

The influence of shrub species and fine-scale plant density on arthropods in a semiarid shrubland

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Abstract. Plant-resident arthropods are closely tied to the distribution of their hosts across multiple spatial scales. Shrubs provide habitat for a range of arthropods, and variations within shrubland ecosystems may affect arthropod communities. We examined the role of shrub species and density in structuring arthropod communities in an encroached Australian woodland using two common and widespread shrub species, Turpentine (*Eremophila sturtii*) and Silver Cassia (*Senna artemisioides* subsp. *filifolia*). We found five times more arthropods (Psocoptera, Collembola and Hemiptera) on *Eremophila* compared with *Senna*. Furthermore, Psyllidae were found only on *Eremophila*. In total we recorded 39 Hemipteran species; 13 from *Eremophila*, 16 from *Senna* and 10 common to both shrub species. Each shrub species supported a unique arthropod assemblage, even though they grow in close proximity (<15 m). In contrast, we found limited effects of fine-scale plant density, with plants growing in low and high density supporting similar arthropod communities. Our study indicated that isolated shrubs in these woodlands support a variety of arthropods, and shrub species is a more important driver of arthropod community structure than fine-scale density.

Additional keywords: Collembola, Hemiptera, plant density, Psocoptera, resource concentration.

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Introduction

The effects of habitat change on biotic communities are known to vary markedly across spatial scales (Mazerolle and Villard 1999; Driscoll 2004; Goslee and Sanderson 2010). For example, changes in habitat structure at landscape scales can alter patterns of faunal distribution by changing immigration and emigration rates (*sensu* Equilibrium Model of Island Biogeography, MacArthur and Wilson 1967) and interaction networks (Gonzalez *et al.* 2011). Changes at finer spatial scales, such as those around individual plants, can affect the abundance, diversity, and distribution of plant-resident herbivores such as arthropods, and in particular insects (Masumoto *et al.* 2000; Hodkinson *et al.* 2001; Sarin and Bergman 2010). Conversely, insects can affect host-plant biomass (Flynn *et al.* 2006) as well as functions such as photosynthetic rate (Meyer and Whitlow 1992).

The distribution of plant-resident arthropods is closely tied to the distribution of their hosts, and changes in the composition, density and spatial arrangement of host plants can alter the community structure of their residents (Schaffers *et al.* 2008; He *et al.* 2010; Murakami and Hirao 2010). One of the most influential hypotheses guiding the study of herbivore–plant interactions over the past few decades has been the Resource Concentration Hypothesis (Root 1973). This hypothesis predicts that specialist herbivores will be more abundant and

speciose in plant patches of high density as these patches are easier to detect, have a higher concentration of resources, and provide a larger area of contiguous habitat than low density patches or isolated plants. Support for this hypothesis has, however, been mixed (Bach 1980, 1988; Cook and Holt 2006). The Resource Concentration Hypothesis has mainly been tested in agricultural systems and/or through the use of experimental manipulation using arthropod as models (e.g. Bach 1980; Grez and Gonzalez 1995; Long *et al.* 2003; Rhainds and English-Loeb 2003). However, there have been far fewer studies conducted *in situ* within natural ecosystems (except see Masumoto *et al.* 2000; Sholes 2008).

In arid and semiarid ecosystems, a variety of studies have examined how faunal assemblages (e.g. Ayers *et al.* 2001; Blaum *et al.* 2007; Sirami *et al.* 2009) respond to increasing shrub density in the context of shrub encroachment (i.e. a widespread shift from grasslands to dense shrublands, e.g. Van Auken 2009; Eldridge *et al.* 2011). Although shrub encroachment is a major management and environmental issue in eastern Australia (Eldridge *et al.* 2011), individual shrubs may also influence invertebrate communities at the scale of a few plants rather than landscape level changes in plant density (e.g. ‘island’ effects: Doblas-Miranda *et al.* 2009; Zhao and Liu 2013; general effects: Li *et al.* 2013; Sotomayor and Lortie 2015).

In this study we tested three propositions about the effects of shrub species and fine-scale differences in shrub density on plant-resident arthropods in an Australian woodland. First, we expected that our two shrub species, *Eremophila sturtii* R. Br. and *Senna artemisioides* subsp. *filifolia* Gaudich. ex DC, would support different arthropod taxa, given their markedly different size and architecture, and the fact that many insects are commonly host-specific (Peeters *et al.* 2001; Sugiura 2011). Second, consistent with expectations under the Resource Concentration Hypothesis, we predicted that shrubs growing in patches of high density or biomass would support a greater richness and abundance of insect taxa than those growing as isolated individuals. Third, we predicted that the abundance and diversity of arthropods would increase with increasing shrub biomass of the sampled plant, consistent again with the Resource Concentration Hypothesis. This allowed an investigation of the effects of changes to plant biomass at patch scales and at the scale of individual plants.

