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Functional feeding groups as a taxonomic surrogate for a grassland arthropod assemblage

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ABSTRACT

Considering the precarious conservation status of the grassland biome in South Africa, effective assessment and monitoring is imperative. The potential use of terrestrial arthropods in ecological assessment has received much attention, but little headway has been made in formulating standardised bioassessment protocols. A suggested reason for this lack of progress is the high diversity of terrestrial arthropods and the high taxonomic expertise required. Sampling was carried out across 12 months in the Bloemfontein Dry Grassland vegetation type and the potential of using functional feeding groups (FFG) as taxonomic surrogates for family level arthropods was investigated. An *F*-test associated with an analysis of covariance (ANCOVA) found a significant correlation between FFG and families for measures of richness, Shannon and Simpson diversity. Accumulation curves indicated that a higher proportion of FFG than families could be assessed with the same sampling intensity. Both families and FFG best fitted the stochastic normal and geometric series relative abundance distribution models, implying that there is no distinction between the taxonomic units with regard to abundance distributions. The reality remains that information does become lost when using surrogacy, so there will continue to be a need for specialist ecological proficiency for the highest risk assessments. It was concluded that for rapid monitoring and snap-shot assessments, FFG could be used as a valuable and reliable taxonomic surrogate.

KEY WORDS: Ecology, grassland arthropods, functional feeding groups, taxonomic surrogates, ANCOVA, relative abundance distributions.

INTRODUCTION

Grasslands are increasingly being regarded as important to sustainable development and in South Africa 36.7% of the land in the grassland biome has been identified as conservation priority areas (South African National Biodiversity Institute *et al*. 2007). Regrettably, however, only about 2% of the biome is actually being conserved (Mucina *et al.* 2006; O'Conner & Kuyler 2009), the Free State Province being especially ignored in terms of conservation (Reyers *et al*. 2005). Ecological monitoring is central to effective natural resource management (Wintle *et al*. 2010) and the improvement of monitoring techniques in grasslands should be prioritised.

The use of arthropods in terrestrial ecological assessment has long been suggested (Rosenburg *et al.* 1986; McGeoch 1998; Kimberling *et al.* 2001; Karr & Kimberling 2003; Andersen *et al.* 2004). Despite the seemingly obvious benefits of using arthropods for these assessments, little headway has been made towards creating a standardised methodology similar to those used in aquatic ecosystems around the globe (Ollis *et al.* 2006). According to Seaman and Louw (1999) one of the reasons for this is the unmanageably high diversity of taxa in terrestrial, and specifically grassland, habitats. Based on this they proposed using functional feeding groups (FFG) as taxonomic surrogates in the South African Grassland Scoring System (SAGraSS); the terrestrial equivalent of the South African Scoring System version 5 (Dickens & Graham 2002) and, its predecessor, the Index for Biotic Integrity (Chutter 1972) river assessment methodologies used in South Africa. Unfortunately, little research has been carried out to identify whether FFG provide accurate representations of the assemblage as a whole

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or whether their usage provides any benefits other than simplicity; these were therefore the primary objectives of this study.

The use of taxonomic surrogacy, where higher taxa are used to estimate species richness, is not new to ecological assessments. It has been shown that analyses at higher taxonomic levels (family or genus levels) can act as a replacement for species richness in various forms of vegetation (Balmford *et al.* 1996*a*, *b*), Neotropical mammals (Grelle 2002) and Greek vertebrates (Mazaris *et al.* 2008), as well as stream diatoms and macroinvertebrates (Heino & Soininen 2007). In terms of terrestrial arthropods, genus has been shown to be a suitable surrogate for species richness in Australian ant fauna (Andersen 1995), whereas family richness was used as a replacement measure for species richness in Hungarian coleopteran, dipteran and acari assemblages (Báldi 2003). Biaggini *et al.* (2007) even went as far as to show that order level is a suitable representative of species richness in agricultural arthropod assemblages. However, it must be appreciated that higher-taxon surrogacy has its setbacks. Considering that species do not follow Gaussian distributions at higher taxonomic levels, surrogacy would be unreliable once multiple conspecifics coexist, as taxonomic resolution would become lost (Bertrand *et al.* 2006). For this study however, it is assumed that family level provides an accurate representation of the assemblage as a whole and it is from this baseline that analyses will be conducted.

