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ORIGINAL PAPER

Soil compaction and surface-active arthropods in historic, agricultural, alien, and recovering vegetation

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Abstract Soil compaction is a major threat to natural resources. However, little information is available on the impacts of soil compaction on arthropod diversity especially relative to different types of vegetation, land use and restoration activities. In response to this dearth of information, we studied soil compaction, as well as percentage soil moisture and mean leaf litter depth, associated with four vegetation types: natural vegetation (fynbos, the historic condition), agricultural land (vineyards), invasive alien trees, and vegetation cleared of invasive alien trees (recovering vegetation). Our study took place in the Cape Floristic Region, South Africa, a biodiversity hotspot, yet also an area of intense viticulture and heavy invasion by alien plants. We sampled soil surface-active arthropods using pitfall traps, and compared species richness and abundance in different vegetation types with various levels of soil compaction and other soil variables. Overall, vineyards had the highest soil compaction while natural fynbos and aliens had low and comparable compaction. For both arthropod species richness and abundance, the order of the four vegetation types was, from highest to lowest: natural fynbos, alien cleared sites, vineyards, and alien infested sites. Level of soil compaction negatively correlated with arthropod species richness but not with abundance. Neither soil moisture nor leaf litter depth on their own significantly affected arthropod species richness or abundance. While alien trees overall had a strong negative effect on both arthropod species richness and abundance, and much more so than vineyards, the situation is reversible, with removal of aliens being associated with rapid recovery of soil structure and of arthropod assemblages. This is an encouraging sign for restoration.

Keywords Soil disturbance · Invertebrates · Arthropod conservation · Insect conservation · Restoration

Introduction

Human-induced soil compaction (dry bulk density) is one of most important factors threatening natural resources (van den Akker and Soane 2005; Eudoxie and Springer 2006; Kirby 2007). It occurs when soil undergoes mechanical stress, mainly through use of heavy machinery or overgrazing, especially during wet soil conditions. The indirect effects of soil compaction may be less clear, and are often the result of highly variable soil characteristics (Boizard et al. 2000).

Soil compaction warrants further attention as it structures vegetation (Roberts 1987; Mitchell 1991), including that of alien plants (Payet et al. 2001) and therefore, may influence temperature of the soil surface directly due to shade, and amount of leaf litter from vegetation (Farji–Brener et al. 2008) necessary for soil fauna. In addition, soil compaction from farming operations also reduces water infiltration (Chan 2001; Mitchell 1991) and increases

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soil erosion (Chan et al. 2006). Erosion, in turn, reduces vegetation cover (Mitchell 1991). However, the extent of soil compaction and its impact on surface-dwelling arthropods under different land uses has not been investigated to any extent.

Many soil organisms are important members of terrestrial ecosystems (Smit and Van Aarde 2001). While many arthropods spend part or all their lives in the soil (Chan and Barchia 2007), many others feed above ground, using the soil as a pupation or nesting site. The potential benefits from arthropods to agro-ecosystems include improvement of soil structure and nutrient cycling (Edwards and Bohlen 1996).

Plant litter decomposition is an important biological process driven by ground living organisms (Dyer et al. 1990; Lawrence and Samways 2003; Pausas et al. 2004). Knowledge of this process is important for conservation of the soil (Chan 2001). In turn, relationships between soil fauna and soil properties can be used to assess the impact of landscape management (Clapperton et al. 2004). Disturbance of the soil profile can change, directly or indirectly, the composition of arthropod diversity associated with it (Wallwork 1970; Manzer et al. 1984; Wall and Moore 1999; Dunxiao et al. 1999; Holland and Luff 2004; Farji–Brener et al. 2008; Jabin 2008). Moreover, the effects on soil structure may also affect species density through indirect effects mediated by their potential influence on plants (Van Dijck and Van Asch 2002; Coulouma et al. 2006).

