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Diet specialization does not explain occupancy or abundance in a test of the resource breadth hypothesis in a small mammal community

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DIET SPECIALIZATION DOES NOT EXPLAIN OCCUPANCY OR ABUNDANCE IN A TEST OF THE RESOURCE BREADTH HYPOTHESIS IN A SMALL MAMMAL COMMUNITY

by

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THESIS

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ABSTRACT

The abundance-occupancy relationship (AOR) is a recurrent pattern in ecology and biogeography, in which species with expansive distributions are locally common while those with restricted distributions are locally rare. Despite occurring across a wide variety of taxa and spatial scales, the mechanisms underlying AORs are not well understood. I tested two such mechanisms regarding dietary generalism in a guild of 8 small, herbivorous African mammals: (1) the degree to which diet was explained by food availability, and (2) population-level diet breadth. I expected that food availability would better predict diet for abundant, widespread species than rare, restricted species. Additionally, I predicted that species that use a diversity of C_3 and C_4 plants and arthropod resources (dietary generalists) both would occupy more sites and, given occupancy, be more abundant than rare, restricted species (i.e., purported dietary specialists). For two species, diet was related to food availability, albeit weakly; food availability was a poor predictor of diet for the remaining six species. I detected no relationship between population-level diet breadth and abundance, nor between population-level diet breadth and occupancy. My results provide weak support for the resource-breadth hypothesis, which posits that differences in niche width underlie AORs.

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INTRODUCTION

Within closely related or ecologically similar taxa, species tend to be common within expansive geographic ranges, or rare within restricted ranges. Such abundance-occupancy relationships (AORs) are robust to sampling methods, spatial and temporal scales of inquiry (Cowley et al., 2001; Darwin, 1959; Webb et al., 2012; Zuckerberg et al., 2009), and have been noted in taxa as diverse as marine bacteria (Amend et al., 2013), woody plants (Falster et al., 2001), breeding birds (Gaston and Blackburn, 2003), butterflies (Cowley et al., 2001), and primates (Harcourt et al., 2005). Abundance-occupancy relationships have been instrumental in a variety of conceptual and applied advances, including the unification of species-area relationships and species-abundance distributions (Harte et al., 2001; McGill and Collins, 2003), pest control (Nachman, 1984; Topping et al., 2015), population estimation for highly motile species (Webb and Merrill, 2012), and the setting of harvest limits (Swain and Morin, 1996). Additionally, AORs have strong potential to inform reserve design and other efforts to curb extirpation and extinction (Börschig et al., 2013; Gaston et al., 2000; Martinez et al., 2017).

A diversity of explanations for the AOR has been proposed, ranging from sampling artifacts (e.g., Selmi and Boulinier, 2004; Wilson, 2011) to differential rates of dispersal (Hanski, 1982; Hanski and Gyllenberg, 1993; Tempel and Gutiérrez, 2013). Perhaps most prominently, AORs have been hypothesized to reflect differences in resource requirements among species, such that those species that are able to use a broad array of resources should occur at more sites, and be relatively abundant in the sites that they occupy (Brown 1984; Brown et al. 1995). In contrast, locally rare species are hypothesized to be resource specialists, thus restricting their distribution across the landscape in tandem with the availability of preferred resources (Brown 1984; Brown et al. 1995). This idea runs counter to the expectation of trade-offs between rare, restricted species (purported specialists) and those that are abundant and widely distributed (purported generalists): under the resource-breadth hypothesis, specialists do not exhibit sufficiently high population growth to be common in the few places that they occur, so the jack-of-all-trades may well be a master of all (Brown, 1995; MacArthur, 1972). Despite the intuitive appeal of this hypothesis, field tests of it are rare (but see Verberk et al., 2010); indeed, the resource-breadth hypothesis itself has even been deemed "impossible to test" (Gaston et al., 1997).

Often, ecologists have tried to evaluate the resource-breadth hypothesis (and other hypotheses for AORs) by relating species abundance and occupancy over broad spatial scales to (necessarily) coarsely-delineated habitat types (e.g., Faulks et al., 2015; Gaston et al., 2000; Komonen et al., 2013; La Sorte and McKinney, 2007; Tonkin et al., 2016). While this approach has enhanced our appreciation for the generality of AORs, it glosses over the near-universality that individuals use only a subset of resources available to them (Manly et al., 2002; Stamps, 2009). Given data only on species abundance and occupancy across habitat types, it remains difficult to discriminate between preferences (which are flexible) and requirements (which are fixed). Moreover, intraspecific variation in resource use can account for most of a population's total niche width (Bolnick et al., 2007, 2011; Maldonado et al., 2017; Newsome et al., 2009; Roughgarden, 1974; Van Valen, 1965). In short, the resource-breadth hypothesis is a macroecological hypothesis that may be challenging to test with macroecological data.

