

Effects of indigenous crop cultivation on mite biodiversity in a biodiversity hotspot

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Exotic crop production negatively affects native biodiversity and alters ecosystem functions and services. Cultivation of indigenous crops can mediate some biodiversity impacts, as these are often less intensively managed than exotic crops and they provide familiar niches for native organisms. *Protea* (Proteaceae), a floricultural crop with high economic value and ecological significance, is harvested within both natural and cultivated systems in South Africa. A multitude of organisms are intimately involved in *Protea* ecology, but many are also pests and pose significant phytosanitary risks. Here we evaluated the impact of *Protea* cultivation on the diversity of mites associated with inflorescences, infructescences, and the rhizosphere in the Greater Cape Floristic Region biodiversity hotspot of South Africa. Natural sites harboured higher mite diversity than cultivated sites, although this was only significant for those mites associated with the rhizosphere or when *Protea* crops were intensively managed. Mite community assemblage composition differed between different management types, localities, and niches. Management actions had little effect on mite assemblage composition in inflorescences and infructescences, likely due to continuous long-distance colonisation from natural areas via pollinators. In contrast, mite assemblages associated with the rhizosphere were highly impacted in all cultivated sites. These results indicate that indigenous crops can sustain substantial above-ground native mite biodiversity, but ecologically important soil assemblages may be severely impacted. Current field-based management strategies are not effective in controlling mite assemblages within *Protea* inflorescences, posing significant phytosanitary risks.

INTRODUCTION

Human population growth continuously places pressure on the natural environment by conversion of natural areas for urbanisation, mining and agriculture (Hooke et al. 2012). About 47% of the earth's land surface area has already been modified, which has substantial negative impacts on biodiversity and ecosystem functions worldwide (Hooke et al. 2012). Most agricultural crops are exotic and are planted as monocultures. Therefore, in addition to replacing natural flora, it leaves very few habitat alternatives for native fauna. Combined with the overuse of pesticides, this leads to substantial biodiversity reduction within nearly all agricultural landscapes, and subsequent reductions in important ecological services (Kremen et al. 2002; Tscharntke et al. 2005).

Negative effects of agricultural intensification (Swinton et al. 2007; Zhang et al. 2007; Power 2010) have been documented for nearly all taxa (e.g., birds and mammals: Andrén 1994; insects: Perfecto et al. 1997; arthropods: Witt and Samways 2004; mites: Bedano et al. 2006). Numerous studies have documented the impact of agricultural practices specifically on mites (e.g., Cortet et al. 2002 – pesticides in a maize field in France; Michereff-Filho 2004 – pesticides in cornfields in Brazil; Bedano et al. 2006 – conversion of agroecosystems to pastures in Argentina; Vanolli et al. 2024 – land use change in sugarcane in Brazil). Ecological studies on mites in agriculture in South Africa are scarce or only alluded to within taxonomic articles (Smith Meyer and Craemer 1999; Halliday 2005) and are mostly limited to unpublished student works (Chikomo 2023).

More sustainable farming practices that promote normal ecosystem processes can assist in biodiversity conservation and the conservation of many ecosystem services (Swinton et al. 2007; Zhang et al. 2007; Power 2010). Also, planting native crops in native ranges may decrease the need for intensive management as native pests are more easily controlled by abundant native predators and parasitoids (Tomich et al. 2011; Wezel et al. 2014; Sasa and Samways 2015). These native crops provide at least some familiar niches for native biota leading to increased biodiversity value (Gurr et al. 2003; Joubert et al. 2009). For example, both wild and cultivated *Cyclopia* species (*Cyclopia maculata* and *Cyclopia genistoides*) maintain high numbers of diverse arthropod communities in the Overberg region of the Western Cape Province, South Africa (Slabbert et al. 2019).

Protea L. (Proteaceae) plants are extensively planted globally for the floricultural industry. Most species and production emanate from the Greater Cape Floristic Region biodiversity hotspot in South Africa (Gerber and Hoffman 2014), where flowers (inflorescences) and fruit (infructescences) are commercially harvested in both cultivated and natural populations (Coetzee et al. 2007). This forms part of a very lucrative fynbos cut-flower market in South Africa that is currently valued at almost R1 billion, and provides employment for nearly 2 500 people (DTIC 2023). However,

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SUPPLEMENTARY DATA

Supplementary Tables S1 and S2 are available online in a separate pdf

these flowers often contain pests (Myburgh et al. 1973; Myburgh and Rust 1975; Coetzee and Giliomee 1985, 1987; Wright 2003; Wright and Saunderson 1995) that pose phytosanitary risks (Hansen and Hara 1994; Reinten and Coetzee 2002; Reinten et al. 2011). Due to their small size and abundance within *Protea* spp., mites (Acari) represent a substantial component of this phytosanitary risk (Myburgh et al. 1973). However, many mite species are saprophytes, detritivores, and microbivores that are essential for natural soil processes (Behan-Pelletier and Walter 2000; Krantz and Walter 2009) or predators that are important for controlling pests (McMurtry et al. 2013).

In addition to the high economic value, *Protea* is also of considerable ecological importance as numerous organisms utilise these plants for shelter, food and movement across the landscape, for example, fungi (Roets et al. 2006, 2012, 2013, Ngubane et al. 2018), insects (Coetzee and Giliomee 1987; Roets et al. 2011; Wright and Samways 2000), and spiders (Coetzee et al. 1990; Zachariades and Midgley 1999). The recent discovery of the complex *Protea*-fungal-mite-bird symbioses (Theron-De Bruin et al. 2018) and the impact of mites on *Protea* pollination (Theron-De Bruin et al. 2024) highlight the importance of investigating the diversity and ecology of mites within the *Protea* system.

As a dominant taxon, *Protea* plays a vital role in maintaining biodiversity in natural systems. However, it is unclear how this role changes under cultivation. An estimated 75% of *Protea* producers use chemical fertilisers and 79% use pesticides (Conradie and Knoesen 2010). Despite this, cultivated Proteaceae may provide habitats for indigenous arthropods and add to the biodiversity value of these production landscapes (Sasa and Samways 2015). The vast number of environments occupied, the large number of different feeding guilds, and their niche specificity and sensitivity, make mites an ideal bioindicator for assessing environmental change (Gulvik 2007). In the present study, we evaluated the impact of agricultural practices on mite assemblages from *P. repens* (L.) L. that may pose phytosanitary problems in inflorescences and infructescences, and also ecologically important assemblages associated with the rhizosphere. We hypothesised that cultivated plants would provide habitat for numerous mite taxa, but that both commercially detrimental (associated with inflorescences and infructescences) and beneficial (associated with rhizosphere) mite biodiversity components would be reduced in commercially grown *P. repens* populations.

METHODS

Study area and design

We identified three study localities in the Western Cape Province of South Africa where natural and cultivated populations of *P. repens* (Figure 1a) occur in close proximity (Figure 2). At each locality, a natural site within a protected area (Figure 1b) [Piketberg, Tamarak farm (32°48'16.3" S 18°38'11.0" E), Kleinmond, Heuningklip farm (34°19'44.9" S 19°04'10.4" E) and Gansbay, Flower valley farm (34°33'11.2" S 19°28'01.9" E)] and a nearby site where *P. repens* was cultivated [(Piketberg, Boesmanzicht farm (Figure 1c) (32°47'31.1" S 18°40'18.3" E), Kleinmond, Honingklip farm (Figure 1d) (34°17'27.5" S 19°08'03.5" E) and Gansbay, Ben Lomond farm (Figure 1e) (34°32'44.9" S 19°30'44.4" E)] were selected no further than 6 km apart (Table 1). At each site, 20 inflorescences (Figure 1f) at the mid-flowering stage (30–50% of individual flowers within inflorescences open), 20 infructescences (Figure 1g) (6–12 months old), and 10 soil samples from the rhizosphere were collected during August to November 2013. Initially, we also collected 50 mature leaves per plant ($n = 10$ plants per site) for

assessing foliar mite communities, but mites were largely absent from leaves so leaves were therefore excluded from further study.

