RESEARCH PAPER

High spatial turnover in springtails of the Cape Floristic Region

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Abstract

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

Location: The south-western Cape, South Africa.

Taxon: Springtails (Hexapoda: Collembola).

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

Results: A total of 114 morphospecies from 14 families was collected. Species richness of Fynbos sites ranged from 14 to 31 species, which was not significantly different to that previously reported for non-Fynbos locations and generally within expectations given the temperature, rainfall and productive energy of each site. Beta diversity was high across all pairwise comparisons of Fynbos sites and dominated by species replacement rather than assemblage nestedness. Relative to the distance between sites, Fynbos assemblages, with a median inter-site distance of 140 km, showed beta diversity substantially higher than in European assemblages, which had a median inter-site distance of 1,270 km.

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

KEYWORDS

arthropods, belowground fauna, beta diversity, nestedness, soil diversity, species energy, turnover

1 | INTRODUCTION

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

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

For arthropods, and notably the insects, the Fynbos was long thought to be low in diversity generally (Giliomee, 2003; Johnson, 1992), though often without considering the distinction between local and regional richness. Yet, in some endophagous Fynbos insects, diversity is high (Wright & Samways, 2000). Indeed, species richness on a par with other areas seems to be the general pattern for phytophagous groups, with regional richness no lower than in other southern Africa biomes (Procheş & Cowling, 2006). Despite a focus on relationships between local richness and turnover to elucidate potential underlying mechanisms for plants, only two investigations of arthropods in the CFR have dealt explicitly with turn-over, concluding that monkey beetles (Scarabaeidae: Hopliini) and leafhoppers (Cephalelini: Cicadellidae) show high turnover among sites (Colville, Picker, & Cowling, 2002; Kemp & Ellis, 2017; Kemp, Linder, & Ellis, 2017). This turnover is linked to variation in plant diversity and independent of other environmental drivers in the case of leafhoppers. For non-phytophagous species, a single study has suggested that for epigaeic ants, local richness is in keeping with what might be expected from available energy (Braschler, Gaston, & Chown, 2012).

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

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

Here, we investigate local richness, turnover and regional richness of the litter-dwelling springtails (Collembola) of the Fynbos Biome. This group is typically not directly associated with vascular plants and mainly subsists on diets linked to soil fungi and microorganisms (Hopkin, 1997). Indeed, Collembola are not at all known for narrow host-plant specificity. Neither do they show direct, consistent relationships with plant richness, despite litter quality effects on their diversity (González-Macé & Scheu, 2018; Leinaas, Bengtsson, Janion, & Chown, 2015; Milcu, Partsch, Langel, & Scheu, 2006; Raymond-Léonard, Gravel, Reich, & Handa, 2018; Sabais, Scheu, & Eisenhauer, 2011; Salamon, Schaefer, Alphei, Schmid, & Scheu, 2004; Salmon et al., 2014). However, edaphic and landscape-level factors nonetheless have a strong influence on its patterns of diversity (Ponge et al., 2003). Thus, springtails make a useful model to examine whether drivers of the unusually high turnover in the vascular plants of the Fynbos Floristic Radiation have also manifested in diversity patterns of arthropod groups with indirect relationships to plants, which contrast strongly with the tight relationships of host-specific insects.

2 | MATERIALS AND METHODS

2.1 | Sites and sampling

Six sites within relatively unmodified landscape were sampled between 2008 and 2011 in the Western Cape of South Africa, with the sites ranging from Cape Peninsula (34.26°S, 18.39°E) in the west to Wilderness (33.99°S, 22.73°E) in the east (Figure 1). The Collembola fauna of the region has recently been the subject of an intense systematic and ecological campaign (e.g. Janion, Bedos, Bengtsson, et al., 2011; Janion, Bedos & Deharveng, 2011; Janion, Deharveng, &
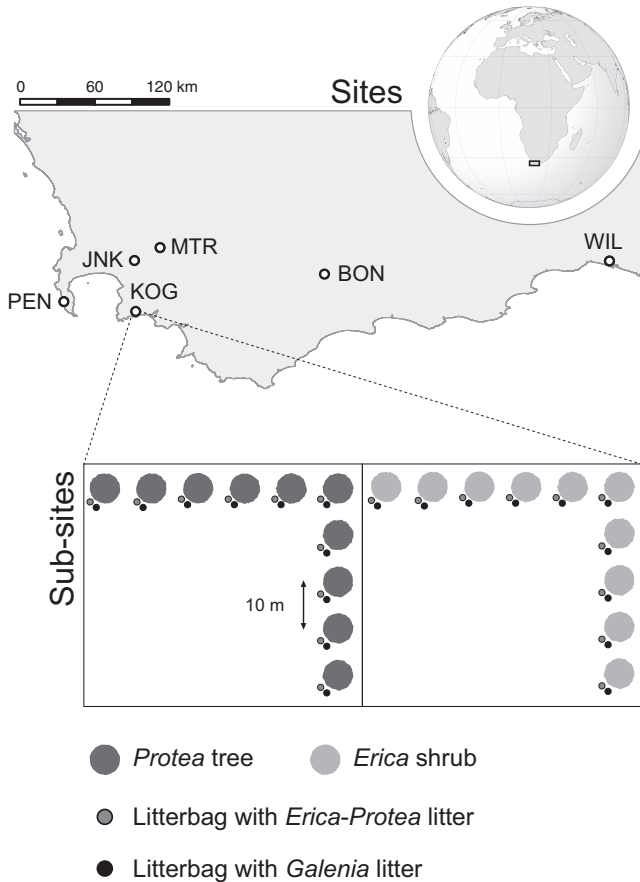
and also allow direct comparison to previous studies (see Bengtsson, Janion, Chown, & Leinaas, 2012; Janion-Scheepers et al., 2016). *Galenia africana* is an indicator of disturbance such as overgrazing and its nutrient content and decomposition rate is high relative to *Protea* and *Erica* species (Bengtsson et al., 2012). Although this species is not a common Fynbos species, it was included because of its attractiveness to springtails (Leinaas et al., 2015). All litterbags were embedded in the soil such that the top of the litterbag was at ground level, allowing unimpeded movement of litter-dwelling invertebrates. Litterbags were always deployed on a Southern bearing <40 cm from the base of a dominant plant. They were left undisturbed and subsequently collected in either September (2008), or in July/August (2009–2011). This timing ensured that litterbags were in the field during the wet season (July/August), when Collembola are particularly abundant (Liu et al., 2012). On collection, the litterbags were wrapped in aluminium foil to prevent any animals from escaping and immediately placed in individual plastic bags and stored upright in a cool, thermally insulated container and returned to the laboratory within 5 hr of collection.

All invertebrates were extracted into 100% propylene glycol using a custom-built high-gradient extractor (Central Mechanical Services, Stellenbosch University), which used a heat source and temperature-controlled water bath (Grant Instruments R2, Cambridge, UK) to generate a thermal gradient along which invertebrates migrated (Block, 1966; Leinaas, 1978; Macfadyen, 1953). The extraction process took approximately 4 days for each litterbag. After extraction, the animals were transferred to 99.9% ethanol for sorting and identification.

