus on relationships between local

84 richness and turnover to elucidate potential underlying mechanisms for plants, only
85 two investigations of arthropods in the CFR have dealt explicitly with turnover,
86 concluding that monkey beetles (Scarabaeidae: Hopliini) and leafhoppers
87 (Cephalelini: Cicadellidae) show high turnover among sites (Colville et al., 2002;
88 Kemp & Ellis, 2017; Kemp et al., 2017). This turnover is linked to variation in plant
89 diversity and independent of other environmental drivers in the case of leafhoppers.
90 For non-phytophagous species, a single study has suggested that for epigaeic ants,
91 local richness is in keeping with what might be expected from available energy
92 (Braschler et al., 2012).

93 Yet, this picture rests on a relatively narrow empirical foundation and one that
94 typically has not carefully examined local richness and its patterns of turnover
95 simultaneously (Kemp et al., 2017 being a notable exception). In effect, whether the
96 drivers of the remarkable diversity of the Cape Floristic Radiation (Linder &
97 Verboom, 2015) also have influenced the diversity of other groups, remains
98 underexplored. In particular, an important question to address is to what extent non-
99 phytophagous arthropods will differ from the phytophagous insects in diversity
100 patterns.

101 The paucity of empirical work on CFR fauna constrains understanding of the
102 eco-evolutionary dynamics of the region, so precluding more general insight into the
103 circumstances that might promote unusually high diversity (Kreft & Jetz, 2007;
104 Jiménez & Ricklefs, 2014; Kemp et al., 2017). But it is also of practical concern given
105 on-going modification of the region by agriculture, urbanization, invasive species and
106 climate change (Rouget et al., 2003; Rouget et al., 2014). If turnover among sites is
107 indeed high in animal groups, the degradation or elimination of local habitat patches
108 will be as much a threat to them as it is to the flora.

109 Here, we investigate local richness, turnover and regional richness of the litter-
110 dwelling springtails (Collembola) of the Fynbos Biome. This group is typically not
111 directly associated with vascular plants and mainly subsists on diets linked to soil
112 fungi and microorganisms (Hopkin, 1997). Indeed, Collembola are not at all known
113 for narrow host-plant specificity. Neither do they show direct, consistent relationships
114 with plant richness, despite litter quality effects on their diversity (Salmon et al. 2004;
115 Milcu et al. 2016; Sabais et al. 2011; Salmon et al., 2014; Leinaas et al. 2015;
116 González-Macé & Scheu 2018; Raymond-Léonard et al. 2018). However, edaphic
117 and landscape-level factors nonetheless have a strong influence on its patterns of

118 diversity (Ponge et al., 2003). Thus, springtails make a useful model to examine
119 whether drivers of the unusually high turnover in the vascular plants of the Fynbos
120 Floristic Radiation have also manifested in diversity patterns of arthropod groups with
121 indirect relationships to plants, which contrast strongly with the tight relationships of
122 host-specific insects.

123

124

125 **2 | MATERIALS AND METHODS**

126 **Sites and sampling**

127 Six sites within relatively unmodified landscape were sampled between 2008 and
128 2011 in the Western Cape of South Africa, with the sites ranging from Cape Peninsula
129 (34.26°S, 18.39°E) in the west to Wilderness (33.99°S, 22.73°E) in the east (Fig. 1).

130 The Collembola fauna of the region has recently been the subject of an intense
131 systematic and ecological campaign (e.g. Janion, et al., 2011a; Janion, Bedos,
132 Deharveng, 2011b; Potapov et al. 2011; Janion, et al., 2012; Liu et al., 2012; Janion et
133 al. 2013; Janion-Scheepers et al., 2015; Leinaas et al., 2015; Janion-Scheepers et al.,
134 2016; Weiner et al. 2017). In the present study, Collembola were sampled in a
135 standardised way using litterbags constructed from cylindrical plastic containers
136 (height = 4 cm, \varnothing = 7.5 cm) with a 0.5 mm aperture steel mesh bottom and 1.6 mm
137 aperture mesh lid, filled with approximately 150 cm³ of air-dried uncondensed litter
138 (Leinaas et al., 2015 and references therein). Litter was prepared by harvesting plant
139 material of the chosen plant species, drying this material at 40°C for at least 24 hours
140 and cutting it into approximately 1 cm long pieces. The filled litterbags were stored
141 dry at room temperature before being deployed in the field. At each of the six sites,
142 two sub-sites, at least 200 m apart, were identified where the dominant flora
143 comprised either Ericoid or Proteoid plants. At each of these sub-sites, 10 pairs of
144 litterbags were deployed at the end of the austral summer (March/April). Each pair
145 comprised one litterbag filled with *Galenia africana* litter and one litterbag filled with
146 a 1:1 mixture of *Erica* and *Protea* litter (see details in Supplementary Material) placed
147 under the dominant plant (Ericoid or Proteoid) at approximately 10 m intervals in an
148 L-shaped configuration to cover a wide area of each of the Proteoid and Ericoid sites
149 (Fig. 1), and also allow direct comparison to previous studies (see Bengtsson et al.
150 2012, Janion-Scheepers et al., 2016). *Galenia africana* is an indicator of disturbance
151 such as overgrazing and its nutrient content and decomposition rate is high relative to

152 *Protea* and *Erica* species (Bengtsson et al. 2012). Although this species is not a
153 common Fynbos species, it was included because of its attractiveness to springtails
154 (Leinaas et al., 2015). All litterbags were embedded in the soil such that the top of the
155 litterbag was at ground level, allowing unimpeded movement of litter-dwelling
156 invertebrates. Litterbags were always deployed on a Southern bearing less than 40 cm
157 from the base of a dominant plant. They were left undisturbed and subsequently
158 collected in either September (2008), or in July/August (2009-2011). This timing
159 ensured that litterbags were in the field during the wet season (July/August), when
160 Collembola are particularly abundant (Liu et al., 2012). On collection, the litterbags
161 were wrapped in aluminium foil to prevent any animals from escaping and
162 immediately placed in individual plastic bags and stored upright in a cool, thermally
163 insulated container and returned to the laboratory within five hours of collection.

164 All invertebrates were extracted into 100% propylene glycol using a custom-
165 built high-gradient extractor (Central Mechanical Services, Stellenbosch University),
166 which used a heat source and temperature-controlled water bath (Grant Instruments
167 R2, Cambridge, UK) to generate a thermal gradient along which invertebrates
168 migrated (Macfadyen, 1953; Block, 1966; Leinaas, 1978). The extraction process
169 took approximately four days for each litterbag. After extraction the animals were
170 transferred to 99.9% ethanol for sorting and identification.

171 Individuals were sorted into morphospecies based on our taxonomic
172 experience of the group. Morphospecies were then identified to the lowest taxonomic
173 level possible using available keys (e.g. Fjellberg, 1998; Potapov, 2001; Fjellberg,
174 2007; Hopkin, 2007). Whenever possible, springtails were identified to species level.
175 However, much of the springtail fauna of South Africa is not well described (Janion et
176 al., 2011a, Janion-Scheepers et al., 2015; Janion-Scheepers et al., 2016). Nevertheless,
177 the morphospecies approach is widely used and the level of systematic knowledge for
178 the group for the region developed by the broader project (see Janion et al., 2011a) is
179 sufficient to provide confidence that morphospecies are representative of the
180 biological situation (i.e. species level differences are being assessed, rather than genus
181 level or some other arbitrary criterion). After assignment to morphospecies,
182 individuals were then counted for each trap. For analyses, species counts from all
183 samples using *Galenia* and *Erica-Protea* litterbags across each site were pooled to
184 represent a complete picture of species diversity at each site regardless of litter
185 species/litter-type preferences.

186

187 **Quantification of α -diversity and assemblage evenness**

188 To determine sampling efficacy at each site, randomised (10 000 permutations)
189 sample-based species accumulation curves were plotted using the *vegan* (Dixon,
190 2003) package in R statistical software (R Core Team, 2017). Individual litterbags
191 were used as sample units (see Janion-Scheepers et al. 2016). Plots of species
192 accumulation curves were qualitatively assessed to determine if they were
193 approaching an asymptote, an indication that most species present at a site have been
194 observed.

195 Hill numbers (qD ; Hill, 1973), metrics of alpha diversity that scale linearly,
196 incorporate species abundance, and represent the effective number of species (Jost,
197 2007), were used to quantify the richness of each site and to enable direct and easily
198 interpretable comparisons amongst sites. Hill numbers were calculated for orders (q)
199 0, 1 and 2 where:

200

$$201 \quad {}^qD = \left(\sum_{i=1}^S p_i^q \right)^{1/(1-q)} \quad (1)$$

202

203 The parameter q determines the sensitivity of the metric to species relative abundance
204 (p). Therefore, when $q = 0$, relative abundance is not included in the sum (i.e. ${}^0D =$
205 Species richness). When $q = 1$, species are weighted relative to their frequency (note
206 when $q = 1$ the equation is undefined, but limits ${}^1D \approx \exp(\text{Shannon entropy})$), and
207 when $q = 2$, common species are heavily weighted (${}^2D = 1/\text{Simpson index}$) (Gotelli &
208 Chao, 2013). Hill numbers were directly compared amongst pairs of sites. Because
209 Hill numbers scale linearly, Hill ratios (the ratio of qD for paired sites) can be used for
210 orders 1D and 2D to compare directly the effective number of species between two
211 sites (Jost, 2007; i.e. a Hill ratio of 2.0 indicates that site one has double the diversity
212 of site two).

213 Hill numbers give more weight to common species with increasing order and
214 can be calculated for orders on a continuous scale (i.e. using non-integer values for q),
215 thus their decline with increasing order can be used as an indicator of assemblage
216 evenness. Diversity profiles, calculating qD for continuous orders between 0 – 5,
217 were, therefore, also generated by to assess the evenness of the Collembola

218 assemblage at each site so that the roles of common and rare species could be considered
219 in between-site comparisons.

220

221 **Comparisons of Fynbos richness with sites elsewhere**

222 Variation in local species richness is typically a function of area and energy (Wylie &
223 Currie, 1993; Storch et al., 2005; Ulrich & Fiera, 2009). To determine if the local
224 richness estimates for the assemblages sampled here significantly differ from those
225 globally or are in keeping with what might be expected from energy availability (e.g.
226 Braschler et al., 2012), information on local springtail richness was compiled from the
227 published literature. Studies documenting the Collembola species richness of sites
228 across the globe were collated by the lead author (CJS). The studies included were
229 undertaken predominantly in natural systems, and, based on the conclusions of the
230 authors of these studies, with the assumption that these studies had sampled species
231 richness (i.e. alpha diversity) in a comprehensive manner. Owing to the range of
232 collection methods used to sample Collembola, a quantitative comparison of sampling
233 effort and completeness was not possible. Therefore, only studies where multiple
234 samples were taken (minimum = 22 samples - Convey et al. 1999), or a large number
235 of individuals collected (minimum = 2505 - Querner et al. 2010) were included. We
236 assumed, therefore, that species richness estimates were unlikely to be substantially
237 inaccurate and that any noise introduced by this approach was also unlikely to be
238 biased in any way.

