

Comparative footprint of alien, agricultural and restored vegetation on surface-active arthropods

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Received: 21 October 2010 / Accepted: 4 April 2011 / Published online: 19 April 2011
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Abstract Both invasive alien trees and agricultural conversion have major impacts on biodiversity. We studied here the comparative impact of these two types of land transformation on a wide range of surface-active arthropod species using pitfall traps, with evergreen sclerophyllous natural vegetation (fynbos) as the control. The study was in the Cape Floristic Region, a global biodiversity hotspot, where alien trees are of major concern and where vineyards replace natural fynbos vegetation. Surface-active arthropods were selected as they are species rich, relatively immobile, and occur in high abundance. We hypothesized that the impact of the two types of land cover transformation would produce similar qualitative and quantitative effects on the arthropods. We also compared the results in the transformed and natural areas with those in areas cleared of alien trees. Arthropod species richness in cleared areas was higher than in vineyards and more similar to that in natural fynbos, while alien trees had the lowest. Overall abundance scores were highest in cleared areas, closely followed by fynbos, then vineyards and

lowest in alien trees. Several species were restricted to each vegetation type, including alien trees. In terms of assemblage composition, all vegetation types were significantly different, although fynbos and vineyards grouped, suggesting that vineyards have less impact on the arthropod community than do alien trees. When rare species were excluded, vineyards and cleared sites grouped, indicating some recovery but only involving those species that were common and habitat tolerant. Our results suggest that vineyards retain a greater complement of indigenous species than alien trees, but that clearing of these aliens soon encourages establishment of indigenous species. Although there were significant differences in soil moisture and litter depth within and between vegetation types, we did not record them as significantly affecting species richness or abundance, even in alien vegetation, an encouraging sign for restoration.

Keywords Alien vegetation · Agricultural conversion · Restoration · Arthropods · Cape Floristic Region

Electronic supplementary material The online version of this article (doi:[10.1007/s10530-011-9994-x](https://doi.org/10.1007/s10530-011-9994-x)) contains supplementary material, which is available to authorized users.

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Introduction

Invasion by alien tree species is a global environmental problem (Mack et al. 2000; Richardson and Pyšek 2006), affecting movement patterns of animals, including insects (Wood and Samways 1991), and threatening their habitats (Armstrong and van

Hensbergen 1996; Samways et al. 1996; Richardson and van Wilgen 2004; Samways and Taylor 2004). However, different ecosystems vary considerably in their susceptibility to invasion (Chytrý et al. 2008), with the impacts of alien tree species in natural systems being dependent on invader attributes and on characteristics of the invaded community (Mason and French, 2008). Invasive alien trees (IATs) are widespread in the Cape Floristic Region (CFR), South Africa, and their success attributed to their good colonizing abilities, especially in disturbed areas (Holmes and Richardson 1999). In many parts of the world, alien trees are the main component of commercial forestry, with these trees often spreading from planting sites (Simberloff et al. 2010). IATs such as *Pinus*, *Acacia* and *Eucalyptus* species are of major commercial importance in South Africa, but they are also a threat to water supplies and biodiversity (Wittenberg and Cock 2001; Le Maitre et al. 2004), especially in the CFR (Macdonald and Richardson 1986).

Another impact on natural systems is conversion to agriculture, which changes ecosystem composition and function (Donald and Evans 2006), and its biodiversity (Turin and den Boer 1988; Newton 2004; Gaigher and Samways 2010). Agriculture is one of the most significant human-induced disturbances that threatens terrestrial biodiversity (Sala et al. 2000; Tilman et al. 2001), affecting the availability of suitable terrestrial habitats (Feber et al. 1996; Warren et al. 1997; Jeanneret et al. 2003; Kleijn and van Langevelde 2006). For example, vegetation structure is important to some arthropods because it can affect their ability to thermoregulate and reproduce (Holl 1996). However, vegetation loss for agricultural purposes does not threaten all arthropods equally (Fleishman et al. 1999), with some relatively small-scale agriculture maintaining open, early seral biotopes favoured by some arthropod species (Shreeve and Mason 1980; Sibatani 1980).

The regional focus for this study is the CFR, a global biodiversity hotspot (Mittermeier et al. 2005) and a world centre of plant diversity and endemism (Linder 2005; Procheş and Cowling 2006), with 67% of plant species endemic to the region (Linder 2005). It is also an important area for many rare and endemic arthropod species (Johnson 1992; Picker and Samways 1996; Wright and Samways 1998; Giliomee 2003; Procheş and Cowling 2006; Procheş

et al. 2009). Of significance here is that both invasive alien trees (IATs) and agriculture, especially vineyards, have an impact on this biodiversity (Rouget et al. 2003). Yet there is little knowledge on the comparative impact, or footprint, of these two types of human-induced land transformations on this biodiversity, so we investigate here the comparative impact of IATs and vineyards on soil-surface arthropod diversity, and compare it with patches where IATs had been removed. We chose this group of arthropods as it is species-rich, occurs in high abundance, and most species are relatively immobile (therefore allowing spatially-explicit interpretation of the arthropod data). We hypothesized that the quantitative and qualitative adverse footprint in its entirety (interior and edge) of IATs and vineyards on arthropod diversity is the same, as they are both, at least to the human eye, major transformations of landscape matrix at the spatial scale of the patch.

