



Abandoned fields and high plant diversity support high spider diversity within an agricultural mosaic in a biodiversity hotspot

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Abstract

Protected areas alone cannot conserve all biodiversity; we must also conserve biodiversity within production landscapes. Little is known about spider diversity in the Cape Floristic Region (CFR) biodiversity hotspot and factors driving spider diversity in transformed landscapes. Here, we assess spatial patterns of spiders in different transformed biotopes bordering remnant fynbos natural vegetation patches, determine direction of associated edge effects, and identify environmental factors influencing spider local distribution. Spiders were sampled along replicated transects running from remnant patches into three different transformed biotopes: old-fields (abandoned farmland), vineyards, and alien tree plantations. Spider Shannon diversity within old-fields and plantations did not differ from remnant patches, which had the highest diversity, whereas vineyards had the lowest. Overall, spider diversity was consistently high around habitat boundaries, regardless of land use type. Vineyards showed sharp declines in spider diversity along the remnant-vineyard transect, compared to other transects. Spider assemblages within vineyards was significantly different compared to remnant patches and old-fields, whereas other land-uses showed greater similarity. Plant species richness within the transformed biotope core increased overall spider diversity, benefiting plant-dwelling assemblages, but negatively influencing ground-dwelling assemblages. Herbaceous plant cover was driving assemblages within vineyards, whereas Restionaceae plant cover drove assemblages within old-fields. Furthermore, amount of natural vegetation in the landscape influenced spider assemblages within transformed biotopes. Our results show that old-fields have great potential to increase structural and functional connectivity within agricultural mosaics, and their rehabilitation is recommended. Furthermore, increasing plant diversity throughout the transformed landscape can soften the landscape and benefit spider diversity.

Keywords Araneae · Cape Floristic Region · Habitat boundaries · Old-fields · Supplementary habitat · Surrounding habitat

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Introduction

Rapid anthropogenic change has resulted in loss of biodiversity (Pimm et al. 2014), with insects of particular concern (Cardoso et al. 2020). Private and proclaimed protected areas alone will not conserve all biological diversity as > 80% of land is not formally protected (Fischer et al. 2013). This realization has sparked considerable interest in conservation of biodiversity within production landscapes through sparing remnants of natural vegetation (Ekroos et al. 2016; Balmford et al. 2018). Sparing these remnants effectively conserves a variety of farmland biodiversity (Phalan et al. 2011; Vrdoljak and Samways 2014; Gaigher et al. 2015; Theron et al. 2020), as well as enhancing ecosystem services for crop production (Isaacs et al. 2008; Carvalheiro et al. 2011).

The surrounding transformed landscape, when managed correctly, can also contribute to conservation of farmland biodiversity (Perfecto and Vandermeer 2010). In addition, the functioning of source patches in terms of arthropod-mediated ecosystem services, benefits from the sustainable management of the surrounding landscape (Garibaldi et al. 2019). However, high intensity management within the production landscape influences an organisms' ability to move within it (Martin and Fahrig 2015), which in turn, influences the organisation of species, impacting ecosystem functioning. In contrast, farmland conservation measures, such as increasing the amount of vegetation within the production landscape can help soften it, leading to improved arthropod-mediated ecosystem services (Isaacs et al. 2008). However, these management decisions need to be guided by land use management that considers arthropod response to land use (Birkhofer et al. 2018). Therefore, studying species' responses within the transformed landscape is important for understanding how species utilise diverse elements throughout the landscape and neighbouring regions (Rosas-Ramos et al. 2018). In addition, assessing distribution patterns across habitat edges of different land uses is important for identifying and understanding the mechanisms of hard and soft boundaries needed to increase successful arthropod boundary crossings throughout the landscape mosaic (Guiller et al. 2016).

The Cape Floristic Region (CFR) biodiversity hotspot is renowned globally for its exceptionally high plant diversity and endemism (Myers et al. 2000), yet has historically undergone extensive land transformation and fragmentation (Rouget et al. 2003), creating a complex tapestry of different land uses, as well as edge effects at biotope boundaries. The relative value, in terms of biodiversity, of these different land uses within the CFR agricultural landscape is poorly understood, with only a few studies documenting the diversity patterns of ground-dwelling arthropods (Gaigher and Samways 2010, 2014), parasitoids and predatory arthropods (Gaigher et al. 2016), flower-visiting insects (Kehinde and Samways 2012, 2014; Vrdoljak and Samways 2014), and grasshoppers (Adu-Acheampong et al. 2017) across farmland mosaics of the CFR. Although conservation of remnants is critical for maintaining unique biodiversity in these landscapes, certain transformed landscape elements can also make a significant contribution to landscape-scale biodiversity (Dominik et al. 2018). Thus, understanding how arthropods respond to different landscape elements throughout the farmland mosaic will help CFR conservancies to better inform land managers on sustainable land use practices which promote arthropod conservation.

Spiders are highly mobile predators, and functionally important components of food webs in natural ecosystems (Nyffeler and Sunderland 2003). Their high mobility enables them to be one of the first groups to colonise new areas (Blandenier 2009), making them ideally suited to study the functional aspect of landscape connectivity within an agricultural mosaic. However, to date, sampling effort for spiders within CFR remnants of natural

vegetation has been low (Dippenaar-Schoeman et al. 2015). Furthermore, spider diversity within different land use types of CFR agricultural mosaics is even less well known (Gaigher and Samways 2010, 2014; Gaigher et al. 2016; Arvidsson et al. 2020). Studying their distribution patterns throughout the mosaic can provide a better understanding of the degree to which different landscape elements can facilitate persistence within a fragmented landscape (Rosas-Ramos et al. 2018). Managing the production landscape with the conservation of arthropod predators in mind, will promote the protection of ecosystem services, such as the biological control of crop pests (Birkhofer et al. 2018), benefiting not only biodiversity, but crop production as well (Garibaldi et al. 2019).

Here, we focus on patterns of spider diversity within different land use types throughout the agricultural mosaic of the CFR. Specifically, we assess spider diversity and assemblage patterns across edges of remnant sclerophyllous fynbos vegetation typical of the CFR, and three different land-use types, to address the following: (1) whether patterns of spider diversity and assemblage structure differ between different human modified land-use types, (2) how the associated edge effects differ between different transformed biotopes, and the direction of these edge effects, (3) which features of the transformed landscape can help soften transformed areas and improve functional connectivity throughout the agricultural mosaic, and (4) how plant communities drive spider assemblage patterns within modified landscapes. These findings would contribute to greening initiatives within other modified landscapes, especially where arthropod conservation can be promoted.

Methods

Study area and sampling design

This study was carried out in the fynbos biome of the Western Cape Province of South Africa. This region forms much of the CFR, characterised by its Mediterranean climate, where average rainfall varies from < 100 to 2 000 mm, with most rain falling in winter (Goldblatt 1997). Two main soil types occur within the fynbos biome: coarse-grained sandy soils poor in essential plant nutrients, and nutrient rich clay soils, weathered from Carboniferous rocks (Goldblatt 1997). Large portions of the CFR have been transformed for agricultural and urban use and invaded by stands of alien invasive trees (Rouget et al. 2003). Agriculture, especially dairy, vineyards and deciduous fruit orchards, as well as some forestry plantations, cover 26% of the fynbos biome, mostly on nutrient rich soils of the renosterveld component (Rouget et al. 2003).

To investigate the potential influence of the production landscape on spider diversity within the CFR, a total of 18 transects were established where remnant natural vegetation was adjacent to one of three different transformed biotopes (Fig. 1). Transects ran from remnant natural vegetation into the adjacent transformed biotopes, and were sampled once per season, over two seasons (Summer 2015 and Autumn 2016). Three different transformed biotopes were sampled: old-fields (vineyards that had been abandoned for economic reasons), currently productive vineyards, and pine tree plantations. Six replicates were sampled for every combination. None of the areas contained livestock, and only very light grazing by small wild antelopes occurs within larger connected remnant patches.