Methods

Study area

This study was conducted at the Australian Wildlife Conservancy's Scotia Sanctuary, which is located ~150 km south of Broken Hill, New South Wales, Australia (33°43'S, 143°02'E). The climate is characterised by low and variable rainfall (250 mm mean annual rainfall), high evapotranspiration (~1500 mm year⁻¹), hot summers (daily mean temperature: 30°C, daily maximum: 47.8°C, daily minimum: >15°C) and cool winters (daily mean: ≤17°C, daily maximum: 32.2°C, daily minimum: ≤6°C) (Australian Wildlife Conservancy 2011).

Site features, vegetation community and target plant species

This study was conducted within *Eremophila*- and *Senna*-dominated communities. The study area is dominated by a wide variety of native shrubs of the genera *Eremophila*, *Dodonaea*, *Senna* and *Rhagodia*. Two shrub species were investigated in this study: *Eremophila sturtii* R. Br. (Turpentine, hereafter *Eremophila*), and *Senna artemisioides* subsp. *filifolia* Gaudich. ex DC (Silver Cassia, hereafter *Senna*). Both shrub species are widely distributed in semiarid eastern Australia, occurring as either scattered individuals within woodland communities, or in extensive dense monocultures (Noble 1997). Within the study area these two species are co-dominant, accounting for over 70% of all individual shrubs (A. Kwok, pers. obs.). *Eremophila*, including *E. sturtii*, are known to contain a wide range of chemical compounds, including some which have antimicrobial properties (e.g. Liu *et al.* 2006; Ndi *et al.* 2007). Virtually nothing is known of the chemical makeup of *Senna artemisioides*.

At our study sites, there are few differences between *Eremophila* and *Senna* in terms of soil surface condition, foliage cover, soil texture, litter cover, and soil carbon and nitrogen (Howard *et al.* 2012). Open patches of bare ground between *Eremophila* and *Senna* have slightly less litter cover, soil carbon, and soil nitrogen, but greater cryptogam cover (Howard *et al.* 2012). However, open patches do not differ from

Eremophila or *Senna* patches in terms of soil texture, basal cover, or indicators of soil stability (Howard *et al.* 2012). Shrub patches do tend to support a higher number of plant species and individuals than open patches, and most of these species were found under both *Senna* and *Eremophila* (Howard *et al.* 2012).

Experimental design and shrub density

Ten sites were chosen within *Eremophila*–*Senna* shrublands. Individual sites occurred in the swales between low, east–west trending dunes. The soil in the swales consists of small areas of calcareous earths and brown, highly calcareous earths (Eldridge *et al.* 2008). Sites were separated by distances of at least 500 m. At each site, we chose four sections at opposite ends of the swale within a plot ~300 m by 300 m in size. Within two of the four sections we chose a shrub growing in a patch considered to be at a low density. 'Low density' was defined as having fewer than two conspecific shrubs within a radius of 5 m (i.e. over an area of ~80 m²). Within the other two sections, we selected two shrubs growing in 'high density' patches, defined as 10–20 conspecific shrubs within an area of 80 m². These treatments therefore are akin to 'patches', which may differ from each other in the resources and habitat they provide (Bach 1988; Rhoads and English-Loeb 2003). We based our definitions of low and high density on an assessment of density specifically at our study sites as we are predominantly concerned with patterns within our study area, and also because plant density in arid shrublands is remarkably variable (e.g. 100-fold variation within a region; Ayers *et al.* 2001). Although we acknowledge that this limits the generalisation of density effects at a broader context, we felt these definitions were those most relevant to our study sites. The biomass of each shrub was calculated using published allometric relationships relating shrub height to biomass (Harrington 1979). We refer to this value herein as 'calculated biomass'. Thus, in total, we sampled 80 shrubs (two species × two treatment configurations (densities) × two subsamples × 10 sites).

We acknowledge that our definitions of density are based only at the scale of individual plants, and density and host-biomass represent only one factor that might affect arthropods in shrublands. For example, it is possible that the biomass of surrounding shrubs is more important than host-plant biomass, or fine-scale density *per se* (e.g. associational effects, Hambäck *et al.* 2000; Karban 2007); however, in this study we focus on conspecific shrub density, as this is the most consistently variable factor at our study sites.