239 Species richness values of sites from this study were first directly compared to
240 species richness values from this compiled dataset through means of a Mann-Whitney
241 U test. Then, using data from non-Fynbos sites, as the data was overdispersed, a
242 negative binomial generalised linear model (GLM) was used (Zuur et al. 2009) to
243 model Collembola species richness of sites as a function of four environmental
244 variables describing upper and lower temperature, precipitation, and productive
245 energy. These variables are all known to affect arthropod diversity variation in
246 general and springtails in particular (Ulrich & Fiera, 2009; Braschler et al., 2012;
247 Overgaard, Kearney, Hoffmann, 2014; Ballesteros-Mejia, Kitching, Jetz, Beck, 2017).
248 Temperature metrics were calculated as the mean day-time temperature of the
249 warmest month and mean night-time temperature of the coldest month, respectively,
250 across a 14-year recent time-series (January 2001 – December 2015) from monthly
251 remote-sensed MODIS/Terra Land Surface Temperature data (MOD11C3; 0.05°

252 resolution) (see also Janion-Scheepers, et al., 2018). As a proxy of productive energy,
253 mean Normalized Difference Vegetation Index (NDVI; MODIS/Terra MOD13C2;
254 0.05° resolution) was calculated for the same period. Annual precipitation was
255 extracted from the WorldClim2 dataset (Fick & Hijmans, 2017). The variance
256 inflation factor was calculated for all variables used to ensure that collinearity of
257 variables would not increase the chance of Type I error in the GLM.

258 For the GLM, precipitation and NDVI were included as independent terms
259 and upper and lower land surface temperature were included as interactive terms as
260 the effect of one variable on the species richness of a site is expected to be dependent
261 on the value of the other variable through means of temperature range/seasonality
262 effects on species richness (Tello & Stevens, 2010; Hua, 2016). No variables were
263 scaled. To determine whether Fynbos Collembola species richness differed from
264 expected species richness given the energy availability and climate of the region, this
265 GLM was then used to generate a richness estimate with 95% confidence intervals for
266 each Fynbos site. Predictions were made using the same four environmental variables
267 described above (upper and lower temperature, precipitation, NDVI). Estimated
268 richness was then compared to observed richness of each Fynbos site. GLM analyses
269 used the *MASS* package in R statistical software (R Core Team, 2017).

270

271 **Beta diversity**

272 Several approaches can be used to assess beta diversity (Koleff, Gaston, Lennon,
273 2003; Baselga & Leprieur, 2015). The equal sampling effort applied to all sites meant
274 that we were able to incorporate species abundance into our beta-diversity analyses.
275 Partitioned Bray-Curtis dissimilarity (Baselga, 2013) was, therefore, calculated
276 between pairs of sites to quantify the relative contributions of variation in abundance
277 and abundance gradients to patterns of beta-diversity between all pairwise
278 combinations of sites.

279 To compare patterns of diversity of the Collembola assemblages described
280 here with those of a non-Fynbos region, the published results of Petersen (2011) were
281 used. Petersen described the species-density of six well-sampled Collembola
282 assemblages across Europe. Due to methodological differences between this study
283 and that of Petersen the abundance-dependent metrics of diversity are not comparable
284 between studies. As a result, higher order Hill numbers and Partitioned Bray-Curtis
285 dissimilarity were not calculated. Thus, incidence-based beta-diversity metrics

286 (Baselga, 2010) were instead calculated for the Fynbos Collembola assemblages from
287 this study and for Collembola incidence data reported by Petersen (2011). Beta-
288 diversity analyses were performed using the *betapart* package (Baselga & Orme,
289 2012) in R statistical software (R Core Team, 2017).

290

291 **Results**

292 A total of 17 408 Collembola comprising 114 morphospecies from 14 families was
293 collected from the six sampled sites (Table 1, Table S1.1, Appendix S1). Kogelberg
294 had the highest species richness (31 species) and Bontebok the lowest (14 species).
295 Bontebok also had the lowest Collembola abundance (295 individuals), in contrast to
296 Peninsula, which had the highest abundance of all sites (6 731 individuals). Although
297 species accumulation curves did not reach an asymptote for any sites (Figs. S1-S6),
298 sampling effort was equal across all sites, enabling among-site comparisons to be
299 made.

300 Comparing the effective number of species amongst sites using Hill numbers
301 where $q \geq 1$, incorporates the relative abundance of each species. While Kogelberg
302 remains the most diverse site based on higher order Hill numbers, Jonkershoek
303 supplants Bontebok as the least diverse site when relative abundance is considered
304 (Table 1). This is indicative of the uneven composition of the Jonkershoek
305 assemblage, which is dominated by an apparently endemic species, *Parisotoma* sp. 5
306 (Table S1.1, Appendix S1). The unevenness of Jonkershoek is also reflected in the
307 steep diversity-profile decline of this site (Fig. S8.1, Appendix S8).

308 Collembola species richness of the South African sites described in this study
309 was not significantly different to Collembola species richness of sites globally (Fig. 2,
310 Table 1; Table S2.1, Appendix S2; MWU; $U = 40$, $Z = -1.2188$, $p = 0.2355$, $r = -$
311 0.0469), acknowledging substantial variation in the compiled data. The fitted GLM
312 explained 30.6 % of species richness deviance (Cox-Snell pseudo- $R^2 = 0.36$) observed
313 across the assemblages compiled from the literature, with productive energy (NDVI)
314 identified as a significant predictor variable (Table S3.1, Appendix S3). Observed
315 Fynbos Collembola species richness of four sites (PEN, MTR, WIL, KOG) was
316 within 95 % confidence intervals predicted using this model. Observed species
317 richness of the two remaining sites (JNK, BON) was below the lower 95 %
318 confidence interval (Table 1).

319 Beta diversity was high across all pairwise comparisons of Fynbos sites (Table
320 2; Table S1.1, Appendix S1, Table S4.1, Appendix S4). Partitioning of Bray-Curtis
321 dissimilarity (Baselga, 2013) indicates that balanced variation in abundance, which is
322 comparable to species turnover in incidence-based beta diversity partitioning, was
323 almost wholly responsible for observed differences between sites. Abundance
324 gradients, comparable to nestedness, contributed very little to the among-site
325 differences (Table 2).

326 Partitioned incidence-based beta diversity metrics for Fynbos Collembola
327 mirror abundance-based metrics, with species turnover contributing almost
328 exclusively to the high beta diversity between pairs of sites (Figs. 3 and 4, Table 3).
329 Beta diversity, measured as total Sørensen Dissimilarity, was higher than that
330 calculated from Collembola incidence data reported by Petersen (2011) for six sites
331 across Europe (Fig. 4; Table S5.1, Appendix S5; Fynbos β_{sor} : $Q_1 = 0.823$, median =
332 0.900 , $Q_3 = 0.918$; Europe β_{sor} : $Q_1 = 0.694$, median = 0.875 , $Q_3 = 0.906$). This
333 difference was not significant (Mann-Whitney U test: $U = 145$, $p = 0.184$, $r = 0.174$).
334 Fynbos sampling sites in this study were, however, almost an order of magnitude
335 closer together than those used by Petersen (Fig. 4; Fynbos intra-site distance, Table
336 S2.1, Appendix S2: $Q_1 = 57$ km, median = 140 km, $Q_3 = 270$ km; Europe intra-site
337 distance, Table S5.1, Appendix S5: $Q_1 = 1033$ km, median = 1272 km, $Q_3 = 1613$
338 km). This difference was significant with a large effect size (Mann-Whitney U test: U
339 = 218 , $p \leq 0.001$, $r = 0.799$).

340

341 Discussion

342 We found that while local (alpha) diversity in springtails in the Fynbos biome
343 was similar to what would be expected from environmental conditions, the beta
344 diversity over small distances (50-250 km) was exceptionally high compared to
345 springtail assemblages elsewhere. Most of this beta diversity was a result of species
346 turnover. This suggests that there is a high diversity of soil animals in the Fynbos, as a
347 result of factors such as a long history of isolation and variable geography, similar to
348 what has been found for plants (e.g. Linder & Verboom 2015).

349 Several studies have demonstrated that the species richness of arthropods in
350 areas of the Cape Floristic Region is similar to that of other southern African biomes,
351 either within the expectations of species-energy theory, or strongly related to plant
352 diversity (Wright & Samways, 2000; Procheş & Cowling, 2006; Procheş et al., 2009;

353 Braschler et al., 2012; Kemp & Ellis, 2017; Kemp et al., 2017). Most of these
354 investigations have, however, concerned phytophagous species, which often have
355 strong associations with plants (Strong, Lawton, Southwood, 1984; Novotný, Drozd,
356 Miller, Kulfan, Janda, Basset, Weiblen, 2006; Castagneyrol & Jactel, 2012; Kemp et
357 al., 2017).

358 Here we showed similar results for a group that subsists on soil fungi and
359 microorganisms (Hopkin, 1997) and is not, therefore, directly linked through diet with
360 vascular plants, suggesting again that Fynbos arthropods in general are not as species
361 poor as originally thought (Marloth, 1908, see also Johnson, 1992). Rather, alpha
362 diversity at each sampled site is in keeping with what might be expected for similar
363 systems globally given energy availability, bearing in mind that the richness-
364 environmental variable analysis accounted for only 30% of the variation in richness
365 (although a value not dissimilar to other studies at this scale – see e.g. Braschler et al.,
366 2012; Gillman et al., 2015; Beck et al., 2017). Other factors, such as regional area
367 effects and long-term climatic stability (Galley, Linder, Zimmerman, 2009; Ulrich &
368 Fiera, 2009), may be important contributors to richness, and will require further
369 investigation. For the two sites with lower than expected species richness (Bontebok
370 and Jonkershoek), more frequent disturbance than the other sites may have played a
371 role (Supplementary Material Figs S7.3, S7.5 and S8.1, Appendices S7 and S8),
372 though causes for richness variation among sites remain to be investigated. The
373 unevenness of the Jonkershoek assemblage, which was dominated by *Parisotoma* sp.
374 5, is particularly conspicuous, but whether this is related to specific species traits is
375 not currently known. This species was dominant both before and after a fire in this
376 area, showing high resistance to this disturbance, which is frequent in the Fynbos (see
377 Janion-Scheepers et al. 2016). Such species-specific traits may play an important role
378 in structuring Collembola assemblages in the Fynbos.

379 In contrast to the unexceptional alpha diversity, beta diversity of Collembola
380 between Fynbos sites was higher than reported from sites across Europe, despite
381 geographic distances between Fynbos sites being significantly shorter by almost an
382 order of magnitude (Fig. 4). Beta diversity was primarily due to species turnover
383 (change in species identity) rather than species nestedness, as indicated by beta-
384 diversity partitioning. Indeed, compared against many other assemblages across a
385 broad range of taxa (Soininen, Heino, Wang, 2018), the turnover found here is
386 extraordinarily high and nestedness unusually low (Fig. 3). A study of springtail

387 assemblages from 16 Swedish pine forest sites, encompassing a comparable spatial
388 scale as the present study, found Sørensen dissimilarity indices of ≈ 0.15 - 0.25 , which
389 are substantially lower than the turnover metrics reported here (Figs. 3 and 4;
390 Widenfalk et al. 2017; see also Perez et al. 2013). Similarly, an investigation of
391 springtail diversity among two major areas of Eastern Europe revealed high turnover
392 of springtails, but again across a 1200 km gradient (Kuznetsova & Saraeva 2018).
393 Elsewhere, across the whole of the Antarctic region (including the Southern Ocean
394 Islands), with distances among sites spanning thousands of kilometres (Baird et al.
395 2019), turnover values (β_{sim}) similar to those found here over the much shorter
396 distances we sampled were found. The European regions were substantially affected
397 by the last glacial maximum, with evidence for postglacial colonization of
398 Collembola from a South-Western European centre (Ulrich & Fiera, 2009), thus
399 potentially accounting for low turnover. By contrast, strong evidence exists for
400 persistence across several glacial cycles of the Antarctic arthropod fauna of many
401 sites (Moon et al. 2017), yet turnover is still lower than in Fynbos given the different
402 spatial extents. Thus, as is the case for previously studied phytophagous insects
403 (Kemp et al. 2017), springtails across the CFR appear to follow similar patterns of
404 spatial variation in species diversity as documented for fynbos vegetation (Cowling,
405 1990; Cowling et al., 1992, Cowling et al., 1996; Cowling & Lombard, 2002; Buerki
406 et al., 2012). How this spatial turnover is established relative to, for example, rates of
407 movement and habitat preference in springtails (see e.g. Treasure & Chown 2013)
408 remains to be determined.