Remnant patches were dominated by shrubs and were relatively undisturbed (no recent fires and little to no invasive plant species). Transformed biotopes all had different vegetation composition and level of disturbance (See Fig. 6 in Appendix). Old-fields contained indigenous plant communities similar to those of remnants, depending on the time since

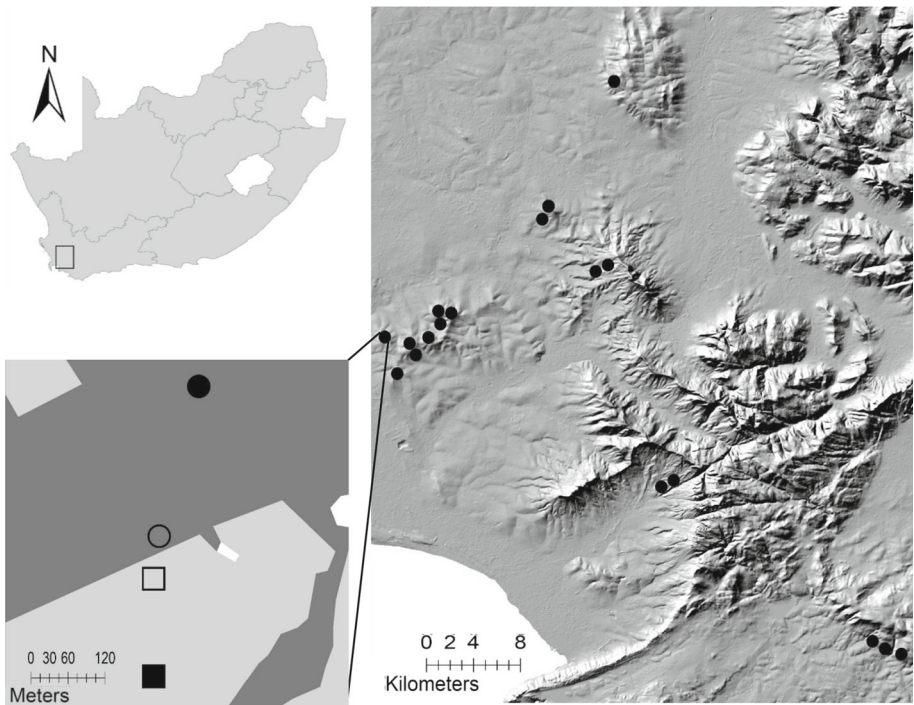


Fig. 1 Map of study area. Righthand side map shows sampling locations throughout the Cape Floristic Region. Bottom left map shows sampling plots at sampling locations. White areas represent urban, light grey represents the transformed biotopes and dark grey represents natural vegetation. Circles are sampling locations in the natural vegetation, the filled circle represents the core (interior) location and hollow circle represents the edge location. Squares are sampling area in the transformed biotopes, the filled square represents core location and hollow square represents edge location

the vineyards had been removed, as well as some weedy herbaceous species. Vineyards contained a greater proportion of weedy herbaceous plant species and bare ground, depending on the cover crop management regime. All vineyards operated under integrated production regimes according to the South African Integrated Production of Wine certification programme (<https://www.ipw.co.za/>). In turn, plantations had low plant cover, most often weedy herbaceous plant species and some hardy native fynbos shrubs. Geographical co-ordinates of sampling locations with details of site characteristics are given in Appendix (see Table 5).

Spider sampling was undertaken at the core (interior) and edge of every transformed biotope, as well as the core and edge of every adjacent remnant natural vegetation patch. Edge plots were about 10 m from the boundary. Locations of plots along each transect were selected to be as linear as possible, while avoiding external influences from other transformed biotopes. The average transect length was 340 m. Only large remnant patches were selected to avoid core plots being influenced by edge effects (average distance of 180 m from boundary). Transects on the same farm were on average separated by 220 m.

Data collection

Pitfall trapping and vacuum sampling was used to sample spiders. Two pitfall traps (6.5 cm wide and 9 cm deep), separated by 2 m, were filled with 70% ethylene glycol to target ground-dwelling spiders. Pitfalls were left open for six days at a time, once per sampling season. After retrieving the pitfalls, the spiders were removed and stored in 75% ethanol for later identification.

A fuel powered handheld leaf blower (Stihl BG 56 C) set to vacuum with a mesh bag attached to the front of the nozzle was used to capture vegetation-dwelling spiders. Two parallel transects were walked with the vacuum sampler across the pitfall sampling locations after pitfalls were collected. To standardise vacuum sample size, the nozzle was inserted into the vegetation 50 times per vacuum transect, resulting in a total of 100 insertions per plot. Transect length varied due to amount of dead vegetation at each plot, with an average length of 75 m. Dead vegetation was not sampled. Vacuum samples were transferred into plastic bags and stored at -40°C before sorting.

Spiders from the pitfalls and vacuum sampling were sorted to morphospecies level (Oliver and Beattie 1996) before being identified by a spider taxonomist. All reference spider species (including juveniles) were identified to at least genus level, and where possible, to species level. However, to avoid unintentional duplication of species identified to genus level only, spiders were grouped and analysed at the genus level for all statistical analyses. Each genus was classified as either web-, plant- or ground-dwelling (Dippenaar-Schoeman et al. 2010). Furthermore, to gain insight into the response of sensitive spiders, species, where possible, were assigned an Arachnida Biodiversity Index (ABI) score. Dippenaar-Schoeman et al. (2010) developed the ABI, which uses data on a species geographic distribution and local abundance, to indicate the geographical extent of rare and range-restricted species. An ABI of 1 indicates a common widespread and habitat-generalist species, whereas an ABI of 9 indicates a highly sensitive, range-restricted species (Dippenaar-Schoeman et al. 2010).

A total of 64 plots were sampled. Two plantation transects were destroyed by a natural fire, and so only four plantation transects, but six old-field and vineyard transects, are used here. Plant surveys were conducted at every site using the point intercept line transect method. At every 1 m interval along the 50 m transect, a 5 mm thick, 3 m long rod was placed perpendicular to the ground. All plant species intercepting the rod were recorded. At every 5 m interval, vegetation height was measured, along with percentage presence of rocks. Two parallel 50 m plant transects were surveyed at each plot, spanning over the pitfall and vacuum sampling area. Plant species and their associated growth form (tree, shrub, succulent, fern, geophyte, herbaceous, graminoid and restio) were later identified for statistical analysis.

Environmental variables collected at each site included plant species richness, plant growth form cover, average vegetation height, % rockiness, amount of natural vegetation within a 500 m buffer, and topographic complexity measured as the standard deviation of the slope of the soil surface within a 50 m buffer. Amount of natural vegetation and topographic complexity was calculated in ArcMap. Along with these continuous environmental variables, additional categorical variables were created, which included land use (remnant natural vegetation, old-field, plantation, or vineyard), transect type (old-field, vineyard or plantation transects), and transect location (natural core/edge or associated transformed core/edge) (see Table 6 in Appendix).

Data analyses

Spider data for the two sampling methods and seasons were pooled and grouped at the genus level. Rarefaction curves plotted per transect (see Fig. 7 in Appendix) were not fully saturated, which further motivated the analysis of spiders at the genus level. Thus, spider genus richness was used as response variable in univariate analyses, and assemblage composition based on spider genera was used in multivariate analyses. All analyses were done for overall spiders, as well as web-, plant- and ground-dwelling spiders. The exponent of Shannon diversity index was calculated for all univariate response variables to allow for comparison between sampling locations. Furthermore, the exponent Shannon diversity index takes into account the rarity and commonness of species at each site. Exponent Shannon diversity index values were calculated using the *vegan* package (Oksanen et al. 2019). Moran's I autocorrelation index, as well as Monte-Carlo test, in the *ape* package (Paradis and Schliep 2018), was used to test whether response variables and assemblages were spatially auto-correlated.

As exponent Shannon diversity showed normal and Poisson distribution, we used generalised linear mixed modelling from the *glmmTMB* package, which allows for more varying response distributions (Brooks et al. 2017). A Gaussian distribution was specified for overall Shannon index, ground-dwelling Shannon index, and plant-dwelling Shannon index, while a Poisson distribution was specified for web-dwelling Shannon index. In all *glmm* models, transect type was used as a random variable to address the hierarchically nested nature of our sampling design. A correlation matrix was first calculated to determine whether explanatory variables were correlated (see Fig. 8 in Appendix).

To address our first two aims, whether spider diversity differs between different land use types and the severity of associated edge effects, we created two models. The first model contained only land use type (4-level factor) e.g. remnant natural vegetation patches, old-fields, plantations, and vineyards, with transect type as random effect (*Land use* model). The second model only contained the sampling locations along the transect for every transect type (12-level factor) e.g. old-field core and edge, as well as the paired adjacent remnant natural vegetation patch core and edge, and transect type as random effect (*Transect* model). Post hoc tests were performed using the *TukeyHSD* function to identify significant differences between categorical variables.