Inflorescences and infructescences were collected from randomly chosen plants (1 structure per plant, plants ~10 m apart) in each population. Soil samples (250 ml, taken from the O horizon – excluding the O_i layer (leaf litter) (Sayer 2006)) (Figure 1h) were collected from the rhizosphere of 10 randomly chosen mature individual plants (10 years and older). Soil and plant structures were individually placed in brown paper bags and stored at 4 °C until further processing within a week after collection.

The collection of mites from inflorescences and infructescences followed methods described in Theron et al. (2012). Briefly, secateurs were used to open the structures by cutting them in half, whereafter the arthropods were shaken out onto a Petri dish from where all mite individuals were collected with fine tweezers and stored in 70% ethanol until sorting. Soil-associated mites were extracted using Berlese funnels (Krantz and Walter 2009) with ethylene glycol (AutoZone Chemicals, South Africa) as a preservative. After four days of extraction, 70% ethanol was added to the ethylene glycol (1:1 ratio) and samples were stored at 4 °C until the individuals were sorted.

Mites were sorted according to the morphospecies concept (Mayr 1996, Oliver and Beattie 1993, Hackman et al. 2017) and counted, whereafter representatives of morphospecies were mounted in HPVA medium (Krantz and Walter 2009) on microscope slides and examined using a Zeiss Axioskop Research microscope. Mites were identified to the lowest taxonomic rank possible using appropriate guides (Krantz and Walter 2009) and with the help of expert mite taxonomists (D. Saccaggi). Reference material was deposited in the National Collection of Arachnida, ARC-Plant Protection Research Institute, Pretoria, South Africa, as well as in the Department of Conservation and Entomology Museum, Stellenbosch University, Stellenbosch, South Africa.

Statistical analyses

Mite communities were compared between the two biotopes (natural and cultivated), the three niche types (inflorescences, infructescences and soil), and the three sample localities (Piketberg, Kleinmond and Gansbay). Diversity measures evaluated included: 1) alpha-diversity (α), including comparisons of mite morphospecies richness and abundance; 2) beta-diversity 1 (β_1), as the changeover in mite community assemblage composition within a particular locality, biotope, or niche (i.e., a measure of beta diversity within a sample type), and; 3) beta-diversity 2 (β_2), as comparisons in mite community assemblage composition between different localities, biotopes or niches (i.e., a measure of beta-diversity between different sample types) (Pryke et al. 2013).

Species richness was estimated using ICE, Chao2 and Jackknife2 (Table 2) in EstimateS TM v.7.5.2 (Colwell 2005, USA) for mite assemblages from each niche within each locality and biotope using 9999 randomisations of samples. These non-parametric and least biased species richness estimators provided the best overall estimates (Hortal et al. 2006). Generalized Linear Models (GLM) performed in Statistica 13 (StatSoft Inc, Tulsa, OK, USA) were used to test factor influence (locality, niche or biotope) on alpha-diversity (species richness and mite abundance). Data sets were tested for normality using Shapiro–Wilk tests and Levene's Test for Homogeneity of Variances and then BoxCox transformed (Osborne 2010). For significant factors, a Games–Howell post hoc test was performed (calculated in R software (R Development Core Team 2013)). For β_1 , presence-absence data were used to calculate Jaccard similarity measures, which were used to evaluate the changeover



Figure 1: a) *Protea repens* mature plant with inflorescences and infructescences, b) *P. repens* in its natural environment, c) Cultivated *P. repens* biotope at Piketberg, d) Cultivated *P. repens* biotope at Kleinmond, e) Cultivated *P. repens* biotope at Gansbay, f) Close-up of mature *P. repens* inflorescence, g) Close-up of *P. repens* infructescence, h) Soil surface above *P. repens* rhizosphere covered with litter.

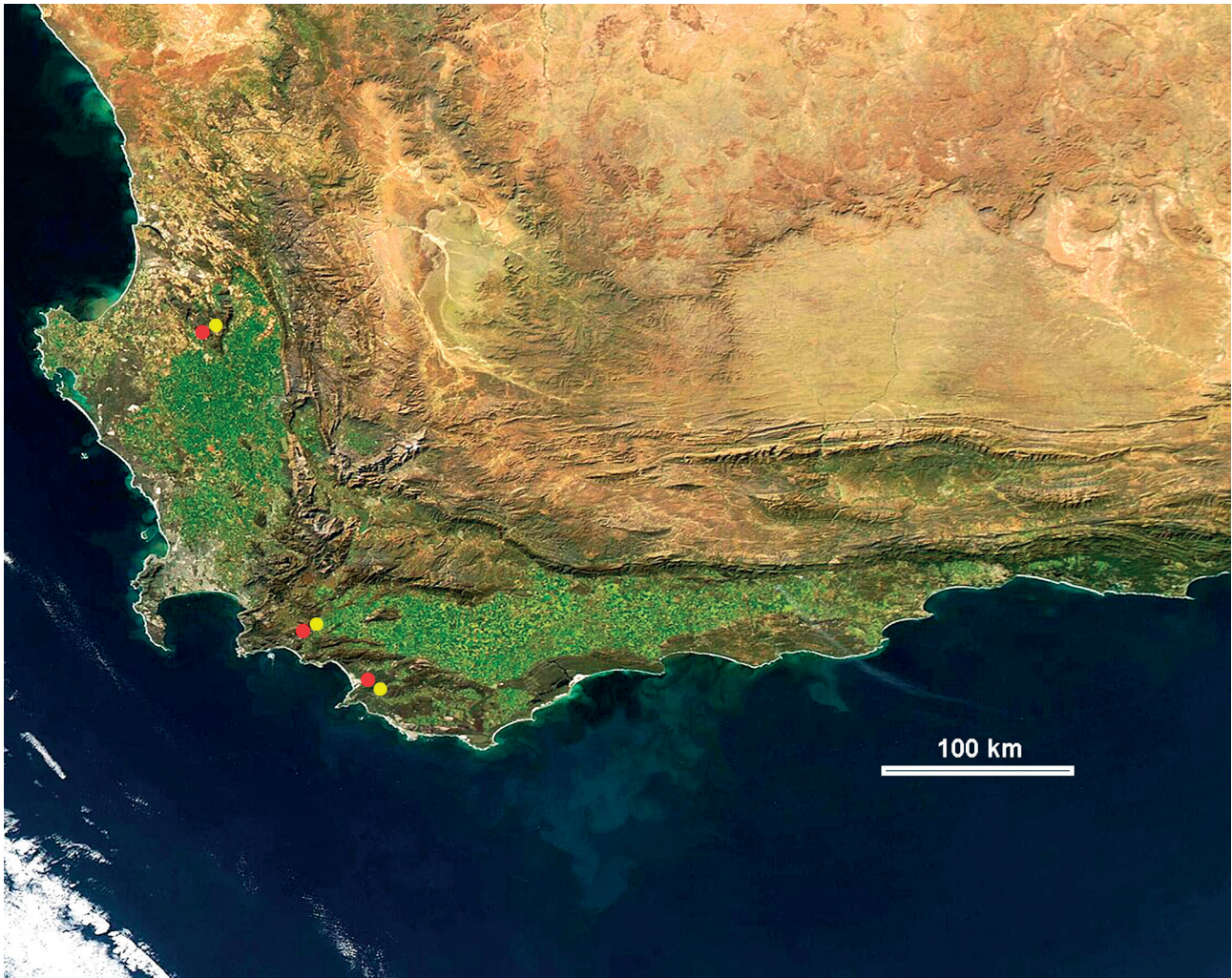


Figure 2: Location of study sites in the Western Cape province of South Africa in protected areas (red) and where *Protea repens* is cultivated (yellow).

in mite assemblage structure within different localities, biotopes and niches (and the interactions between these factors) using permutational analyses of dispersion (PERMDISP) and 9999 permutations in PRIMER 6 (PRIMER-E 2008) (Anderson 2006; Pryke et al. 2013). For β_2 , Bray–Curtis similarity measures using square root transformed abundance data (Anderson 2001) were calculated to compare mite community assemblage structure between factors and their interactions using permutational analysis of variance (PERMANOVA) with 9999 permutations in PRIMER 6 (PRIMER-E 2008). Significant differences within and between factors are reported when $p \leq 0.05$.