Study area and methods

Study sites

Sampling was in three nature reserves and seven wine estates within the CFR (Table 1). At each of these ten localities, transects were established, so that the focal land cover/land use types (hereafter referred to as 'vegetation type') were adjacent to each other. In total, there were 36 transects, each 256 m in length. Half of the transect, i.e. 128 m, was on either side of the boundary of land use/land cover types, with the exception of two transects (128 m in length) that were established across native vegetation and small IAT fragments (Table 1). Vegetation type was in four categories: natural fynbos (evergreen sclerophyllous shrublands characterized by graminoids of the Restionaceae, and shrubs of the Ericaceae and Proteaceae), IATs, cleared of invasive alien trees (CIATs), and vineyards. These resulted in six different pairs of vegetation types (Table 1).

Natural fynbos was relatively untransformed by human activity and selected from the nature reserve and the wine farms with less than 10% alien tree vegetation. Natural fynbos was predominantly mountain fynbos, with common plant species being geophytes *Watsonia borbonica*, *Cyphia phyteuma* and *Chasmanthe aethiopica*; herbs *Gymnodiscus capillaris*

Table 1 Details of the study sites and transects

Category	Site name	Locality	Pair of vegetation		Transect length (m)	No. pitfall traps
Vineyards	Vergelegen	E: 34.09206 S: 18.89851	Cleared IATs	Natural Fynbos	256	28
			Cleared IATs	Natural Fynbos	256	28
		Cleared IATs	Natural Fynbos	256	28	
		Cleared IATs	Natural Fynbos	256	28	
		IATs	Natural Fynbos	256	28	
		IATs	Cleared IATs	256	28	
		IATs	Cleared IATs	256	28	
	Bilton	E:34.01431 S:18.87259	Vineyard	IATs	256	28
			Vineyard	IATs	256	28
		Vineyard	IATs	256	28	
		Vineyard	Natural Fynbos	256	28	
		Vineyard	Natural Fynbos	256	28	
	Stellenzicht-Driekoppen	E:34.98575 S:18.95216	Vineyard	Cleared IATs	256	28
			Vineyard	Cleared IATs	256	28
	Waterford	E: 34.06625 S: 18.87626	Vineyard	IATs	256	28
			IATs	Cleared IATs	256	28
	Rustenberg	E: 33.96862 S: 18.9354	Vineyard	Cleared IATs	256	28
			Vineyard	Cleared IATs	256	28
		Vineyard	Natural Fynbos	256	28	
		Vineyard	Natural Fynbos	256	28	
		Vineyard	Natural Fynbos	256	28	
		Vineyard	Natural Fynbos	256	28	
		Vineyard	IATs	256	28	
	Dornier	E: 34.01731 S: 18.86607	Vineyard	IATs	256	28
			Vineyard	Cleared IATs	256	28
	Waterford-Driekoppen	E: 34.0063 S: 18.87639	Vineyard	Cleared IATs	256	28
Vineyard			Cleared IATs	256	28	
Nature Reserves	Jonkershoek	E: 33.98317 S: 18.94967	IATs	Natural Fynbos	256	28
			IATs	Natural Fynbos	256	28
		IATs	Natural Fynbos	128	24	
		IATs	Natural Fynbos	128	24	
	Helderberg	E: 34.00535 S: 18.8748	IATs	Cleared IATs	256	28
			IATs	Natural Fynbos	256	28
	Hottentots Holland	E: 34.06436 S: 18.87469	IATs	Cleared IATs	256	28
			IATs	Cleared IATs	256	28
		Cleared IATs	Natural Fynbos	256	28	
		Cleared IATs	Natural Fynbos	256	28	
Total number of pitfall traps						1000

IATs invasive alien trees

and *Dimorphotheca pluvialis*; shrubs *Aspalathus forbesii*, *A. aspalathoides*, *Lebeckia sepiaria*, *Lotononis prostrata*, *Hymenolepis crithmoides*, *Protea compacta*,

P. repens, *P. neriifolia*, and *Salix* species, as well as various ericas. IATs was considered a vegetation type with more than 90% alien trees, mainly *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. Since 2000, farmers together with government authorities started clearing these invasive alien trees, with follow-up clearing undertaken at least every 3 years. Physical or manual and chemical control methods were applied during IAT clearing. In essence, IATs were cut and herbicides applied to the remaining mainstem. Only organic vineyards were considered. Organic vineyard management involves no application of artificial fertilizers as the soils are relatively fertile through permanent cover crop (i.e. wheat), and only apply pesticides when absolutely necessary. One application of chemical agent chlorpyrifos was applied during early August to control mealybugs which are the vectors of a viral disease of the vines.