In the Cape Floristic Region (CFR), the comparative influence of soil compaction on ground arthropod assemblages under various conditions of land use has not been investigated, despite this region being a global biodiversity hotspot (Mittermeier et al. 2005). There are severe stressors to the biodiversity of the region, especially from agricultural conversion (especially to vineyards) and from the extensive impact of invasive alien plants (Rouget et al. 2003; Gaertner et al. 2009; Fairbanks et al. 2004).

It is unknown how infestation by alien trees and from agricultural practices (specifically viticulture) influence soil compaction and associated arthropod diversity. Apart from Magoba and Samways (2012), there is little knowledge on how these assemblages recover when the alien trees are removed, a significant mitigation measure in the region which has been assessed using aerial taxa (Samways and Sharrat 2010). To date there is no information focusing on the role of soil compaction in this process of recovery. In view of this dearth of information, we pose two hypotheses. Firstly, we hypothesize that a change in vegetation structure will alter soil compaction. Secondly, we hypothesize that there are significant correlations between arthropod diversity, soil compaction, leaf litter, site location or soil moisture content under the four main vegetation types (natural vegetation, agricultural production, invasive alien trees, and recovering vegetation).

Study area and methods

Study sites

Vegetation of the study area (between Stellenbosch and Somerset West, South Africa: 18°15′E, 34°00′S) included many species-rich communities, occurring on highly infertile soils derived from sandstone of the Table Mountain Group. These communities range from upland study sites where soils are well drained and rocky to sand-loamy soil on the foothills and in the valleys. Intrusion of shale in some vineyards (i.e. Rustenberg) is evident. Boucher and Moll (1981) recognize two main soil types in the area. Lithosols, are generally shallow (<30 cm), grey sandy soils associated with the Table Mountain Group (TMG) sandstone, have a weak profile differentiation and contain coarse fragments and solid rock, and are largely the soil type studied here. Selected sites had similar edaphic conditions derived from the same parent material, TMG sandstone. For each site, the topographical conditions of adjacent distinct vegetation were similar.

At each of ten localities (three protected areas (PAs): Jonkershoek, Helderberg and Hottentots Holland; and seven wine estates: Vergelegen, Bilton, Stellenzicht, Driekoppen, Waterford, Rustenberg and Dornier) four vegetation types were selected: natural fynbos, alien invasive trees (IATs), cleared of invasive alien trees (CIATs), and vineyards. Transects (see details below) were established, so that the four vegetation types were adjacent to each other in their various combinations. This resulted in six different pairs of vegetation types (Natural fynbos-IATs; Natural fynbos-CIATs; IATs-CIATs; Natural fynbos-vineyards; vineyards-IATs; and vineyards-CIATs). In total, there were 36 transects.

The natural fynbos sites were untransformed by human activity and selected from the PAs and wine farms with <10 % alien tree cover. Natural fynbos was predominantly mountain fynbos, with common plant species being *Aspalathus forbesii*, *A. aspalathoides*, *Lebeckia sepiaria*, *Lotononis prostrata*, *Cyphia phyteuma*, *Chasmanthe aethiopica*, *Watsonia borbonica*, *Gymnodiscus capillaris*, *Dimorphotheca pluvialis*, *Hymenolepis crithmoides Protea compacta*, *P. repens*, *P. neriifolia*, and *Salix* species, as well as various ericas. The IAT sites had >90 % alien tree cover, represented mainly by *Acacia mearnsii*, *A. longifolia*, *A. saligna*, *Hakea sericea*, *H. drupacea*, *Pinus pinaster*, *P. radiata*, *Eucalyptus lehmannii*, *E. diversicolor* and *Populus* trees, with an understorey of grasses and forbs. The CIAT sites had been cleared of the alien trees in 2000, by felling and herbicide treating of stumps, and allowing the indigenous fynbos to recover of its own accord. After 6 years of recovery, the vegetation at these cleared sites was comparable in dominant species to that in natural fynbos (see above). The fourth vegetation type was organic vineyards, where there was no application of artificial fertilizers as the soils are relatively fertile through permanent crop cover (i.e. wheat), and pesticides were only applied as a last resort when necessary. One application of the chemical agent chlorpyrifos was applied during early August to control the mealybug *Planococcus ficus* which is the vector of a viral disease of the vines.

