

Epigaeic invertebrate community structure in two subtropical nature reserves, Eastern Cape, South Africa: Implications for conservation management

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Abstract. Epigaeic invertebrates were sampled at non-invaded ('Indigenous Forest' and 'Indigenous Grassland') and alien-invaded ('Eucalyptus' and 'Mixed alien') sub-sites in the Nduli and Luchaba Nature Reserves using pitfall traps. A total of 2054 specimens belonging to three phyla (Arthropoda, Mollusca and Annelida) was caught and sorted into seven orders, 18 families, one tribe, 45 genera (22 identified to species level) and 20 morphospecies. Higher species richness occurred in 'Indigenous Forest' and 'Mixed Alien' sub-sites while higher specimen counts were made in invaded ('Mixed Alien' and 'Eucalyptus') sub-sites during summer months, peaking in January. Canonical Correspondence Analysis results show that some measured site variables, e.g. litter depth, grazing intensity, percentage of alien vegetation cover, and soil chemical properties accounted for invertebrate taxa composition and distribution trends at sub-sites. Although habitat-patch level characteristics (including abiotic factors) were important for determining species distributions, increased levels of infestation by invasive alien vegetation across sub-sites did not necessarily impact on epigaeic invertebrates in a predictable manner. For guiding management decisions, future studies on the effects of invasive alien plants on epigaeic invertebrates should distinguish between ecological effects and adverse impacts on species of conservation concern.

Keywords: alien and indigenous vegetation, environmental variables, epigaeic invertebrates, nature reserves, ordination

Biological invasions are a main component of global change with strong ecological and socio-economic consequences (Simberloff et al. 2013, Schirmel et al. 2016). Such changes can affect resident animal communities by modifying habitats (Schirmel et al. 2011), food resources (Wolkovich et al. 2009) or biotic interactions (Schweiger et al. 2010). Effects on local fauna can be negative in terms of abundances and diversity (Hanula & Horn 2011, Holmquist et al. 2011), and functional diversity (Schirmel & Buchholz 2013). Reported effects of invasive species are often biased towards negative consequences (Kumschick & Richardson 2013), but positive effects of invasive plants on animals are also known (Schlaepfer et al. 2011).

Monitoring biodiversity in protected areas (PAs) forms an integral component of assessing their performance and providing the necessary information for effective management. In South Africa, PAs play a significant role as refugia, providing high quality habitat patches for invertebrate biodiversity conservation even though challenges resulting from their size and numbers do arise (Samways 2005, Foxcroft et al. 2011, Samways et al. 2012). Even within these reserves, alien invasive plants impact invertebrate species composition and distribution patterns differently (Richardson & van Wilgen 2004, Halaj et al. 2008, Foxcroft et al. 2010). Invertebrates constitute a significant proportion of terrestrial and freshwater biodiversity (Hamer & Slotow 2002), serve a series of critical ecosystem functions (McGeoch et al. 2011) and, as a consequence, must necessarily be considered in protected area monitoring systems (Vane-Wright 1993).

Little is known about habitat-level impacts of invasive and indigenous vegetation on the richness, abundance and diversity of epigaeic invertebrate taxa within PAs of the Eastern Cape Province of South Africa. Such studies are likely

to yield additional insight into how and under which conditions invasive plants alter ecosystem function and biodiversity patterns in such habitats (Samways et al. 2012, Samways & Bohm 2012).

The Nduli and Luchaba Nature Reserves (protected areas), situated in the Eastern Cape Province of South Africa fall within the Albany Centre of Endemism, which has high levels of endemic plant and animal extinctions due to several stressors including invasive alien plants (Smith & Wilson 2002, Preston 2003, Oxborough et al. 2010, Egoh et al. 2011). These reserves are growing in significance as elements of the matrix within which raising public awareness for conserving indigenous biodiversity can be undertaken.

The goal of this preliminary study was to assess habitat characteristics at a priori selected invaded and non-invaded vegetation patches and compare their effects on epigaeic invertebrate assemblages.

Study area, material and methods

The study was carried out in the Nduli and Luchaba Nature Reserves (Fig. 1). These are situated at 31°30'S, 28°42'E and 31°35'S, 28°45'E, respectively, in the King Sabata Dalindyebo (KSD) Municipality. The two reserves are located about 3.5 km apart and fall within the Mthatha moist grassland biome. Nduli Nature Reserve (170 ha) was originally established in 1951 and re-proclaimed in 1972 in terms of the Cape Nature Conservation Ordinance of 1965. Luchaba Nature Reserve (460 ha) is an un-proclaimed protected area on state land, managed as a nature reserve by the Operations Directorate of the Eastern Cape Parks & Tourism Agency (ECPTA). Climate at both reserves is characterized by average winter and summer temperatures of 13 °C and 26 °C respectively, with average annual precipitation of 634 mm (DWAf 2005). Natural forest in the reserve area is made up of indigenous trees, e.g. *Acacia karroo*, *A. sieberiana*, *A. xanthophloea*, *Erythrina caffra* and *Zanthoxylum capense* (Palgraves 2002). Common grass species in the reserves are *Eragrostis curvula*, *E. plana*, *E. racemosa*, *Paspalum dilatatum*, *Themeda triandra* and *Pennisetum* spp., while invasive alien plant species present in Luchaba Nature Reserve comprise *Eucalyptus grandis*, *Acacia mearnsii*, *Lantana camara*, *Solanum mauritianum* and *Cestrum laevigatum* (Olckers & Hulley 1991). The geology of the re-