Simple linear regression analysis has been used to identify the relationships between taxonomic units (Andersen 1995; Balmford *et al.* 1996*a, b*). As this study was carried out across a seasonal gradient, the month in which the sample was taken became an additional confounding variable. This meant that linear regression was not suitable for this comparison. To overcome this, an analysis of covariance (ANCOVA) was performed which allowed a dependent variable (FFG), within numerous factors (sampling months), to be compared to a covariable (family). Previous analyses generally have only correlated measures of richness, but this study also investigated other diversity measurement indices so that the relationship between taxonomic units could be further investigated with regard to disparities in the abundances of taxa. Beside the ANCOVA analysis, taxonomic accumulation curves were used to determine how the representation of taxonomic units varies with sample intensity (following the precedent set by Andersen 1995; Balmford *et al.* 1996*b*; Biaggini *et al.* 2007).

It is commonly known that abundance varies among taxonomic units, and multiple models have been developed to describe and explain these patterns (McGill *et al.* (2007) give a summary of 27 such models). If taxonomic surrogates are to be considered as suitable representations, then it is necessary that they demonstrate similar abundance distributions to the taxonomic units they aim to replace. This study therefore compared the relative abundance distributions of arthropod families and functional feeding groups. For the purpose of this study, however, the theory behind the models is not imperative since they are utilised solely for descriptive purposes and not explanatory ones.

This study did not address the potential of arthropods as indicators of grassland ecological integrity as suggested by the SAGraSS method. It only addresses one of the fundamental assumptions on which it is based. Even if the SAGraSS method is deemed non-viable, this study is still applicable to other ecological assessments. Additionally, if FFG is deemed a viable taxonomic replacement, it means that ecological assessment is no longer restricted to highly qualified specialists. The simpler identification would mean

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that technicians could easily be trained as para-taxonomists, human capacity restrictions could be overcome and new ecological information would readily be made available. The collective consequences of this would contribute to the advancement of grassland management as a whole and improve the efficacy of sustainable resource usage.

MATERIAL AND METHODS

Sampling

Sampling was carried out on an area of woody grassland at the Free State National Botanical Gardens (29°03.047'S:26°12.682'E) on the outskirts of Bloemfontein, South Africa, which falls within the endangered Bloemfontein Dry Grassland vegetation type (Mucina *et al*. (2006) provides a complete description of this vegetation type). The site was selected on the basis that it is largely pristine with high levels of control. The only grazing in the area was by small rodent, lagomorph and antelope species, as livestock did not have access to the area.

Thirty randomly positioned points were marked out across the one-hectare study site and sampling was carried out in the immediate area within a 7 m radius of each point using 100 sweeps of a standard sweep net (120 cm circumference). This plot-based sampling regime was preferred to linear transects because there were Karee trees (*Searsia lancea*) scattered across the site and therefore fewer linear transects could have been fitted into the area. The process was repeated, for the exact same sampling plots, once monthly for 12 months from April 2009 until March 2010, giving a total of 360 samples of 100 sweeps. All sampled insects were sorted, counted and identified to family level as well as being assigned to functional feeding groups (FFG). The functional feeding groups were assigned as follows: each taxon was broadly categorised into the feeding group in which it exists and then further subdivided in terms of the taxonomic order (or in the case of Hemiptera, suborder) (Table 1). Non-insect arthropods were included, but were only classified to the highest practically distinct taxonomic level; *i.e.* class (e.g. Diplopoda) or subclass (Araneae and Acari). In many cases, assignment of FFG can be performed with less taxonomic expertise than family level as many orders and/or superfamilies only have one feeding style. In the few cases where this is not the case, it is possible to learn the exceptions using taxonomic expertise equal to that required for family-level identifications. It is also important to realise that many of the FFG are strictly not *feeding* groups; weevils are, for example, also phytophagous but were placed in their own group to add resolution to the taxonomic surrogate.