Sampling

Sampling of arthropods was on three occasions (August–October 2006, May–July 2007 and November 2007–January 2008) using pitfall traps (Samways et al. 2010). Each sampling occasion was for 5 days. Soil compaction and percentage (%) soil moisture content measurements at each sampling station were undertaken using a Radioactive moisture-density gauge instrument (Troxler 3411-B). Leaf litter depth was determined by inserting a steel rod, 4 mm in diameter, into the leaf-litter until the harder soil layer was reached (Lawes et al. 2005). Mean leaf-litter depth was then estimated from three random measurements in each 2 m^2 quadrat created at each sampling station around the trap set.

The 256 m transects consisted of a trap-set of two individual pitfall traps, 1 m apart, placed at log 2 intervals: 2, 4, 8, 16, 32, 64 and 128 m on either side of the boundary between two adjoining vegetation types. Every patch on either side of the boundary was >100 m × 100 m, and all but one >250 m × 250 m. This spacing gave equal weighting to edges and interiors of patches. However, two transects, between alien vegetation and fynbos, were each four traps short, owing to unavailability of extensive sites. The total was 1000 pitfall traps (two per set, fourteen sets per transect, six transects per vegetation type pair and six vegetation pairs from four vegetation types, minus eight traps).

Pitfall traps for sampling arthropods were 500 ml plastic honey jars, each containing a replaceable paper cup, 8 cm diameter, 12 cm deep. Each trap was one-third filled with 70 % ethanediol. Traps remained closed during non-sampling periods, and opened for 5 consecutive days without rain during sampling periods (Borgelt and New 2006). Samples were then washed in water, and later transferred to 70 % ethanol for later identification in the laboratory. The collected surface-active arthropods were sorted and allocated to families. Where possible, they were identified to species level. Voucher specimens are in the Entomology Museum, Stellenbosch University, although spiders are in the National Collection of Arachnida, National Museum, Pretoria. Identification was by keys and expert opinion.

Data analyses

One-way analysis of variance (ANOVA) using SPSS v17 software (SPSS Inc. 2006), was performed on the selected soil factors comparing the different vegetation types. Classification trees for all the vegetation types in terms of soil compaction, leaf litter depth, percentage soil moisture and species richness were produced separately using CHAID growth limits incorporated in SPSS v17 software (SPSS Inc. 2006). Significance level for splitting nodes and merging categories was 0.05 and the significance values adjusted using the Bonferroni method. A variety of non-parametric species estimators were used to provide the best overall arthropod species estimates for all the vegetation types (Hortal et al. 2006). Incidence-based Coverage Estimator (ICE) is a robust and accurate estimator of species richness (Chazdon et al. 1998), whereas Chao2 and Jackknife estimators provide the least biased estimates for insufficient sampling (Colwell and Coddington 1994). Therefore, we calculated these estimators using EstimateS (Colwell 2006) for all the vegetation types separately and for a combination of these. One-way ANOVA was performed on the species and the log transformed abundance data comparing the different vegetation types with multiple comparisons of the means, using Tamahane's post hoc. We used SpatialPack (version 0.2–3) in R (R Core Team 2013) to calculate the corrected Pearson's correlations for spatial autocorrelation between assemblage composition and soil factors.