Arboreal arthropods were sampled from all 80 shrubs by fogging each plant with a pyrethrum-based insecticide (Pyzap, 40 g L⁻¹ Pyrethrins, 160 g L⁻¹ piperonylbutoxide, Agserv-Ruddock Agriculture, Silverwater, NSW, Australia). Spraying was only conducted on wind-free days over a period of 1 week in May 2009. Thirty minutes after spraying, each shrub was shaken for 1 min to dislodge any arthropods. Arthropods were collected from a sheet placed below the shrub, and transferred to vials of ethanol for storage. Foliage dislodged from the shrubs during shaking was inspected separately for arthropods. These two sources of arthropods were pooled for our analyses.

We acknowledge that our sampling was relatively limited, particularly given that arthropod communities can change across seasons (e.g. Moir *et al.* 2011). For example, we sampled in May, which is a relatively cool time of year. In arid ecosystems, lower temperatures generally lead to reduced invertebrate numbers as they are heavily influenced by temperature (Palmer 2010). Similarly, the general productivity of arid systems at any given point of time is heavily influenced by climate and in particular rainfall (Morton *et al.* 2011). Thus, the limited temporal replication of our sampling should be considered when interpreting the results of this study.

From all the taxa sampled, results were recorded only for Collembola, Hemiptera (including a large number of Psyllidae) and Psocoptera. These taxa represented over 90% of the total number of arthropods sampled (unpubl. data). Psocoptera were only identified at the ordinal level. Collembola were identified to the family level. Hemiptera were further identified to morphospecies and verified by a taxonomic expert (Gerrosimus Cassis, University of New South Wales). Analyses of species richness, diversity and composition were restricted to the Hemiptera.

Statistical analyses

For statistical analyses, the abundance of each arthropod taxon was based on the mean of the two subsamples for each treatment configuration at each site. Generalised Linear Models (GLM) were used to test for differences in arthropod (Hemiptera, Psyllidae, Collembola and Psocoptera) abundance between shrub species (*Eremophila*, *Senna*), shrub density (low, high), and the interaction of these factors. Although Psyllidae is a family of Hemiptera, it was treated separately in our analyses due to the presence and numerical dominance of only one Psyllid species. GLM were also used to test for differences between shrub density and shrub species in the species richness and diversity of Hemiptera. For a diversity measure, we used a bias-controlled effective number of species (Jost 2006), which has been shown to be one of the least biased diversity estimates (Beck and Schwanghart 2010). Bias-controlled effective number of species (hereafter 'effective species diversity') was calculated using the program SPADE (Chao and Shen 2003). Each arthropod taxon was analysed in a separate model, using either a negative binomial (number of arthropods) or Gaussian (number of hemipteran species, effective species diversity) distribution. The choice of distribution was based on visual analysis of the residual graphs (following Zuur *et al.* 2009). All GLM analyses were conducted in the program R (R Development Core Team 2015) using the MASS package (Venables and Ripley 2002). Deviance explained by the model (also known as the Pseudo- R^2) was calculated as per Zuur *et al.* (2009).

We used linear regression to examine the relationship between calculated plant biomass and the abundance of Psocoptera, Collembola and Hemiptera, for each shrub species and density treatment. Additionally, the abundance of Psyllidae and calculated biomass was regressed for *Eremophila* only, as Psyllids were found only on this shrub species. For Hemiptera, we examined the relationship between calculated

plant biomass and the number of species and effective species diversity.

Hemipteran species composition

A two-way Permutational Multivariate Analysis of Variance (PERMANOVA, Anderson and Gorley 2008) was used to test for differences in the hemipteran species composition between shrub species and shrub density, and the interaction of these factors. We used non-metric multi-dimensional scaling to display patterns of community composition within each shrub species and shrub configuration. These analyses were based on square-root transformed data and a zero-adjusted Bray–Curtis resemblance matrix (Clarke and Gorley 2006). The closer any given points are to each other in the resulting ordination, the greater their similarity in terms of species composition. The PRIMER (Version 6) (Clarke and Gorley 2006) + PERMANOVA (Anderson and Gorley 2008) package was used for all multivariate analyses, including the creation of species accumulation and dominance curves. Analyses of species composition excluded rare species. For the purposes of our analyses, 'rare' species were defined as those that were recorded on less than five shrubs, or had less than five individuals sampled in total.