Analyses

For each of the 360 samples the richness (S), Shannon (D(H')) and Simpson (D(λ)) diversities (these are the true diversities obtained from their respective entropies as demonstrated by Jost (2006)) were determined for both families and FFG using Primer Version 6.1.10 (Primer-E 2007). These three measures of diversity were used because they each represent the taxon abundance disproportionally due to the differing diversity of order (q) used by most nonparametric diversity indices (Jost 2006). Family richness (q=0) disproportionally favours rare taxa, as all taxa are considered as equivalent despite their disparities in abundance. Shannon diversity ($q\approx1$) favours neither rare nor common taxa and weighs elements based on their relative abundances. Simpson diversity (q=2) disproportionally favours common taxa as it determines diversity based on squared

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TABLE 1

The broad functional feeding groups (FFG) into which grassland insect families were assigned. FFG were obtained by classifying taxa in terms of Part A: Feeding Group and Part B: Order. (*Example*: Acrididae grasshoppers are ORTH_Phy.)

PART A: Feeding Group	**Description**	
Predator (Pr)	This broad group comprises arthropods which feed on other arthropods, irrespective of the mode of feeding.	
Phytophagous (Phy)	This group includes arthropods which feed on plant matter and possess biting/chewing mouthparts.	
Parasitoid (Par)	Includes arthropods which feed in or on another living animal for a relatively long time during one or all of their life-stages.	
Nectar Feeder (NF)	Arthropods feeding on nectar in some way or form during any of their life-stages.	
Weevil (Weev)	Coleoptera which feed on plant material by making holes into plant parts for feeding on the internal plant tissues and oviposition.	
Saprophagous (Sap)	Arthropods feeding on dead and decaying plant or animal matter by using enzymes to first liquefy the material, which is subsequently ingested.	
Fungus Feeder (FF)	Arthropods feeding on fungi.	
Sap-sucking (SS)	This group includes organisms which feed on plant matter and possess piercing/sucking mouthparts.	
Seed feeder (SF)	Arthropods feeding primarily (or exclusively) on the seeds of plants.	
Scavenger (Sca)	Arthropods which feed on dead plants or animals, or any other form of animal waste.	
Tourist (Tou)	Arthropods which are only present in the habitat for reasons other than feeding.	
Rasper (Rp)	Arthropods where the mandible is used to rupture plant tissues from which plant liquids are sucked up and ingested.	
PART B: Order		
Araneae (ARA) Acari (ACA) Diplopoda (DIP) Ephemeroptera (EPH) Odonata (ODO) lattodea (BLAT) Isoptera (ISO)	Mantodea (MAN) Orthoptera (ORTH) Phasmatodea (PHAS) Psocoptera (PSOC) Hemiptera: Heteroptera (HET) Hemiptera: Homoptera (HOM) Thysanoptera (THY)	Neuroptera (NEU) Coleoptera (COL) Diptera (DIP) Trichoptera (TRIC) Lepidoptera (LEP) Hymenoptera (HYM)

relative abundances; hence taxa with higher abundance will carry greater weight in the index. An analysis of covariance (ANCOVA) was performed comparing families and FFG, while correcting for sampling months, for each of the three measures of diversity using MedCalc Version 11.5.1.0 (MedCalc Software 2011). ANCOVA combines analysis of variance with linear regression for two variables within multiple factors. The coefficient of determination (r^2) demonstrated the proportion of change in the dependent variable (FFG) that was caused by changes in the independent variable (family). The *p*-value associated with a *F*-test was used to determine the significance of the relationship between the dependent variable (FFG) and the independent covariable (family) as well as the confounding factor of sampling month. Significance was determined within a confidence level of 95% (α=0.05).

Family and FFG accumulation curves were used to compare how sampling intensity influenced the representation of the entire population. Observed accumulation curves plotted the cumulative family and FFG abundances in the order in which samples were

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TABLE 2

The relative abundance distributions fitted to the observed data for both family and functional feeding group abundance distributions of a grassland arthropod community.

Model	Abbreviation	Type of Model
Log Series	Log_ser	Statistical
Stochastic Normal	Stoc_norm	Statistical
Zipf-Mandelbrot	Zipf_Man	Statistical
Stochastic Zipf-Mandelbrot	Stoc_ZM	Statistical
Geometric series	Geo_ser	Niche-based
Broken Stick	Brok_st	Niche-based
Over-lapping Niche	OvL_niche	Niche-based
Particulate Niche	Par_niche	Niche-based
Sugihara sequential break-down	Sug_seq	Niche-based
Dominance Decay	Dom_dec	Niche-based
Random Assortment	Ran_ass	Niche-based
Random Fraction	Ran_frac	Niche-based
Power Fraction	Pow_frac	Niche-based
Hubbell's neutral	Hubb	Neutral

carried out. Smoothed accumulation curves were obtained through permutation (999 times, without replacement) in Primer Version 6.1.10 (Primer-E 2007).