Results

Soil factors among the four vegetation types

Soil compaction was highest in vineyards, followed by cleared sites and fynbos, and lowest in aliens (Table 1). In turn, percentage moisture content was lowest in vineyards, followed by cleared sites, aliens, and finally fynbos with the highest. Litter depth was greatest by far in aliens, followed by fynbos and closely by cleared sites, with vineyards with by far the least. ANOVA among the four vegetation types showed that there were significant differences in soil compaction ($df = 3$, $f = 19.36$, $p < 0.001$), litter depth ($df = 3$, $f = 296.6$, $p < 0.001$) and percentage soil moisture ($df = 3$, $f = 15.8$, $p < 0.001$).

The classification tree of significant soil compaction values indicated similarity between fynbos and cleared sites (Table 1; online Figure 1). Aliens and vineyards were significantly different from each other, but neither was comparable to either fynbos or cleared sites. Classification of site locations based on soil compaction resulted in three nodes (Fig. 1; online Figure 2). All three nature reserves had similar low soil compaction (Node 1). Some vineyards

Table 1 Soil factor means (±1SE) for fynbos, invasive alien trees (IATs), cleared invasive alien trees (CIATs), and vineyard sites

Variable	Vegetation type	Mean	N	SE	Node
Soil compaction (Kg/m^3)	CIATs	1277.1	115	12.06	1
	Fynbos	1270.7	145	11.83	1
	IATs	1205.4	124	15.77	2
	Vineyard	1341.6	126	9.75	3
	All groups	*1273.8*	*510*	*6.59*	
Percentage soil moisture	CIATs	8.78	115	0.27	1
	Fynbos	9.76	145	0.28	2
	IATs	9.49	124	0.30	2
	Vineyard	8.36	126	0.22	1
	All groups	*9.13*	*510*	*0.14*	
Leaf litter depth (mm)	CIATs	13.65	115	0.52	1
	Fynbos	15.57	145	0.39	2
	IATs	20.80	124	0.58	3
	Vineyard	2.74	126	0.21	4
	All groups	*13.24*	*510*	*0.36*	

Values in Italic refer to the averages for the four vegetation types combined

(Node 2) had significantly higher soil compaction than any other location. Rustenberg, Bilton, and Dornier vineyards had more comparable soil compaction (Node 3).

Classification of the different vegetation types in terms of litter depth resulted in four separate categories (Table 1, online Figure 3). Vineyard clustering (Node 4) showed low leaf litter depth. Moreover, there were significant differences between the ten site locations (*df* = 506, f = 35.36, $p < 0.001$) in terms of litter depth, with the highest leaf litter depths recorded from Jonkershoek and Hottentots Holland nature reserves respectively (online Figure 4). However, Helderberg nature reserve was associated with relatively lower litter depth, which was comparable to those in some vineyards. Classification of different vegetation types using percentage soil moisture resulted in two vegetation categories: cleared sites were comparable to vineyards, and fynbos to aliens (online Figure 5).

Arthropod species richness among the four vegetation types

A total of 22,255 individuals were sampled, and assigned to 198 morphospecies/species. In terms of both arthropod species and abundance, the four vegetation types followed the same sequence, from highest to lowest: fynbos, cleared sites, vineyards, and aliens (Table 2). ANOVA among the four vegetation types gave significant differences among (*df* = 3, f = 41.65, $p < 0.0001$), and within (*df* = 509, f = 41.65, $p < 0.0001$) them in terms of species richness. Any one vegetation type shared at least 77 % of all sampled species, with fynbos having 90 % and cleared sites 85 % (Table 2). A Tamhane's post hoc test after ANOVA among the four vegetation types (Fig. 1) gave significant differences in species richness between fynbos and aliens ($p < 0.001$); fynbos and vineyards ($p < 0.001$); cleared sites and alien sites ($p < 0.001$); and cleared sites and vineyard ($p < 0.001$). However, there were no statistically significant differences between cleared sites and fynbos ($p = 1.00$) in terms of species richness (online Figure 6). Although vineyards had relatively higher mean arthropod abundance than aliens (Table 2), the difference was not significant ($p = 1.00$). All other combinations of abundance were significant.