The 9800 ha Jonkershoek nature reserve comprises the Jonkershoek mountains and portions of the upper Jonkershoek valley where large *Radiata* pine (*Pinus radiata*) plantations are a distinctive feature bordering fynbos vegetation. This reserve was considered due to the presence of mountain fynbos adjacent to invasive alien trees (i.e. *Pinus* and *Hakea* spp.). The 286 ha Helderberg nature reserve has mountain fynbos dominated mainly by protea species. This site was chosen for its IATs adjacent to a site cleared of IATs (i.e. *Pinus* spp.). The Hottentots Holland nature reserve is 42 000 ha and comprises the Hottentots Holland mountains with the presence of pristine mountain fynbos adjacent to IATs (i.e. *P. radiata*).

Sampling

Sampling of the arthropods was on three occasions (August–October 2006, May–July 2007 and November 2007–January 2008), when soil surface characteristics (i.e. soil moisture with radioactive moisture-density gauge (Troxler 3411-B) and leaf litter depth by inserting a steel rod, 4 mm in diameter, into the leaf-litter until the harder soil layer was reached) were also measured. Pitfall traps were used to sample arthropods as this method is particularly good for comparative studies of soil-surface active arthropods (Samways et al. 2010). 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 to ensure all species across the whole vegetation type were accounted for. The reason for this layout of traps was because the ‘footprint’ of any one patch has both interior and edge, with a cross over at approximately 30 m (Samways and Moore 1991; J.S. Pryke unpublished data). The aim was to give approximate equal weighting to both interior and edge, while at the same time having a sampling programme that was practical in terms of time, hence the log 2 intervals. This is a study of a land mosaic consisting of patchwork of land use types, making a reference site of a small-sized patch of fynbos being more appropriate than an extensive nature reserve so as to compare different types of patches of comparative size. Furthermore, beta diversity is very high in extensive natural habitats and we did not want to invoke another variable into the data. It was not the intention here to unpack all the complex details of edge effects for the different taxa but rather to compare patches in their entirety in a variety of landscape contexts (see Wiens et al. 1993). However, two transects, between IATs and fynbos, were each four traps short, owing to unavailability of extensive sites (Table 1). 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) (Table 1).

Pitfall traps for sampling arthropods were 500 ml plastic honey jars, each containing a replaceable paper cups, 8 cm diameter, 12 cm deep. Each trap was one-third filled with 70% ethylene glycol. Traps remained closed during non-sampling periods, and opened for five consecutive days without rain (Borgelt and New 2006). Samples then were washed in water, and transferred to 70% ethanol.

Sampling in vineyards was under vine rows to minimize impact of disturbance by farm activity. All pitfall traps were established three months prior initial sampling to eliminate ‘digging effects’. Arthropod samples from each trap set were combined, resulting in one sample per sampling station (i.e. 1000 pitfall traps gave 500 samples per sampling period, making 1 500 samples over the three sampling periods).

Arthropods were identified to species, or where this was not possible, assigned to morphospecies. 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

Species accumulation curves, using EstimateS version 8.0.0 with samples randomized 50 times (Colwell 2006), were produced for all vegetation types separately, and for all combined. Non-parametric species estimators were used to provide the best overall arthropod species estimates for all vegetation types (Hortal et al. 2006). The 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 should insufficient sampling be an issue (Colwell and Coddington 1994), and were calculated here using EstimateS (Colwell 2006) for all vegetation types separately and for all combined.

As arthropod species richness was normally distributed and variance homogeneous, one-way analysis of variance (ANOVA) was performed on species richness data. However, log transformations were used for abundance data. Multiple comparisons of the means were made using Bonferroni methodology (Legendre and Legendre 1998). ANOVA was used to test for differences between means of populations.

ANOVAs were performed on the selected environmental variables in the different vegetation types using SPSS v17 software (SPSS Inc. 2006), and significance level was set at a P-value > 0.05 . Where the ANOVAs were not significant, the analysis was terminated. However, where the result was significant, it was investigated further using multi-comparison tests.

Classification trees, using CHAID growth limits (SPSS Inc. 2006) determined the relationship between the vegetation types in terms of species richness and abundance relative to environmental variables. Significance level for splitting nodes and merging categories was 0.05, and the significance values were adjusted using Bonferroni methodology. Correlations between species richness and abundance with environmental variables for all vegetation types, separately and collectively, were calculated using Spearman's Rank Order Coefficient, since the data were not normally distributed.

Multivariate analysis, using Primer Ver. 5 (Clarke and Gorley 2001), was used to detect trends and to explore the differences in arthropod assemblages between different vegetation types. Bray-Curtis similarity coefficients were used to derive similarity matrices of arthropod data, then clustering dendrograms and non-metric, multi-dimensional scaling (NMDS) ordination plots to detect trends in similarity. The main advantage of NMDS is its greater ability to represent complex relations accurately in low-dimensional space (Clarke and Warwick 2001). Joint absences in the NMDS were ignored to emphasize similarity in common or rare species, comparing only percentage composition (Clarke and Warwick 2001). The dendrograms were group-average linking on Bray-Curtis species similarities from standardized abundance data.