It was not possible to directly compare the relative abundance distributions of families and FFG populations since they contained the same number of individuals (*N*) while demonstrating vastly different richness (*S*). It was therefore necessary to fit each abundance distribution to pre-existing models and then try to compare the models. The relative abundance distribution of both family and FFG were analyzed using RAD version 4.1 (Ulrich 2002), a relative abundance distribution calculator. The 14 abundance distribution models that were fitted are shown in Table 2. The goodness-of-fit was determined using a combination of techniques. A distribution test statistic (r_{test}) and an octave test statistic (oc_{test}) were computed in RAD version 4.1, lower values, ideally less than 10, indicated greater fit. The proportion of observed abundance distribution values which fell within the 95% confidence level of stochastic distribution models (FR < *conf.* 95) was also used to determine goodness-of-fit (Tokeshi 1990). A similar measure (R_{sum} < *conf.* 95) was also calculated in RAD version 4.1 which represents the proportion of observed abundance distribution values which fell within the 95% confidence level of stochastic distribution models which has been corrected for sample size. Often these fitting techniques give contradictory results, so visual observation of Whittaker abundance distribution plots (Whittaker 1965) were also used to verify the measurements of fit.

RESULTS

Over the course of 12 months, 61,022 individuals from 108 arthropod families and 36 functional feeding groups (FFG) were sampled in the grassland habitat. ANCOVA demonstrated a strong correlation between family and FFG diversity (Figs 1A–C). For all measures of diversity, the coefficient of determination demonstrated that more than 90%

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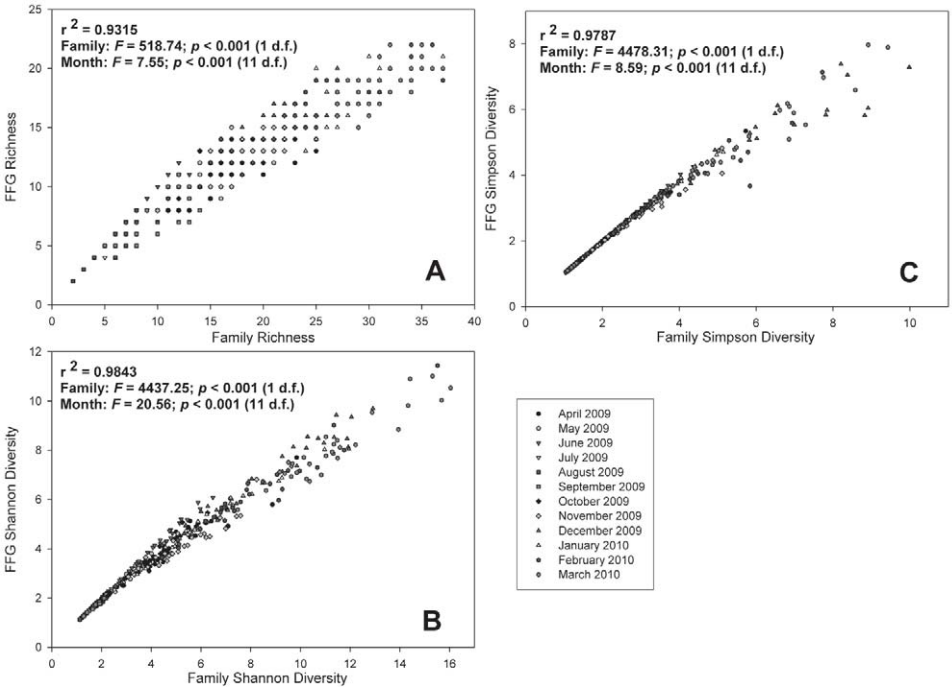


Fig. 1. The relationship between family and functional feeding group (FFG) richness (A), Shannon diversity (B) and Simpson diversity (C) of arthropods in a grassland habitat in the Free State Province, South Africa between April 2009 and March 2010. Text represents the results of an *F*-test associated with an ANCOVA analysis comparing FFG with the covariable family and the confounding factor of sampling month.