Results

We collected a total of 9102 arthropods in this study, mostly (85%) from *Eremophila sturtii*. Fifty-one percent of individuals on *Eremophila* were Psocoptera, 28% Hemiptera, 15% Psyllidae and 6% Collembola. The fauna on *Senna* was dominated by Psocoptera (69%) with smaller numbers of Hemiptera (22%), Collembola (8%) and Psyllidae (1%). All Collembola were from the family Sminthuridae. Species accumulation curves indicated that a high proportion of species were recorded for both shrubs, but that a greater number of additional samples would be required to record all species for *Senna* compared with *Eremophila* (Fig. 1).

Effect of shrub density on the arthropod fauna

There was no effect of shrub density on the total abundance of arthropods (Density (D): $P > 0.05$), and this was consistent for both *Eremophila* and *Senna* (shrub species (SS) \times D interaction: $P > 0.05$; Tables 1 and 2). This was also the case for the number of Psocoptera, Psyllidae, and Collembola when analysed separately (Tables 1 and 2). The abundance of Hemiptera was significantly greater on low density shrubs, for both *Senna* and *Eremophila* (D: $P < 0.05$, SS \times D interaction $P > 0.05$; Table 2, Fig. 2a). The number of hemipteran species was higher on low density shrubs for *Senna*, but this was not statistically significant ($P > 0.05$; Table 2; Fig. 2b). The effective species diversity of hemipterans was 35–43% lower on high density *Senna* compared with all other density and shrub species groups (SS: $P < 0.01$; D: $P < 0.01$; SS \times D interaction: $P < 0.01$; Table 2, Fig. 2c).

The hemipteran species assemblage also differed markedly between high and low density shrubs (PERMANOVA Pseudo- $F_{1,36} = 2.28$, $P = 0.02$; Fig. 3a), and this was the case for both *Eremophila* and *Senna* (SS \times D interaction: Pseudo- $F_{1,36} = 1.73$, $P = 0.08$).

Effect of shrub species on the arthropod fauna

Arthropods were more abundant on *Eremophila* than *Senna* (SS: $P < 0.001$) and the trends were similar for all arthropod groups when analysed separately (Table 1, 2). Across both shrub species, 39 hemipteran species from the sub-orders Auchenorrhyncha and Heteroptera were recorded across seven families: Cicadellidae (19 spp.), Delphacidae (8 spp.), Miridae (6 spp.), Pentatomidae (3 spp.), Tingidae (1 sp.), Lygaeidae (1 sp.), and Nabidae (1 sp.).

Thirteen species of Hemiptera were recorded only on *Eremophila*, 16 only on *Senna*, and 10 were sampled on both shrub species. Of the 10 species sampled on both *Eremophila* and *Senna*, seven of these could be defined as rare on *Senna* by our definition (i.e. fewer than five individuals sampled or sampled on fewer than five shrubs in total). On *Eremophila*, the mean abundance of these seven species ranged from 0.4 ± 0.13 to 28.6 ± 4.63 individuals per shrub (24–1143 individuals in total), and were therefore not rare. The remaining three species common to both *Eremophila* and *Senna* were rare on both

shrub species. Of the 16 species sampled only on *Senna*, 11 could be considered rare. This number was the same for those occurring only on *Eremophila*.

Eremophila supported a greater number of hemipteran species, irrespective of shrub density (4.78 ± 0.31 cf. 2.38 ± 0.3 ; SS: $P < 0.001$, Table 2, Fig. 2b). When shrub density was pooled and the abundance of individuals standardised (rarefaction), hemipteran species richness was higher on *Senna* ($n = 17$) than *Eremophila* ($n = 10$; 95% confidence interval = 7–13; Fig. 4). As noted above, hemipteran effective species diversity was dependent upon shrub species and density (SS \times D interaction: $P = < 0.01$, Table 2, Fig. 2c), and was significantly lower on high density *Senna* compared with all other treatments. The species assemblage of hemipterans differed markedly between shrub species (PERMANOVA Pseudo- $F_{1,36} = 51.61$, $P = 0.0001$), and as noted above this was the case regardless of shrub density (Fig. 3b).