Principal Components Analysis (PCA) was used to determine whether arthropods from the different vegetation types fell into distinct groups (Clarke and Warwick 2001). PCA considers a different starting point by making different assumptions about the definition of (dis)similarity of samples being compared. Rare species were excluded from the PCA, so that the species retained were more comparable with the number of samples (Clarke and Warwick 2001). Distances between vegetation types on the ordination attempt to match the corresponding dissimilarities in arthropod assemblage composition i.e. similar vegetation types would have very similar arthropod assemblages, while vegetation types that are dissimilar would have few species in common, or the same species at very different levels of abundance. However, PCA can produce inconclusive results, so the data were further analyzed using cluster analysis for determining how the vegetation types varied, and how they grouped in terms of their arthropod assemblages. Cluster analysis produces results that broadly agree with PCA (Clarke and Warwick 2001), and usually it is much easier to observe grouping in cluster analysis than in PCA. Nevertheless, it may be easier to understand what the groupings indicate if they have been produced by PCA. Therefore, using a combination of cluster analysis and PCA is an effective approach.

Analysis of similarity (ANOSIM) tests the hypothesis that there are no assemblage differences between groups of samples specified, here vegetation type (Clarke and Warwick 2001). R is approximately zero

if the null hypothesis is true, indicating that similarities between and within vegetation types will be the same on average (Clarke and Warwick 2001).

Because of the large number of species sampled, a more automatic, analytical procedure for identifying influential species (typifying species) was carried out.

Results

Species richness and abundance

In total, 25 225 individuals were sampled, and allocated to 198 species, 106 families and 24 orders (Electronic Supporting Table 1). Species accumulation curves for the four vegetation types, fynbos, IATs, CIATs and vineyards, although flattening, did not quite reach an asymptote, despite the large number of individuals sampled. Nevertheless, an overall species accumulation curve combining all vegetation types did reach an asymptote after counting over 400 samples and 20 000 individuals, the latter of which was exceeded here.

CIATs and fynbos supported highest and next highest mean species richness and abundance respectively (Table 2). Vineyards and particularly IATs had the least number of species and lowest overall abundance (Table 2). ANOVA among the four vegetation types showed significant differences in arthropod species richness ($df = 509$, $F = 41.65$, $P < 0.001$) and abundance ($df = 509$, $F = 62.59$, $P < 0.001$). Nested ANOVAs for arthropod species richness

Table 2 Mean (\pm SE) species richness and abundance for fynbos, invasive alien trees (IATs), cleared invasive alien trees (CIATs), and vineyard sites

Variable	Vegetation	Mean	<i>N</i>	SE
Species richness	Cleared IATs	18.130	115	0.535
	Fynbos	18.062	145	0.522
	IATs	11.573	124	0.413
	Vineyard	14.056	126	0.494
	All vegetation types	15.510	510	0.276
Abundance	Cleared IATs	65.765	115	3.660
	Fynbos	53.421	145	2.765
	IATs	38.105	124	2.379
	Vineyard	41.437	126	2.306
	All vegetation types	49.520	510	1.472

N refers to the number of samples with one or more individuals

among all four vegetation types revealed significant differences between all vegetation pairs except fynbos and CIATs (Table 3). For abundance, all pairs of vegetation types were significantly different, except vineyards and IATs (Table 3).

Of the sampled arthropods, 77 species were restricted to 1–3 of the four possible vegetation types, with some being restricted to only one vegetation type: fynbos (6 spp.); IATs (4 spp.); CIATs (3 spp.) and vineyards (5 spp.) (Electronic Supporting Table 2).

The classification tree for vegetation based on arthropod species richness indicated some similarity between fynbos and CIATs (Fig. 1). In turn, IATs and vineyards were significantly different from each other in species richness, and both were not comparable to either fynbos or CIATs (Fig. 1). Classification of different vegetation types in terms of arthropod abundance gave three different nodes (Fig. 2). IATs and vineyards clustered together and had significantly lower species abundance than fynbos or CIATs.

Arthropod assemblage composition

Results on assemblage composition, where both species and their abundances are considered together, gave a different arrangement of vegetation types compared to the results from species richness and abundance above. Cluster analysis showed that fynbos and vineyards were most similar, followed by IATs and then CIATs (Fig. 3). NMDS gave similar results. In short, while IATs and vineyards were species poor and low in abundance, when it came to the species characterizing the assemblages, vineyards and fynbos were similar, and CIATs still had an arthropod legacy of the IATs, even though there was an increase in species richness and abundance. However, when vegetation types were grouped by assemblage composition, there were statistically significant differences between these vegetation types ($R = 0.149$, $P = 0.001$) using ANOSIM. Yet PCA, which excluded the rare species, gave a slightly different picture from the cluster analysis, with IATs and fynbos as outliers, and vineyards and CIATs close to each (Fig. 4).