To address our third aim, understanding the mechanisms driving spider diversity within the transformed landscape, we created a model using a subset from the overall dataset, which contained data on only the transformed biotope cores. We used plant species richness, average vegetation height, % rockiness, amount of natural vegetation, and topographic complexity, as well as transect type as a random effect, in the model (*Transformed biotope* model). These variables were used in a global model to perform model selection using the *dredge* function within the *MuMIn* package (Barton, 2019). After model selection, model averaging was performed on a subset of the best models ($AICc < 2$) using the *MuMIn* package (Barton 2019). Averaging could not be performed when the top subset of models only contained one model. In these cases, estimates for the top model are reported.

To test the response of spider assemblages, we used the *manyglm* function within the *mvabund* package (Wang et al. 2012). This function fits multiple generalised linear models to all combinations of variables between an assemblage and environmental data set, thus allowing effects to be identified at the assemblage level. The *Land use*, *Transect* and *Transformed biotope* models used in the univariate modelling were also used for multivariate modelling. For the *Transect* model, we modelled transects separately. All the multivariate models were fitted with negative binomial distribution, assuming a quadratic

mean–variance. Test statistics were calculated based on the ‘pit-trap’ resampling method, with 999 permutations. To identify significant differences between categorical variables, pairwise comparisons were performed using 999 permutation within the *mvabund* package (Wang et al. 2012).

To visualise the direction of spider response at the family level, we performed a fourth corner analysis using the *traitglm* function in the *mvabund* package (Wang et al. 2012). The fourth corner analysis pertains to how traits of organisms can explain variation in environmental response across assemblages. However, here, we did not use trait data, but rather spider family as a grouping variable, thereby allowing us to identify which spider families respond to specific modelled variables. The fourth corner model was fitted with negative binomial distribution and with a LASSO penalty. The LASSO penalty reduces small environmental-trait relationship coefficients to 0, thereby reducing the effects from spider families with small numbers of individuals.

Lastly, to address our fourth aim, how plant communities drive spider assemblage patterns within modified land use types, we performed non-metric multidimensional scaling (NMDS) using the *metaMDS* function within the *vegan* package (Oksanen et al. 2019). NMDS is an unconstrained ordination method that represents pairwise dissimilarity between objects in low dimensional space, where sites with similar species are plotted close together, and sites with dissimilar species are placed further apart. Furthermore, using the *envfit* function, environmental variables can be identified which are driving the site distribution pattern (Oksanen et al. 2019). Thus, we used NMDS to identify the influence that plant growth forms have on shaping spider assemblages among different transformed biotopes. NMDS was performed using Bray–Curtis dissimilarity. All statistical analyses were performed in R version 3.6.1 (R Core Team 2013).

Results

Spider diversity throughout the agricultural mosaic

No spatial autocorrelation was detected for univariate response variables (at $p < 0.1$) or assemblages (at $p < 0.07$). A total of 1 426 spider individuals (with juveniles included) were collected during this study, with a total of 71 spider genera from 30 families (see Table 7 in Appendix). A total of 761 individuals were plant-dwelling, 495 were ground-dwelling and 170 were web-dwelling spiders. The most diverse families were Thomisidae consisting of 11 genera, followed by Gnaphosidae and Salticidae with eight genera each. The most abundant families were Thomisidae with 256 individuals, followed by Salticidae with 222 individuals and Oxyopidae with 219 individuals. Spider families within old-fields were very similar to those of remnant natural vegetation patches in terms of diversity and abundance, with Thomisidae, Oxyopidae, Salticidae, and Philodromidae being the most abundant families within old-fields and remnants. Gnaphosidae, Oxyopidae, and Amaurobiidae were the most abundant families within vineyards, whereas, Thomisidae, Philodromidae and Amaurobiidae were the most abundant families within alien tree plantations.

When considering rare and range restricted species, numerous species of conservation concern were sampled. *Diores simoni* (ABI of 7) was sampled within all the different land use types. *Drassodella septemmaculata* (ABI of 7) occurred within an old-field and a plantation site, whereas *Zelotes broomi* (ABI of 7) only occurred within a plantation site. *Chresiona invalida* (ABI of 6) was sampled within vineyards.

Factors driving spider diversity

Overall and plant-dwelling spider diversity was significantly affected by land use type (Table 1). Post hoc tests showed that overall spider diversity was significantly lower in vineyards than in remnants and old-fields, whereas spider diversity in the other three land use types did not significantly differ (Fig. 2). Additionally, overall, plant-, and ground-dwelling spider diversity was significantly affected by transect location (Table 1). Transformed cores consistently had the lowest spider diversity compared to other sampling locations along transects (Fig. 3). Spider diversity declined sharply across the remnant-vineyard edge, with the lowest diversity of all the sampling locations in the vineyard core (Fig. 3). However, diversity at the remnant edge bordering vineyards was relatively high. Spider diversity along the old-field transects changed little, and contained the highest spider diversity compared to all other sampled plots, except for natural edge adjacent to vineyards. (Fig. 3). Spider diversity within remnant natural vegetation patches adjacent to plantations had the lowest diversity (edge and core) compared to remnants adjacent to the other land uses. Post hoc tests did not reveal any significant differences in ground-dwelling spider diversity, while plant-dwelling spider diversity showed similar patterns to that of overall spider diversity (see Fig. 9 in Appendix). Within transformed biotope cores, plant species richness had a significant positive effect on overall spider diversity, as well as on plant-dwelling spider diversity (Table 2, see Fig. 9 in Appendix).

Factors influencing spider assemblage composition

Overall, web-, plant-, and ground-dwelling spider assemblages were significantly influenced by land use type (Table 3). Post hoc tests showed that the overall and plant-dwelling spider assemblages within vineyards was significantly different from that of old-fields (deviance: 112.19, p-value: 0.036; deviance: 55.95, p-value: 0.037) and remnant natural vegetation (deviance: 130.26, p-value: 0.01; deviance: 66.90, p-value: 0.013). The web-dwelling spider assemblages within plantations was significantly different from that of remnant natural vegetation (deviance: 33.14, p-value: 0.011). No difference was detected between old-fields and remnant natural vegetation or plantations. Post hoc tests did not reveal any significant differences in ground-dwelling spider assemblage structure. The fourth corner analysis revealed that abundances of Araneidae, Philodromidae, Salticidae and Thomisidae negatively correlated with vineyards, whereas Clubionidae, Gnaphosidae

Table 1 Results obtained from generalised linear mixed effects models using the exponent of the Shannon index

Model	Response variable	Explanatory variables	χ^2	p-value
Land use	Overall exp Shannon index	Land use	13.794	0.003
	Web-dwelling exp Shannon index	Land use	3.317	0.345
	Ground-dwelling exp Shannon index	Land use	3.688	0.297
	Plant-dwelling exp Shannon index	Land use	16.746	0.001
Transect	Overall exp Shannon index	Transect location	26.647	0.005
	Web-dwelling exp Shannon index	Transect location	7.061	0.794
	Ground-dwelling exp Shannon index	Transect location	19.868	0.047
	Plant-dwelling exp Shannon index	Transect location	24.554	0.011

Significant variables in bold

Fig. 2 Box plots indicating significant results between overall exponent of the Shannon index and land use type. Different characters above box plots indicate significant differences