(r^2>0.90) of the change in the dependent variable could be accounted for by changes in the dependent variable. The *F*-test showed a significant correlation (p<0.001) between family and FFG for all measures of diversity. The sampling month was also significantly correlated (p<0.001) to FFG for each of the three diversity measures.

Both observed and smoothed accumulation curves indicate that it takes fewer samples to reach a proportion of the total FFG richness than it would to sample the same proportion of family richness (Figs 2A, 2B). This must be considered with the total richness of each taxonomic unit; family (n=108) and FFG (n=36), because the same proportion would comprise of different number of taxonomic units.

The relative abundance distributions of the arthropod family and FFG were fitted to multiple abundance distribution models (Table 3). The results were ambiguous for family fitting. No model has a low distribution test statistic (r_{test}<10) and only the Geometric series model (Geo_ser) had a low octave test statistic (oc_{test}=7.57). More than 95% of observed family data fell within a 95% confidence level for four models (Stoc_norm; Stoc ZM; Geo_ser; Brok_st). Observed family data had corrected proportions within 95% confidence levels statistics lower than 0.1 for five models (Stoc_norm; Geo_ser; Brok_st; Ran_ass; Pow_frac). Visual observations of Whittaker plots showed that Stochastic normal and Random fraction models best fitted the observed family data (Fig. 3B). Based on all these measures it is possible to suggest that Stochastic normal

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and Geometric series are the models which best describe the abundance distribution of arthropod families.

For functional feeding groups, Stochastic normal, Random fraction and Power fraction models all showed r_{test} values lower than 10, indicating good fit. Six models had oc-