Correlation between soil factors and arthropod species richness and abundance among the four vegetation types

There was a significant negative correlation between soil compaction and species richness, but not abundance (Table 3). High soil compaction in vineyards did not correlate with reduced species richness. However, percentage soil moisture content and leaf litter depths were significantly negatively correlated with the soil compaction, and leaf litter depth was positively correlated to the percentage soil moisture, although neither soil moisture or litter depth on their own significantly affected arthropod species richness or abundance (Table 3).

Discussion

Soil factors associated with the vegetation types

We found high soil compaction in the vineyards, which comes about from many activities associated with grape production (Ferrero et al. 2005). At the other end of the

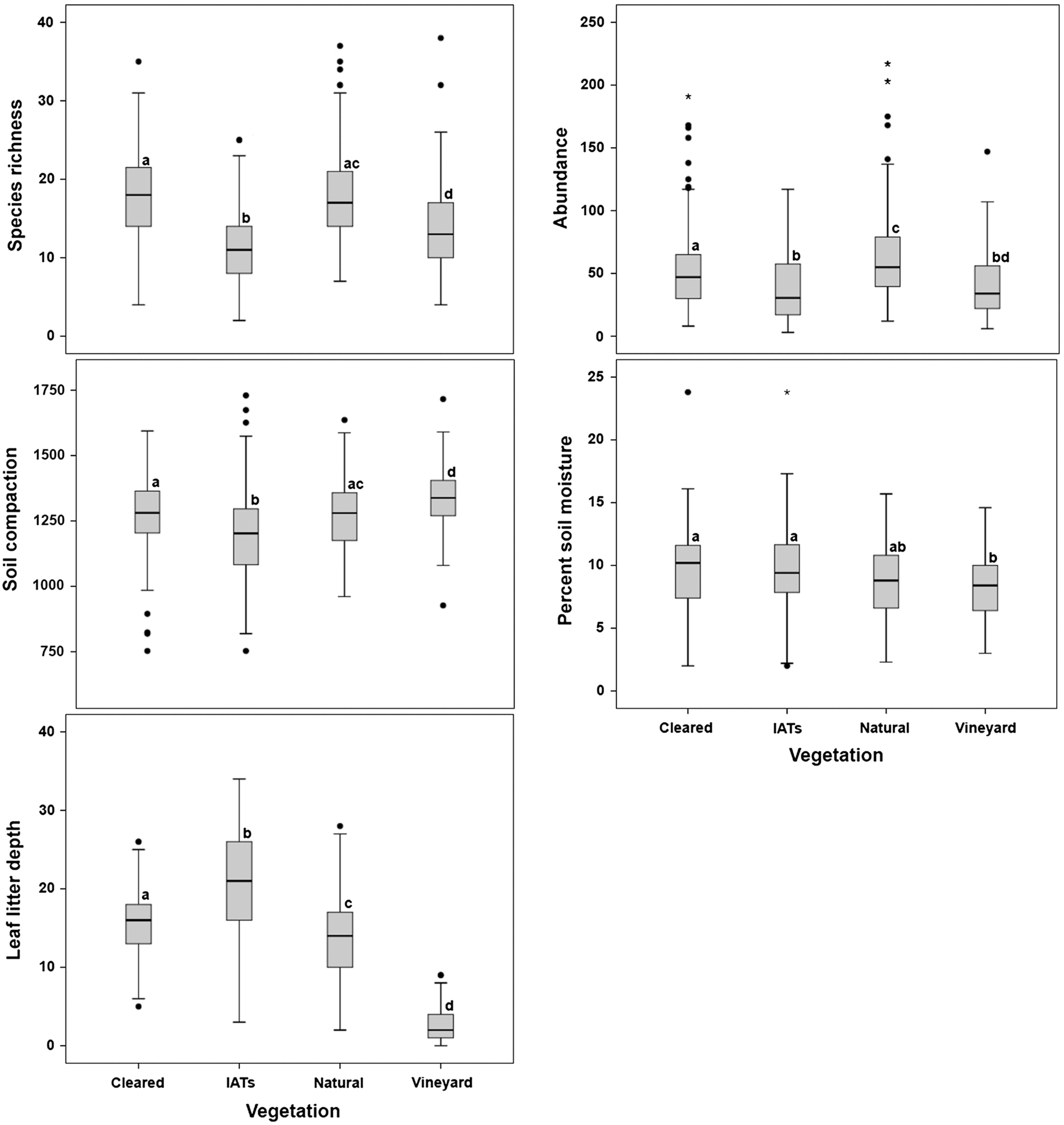

Fig. 1 *Boxplots* comparing means among fynbos (natural), invasive alien trees (IATs), cleared invasive alien trees and vineyard sites in terms of species richness, species abundance, soil compaction (kg/m^3), percentage soil moisture and leaf litter depth (mm). *Letters* at the *boxplots* (*a–d*) indicate significant differences between means, based on the results of a Tamahane's post hoc test after an analysis of variance test. The *dark middle line* of the *box* is the median. *Whiskers* (*vertical lines*) represent maximum and minimum values that are not statistical outliers. *Black dots* and *stars* are statistical outliers

spectrum, we found alien trees had significantly lower soil compaction compared to either fynbos or the sites cleared of alien trees, possibly due to a combination of root activity and accumulation of litter. As well as having highest compaction, vineyards also had lowest percentage moisture content, probably due to high evaporation rates associated with the structurally open production system, in comparison with the dense fynbos or alien vegetation. Overall, soil moisture was highly responsive to the type and structure of associated vegetation. While fynbos and alien vegetation