409 Spatial variation in diversity has been at the heart of characterisations of the
410 high richness of plant species in the Fynbos biome (Cowling, 1990; Buerki et al.,
411 2012). In particular, alpha diversity tends to be low, but beta diversity is high, leading
412 to the exceptionally high regional diversity that is characteristic of the Fynbos
413 (Cowling, 1990; Cowling et al., 1992, Cowling et al., 1996; Cowling & Lombard,
414 2002). A similar situation seems to be true of the Collembola examined in this study.

415 Although the idea that high beta diversity of insects might explain high
416 regional insect diversity in the Fynbos has been proposed previously (Procheş et al.
417 2009), it has not been comprehensively examined for any arthropods. The most
418 sophisticated assessment of arthropod diversity variation in the region has come from
419 a study of cicadellid bugs associated with the plant family Restionaceae (Kemp et al.
420 2017). Three likely hypotheses for similar patterns in host and insect spatial diversity

421 variation were proposed: 1. insect host specificity; 2. similar responses of insects and
422 their hosts to climatic gradients; 3. similar biogeographic influences on each of the
423 groups. For these relatively host-specific cicadelids, host specificity was identified as
424 the likely underlying cause of similarity in spatial diversity patterns (Kemp et al.,
425 2017). In the succulent Karoo, plant beta diversity was also identified as being a
426 major factor influencing beta diversity of the flower visiting beetles (Scarabaeidae:
427 Hopliini) (Colville et al., 2002).

428 In contrast to phytophagous insects, springtails mainly belong to the soil detritus
429 food chain, and are not, therefore, closely associated with individual plant species
430 (Hopkin, 1997; Salamon, Schaefer, Alpehi, Schmid, Scheu, 2004), although they are
431 responsive to plant richness and functional diversity (Sabais, Scheu, Eisenhauer,
432 2011; Henneron et al., 2017). Accordingly, the majority of springtail species were
433 found in both nutrient-rich and nutrient-poor litter types during preliminary litter-type
434 studies the Jonkershoek site (Table S6.1), further bearing out the generalist foraging
435 behaviour of these animals (see also Leinaas et al., 2015). In consequence, either
436 responses to climatic gradients or biogeographic features similar to those found in
437 many vascular plant groups of the Fynbos are likely responsible for high beta
438 diversity in the springtails. A strong relationship was also found between plant
439 phylogenetic diversity and detritivore insect richness within the Fynbos at the 20 m
440 sampling scale in a previous investigation (Proçhes et al. 2009), bearing out the
441 independent, but likely similar, influence of environmental drivers on plants and on
442 detritivorous arthropods. Understanding just what these mechanistic drivers are will
443 require the kinds of coupled ecological and phylogenetic work that has provided so
444 much insight into the mechanisms underlying plant diversity in the region (Linder,
445 2003; Dupont et al., 2011; Cowling et al., 2015; Linder & Verboom, 2015; Rundel et
446 al., 2016), including explicit tests of Kemp et al.'s (2017) hypotheses and other
447 drivers such as interspecific interactions (Augustyn et al., 2017). Initial evidence
448 suggests that some springtail genera, such as *Seira*, may have undergone significant
449 radiations in the CFR (Janion, Bedos, Deharveng, et al. 2011; Liu, 2015), which
450 points to the importance of eco-evolutionary processes, as is the case in the plants.
451 Notwithstanding uncertainty about mechanisms, the level of replacement among sites
452 was high, with more than 85% of species unique to one site (Table S1.1, Appendix
453 S1). Such a high number of site-specific species contrasts strongly with what has been
454 found for springtails of other areas at similar scales (Ulrich & Fiera, 2009). Although

455 our sampling was not comprehensive across the entire Fynbos Biome, and some
456 species may not have been detected at each of the sites, other approaches in the
457 region, which have demonstrated many local springtail endemics (Liu, 2015), suggest
458 that the patterns are likely to be upheld. Thus, the CFR may be as important a
459 biodiversity hotspot for belowground systems as it is for those more visible on the
460 surface. Loss or degradation of local sites may thus have more of an impact on
461 Fynbos biodiversity than is currently estimated (Rouget et al., 2014).

462

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747

748 **Biosketches**

749 **Charlene Janion-Scheepers** is interested in the adaptation and plasticity of
750 organisms' responses to climate change and how these responses differ between
751 introduced and indigenous species.

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754 Author contribution:

755 CJ-S, JB, HPL and SLC designed the study, CJ-S, JB and HPL performed the
756 collection and processing of samples, CJ-S and LD identified the species, CJ-S and

757 GAD analysed collected biodiversity data, CJ-S, GAD and SLC wrote the manuscript,
758 and all authors provided comments on manuscript drafts.

759 **Table 1:** Collembola assemblage sampling sites used in this study. Diversity metrics
760 were calculated for Collembola from collected material. Annual precipitation, upper
761 and lower land surface temperature, and Normalized Difference Vegetation Index
762 (NDVI) of each site were used to predict Collembola species richness through the
763 application of a generalized linear model (GLM) constructed from reported species
764 richness of Collembola globally (Table S3.1).
765

	Peninsula	Jonkershoek	Kogelberg	Mont Rochelle	Bontebok	Wilderness
	(PEN)	(JNK)	(KOG)	(MTR)	(BON)	(WIL)
Latitude	-34.2601	-33.9886	-34.3248	-33.9034	-34.0784	-33.9916
Longitude	18.3934	18.9552	18.9650	19.1590	20.4671	22.7349
Diversity metrics						
Collembola richness (⁰ D)	26	20	31	27	14	25
Collembola abundance ¹ D	6731	2948	2581	2281	295	2572
² D	4.63	3.75	9.69	7.15	6.17	7.00
	3.17	2.08	6.34	4.03	4.32	4.71
Environmental data						
Precipitation (mm)	681	1032	811	949	557	737
Lower temperature (°C)	5.75	3.53	5.61	3.85	4.99	4.41
Upper temperature (°C)	24.85	33.01	32.43	31.07	38.29	28.07
NDVI	0.47	0.57	0.50	0.53	0.46	0.68
GLM predictions						
Prediction	21.93	32.49	28.05	30.32	34.97	36.49
Lower 95% estimate	10.30	23.82	18.56	21.77	19.34	24.94
Upper 95% estimate	33.55	41.16	37.55	38.87	50.60	48.03

766

767

768 **Table 2:** Asymmetric distance matrix for abundance-based partitioning of pairwise
769 Bray-Curtis dissimilarity (Baselga 2013) between Collembola assemblages of the
770 Western Cape. The relatively large values for dissimilarity derived from balanced
771 variation in abundance between sites (grey) indicates that species turnover is the main
772 contributor of observed pairwise dissimilarity, while dissimilarity derived from
773 unidirectional abundance gradients (white) contributes relatively little.
774

	PEN	MTR	WIL	KOG	JNK	BON
PEN		0.0264	0.0043	0.1328	0.0170	0.0093
MTR	0.9465		0.0001	0.0026	0.0043	0.0000
WIL	0.9903	0.9982		0.0000	0.0007	0.0000
KOG	0.7021	0.9579	0.9817		0.0048	0.0539
JNK	0.9566	0.9667	0.9891	0.9272		0.0111
BON	0.9898	1.0000	1.0000	0.9322	0.9864	

775

776 **Table 3:** Asymmetric distance matrix for incidence-based partitioning of pairwise
 777 beta diversity metrics (Baselga 2010; Table S2.1) between Collembola assemblages
 778 of the Western Cape. The relatively large values for the turnover component
 779 measured as Simpson dissimilarity (grey), indicates that species turnover is the main
 780 contributor of observed pairwise dissimilarity, while the nestedness component
 781 measured as the nestedness-resultant fraction of Sørensen dissimilarity (white),
 782 contributes relatively little.
 783

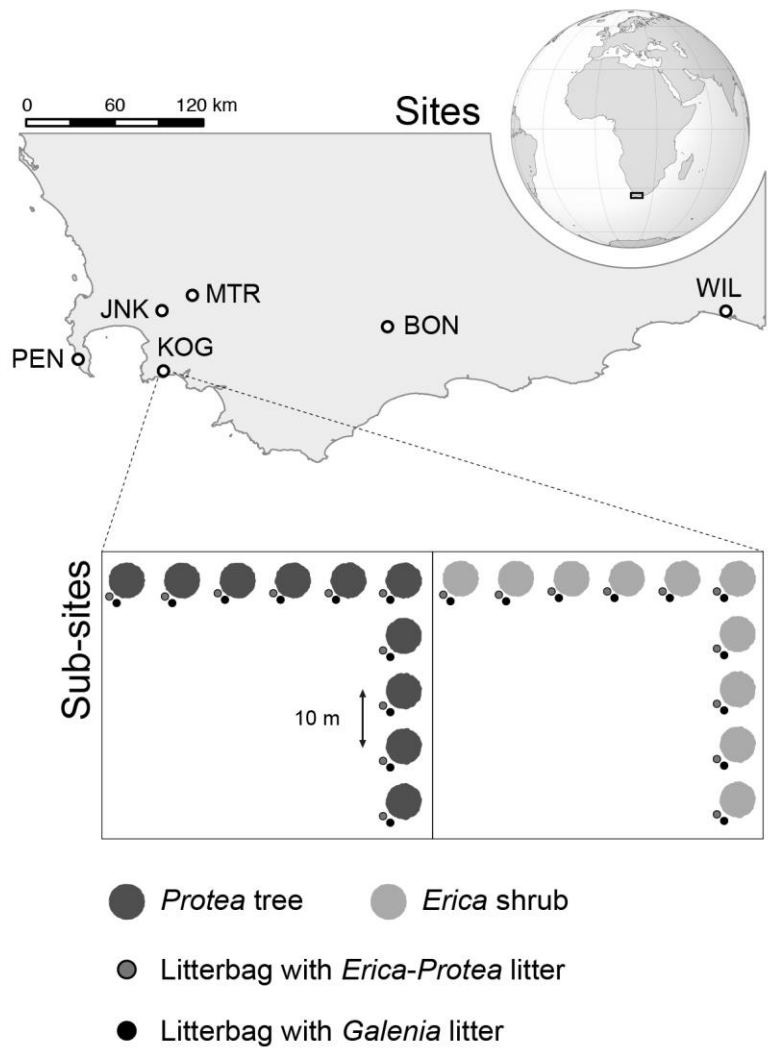
	PEN	MTR	WIL	KOG	JNK	BON
PEN		0.0029	0.0016	0.0202	0.0261	0.0429
MTR	0.8462		0.0031	0.0153	0.0149	0.0000
WIL	0.9200	0.9200		0.0214	0.0111	0.0000
KOG	0.7692	0.7778	0.8000		0.0647	0.0540
JNK	0.8000	0.9000	0.9000	0.7000		0.0378
BON	0.8571	1.0000	1.0000	0.8571	0.7857	