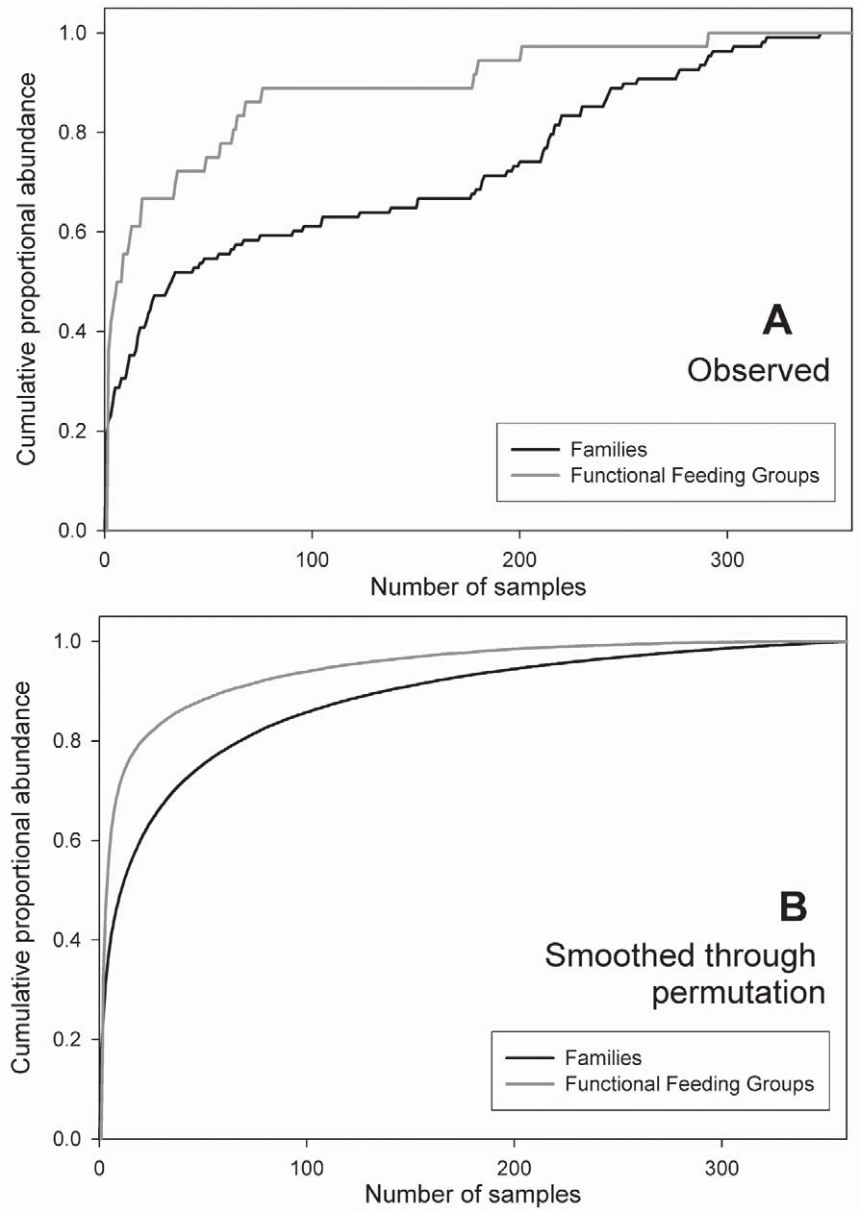


Fig. 2. The observed (A) and smoothed through permutation (999 times, without replacement) (B) proportional accumulation curves for arthropod family (n=108) and functional feeding group (n=36) richness occurring in 360 (100 sweeps) samples of grassland habitat in the Free State Province, South Africa.

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TABLE 3

The goodness-of-fit statistics for the family and functional feeding group relative abundance distribution for each of the 14 relative abundance distribution models for arthropods of grassland habitat in the Free State Province, South Africa. Bold values indicate a strong fit between the models for that specific goodness of fit measure. (*** indicates that this measure was not considered for the model which was deterministic; hence having no 95% confidence levels.)

	Family			
Model	**r_{test}**	**oc_{test}**	**FR < *conf.* 95**	**R_{sum} < *conf.* 95**
Log_ser	111.84	41.31	0.38	0.27
Stoc_norm	48.29	65.55	**0.95**	**0.08**
Zipf_Man	27.72	105.26	0.67	0.44
Stoc_ZM	24.22	107.12	**0.95**	0.10
Geo_ser	127.07	**7.57**	**0.99**	**0.01**
Brok_st	1217.9	88.68	**0.98**	**0.02**
OvL_niche	428.72	158.86	0.37	0.45
Par_niche	562.29	168.30	0.31	0.69
Sug_seq	67.04	333.41	0.18	0.13
Dom_dec	1341.0	380.18	***	***
Ran_ass	1510.4	326.61	0.01	**0.07**
Ran_frac	194.77	108.54	0.77	0.28
Pow_frac	69.04	58.45	0.01	**0.06**
Hubb	1641.8	225.17	0.92	0.19
	Functional feeding group			
	r_{test}	**oc_{test}**	**FR < *conf.* 95**	**R_{sum} < *conf.* 95**
Log_ser	20.64	5.04	0.36	0.26
Stoc_norm	**2.99**	**2.87**	**1.0**	**0**
Zipf_Man	18.27	28.38	0.5	0.61
Stoc_ZM	15.78	24.40	**1.0**	**0**
Geo_ser	14.60	**2.67**	**0.97**	**0.02**
Brok_st	153.78	19.25	**0.97**	0.2
OvL_niche	16.78	10.63	0.92	**0.05**
Par_niche	33.96	12.07	0.56	0.17
Sug_seq	10.20	99.54	0.11	0.15
Dom_dec	219.85	67.80	***	***
Ran_ass	12.70	**2.67**	0.83	**0.07**
Ran_frac	**6.14**	**4.31**	0.89	**0.05**
Pow_frac	**9.41**	**2.22**	0.22	**0.09**
Hubb	232.88	110.03	0.92	2.21

tave tests statistics smaller than 10 (Log_ser; Stoc_norm; Geo_ser; Ran_ass; Ran_frac; Pow_frac). More than 95% of observed data fell within a 95% confidence level for four models (Stoc_norm; Stoc ZM; Geo_ser; Brok_st). Observed family data had corrected proportions within 95% confidence levels statistics lower than 0.1 for seven models (Stoc_norm; Stoc_ZM; Geo_ser; OvL_niche; Ran_ass; Ran_frac; Pow_frac). Like family abundance distributions, visual observations of Whittaker plots showed that Stochastic normal and Random fraction models best fitted the observed FFG data