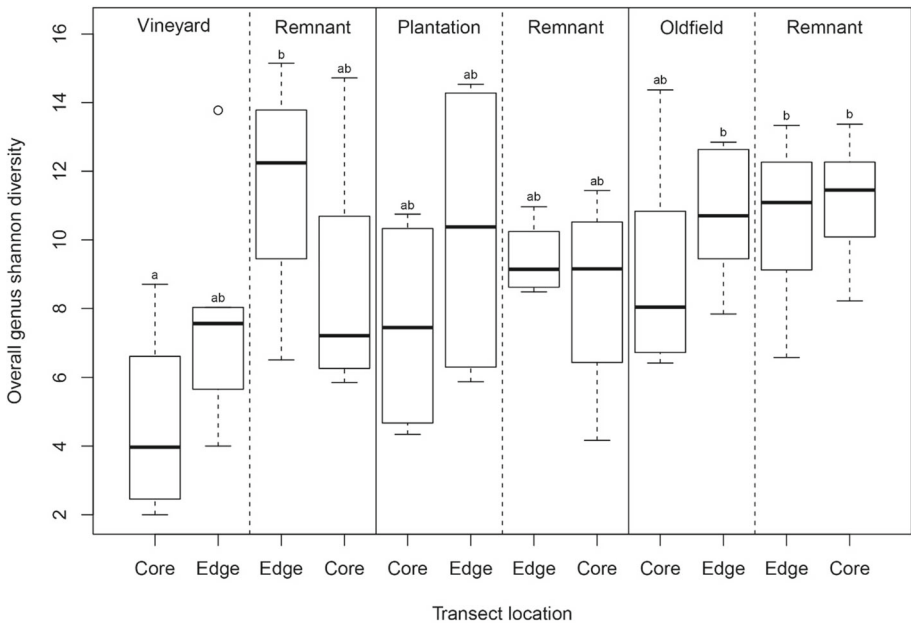
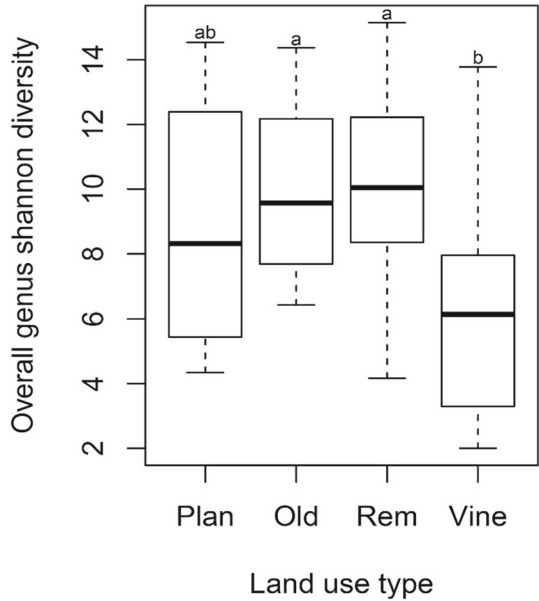


Fig. 3 Box plots indicating significant results between overall exponent of the Shannon index and transect location. Characters above box plots indicate significant differences

and Zodariidae responded positively (Fig. 4). Ammoxenidae responded negatively towards old-fields, whereas Scytodidae responded positively (Fig. 4). Lastly, Linyphiidae showed a positive response towards plantations (Fig. 4).

Table 2 Model-averaged estimates (conditional average) of explanatory variables within the transformed landscape, predicting overall, plant-dwelling, web-dwelling and ground dwelling exponent (exp) Shannon index

Model	Response variable	Explanatory variables	Estimate	SE	95% CI	RI	#Models
Transformed biotope	Exp Shannon index	Plant richness	2.060	0.686	0.715; 3.405	NA	1
	Web-dwelling exp Shannon index	Average plant height	0.254	0.192	– 0.159;	0.33	1
	Ground-dwelling exp Shannon index	Amount of natural habitat	0.528	0.329	– 0.189;	0.35	1
	Plant-dwelling exp Shannon index	Plant richness	1.582	0.428	0.648; 2.517	1	2
		Amount of natural habitat	– 0.671	0.405	– 1.562;	0.29	1

Significant variables in bold

RI relative importance

#Models = number of containing models. Relative importance for top model only could not be calculated and indicated by NA

Table 3 Results from *manyglm* for *Land* use model as well as for *Transect* model separately

Model	Community	Explanatory variables	Deviance	p value
Land use	Overall	Land use	321.2	0.001
	Web dwelling	Land use	69.18	0.007
	Plant dwelling	Land use	132.3	0.003
	Ground dwelling	Land use	119.7	0.019
Old-field	Overall	Transect location	165.8	0.326
	Web dwelling	Transect location	23.6	0.711
	Plant dwelling	Transect location	65.55	0.526
	Ground dwelling	Transect location	76.6	0.09
Vineyard	Overall	Transect location	231.2	0.005
	Web dwelling	Transect location	24.2	0.298
	Plant dwelling	Transect location	107.7	0.009
	Ground dwelling	Transect location	99.28	0.02
Plantation	Overall	Transect location	158.5	0.145
	Web dwelling	Transect location	45.57	0.039
	Plant dwelling	Transect location	61.45	0.268
	Ground dwelling	Transect location	51.5	0.345

Significant variables are in bold

Overall, plant- and ground-dwelling spider assemblages were significantly influenced by transect location along the vineyard transect, whereas web-dwelling spider assemblages were significantly influenced by transect location along the plantation transect (Table 3). Post hoc tests showed that overall spider assemblages within vineyard core sites were

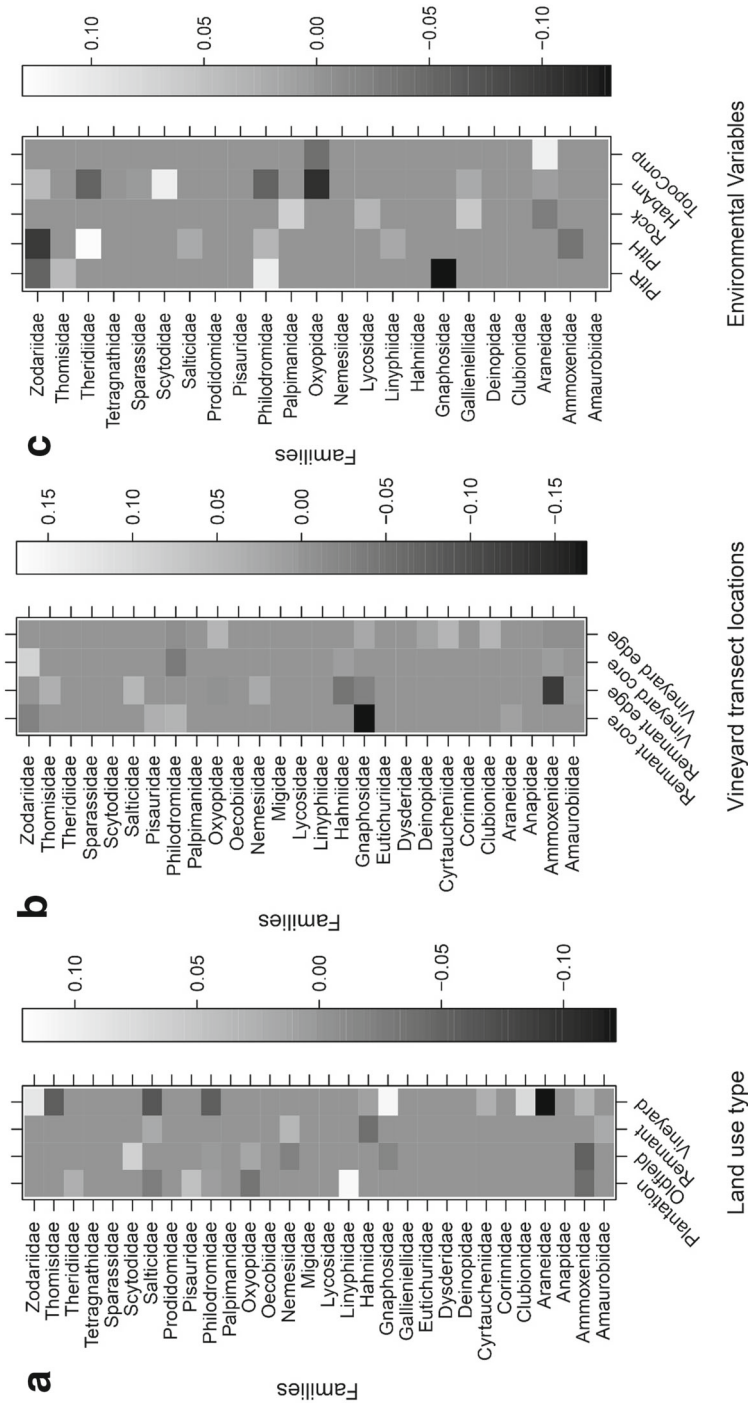


Fig. 4 Fourth corner analysis showing coefficients for **a** family and land use type, **b** family and vineyard transect location, and **c** family and environmental variables

Table 4 Results from *manyglm* for the *Transformed biotope* model

Community	Explanatory variables	Deviance	p-value
Overall	Plant richness	89.86	0.024
	Average plant height	48.44	0.28
	Rockiness	73.24	0.062
	Amount of natural habitat	83.94	0.021
	Topographic complexity	63.93	0.017
Web dwelling	Plant richness	4.802	0.655
	Average plant height	14.897	0.105
	Rockiness	28.293	0.003
	Amount of natural habitat	11.379	0.091
	Topographic complexity	11.352	0.057
Plant dwelling	Plant richness	60.25	0.013
	Average plant height	16.26	0.377
	Rockiness	17.42	0.434
	Amount of natural habitat	45.03	0.013
	Topographic complexity	43.34	0.008
Ground dwelling	Plant richness	24.808	0.136
	Average plant height	17.278	0.406
	Rockiness	27.534	0.082
	Amount of natural habitat	27.538	0.078
	Topographic complexity	9.234	0.5

Significant variables are in bold

significantly different to those of the adjacent remnant edge (deviance: 94.53, p-value: 0.046). No other significant difference was detected between any sampling locations within all other transects. For the vineyard transect, the fourth corner analysis showed that Ammoxenidae responded negatively towards the remnant edge adjacent to vineyards, and Gnaphosidae responded negatively towards remnant core adjacent to vineyards (Fig. 4). Zodariidae showed a positive response towards vineyard cores (Fig. 4).