784

785 **Figures**

786

787

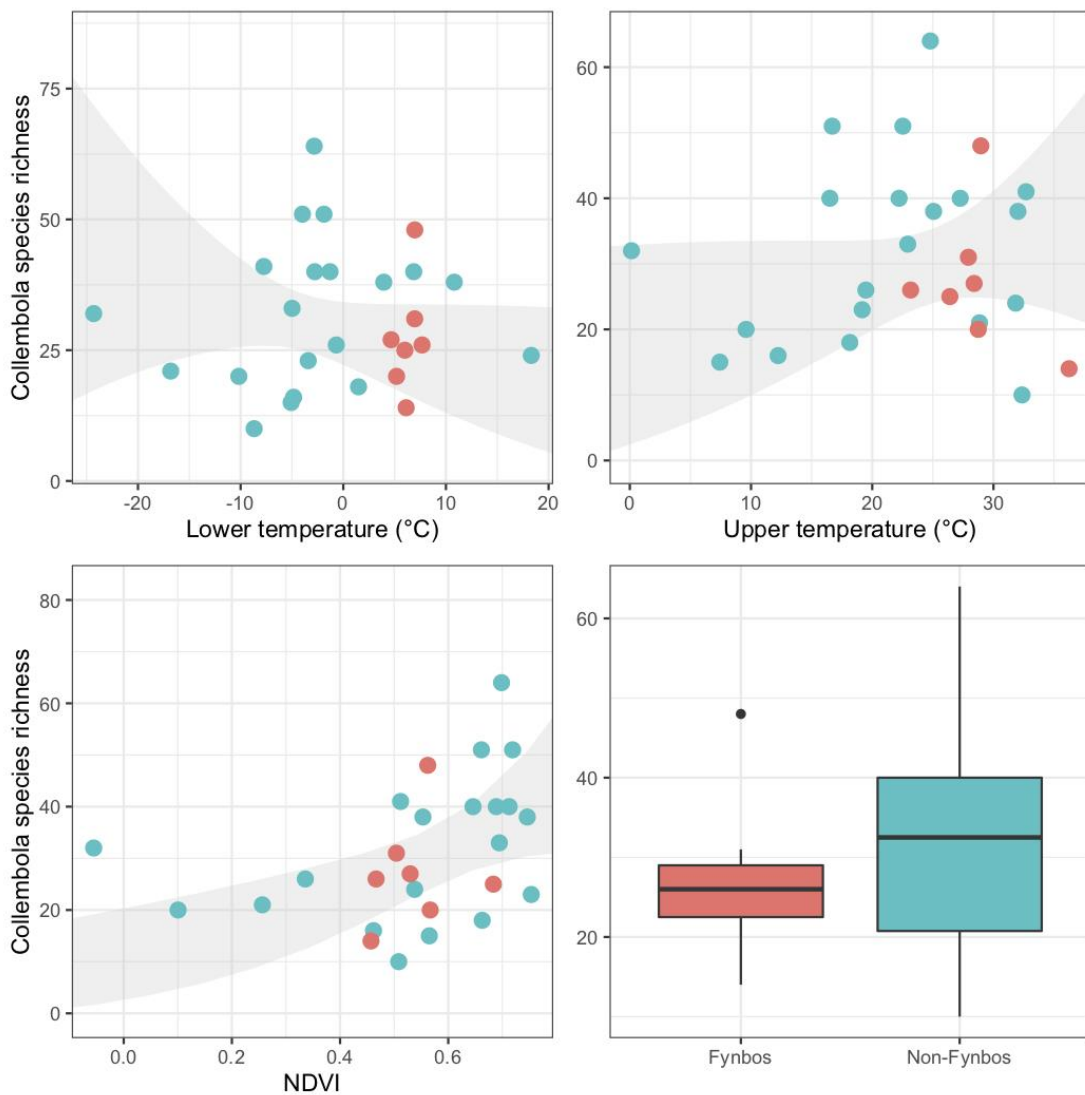


788

789 **Fig. 1:** Experimental design used at each site in this study.

790

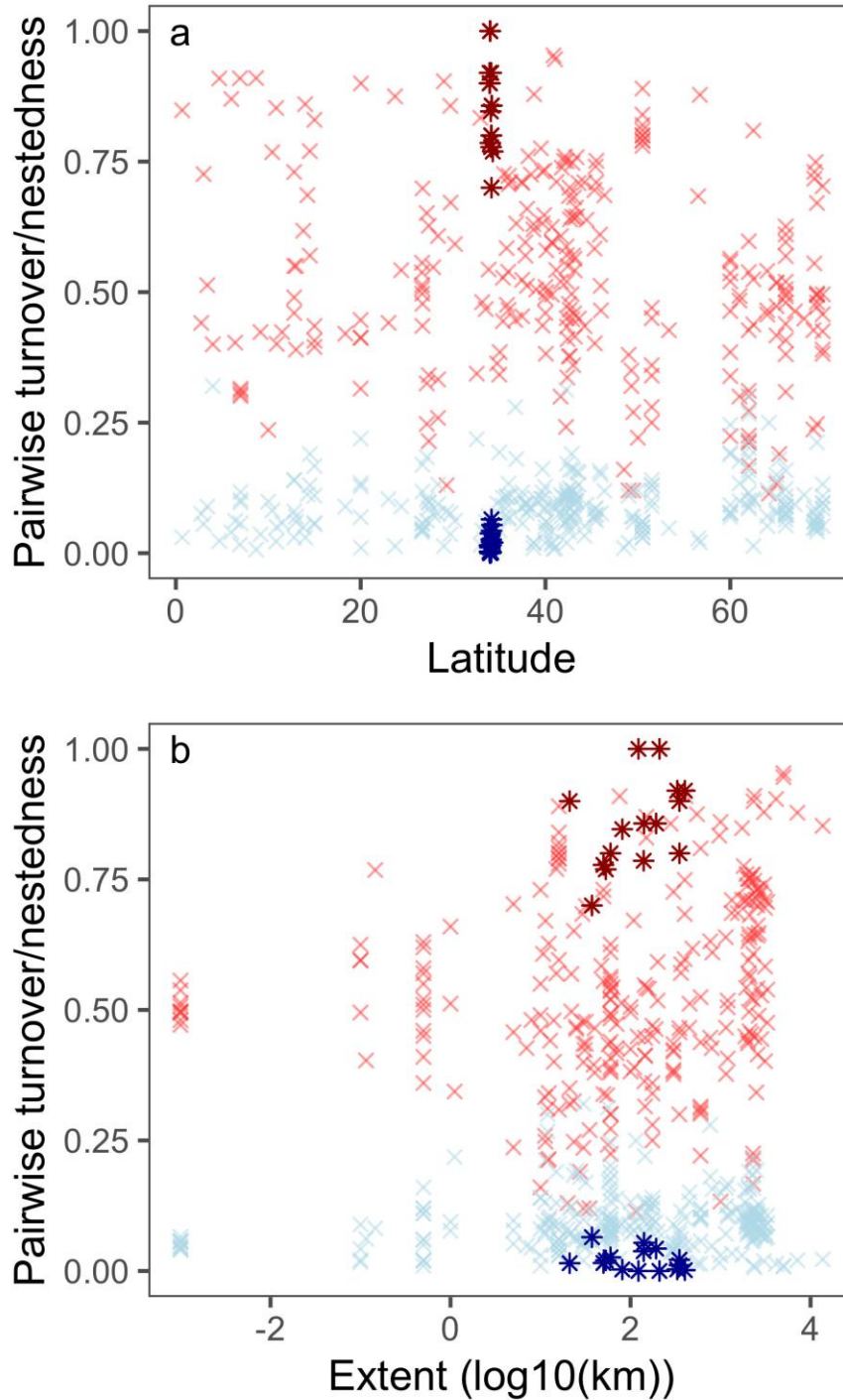
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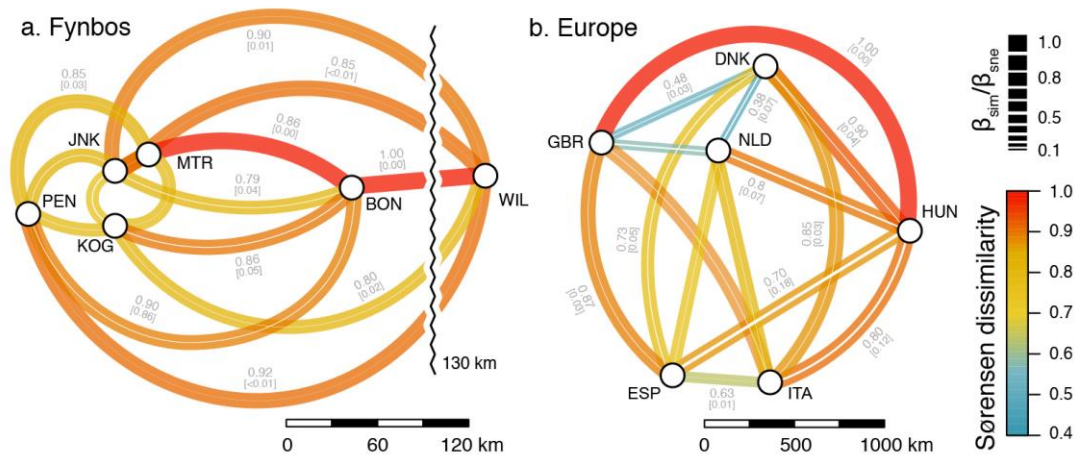
794 **Fig. 2.** Species richness of Collembola against the three most influential
795 environmental variables of our generalised linear model (Table S4.1). Grey ribbons
796 represent the 95% confidence intervals for each variable assuming all other variables
797 are held at their respective mean. Blue points represent species richness of sites from
798 published literature (excluding Liu et al. 2012) that were used to build the GLM. Red
799 points represent Fynbos sites (i.e. all sites from this study and Liu et al. 2012). The
800 boxplot directly compares species richness of Fynbos and non-Fynbos sites.



801
 802 **Fig. 3.** Pairwise turnover (red) and nestedness (blue) components of incidence-based
 803 beta diversity metrics across latitude (a; mean latitude of site pair) and spatial extent
 804 (b; log₁₀ distance between site pair) for the range of taxa compiled by Soininen,
 805 Heino, Wang, 2018 (lighter crosses) and springtail data from this study (darker
 806 asterisks; Table 3).