Selected environmental variables influencing arthropod biodiversity

Vineyards supported the lowest percentage soil moisture followed by CIATs, whereas fynbos had

Table 3 Nested analysis of variance (ANOVA) among fynbos, invasive alien trees (IATs), cleared invasive alien trees (CIATs), and vineyard site species richness

Variable	Vegetation (I)	Vegetation (J)	(I-J) Mean species richness/ abundance difference	SE	Sig.	95% Confidence interval	
						Lower bound	Upper bound
Species richness	Fynbos	IATs	6.489*	0.685	0.000	4.67	8.30
		Vineyard	4.007*	0.682	0.000	2.20	5.81
	CIATs	Fynbos	0.068	0.700	1.000	-1.78	1.92
		IATs	6.558*	0.725	0.000	4.64	8.48
	Vineyard	IATs	4.075*	0.723	0.000	2.16	5.99
Abundance	Fynbos	IATs	15.316*	3.866	0.001	5.08	25.55
		Vineyard	11.984*	3.849	0.012	1.79	22.18
	CIATs	Fynbos	12.345*	3.946	0.011	1.89	22.80
		IATs	27.660*	4.092	0.000	16.82	38.50
	Vineyard	IATs	24.329*	4.076	0.000	13.53	35.12
	Vineyard	IATs	3.332	3.998	1.000	-7.26	13.92

* indicates that the mean difference is significant at the 0.05 level. (I) and (J) represent two different vegetation types being compared

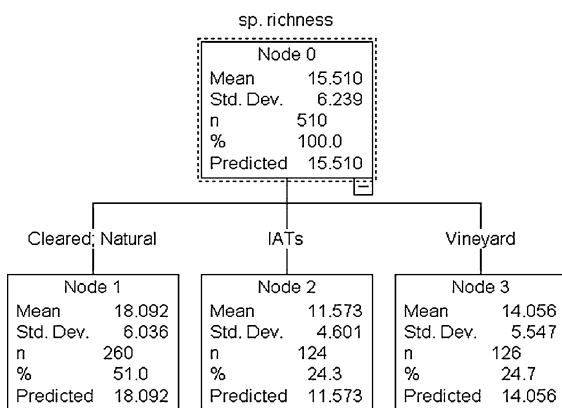


Fig. 1 Classification tree of the four vegetation types (at all locations combined) for mean arthropod species richness. Cleared = vegetation cleared of invasive alien trees, natural = fynbos, IATs = invasive alien trees

the highest (Table 4). Greatest leaf litter depth was in IATs, while vineyards had a very shallow leaf litter (Table 4). ANOVA of fynbos, IATs, CIATs, and vineyards showed that there were significant differences among (df = 3, F = 5.81, P < 0.01), and within (df = 509, F = 5.81, P < 0.01) sites in terms of percentage soil moisture. There were also significant differences, among fynbos, IATs, CIATs, and vineyards in terms of leaf litter depth (df = 3, F = 296.6, P < 0.0001). Vineyards had significantly

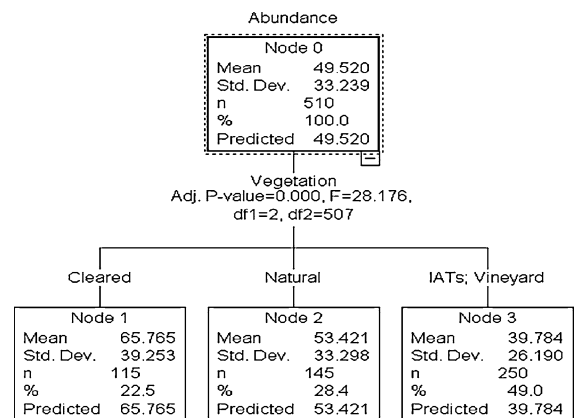


Fig. 2 Classification tree of vegetation in terms of mean arthropod abundance. Cleared = vegetation cleared of invasive alien trees, natural = fynbos, IATs = invasive alien trees

different soil moisture content compared to fynbos and IATs, but comparable with CIATs (Table 5).

Overall, there were no significant correlations between percentage soil moisture and species richness (Spearman’s Coefficient = 0.05; P < 0.919, n = 510), as well as abundance (Spearman’s Coefficient = 0.061; P < 0.171, n = 510). Moreover, there were no significant correlations between leaf litter depth and species richness (Spearman’s Coefficient = -0.20; P = 0.651, n = 510), nor abundance (Spearman’s Coefficient = -0.033; P < 0.454, n = 510).