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serves comprises predominantly shales and sandstones of the Beaufort series of the Karoo system. These land forms are interlaced with dolerite dykes (Acocks 1988).

Sampling site stratification

Site one in the Nduli Nature Reserve (dominated by indigenous vegetation), measuring 130 m², was mapped out and divided into two sub-sites comprising 'Indigenous Forest patch' and 'Indigenous Grassland patch' each measuring 60 m². The second site is in the Luchaba Nature Reserve (comprising predominantly invasive alien plants), measured 250 m² and was also divided into two sub-sites, each measuring 60 m²

for the study. These sub-sites were a 'Eucalyptus patch' and 'Mixed Alien patch' (Tab. 1). Each of the four sub-sites was further stratified into four square grids (sampling units = SU) measuring 10 m² and separated from each other by 8–9 m.

Invertebrate species sampling using pitfall traps

Although the interpretation of pitfall trap data is contentious because the size of catch is not only affected by density, but also the activity of the species being sampled (Saska et al. 2013), this method has been widely used for sampling epigaeic invertebrates because it is less costly, efficient and easy to use (Southwood & Henderson 2000, Parr & Chown 2001, Un-

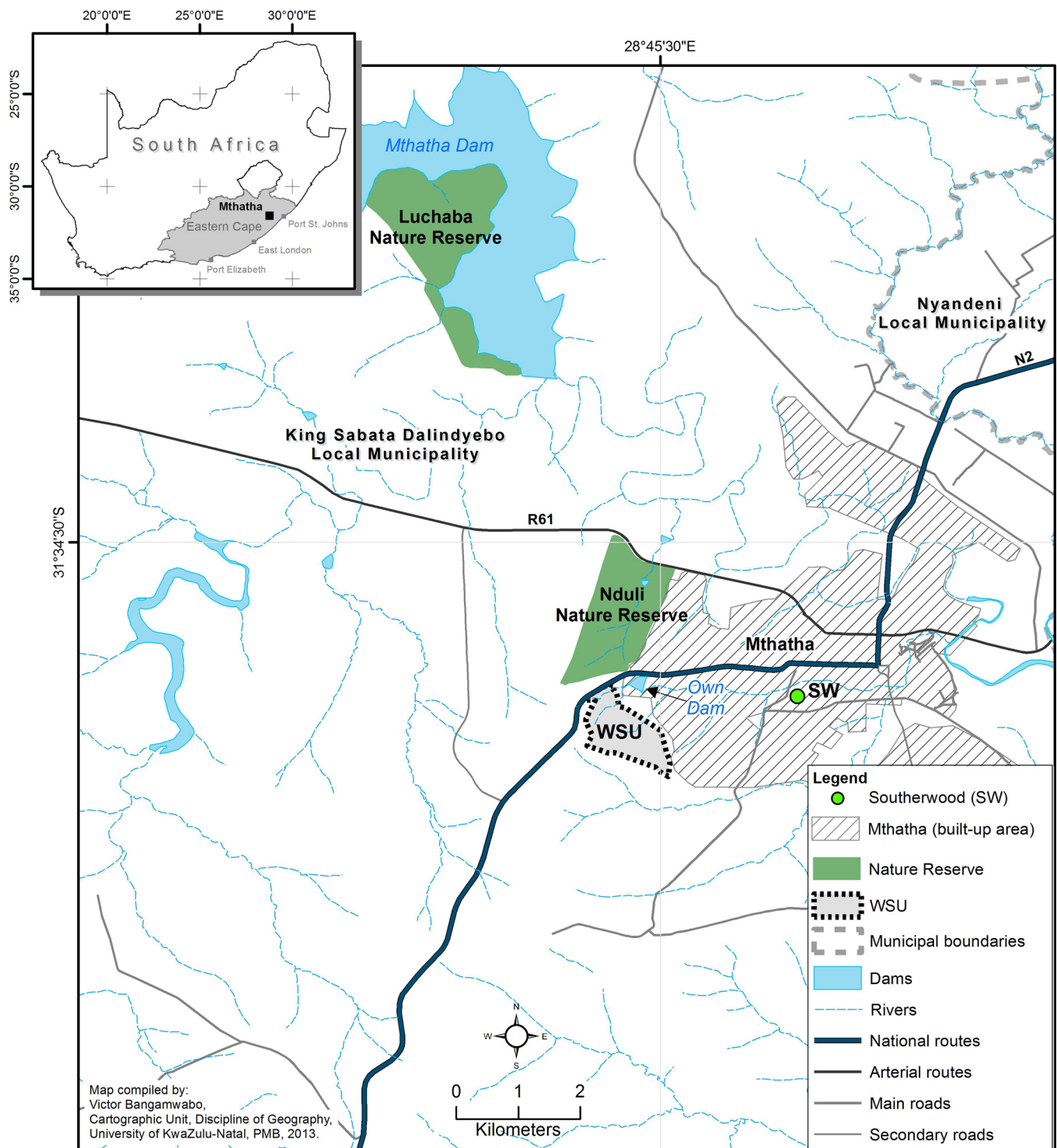


Fig. 1: Map of the study area, King Saba Dalindyebo (KSD) Municipality, Eastern Cape Province, South Africa

Tab. 1: Site description and sampling unit labels at Nduli and Luchaba Nature Reserves

Site Name	Sub-sites	Sampling unit labels	Dominant vegetation /disturbance regime
Site 1: Nduli Nature Reserve	Indigenous Forest patch (IF)	IFA, IFB, IFC, IFD	Native acacias, <i>Podocarpus</i> sp., <i>Erythrina</i> sp. Minimally grazed
	Indigenous Grassland patch (IG)	IGA, IGB, IGC, IGD	Native grasses e.g. <i>Eragrostis curvula</i> , <i>Paspalum dilatatum</i> , <i>Pennisetum</i> sp. Rich and sedges Moderately grazed
Site 2: Luchaba Nature Reserve	Eucalyptus patch (EU)	EUA, EUB, EUC, EUD	Gum trees (<i>Eucalyptus grandis</i>) Highly grazed
	Mixed Alien patch (MA)	MAA, MAB, MAC, MAD	<i>Lantana camara</i> , <i>Acacia mearnsii</i> , <i>Solanum mauritianum</i> Indigenous herbs Highly grazed