Table 2 Arthropod species richness and abundance sampled from different vegetation types: fynbos, invasive alien trees (IATs), cleared of invasive alien trees (CIATs) and vineyard sites

Arthropod species	Fynbos	IATs	CIATs	Vineyard	Combined
Total no. of sampled individuals	7746	4725	7563	5221	25,255
Total no. of sampled species	179	153	169	159	198
% Total sampled species	90	77	85	80	
ICE	186.42	164.87	176.99	173.14	203.83
Jackknife2	193.04	177.93	187.95	193.76	215.96

Table 3 Corrected Pearson's correlations for spatial autocorrelation between soil factors and overall arthropod assemblages in fynbos, invasive alien trees (IATs), cleared invasive alien trees (CIATs) and vineyard sites

Variable	Spearman's rho correlations	Abundance	Soil compaction (Kg/m^3)	Percentage soil moisture	Leaf litter depth (mm)
Species richness	Correlation coefficient	0.644	0.003	−0.023	−0.008
	p-value	0.001	0.952	0.579	0.861
Abundance	Correlation coefficient		0.018	0.006	−0.026
	p-value		0.713	0.142	0.585
Soil compaction (Kg/m^3)	Correlation coefficient			−0.464	−0.267
	p-value			0.001	0.001
Percentage soil moisture	Correlation coefficient				0.197
	p-value				0.001

N = 500

had highest soil moisture, clearing of alien trees resulted in slightly reduced soil moisture. In addition to relatively higher soil moisture content, alien vegetation and fynbos both had deep litter layers, while vineyards and cleared sites had the shallowest layers, apparently due to increased exposure leading to increased decomposition.

All vineyards had similar and high levels of soil compaction, suggesting that compaction levels are not restricted to a particular local area but are relative to land use, with farming operations often occurring when the soils are moist and prone to compaction (Chan et al. 2006). This increased compaction can potentially reduce root penetration, water extraction and plant growth (Kirkegaard et al. 1992; Passioura 2002), leading to reduced crop production (McGarry and Chan 1984; McGarry 1990; Radford et al. 2001; Hamza and Anderson 2003).