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

2.2 | Quantification of α-diversity and assemblage evenness

To determine sampling efficacy at each site, randomised (10,000 permutations) sample-based species accumulation curves were plotted using the 'vegan' (Dixon, 2003) package in R statistical software (R Core Team, 2017). Individual litterbags were used as sample units

FIGURE 1 Experimental design used at each site in this study. BON, Bontebok; JNK, Jonkershoek; KOG, Kogelberg; MTR, Mont Rochelle; PEN, Peninsula; WIL, Wilderness

Weiner, 2013; Janion, D'Haese, & Deharveng, 2012; Janion-Scheepers, Bengtsson, Leinaas, Deharveng, & Chown, 2016; Janion-Scheepers, Deharveng, Bedos, & Chown, 2015; Leinaas et al., 2015; Liu, Janion, & Chown, 2012; Potapov, Janion, & Deharveng, 2011; Weiner, Janion-Scheepers, & Deharveng, 2017). In the present study, Collembola were sampled in a standardized way using litterbags constructed from cylindrical plastic containers (height = 4 cm, Ø = 7.5 cm) with a 0.5 mm aperture steel mesh bottom and 1.6 mm aperture mesh lid, filled with approximately 150 cm^3 of air-dried uncondensed litter (Leinaas et al., 2015 and references therein). Litter was prepared by harvesting plant material of the chosen plant species, drying this material at 40°C for at least 24 hr and cutting it into approximately 1 cm long pieces. The filled litterbags were stored dry at room temperature before being deployed in the field. At each of the six sites, two sub-sites, at least 200 m apart, were identified where the dominant flora comprised either Ericoid or Proteoid plants. At each of these sub-sites, 10 pairs of litterbags were deployed at the end of the austral summer (March/April). Each pair comprised one litterbag filled with *Galenia africana* litter and one litterbag filled with a 1:1 mixture of *Erica* and *Protea* litter (see details in Supplementary Material) placed under the dominant plant (Ericoid or Proteoid) at approximately 10 m intervals in an L-shaped configuration to cover a wide area of each of the Proteoid and Ericoid sites (Figure 1),

(see Janion-Scheepers et al., 2016). Plots of species accumulation curves were qualitatively assessed to determine if they were approaching an asymptote, an indication that most species present at a site have been observed.

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

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

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

Hill numbers give more weight to common species with increasing order and can be calculated for orders on a continuous scale (i.e. using non-integer values for q), thus their decline with increasing order can be used as an indicator of assemblage evenness. Diversity profiles, calculating ^qD for continuous orders between 0 and 5, were, therefore, also generated to assess the evenness of the Collembola assemblage at each site so that the roles of common and rare species could be considered in between-site comparisons.

2.3 | Comparisons of Fynbos richness with sites elsewhere

Variation in local species richness is typically a function of area and energy (Storch, Evans, & Gaston, 2005; Ulrich & Fiera, 2009; Wylie & Currie, 1993). To determine if the local richness estimates for the assemblages sampled here significantly differ from those globally or are in keeping with what might be expected from energy availability (e.g. Braschler et al., 2012), information on local springtail richness was compiled from the published literature. Studies documenting the Collembola species richness of sites across the globe were collated by the lead author (CJS). The studies included were undertaken predominantly in natural systems, and, based on the conclusions of the authors of these studies, with the assumption that these studies had sampled species richness (i.e. alpha diversity) in a comprehensive manner. Owing to the range of collection methods used to sample Collembola, a quantitative comparison of sampling effort and

completeness was not possible. Therefore, only studies where multiple samples were taken (minimum = 22 samples—Convey, Greenslade, Arnold, & Block, 1999), or a large number of individuals collected (minimum = 2,505—Querner, Bruckner, Weigand, & Prötsch, 2010) were included. We assumed, therefore, that species richness estimates were unlikely to be substantially inaccurate and that any noise introduced by this approach was also unlikely to be biased in any way.

Species richness values of sites from this study were first directly compared to species richness values from this compiled dataset through means of a Mann–Whitney U-test. Then, using data from non-Fynbos sites, as the data were overdispersed, a negative binomial generalized linear model (GLM) was used (Zuur et al., 2009) to model Collembola species richness of sites as a function of four environmental variables describing upper and lower temperature, precipitation and productive energy. These variables are all known to affect arthropod diversity variation in general and springtails in particular (Ballesteros-Meija, Kitching, Jetz, Beck, 2017; Braschler et al., 2012; Overgaard, Kearney, Hoffmann, 2014; Ulrich & Fiera, 2009). Temperature metrics were calculated as the mean day-time temperature of the warmest month and mean night-time temperature of the coldest month, respectively, across a 14-year recent time-series (January 2001–December 2015) from monthly remote-sensed MODIS/Terra Land Surface Temperature data (MOD11C3; 0.05° resolution; see also Janion-Scheepers et al., 2018). As a proxy of productive energy, mean Normalized Difference Vegetation Index (NDVI; MODIS/Terra MOD13C2; 0.05° resolution) was calculated for the same period. Annual precipitation was extracted from the WorldClim2 dataset (Fick & Hijmans, 2017). The variance inflation factor was calculated for all variables used to ensure that collinearity of variables would not increase the chance of Type I error in the GLM.

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

2.4 | Beta diversity

Several approaches can be used to assess beta diversity (Baselga & Leprieur, 2015; Koleff, Gaston, Lennon, 2003). The equal sampling effort applied to all sites meant that we were able to incorporate

species abundance into our beta-diversity analyses. Partitioned Bray–Curtis dissimilarity (Baselga, 2013) was, therefore, calculated between pairs of sites to quantify the relative contributions of variation in abundance and abundance gradients to patterns of beta-diversity between all pairwise combinations of sites.

To compare patterns of diversity of the Collembola assemblages described here with those of a non-Fynbos region, the published results of Petersen (2011) were used. Petersen described the species-density of six well-sampled Collembola assemblages across Europe. Due to methodological differences between this study and that of Petersen the abundance-dependent metrics of diversity are not comparable between studies. As a result, higher order Hill numbers and Partitioned Bray–Curtis dissimilarity were not calculated. Thus, incidence-based beta-diversity metrics (Baselga, 2010) were instead calculated for the Fynbos Collembola assemblages from this study and for Collembola incidence data reported by Petersen (2011). Beta-diversity analyses were performed using the 'betapart' package (Baselga & Orme, 2012) in R statistical software (R Core Team, 2017).

3 | RESULTS

A total of 17,408 Collembola comprising 114 morphospecies from 14 families was collected from the six sampled sites (Table 1; Table S1.1 in Appendix S1). Kogelberg had the highest species richness (31 species) and Bontebok the lowest (14 species). Bontebok also had the lowest Collembola abundance (295 individuals), in contrast to

Peninsula, which had the highest abundance of all sites (6,731 individuals). Although species accumulation curves did not reach an asymptote for any sites (Figures S7.1–S7.6 in Appendix 7), sampling effort was equal across all sites, enabling among-site comparisons to be made.

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

Collembola species richness of the South African sites described in this study was not significantly different to Collembola species richness of sites globally (Figure 2, Table 1; Table S2.1 in Appendix S2; MWU; $U = 40$, $Z = -1.2188$, $p = .2355$, $r = -0.0469$), acknowledging substantial variation in the compiled data. The fitted GLM explained 30.6% of species richness deviance (Cox-Snell pseudo-R^2 = 0.36) observed across the assemblages compiled from the literature, with productive energy (NDVI) identified as a significant predictor variable (Table S3.1 in Appendix S3). Observed Fynbos Collembola species richness of four sites (PEN, MTR, WIL, KOG) was within 95% confidence intervals predicted using this model. Observed species richness of the two remaining sites (JNK, BON) was below the lower 95% confidence interval (Table 1).