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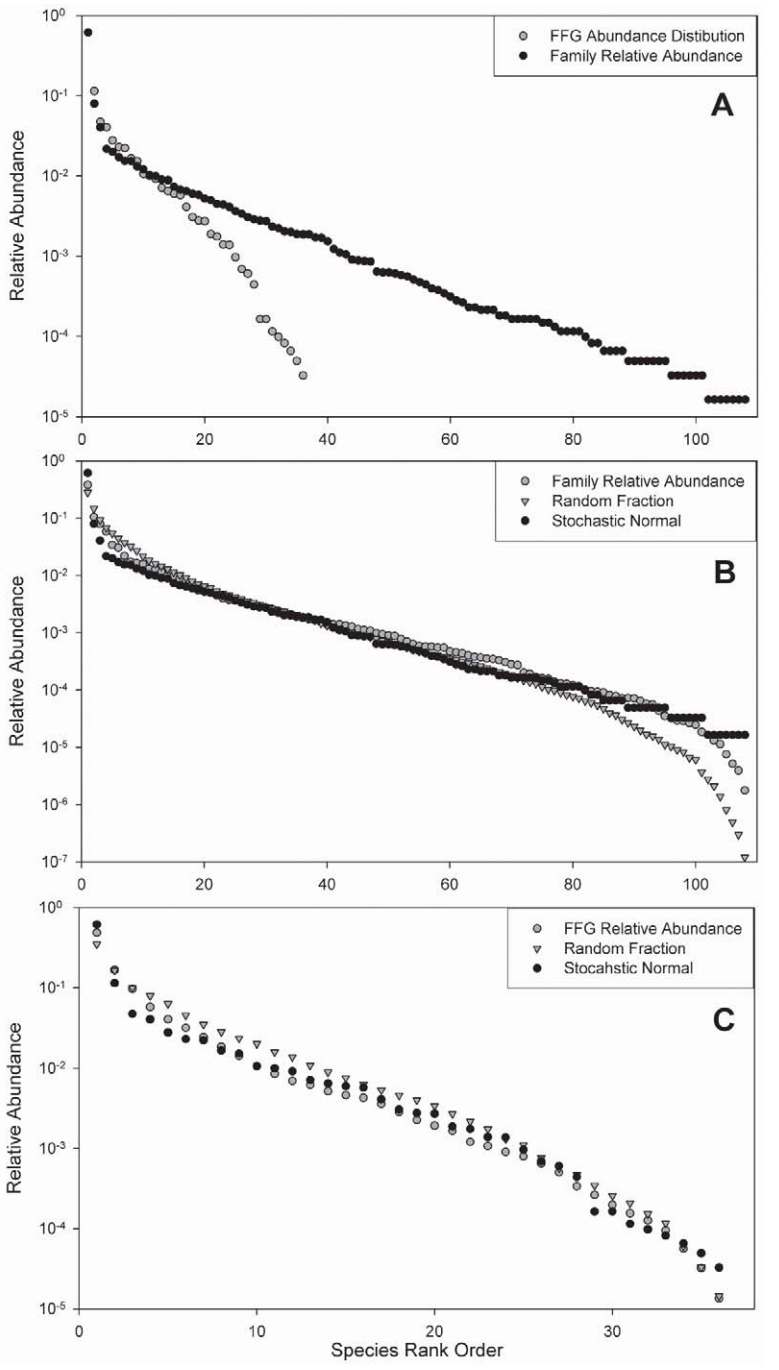


Fig. 3. The relative abundance distribution Whittaker plots comparing families and functional feeding groups (FFG) (A), family to the Stochastic normal and Random fraction models (B) and FFG to the Stochastic normal and Random fraction models (C) for an arthropod community of grassland habitat in the Free State Province, South Africa.

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(Fig. 3C). From this collection of data it can be suggested that the Stochastic normal, Geometric series or Random fraction models best fit the observed abundance distributions for functional feeding group data. Similar patterns in these goodness-of-fit techniques for both family and FFG data were apparent despite the disparities in richness. This is suggestive that there is correspondence between families and FFG with regard to how abundance is distributed across taxa.