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811 **Fig. 4.** Comparison of incidence-based beta diversity metrics from Fynbos sites in this
 812 study and from sites across Europe from Petersen (2011). The colour of each line
 813 represents combined turnover and nestedness, measured as Sørensen pair-wise
 814 dissimilarity. The width of each coloured line represents spatial turnover (β_{sim}),
 815 measured as Simpson pair-wise dissimilarity, while the width of each interior white
 816 line represents nestedness-resultant dissimilarity (β_{sne}), measured as the nestedness-
 817 fraction of Sørensen pair-wise dissimilarity. The relative proportions of coloured line
 818 and white line thickness are, therefore, indicative of turnover and nestedness,
 819 respectively, contributions to overall beta-diversity (actual values are shown in grey
 820 lettering with β_{sim} being the upper value). Distances between sites in each sub-figure
 821 are to scale.

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835 **Supporting Information**

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837 **Table S1.1:** Complete assemblage results from litter-traps deployed across the
838 Western-Cape. See Table 1 for site location details.

839

840 **Table S2.1:** Studies synthesised to identify the global environmental correlates of
841 Collembola species richness, with associated NDVI and WorldClim2 (Fick &
842 Hijmans 2017) environmental data.

843

844 **Table S3.1:** Results of generalised linear model (GLM) with Collembola species
845 richness from all non-Fynbos sites (Table S2.1) as a response to annual precipitation,
846 temperature of the warmest and coldest month, and their interaction, and mean NDVI.

847

848 **Table S4.1:** Asymmetric distance matrix for pairwise comparisons between Fynbos
849 sites described in this study. Values shown are Sørensen dissimilarity (grey), an
850 incidence-based metric of beta diversity, and geographic distance (white).

851

852 **Table S5.1:** Asymmetric distance matrix for pairwise comparisons between European
853 non-Fynbos sites described in Petersen (2011). Values shown are Sørensen
854 dissimilarity (grey), an incidence-based metric of beta diversity, and geographic
855 distance (white).

856

857 **Table S6.1:** Abundance of species in different litter types in Jonkershoek Nature
858 Reserve.

859

860

861 **Figure S7.1-S7.6:** Randomised Collembola species accumulation curves for the sites
862 described in this study.

863

864 **Figure S8.1:** Diversity profile using Hill numbers – steep declines suggest abundance
865 unevenness of samples, i.e. assemblages dominated by a few species.

866

867

High spatial turnover in springtails of the Cape Floristic Region

Charlene Janion-Scheepers | Jan Bengtsson | Grant A. Duffy | Louis Deharveng | Hans Petter Leinaas | Steven L. Chown

Supporting Information

Appendices S1-S7

Appendix S1

Results from sampling litter traps across six sites in the Western Cape.

Table S1.1: Complete springtail assemblage results from litter-traps deployed across the Western-Cape. See Table 1 in main text for site location details.

	PEN	MTR	WIL	KOG	JNK	BON
Order Poduromorpha						
Family Neanuridae						
<i>Neanura muscorum</i>	0	3	0	12	0	0
cf. <i>Aethiopella</i> sp. 1	0	0	1	0	0	0
cf. <i>Aethiopella</i> sp. 2	7	0	0	0	2	2
cf. <i>Tasmanura</i> sp.	0	0	0	0	2	0
<i>Ectonura</i> sp. 1	0	0	0	0	8	0
<i>Ectonura</i> sp. 2	0	50	0	0	0	0
<i>Friesea</i> sp.	0	0	0	0	0	122
<i>Micranurida</i> sp. 1	0	0	0	9	0	0
<i>Micranurida</i> sp. 2	0	3	0	0	0	0
<i>Micranurida</i> sp. 3	19	0	0	0	0	0
Neanuridae sp.	1	0	0	0	0	0
<i>Pseudachorutes</i> sp. 1	0	0	0	65	0	0
<i>Pseudachorutes</i> sp. 2	0	19	0	0	0	0
<i>Pseudachorutes</i> sp. 3	12	0	0	0	0	0
<i>Pseudachorutes</i> sp. 4	0	0	41	0	0	0
<i>Pseudachorutes</i> sp. 5	0	0	0	0	10	1
Family Tullbergiidae						
<i>Tullbergia</i> sp. 1	0	0	0	0	0	2
<i>Tullbergia</i> sp. 2	0	0	0	0	2	0
<i>Tullbergia</i> sp. 3	0	0	0	19	0	0
<i>Tullbergia</i> sp. 4	0	5	0	0	0	0
<i>Tullbergia</i> sp. 5	7	0	0	0	0	0

<i>Tullbergia</i> sp. 6	0	0	89	0	0	0
<i>Mesaphorura</i> sp. 1	0	0	63	20	25	0
<i>Mesaphorura</i> sp. 2	0	3	0	0	0	0
<i>Mesaphorura</i> sp. 3	2	0	0	0	0	0
Family Odontellidae						
cf. <i>Afrodontella</i> sp.	2	0	0	0	0	0
Odontellidae sp.	0	0	0	1	0	0
Family Brachystomellidae						
<i>Brachystomella georgensis</i>	0	0	0	0	170	0
<i>Brachystomella platensis</i>	0	51	0	0	0	0
<i>Brachystomella</i> sp. 1	0	0	98	0	0	0
<i>Brachystomella</i> sp. 2	0	0	0	243	0	0
<i>Brachystomella</i> sp. 3	158	0	0	0	0	0
Family Hypogastruridae						
<i>Austrogastrura</i> sp. 1	0	55	0	0	0	0
<i>Austrogastrura</i> sp. 2	2	0	0	0	0	0
<i>Austrogastura</i> sp. 3	0	0	845	0	0	0
<i>Ceratophysella denticulata</i>	3242	1	0	691	0	0
Hypogastruridae sp.	0	2	0	0	0	0
<i>Triacanthella</i> sp. 1	0	0	0	0	248	0
<i>Triacanthella</i> sp. 2	0	0	0	70	0	0
<i>Triacanthella</i> sp. 3	0	260	0	0	0	0
<i>Triacanthella</i> sp. 4	4	0	0	0	0	0
<i>Willemia</i> sp. 1	0	0	0	1	0	0
<i>Willemia</i> sp. 2	0	0	5	0	0	0
<i>Xenylla</i> sp.	0	178	1	38	0	0
Order Entomobryomorpha						
Family Isotomidae						
<i>Mucrosomia</i> cf. <i>caeca</i>	769	59	3	24	107	0
<i>Folsomides parvulus</i>	0	0	81	1	0	0
<i>Hemisotoma</i> sp.	0	0	9	0	0	0
<i>Isotoma</i> sp. 1	0	0	0	0	0	1

<i>Isotoma</i> sp. 2	0	15	0	0	0	0
<i>Isotoma</i> sp. 3	4	0	0	0	0	0
<i>Isotoma</i> sp. 4	0	0	0	355	0	0
<i>Parisotoma</i> sp. 1	0	0	0	0	0	7
<i>Parisotoma</i> sp. 2	0	0	0	582	0	0
<i>Parisotoma</i> sp. 3	0	1052	0	0	0	0
<i>Parisotoma</i> sp. 4	1735	0	0	0	0	0
<i>Parisotoma</i> sp. 5	0	0	0	0	2014	0
<i>Parisotoma</i> sp. 6	0	0	474	0	0	0
<i>Proisotoma</i> sp. 1	0	8	0	0	0	0
<i>Proisotoma</i> sp. 2	0	0	2	0	0	0
<i>Isotomurus</i> sp.	2	0	0	3	17	1
<i>Cryptopygus</i> sp. 1	0	0	0	0	76	0
<i>Cryptopygus</i> sp. 2	2	0	0	0	0	0
<i>Cryptopygus</i> sp. 3	0	3	0	2	0	0
<i>Cryptopygus</i> sp. 4	0	0	0	133	0	0
<i>Cryptopygus</i> sp. 5	0	0	0	0	0	29
<i>Cryptopygus</i> sp. 6	0	174	0	0	0	0
<i>Cryptopygus</i> sp. 7	0	0	0	29	0	0
Family Entomobryidae						
Entomobryidae sp.	0	0	5	0	0	0
<i>Lepidocyrtus</i> sp. 1	0	0	0	118	113	0
<i>Lepidocyrtus</i> sp. 2	0	168	0	0	0	0
<i>Lepidocyrtus</i> sp. 3	288	0	0	0	0	0
<i>Lepidocyrtus</i> sp. 4	0	0	654	0	0	0
<i>Pseudosinella</i> sp. 1	0	0	0	19	0	22
<i>Pseudosinella</i> sp. 2	0	2	0	0	0	0
<i>Pseudosinella</i> sp. 3	63	0	0	0	0	0
<i>Pseudosinella</i> sp. 4	0	0	9	0	0	0
<i>Seira</i> sp. 1	0	0	0	1	0	0
<i>Seira</i> sp. 2	0	1	0	0	0	0
<i>Seira</i> sp. 3	0	0	2	0	0	0

<i>Seira</i> sp. 4	0	0	0	7	0	0
<i>Seira</i> sp. 5	0	2	0	0	0	0
<i>Seira</i> sp. 6	0	0	0	0	0	43
<i>Seira</i> sp. 7	0	0	50	0	0	0
<i>Seira</i> sp. 8	0	0	0	0	0	41
<i>Seira</i> sp. 9	0	0	0	11	18	0
<i>Seira</i> sp. 10	3	0	0	0	0	0
<i>Seira</i> sp. 11	0	0	0	21	0	0
<i>Seira</i> sp. 12	12	0	0	0	0	0
<i>Seira</i> sp. 13	21	28	0	31	17	0
<i>Seira</i> sp. 14	0	0	16	0	0	0
<i>Seira</i> sp. 15	0	13	0	0	0	0
<i>Seira</i> sp. 16	0	0	24	0	0	0
<i>Seira</i> sp. 17	0	0	0	0	3	0
Family Cyphoderidae						
Cyphoderidae sp. 1	8	0	0	0	0	0
Cyphoderidae sp. 2	0	0	1	0	0	0
Order Neelipleona						
Family Neelidae						
<i>Megalothorax</i> cf. <i>minimus</i>	171	0	0	3	0	0
Order Symphypleona						
Family Bourletiellidae						
Bourletiellidae sp. 1	0	0	0	0	0	1
Bourletiellidae sp. 2	0	0	0	0	2	0
Family Dicyrtomidae						
Dicyrtomidae sp. 1	0	0	0	6	0	0
Dicyrtomidae sp. 2	0	1	0	0	0	0
Family Katiannidae						
<i>Sminthurinus</i> sp. 1	0	0	43	0	0	0
<i>Sminthurinus</i> sp. 2	0	0	0	0	9	0
<i>Sminthurinus</i> sp. 3	0	0	0	0	81	0
<i>Sminthurinus</i> sp. 4	0	0	2	0	0	0

<i>Sminthurinus</i> sp. 5	0	0	32	0	0	0
<i>Sminthurinus</i> sp. 6	0	5	0	0	0	0
<i>Sminthurinus</i> sp. 7	0	0	0	37	0	0
<i>Sminthurinus</i> sp. 8	41	120	0	0	0	0
<i>Sminthurinus</i> sp. 9	0	0	0	0	0	6
<i>Sminthurinus</i> sp. 10	0	0	0	0	0	17
Family Sminthuridae						
Sminthuridae sp. 1	0	0	0	1	0	0
Sminthuridae sp. 2	1	0	0	0	0	0
Family Sminthurididae						
<i>Sphaeridia</i> sp. 1	0	0	0	0	24	0
<i>Sphaeridia</i> sp. 2	155	0	22	28	0	0

Appendix 2

Summaries of studies

Table S2.1 Studies synthesised to identify the global environmental correlates of Collembola species richness, with associated NDVI and WorldClim (Fick & Hijmans 2017) environmental data.