derwood & Fisher 2006). In this study, four pitfall traps, each made up of a 250 ml blue plastic cup with a rim diameter of 7.5 cm and 9.5 cm deep were sunk into the ground in square grids within each sampling unit such that the open end of the cup was flush with the ground surface. Traps were filled with soapy water as a trapping medium, and left open in the ground for 24 hours to capture soil-surface dwelling (epigaeic) invertebrate specimens (Forbanka & Niba 2013). Trapped specimens were sorted from flying arthropods, preserved in 70 % alcohol, and transported to the laboratory for preliminary identification. Identification was done using a Zeiss stereo dissecting microscope (Model STEMI DV4) and field guides (Picker et al. 2004). Spider identities were confirmed using reference works by Dippenaar-Schoeman & Jocqué (1997). Ants were identified at the Biosystematics Division of the Agricultural Research Council (ARC) in Pretoria. Unidentified morpho-species were coded and preserved in 70 % alcohol for future identification by taxon specialists. Specimen data was collected in 64 traps per month across all sites during 12 sampling months from May 2010 to April 2011.

Measurement of environmental variables

A number of environmental variables were hypothesized to be important in determining faunal composition and distribution across sampling units at the sites (Avuletey & Niba 2014) and were measured as follows:

- Soil pH, phosphorus, potassium and zinc contents were determined by collecting (through digging) 200 g of top soil samples to the depth of 10 cm in each SU. The samples were analysed at the Mthatha Dam Soil Analytical Services Laboratory using standardized protocols for measuring soil chemical properties (Soon & Warren 1993)
- Litter depth (cm) was measured using a calibrated wooden ruler placed perpendicularly on the soil surface to determine the depth and thickness of the litter
- Grazing intensity was assessed by classifying available dung and degree of trampling as 0 (none), 1 (low), 2 (medium) and 3 (high)
- Extent of alien plant cover was estimated by determining the percentage of total area of SU surface covered by these plants
- Percentage (%) shade (insolation) was estimated as amount of sunlight that penetrated the SU during the sampling interval between 11:30 am and 13:30 pm on clear sunny days

Data on soil characteristics were collected once during each of the four seasons of the year while the rest of the measured variables were collected monthly.