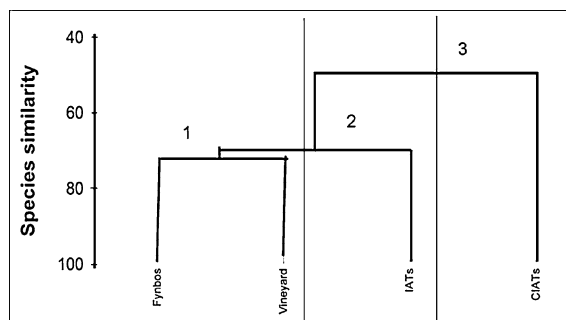


Fig. 3 Classification tree of vegetation types in terms of arthropod assemblages using group-average linking on Bray-Curtis species similarities. CIATs = vegetation cleared of invasive alien trees, IATs = invasive alien trees

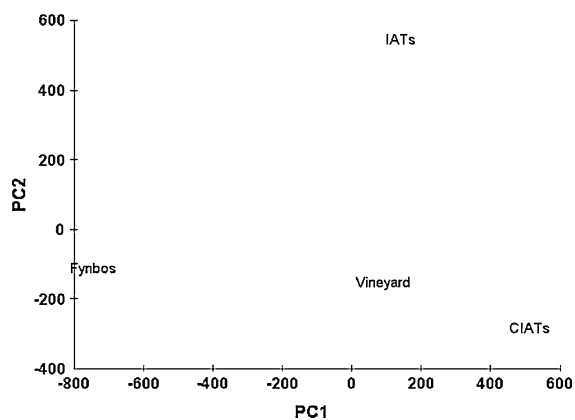


Fig. 4 Principal components analysis (PCA) ordination of Bray-Curtis similarity between arthropod samples from different vegetation types (i.e. fynbos, vineyard, invasive alien trees (IATs), vegetation cleared of invasive alien trees (CIATs))

Species typifying vegetation types

The similarity between all pairs of sites in fynbos was made up mainly of contributions from eight species including *Camponotus* sp.2, *Linepithema humile* and *Gryllus bimaculatus* with a cumulative contribution of over 60% of the total similarity of 16.32 (Table 6). These arthropod species can be considered as typical of associated vegetation types, although *L. humile* is alien (Table 6). The lower ratio of their contribution to the SD was an indication that the species were inconsistently present in large numbers.

Some species such as *L. humile* were typical of different vegetation types (i.e. fynbos, CIATs, and vineyards), an indication of its strong adaptation towards different vegetation conditions (Table 6).

Table 4 Environmental variable means (± 1 SE) for fynbos, invasive alien trees (IATs), cleared invasive alien trees (CIATs), and vineyard sites

Environmental variable	Vegetation	Means	N	SE
% Soil moisture	CIATs	8.778	115	0.272
	Fynbos	9.761	145	0.276
	IATs	9.491	124	0.300
	Vineyard	8.362	126	0.223
	All vegetation types	9.128	510	0.137
Leaf litter depth (mm)	CIATs	13.652	115	0.516
	Fynbos	15.572	145	0.385
	IATs	20.798	124	0.578
	Vineyard	2.738	126	0.211
	All vegetation types	13.239	510	0.363

Nevertheless, alien *L. humile* was not typical of IATs, suggesting that this species had a preference of various vegetation types but not IATs. An overlap of typifying arthropod species may also indicate that some vegetation types have similar resources required by arthropods and that not all arthropod species are vegetation specific.

Discussion

Species richness and abundance in the different vegetation types

As none of the species accumulation curves in the various individual vegetation types reached an asymptote, species estimates were underestimates. Nevertheless, the overall species accumulation curve did reach an asymptote, indicating that the sample size ($> 25\ 000$ individuals) was enough to estimate surface-active arthropod species richness using both number of samples or individuals.

We found that the overall results were categorical, with all species estimators showing highest species richness in fynbos, with cleared areas and vineyards having the next highest estimates. Lowest species richness was in invaded areas, supporting other findings that invasion of fynbos by alien trees is highly impoverishing in the CFR (Ratsirarson et al. 2002; Pryke and Samways 2009). In terms of overall

Table 5 Nested analysis of variances (ANOVA) among natural fynbos, invasive alien trees (IATs), cleared invasive alien trees (CIATs), and vineyard sites in terms of percentage (%) soil moisture

Dependent Variable	Primary vegetation type (I)	Adjacent vegetation type (J)	(I-J) Mean Difference	SE	Sig.	95% confidence interval	
						Lower bound	Upper bound
% Soil moisture	Fynbos	IATs	0.270	0.373	1.000	-0.719	1.260
		CIATs	0.983	0.381	0.061	-0.027	1.993
	IATs	Vineyard	1.399*	0.372	0.001	0.414	2.385
		CIATs	0.712	0.395	0.432	-0.334	1.760
	CIATs	Vineyard	1.129*	0.386	0.022	0.106	2.152
		Vineyard	0.416	0.394	1.000	-0.627	1.459
Leaf litter depth (mm)	Fynbos	CIATs	1.920*	0.618	0.012	0.280	3.560
		Vineyard	12.834*	0.603	0.000	11.240	14.430
	IATs	Fynbos	5.226*	0.605	0.000	3.620	6.830
		CIATs	7.146*	0.641	0.000	5.450	8.840
	CIATs	Vineyard	18.060*	0.626	0.000	16.400	19.720
		Vineyard	10.914*	0.638	0.000	9.220	12.600