RESULTS

Overall, 4 395 individuals from ~82 mite morphospecies (Mayr 1996) were collected (Supplementary Table S1). Species estimates indicated that sampling was adequate to assess mite diversity in our samples (Table 2). All factors tested had a significant influence on mite species richness and abundance, except locality (Table 3). Mite richness and abundance were the highest in soils, then in infructescences, and the lowest in inflorescences (Table 3). However, all factors interacted significantly (Table 3, Figure 3). Piketberg had much lower mite species richness and abundance in the cultivated biotope versus the natural biotope (Figure 3). Mite species richness and abundance were higher within all niches from natural sites compared to niches in cultivated sites, but these differences were small in Kleinmond (Table 2, Figure 3). Mite numbers in the infructescences and inflorescences changed only marginally between the two

biotopes at this locality (Figure 3). At the Gansbay locality, mite numbers were always lower in all niches when plants were in cultivation, but never significantly so (Figure 3).

PERMDISP analyses indicated that the magnitude of changeover in mite assemblage composition differed within different niches and biotopes, but not for localities when overall assemblages were considered (Table 3). When considering niche, β_1 was similar for inflorescences and infructescences, but these were significantly higher than for soil assemblages (Table 3). Cultivated areas had significantly higher β_1 than natural areas when considering overall assemblages (Table 3). However, all factors interacted significantly (Table 3, Figures 4 and 5). When considering the interaction between niche and locality, Piketberg generally had higher β_1 for infructescences and soil than the other localities, but inflorescences were similar (Figures 4a and 5). This was largely due to significantly higher β_1 in the cultivated area at Kleinmond (Figure 4b) that had significant positive impacts on the mite assemblage turnover in inflorescences and soil (Figure 5). In general, however, mite assemblage turnover within inflorescences and infructescences increased due to cultivation (Figure 4c). When investigating the interaction of all three factors, we found a general trend for less change in β_1 diversity in inflorescences and infructescences from cultivated and natural sites (except at Kleinmond), with soil communities particularly significantly affected at Piketberg and Kleinmond (Figure 5).

PERMANOVA analyses indicated that mite assemblage composition was significantly different between nearly all factors tested (Table 3, Supplementary Table S2). The main

Table 1: Sampling sites of *Protea repens* populations assessed in this study, with indication of natural or cultivated status and farming practice.

Locality	Status	Farming practice (as verbally indicated by the landowners)
Piketberg, Tamarak farm	Natural	n.a
Piketberg, Boesmanzight farm	Cultivation	Direct pesticide control and intensive management
Kleinmond, Heuningklip farm	Natural	n.a
Kleinmond, Honingklip farm	Cultivation	Indirect pesticides from surrounding crops with less intensive management
Gansbay, Flower Valley farm	Natural	n.a
Gansbay, Ben Lomond farm	Cultivation	No pesticides with no management as the site will be rehabilitated

Table 2: Observed and estimated species richness of mites associated with *Protea repens* from three different sites (Piketberg, Kleinmond and Gansbay), two biotopes (natural and cultivated) and three niche types (inflorescences, infructescences and soil) in the Western Cape Province, South Africa.

Samples	Observed richness	Overall abundance	ICE*	Chao2** (±SD)	Jackknife2***
Inflorescences					
Natural all	11	606	12.26	11.66 (1.29)	12.05
Cultivated all	10	63	11.34	10.49 (1.28)	12.95
Piketberg natural	6	66	6.33	6 (0.53)	7.85
Piketberg cultivated	3	5	6.67	3.95 (2.02)	6.7
Kleinmond natural	7	495	10.29	11.28 (6.85)	11.7
Kleinmond cultivated	9	27	13.29	16.6 (11.1)	15.55
Gansbay natural	6	45	6.4	6 (0.24)	7
Gansbay cultivated	6	31	7.32	6.95 (2.12)	9.7
Infructescences					
Natural all	16	422	19.47	18.21 (3.34)	19.95
Cultivated all	15	290	16.79	16.47 (2.55)	19.87
Piketberg natural	11	135	11.93	11.95 (1.79)	12.99
Piketberg cultivated	5	49	6.48	6.71 (3.25)	7.55
Kleinmond natural	9	122	10.49	9.95 (2.16)	12.7
Kleinmond cultivated	7	150	7	7 (0.4)	6.15
Gansbay natural	9	165	9.37	9 (0.54)	10.85
Gansbay cultivated	9	91	10.88	9.63 (1.25)	10.14
Soil					
Soil natural all	52	2573	55.3	54.26 (2.48)	58.09
Soil cultivated all	25	442	40.69	54.24 (27.71)	44.1
Piketberg natural	19	688	19.84	19.45 (1.19)	21.69
Piketberg cultivated	12	182	13.14	12.45 (1.19)	14.69
Kleinmond natural	18	440	20.71	19.8 (2.63)	23.38
Kleinmond cultivated	16	131	24.39	23.35 (7.5)	25.77
Gansbay natural	24	1444	24.99	24.13 (0.45)	23.13
Gansbay cultivated	11	129	15.23	14.6 (4.8)	16.38

* Incidence-based coverage estimator, **Second order Chao estimator, *** Second order Jackknife estimator

mite taxa that contributed to this result were the oribatid mite *Antarctozetes translamellatus* (Mahunka) and Stigmaeidae sp.1 for soil, the Tarsonemidae sp.1 and Glycyphagidae sp.1 for inflorescences, Tydeidae sp.1 and *Trichouropoda* sp.1 for inflorescences, and *Proctolaelaps vanderbergi* Ryke that was associated with both inflorescences and infructescences (data not shown). Communities from soil were more tightly grouped (smaller values) than assemblages from inflorescences or from infructescences, indicating overall less within-niche turnover

(β 1 diversity). In addition to dissimilarities in mite assemblages due to niche type, separation of communities based on location was evident (Piketberg, Kleinmond, and Gansbay) (Table 3, Supplementary Table S2). The main mite taxa that contributed to this result were Cunaxidae sp.1 and Cunaxidae sp.2 from Kleinmond, the Anystidae sp.1 from Gansbay, and *Proctolaelaps vanderbergi* that was associated with both Gansbay and Piketberg (data not shown).

Table 3: The effect niche (soil = S, infructescences = lfr and inflorescences = lfl), locality (Piketberg = PB, Kleinmond = KM, Gansbay = GB) and biotope (natural = N, cultivated = C) on alpha- and beta-diversity (within and between factors) on mite assemblages associated with *Protea repens*.