Data analysis

Data sets were collated for each sampling unit (SU) for each month and arranged in data matrices as proposed by Clarke & Gorley (2006). The statistical software program DIVERSE in PRIMER V 6 (Clarke & Warwick 2001) was used to determine Shannon diversity index (H') and Pielou's evenness index (J) for species data. Ordination methods attempt to give a broad overview of invertebrate community structure and patterns across site sampling units (Clark & Gorley 2006, Ter Braak & Looman 1995). The computer software package CANOCO (Ter Braak & Šmilauer 2002), which combines into one algorithm Correspondence Analysis (CA) on species data and weighted multiple regressions on environmental variable data, was used. This technique related species composition to known variations in the environment. Canonical Correspondence Analysis (CCA) in CANOCO produced an ordination diagram in which points represented species and sites, and vectors (arrows) represented measured site (environmental) variable gradients. Such a diagram shows patterns of variation in species composition that can be explained best by the measured site variables (Ter Braak & Looman 1995).

Results

A total of 2054 specimens belonging to three phyla (Arthropoda, Mollusca and Annelida) was caught and sorted into seven orders, 18 families, one tribe, 45 genera (22 identified to species level) and 20 morphospecies. The Araneae constituted the richest order with eleven families and 21 genera (10 identified species) followed by the Coleoptera with four families, one tribe (Hopliini), and 13 genera (seven identified to species). Most specimens collected belonged to the order Hymenoptera at 60% (58% Formicidae) while the Stylomatophora was represented by one family and one species. A total of 20 morphospecies collected from traps were sorted into two morphospecies of the Annelida, three of woodlice (Crustacea), two of millipedes and centipedes (Myriapoda) and 13 morphospecies of ticks, mites and scorpions (other Arachnida). Indices of species diversity and evenness trends at across sub-sites are shown in Tab. 2. Only specimens identified to tribe, genus and species levels were included in the multivariate analyses.

Tab. 2: Taxonomic profile and abundance of epigeic invertebrate taxa sampled at sub-sites in the Nduli and Luchaba Nature Reserves^aOrder or higher taxonomic level (Phylum/Class), ^bCode names used in analyses

ORDER ^a /Family/Tribe/ Genus/Species	Code ^b	EU	MA	IF	IG	total
ARANEAE						
Araneidae						
<i>Cyclosa</i> sp.	Cycsp	.	.	3	.	3
Clubionidae						
<i>Clubiona</i> sp.	Clusp	.	.	2	.	2
Dysderidae						
<i>Dysdera crocata</i> C.L. Koch, 1838	Dys	3	3	1	2	9
Eutichuridae						
<i>Cbeiracanthium furculatum</i> Karsch, 1879	Che	1	.	2	6	9
Eresidae						
<i>Dresserus</i> sp.	Dresp	.	.	1	2	3
Gnaphosidae						
<i>Xerophaeus crustosus</i> Purcell, 1907	Xer	.	.	2	.	2
<i>Zelotes uquathus</i> FitzPatrick, 2007	Zel	3	1	2	.	6
Lycosidae						
<i>Hogna</i> sp.	Hogsp	.	.	2	1	3
<i>Pardosa crassipalpis</i> Purcell, 1903	Par	211	184	10	35	440
<i>Pardosa</i> sp.	Parsp	12	9	2	4	27
Pisauridae						
<i>Afropisaura</i> sp.	Afrsp	2	.	.	.	2
<i>Nilus (Thalassius)</i> sp.	Thasp	.	5	19	1	25
Salticidae						
<i>Evarcha</i> sp.	Evasp	2	15	1	5	23
<i>Habrocestum dotatum</i> Peckham & Peckham, 1903	Hab	1	4	2	.	7
<i>Hyllus argyrotroxus</i> Simon, 1902	Hyl	.	5	2	3	10
<i>Langona warchalowskii</i> Wesołowska, 2007	Lan	2	.	1	11	14
<i>Thyene</i> sp.	Thysp	.	.	.	2	2
<i>Thyenula aurantiaca</i> (Simon, 1902)	Thy	2	.	.	3	5
<i>Thyenula juvenca</i> Simon, 1902	Thyj	.	.	.	3	3
Theridiidae						
<i>Theridion</i> sp.	Thesp	.	1	.	.	1
Thomisidae						
<i>Xysticus</i> sp.	Xyssp	10	2	2	5	19
COLEOPTERA						
Chrysomelidae						
<i>Plagioderma</i> sp.	Plasp	.	1	.	.	1
<i>Sagra</i> sp.	Sagsp	.	.	.	1	1
<i>Sonchbia sternalis</i> (Fairmaire, 1888)	Son	.	3	1	.	4
Hydrophilidae						
<i>Hydrophilus</i> sp.	Hydsp	.	1	.	3	4