* indicates that the mean difference is significant at the 0.05 level

abundance, invaded areas were much poorer than vineyards, indicating greater impact of alien trees over that of vineyards. Fynbos had very high arthropod abundance, the highest of all the vegetation types, even though this footprint study was highly conservative with similar weight being given to edge species as to interior species. Yet species richness of the cleared areas was close to that of fynbos, showing that clearing of alien trees increases species richness, an encouraging sign for restoration. However, we must not over-simplify here, because as pointed out by Holl (1996) and Brändle et al. (2000), the restoration process can be very dynamic, with different species and population abundance being favoured at different times during the recovery process.

Arthropods restricted to particular vegetation types

All vegetation types had some unique arthropod species, with only five being unique to natural vegetation. This figure would in all likelihood be higher if extensive natural reference sites had been used, but the aim here was to compare patches of comparative size. In turn, four species were unique to vineyards, and three to each in invaded and cleared areas. However, as species richness was lowest in

invaded areas, this tantamounts to the largest number of absentees compared to all the other vegetation types. This is not surprising because alien trees can impoverish the local terrestrial fauna even over a few metres (Samways et al. 1996). However, some species such as the thomisid spider *Ozyptila* sp., the chrysidid hymenopteran *Spintharina* sp., the millipede *Centrobolus* sp.2 and the army ant *Dorylus helvolus* were only in invaded areas, indicating that although the majority of arthropods cannot tolerate alien trees, some thrive under such conditions, as is the case with dragonflies under alien trees on Mayotte Island (Samways 2003). Presumably, in the wild, they are restricted to heavily shaded, highly local habitats, which prevail in the sheltered ravines of the Cape Fold Mountains (Pryke and Samways 2008). In contrast, certain species such as the calliphorid fly *Chrysomya chloropyga* and cicadellid hemipteran *Ciphalilus* sp. preferred vegetation types other than IATs.

Effectiveness of clearing of alien trees varies with density of the original plant infestation, species type, and time that the site has been invaded (Holmes and Richardson 1999). Removal of the dense stands here led to the remarkable recovery of certain arthropod species (e.g. the cantharid beetle *Cantharis* sp., the chrysomelid beetle *Leptinotarsa* sp., *C. chloropyga*,

Table 6 Arthropod species typifying vegetation types

Species	Av. Abund	Av. Sim	Sim/SD	Contrib%	Cum%
Typical of fynbos vegetation type (Overall average similarity: 16.32)					
<i>Camponotus</i> sp.2	5.23	3.81	0.64	23.33	23.33
<i>Linepithema humile</i>	2.48	1.34	0.45	8.18	31.51
<i>Gryllus bimaculatus</i>	1.35	1.05	0.51	6.45	37.96
<i>Microhodotermes viator</i>	5.35	1.02	0.21	6.23	44.19
<i>Centrobolus</i> sp.2	2.80	0.80	0.27	4.93	49.12
<i>Zophosis boei</i>	2.19	0.74	0.37	4.55	53.67
<i>Diores youngai</i>	1.28	0.74	0.47	4.52	58.19
<i>Tetramorium capense</i>	1.66	0.73	0.32	4.45	62.64
Typical of IATs vegetation type (Overall average similarity: 13.05)					
<i>Centrobolus</i> sp.2	5.92	3.77	0.47	28.92	28.92
<i>Porcello</i> sp.	4.59	2.49	0.36	19.09	48.02
<i>Gryllus bimaculatus</i>	0.75	0.73	0.39	5.57	53.58
Typical of CIATs vegetation type (Overall average similarity: 19.79)					
<i>Microhodotermes viator</i>	11.88	3.74	0.41	18.93	18.93
<i>Centrobolus</i> sp.2	5.66	2.73	0.49	13.82	32.75
<i>Camponotus</i> sp.2	5.11	2.72	0.62	13.75	46.50
<i>Zophosis boei</i>	3.90	1.68	0.53	8.47	54.97
<i>Linepithema humile</i>	3.18	1.30	0.45	6.58	61.55
<i>Porcello</i> sp.	2.92	1.07	0.31	5.42	66.97
<i>Tetramorium capense</i>	2.76	1.07	0.38	5.39	72.35
Typical of vineyard vegetation type (Overall average similarity: 12.09)					
<i>Linepithema humile</i>	3.71	1.64	0.35	13.61	13.61
<i>Zophosis boei</i>	2.90	1.55	0.35	12.82	26.42
<i>Centrobolus</i> sp.2	3.31	0.92	0.22	7.63	34.05
<i>Camponotus</i> sp.2	2.01	0.82	0.27	6.81	40.85
<i>Gryllus bimaculatus</i>	0.73	0.52	0.37	4.26	45.12
<i>Xestobium</i> sp.	1.88	0.51	0.17	4.24	49.36
Halictidae sp.1	0.94	0.44	0.29	3.62	52.98
Curculionidae sp.1	0.57	0.43	0.28	3.60	56.58
<i>Tetramorium capense</i>	1.26	0.42	0.24	3.45	60.03
<i>Porcello</i> sp.	1.70	0.42	0.19	3.44	63.47