Variables	df	χ^2	<i>p</i>	Post hoc
Richness				
Niche	2	130.97	0.000	S > lfr > lfl
Locality	2	1.61	0.202	KM = GB = PB
Biotope	1	53.83	0.000	N > C
Niche* Locality* Biotope	4	3.76	0.005	Figure 3
Abundance				
Niche	2	104.82	0.000	S > lfr > lfl
Locality	2	2	0.137	KM = GB = PB
Biotope	1	52.3	0.000	N > C
Niche* Locality* Biotope	4	4.34	0.002	Figure 3
Variables- PERMDISP	df	F	<i>p</i>	Post hoc
Beta-diversity 1 (β_1)				
Niche	2	4.98	0.0115	lfr = lfl > S
Locality	2	0.40	0.7084	KM = GB = PB
Biotope	1	16.93	0.0001	C > N
Niche*Locality	8	1.91	0.0973	Figure 4
Locality*Biotope	5	3.71	0.0075	Figure 4
Biotope*Niche	4	7.62	0.0001	Figure 4
Niche* Locality* Biotope	14	4.35	0.0001	Figure 5
Variables- PERMANOVA	df	Pseudo F	<i>p</i>	Post hoc
Beta-diversity 2 (β_2)				
Niche	2	27.48	0.0001	All differ
Locality	2	5.32	0.0001	All differ
Biotope	1	10.47	0.0001	Both differ
Niche*Locality	4	4.71	0.0001	Supplementary Table S2
Locality*Biotope	2	4.67	0.0001	Supplementary Table S2
Biotope*Niche	1	7.51	0.0001	Supplementary Table S2

DISCUSSION

There is a rich assemblage of mites associated with *Protea repens* in natural populations. All niches investigated differed in terms of their mite assemblage composition, with those from soil substantially different from mite assemblages associated with inflorescences and infructescences, with oribatid mites almost entirely absent from the latter two niches, true to their predominantly soil inhabiting nature (Norton and Behan-Pelletier 2009). In cultivated *Protea* stands, species numbers and abundance of mites decreased, but the extent of this reduction depended strongly on the intensity of management and potential exposure to pesticides. Similar findings were reported in a study on mites in Italian vineyards where species richness and abundance on leaves were lower in cultivated compared to organic and untreated vineyards (Sabbatini Peverieri et al. 2009). Furthermore, the assemblage structure of mites also changed within all niches associated with *Proteas* under cultivation. Mite biodiversity changes were, however, the strongest for the

particularly rich soil-associated assemblages. This finding aligns with other studies, such as those in Europe where agricultural intensification has had a negative impact on soil fauna, including mites (Tsiadouli et al. 2015)

At Piketberg cultivation practices were most intense, with various pesticides and fertilisers applied to plants and the soil. At this site, there is also limited diversity within the landscape, such that there were no natural stepping-stones or corridors in the form of other plants (Tscharntke et al. 2005). Despite this, the alpha-diversity in the natural area at this site was still comparable to the other natural sites sampled. Therefore, changes in natural site conditions (higher elevation and drier climate in this case) may not have a large influence on mite alpha-diversity associated with *Protea*. Interestingly, mite numbers within inflorescences at this site, even though reduced in comparison to those from the natural site, were not significantly different from the numbers of mites within the inflorescences from both natural and cultivated populations at other sites sampled. This indicates that, even though there is an intensive spraying regime,

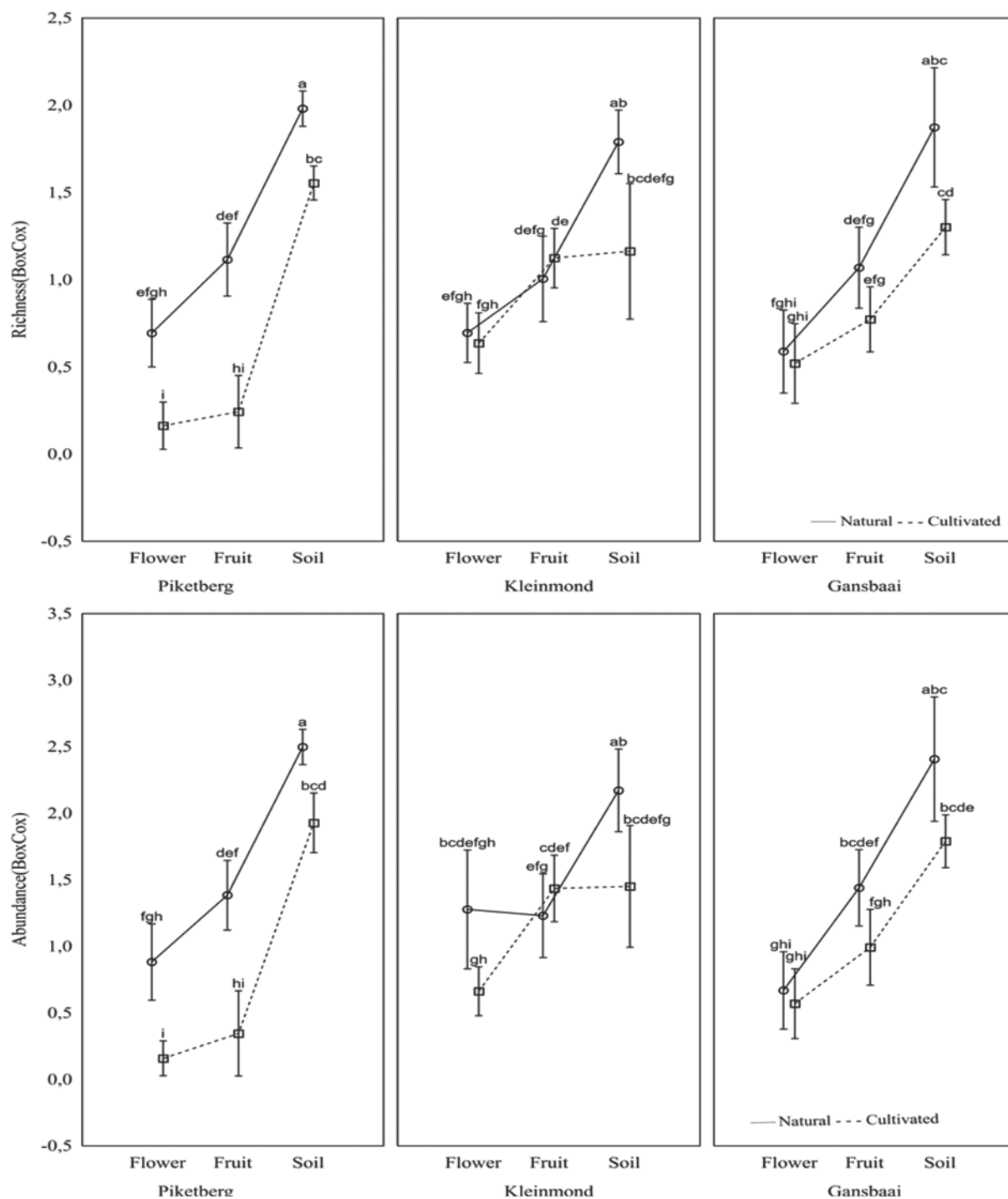


Figure 3: Comparisons between mean BoxCox transformed (\pm 95%) species richness (top) and abundance (bottom) (alpha-diversity (α)) between localities (Piketberg, Kleinmond, Gansbay), biotopes (natural, cultivated) and niche types (Soil, Inflorescences = Flower, Inflorescences = Fruit). Different letters above bars indicate significantly different means ($p < 0.05$) (see Supplementary Table S2 for Post hoc test results).

it is not sufficient to reduce mites associated with inflorescences to lower-than-expected levels. Most mites associated with inflorescences of *Protea* are likely phoretic on pollinators such as insects and birds (Roets et al. 2009; Theron-De Bruin et al. 2018). These pollinators are known to disperse the mites between *P. repens* stands over vast distances (> 200 km based on population genetics of associated fungal species for some mites (Aylward et al. 2015, 2023) and could easily continuously introduce at least some mites when these inflorescences are open, irrespective of spraying regime. These assemblages are, unfortunately, also those that pose the most significant phytosanitary risks, either on their own or due to the fungi that they are known to vector (Roets et al. 2009; Theron-De Bruin et al. 2018).