ORDER ^a /Family/Tribe/ Genus/Species	Code ^b	EU	MA	IF	IG	total
Scarabaeidae						
<i>Anachalcos convexus</i> Boheman, 1857	Ana	.	.	2	.	2
<i>Anisonyx editus</i> Péringuey, 1902	Ani	.	4	.	.	4
<i>Aphodius</i> sp.	Aphsp	.	.	2	.	2
<i>Diplognatha gagates</i> Forster, 1771	Dip	1	2	.	.	3
<i>Gymnopleurus</i> sp.	Gymsp	.	.	4	.	4
Hopliini [tribe]	Hoptr	23	.	10	.	33
<i>Kheper nigroaeneus</i> (Boheman, 1857)	Khe	.	1	3	.	4
<i>Sisyphus</i> sp.	Sissp	.	2	.	4	6
Tenebrionidae						
<i>Pachyphaleria capensis</i> Laporte de Castelnau, 1840	Pac	5	1	2	.	8
<i>Psammodes bertolonii</i> Guérin-Méneville, 1844	Psa	.	.	.	5	5
HYMENOPTERA						
Formicidae						
<i>Camponotus</i> sp.	Camsp	71	258	179	112	806
<i>Carebara vidua</i> F. Smith, 1858	Car	1	.	3	.	4
<i>Messorcapensis</i> (Mayr, 1862)	Mes	.	1	.	.	1
<i>Pheidole</i> sp.	Phesp	117	74	32	16	223
<i>Polyrhachis gagates</i> F. Smith, 1858	Pol	.	3	.	.	3
<i>Streblognathus aethiopicus</i> (F. Smith, 1858)	Stre	.	3	.	2	5
<i>Tetraponera</i> sp.	Tetsp	.	.	2	.	2
<i>Technomyrmex</i> sp.	Tecsp	60	49	67	46	252
BLATTODEA						
Blaberidae						
<i>Bantua</i> sp.	Bansp	.	3	1	.	4
Blattidae						
<i>Deropeltis erythrocephala</i> (Fabricius, 1781)	Der	.	2	2	13	17
STYLOMMATOPHORA						
Valloniidae						
<i>Vallonia</i> sp.	Valsp	2	4	.	.	6
DIPLOPODA						
2 morphospecies						10
ISOPODA						
3 morphospecies						2
ANNELIDA						
2 morphospecies						2
ARACHNIDA						
(Acari, Scorpiones)						
13 morphospecies						41
Total no. of taxa		18	26	29	23	
[only tribe or lower]/sub-site						
Total no. of individuals/ sub-site (N)		529	635	447	270	
Margalef's index (d')		3.4	3.6	3.9	4.3	
Shannon diversity index (H')		1.8	1.6	1.3	2.0	
Pielou's evenness Index (J)		0.55	0.52	0.42	0.63	

Spatio-temporal distribution of species across sites

Three invertebrate species (*Pardosa crassipalpis*, *Camponotus* sp. and *Technomyrmex* sp.) occurred throughout the year at all sub-sites, and fourteen taxa (genus and species) were recorded only from indigenous (forest and grassland) vegetation sub-sites while eight were sampled exclusively from invaded (Eucalyptus and Mixed alien) sub-sites. 24 taxa including one tribe (Hopliini) occurred in both invaded and non-invaded sampling units. The Mixed Alien patch had the highest specimen count while the grassland patch had the lowest (Tab. 2). Species richness peaked in summer (January and February) while highest specimen counts occurred in January at the Mixed Alien and Eucalyptus sub-sites. Specimen counts for *Camponotus* sp. accounted for overall high abundance trends in August at the Indigenous Forest sub-site.

Response of epigaic invertebrates to measured site variables

Results of all measured environmental variables are shown in Tab. 3. The species – sampling units – environmental variable (CCA ordination) tri-plot (Fig. 2) indicated that most spe-

cies were clumped at the centre of the ordination, and related to certain measured environmental variable gradients. CCA ordination axes one and two (Tab. 4a) suggested that neither axis accounted for much variation in species data. Variance accounted for by measured environmental variables for both axes was 45.1 %. Monte-Carlo permutation tests were not significant for axis one ($F=1.54$, $P>0.05$). However, intra-set correlations extracted gradients of soil chemical properties (e.g. pH and Potassium (K) content), percentage shade (insulation) and grazing intensity that positively correlated with axis one of the ordination tri-plot, and may have determined the occurrence of most taxa at the Indigenous Grassland sampling units, e.g. *Cheiracanthium furculatum* and *Psammodes bertolonii* at SU IGB and *Dresserus* sp. at SU IGA.

Gradients of percentage alien vegetation cover and litter deposition negatively correlated with axis one of the ordination output (Tab. 4b). These variables were mostly important in determining species composition and distribution at the Eucalyptus, Mixed Alien and Indigenous Forest sub-sites. Litter depth explained the distribution of habitat-restricted specific species e.g. *Carebara vidua* at sampling unit EUA.