Av.Abund average abundance, Av.Sim average similarity, Sim/SD average similarity/standard deviation of the average, Contrib% contributed towards total average similarity per taxon, Cum% cumulative percentage total of all taxa towards average similarity

the reduviid hemipteran *Ectrichodia crux*, the nemopterid neuropteran *Laurhervasia setacea* and the ant *Componotus maculatus*), as is the case with aquatic arthropods when IATs are removed from river banks (Magoba and Samways 2010).

We also found the alien ant *Linepithema humile* to be common in fynbos, which may seem to contradict earlier findings where it is usually associated with disturbed areas (Suarez et al. 1998; Suarez et al.

2000; Holway et al. 2002; Carpintero et al. 2005; Ward 2005). This suggests that while the fynbos may appear relatively undisturbed from a vegetation point of view, the context of the fynbos patches (i.e. adjacent to very disturbed patches) has an influence, which would reconcile the two sets of findings. This was confirmed by the fact that the ant was common in vineyards, and from these agricultural areas it is apparently able to penetrate the adjacent fynbos.

Arthropod assemblage composition

The four vegetation types had distinct arthropod assemblages, based on cluster, NMDS and ANOSIM analyses. Even though fynbos was much more species rich than vineyards, their assemblages nevertheless grouped close together, suggesting that the conversion to vineyards was much more faithful in maintaining indigenous ecological integrity than was conversion caused by alien trees. Why this is so is not clear but shading might play a role, because shade from alien trees is the key factor affecting some aerial insects in the same area (Samways and Sharratt 2010). However, as the arthropods here are living in, and dependent on, the litter and soil, there is likely to be a whole host of chemical and physical factors, not measured here, playing a role at various spatial scales from a meter or two to several hundreds of kilometres.

The invaded and cleared areas also grouped together in the multivariate analyses, indicating, not surprisingly, that the recovery process follows a trajectory based on the existing fauna in the invaded areas. Interestingly, when rare species were excluded from the analyses in the PCA, fynbos and cleared areas were no longer comparable in terms of assemblage composition, indicating that the arthropod recovery in the cleared areas was mostly the result of re-establishment by common species, including some that appeared very opportunistic, such as the termite *Microhodotermes viator*. Then, as vineyards and cleared areas had a similar species composition, it is likely that both vegetation types supported species that preferred more open areas rather than dense and shady fynbos vegetation, but nevertheless re-inforces the fact that vineyards have less impact on species composition than do alien trees.

Arthropod species and environmental variables

Soil under natural fynbos, alien trees, and in cleared areas had comparable percentage soil moisture, which appeared to be a result of comparable ground cover. In contrast, vineyards with their bare surface between the vine rows, had lower percentage soil moisture than fynbos or cleared areas, with resultant lower arthropod abundance than even in invaded areas. However, soil moisture did not statistically correlate with arthropod species richness or abundance. On the other hand, alien tree areas had

significantly deeper leaf litter compared to either natural vegetation or cleared areas, possibly due to lack of decomposers necessary to reduce the leaf litter. Nevertheless, there was no significant correlation between leaf litter and arthropod species richness and abundance, despite vineyards having the lowest. Overall, these results, being not very categorical, are encouraging for restoration, as soil conditions under both vineyards and alien trees are not sufficiently adverse to be of concern, at least in terms of the arthropods we studied.

Conclusions

Our results emphasize that the impoverishing effect of a particular type of agriculture (vineyards) on indigenous surface-active arthropods is not as great as that of invasive alien trees in patches of comparative size. Furthermore, the remnant assemblage in vineyards is more of a subset of that in natural fynbos than is the case with alien trees. This suggests that conversion of vineyards to more biodiversity friendly farming methods, as outlined by Gaigher and Samways (2010), has a good base on which to work. In turn, clearing of alien trees will continue to benefit biodiversity recovery, but it will take time for the original set of species to return, as it is only the common, and presumably more habitat-tolerant, species which readily recover. This re-establishment of the original set of arthropod species would be promoted by clearing alien trees in close proximity to large patches of natural fynbos, to enable easy movement and recolonization of the areas being restored.

Acknowledgments Financial support was from the Centre for Invasion Biology and the Andrew Mellon Foundation. Rejoyce Gavhi, Rozwivhona Magoba, Mbula Tshikalange, Adam Johnson, Tshilidzi Muofhe and Sne Mchunu kindly assisted in the field. Ansie Dipenaar identified spiders, and Henk Geertsema assisted with other identifications. We also appreciate the very constructive criticisms of two anonymous referees which greatly improved the manuscript.

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