TABLE 1 Collembola assemblage sampling sites used in this study

	Peninsula (PEN)	Jonkershoek (JNK)	Kogelberg (KOG)	Mont Rochelle (MTR)	Bontebok (BON)	Wilderness (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	6,731	2,948	2,581	2,281	295	2,572
^{1}D	4.63	3.75	9.69	7.15	6.17	7.00
^{2}D	3.17	2.08	6.34	4.03	4.32	4.71
Environmental data						
Precipitation (mm)	681	1,032	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

Note: Diversity metrics were calculated for Collembola from collected material. Annual precipitation, upper and lower land surface temperature, and Normalized Difference Vegetation Index (NDVI) of each site were used to predict Collembola species richness through the application of a generalized linear model (GLM) constructed from reported species richness of Collembola globally (Table S3.1).
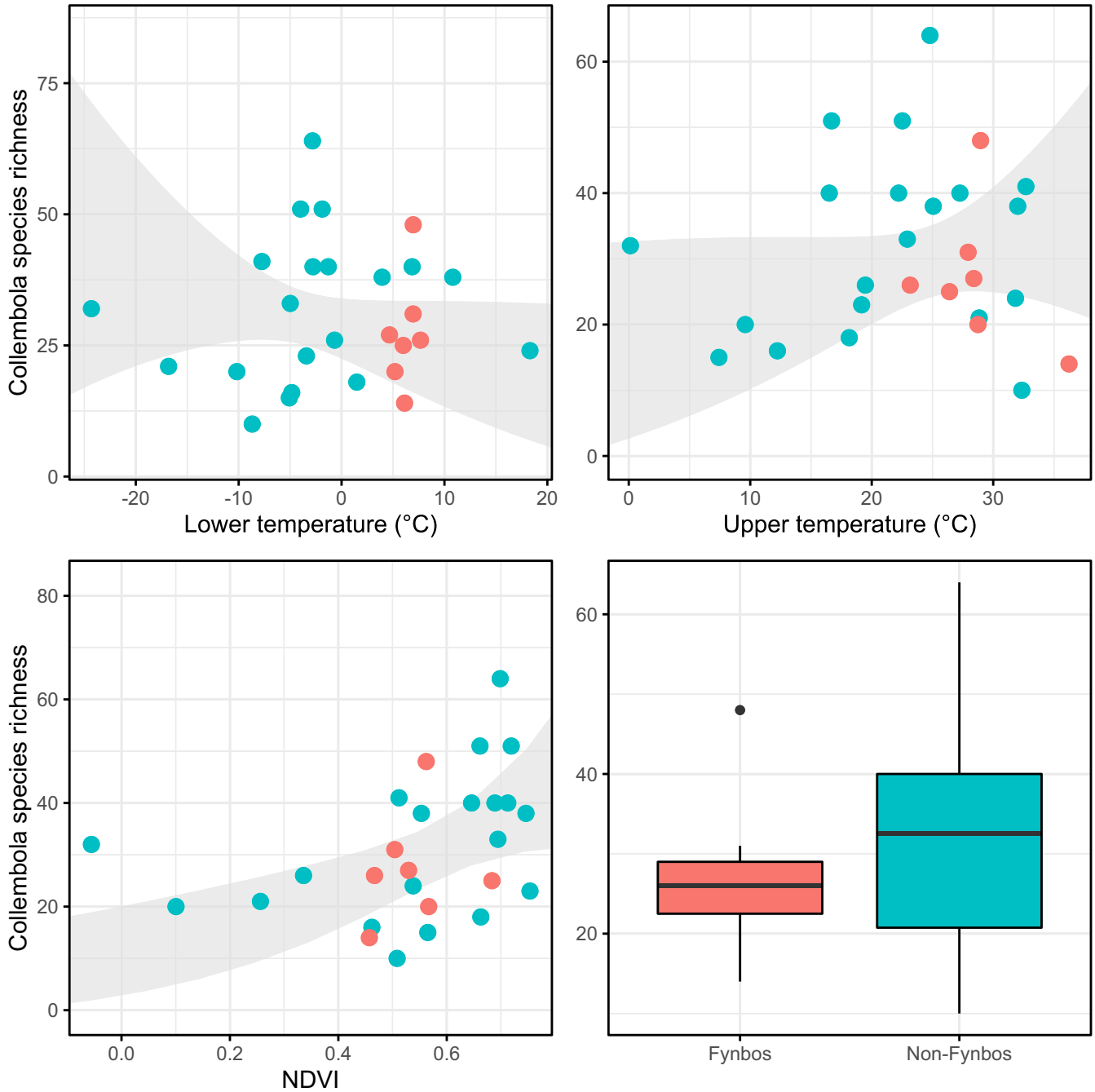
FIGURE 2 Species richness of Collembola against the three most influential environmental variables of our generalized linear model (GLM; Table S4.1 in Appendix S4). Grey ribbons represent the 95% confidence intervals for each variable assuming all other variables are held at their respective mean. Blue points represent species richness of sites from published literature (excluding Liu et al., 2012) that were used to build the GLM. Red points represent Fynbos sites (i.e. all sites from this study and Liu et al., 2012). The boxplot directly compares species richness of Fynbos and non-Fynbos sites

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

Partitioned incidence-based beta diversity metrics for Fynbos Collembola mirror abundance-based metrics, with species turnover contributing almost exclusively to the high beta diversity between pairs of sites (Figures 3 and 4, Table 3). Beta diversity, measured as total Sørensen Dissimilarity, was higher than that calculated from Collembola incidence data reported by Petersen (2011) for six sites across Europe (Figure 4; Table S5.1 in Appendix S5; Fynbos β_{sor}: $Q_1 = 0.823$, median = 0.900, $Q_3 = 0.918$; Europe β_{sor}: $Q_1 = 0.694$,

TABLE 2 Asymmetric distance matrix for abundance-based partitioning of pairwise Bray–Curtis dissimilarity (Baselga, 2013) between Collembola assemblages of the Western Cape

	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	

Note: The relatively large values for dissimilarity derived from balanced variation in abundance between sites (grey) indicates that species turnover is the main contributor of observed pairwise dissimilarity, while dissimilarity derived from unidirectional abundance gradients (white) contributes relatively little.
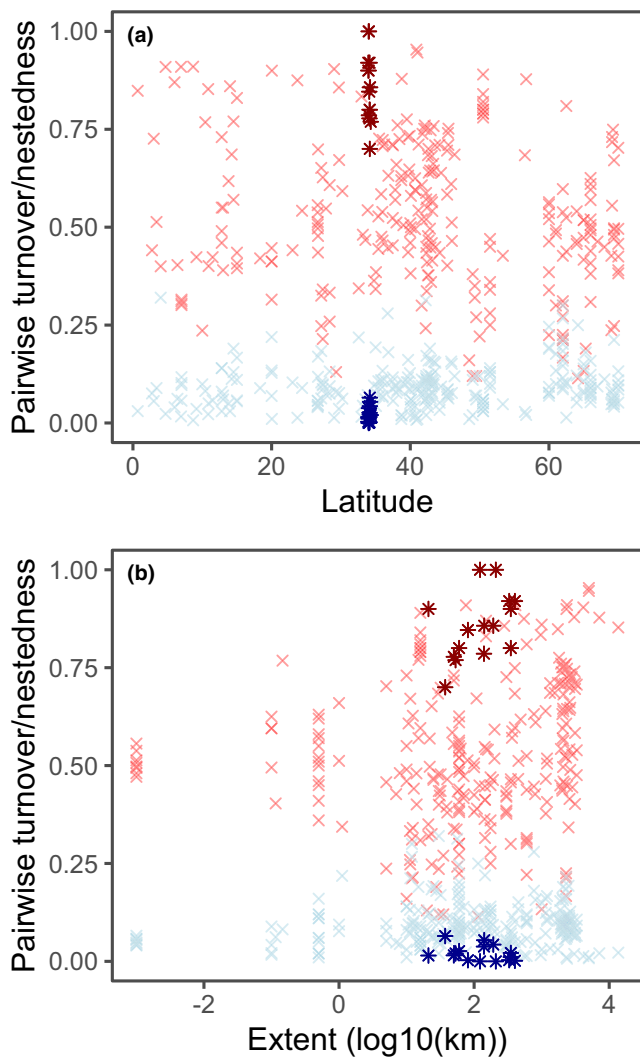