Tab. 3: Mean and range (in brackets) of measured environmental variables at sampling units (A-D) during the sampling period in the Nduli and Luchaba Nature Reserves. EUA-EUD (Eucalyptus), MAA-MAD (Mixed Alien), IFA-IFD (Indigenous Forest), IGA-IGD (Indigenous Grassland) sub-sites

Variables (Units)	EUA	EUB	EUC	EUD	MAA	MAB	MAC	MAD	IFA	IFB	IFC	IFD	IGA	IGB	IGC	IGD
Leaf litter depth (cm)	3.6 (1.5-5)	3.5 (1-7)	4.7 (2-8)	3.9 (2-5)	0.3 (0-2)	0.5 (0-3)	0.5 (0-2)	0.5 (0-2)	1.7 (0-3)	3.8 (2.5-6.5)	2.5 (1-4)	2.5 (1-3)	0 (0)	0 (0)	0 (0)	0 (0)
Alien veg. (%)	54 (30-80)	54 (30-100)	79 (50-100)	70 (20-100)	70 (40-90)	68 (60-90)	71 (50-90)	72 (50-80)	0.8 (0-5)	0.4 (0-5)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
Shade (%)	50 (30-70)	31 (20-40)	72 (30-80)	68 (30-90)	62 (30-90)	63 (40-90)	67 (40-90)	67 (40-90)	85 (70-100)	81 (70-90)	67 (50-80)	71 (50-100)	87 (70-100)	90 (80-100)	84 (70-100)	91 (70-100)
Potassium (ppm)	187 (90-220)	169 (80-190)	194 (75-210)	162 (100-180)	231 (200-250)	167 (120-186)	179 (144-220)	164 (98-193)	233 (210-256)	194 (200-263)	232 (183-231)	217 (184-224)	3348 (250-368)	392 (320-410)	381 (340-422)	273 (210-310)
Phosphorus (ppm)	20 (14-23)	27 (11-45)	15 (11-21)	17 (14-21)	34 (24-48)	23 (12-26)	24 (14-30)	22 (15-25)	12 (9-18)	22 (10-24)	21 (13-27)	19 (15-30)	18 (8-31)	22 (11-31)	17 (12-26)	30 (11-35)
Zinc (ppm)	0.3 (0.2-0.5)	0.4 (0.1-0.6)	0.05 (0.1-0.8)	0.4 (0.1-0.8)	0.4 (0.2-0.8)	0.2 (0.1-0.3)	0.3 (0.1-0.6)	0.2 (0.1-0.3)	0.2 (0.1-0.4)	1.1 (0.2-1.7)	0.8 (0.4-1.6)	0.9 (0.1-0.6)	0.4 (0.2-0.5)	0.3 (0.2-0.8)	0.4 (0.2-0.8)	0.4 (0.2-0.6)
Grazing intensity	2 (1-3)	2 (1-3)	3 (0-3)	2 (2-3)	2 (1-3)	2 (1-3)	2 (1-3)	2 (1-3)	1 (0-2)	1 (0-2)	0 (0-0)	0 (0-0)	2 (0-3)	2 (1-3)	1 (0-2)	1 (0-2)
pH	4.9 (4-5.5)	4.2 (4-6)	3.9 (4-6.6)	4 (3.8-4.5)	3.5 (3.8-5)	3.1 (3-4.2)	3.2 (3-4)	3.9 (4-5.1)	4.8 (4.5-6)	5.6 (4.3-7)	6.5 (5.2-7.5)	5.9 (5-6.2)	4.3 (4-5)	4.7 (4-7.8)	4.5 (4-5.5)	4.5 (4-5.8)

Tab. 4a: Summary of the first two CCA axes weightings. Variances explained by the two axes are given. Monte-Carlo permutation tests for Axis 1: ($F=1.154$, $P>0.05$) and for all four axes (Global: $F=1.68$, $P<0.05$). *Significant

Axes	1	2	All four axes
Eigen values	0.27	0.20	.
Species-environmental variable correlations	0.97	0.94	.
Cumulative percentage variance of species data	14.7	26	.
Cumulative % variance species/envir. var. relations	25.5	45.1	.
Total inertia	.	.	1.85
F-ratio	1.54	.	1.68
p-value	0.33	.	0.04*

Tab. 4b: Intra-set correlations between each of the measured environmental variables and the first two canonical axes using pooled invertebrate species data recorded at sub-sites in the Nduli and Luchaba Nature Reserves

Variable	Intra-set Correlation		Inter-set Correlation	
	CCA1	CCA2	CCA1	CCA2
Litter deposition	-0.40	-0.37	-0.29	-0.39
Grazing Intensity	0.54	0.34	0.41	0.55
pH	0.03	-0.32	0.74	0.03
Potassium K	0.52	0.55	0.51	0.52
Phosphorus P	0.24	-0.26	-0.06	0.24
Zinc Z	-0.26	-0.44	0.43	-0.27
Alien vegetation	-0.34	0.02	-0.67	-0.34
Shade	0.55	0.32	0.38	0.56