Within the transformed core, overall and plant-dwelling spider assemblages were significantly influenced by plant species richness, amount of natural vegetation within the landscape, as well as by topographic complexity (Table 4). The web-dwelling spider assemblage was significantly influenced by rockiness (Table 4). The fourth corner analyses revealed that Gnaphosidae and Zodariidae were negatively influenced by plant species richness within the production landscape, whereas Philodromidae were positively influenced (Fig. 4). Furthermore, Zodariidae and Ammoxenidae were negatively influenced by average vegetation height, whereas Theridiidae was positively influenced (Fig. 4). Rockiness had a positive influence on Gallieniellidae and Palpimanidae, but a negative influence on Araneidae (Fig. 4). The amount of natural vegetation within the landscape had a negative influence on Oxyopidae, Philodromidae and Theridiidae, but a positive influence on Scytodidae (Fig. 4). Lastly, Araneidae was positively influenced by topographic complexity (Fig. 4).

Herbaceous plant cover and restio cover had a significant effect (r^2 : 0.4; p-value: 0.03 and r^2 : 0.43; p-value: 0.025) on spider assemblage patterns within the production landscape. Restio cover was driving spider assemblages within old-fields, whereas herbaceous plant cover was driving assemblages within vineyards (Fig. 5), which were characterised

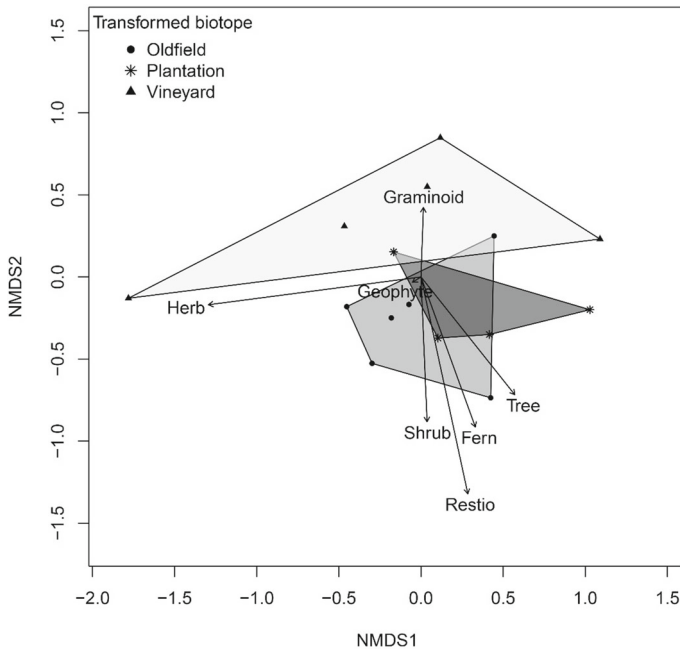


Fig. 5 NMDS plot showing spider genera grouping per transformed biotope and plant growth form cover as vectors driving spider site distribution patterns (2 dimension, stress = 0.155)

by graminoid and herbaceous plants (see Fig. 6 in Appendix). Old-fields and plantations both had similar plant growth form diversity compared to remnant patches of natural vegetation. However, old-fields had higher cover of graminoid, herbaceous, restio and shrub growth forms compared to plantations, whereas plantations had higher tree cover (see Fig. 6 in Appendix).

Discussion

Spider diversity within the agricultural mosaic

The agricultural mosaic of the CFR supports high spider diversity and diverse assemblages, with numerous rare and range-restricted spider species occurring throughout the mosaic, indicating the value of the mosaic for spider conservation. Furthermore, the number of spider individuals sampled within this study is comparable to other studies conducted within the CFR (Gaigher and Samways 2014; Gaigher et al. 2016; Theron et al. 2020). However, sampling effort for spiders within fynbos has been low (Foord et al. 2011), but with some studies focused on the agricultural mosaic (Gaigher and Samways 2010, 2014; Gaigher et al. 2016; Arvidsson et al. 2020), which suggests that more research on spider diversity within the CFR mosaic is needed.

Factors driving spider diversity within the agricultural mosaic

Remnant natural vegetation patches had the highest spider diversity, as previously reported for the CFR (Gaigher et al. 2016). Sparing remnants of natural vegetation within a

production landscape is an effective tool for conserving biodiversity across farmland mosaics (Ekroos et al. 2016; Balmford et al. 2018), especially through provision of source habitats (Duelli and Obrist 2003), and as refuges during times of high disturbance within the production landscape (Gaigher and Samways 2014), while enabling species persistence across spatial and temporal scales (Saura et al. 2014). The effectiveness of these remnant habitats for biodiversity ultimately depends on the surrounding landscape. More so, if managed sustainably, is pivotal for arthropod conservation moving forward (Samways 2015), especially if different land use types with varying management intensities are maintained (Birkhofer et al. 2017).

The agricultural mosaic supports diverse spider assemblages (Birkhofer et al. 2017), thereby contributing to spider conservation at the landscape scale. Here, we found that vineyards contained different spider assemblages compared to old-fields and remnant patches. Also, vineyards had lowest spider diversity, which mirrors earlier results (Gaigher and Samways 2010, 2014). The sampled vineyards all operate under integrated production regimes. This approach allows careful use of agrochemicals, and therefore the low diversity might be caused by pesticide application. Nevertheless, actively managed vineyards can still support distinct spider assemblages, and diversity can be improved within vineyards by increasing plant species richness, specifically herbaceous plant species (Winter et al. 2018; Paiola et al. 2020). Here, we add to this, showing that herbaceous plant species influence assemblage patterns within vineyards. The effect of plant richness on spiders might be indirect via its arthropod prey species, as spiders within the CFR mosaic are strongly influenced by prey abundance (Gaigher et al. 2016). This corresponds with findings from organic fruit orchards of South Africa, showing that the type of weed species occurring within an orchard plays an important role in spider predator–prey interactions (Arvidsson et al. 2020).

Old-fields supported high spider diversity, and contained similar spider assemblages to remnant patches of natural vegetation. Similar patterns of diversity have previously been shown for parasitoids within the CFR production landscape (Gaigher et al. 2016). However, spider families responded differently towards old-fields, which could be due to differences in the ecological traits of different families (Schmidt et al. 2005; Gallé et al. 2019). Ammoxenidae, also known as termite hunters, showed a negative response, whereas Scytodidae, also known as spitting spiders, showed a positive response. Both these families contain mostly ground dwelling spiders and difference in response might be attributed to their different ecological traits. Additionally, the negative response of Ammoxenidae might be seasonal, corresponding to the seasonal occurrence of their termite prey (Haddad et al. 2016). Thus, sampling spiders throughout the year might provide further, nuanced results.

Plant composition within old-fields was similar to that of remnant patches when compared to other transformed biotopes, and restios were found to influence old-field spider assemblages. Old-fields retained herbaceous and graminoid species in high abundance, similar to the plant composition of vineyards, which suggests that some old-fields might suffer from legacy effects from vineyard abandonment (Helm et al. 2019). However, results from Europe indicate that fallow fields, independent of age, can still act as a source habitat with high activity density and spillover for some spider families (Birkhofer et al. 2018). Nevertheless, our results show that old-fields may be able to increase the functional connectivity within the agricultural mosaic by providing greater permeability for fynbos spiders.