FIGURE 3 Pairwise turnover (red) and nestedness (blue) components of incidence-based beta diversity metrics across latitude (a; mean latitude of site pair) and spatial extent (b; log10 distance between site pair) for the range of taxa compiled by Soininen et al. (2018) (lighter crosses) and springtail data from this study (darker asterisks; Table 3)

median = 0.875, Q_3 = 0.906). This difference was not significant (Mann–Whitney *U*-test: U = 145, p = .184, r = 0.174). Fynbos sampling sites in this study were, however, almost an order of magnitude

closer together than those used by Petersen (Figure 4; Fynbos intra-site distance, Table S2.1 in Appendix S2: Q_1 = 57 km, median = 140 km, Q3 = 270 km; Europe intra-site distance, Table S5.1 in Appendix S5: Q1 = 1,033 km, median = 1,272 km, Q_3 = 1613 km). This difference was significant with a large effect size (Mann–Whitney *U*-test: U = 218, $p \leq$ .001, r = 0.799).

4 | DISCUSSION

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

Several studies have demonstrated that the species richness of arthropods in areas of the CFR is similar to that of other southern African biomes, either within the expectations of species-energy theory, or strongly related to plant diversity (Braschler et al., 2012; Kemp & Ellis, 2017; Kemp et al., 2017; Proceş & Cowling, 2006; Proceş et al., 2009; Wright & Samways, 1998, 2000). Most of these investigations have, however, concerned phytophagous species, which often have strong associations with plants (Castagneyrol & Jactel, 2012; Kemp et al., 2017; Novotný et al., 2006; Strong, Lawton, Southwood, 1984).

Here we showed similar results for a group that subsists on soil fungi and microorganisms (Hopkin, 1997) and is not, therefore, directly linked through diet with vascular plants, suggesting again that Fynbos arthropods in general are not as species poor as originally thought (Marloth, 1908, see also Johnson, 1992). Rather, alpha diversity at each sampled site is in keeping with what might be expected for similar systems globally given energy availability, bearing in mind that the richness-environmental variable analysis accounted for only 30% of the variation in richness (although a value not dissimilar to other studies at this scale—see e.g. Beck et al., 2017; Braschler et al., 2012; Gillman et al., 2015). Other factors, such as regional area
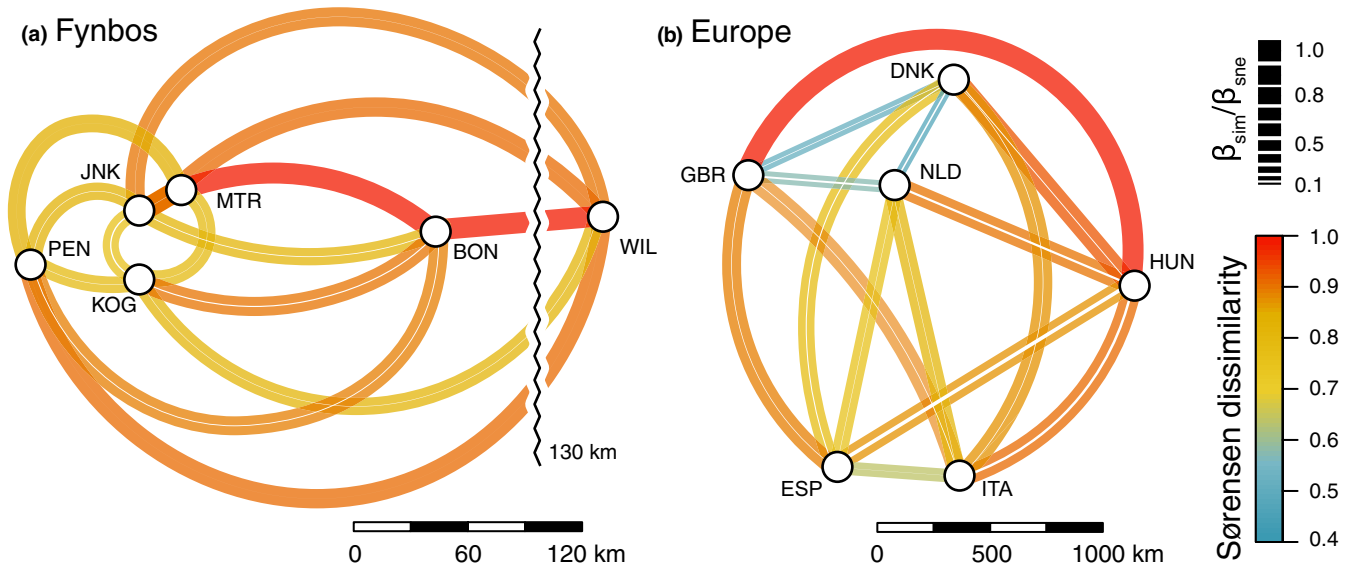
(a) Fynbos

(b) Europe

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

TABLE 3 Asymmetric distance matrix for incidence-based partitioning of pairwise beta diversity metrics (Baselga, 2010; Table S2.1) between Collembola assemblages of the Western Cape

	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	

Note: The relatively large values for the turnover component measured as Simpson dissimilarity (grey), indicates that species turnover is the main contributor of observed pairwise dissimilarity, while the nestedness component measured as the nestedness-resultant fraction of Sørensen dissimilarity (white), contributes relatively little.

effects and long-term climatic stability (Galley, Linder, Zimmerman, 2009; Ulrich & Fiera, 2009), may be important contributors to richness, and will require further investigation. For the two sites with lower than expected species richness (Bontebok and Jonkershoek), more frequent disturbance than the other sites may have played a role (Figures S7.3, S7.5 and S8.1, Appendices S7 and S8), though causes for richness variation among sites remain to be investigated. The unevenness of the Jonkershoek assemblage, which was dominated by *Parisotoma* sp. 5, is particularly conspicuous, but whether this is related to specific species traits is not currently known. This species was dominant both before and after a fire in this area, showing high resistance to this disturbance, which is frequent in the Fynbos (see Janion-Scheepers et al., 2016). Such species-specific traits may play an important role in structuring Collembola assemblages in the Fynbos.