Protea cultivation at Kleinmond was less intense in the sense that *Protea* pests are not directly controlled via the spraying of pesticides. However, this site is surrounded by other crop species, including fruit trees that are regularly sprayed. Here wind may carry spray mists to the neighbouring *Protea* stands, where these chemicals likely affect mite assemblages outside the target areas. Even so, mite numbers on aboveground plant parts did not differ between the plants that were under cultivation and those from the nearby natural area. Even though not significantly so, the belowground mite numbers were the most negatively influenced, likely due to weed control and other management practices (Seniczak et al. 2018). At Gansbay, there was no contact with chemical sprays and the site was left for natural regeneration.

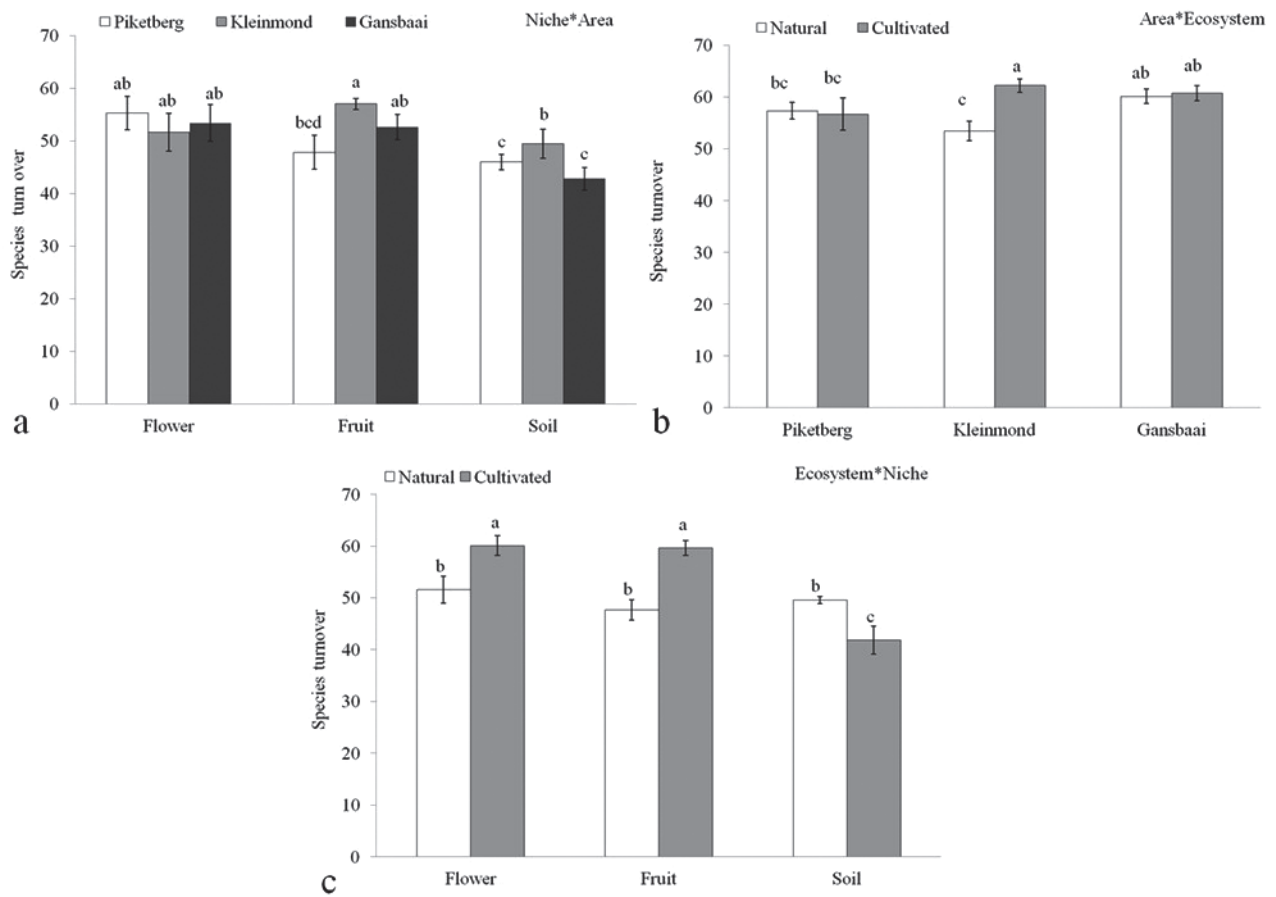


Figure 4: Between site comparisons for beta-diversity (β_1) for the interaction: a) locality*niche type, b) locality*biotope type, c) biotope*niche type. Mean (\pm SE). Letters above bars indicate significantly different means ($p < 0.05$). Inflorescences = Flower, Infructescences = Fruit.

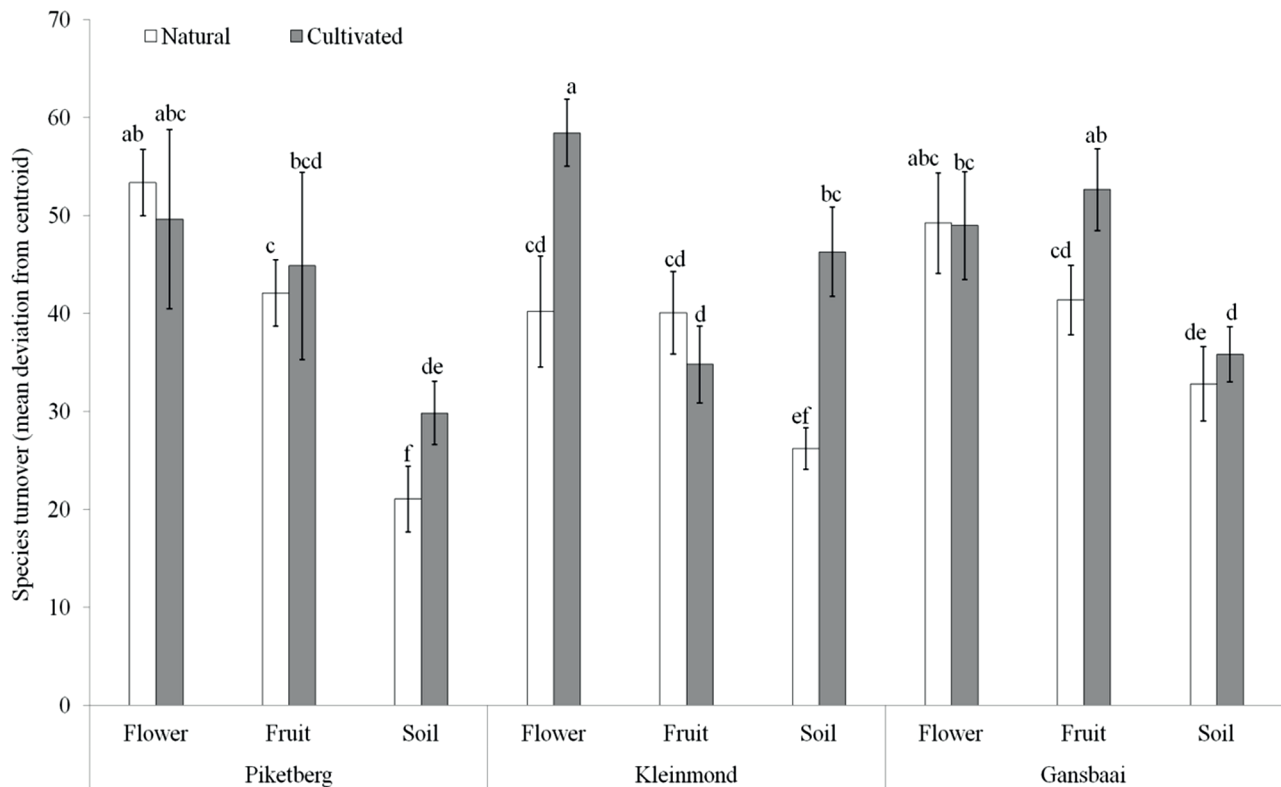


Figure 5: Pairwise comparisons of mite community assemblage composition (β_1) for interactions within localities (Piketberg, Kleinmond, Gansbaai) and biotopes (natural = white, cultivated = grey) and niche types (Soil, Inflorescences = Flowers, Infructescences = Fruit). Comparisons of distance from the centroids (Mean, \pm SE) within factors are presented. Letters above bars indicate significantly different means ($p < 0.05$).