Overall, spider diversity can be enhanced within the production landscape through increasing plant species richness. Here, even plantation sites were able to support fairly

high spider diversity. This contrasts with previous findings that show plantations to affect spider diversity worse than vineyards (Magoba and Samways 2012). One explanation for this could be due to the plant species sampled within our plantations, as plantations had some of the same components of remnants, but in lower abundance. Web-dwelling spiders responded positively towards plantations, specifically the Linyphiidae, and these web building spiders might benefit from heterogeneity in vegetation structure within the plantations (Oxbrough et al. 2005). In general, exotic timber plantations have significant negative impact on arthropod diversity. However, spider assemblages can recover quickly once plantations are removed (Magoba et al. 2015).

How the production landscape is managed will ultimately influence the outcome of conservation goals (e.g. increasing function connectivity) within an agricultural mosaic (Driscoll et al. 2013). Not all transformed biotopes are similar, and some provide greater resistance to movement than others. This differential permeability of different land-uses is likely to influence patterns at habitat edges. Here, we consistently found highest spider diversity at the habitat boundary, except for remnant edges adjacent to plantations where we found low spider diversity. Nevertheless, the trend of aggregated richness at habitat boundaries is also supported by other studies (Evans et al. 2016; Guiller et al. 2016), and can be explained through the proliferation of generalist species that can exploit resources in multiple land uses (Pardini et al. 2009). Dennis and Fry (1992) showed that field margins can increase arthropod diversity on farmland, especially predatory arthropods, due to an increase in prey species at habitat edges. In addition, the permeability of the biotope is dependent on plant cover density within it, which can change throughout the year (Vasseur et al. 2013), impacting local arthropod distribution patterns across the production landscape.

Not all spiders here responded similarly to plant richness within the production landscape. Ground-dwelling spiders within the Gnaphosidae and Zodariidae were negatively affected by plant richness, whereas plant-dwelling spiders (Philodromidae) were positively influenced. Increasing the proportion of natural vegetation cover at the landscape scale within the agricultural mosaic had a strong positive influence on the spider assemblages, supporting results from Europe (Schmidt et al. 2008). However, there were contrasting responses, with Oxyopidae, Philodromidae and Theridiidae responding negatively, whereas Scytodidae responded positively. Oxyopidae, Philodromidae and Theridiidae are common spider families within the agricultural landscape (Dippenaar-Schoeman et al. 2013) and might benefit from increased cropland within the landscape. Furthermore, the structure of the vegetation can also play an important role for spiders, as ground dwelling spiders (Zodariidae and Ammoxenidae) responded negatively to average vegetation height. Entling et al. (2007) found that shading from vegetation was an important predictor for spiders, which might be an important driver here for ground dwelling spiders. Differential responses of different families could also be due to different dispersal abilities. Ballooning of certain spider taxa can enable relatively long-distance passive dispersal (Hogg and Daane 2010) and may obscure species responses to habitat quality (Schmidt et al. 2005). Although data are not currently available on this trait for the local taxa, this would nonetheless be an interesting topic for future assessments.

In our rocky sclerophyllous sampling area, rockiness had a negative influence on web-building spider assemblage, specifically spiders within the Araneidae, potentially due to reduced opportunity for web attachments. Additionally, rockiness positively influenced ground-dwelling families (Gallieniellidae and Palpimanidae), which supports previous findings (Theron et al. 2020). Rockiness creates microclimatic conditions that influences a variety of taxa (Crous et al. 2013), thereby adding to the heterogeneity of landscapes.

Spider conservation and management implications

An effective agro-ecological conservation framework requires incorporation of both the protection of remnant patches of natural vegetation and sustainable management of the production landscape (Perfecto and Vandermeer 2010). However, production landscapes comprise a variety of landscape elements, and to prioritise conservation effort and improve landscape management in agricultural environments, keystone structures need to be identified (Tews et al. 2004; Rosas-Ramos et al. 2018). Here we identified old-fields as an important supplementary habitat element to remnant patches, conserving high spider diversity and sustaining spider assemblages similar to those of remnant natural vegetation. Old-fields therefore increase the area of occupancy for many spider species through an increase in the structural and functional connectivity across the landscape mosaic (Tischendorf and Fahrig 2000). However, some old-fields, especially those with high amounts of graminoids and weedy herbaceous plant species, suffer from legacy effects, and active old-field restoration is recommended (Helm et al. 2019). Midoko-Iponga et al. (2005) demonstrated that by reducing weedy herbaceous species within old-fields of the CFR, native plant species establishment can be improved, thereby allowing old-fields to resemble native remnant vegetation more closely. To add to this, future work could focus on how the amount of natural vegetation in the surrounding landscape influences plant composition within old-fields, and how different plant assemblages within old-fields impact arthropod predators. Nonetheless, old-fields hold great conservation value, and their restoration should be incorporated into agri-environmental schemes, especially as fallow fields have been shown to be important for conservation biological control in Europe (Birkhofer et al. 2018).

Protecting semi-natural habitat features within the production landscape helps conserve farmland biodiversity in the CFR (Vrdoljak and Samways 2014; Gaigher et al. 2016). Here we add to this evidence that improving the proportion of natural and semi-natural vegetation throughout the landscape sustains spider assemblages across the production mosaic. It is well known that establishing vegetation within the inter-rows of vineyards can increase farmland biodiversity (Winter et al. 2018; Katayama et al. 2019). Therefore, increasing the complexity and quality of the transformed landscape, via establishment of cover crops, protecting remnant natural vegetation and restoring old-fields, will increase natural enemy diversity, soften the transformed landscape, and allow for more effective habitat boundary crossings. This will help ensure that agro-ecological mosaics function as close as possible to natural systems, thereby providing guarantees for biodiversity and better resilience in these times of great environmental change.

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Data availability Data will be made available upon request.

Compliance with ethical standards

Conflicts of interest Not applicable.

Appendix

See Figs. 6, 7, 8, 9 and Tables 5, 6, 7.

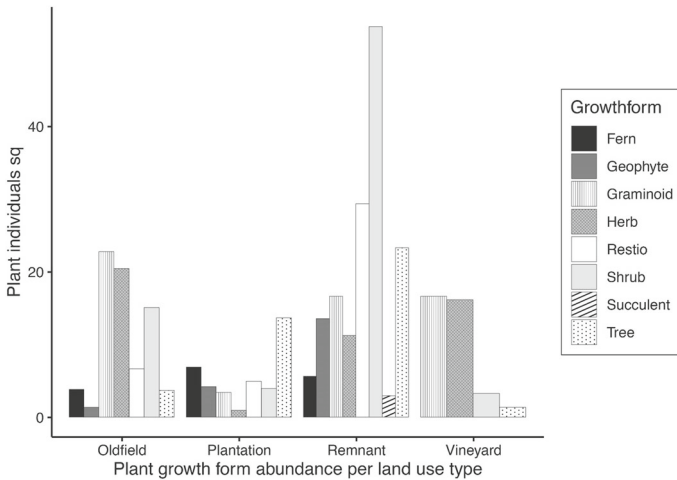


Fig. 6 Bar plot of squared number of plant individuals per growth form grouped within different land use types

Fig. 7 Rarefaction curves per sampling transect

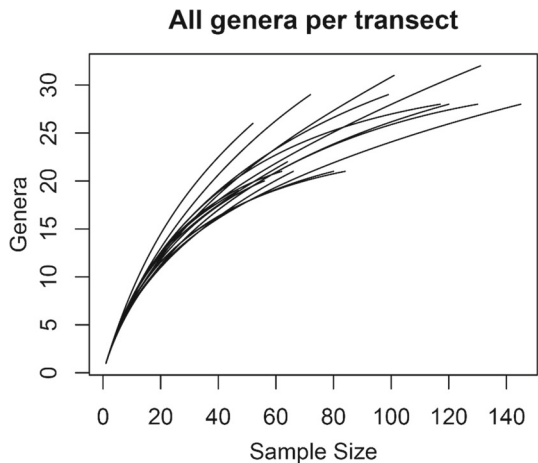
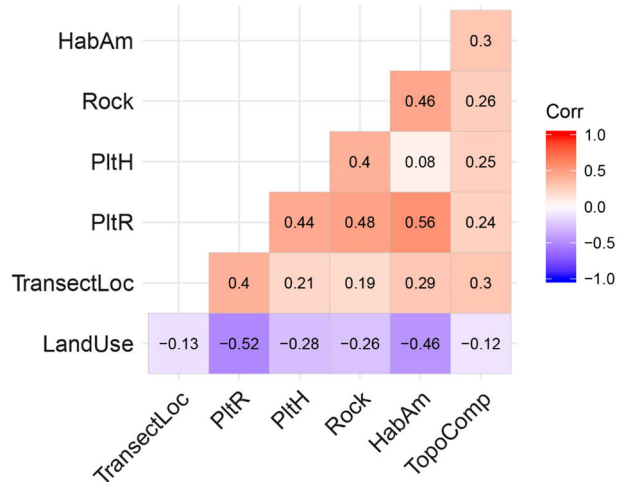