Discussion

It is still poorly understood whether general patterns in impacts of invasive plants exist and whether these patterns are related to certain ecosystems or animal traits (Kumschick et al. 2015). Moreover, progress in understanding invasion impacts is challenged in several ways (Schirmel et al. 2016). Impacts are often not or differently defined (Jeschke et al. 2014), controversies about invasion impacts often rely on case studies, but meaningful generalisations based on single cases do not exist (Ricciardi et al. 2013). In this study, the impact of invasive plants on epigeic invertebrates varied across sub-sites with neutral and decreasing effects on species diversity and abundance. The majority (24 taxa) occurred at both invaded and non-invaded vegetation sub-sites, while 14 taxa occurred exclusively at indigenous (forest and grassland) vegetation sub-sites, possibly due to the fact that these sites had minimal

and moderate grazing intensity respectively, and are more stable ecosystems. Generally, native plants are associated with a higher diversity and abundance of herbivore insects (Schirmel et al. 2016). This is often explained by co-evolutionary adaptations of native insects to leaf structural traits or to chemical compounds of native plants (Harvey & Fortuna 2012). Eight invertebrate species occurred only at the highly grazed invaded (*Eucalyptus* and Mixed Alien) sub-sites.

High invertebrate species richness and abundance occurred during the rainy summer months of January–February probably as a result of optimal habitat conditions which favoured maturation for various invertebrate taxa. This period is also characterized by high ambient temperatures which may have resulted in higher levels of invertebrate activity and their catch rates in traps. Even though the diversity and abundance patterns of invertebrate taxa (e.g. beetles, ants)