The thick litter layer under alien vegetation may have lacked essential detritivores. This is suggested from the fact that the dense fynbos vegetation had much less litter than the aliens, probably because it supported the indigenous detritivores leading to the highly decomposed materials under fynbos compared to aliens and even vineyards.

Arthropod diversity in the different vegetation types

Arthropod species richness in cleared sites was high and similar to that in fynbos, and supported about 90 and 85 % of the total sampled species respectively. On the other hand, vineyards and alien sites had the lowest number of species respectively. Farm activities cause high soil compaction in vineyards, with the intensity of this compaction aggravated by relatively higher soil water content associated with vineyards (Usowicz 1992). Interestingly, species richness in vineyards was higher than in aliens, with vineyards being far from species poor. This suggests that the local surface-active fauna are well adapted to drier conditions, probably by being selected through the regular appearance of drought conditions in summer in this Mediterranean-type climate. Associated with this, is location, which also plays an important role, with Vergelegen Estate, for example, supporting more species than the Jonkershoek PA, suggesting that some vineyards can have value in maintaining an important component of arthropod diversity.

The aliens here supported fewer arthropod species than did those of indigenous vegetation, supporting the findings of Watts (1951) and Samways et al. (1996). The alien sites were drier than native vegetation but also had a dense (canopy giving deep shade) and a litter cover physically and chemically different from the historic condition. This meant that the alien tree cover was functionally different from the native vegetation, as in Michigan (Leege and Murphy 2001). Furthermore, arthropod species richness was relatively high in the native fynbos, with its low and varied soil compaction levels, compared to aliens, which had relatively uniform and low compaction levels.

Correlation between soil factors and arthropod species richness and abundance in different vegetation types

Density of soil fauna in agricultural areas is closely linked to soil structure (Usher 1975). Furthermore, increased soil compaction leads to a reduction in arthropod species diversity (Heisler and Kaiser 1995; Schrader and Lingnau 1997; Dittmer and Schrader 2000), with vineyard activities increasing soil compaction and altering the characteristics of the soil, leading to a reduction in habitats for the soil mesofauna (Larsen et al. 2004; Watson and Kelsey 2006). However, our study does not confirm these findings. This implies that disturbance of soil profile alone does not necessarily have as great an impact on the associated surface-active arthropods, as other studies might suggest. Nevertheless, soil has an effect on the amount of water held to enhance plant growth (Thomas and Squires 1991), and so provision of habitat for arthropods, which is reduced when the soil is compacted.

The differences in compaction levels between natural fynbos and cleared sites were small. It is interesting to view this in terms of restoration, with natural fynbos and cleared sites having similar soil compaction, and comparable arthropod species richness. This implies that, in terms of compaction at least, that alien trees leave the ground in a reduced state of compaction which, from our results, suggests that this enables good ground-living arthropod species recovery. In short, clearing alien trees sets the stage for recovery of arthropod assemblages to levels similar to those in natural vegetation, bearing in mind however, that aliens can change soil chemistry (Payet et al. 2001).

Conclusions and recommendations

We show here that vineyard soils are subject to some compactive degradation. This means that proficiency of soil to support higher arthropod diversity within the vineyards can be increased when operations are scheduled at appropriate moisture content (i.e. in dry soils). This is not to say that vineyards were poor in species, with 80 % of the total sampled accounted for. Even the alien plants, probably because of their ability to reduce compaction and increase leaf litter and moisture, had 77 % of the total arthropod fauna. However, arthropods were not so numerous or evenly distributed in the soil under alien trees than in natural vegetation, suggesting perhaps there could be ongoing impoverishment of the fauna should the alien trees not be removed. Overall, these results indicate the negative impact of alien invasive vegetation, more so than soil compaction in vineyards. Yet, this negative situation is reversible, with removal of invasive alien trees being associated with rapid recovery of certain soil conditions, enough to improve arthropod diversity.

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