Literature	longitude	latitude	SR	n sample	method	total Collembola	metric	fynbos	WorldClim bio12	Max LST	Min LST	Mean NDVI
Cassagne et al. 2006	1.07	42.86	51	60	gradient extraction: litter + soil	7187	n individuals	0	1158	26.37	-7.07	0.661
Chauvat et al. 2011	1.3	49.73	40	32	gradient extraction: soil	7231	n individuals	0	734	25.69	-5.59	0.697
Convey et al. 1999	-36.67	-54.2	20	22	gradient extraction: litter + soil	not stated	NA	0	1600	11.81	-15.39	0.101
Culik et al. 2002	-41.05	-20.38	38	88	gradient extraction: soil	9650	n individuals	0	1352	27.83	9.93	0.734
Driessen & Greenslade 2004	146.2	-42.85	40	604	sweep net + pitfall traps	28162	n individuals	0	2024	18.15	-3.11	0.744
Driessen 2006	145.97	-41.8	51	576	sweep net + pitfall traps	not stated	NA	0	2225	19.41	-3.17	0.719
Gabriel et al. 2001	37.74	-46.89	16	1008	gradient extraction: soil	300 - 60 733	individuals/m2	0	2664	17.27	-5.51	0.462

Greenslade & Driessen 1999	146.17	-43.47	18	63	sweep net	8282	n individuals	0	1589	22.37	0.11	0.663
Liu et al. 2012	18.43	-34.06	48	80	gradient extraction: litter suction sampling	21278	n individuals	1	873	33.81	5.55	0.562
Petersen 2011_GBR	-3.47	53.05	23	30	+ gradient extraction: soil suction sampling	12 533 - 20 249	individuals/m2	0	1189	21.31	-5.77	0.744
Petersen 2011_DNK	10.95	56.38	26	30	+ gradient extraction: soil suction sampling	16 913 - 23 372	individuals/m2	0	571	24.25	-12.45	0.583
Petersen 2011_NLD	5.92	52.4	33	30	+ gradient extraction: soil suction sampling	7 789 - 15 934	individuals/m2	0	794	31.21	-8.37	0.656
Petersen 2011_ESP	1.82	41.3	38	30	+ gradient extraction: soil suction sampling	8 905 - 22 810	individuals/m2	0	906	36.17	-9.29	0.71
Petersen 2011_ITA	8.15	40.6	40	30	+ gradient extraction: soil suction sampling	3 190 - 5962	individuals/m2	0	608	29.73	5.63	0.578
Petersen 2011_HUN	19.38	46.88	10	30	+ gradient extraction: soil suction sampling	4 898 - 12 173	individuals/m2	0	535	36.51	-14.93	0.508
Querner et al. 2010	16.95	48.07	41	30	gradient extraction: soil	2505	n individuals	0	640	37.41	-11.85	0.507

Rochefort et al. 2006	-71.22	46.82	21	150	gradient extraction: soil	101311	n individuals	0	1108	31.03	-20.51	0.256
Salmon et al. 2010	0.69	42.96	64	54	gradient extraction: pitfall + litter + soil	7506	n individuals	0	976	30.35	-5.31	0.699
Terauds et al. 2011	158.95	-54.5	15	72	gradient extraction: soil	3351 - 194 330	individuals/m2	0	942	10.35	-6.29	0.535
This study (BON)	20.47	-34.08	14	40	gradient extraction: litter bags	295	n individuals	1	557	38.29	4.99	0.457
This study (JNK)	18.96	-33.99	20	40	gradient extraction: litter bags	2948	n individuals	1	1032	33.01	3.53	0.567
This study (KOG)	18.97	-34.32	31	40	gradient extraction: litter bags	2581	n individuals	1	811	32.43	5.61	0.504
This study (MTR)	19.16	-33.9	27	40	gradient extraction: litter bags	2281	n individuals	1	949	31.07	3.85	0.53
This study (PEN)	18.39	-34.26	26	40	gradient extraction: litter bags	6731	n individuals	1	681	24.85	5.75	0.467
This study (WIL)	22.73	-33.99	25	40	gradient extraction: litter bags	2572	n individuals	1	737	28.07	4.41	0.683
Uvarov & Byzova 1995	16.09	77.14	32	912	gradient extraction: soil	not stated	NA	0	359	1.15	-28.73	-0.056
Zeppelini et al. 2009	-34.97	-6.51	24	30	malaise traps	12183	n individuals	0	1643	33.93	16.45	0.538

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Appendix S3

Results of generalised linear model (GLM)

Table S3.1 Results of generalised linear model (GLM) with Collembola species richness from all non-Fynbos sites (Table S3) as a response to annual precipitation, temperature of the warmest and coldest month, and their interaction, and mean NDVI.

	Estimate	Standard error	z value	p
(Intercept)	1.9379	0.7495	2.5856	0.0097 *
Annual precipitation	< 0.0000	0.0002	-0.0939	0.9252
Mean NDVI	1.6984	0.6312	2.6906	0.0071*
Temperature of the coldest month	-0.0663	0.0354	-1.8741	0.0609
Temperature of the warmest month	0.0219	0.0174	1.2575	0.2086
Interaction between temperatures	0.0021	0.0011	1.8541	0.0637

Null deviance: 29.615 on 19 degrees of freedom

Residual deviance: 20.565 on 14 degrees of freedom

AIC: 166.68

Appendix 4

Asymmetric distance matrix

Table S4.1 Asymmetric distance matrix for pairwise comparisons between Fynbos sites described in this study. Values shown are Sørensen dissimilarity (grey), an incidence-based metric of beta diversity, and geographic distance (white).

	PEN	MTR	WIL	KOG	JNK	BON
PEN		92.7185	481.4741	63.6445	68.4651	230.3502
MTR	0.8491		396.0181	49.2797	24.2795	145.9669
WIL	0.9216	0.9231		418.8200	418.4723	251.2622
KOG	0.7895	0.7931	0.8214		35.4213	168.2755
JNK	0.8261	0.9149	0.9111	0.7647		167.6352
BON	0.9000	1.0000	1.0000	0.9111	0.8235	

Appendix S5

Asymmetric distance matrix

Table S5.1 Asymmetric distance matrix for pairwise comparisons between European non-Fynbos sites described in Petersen (2011). Values shown are Sørensen dissimilarity (grey), an incidence-based metric of beta diversity, and geographic distance (white).

	DK	GB	NL	HU	ES	IT
DK		2616.0446	1382.2709	1605.2728	1992.1506	1415.8447
GB	0.5102		1636.4767	1040.0965	922.8750	1887.1008
NL	0.4576	0.5714		708.6487	1536.8121	1759.9269
HU	0.9444	1.0000	0.9070		842.7948	1326.8212
ES	0.7813	0.9016	0.7465	0.8750		979.4407
IT	0.8788	0.9048	0.8082	0.9200	0.6410	

Appendix S6

Table S6.1 Abundance of species in different litter types in Jonkershoek Nature Reserve, (experiment performed in 2008, before a fire hit the area; decomposition rates reported in Bengtsson et al. 2012, see also Janion-Scheepers et al 2016).

	<i>Galenia</i>	<i>Erica</i>	<i>Protea</i>	<i>Erica-Protea mixture</i>	<i>Restio</i>
Order Poduromorpha					
Family Neanuridae					
cf. <i>Aethiopella</i> sp.	0	0	1	2	0
cf. <i>Tasmanura</i> sp.	0	5	8	4	2
<i>Ectonura</i> sp.	4	1	25	4	1
cf. <i>Micranurida</i> sp.	1	1	4	0	7
<i>Pseudachorutes</i> sp.	2	11	15	8	10
Family Tullbergiidae					
<i>Mesaphorura</i> sp.	127	5	49	21	30
<i>Tullbergia</i> sp.	0	0	0	2	0
Family Brachystomellidae					
<i>Brachystomella</i> sp.	153	39	159	75	208
Family Hypogastruridae					
<i>Austrogastura</i> sp.	0	0	0	0	3
<i>Hypogastrura</i> sp.	0	2	0	0	1
<i>Triacanthella</i> sp.	212	19	15	91	5
<i>Xenylla</i> sp.	0	0	8	1	1
Order Entomobryomorpha					
Family Isotomidae					
<i>Cryptopygus</i> sp. 1	87	22	76	32	85
<i>Cryptopygus</i> sp. 2	0	0	1	0	0
<i>Folsomides parvulus</i>	2	0	0	1	0
<i>Isotoma</i> sp. 1	0	0	1	0	11

<i>Isotoma</i> sp. 2	15	0	4	1	0
<i>Isotomurus</i> sp.	4	6	6	3	9
<i>Mucrosomia</i> cf. <i>caeca</i>	59	24	136	53	44
<i>Parisotoma</i> sp.1	0	0	0	0	11
<i>Parisotoma</i> sp. 2	1031	223	823	1007	584
<i>Parisotoma</i> sp. 3	76	52	91	94	14
<i>Proisotoma</i> sp.	0	2	2	0	0
Family Entomobryidae					
<i>Lepidocyrtus</i> sp.	85	126	48	65	72
<i>Seira</i> sp. 1	16	7	8	3	14
<i>Seira</i> sp. 2	0	1	0	0	0
<i>Seira</i> sp. 3	0	1	2	4	8
<i>Seira</i> sp. 4	20	14	11	7	4
Order Symphypleona					
Family Katiannidae					
<i>Sminthurinus</i> sp. 1	17	15	29	12	19
<i>Sminthurinus</i> sp. 2	45	85	19	48	50
<i>Sminthurinus</i> sp. 3	3	2	3	2	18
<i>Sminthurinus</i> sp. 4	0	3	12	4	0
Family Arrhopalitidae					
<i>Arrhopalites</i> sp.	0	0	1	0	0
Family Sminthurididae					
<i>Sphaeridia</i> sp.	25	0	14	1	4