Relationships between calculated plant biomass and the arthropod fauna

For *Eremophila* at low densities, the number of individuals increased with plant biomass for all arthropod taxa (Psocoptera, Hemiptera, Psyllidae, and Collembola), as did the number of hemipteran species ($R^2 = 0.21\text{--}0.31$; Table 3). At high plant density, relationships between our measure of plant biomass and arthropod abundance were not statistically significant (Table 3). In contrast, for *Senna* the number of Hemiptera (individuals and species) and effective species diversity decreased with plant biomass, but only for plants growing at high density ($R^2 = 0.15\text{--}0.18$; Table 3).

Discussion

Our data indicated that the semiarid woodlands in our study area supported a wide range of arthropods, and shrub species was a more important discriminator of arthropod community structure than fine-scale shrub density. The two shrub species in our system (*Eremophila sturtii* and *Senna artemisioides* subsp. *filifolia*) supported markedly different assemblages of arthropods, even at the ordinal level, irrespective of whether they were growing in low or high density patches. This was evident at finer taxonomic scales for the Hemiptera, for which we had species level data.

It is important to note that a variety of factors other than those that we measured may also influence arthropod communities.

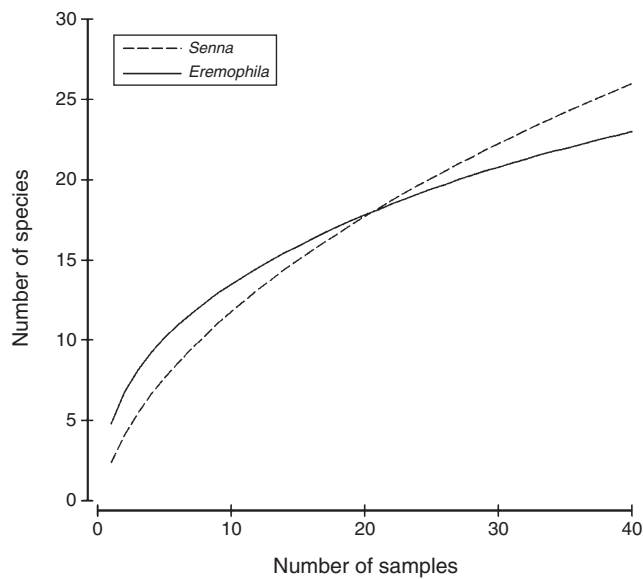


Fig. 1. Species accumulation curves for *Senna artemisioides* (dashed line) and *Eremophila sturtii* (solid line), using number of observed hemipteran species.

Table 1. Mean (\pm s.e.) abundance of total arthropods, Psocoptera, Collembola and Psyllidae in relation to shrub species and shrub density

Different letters within a row indicate a significant difference at $P < 0.01$. Shrub density refers to comparison of abundance between low and high treatments. Shrub species refers to comparison of abundance between shrub species. L = low density, H = high density, E = *Eremophila sturtii*, S = *Senna artemisioides*. For Hemiptera (non-Psyllidae) see Fig. 2

Taxon	<i>Eremophila sturtii</i>		<i>Senna artemisioides</i>		Shrub density	Shrub species
	Low	High	Low	High		
All arthropods	216.1a (40.9)	313.3a (30.1)	43.7b (7.8)	41.9b (5.8)	L = H	E > S
Psocoptera	88.6a (20.7)	111.0a (20.5)	21.9b (6.1)	24.0b (4.6)	L = H	E > S
Collembola	11.9a (3.5)	10.8a (1.4)	1.9b (0.6)	3.4b (0.8)	L = H	E > S
Psyllidae	32.8a (9.6)	24.3a (7.2)	0.5b (0.3)	0.4b (0.1)	L = H	E > S

Table 2. Summary statistics for generalised linear model analyses on abundance of arthropods taxa sampled from *Eremophila* and *Senna* (shrub species, SS) and in low and high shrub density (density, D)
The pseudo- R^2 is given in parentheses

	Deviance	Residual deviance	P
<i>Total arthropods</i> (0.61)			
Null	–	107.91	–
Shrub species	65.86	42.05	<0.001
Density	0.02	42.03	0.89
Shrub species × Density	0.01	42.02	0.94
<i>Collembola</i> (0.56)			
Null	–	85.83	–
Shrub species	40.12	45.71	<0.001
Density	0.42	45.29	0.52
Shrub species × Density	1.9	43.39	0.17
<i>Psocoptera</i> (0.38)			
Null	–	72.8	–
Shrub species	27.03	45.78	<0.001
Density	0.34	45.43	0.82
Shrub species × Density	0.06	45.37	0.81
<i>Psyllidae</i> (0.72)			
Null	–	135.38	–
Shrub species	96.62	96.62	<0.001
Density	0.56	38.20	0.14
Shrub species × Density	0.019	38.18	0.91
<i>Hemiptera</i> (0.73)			
Null	–	140.45	–
Shrub species	97.19	43.27	<0.001
Density	4.67	38.59	0.03
Shrub species × Density	0.01	38.58	0.91
<i>Number of species (Hemiptera)</i> (0.50)			
Null	–	39.06	–
Shrub species	15.8	23.26	<0.001
Density	1.48	21.78	0.22
Shrub species × Density	2.41	19.37	0.12
<i>Effective species diversity (Hemiptera)</i> (0.24)			
Null	–	46.02	–
Shrub species	2.75	43.27	0.004
Density	1.94	41.33	0.008
Shrub species × Density	6.47	34.85	0.014