In contrast to the unexceptional alpha diversity, beta diversity of Collembola between Fynbos sites was higher than reported from sites across Europe, despite geographical distances between Fynbos sites being significantly shorter by almost an order of magnitude (Figure 4). Beta diversity was primarily due to species turnover (change in species identity) rather than species nestedness, as indicated by beta-diversity partitioning. Indeed, compared against many other assemblages across a broad range of taxa (Soininen, Heino, Wang, 2018), the turnover found here is extraordinarily high and nestedness unusually low (Figure 3). A study of springtail assemblages from 16 Swedish pine forest sites, encompassing a comparable spatial scale as the present study, found Sørensen dissimilarity indices of *c.* 0.15–0.25, which are substantially lower than the turnover metrics reported here (Figures 3 and 4; Widenfalk et al. 2017; see also Perez et al., 2013). Similarly, an investigation of springtail diversity among two major areas of

Eastern Europe revealed high turnover of springtails, but again across a 1,200 km gradient (Kuznetsova & Saraeva, 2018). Elsewhere, across the whole of the Antarctic region (including the Southern Ocean Islands), with distances among sites spanning thousands of kilometres (Baird, Janion-Scheepers, Stevens, Leihy, & Chown, 2019), turnover values (β_{sim}) similar to those found here over the much shorter distances we sampled were found. The European regions were substantially affected by the last glacial maximum, with evidence for postglacial colonization of Collembola from a South-Western European centre (Ulrich & Fiera, 2009), thus potentially accounting for low turnover. By contrast, strong evidence exists for persistence across several glacial cycles of the Antarctic arthropod fauna of many sites (Moon, Chown, & Fraser, 2017), yet turnover is still lower than in Fynbos given the different spatial extents. Thus, as is the case for previously studied phytophagous insects (Kemp et al., 2017), springtails across the CFR appear to follow similar patterns of spatial variation in species diversity as documented for fynbos vegetation (Buerki et al., 2012; Cowling, 1990; Cowling et al., 1992, 1996; Cowling & Lombard, 2002). How this spatial turnover is established relative to, for example, rates of movement and habitat preference in springtails (see e.g. Treasure & Chown, 2013) remains to be determined.

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

Although the idea that high beta diversity of insects might explain high regional insect diversity in the Fynbos has been proposed previously (Proches et al., 2009), it has not been comprehensively examined for any arthropods. The most sophisticated assessment of arthropod diversity variation in the region has come from a study of cicadellid bugs associated with the plant family Restionaceae (Kemp et al., 2017). Three likely hypotheses for similar patterns in host and insect spatial diversity variation were proposed: (a) insect host specificity; (b) similar responses of insects and their hosts to climatic gradients; (c) similar biogeographical influences on each of the groups. For these relatively host-specific cicadelids, host specificity was identified as the likely underlying cause of similarity in spatial diversity patterns (Kemp et al., 2017). In the succulent Karoo, plant beta diversity was also identified as being a major factor influencing beta diversity of the flower visiting beetles (Scarabaeidae: Hopliini; Colville et al., 2002).

In contrast to phytophagous insects, springtails mainly belong to the soil detritus food chain, and are not, therefore, closely associated with individual plant species (Hopkin, 1997; Salamon, Schaefer, Alphei, Schmid, & Scheu, 2004), although they are responsive to plant richness and functional diversity (Henneron et al., 2017; Sabais et al., 2011). Accordingly, the majority of springtail species were found in both nutrient-rich and nutrient-poor litter types during preliminary litter-type studies the Jonkershoek site (Table S6.1 in Appendix 6), further bearing out the generalist foraging behaviour of these animals (see also Leinaas et al., 2015). In consequence, either responses to climatic gradients or biogeographical features similar to those found in many vascular plant groups of the Fynbos are likely responsible for high beta diversity in the springtails. A strong relationship was also found between plant phylogenetic diversity and detritivore insect richness within the Fynbos at the 20 m sampling scale in a previous investigation (Proches et al., 2009), bearing out the independent, but likely similar, influence of environmental drivers on plants and on detritivorous arthropods. Understanding just what these mechanistic drivers are will require the kinds of coupled ecological and phylogenetic work that has provided so much insight into the mechanisms underlying plant diversity in the region (Cowling et al., 2015; Dupont et al., 2011; Linder, 2003; Linder & Verboom, 2015; Rundel et al., 2016), including explicit tests of Kemp et al. (2017) hypotheses and other drivers such as interspecific interactions (Augustyn, Anderson, Merwe, & Ellis, 2017). Initial evidence suggests that some springtail genera, such as *Seira*, may have undergone significant radiations in the CFR (Janion, Bedos, Bengtsson, et al., 2011; Liu, 2015), which points to the importance of eco-evolutionary processes, as is the case in the plants. Notwithstanding uncertainty about mechanisms, the level of replacement among sites was high, with more than 85% of species unique to one site (Table S1.1 in Appendix S1). Such a high number of site-specific species contrasts strongly with what has been found for springtails of other areas at similar scales (Ulrich & Fiera, 2009). Although our sampling was not comprehensive across the entire Fynbos Biome, and some species may not have been detected at each of the sites, other approaches in the region, which have demonstrated many local springtail endemics (Liu, 2015), suggest that the patterns are likely to be upheld. Thus, the CFR may be as important a biodiversity hotspot for belowground systems as it is for those more visible on the surface. Loss or degradation of local sites may thus have more of an impact on Fynbos biodiversity than is currently estimated (Rouget et al., 2014).

CONFLICT OF INTEREST

The authors declare they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All data are found in Appendices S1, S2 and S6.

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REFERENCES

Augustyn, W. J., Anderson, B., van der Merwe, J. F., & Ellis, A. G. (2017). Spatial turnover in host-plant availability drives host-associated divergence in a South African leafhopper (*Cephalelus uncinatus*). *BMC Evolutionary Biology*, *17*, 72. 10.1186/s12862-017-0916-0

Baird, H. P., Janion-Scheepers, C., Stevens, M. I., Leihy, R. I., & Chown, S. L. (2019). The ecological biogeography of indigenous and introduced Antarctic springtails. *Journal of Biogeography*, *46*, 1959–1973. https://doi.org/10.1111/jbi.13639

Ballesteros-Meija, L., Kitching, I. J., Jetz, W., & Beck, J. (2017). Putting insects on the map: Near-global variation in sphingid moth richness along spatial and environmental gradients. *Ecography*, *40*, 698–708. https://doi.org/10.1111/ecog.02438

Barraclough, T. G. (2006). What can phylogenetics tell us about speciation in the Cape flora? *Diversity and Distributions*, *12*, 21–26. https://doi.org/10.1111/j.1366-9516.2006.00208.x

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*, 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A. (2013). Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography*, *36*, 124–128. https://doi.org/10.1111/j.1600-0587.2012.00124.x

Baselga, A., & Leprieur, F. (2015). Comparing methods to separate components of beta diversity. *Methods in Ecology and Evolution*, *6*, 1069–1079. https://doi.org/10.1111/2041-210X.12388

Baselga, A., & Orme, C. D. L. (2012). betapart: An R package for the study of beta diversity. *Methods in Ecology and Evolution*, *3*, 808–812.