Appendix S7

Rarefaction curves and diversity profile of all sites investigated

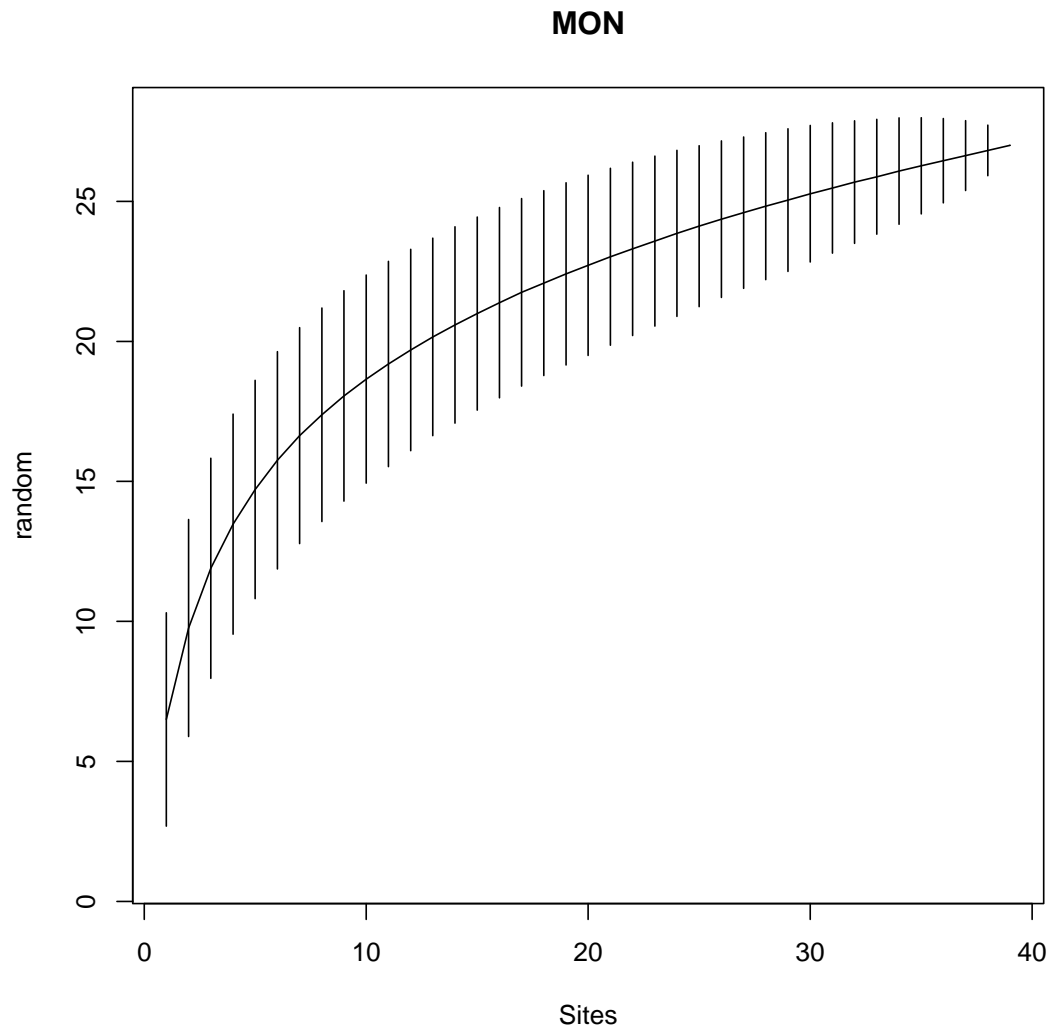


Fig. S7. 1 Species accumulation curve for Mont Rochelle.

KLG

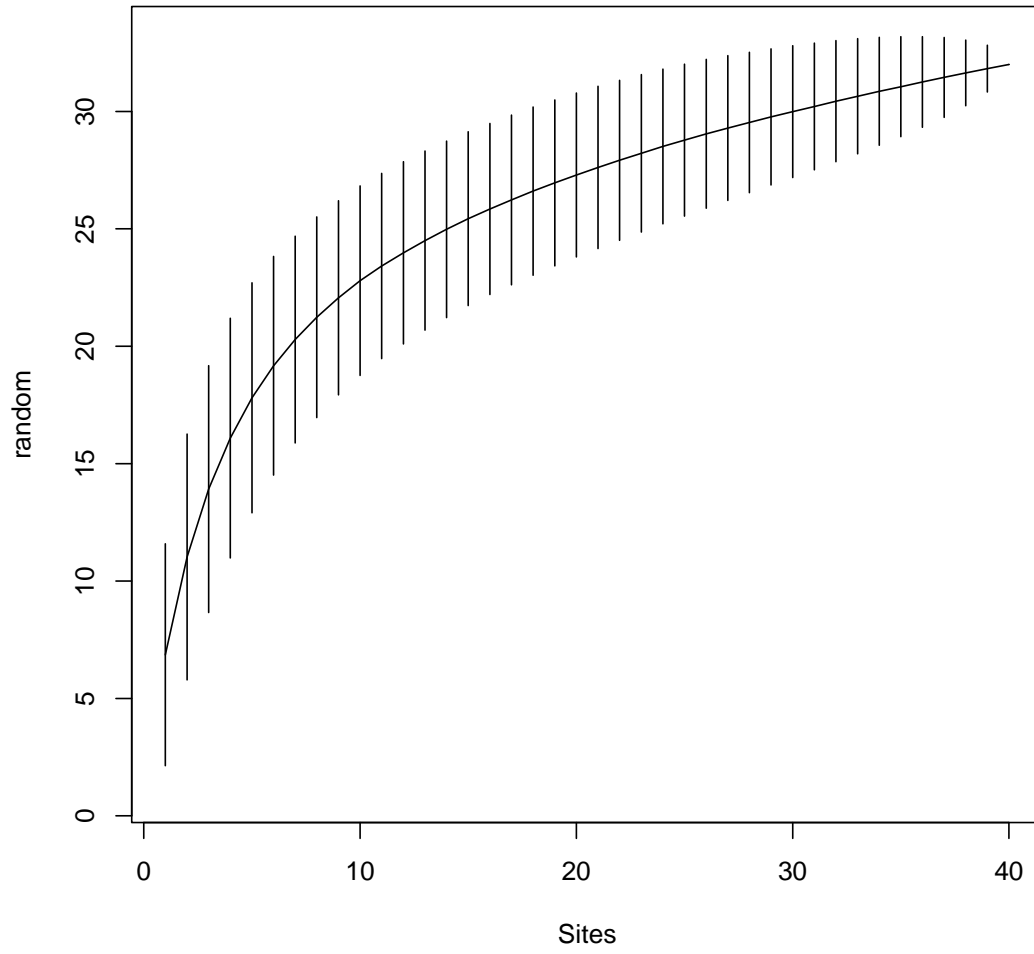


Fig. S7.2 Species accumulation curve for Kogelberg.

BON

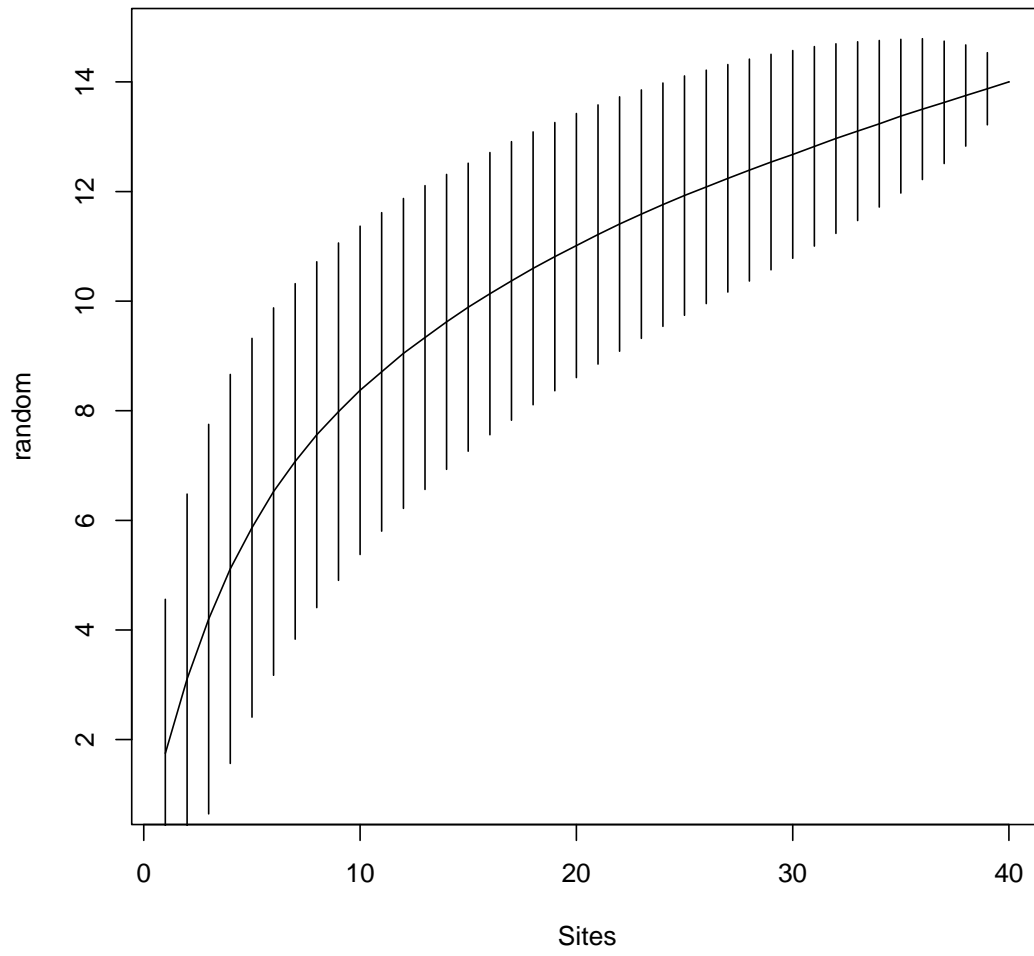


Fig. S7.3 Species accumulation curve for Bontebok.

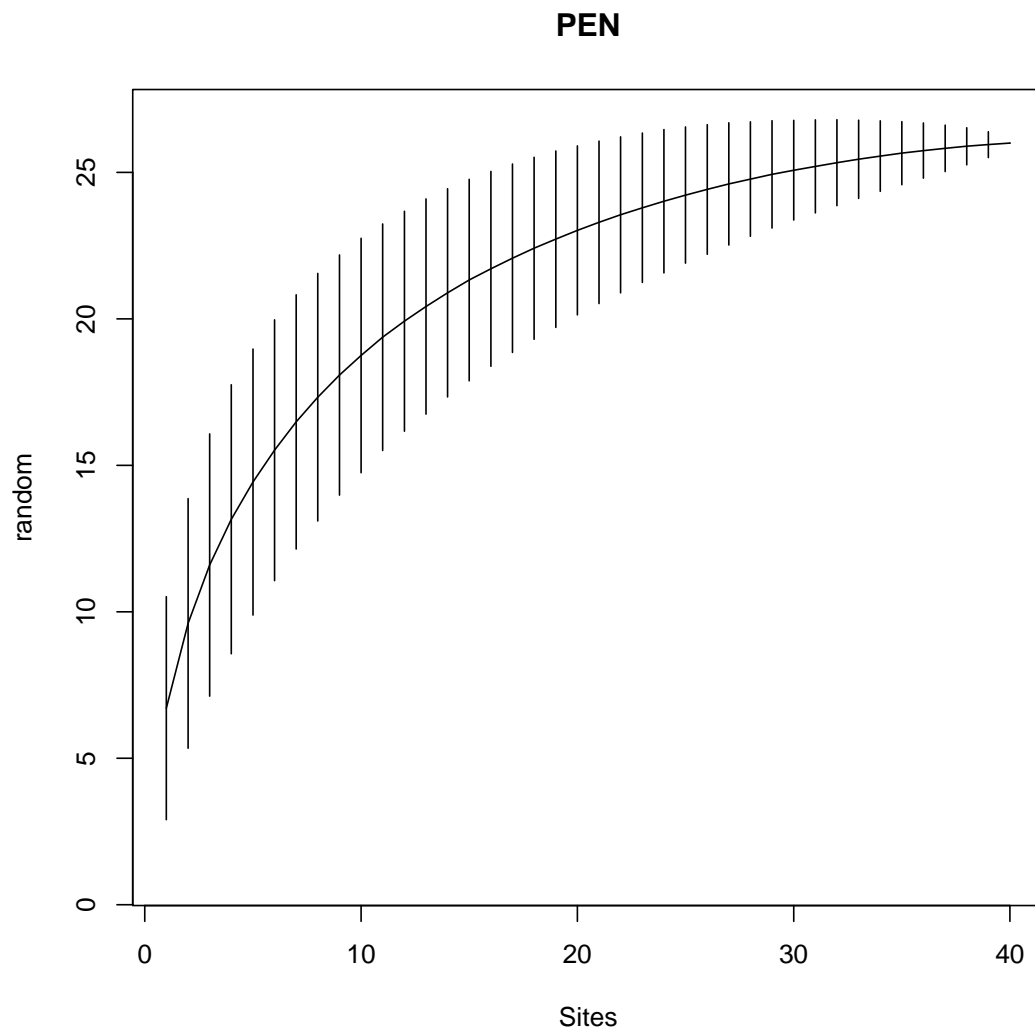


Fig. S7.4 Species accumulation curve for Peninsula.