Degrees of freedom (d.f.) for shrub species, density, and their interaction all 1, whereas residual d.f. are 38, 37 and 36, respectively. Total residual d.f. are 39. Pseudo R -values of 1 indicate that all variation in the model was explained by the predictor variables.

For example, though non-*Eremophila* or *Senna* shrubs were relatively uncommon at our study sites, it is possible that their presence influences the distribution of arthropods. Similarly, differences in the composition of the understorey of *Eremophila* and *Senna* (Howard *et al.* 2012) may also have associational effects that we did not account for. Variation in plant density, at a different scale to our treatments, might also affect our results (Grez and Gonzalez 1995). Lastly, arthropod communities are variable over time, often showing marked seasonal differences (e.g. Moir *et al.* 2011). Such factors should be taken into consideration when interpreting the results and conclusions of this study.

Eremophila and *Senna* support different arthropod assemblages

In this study we sampled about five times more arthropods on *Eremophila* than *Senna*, and this was consistent for every arthropod group sampled (Collembola, Hemiptera, and Psocoptera). These results are consistent with a variety of studies indicating the effect of plant species on a range of arthropod taxa (e.g. Coleoptera, Katakura *et al.* 1989; Hemiptera, Novotny and Basset 1998; Moir *et al.* 2011; Lepidoptera, Thompson and Pellmyr 1991; Dyer *et al.* 2007). Additionally, hemipteran species differed between *Eremophila* and *Senna*, and Psyllids were restricted to *Eremophila*. These results suggest that Hemiptera, at least, are abundant in our system but are specifically restricted or 'specialised' to a particular shrub species, regardless of plant density.

For the phytophagous Hemiptera, differences between shrub species are not surprising given that they are often host-specific (e.g. Moir *et al.* 2010). Non-herbivorous taxa (e.g. the Collembola and the Psocoptera), however, are not thought to show strong host preference (Broadhead and Thornton 1955; Smithers 1991) as they tend to be affected by factors that could be expected to be influenced by plant density (e.g. relative humidity, Greenslade 1991). The composition of Collembola is often affected by the cover of leaf litter (Ponge *et al.* 1993). Although litter cover at our study sites does not differ dramatically between *Eremophila* and *Senna* (Howard *et al.* 2012), it is possible that there are differences in the microclimate or food resources provided by the litter, and these may drive the distribution of Collembola (Greenslade and Greenslade 1973). The presence of host-specific arthropod communities suggests that associational effects (e.g. presence of species on *Eremophila* due to the nearby presence of *Senna*) are minimal in our system (e.g. Agrawal *et al.* 2006), though these are possible as our shrub species do facilitate a variety of other species (Howard *et al.* 2012).

A range of species-specific plant characteristics may explain why our shrub species had different levels of arthropod richness. Arthropod richness is often positively correlated with plant size or biomass (Masumoto *et al.* 2000; Hodkinson *et al.* 2001), though we did not find that in the present study. The plants in our study area do appear to have different leaf architecture, with *Eremophila* having a greater number and more variation in leaf orientation and spacing than *Senna*. Similarly, the bark of *Eremophila* is more fissured than that of *Senna*, and this may affect animals such as Psocoptera, who rely on resources on the bark surface (Smithers 1991). Such differences can exert strong effects on insect individuals and communities, both within and between plant species (Lawton 1983; Reid and Hochuli 2007), by altering predation pressure (e.g. Jeffries and Lawton 1984; Obermaier *et al.* 2008), resource provision (Marques *et al.* 2000), and microclimate (Larsson 1989; Raghu *et al.* 2004). Differences between plant species in plant chemistry (e.g. foliar nutrients) may also affect arthropod feeding, abundance, and composition (Recher *et al.* 1996; Lavandero *et al.* 2009; Joern *et al.* 2012).