Beck, J., McCain, C. M., Axmacher, J. C., Ashton, L. A., Bärtschi, F., Brehm, G., … Novotny, V. (2017). Elevational species richness gradients in a hyperdiverse insect taxon: A global meta-study on geometrid moths. *Global Ecology and Biogeography*, *26*, 412–424. https://doi.org/10.1111/geb.12548

Bengtsson, J., Janion, C., Chown, S. L., & Leinaas, H. P. (2012). Litter decomposition in fynbos vegetation, South Africa. *Soil Biology & Biochemistry*, *47*, 100–105. https://doi.org/10.1016/j.soilbio.2011.11.023

Block, W. (1966). Some characteristics of the Macfadyen high gradient extractor for soil micro-arthropods. *Oikos*, *17*, 1–9. https://doi.org/10.2307/3564777

Braschler, B., Gaston, K. J., & Chown, S. L. (2012). The Fynbos and Succulent Karoo biomes do not have exceptional local ant richness. *PloSONE*, *7*, e31463. https://doi.org/10.1371/journal.pone.0031463

Buerki, S., Jose, S., Yadav, S. R., Goldblatt, P., Manning, J. C., & Forest, F. (2012). Contrasting biogeographic and diversification patterns in two Mediterranean-type ecosystems. *PLoS ONE*, *7*, e39377. https://doi.org/10.1371/journal.pone.0039377

Castagneyrol, B., & Jactel, H. (2012). Unravelling plant-animal diversity relationships: A meta-regression analysis. *Ecology*, *93*, 2115–2124. https://doi.org/10.1890/11-1300.1

Colville, J., Picker, M. D., & Cowling, R. M. (2002). Species turnover of monkey beetles (Scarabaeidae: Hopliini) along environmental and disturbance gradients in the Namaqualand region of the succulent Karoo, South Africa. *Biodiversity & Conservation*, *11*, 243–264.

Convey, P., Greenslade, P., Arnold, P. J., & Block, W. (1999). Collembola of sub-Antarctic South Georgia. *Polar Biology*, *22*, 1–6. https://doi.org/10.1007/s003000050383

Cowling, R. M. (1990). Diversity components in a species-rich area of the Cape Floristic Region. *Journal of Vegetation Science*, *1*, 699–710. https://doi.org/10.2307/3235578

Cowling, R. M., Holmes, P. M., & Rebelo, A. G. (1992). Plant diversity and endemism. In R. M. Cowling (Ed.), *The ecology of Fynbos: Nutrients, fire and diversity* (pp. 62–112). Cape Town: Oxford University Press.

Cowling, R. M., & Lombard, A. T. (2002). Heterogeneity, speciation/extinction history and climate: Explaining regional plant diversity patterns in the Cape Floristic Region. *Diversity and Distributions*, *8*, 163–179. https://doi.org/10.1046/j.1472-4642.2002.00143.x

Cowling, R. M., MacDonald, I. A. W., & Simmons, M. T. (1996). The Cape Peninsula, South Africa: Physiographical, biological and historical background to an extraordinary hot-spot of biodiversity. *Biodiversity and Conservation*, *5*, 527–550. https://doi.org/10.1007/BF00137608

Cowling, R. M., Potts, A. J., Bradshaw, P. L., Colville, J., Arianoutsou, M., Ferrier, S., … Zutta, B. R. (2015). Variation in plant diversity in Mediterranean-climate ecosystems: The role of climatic and topographical stability. *Journal of Biogeography*, *42*, 552–564. https://doi.org/10.1111/jbi.12429

Cowling, R. M., Rundel, P. W., Desmet, P. G., & Esler, K. J. (1998). Extraordinary high regional-scale plant diversity in southern African arid lands: Subcontinental and global comparisons. *Diversity and Distributions*, *4*, 27–36.

Dixon, P. (2003). VEGAN, a package of R functions for community ecology. *Journal of Vegetation Science*, *14*, 927–930. https://doi.org/10.1111/j.1654-1103.2003.tb02228.x

Dupont, L. M., Linder, H. P., Rommerskirchen, F., & Schefuß, E. (2011). Climate-driven rampant speciation of the Cape flora. *Journal of Biogeography*, *38*, 1059–1068. https://doi.org/10.1111/j.1365-2699.2011.02476.x

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*, 4302–4315. https://doi.org/10.1002/joc.5086

Fjellberg, A. (1998). *Fauna Entomologica Scandinavica Volume 35. The Collembola of Fennoscandia and Denmark. Part I: Poduromorpha*. Leiden: Brill.

Fjellberg, A. (2007). *Fauna Entomologica Scandinavica Volume 42. The Collembola of Fennoscandia and Denmark. Part II: Entomobryomorpha and Symphypleona*. Leiden: Brill.

Galley, C., Linder, H. P., & Zimmerman, N. E. (2009). *Pentaschistis* (Poaceae) diversity in the Cape Mediterranean region: Habitat heterogeneity and climate stability. *Global Ecology & Biogeography*, *18*, 586–595. https://doi.org/10.1111/j.1466-8238.2009.00468.x

Giliomee, J. H. (2003). Insect diversity in the Cape Floristic Region. *African Journal of Ecology*, *41*, 237–244. https://doi.org/10.1046/j.1365-2028.2003.00442.x

Gillman, L. N., Wright, S. D., Cusens, J., McBride, P. D., Malhi, Y., & Whittaker, R. J. (2015). Latitude, productivity and species richness. *Global Ecology and Biogeography*, *24*, 107–117. https://doi.org/10.1111/geb.12245

Goldblatt, P. (1978). An analysis of the flora of Southern Africa: Its characteristics, relationships, and origins. *Annals of the Missouri Botanical Garden*, *65*, 369–436. https://doi.org/10.2307/2398858

González-Mace, O., & Scheu, S. (2018). Response of Collembola and Acari communities to summer flooding in a grassland plant diversity experiment. *PLoS ONE*, *13*, e0202862. https://doi.org/10.1371/journal.pone.0202862

Gotelli, N. J., & Chao, A. (2013). Measuring and estimating species richness, species diversity and biotic similarity from sampling data. In S. A. Levin (Ed.), *Encyclopaedia of biodiversity*, Vol. *5* (pp. 195–211). Waltham: Academic Press.

Hawkins, J. A. (2006). Using phylogeny to investigate the origins of the Cape flora: The importance of taxonomic, gene and genome sampling strategies. *Diversity and Distributions*, *12*, 27–33. https://doi.org/10.1111/j.1366-9516.2006.00209.x

Henneron, L., Aubert, M., Archaux, F., Bureau, F., Dumas, Y., Ningre, F., … Chauvat, M. (2017). Forest plant community as a driver of soil

biodiversity: Experimental evidence from collembolan assemblages through large-scale and long-term removal of oak canopy trees *Quercus petraea*. *Oikos*, *126*, 420–434. https://doi.org/10.1111/oik.03677

Hill, M. O. (1973). Diversity and evenness: A unifying notation and its consequences. *Ecology*, *54*, 427–432. https://doi.org/10.2307/1934352

Hopkin, S. (1997). *Biology of the Springtails. Insecta: Collembola*. Oxford: Oxford University Press.

Hopkin, S. (2007). *A key to the Collembola (Springtails) of Britain and Ireland*. London, UK: FSC.

Hua, X. (2016). The impact of seasonality on niche breadth, distribution range and species richness: A theoretical exploration of Janzen's hypothesis. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20160349.

Huntley, B. J. (1989). *Biotic diversity in Southern Africa. Concepts and conservation*. Oxford: Oxford University Press.