Fig. 9 Significant results obtained through generalized linear mixed effect models. Characters above box plots indicate significant differences. **a** Plant-dwelling exponent of the Shannon index and land use type, **b** Plant-dwelling exponent of the Shannon index and transect location, **c** Overall exponent of the Shannon index and plant richness, and **d** Plant-dwelling exponent of the Shannon index and plant richness

Fig. 8 Correlation matrix based on spearman rank coefficients of explanatory variables



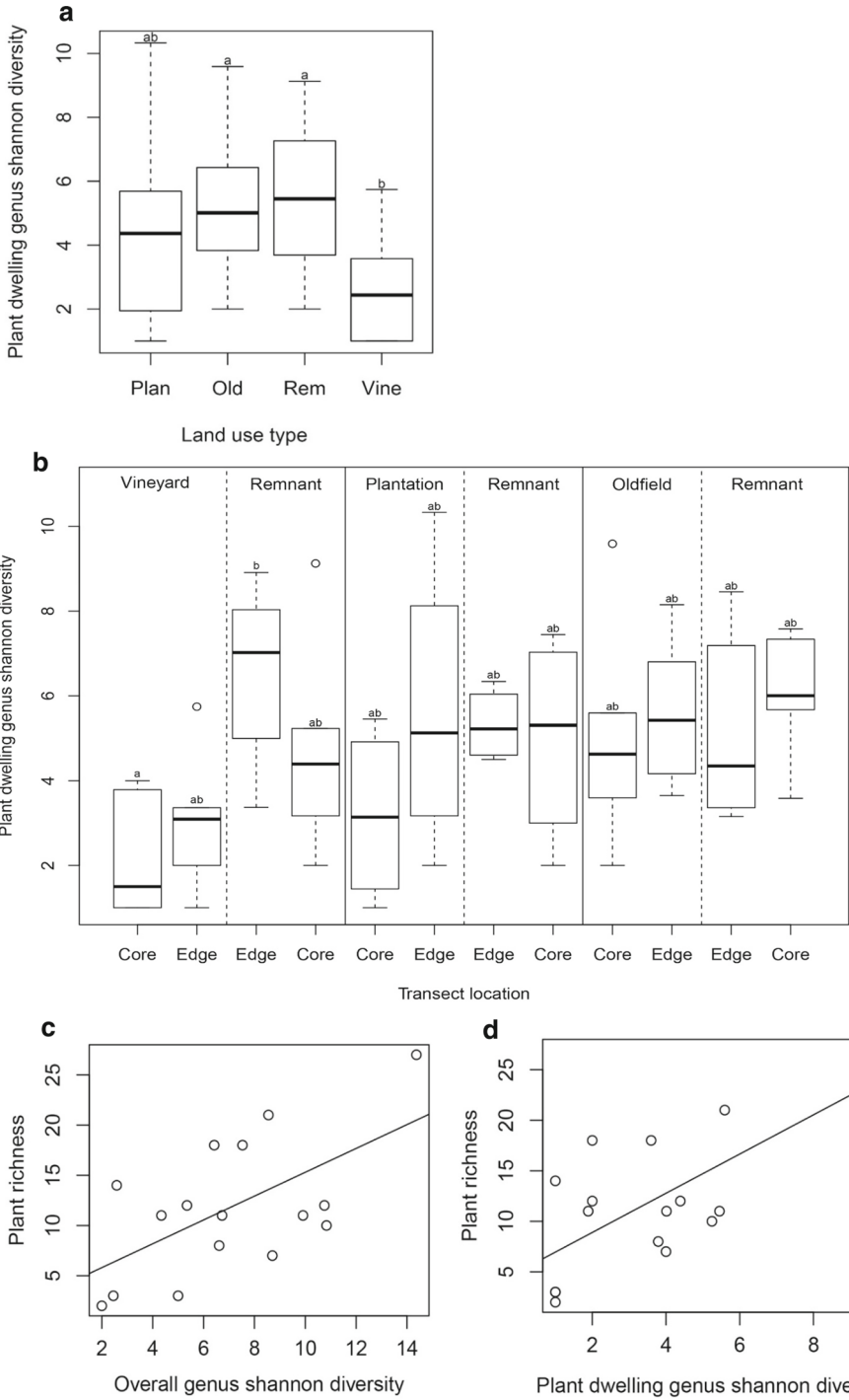


Table 5 Geographical co-ordinates of sampled sites throughout the Cape Floristic Region with additional site characteristics

Land use	Transect	TranLoc	PltR	PltH	Rock	HabAm	TopoComp	LongDD	LatDD
Vine	Vine	VineMC	8	23.41	0	20.05	1.12	18.89	– 33.74
Vine	Vine	VineME	14	39.55	2	31.16	1.54	18.90	– 33.74
Rem	Vine	VineNC	19	111.14	32	48.85	2.22	18.90	– 33.74
Rem	Vine	VineNE	13	131.05	3	33.17	1.57	18.90	– 33.74
Old	Old	OldMC	10	48.36	1	22.03	1.89	18.85	– 33.84
Old	Old	OldME	12	47.73	0	27.00	1.99	18.85	– 33.84
Rem	Old	OldNC	17	79.45	54	57.04	3.04	18.86	– 33.83
Rem	Old	OldNE	17	101.86	0	29.10	2.15	18.85	– 33.84
Vine	Vine	VineMC	3	15.27	5	43.05	2.46	18.86	– 33.84
Vine	Vine	VineME	34	117.50	23	47.77	2.12	18.86	– 33.83
Rem	Vine	VineNC	22	78.86	58	63.93	2.82	18.86	– 33.83
Rem	Vine	VineNE	24	125.00	54	49.06	2.04	18.86	– 33.83
Plan	Plan	InvMC	11	153.89	0	45.95	2.21	19.12	– 34.16
Plan	Plan	InvME	20	37.27	1	51.72	3.03	19.12	– 34.16
Rem	Plan	InvNC	12	87.73	0	77.99	4.16	19.12	– 34.16
Rem	Plan	InvNE	11	73.57	0	54.50	3.43	19.12	– 34.16
Old	Old	OldMC	18	57.14	2	64.41	1.94	19.12	– 34.16
Old	Old	OldME	31	65.45	22	69.85	3.38	19.12	– 34.16
Rem	Old	OldNC	34	75.91	73	78.19	3.14	19.12	– 34.16
Rem	Old	OldNE	34	139.32	49	69.72	3.44	19.12	– 34.16
Vine	Vine	VineMC	7	22.73	0	47.62	1.30	19.12	– 34.16
Vine	Vine	VineME	21	57.86	0	55.41	1.54	19.12	– 34.16
Rem	Vine	VineNC	22	88.41	47	77.19	2.63	19.12	– 34.16
Rem	Vine	VineNE	22	73.86	0	56.00	3.43	19.12	– 34.16
Plan	Plan	InvMC	12	157.73	5	18.91	2.48	18.74	– 33.95
Plan	Plan	InvME	22	132.73	0	18.91	2.91	18.74	– 33.95
Rem	Plan	InvNC	20	127.73	0	12.41	1.97	18.74	– 33.95
Rem	Plan	InvNE	20	104.55	1	18.91	2.85	18.74	– 33.95
Old	Old	OldMC	27	57.18	2	33.66	1.25	18.75	– 33.93
Old	Old	OldME	14	49.50	0	41.37	2.17	18.75	– 33.93
Rem	Old	OldNC	27	110.09	2	60.26	2.04	18.75	– 33.93
Rem	Old	OldNE	21	117.00	0	42.49	2.32	18.75	– 33.93
Vine	Vine	VineMC	14	34.14	0	37.10	1.31	18.75	– 33.93
Vine	Vine	VineME	10	30.77	0	42.65	1.39	18.75	– 33.93
Rem	Vine	VineNC	34	138.95	43	56.26	2.30	18.75	– 33.93
Rem	Vine	VineNE	25	143.68	6	43.93	1.27	18.75	– 33.93
Plan	Plan	InvMC	3	124.55	50	42.31	2.22	18.77	– 33.91
Plan	Plan	InvME	4	94.58	3	51.83	2.27	18.77	– 33.91
Rem	Plan	InvNC	38	140.27	61	69.39	2.89	18.77	– 33.90
Rem	Plan	InvNE	40	112.91	22	54.43	2.15	18.77	– 33.91
Old	Old	OldMC	18	63.27	0	45.73	2.06	18.77	– 33.90
Old	Old	OldME	21	43.27	0	54.26	2.67	18.77	– 33.91
Rem	Old	OldNC	38	94.50	4	74.12	2.74	18.77	– 33.90