Fine-scale density has limited effects on the insect community

Contrary to our predictions, we found that the abundance of three of the four arthropod groups was similar on plants growing

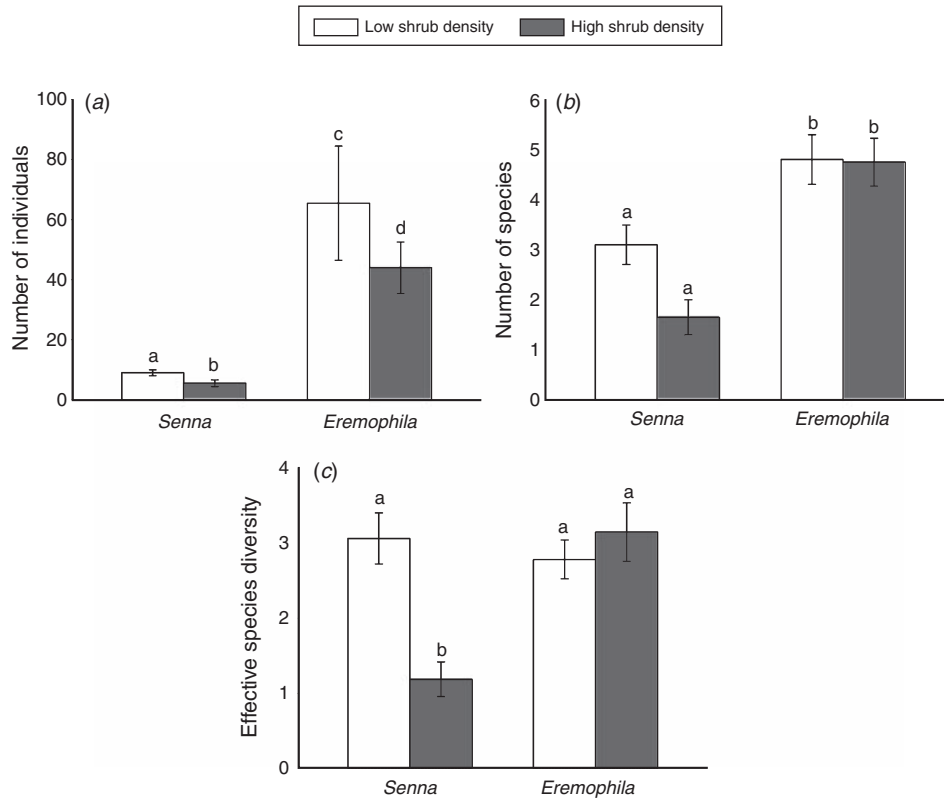


Fig. 2. Mean \pm s.e. (a) number of Hemiptera, (b) number of Hemiptera species and (c) effective number of Hemiptera species (*sensu* species diversity) averaged over two shrub subsamples per site for two shrub species (*Senna artemisioides* and *Eremophila sturtii*) across two shrub densities (low and high). Different letters indicate a significant difference in data at $P < 0.05$.

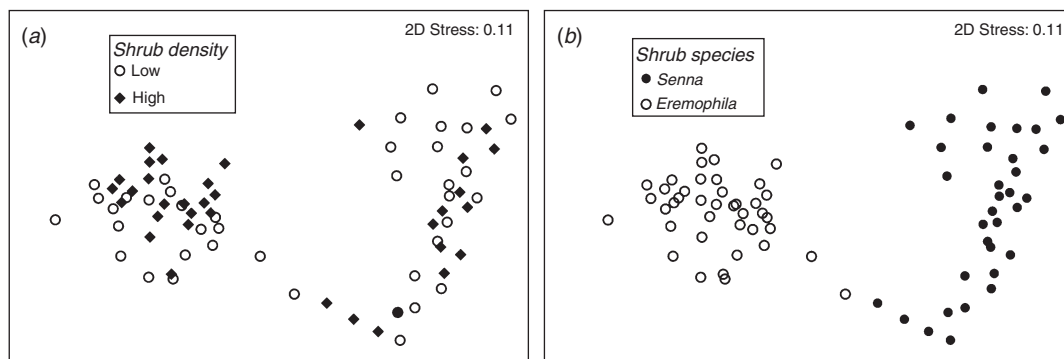


Fig. 3. Non-metric multi-dimensional scaling ordination for hemipteran species composition in relation to (a) shrubs growing in low density (open circles) and high density (closed diamonds), and (b) *Eremophila sturtii* (open circles) and *Senna artemisioides* (closed circles). The closer any given points are to each other, the greater their similarity in terms of species composition.

at low and high densities. Further, differences between low and high density treatments in the hemipteran assemblage were largely due to subtle shifts in the relative abundance of each species, not differences in the species themselves (data not shown). Our results suggest that, for *Senna–Eremophila* shrublands in our study area, differences in the density of resources (i.e. shrubs and their associated patches) at a scale

of tens of metres have only weak effects on the arthropod fauna and community-scale diversity.