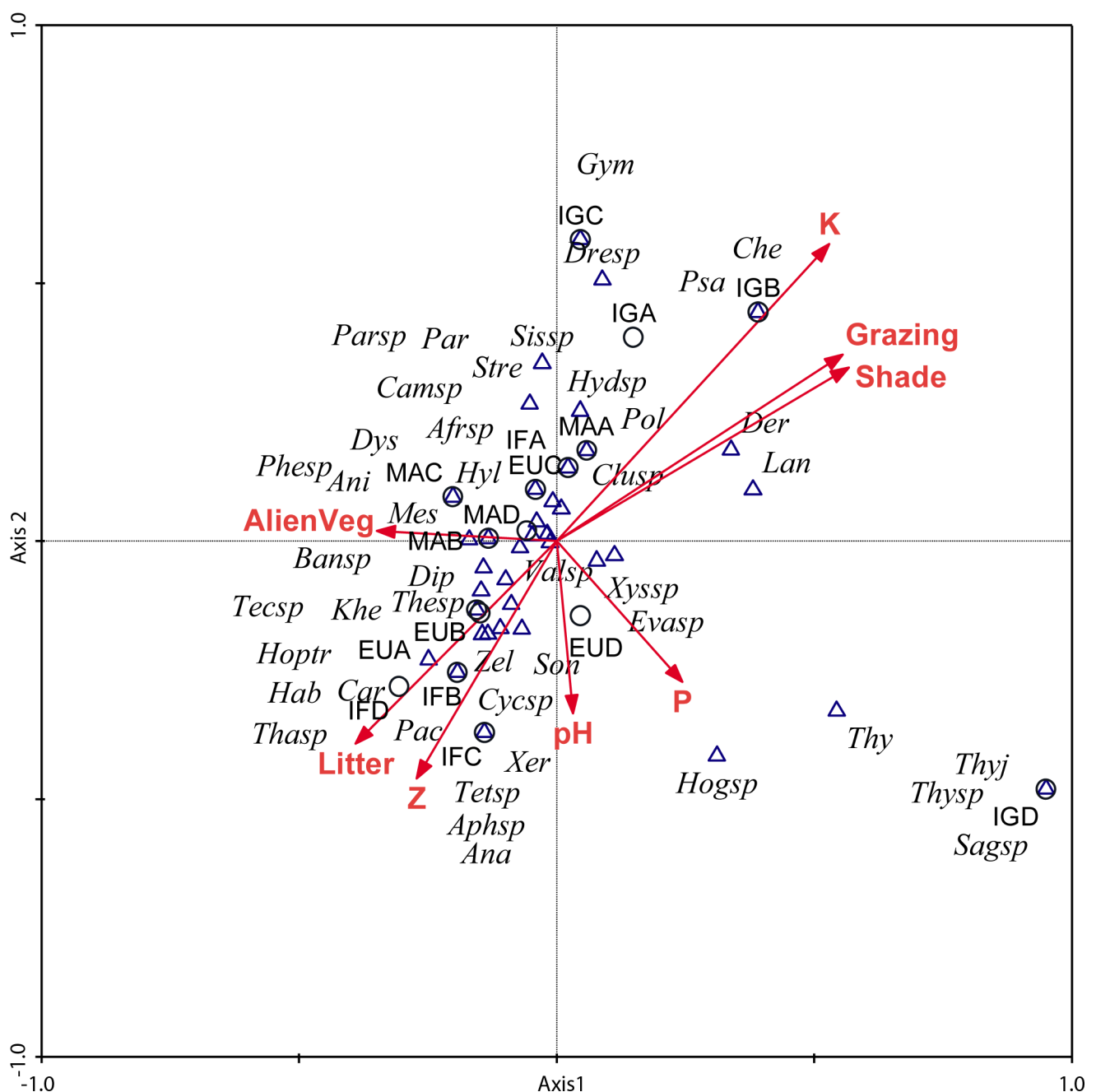


Fig. 2: Canonical Correspondence analysis (CCA) ordination of invertebrate species (Δ), site sampling units (\circ), and measured environmental variables (\rightarrow) using pooled data collected at Nduli and Luchaba Nature Reserves. Site description and sampling unit labels see Tab. 1, species code names see Tab. 2.

have been shown to be influenced significantly by seasonality (rainfall) and temperature (Davis 2002, Hahn & Wheeler 2002), other intrinsic factors could also have influenced the rate at which specimens were caught e.g. thermoregulation, body size, motivation or plasticity in diel rhythms (Atienza & Farinos 1996, Wallin & Ekblom 1994). Extrinsic factors could potentially impact on catch rates e.g. vegetation structure, soil surface litter (Hatten et al. 2007) as well as limitations associated with sampling design or short-term disturbances at sites (Mitchell 1963).

Litter deposition was found to be an important variable gradient influencing the composition and distribution of invertebrates across the Eucalyptus, Mixed Alien and Indigenous Forest sub-sites. High specimen counts at the Eucalyptus dominated sub-site could probably be due to abundant leaf litter deposition used by some taxa e.g. *Pachyphaleria capensis* as growth substrate for egg-laying and shelter from predators and desiccation (Albelho & Graça 1996, Magura et al. 2004, Hills et al. 2008, Tererai et al. 2013).

Grazing intensity can influence the distribution of invertebrate species either positively or negatively depending on grazing pressure (Souminan & Olofsson 2000). Grazing at very high intensities by game can reduce plant diversity leading to a reduction in faunal diversity due to exposure to predators (Allombert et al. 2005, Cheli & Corley 2010).

The composition and distribution patterns of widespread and habitat-restricted taxa e.g. *Langona warchalowskii* and *Cyclosa* sp. respectively were probably influenced by this gradient at the Indigenous Grassland sub-sites.

Soil chemical properties (e.g. pH, zinc and potassium) were also important in determining the occurrence of habitat-restricted invertebrate taxa e.g. *Cyclosa* sp. At Indigenous Forest sub-sites. Agwunobi & Ugwumba (2013) have noted that different faunal species associate with specific soil pH ranges due to their degree of vulnerability and resistance to acidity or alkalinity of the soil. Furthermore, highly acidic soils have fewer nutrients available, thereby providing less suitable environments for epigeic invertebrates (Magura et al. 2004).

Temperature has a significant effect on the activity of epigeic arthropods (Honek 1997, Saska et al. 2013) and therefore on their diversity and abundance (Davis 2002). In this study, CCA ordination axis one extracted percentage shade (insulation). This variable gradient may have influenced species composition and distribution patterns of *Clubiona* sp. (Araneae), *Hydrophilus* sp. and *Psammodes bertolonii* (Coleoptera) at the Indigenous Grassland sub-sites (Fig. 2).

Conclusion and management implications

Both direction and magnitude of plant-mediated invasion effects on animals cannot be generalised as universal response patterns but need specification in relation to ecosystem, taxa and functional groups as significant effects (either positive or negative), may thus remain undetected (Schirmel et al. 2016). This preliminary study shows that even though habitat-patch level characteristics (including abiotic factors) were important in determining invertebrate composition and distribution patterns, increased levels of infestation by invasive alien vegetation across sub-sites in the study did not necessarily impact species in a predictable manner.

There is urgent need to monitor and identify species at sub-sites over a much longer period to obtain a complete in-

ventory for comparison with existing regional baseline data for protected areas in South Africa. Although invertebrates remain critically important across a range of protected areas management objectives in the country, they should be explicitly and clearly linked to these objectives (McGeoch et al. 2011). Furthermore, for guiding management decisions, future studies on the effects of invasive alien plants on epigeic invertebrates should distinguish between ecological effects and adverse impacts on species of conservation concern.

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