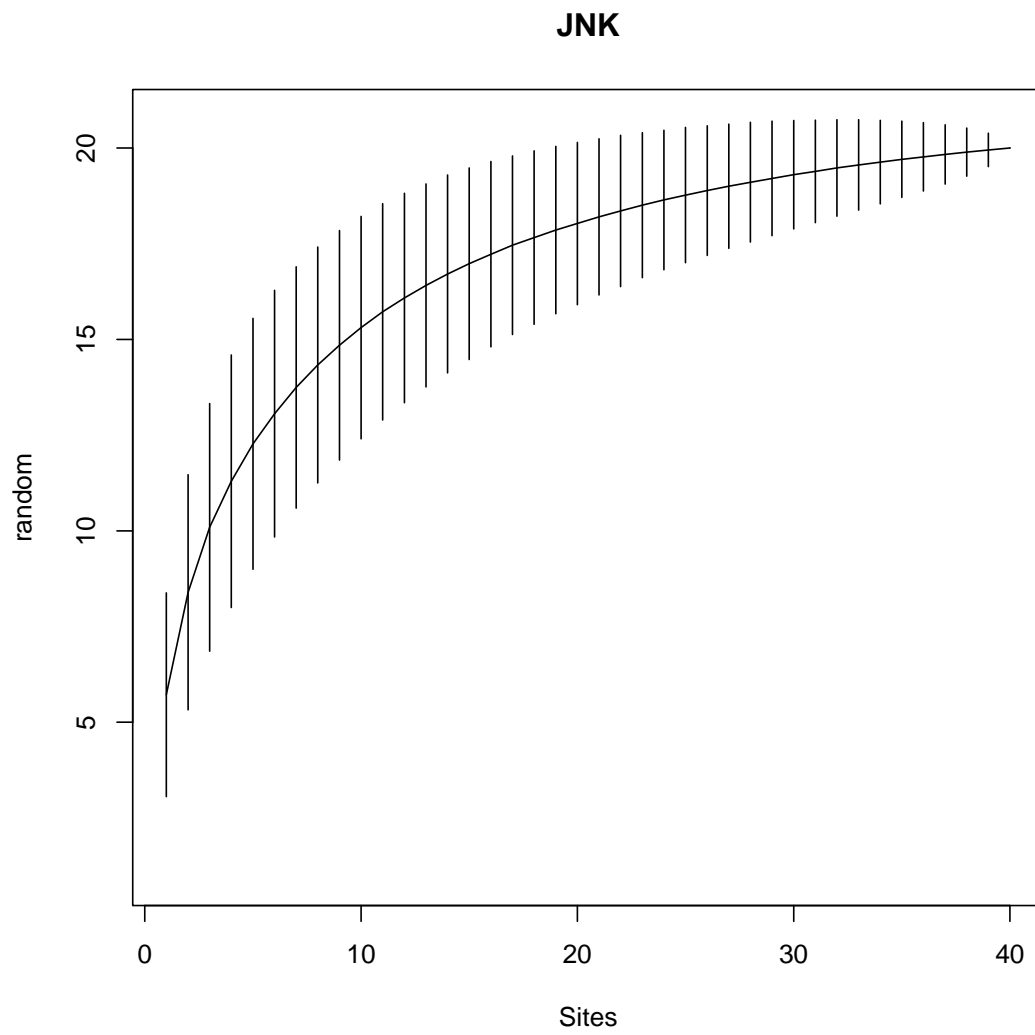


Fig. S7.5 Species accumulation curve for Jonkershoek.

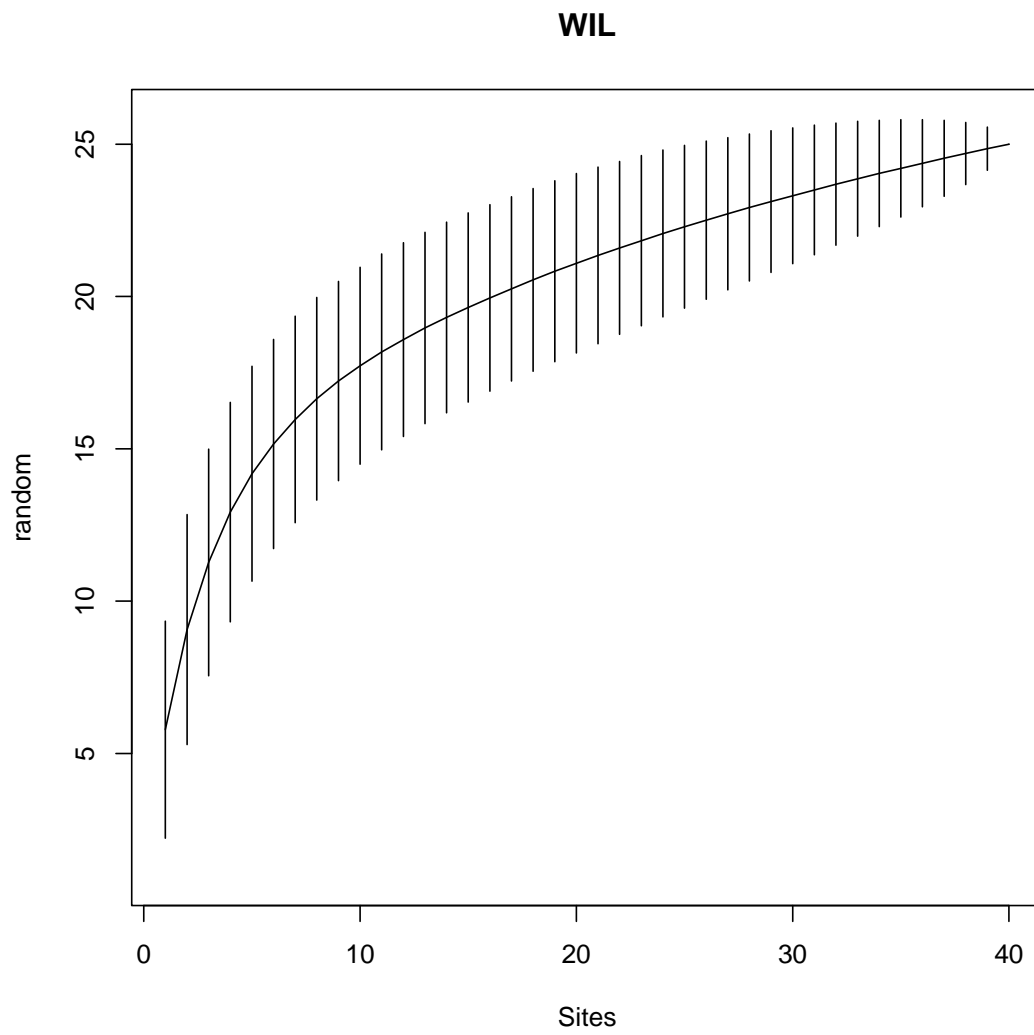


Fig. S7.6 Species accumulation curve for Wilderness.

Appendix S8

Diversity profile of all sites investigated

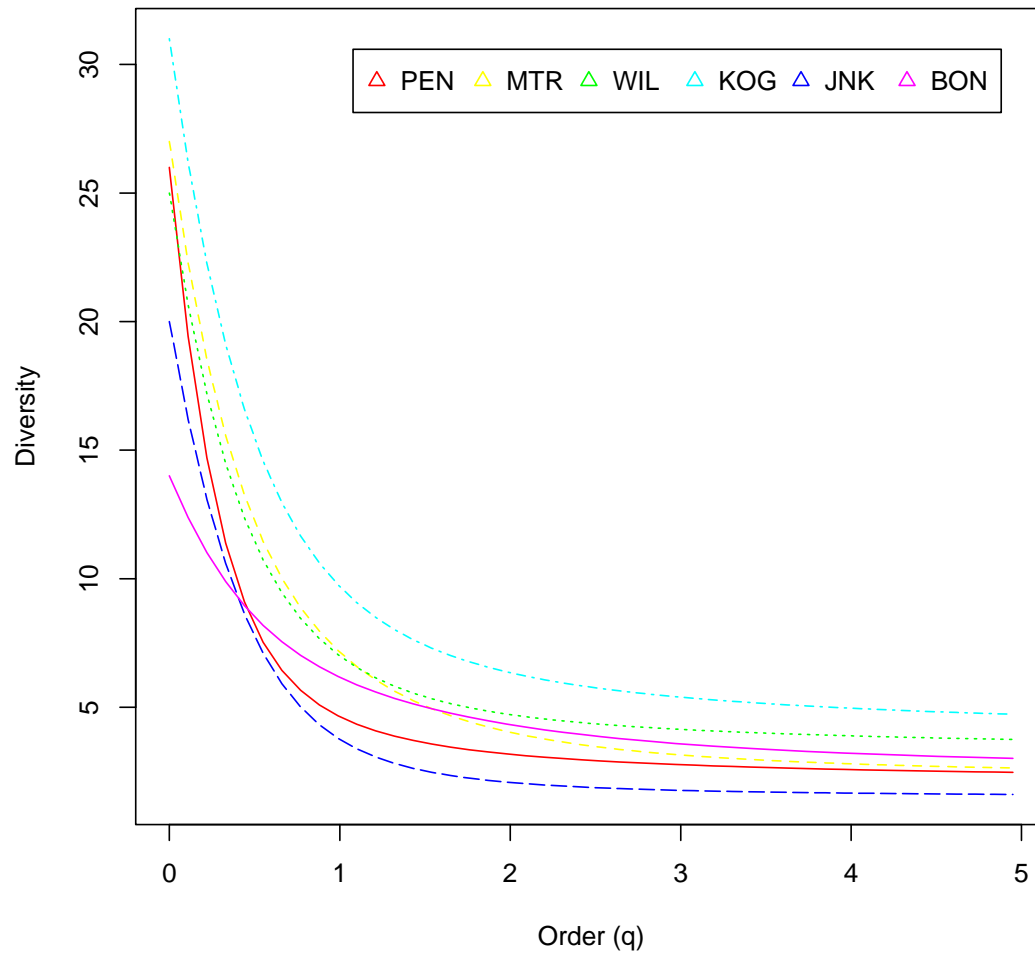


Figure S8.1 Diversity profile using Hill numbers – steep declines show abundances unevenness of samples, i.e. assemblages dominated by a few species.