Janion, C., Bedos, A., Bengtsson, J., Deharveng, L., Jansen van Vuuren, B., Leinaas, L., … Chown, S. L. (2011). Springtails diversity in South Africa. *South African Journal of Science*, *107*, 7. Article #582

Janion, C., Bedos, A., & Deharveng, L. (2011). The genus *Ectonura*, Cassagnau 1980 in South Africa (Collembola: Neanuridae: Neanurinae), with a key to South African Neanurinae. *ZooKeys*, *136*, 31–45. https://doi.org/10.3897/zookeys.136.1744

Janion, C., Deharveng, L., & Weiner, W. M. (2013). Synonymy of *Spicatella* Thibaud, 2002 with *Delamarephorura* Weiner & Najt, 1999, and description of two new species (Collembola: Tullbergiidae). *Raffles Bulletin of Zoology*, *61*, 657–663.

Janion, C., D'Haese, C., & Deharveng, L. (2012). A new species and first record of the genus *Triacanthella* Schaffer, 1897 (Collembola, Hypogastruridae) for Africa. *ZooKeys*, *163*, 57–68. https://doi.org/10.3897/zookeys.163.2298

Janion-Scheepers, C., Bengtsson, J., Leinaas, H. P., Deharveng, L., & Chown, S. L. (2016). The response of springtails to fire in the fynbos of the Western Cape, South Africa. *Applied Soil Ecology*, *108*, 165–175. https://doi.org/10.1016/j.apsoil.2016.08.001

Janion-Scheepers, C., Deharveng, L., Bedos, A., & Chown, S. L. (2015). Updated list of Collembola species currently recorded from South Africa. *ZooKeys*, *503*, 55–88. https://doi.org/10.3897/zookeys.503.8966

Janion-Scheepers, C., Phillips, L., Sgrò, C. M., Duffy, G. A., Hallas, R., & Chown, S. L. (2018). Basal resistance enhances warming tolerance of alien over indigenous species across latitude. *Proceedings of the National Academy of Sciences of the United States of America*, *115*, 145–150. https://doi.org/10.1073/pnas.1715598115

Jiménez, I., & Ricklefs, R. E. (2014). Diversity anomalies and spatial climate heterogeneity. *Global Ecology and Biogeography*, *23*, 988–999. https://doi.org/10.1111/geb.12181

Johnson, S. D. (1992). Plant–animal relationships. In R. M. Cowling (Ed.), *The ecology of Fynbos: Nutrients, fire and diversity* (pp. 175–205). Cape Town: Oxford University Press.

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*, *88*, 2427–2439. https://doi.org/10.1890/06-1736.1

Kemp, J. E., & Ellis, A. G. (2017). Significant local-scale plant-insect species richness relationship independent of abiotic effects in the temperate Cape Floristic Region Biodiversity Hotspot. *PLoS ONE*, *12*, e0168033. https://doi.org/10.1371/journal.pone.0168033

Kemp, J. E., Linder, P., & Ellis, A. G. (2017). Beta diversity of herbivorous insects is coupled to high species and phylogenetic turnover of plant communities across short spatial scales in the Cape Floristic Region. *Journal of Biogeography*, *44*, 1813–1823. https://doi.org/10.1111/jbi.13030

Koleff, P., Gaston, K. J., & Lennon, J. L. (2003). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, *72*, 367–382. https://doi.org/10.1046/j.1365-2656.2003.00710.x

Kreft, H., & Jetz, W. (2007). Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences of the Unites States of America*, *104*, 5925–5930. https://doi.org/10.1073/pnas.0608361104

Kuznetsova, N. A., & Saraeva, A. K. (2018). Beta-diversity partitioning approach in soil zoology: A case of Collembola in pine forests. *Geoderma*, *332*, 142–152. https://doi.org/10.1016/j.geoderma.2017.09.030

Leinaas, H. P. (1978). Sampling of soil microarthropods from coniferous forest podzol. *Norwegian Journal of Entomology*, *25*, 57–62.

Leinaas, H. P., Bengtsson, J., Janion, C., & Chown, S. L. (2015). Indirect effects of disturbance on invasion: Nutritious litter from a grazing resistant plant favours alien over native Collembola. *Ecology and Evolution*, *5*, 3462–3471. https://doi.org/10.1002/ece3.1483

Linder, H. P. (1991). Environmental correlates of patterns of species richness in the south-western Cape Province of South Africa. *Journal of Biogeography*, *18*, 509–518. https://doi.org/10.2307/2845687

Linder, H. P. (2003). The radiation of the Cape flora, southern Africa. *Biological Reviews*, *78*, 597–638. https://doi.org/10.1017/S1464793103006171

Linder, H. P., & Verboom, G. A. (2015). The evolution of regional species richness: The history of the Southern African flora. *Annual Review of Ecology, Evolution, and Systematics*, *46*, 393–412. https://doi.org/10.1146/annurev-ecolsys-112414-054322

Liu, W. P. A. (2015). *Diversity of the genus Seira (Collembola: Entomobryidae: Seirinae) in the Fynbos and Southern Afrotemperate forest*. Stellenbosch University, M.Sc. dissertation.

Liu, W. P. A., Janion, C., & Chown, S. L. (2012). Collembola diversity in the critically endangered Cape Flats Sand Fynbos and adjacent pine plantations. *Pedobiologia*, *55*, 203–209. https://doi.org/10.1016/j.pedobi.2012.03.002

Macfadyen, A. (1953). Notes on methods for the extraction of small soil arthropods. *Journal of Animal Ecology*, *22*, 65–77. https://doi.org/10.2307/1691

Marloth, R. (1908). Some observations on entomophilous flowers. *South African Journal of Science*, *4*, 110–113.

Milcu, A., Partsch, S., Langel, R., & Scheu, S. (2006). The response of decomposers (earthworms, springtails and microorganisms) to variations in species and functional group diversity of plants. *Oikos*, *112*, 513–524. https://doi.org/10.1111/j.0030-1299.2006.14292.x

Mokhatla, M. M., Measey, G. J., Chimimba, C. T., & van Rensburg, B. J. (2012). A biogeographical assessment of anthropogenic threats to areas where different frog breeding groups occur in South Africa: Implications for anuran conservation. *Diversity and Distributions*, *18*, 470–480. https://doi.org/10.1111/j.1472-4642.2011.00870.x

Moon, K. L., Chown, S. L., & Fraser, C. I. (2017). Reconsidering connectivity in the sub-Antarctic. *Biological Reviews*, *92*, 2164–2181. https://doi.org/10.1111/brv.12327

Novotný, V., Drozd, P., Miller, S. E., Kulfan, M., Janda, M., Basset, Y., & Weiblen, G. D. (2006). Why are there so many species of herbivorous insects in tropical rainforests? *Science*, *313*, 1115–1118. https://doi.org/10.1126/science.1129237

Overgaard, J., Kearney, M. R., & Hoffmann, A. A. (2014). Sensitivity to thermal extremes in Australian *Drosophila* implies similar impacts of climate change on the distribution of widespread and tropical species. *Global Change Biology*, *20*, 1738–1750. https://doi.org/10.1111/gcb.12521

Perez, G., Decaëns, T., Dujardin, G., Akpa-Vinceslas, M., Langlois, E., & Chauvat, M. (2013). Response of collembolan assemblages to plant species successional gradient. *Pedobiologia*, *56*, 169–177. https://doi.org/10.1016/j.pedobi.2013.04.001

Péron, G., & Altwegg, R. (2015). Low bird diversity in the Fynbos plant diversity hotspot: Quaternary legacies in the current distributions of passerine birds. *Ecography*, *38*, 992–997. https://doi.org/10.1111/ecog.01176

Petersen, H. (2011). Collembolan communities in shrublands along climatic gradients in Europe and the effect of experimental warming and drought on population density, biomass and diversity. *Soil Organisms*, *83*, 463–488.