Table 5 continued

Land use	Transect	TranLoc	PltR	PltH	Rock	HabAm	TopoComp	LongDD	LatDD
Rem	Old	OldNE	28	119.23	0	54.25	2.75	18.77	– 33.91
Vine	Vine	VineMC	2	12.73	0	18.88	1.02	18.76	– 33.90
Vine	Vine	VineME	5	26.64	2	47.37	1.98	18.77	– 33.90
Rem	Vine	VineNC	54	100.73	33	80.51	3.14	18.77	– 33.90
Rem	Vine	VineNE	17	110.05	2	47.83	1.94	18.77	– 33.90
Plan	Plan	InvMC	11	206.67	21	30.58	3.41	18.95	– 34.03
Plan	Plan	InvME	18	188.64	27	33.59	2.80	18.95	– 34.03
Rem	Plan	InvNC	29	77.05	58	77.88	2.28	18.95	– 34.03
Rem	Plan	InvNE	30	121.09	6	34.94	3.25	18.95	– 34.03
Old	Old	OldMC	21	72.73	8	24.21	0.84	18.94	– 34.03
Old	Old	OldME	20	78.18	7	58.45	1.27	18.95	– 34.03
Rem	Old	OldNC	26	116.82	27	74.40	1.20	18.95	– 34.03
Rem	Old	OldNE	30	121.09	6	67.30	1.05	18.95	– 34.03
Old	Old	OldMC	11	45.68	2	42.15	2.30	18.76	– 33.92
Old	Old	OldME	18	37.73	8	47.87	2.46	18.76	– 33.92
Rem	Old	OldNC	26	90.00	36	60.67	2.72	18.76	– 33.92
Rem	Old	OldNE	30	120.45	17	48.17	2.28	18.76	– 33.92
Vine	Vine	VineMC	12	7.73	1	42.35	2.03	18.73	– 33.93
Vine	Vine	VineME	13	7.00	0	52.76	1.69	18.73	– 33.92
Rem	Vine	VineNC	26	131.86	10	72.41	1.74	18.73	– 33.92
Rem	Vine	VineNE	28	133.77	1	55.43	1.67	18.73	– 33.92

PltR is plant species richness. PltH is the average vegetation height. Rock refers to % rockiness measured. HabAm is the amount of natural vegetation (meter squared) within a 500 m buffer. TopoComp is the topographic complexity measured as the standard deviation of slope within a 50 m buffer

Vine vineyard, *Rem* remnant natural vegetation patches, *Old* old-field and *Plan* plantation. TranLoc refers to sampling location along the transect; where *MC* managed core, *ME* managed edge, *NC* natural core and *NE* natural edge

Table 6 Explanatory variable description used in this study

Variable	Description	Term
Land use	Different land use types sampled. Specifically, natural vegetation, old fields, plantations, vineyards	Fixed
Transect	The transect type containing sampling locations. Specifically, old field transect, plantation transect, and vineyard transect	Random
TranLoc	The sampling location along the transect. Specifically, natural core, natural edge, managed edge type, managed core type	Fixed
PltR	Plant species richness	Fixed
PltH	Average vegetation height	Fixed
Rock	Percentage rockiness	Fixed
HabAm	Amount of natural vegetation measured within 500 m buffer	Fixed
TopoComp	Topographic complexity measured within 50 m buffer	Fixed

Table 7 Spiders collected in this study with functional guild and number of individuals

Family	Genus	Guild	Abundance
Amaurobiidae	<i>Chresiona</i>	Ground dweller	164
Amoxenidae	<i>Amoxenus</i>	Ground dweller	13
	<i>Rastellus</i>	Ground dweller	5
Anapidae	<i>Crozetulus</i>	Web dweller	2
Araneidae	<i>Araneus</i>	Web dweller	4
	<i>Argiope</i>	Web dweller	36
	<i>Hypsacantha</i>	Web dweller	1
	<i>Neoscona</i>	Web dweller	18
Clubionidae	<i>Clubiona</i>	Vegetation dweller	6
Corinnidae	<i>Castianeira</i>	Ground dweller	1
Cyrtacheniidae	<i>Ancylotrypa</i>	Ground dweller	7
	<i>Homostola</i>	Ground dweller	1
Deinopidae	<i>Menneus</i>	Web dweller	7
Dysderidae	<i>Dysdera</i>	Ground dweller	1
Eutichuriidae	<i>Cheiracanthium</i>	Vegetation dweller	9
Gallieniellidae	<i>Drassodella</i>	Ground dweller	3
Gnaphosidae	<i>Camillina</i>	Ground dweller	2
	<i>Leptodrassus</i>	Ground dweller	15
	<i>Megamyraekion</i>	Ground dweller	6
	<i>Nomisia</i>	Ground dweller	1
	<i>Trachyzelotes</i>	Ground dweller	4
	<i>Trephopoda</i>	Ground dweller	2
	<i>Xerophaeus</i>	Ground dweller	40
	<i>Zelotes</i>	Ground dweller	52
Hahniidae	<i>Hahnia</i>	Web dweller	33
Linyphiidae	<i>Agyneta</i>	Web dweller	20
	<i>Erigone</i>	Web dweller	1
Lycosidae	<i>Proevippa</i>	Ground dweller	6
	<i>Trabea</i>	Ground dweller	2
Migidae	<i>Moggridgea</i>	Ground dweller	1
Nemesiidae	<i>Lepthercus</i>	Ground dweller	14
	<i>Pionothele</i>	Ground dweller	2
Oecobiidae	<i>Oecobius</i>	Vegetation dweller	1
Oxyopidae	<i>Hamataliwa</i>	Vegetation dweller	4
	<i>Oxyopes</i>	Vegetation dweller	211
	<i>Peucetia</i>	Vegetation dweller	4
Palpimanidae	<i>Palpimanus</i>	Ground dweller	3
Philodromidae	<i>Philodromus</i>	Vegetation dweller	94
	<i>Thanatus</i>	Vegetation dweller	45
	<i>Tibellus</i>	Vegetation dweller	21
Pisauridae	<i>Afropisaura</i>	Vegetation dweller	9
	<i>Euprostenopsis</i>	Web dweller	2
Prodidomidae	<i>Theuma</i>	Ground dweller	4

Table 7 continued

Family	Genus	Guild	Abundance
Salticidae	<i>Baryphas</i>	Vegetation dweller	63
	<i>Cyrba</i>	Ground dweller	2
	<i>Heliophanus</i>	Ground dweller	107
	<i>Langona</i>	Ground dweller	7
	<i>Pellenes</i>	Ground dweller	6
	<i>Pseudicius</i>	Vegetation dweller	10
	<i>Rhene</i>	Vegetation dweller	1
	<i>Thyenula</i>	Vegetation dweller	26
Scytodidae	<i>Scytodes</i>	Ground dweller	10
Sparassidae	<i>Olios</i>	Vegetation dweller	2
	<i>Palystes</i>	Vegetation dweller	2
Tetragnathidae	<i>Leucauge</i>	Web dweller	1
	<i>Tetragnatha</i>	Web dweller	2
Theridiidae	<i>Latrodectus</i>	Web dweller	1
	<i>Steatoda</i>	Web dweller	2
	<i>Theridion</i>	Web dweller	40
Thomisidae	<i>Avelis</i>	Vegetation dweller	5
	<i>Diaea</i>	Vegetation dweller	29
	<i>Heriaeus</i>	Vegetation dweller	8
	<i>Holopelus</i>	Vegetation dweller	1
	<i>Oxytate</i>	Vegetation dweller	60
	<i>Ozyptila</i>	Ground dweller	1
	<i>Pherecydes</i>	Vegetation dweller	59
	<i>Phrynarachne</i>	Vegetation dweller	3
	<i>Synema</i>	Vegetation dweller	54
	<i>Thomisus</i>	Vegetation dweller	34
Zodariidae	<i>Xysticus</i>	Ground dweller	2
	<i>Diores</i>	Ground dweller	11

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