Here, mite alpha-diversity was similar to the natural site, but soil-associated mites still tended to have the greatest reduction in numbers compared to other niches. This reduction in soil-mite assemblages indicates less optimal soil conditions (Giller et al. 1997; Tsiafouli et al. 2015) and likely has large negative effects on ecosystem services provided (Bedano et al. 2006).

Given the high number of mite species and their apparent sensitivity to ecosystem change detected in this study, mites, especially soil-associated taxa, would make good indicators for *Protea* cultivation system health, habitat quality and management intensity (Carignan and Villard 2002; Duelli and Obrist 2003; Gerlach et al. 2013). Indeed, various mite groups, especially Oribatida mites (Behan-Pelletier 1999; Jamshidian et al. 2015; N'Dri et al. 2016; Mics 2024), are regularly used as bioindicators (O'Neill et al. 2010), while other mite groups are useful for the biological control of pests (Johann et al. 2014). However, in terms of *Protea*, the feeding habits of the predatory mites of the families Ascidae and Laelapidae would first need to be determined before they could be considered viable control options (Beaulieu and Weeks 2007). Although mites can be important indicators of ecosystem health, they can be difficult to correctly identify without the help of trained experts (Behan-Pelletier 1999; Gerlach et al. 2013). This became evident in this study with the Oribatida, where some morphospecies were subsequently found to contain more than one species after identification by experts. This taxonomic hurdle, often called the 'taxonomic impediment' needs urgent attention, not only in South Africa, but globally (Engel et al. 2021; Páll-Gergely et al. 2024), if significant progress into the understanding of the ecological role of mites is to be made.

As with a previous study (Slabbert et al. 2019), the results of this study indicated that cultivated indigenous plant species may be suitable to host natural biodiversity to substantial levels, but this depends strongly on the intensity of cultivation practices. In addition, control of mite numbers within inflorescences and infructescences within cultivated systems, no matter what the level of management, does not seem to be effective. These will no doubt have strong negative effects on the lucrative fynbos cut-flower export industry, which amounts to R766 million per year and for which South Africa is seen as a leader (DTIC 2023). In contrast, management practices seem to affect soil biota negatively, even with minimal management of these systems. Reliance on post-harvest treatments of inflorescences intended for export markets will therefore remain essential. A variety of post-harvesting treatments are currently available (Jamieson et al. 2009), but they are still inadequate to rid fresh plant material of mites without damaging the inflorescences and infructescences (Coetzee et al. 2007). Therefore, future studies should focus on improved treatments or the development of new post-harvest treatments.

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AVAILABILITY OF DATA AND MATERIAL

Reference material was deposited in the National Collection of Arachnida, ARC-Plant Protection Research Institute, Pretoria,

South Africa, and in the Department of Conservation and Entomology Museum, Stellenbosch University, Stellenbosch, South Africa.

AUTHORS' CONTRIBUTIONS

N. T-DB: study design, data collection, laboratory work, statistical analyses, writing of first draft.

F.R., L.L.D: study concept, study design, acquired funding, statistical analyses, writing of the manuscript.

E.A. H-C.: Oribatida identification, writing of the manuscript.

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REFERENCES

- Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology*. 26:32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>.
- Anderson MJ. 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics*. 62:245–253. <https://doi.org/10.1111/j.1541-0420.2005.00440.x>.
- Andrén H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos*. 71:355–366.
- Aylward J, Dreyer LL, Steenkamp ET, Wingfield MJ, Roets F. 2015. Long-distance dispersal and recolonization of a fire-destroyed niche by a mite-associated fungus. *Fungal Biology*. 119:245–256. <https://doi.org/10.1016/j.funbio.2014.12.010>.
- Aylward J, Roets F, Dreyer LL, Wingfield MJ. 2023. Unseen fungal biodiversity and complex interorganismal interactions in *Protea* flower heads. *Fungal Biology Reviews*. 45:100317. <https://doi.org/10.1016/j.fbr.2023.100317>.
- Beaulieu F, Weeks AR. 2007. Free-living mesostigmatic mites in Australia: their roles in biological control and bioindication. *Australian Journal of Experimental Agriculture*. 47:460–478. <https://doi.org/10.1071/EA05341>.
- Bedano JC, Cantú MP, Doucet ME. 2006. Influence of three different land management practices on soil mite (Arachnida: Acari) densities in relation to a natural soil. *Applied Soil Ecology*. 32:293–304. <https://doi.org/10.1016/j.apsoil.2005.07.009>.
- Behan-Pelletier VM. 1999. Oribatid mite biodiversity in agroecosystems: role for bioindication. *Agriculture, Ecosystems and Environment*. 74:411–423. [https://doi.org/10.1016/S0167-8809\(99\)00046-8](https://doi.org/10.1016/S0167-8809(99)00046-8).
- Behan-Pelletier VM, Walter DE. 2000. Biodiversity of oribatid mites (Acari: Oribatida) in tree canopies and litter. In: Coleman DC, Hendrix PF (eds), *Invertebrates as webmasters in ecosystems*. United Kingdom: CABI Publishing. pp 187–202.
- Carignan V, Villard MA. 2002. Selecting indicator species to monitor ecological integrity: a review. *Environmental Monitoring and Assessment*. 78:45–61. <https://doi.org/10.1023/A:1016136723584>.
- Chikomo NN. 2023. Seasonal abundance and diversity of mites in *Coffea arabica* L. at Beaver Creek Coffee Estate, South Africa. MSc dissertation, University of the Witwatersrand, Johannesburg, South Africa.
- Coetzee JH, Dippenaar-Schoeman A.S, Berg A. 1990. Spider assemblages on five species of proteaceous plants in the fynbos biome of South Africa. *Phytophylactica*. 22: 443–447.
- Coetzee JH, Giliomee JH. 1985. Insects in association with the inflorescence of *Protea repens* (L.) (Proteaceae) and their role in pollination. *Journal of the Entomological Society of Southern Africa*. 48:303–314.
- Coetzee JH, Giliomee JH. 1987. Borers and other inhabitants of the inflorescences and infructescences of *Protea repens* in the Western Cape. *Phytophylactica*. 19:1–6.
- Coetzee JH, Littlejohn GM, Janick, J. 2007. *Protea*: a floricultural crop from the Cape Floristic Kingdom. *Scripta Horticulturae*. 5:77–112.
- Colwell RK. 2005. EstimateS: Statistical estimation of species richness and shared species from samples. Version 7.5. <http://purl.oclc.org/estimates>.