DISCUSSION

Functional diversity has been earmarked as an essential feature of biological assemblages due to its ability to predict ecosystem processes (Mason *et al.* 2005). Grassland arthropods can easily be assigned to broad functional feeding groups (FFG) based on feeding style and the taxonomic order into which they fit. The findings of this study indicate that grassland arthropod FFG are very closely correlated to families in terms of richness, Shannon diversity and Simpson diversity. Richness demonstrated the weakest correlation of the diversity measures. Since richness measures disproportionally favour taxa with low abundances, it might be possible to assume that discrepancies from the linear relationship are caused by rare, low abundance taxa. In a similar study, Andersen (1995) found that although a strong relationship existed between species and genera of Australian ant fauna the precise correlation was dependent on habitat type. As this study covered a 12 month period it is possible that the residuals and extended prediction intervals were remnants of intra-annual seasonal variation and the habitat changes associated with it. It is a well known ecological principle that rare taxa are more affected by seasonal variation than more abundant taxa (Levine & Rees 2004). Shannon diversity, which considers all taxa weighted by their relative abundance, showed the closest relationship between family and FFG whereas Simpson diversity, which disproportionally favours abundant taxa, also demonstrated a very significant relationship between family and FFG levels. Nevertheless, the findings of the ANCOVA analysis reveal, with a high degree of certainty, that FFG can be used as taxonomic surrogates for the assemblage as a whole.

Accumulation curves show that the proportional abundance of FFG exceeds that of families with regard to sampling intensity. It is therefore possible to obtain a more reliable representation of the assemblage as a whole in fewer samples using FFG as opposed to families. This has major implications regarding monitoring costs. As there are fewer functional feeding groups than families, data handling is simplified, as is the potential of including arthropods in a uniform biotic index of ecological integrity. Similarly, in all likelihood FFG are more homogeneously dispersed across space than other, more diverse, taxonomic units. This means that comparisons across space are simplified.

Similar trends were found with regard to the relative abundance distributions of families and FFG: both taxonomic units fitted the stochastic normal and geometric series models best, while FFG also fitted the random fraction model. Tokeshi (1993) found that models generally become ambiguous in small assemblages, making distinction between them difficult; so it is not unfounded that FFG fitted more models due to its smaller richness. The stochastic normal is a statistical model designed to describe abundance distributions and is not based on any ecological assumptions, whereas the geometric series model is niche-based, and is meant to be explanatory in terms of how niche space is divided between taxa (Magurran 2004). The theory behind the models

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was not important in the scope of this study because it was not significant which model families and FFG fitted, but rather that they fitted the same models; which is the case here. It can therefore be noted that, despite the reduced number of taxa, FFG do not differ from families in terms of the relative abundance distribution of taxa.

As with any study, there are potential limitations to these findings. The first is the potential misapplication of the findings. These finding have demonstrated that FFG can be used as family replacement taxonomic units for arthropods sampled using sweep nets in Bloemfontein Dry Grassland. This does not by implication mean that similar surrogacy will apply to other faunal groups, sampling methodologies or habitat types. There is the need to determine whether such surrogacy is consistent over various environmental gradients (Shokri & Gladstone 2009), and spatio-temporal scales (Báldi 2003; Mandelik *et al.* 2007). A distinction must also be made between taxonomic surrogates and biodiversity surrogates. Biodiversity surrogacy (or biodiversity indication) is when the diversity of an organism or group of organisms is used to measure the diversity of other organisms in a habitat (McGeoch 1998); new information is obtained through inference. Although it is possible that functional feeding groups may be biodiversity surrogates, this study neither proved nor disproved this. Taxonomic surrogacy, which was demonstrated by this study, implies that the same amount of information (*i.e.* no inference is made about taxa which were not sampled) can be obtained using a simpler methodology. Lastly, unless all species are monophyletic, data will inevitably be lost by the use of taxonomic surrogates (Bertrand *et al.* 2006). The status of rare species might be hidden if those species occur in the same FFG as a more abundant species (Mandelik *et al.* 2007), thereby misinforming conservation strategies.

It can be concluded that functional feeding groups can be used to obtain the same ecological information as family level data, with much less sampling effort and taxonomic expertise. However, the information must be used in the context in which it was intended: rapid monitoring and snap-shot assessments. High-risk ecological scenarios will continue to require specialist ecological inputs and greater investment in environmental information.

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