Several interacting mechanisms could potentially account for greater hemipteran abundance on low density shrubs. Isolated shrubs may be larger in size than those growing in close proximity, and may therefore be able to support more herbivores (e.g. Reznik 1993; or the Plant Size *per se* Hypothesis,

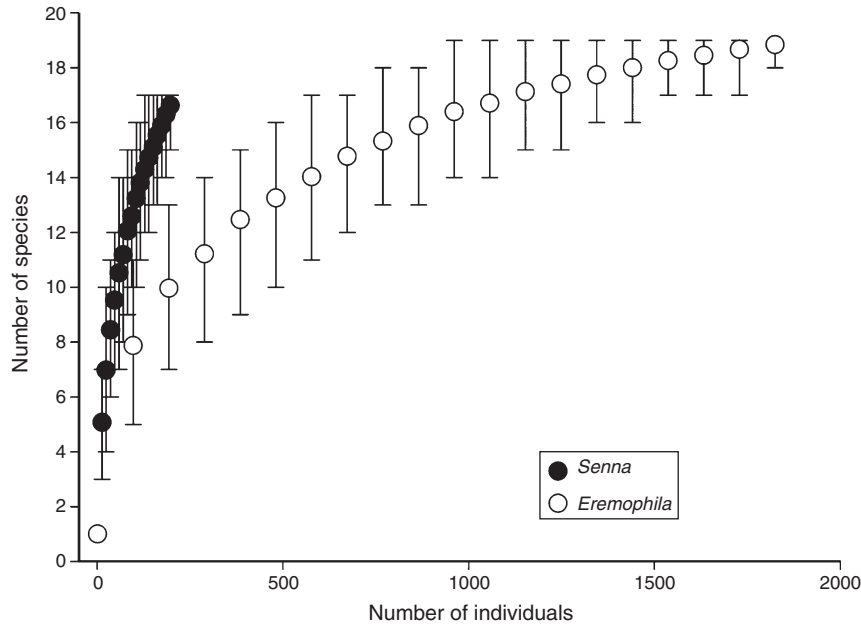


Fig. 4. Rarefaction curves for the number of Hemiptera species on *Senna artemisioides* (closed circles) and *Eremophila sturtii* (open circles).

Table 3. Linear regression results between plant biomass and arthropod abundance or Hemiptera species richness or diversity for *Eremophila* and *Senna* at low and high densities

Values are coefficients of determination (Adjusted- R^2). Significant regressions are always positive for *Eremophila* but negative for *Senna*. n.s. = not significant at $P < 0.05$. * $P < 0.05$; ** $P < 0.01$

Density	<i>Senna artemisioides</i>		<i>Eremophila sturtii</i>	
	Low	High	Low	High
Collembola	n.s.	n.s.	0.21*	n.s.
Psocoptera	n.s.	n.s.	0.25*	n.s.
Psyllidae	n.s.	n.s.	0.21*	n.s.
Hemiptera	n.s.	0.18*	0.31**	n.s.
Number of species (Hemiptera)	n.s.	0.16*	0.23*	n.s.
Species diversity (Hemiptera)	n.s.	0.16*	n.s.	n.s.

Lawton 1983). Animals that are wind-drifting or dispersing may collect in greater numbers on isolated shrubs, compared with shrubs surrounded by neighbouring plants (e.g. ‘target area effect’, Gilpin and Diamond 1976). Furthermore, the abundance of predators, and therefore their prey, may differ depending on local shrub density and associated changes to microhabitats (e.g. Sanchez and Parmenter 2002; Obermaier *et al.* 2008), food resources (Marques *et al.* 2000), and through the creation of predator-free spaces (Jeffries and Lawton 1984; Schowalter 2012). Species-specific foraging and dispersal strategies or mechanisms can also determine patterns of distribution in relation to available resources (Bukovinsky *et al.* 2005; Cook and Holt 2006).

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