- Conradie B, Knoesen H. 2010. A survey of the cultivation and wild harvesting of fynbos flowers in South Africa (No. 1). Report. pp 1–19.
- Cortet J, Gillon D, Joffre R, Ourcival JM. 2002. Effects of pesticides on organic matter recycling and microarthropods in a maize field: use and discussion of the litterbag methodology. *European Journal of Soil Biology*. 38:261–265. [https://doi.org/10.1016/S1164-5563\(02\)01156-1](https://doi.org/10.1016/S1164-5563(02)01156-1).
- Duelli P, Obrist MK. 2003. Biodiversity indicators: the choice of values and measures. *Agriculture, ecosystems and environment*. 98:87–98. [https://doi.org/10.1016/S0167-8809\(03\)00072-0](https://doi.org/10.1016/S0167-8809(03)00072-0).
- DTIC. 2023. Announcement of protection for R1,7 billion cut-flower export industry. Department of Trade, Industry and Competition media statement. <https://www.thedtic.gov.za/announcement-of-protection-for-r17-billion-cut-flower-export-industry/#:~:text=Primary%20fynbos%20cut%2Dflower%20production,are%20women%20from%20rural%20areas>.
- Engel MS, Cerfaco LM, Daniel GM, Dellapé PM, Löbl I, Marinov M, Reis RE, Young MT, et al. 2021. The taxonomic impediment: a shortage of taxonomists, not the lack of technical approaches. *Zoological Journal of the Linnean Society*. 193: 381–387. <https://doi.org/10.1093/zoolinnean/zlab072>.
- Gerber AI, Hoffman EW. 2014. International Protea Association and current global Proteaceae production: Achievements and challenges. *Acta Horticulturae*. 1031:17–28. <https://doi.org/10.17660/ActaHortic.2014.1031.1>.
- Gerlach J, Samways M, Pryke J. 2013. Terrestrial invertebrates as bioindicators: an overview of available taxonomic groups. *Journal of Insect Conservation*. 17:831–850. <https://doi.org/10.1007/s10841-013-9565-9>.
- Giller KE, Beare MH, Lavelle P, Izac A-MN, Swift MJ. 1997. Agricultural intensification, soil biodiversity and agroecosystem function. *Applied Soil Ecology*. 6:3–16. [https://doi.org/10.1016/S0929-1393\(96\)00149-7](https://doi.org/10.1016/S0929-1393(96)00149-7).
- Gulvik M. 2007. Mites (Acari) as indicators of soil biodiversity and land use monitoring: a review. *Polish Journal of Ecology*. 55:415–440.
- Gurr GM, Wratten SD, Luna JM. 2003. Multi-function agricultural biodiversity: pest management and other benefits. *Basic and Applied Ecology*. 4:107–116. <https://doi.org/10.1078/1439-1791-00122>.
- Hackman KO, Gong P, Venevsky S. 2017. A rapid assessment of landscape biodiversity using diversity profiles of arthropod morphospecies. *Landscape Ecology*. 32:209–223. <https://doi.org/10.1007/s10980-016-0440-4>.
- Halliday RB. 2005. Predatory mites from crops and pastures in South Africa: potential natural enemies of redlegged earth mite *Halotydeus destructor* (Acari: Penthalidae). *Zootaxa*. 1079:11. <https://doi.org/10.11646/zootaxa.1079.1.2>.
- Hansen JD, Hara AH. 1994. A review of postharvest disinfestation of cut flowers and foliage with special reference to tropics. *Postharvest Biology and Technology*. 4:193–212. [https://doi.org/10.1016/0925-5214\(94\)90030-2](https://doi.org/10.1016/0925-5214(94)90030-2).
- Hooke RL, Martín-Duque JF, Pedraza J. 2012. Land transformation by humans: a review. *GSA Today*. 22:4–10.
- Hortal J, Borges PV, Gaspar C. 2006. Evaluating the performance of species richness estimators: sensitivity to sample grain size. *Journal of Animal Ecology*. 75:274–287. <https://doi.org/10.1111/j.1365-2656.2006.01048.x>.
- Jamieson LE, Meier X, Page B, Zullhendri F, Page-Weir N, Brash D, McDonald RM, Stanley J, Woolf AB. 2009. A review of postharvest disinfestation technologies for selected fruits and vegetables. Auckland: The New Zealand Institute for Plant and Food Research Ltd. pp 1–11.
- Jamshidian MK, Saboori A, Akrami MA, Van Straalen NM. 2015. Oribatid mite communities in contaminated soils nearby a lead and zinc smelting plant in Zanjan, Iran. *Systematic and Applied Acarology*. 20:251–262. <https://doi.org/10.11158/saa.20.3.3>.
- Johann L, Horn TB, Carvalho GS, Ferla NJ. 2014. Diversity of mites (Acari) in vineyard ecosystems (*Vitis vinifera*) in two viticultural regions of Rio Grande Do Sul State, Brazil. *Acarologia*. 54:137–154. <https://doi.org/10.1051/acarologia/20142122>.
- Joubert L, Esler KJ, Privett SDJ. 2009. The effect of ploughing and augmenting natural vegetation with commercial fynbos species on the biodiversity of Overberg Sandstone fynbos on the Agulhas Plain, South Africa. *South African Journal of Botany*. 75:526–531. <https://doi.org/10.1016/j.sajb.2009.05.002>.
- Krantz G, Walter D. 2009. A manual of Acarology. 3rd edn. Lubbock: Texas Tech University Press.
- Kremen C, Williams NM, Thorp RW. 2002. Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences*. 99:16812–16816. <https://doi.org/10.1073/pnas.262413599>.
- Mayr E. 1996. What is a species, and what is not? *Philosophy of Science*. 63:262–277. <https://doi.org/10.1086/289912>.
- McMurtry JA, De Moraes GJ, Sourassou NF. 2013. Revision of the lifestyles of phytoseiid mites (Acari: Phytoseiidae) and implications for biological control strategies. *Systematic and Applied Acarology*. 18:297–320. <https://doi.org/10.11158/saa.18.4.1>.
- Michereff-Filho M, Guedes, RNC, Della-Lucia TMC, Michereff MF, Cruz I. 2004. *International Journal of Pest Management*. 50:91–99. <https://doi.org/10.1080/09670870410001655885>.
- Mics F. 2024. Ecological indication potential of oribatid mites. *Opuscula Theologica et Scientifica*. 2:59–95. <https://doi.org/10.59531/ots.2024.2.1.59-95>.
- Myburgh AC, Rust DJ. 1975. A survey of pests of the Proteaceae in the Western and Southern Cape Province. *Journal of the Entomological Society of Southern Africa*. 38:55–60.
- Myburgh LC, Rust DJ, Starke LC. 1973. Pests of protea cut-flowers. *Journal of the Entomological Society of Southern Africa*. 36:251–255.
- N'Dri JK, Hance T, André HM, Lagerlöf J, Tondoh JE. 2016. Microarthropod use as bioindicators of the environmental state: case of soil mites (Acari) from Côte d'Ivoire. *Journal of Animal and Plant Sciences*. 29:4622–4637.
- Ngubane NP, Dreyer LL, Oberlander KC, Roets F. 2018. Two new *Sporothrix* species from *Protea* flower heads in South African Grassland and Savanna. *Antonie van Leeuwenhoek*. 111:965–979. <https://doi.org/10.1007/s10482-017-0995-3>.
- Norton RA, Behan-Pelletier VM. 2009. Chapter 15: Suborder Oribatida. In: Krantz G, Walter D (eds), *A manual of Acarology*. Lubbock: Texas Tech University Press. pp 430–564.
- Oliver I, Beattie AJ. 1993. A possible method for the rapid assessment of biodiversity. *Conservation Biology*. 7:562–568. <https://doi.org/10.1046/j.1523-1739.1993.07030562.x>.
- O'Neill KP, Godwin HW, Jiménez-Esquilín AE, Battigelli JP. 2010. Reducing the dimensionality of soil microinvertebrate community datasets using Indicator Species Analysis: Implications for ecosystem monitoring and soil management. *Soil Biology and Biochemistry*. 42:145–154. <https://doi.org/10.1016/j.soilbio.2009.09.024>.
- Osborne JW. 2010. Improving your data transformations: Applying the Box-Cox transformation. *Practical Assessment, Research and Evaluation*. 15:1–9.
- Páll-Gergely B, Krell F-T, Abrahám L, Bajomi B, Balog LE, Boda P, et al. 2024. Identification crisis: a fauna-wide estimate of biodiversity expertise shows massive decline in a Central European country. *Biodiversity and Conservation*. 33:3871–3903. <https://doi.org/10.1007/s10531-024-02934-6>.
- Perfecto I, Vandermeer J, Hanson P, Cartín V. 1997. Arthropod biodiversity loss and the transformation of a tropical agroecosystem. *Biodiversity and Conservation*. 6:935–945. <https://doi.org/10.1023/A:1018359429106>.
- Power AG. 2010. Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*. 365:2959–2971. <https://doi.org/10.1098/rstb.2010.0143>.
- Pryke JS, Roets F, Samways MJ. 2013. Importance of habitat heterogeneity in remnant patches for conserving dung beetles. *Biodiversity Conservation*. 22:2857–2873. <https://doi.org/10.1007/s10531-013-0559-4>.
- Reinten E, Coetzee JH. 2002. Commercialization of South African indigenous crops: aspects of research and cultivation of products. In: Janick J, Whipkey A (eds), *Trends in new crops and new uses*. Alexandria, VA: ASHS Press.
- Reinten EY, Coetzee JH, Van Wyk BE. 2011. The potential of South African indigenous plants for the international cut flower trade. *South African Journal of Botany*. 77:934–946. <https://doi.org/10.1016/j.sajb.2011.09.005>.
- Roets F, Crous PW, Wingfield MJ, Dreyer LL. 2009. Mite-mediated hyperphoretic dispersal of *Ophiostoma* spp. from the infructescences of South African *Protea* spp. *Environmental Entomology*. 38:143–152. <https://doi.org/10.1603/022.038.0118>.
- Roets F, De Beer ZW, Dreyer LL, Zipfel R, Crous PW, Wingfield MJ. 2006. Multi-gene phylogeny for *Ophiostoma* spp. reveals two new