Ponge, J. F., Gillet, S., Dubs, F., Fedoroff, E., Haese, L., Sousa, J. P., & Lavelle, P. (2003). Collembola communities as bioindicators of land use intensification. *Soil Biology & Biochemistry*, 35, 813–826. https://doi.org/10.1016/s0038-0717(03)00108-1

Potapov, M. (2001). In W. Dunger (Ed.), *Synopses on Palaearctic Collembola, Volume 3, Isotomidae*. Görlitz: Staatliches Museum für Naturkunde.

Potapov, M., Janion, C., & Deharveng, L. (2011). Two new species of *Parisotoma* (Collembola: Isotomidae) from the Western Cape, South Africa. *Zootaxa*, 2771, 17–24. https://doi.org/10.11646/zootaxa.2771.1.2

Procheş, S., & Cowling, R. M. (2006). Insect diversity in Cape fynbos and neighbouring South African vegetation. *Global Ecology and Biogeography*, 15, 445–451. https://doi.org/10.1111/j.1466-822X.2006.00239.x

Procheş, S., Forest, F., Veldtman, R., Chown, S. L., Cowling, R. M., Johnson, S. D., ... Savolainen, V. (2009). Dissecting the plant-insect diversity relationship in the Cape. *Molecular Phylogenetics and Evolution*, 51, 94–99. https://doi.org/10.1016/j.ympev.2008.05.040

Querner, P., Bruckner, A., Weigand, E., & Prötsch, M. (2010). Short- and long-term effects of fire on the Collembola communities of a sub-alpine dwarf pine ecosystem in the Austrian Alps. *eco.mont*, 2, 29–36. https://doi.org/10.1553/eco-mont-2-2s29

R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Raymond-Léonard, L. J., Gravel, D., Reich, P. B., & Handa, I. T. (2018). Springtail community structure is influenced by functional traits but not biogeographic origin of leaf litter in soils of novel forest ecosystems. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20180647. https://doi.org/10.1098/rspb.2018.0647

Rouget, M., Barnett, M., Cowling, R. M., Cumming, T., Daniels, F., Hoffman, M. T., ... Rebelo, T. (2014). Conserving the Cape Floristic Region. In N. Allsopp, J. F. Colville, & A. G. Verboom (Eds.), *Fynbos: Ecology, evolution, and conservation of a megadiverse region* (pp. 321–336). New York, NY: Oxford University Press.

Rouget, M., Richardson, D. M., Cowling, R. M., Lloyd, J. W., & Lombard, A. T. (2003). Current patterns of habitat transformation and future threats to biodiversity in terrestrial ecosystems of the Cape Floristic Region, South Africa. *Biological Conservation*, 112, 63–85. https://doi.org/10.1016/S0006-3207(02)00395-6

Rundel, P. W., Arroyo, M. T. K., Cowling, R. M., Keeley, J. E., Lamont, B. B., & Vargas, P. (2016). Mediterranean biomes: Evolution of their vegetation, floras, and climate. *Annual Review of Ecology, Evolution, and Systematics*, 47, 383–407. https://doi.org/10.1146/annurev-ecolsys-121415-032330

Sabais, A. W. C., Scheu, S., & Eisenhauer, N. (2011). Plant species richness drives the density and diversity of Collembola in temperate grassland. *Acta Oecologia*, 37, 195–202. https://doi.org/10.1016/j.actao.2011.02.002

Salamon, J.-A., Schaefer, M., Alphei, J., Schmid, B., & Scheu, S. (2004). Effects of plant diversity on Collembola in an experimental grassland ecosystem. *Oikos*, 106, 51–60. https://doi.org/10.1111/j.0030-1299.2004.12905.x

Salmon, S., Ponge, J. F., Gachet, S., Deharveng, L., Lefebvre, N., & Delabrosse, F. (2014). Linking species, traits and habitat characteristics of Collembola at European scale. *Soil Biology and Biochemistry*, 75, 73–85. https://doi.org/10.1016/j.soilbio.2014.04.002

Soininen, J., Heino, J., & Wang, J. (2018). A meta-analysis of nestedness and turnover components of beta diversity across organisms and ecosystems. *Global Ecology & Biogeography*, 27, 96–109. https://doi.org/10.1111/geb.12660

Storch, D., Evans, K. L., & Gaston, K. J. (2005). The species-area-energy relationship. *Ecology Letters*, 8, 487–492. https://doi.org/10.1111/j.1461-0248.2005.00740.x

Strong, D. J., Lawton, J. H., & Southwood, R. (1984). *Insects on plants. Community patterns and mechanisms*. Oxford: Blackwell Scientific Publications.

Tello, J. S., & Stevens, R. D. (2010). Multiple environmental determinants of regional species richness and effects of geographic range size. *Ecography*, 33, 796–808. https://doi.org/10.1111/j.1600-0587.2009.05991.x

Treasure, A. M., & Chown, S. L. (2013). Contingent absences account for range limits but not the local abundance structure of an invasive springtail. *Ecography*, 36, 146–156. https://doi.org/10.1111/j.1600-0587.2012.07458.x

Ulrich, W., & Fiera, C. (2009). Environmental correlates of species richness of European springtails (Hexapoda: Collembola). *Acta Oecologia*, 35, 45–52. https://doi.org/10.1016/j.actao.2008.07.007

Weiner, W. N., Janion-Scheepers, C., & Deharveng, L. (2017). Two new species of *Friesea* Dalla Torre 1895 (Collembola: Neanuridae) from the Western Cape Province, South Africa; with a key to sub-Saharan Friesea. *Annales Zoologici*, 67, 657–664.

Widenfalk, L. A., Malmström, A., Berggren, Å., Berg, M. P., Leinaas, H. P., & Bengtsson, J. (2017). Regional patterns of species and traits diversity among Collembola in mature pine forests across south-central Sweden. Paper 4 in Widenfalk, L.A., Springtails in Space. Doctoral thesis. 2017:6 Swedish University of Agricultural Sciences, Uppsala, Sweden.

Wright, M., & Samways, M. J. (1998). Insect species richness tracking plant species richness in a diverse flora: Gall insects in the Cape Floristic Region, South Africa. *Oecologia*, 115, 427–433. https://doi.org/10.1007/s004420050537

Wright, M. G., & Samways, M. J. (2000). Biogeography and species richness of endophagous insects associated with Proteaceae in South Africa. *African Journal of Ecology*, 38, 16–22. https://doi.org/10.1046/j.1365-2028.2000.00210.x

Wylie, J. L., & Currie, D. J. (1993). Species-energy theory and patterns of species richness: I. Patterns of bird, angiosperm, and mammal species richness on islands. *Biological Conservation*, 63, 137–144. https://doi.org/10.1016/0006-3207(93)90501-Q

Zuur, A. F., Leno, E. N., Elphick, C. S., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer Verlag.

BIOSKETCHES

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

Author contribution: CJ-S, JB, HPL and SLC designed the study, CJ-S, JB and HPL performed the collection and processing of samples, CJ-S and LD identified the species, CJ-S and GAD analysed collected biodiversity data, CJ-S, GAD and SLC wrote the manuscript, and all authors provided comments on manuscript drafts.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.