- species from *Protea* infructescences. *Studies in Mycology*. 55:199–212. <https://doi.org/10.3114/sim.55.1.199>.
- Roets F, Theron N, Wingfield MJ, Dreyer LL. 2012. Biotic and abiotic constraints that facilitate host exclusivity of *Gondwanamyces* and *Ophiostoma* on *Protea*. *Fungal Biology*. 116:49–61. <https://doi.org/10.1016/j.funbio.2011.09.008>.
- Roets F, Wingfield MJ, Crous PW, Dreyer LL. 2013. Taxonomy and ecology of ophiostomatoid fungi associated with *Protea* infructescences. In: Seifert KA, De Beer ZW, Wingfield MJ (eds), *The Ophiostomatoid Fungi: Expanding Frontiers*. In: CBS Biodiversity Series 12. CBS-KNAW Biodiversity Centre, The Netherlands. pp 177–187.
- Roets F, Wingfield MJ, Wingfield BD, Dreyer LL. 2011. Mites are the most common vectors of the fungus *Gondwanamyces proteae* in *Protea* infructescences. *Fungal Biology*. 115:343–350. <https://doi.org/10.1016/j.funbio.2011.01.005>.
- Sabbatini Peverieri G, Simoni S, Goggioli D, Liguori M, Castagnoli M. 2009. Effects of variety and management practices on mite species diversity in Italian vineyards. *Bulletin of Insectology*. 62: 53–60.
- Sasa A, Samways MJ. 2015. Arthropod assemblages associated with wild and cultivated indigenous proteas in the Grabouw area, Cape Floristic Region. *African Entomology*. 23:19–36. <https://doi.org/10.4001/003.023.0130>.
- Sayer EJ. 2006. Using experimental manipulation to assess the roles of leaf litter in the functioning of forest ecosystems. *Biological Reviews*. 81:1–31. <https://doi.org/10.1017/S1464793105006846>.
- Seniczak A, Seniczak S, García-Parra I, Ferragut F, Xamani P, Graczyk R, Messegueur E, Laborda R, Rodrigo E. 2018. Oribatid mites of conventional and organic vineyards in the Valencian Community, Spain. *Acarologia*. 58 (suppl): 119–133. <https://doi.org/10.24349/acarologia/20184281>.
- Slabbert E, Malgas R, Veldtman R, Addison P. 2019. Honeybush (*Cyclopia* spp.) phenology and associated arthropod diversity in the Overberg region, South Africa. *Bothalia*. 49:179–191. <https://doi.org/10.4102/abc.v49i1.2430>.
- Smith Meyer MKP, Craemer C. 1999. Mites (Arachnida: Acari) as crop pests in southern Africa: an overview. *African Plant Protection*. 5: 37–51.
- Swinton SM, Lupi F, Robertson GP, Hamilton SK. 2007. Ecosystem services and agriculture: cultivating agricultural ecosystems for diverse benefits. *Ecological Economics*. 64:245–252. <https://doi.org/10.1016/j.ecolecon.2007.09.020>.
- Theron-De Bruin N, Dreyer LL, Ueckermann EA, Roets F. 2024. Flower mites steal *Protea* pollen and nectar. *African Entomology*. 32:e18064. <https://doi.org/10.17159/2254-8854/2024/a18064>.
- Theron-De Bruin N, Dreyer LL, Ueckermann EA, Wingfield MJ, Roets F. 2018. Birds Mediate a Fungus-Mite Mutualism. *Microbial Ecology*. 75:863–874. <https://doi.org/10.1007/s00248-017-1093-9>.
- Theron N, Roets F, Dreyer LL, Esler KJ, Ueckermann EA. 2012. A new genus and eight new species of *Tydeidea* (Acari: Trombidiformes) from *Protea* species in South Africa. *International Journal of Acarology*. 38:257–273. <https://doi.org/10.1080/01647954.2011.619576>.
- Tomich TP, Brodt S, Ferris H, Galt R, Horwath WR, Kebreab E, Leveau JH, Liptzin D, Lubell M, Merel P, Michelmore R. 2011. Agroecology: a review from a global-change perspective. *Annual Review of Environment and Resources*. 36:193–222. <https://doi.org/10.1146/annurev-environ-012110-121302>.
- Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C. 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters*. 8:857–874. <https://doi.org/10.1111/j.1461-0248.2005.00782.x>.
- Tsiafouli MA, Thébault E, Sgardelis SP, Rüter PC, Putten WH, Birkhofer K, Hemerik L, Vries FT, Bardgett RD, Brady MV, Bjornlund L. 2015. Intensive agriculture reduces soil biodiversity across Europe. *Global Change Biology*. 21:973–985. <https://doi.org/10.1111/gcb.12752>.
- Vanolli BS, de Andrade N, Canisares LP, Franco ALC, Pereira APA, Cherubin MR. 2024. Edaphic mesofauna responses to land use change for sugarcane cultivation: insights from contrasting soil textures. *Frontiers in Ecology and Evolution*. 11:1305115. <https://doi.org/10.3389/fevo.2023.1305115>.
- Wezel A, Casagrande M, Celette F, Vian JF, Ferrer A, Peigné J. 2014. Agroecological practices for sustainable agriculture. A review. *Agronomy for sustainable development*. 34:1–20. <https://doi.org/10.1007/s13593-013-0180-7>.
- Witt ABR, Samways MJ. 2004. Influence of agricultural land transformation and pest management practices on the arthropod diversity of a biodiversity hotspot, the Cape Floristic Region, South Africa. *African Entomology*. 12:89–95.
- Wright M. 2003. Insect pests of Proteaceae: assessment of predictions of new pests internationally, and management implications. *Acta Horticulturae*. 602:167–171. <https://doi.org/10.17660/ActaHortic.2003.602.24>.
- Wright MG, Samways MJ. 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>.
- Wright MG, Saunderson MD. 1995. *Protea* plant protection: from the African context to the international arena. *Acta Horticulturae*. 387:129–140. <https://doi.org/10.17660/ActaHortic.1995.387.15>.
- Zachariades C, Midgley JJ. 1999. Extrafloral nectaries of South African Proteaceae attract insects but do not reduce herbivory. *African Entomology*. 7:67–7.
- Zhang W, Ricketts TH, Kremen C, Carney K, Swinton, SM. 2007. Ecosystem services and dis-services to agriculture. *Ecological Economics*. 64:253–260. <https://doi.org/10.1016/j.ecolecon.2007.02.024>.