I integrated consumer-resource interactions with intraspecific variation in diet to evaluate the role of diet breadth in driving abundance and occupancy in a species-rich guild of small, mainly herbivorous mammals. Although food represents a single resource, food limitation underlies whole-community abundance in my study system (Goheen et al., 2013; Long et al., 2017), other small-mammal communities in East Africa (Keesing, 1998; Keesing and Young, 2014; Metz and Keesing, 2001; Young et al., 2015), and small-mammal communities elsewhere (e.g., Buesching et al., 2011; Galetti et al., 2015; Herder et al., 2016; Parsons et al., 2013; Steen et al., 2005). Therefore, diet provides an informative lens through which to test predictions of the resource-breadth hypothesis in my study system. In accord with the resource breadth hypothesis, I predicted that more abundant, widespread species would be generalists whose food use would reflect availability (Fig. 1A; Fig. 1Bi). In contrast, rare, restricted species should be specialists whose food use should be relatively invariant, even in the face of shifting availability (Fig. 1A; Fig. 1Bii, 1Biii). Further, I predicted that population-level diet breadth, as assayed by carbon and nitrogen isotopes (i.e. the isotopic niche) would be broadest for abundant, widespread species and narrowest for rare, restricted species. In confronting the AOR with species' differences in diet selection, I hoped to mechanistically link intraspecific variation in resource use to a widespread ecological pattern.

METHODS

Study Area: My research was conducted from 2009–2016 at the Mpala Conservancy in Laikipia County in central Kenya (0°17′N, 37°52′ E, 1600 m elevation), in a semi-arid savanna. This region is characterized by unproductive, red sandy loam soil and has a trimodal rainfall regime. The long rains occur April–May, and two periods of shorter rains may occur in August and October (Augustine, 2002). Mount Kenya casts a rain shadow across my field sites, such that annual rainfall increases by ~45% from the arid north to the mesic south over a short distance (~20 km). Vegetation overstory is dominated by *Acacia etbaica*, *Acacia mellifera*, and *Acacia brevispica*, while understory is a discontinuous mix of grasses and forbs. The most common grasses are *Pennisetum stramineum*, *Cynodon plectostachyus*, and *Cynodon dactylon* (Goheen et al., 2013). The most common forbs are *Gutenbergia cordifolia*, *Commelina africana*, and *Indigofera brevicalyx*. A diversity of large (>5 kg) mammalian herbivores occurs at my sites, of which elephant (*Loxodonta africana*), impala (*Aepyceros melampus*), and dik-dik (*Madoqua guentheri*) account for the highest biomass density (Pringle et al., 2014).

I conducted my work within the UHURU (Ungulate Herbivory Under Rainfall Uncertainty) experiment that consists of four size-selective treatments, in which combinations of mammalian herbivores are excluded or permitted access to 1-ha plots using a series of electrified fences (Goheen et al., 2013). For the purposes of this study, I focused on the two extreme treatments: control (unfenced) plots to which all large mammalian herbivores had access, and total exclusion plots from which all herbivores including and larger than dik-dik (ca. 5 kg) were excluded (hereafter “exclusion plots”). Exclusion plots are permeable to predators (snakes and small carnivores) that consume small mammals (Goheen et al. 2013; Long et al. 2017). These treatments are replicated three times at each of three rainfall levels (Goheen et al. 2013): south (~640 mm/year), central (~580 mm/year), and north (~440 mm/year). In combination, the spatial gradient in rainfall, temporal variability in rainfall, and exclusion of large mammalian herbivores create a shifting mosaic of food availability.

Small Mammal Trapping: Since May 2009, small mammals have been trapped at UHUHU sites; my study uses samples collected July 2009 – January 2013 and March 2015 – August 2016. A 7x7 trapping grid with 10 m spacing is centered within each plot, for a total of 882 traps across all plots. Small mammals were captured with Sherman live traps baited with a peanut butter and oats mixture, placed at each stake for 4 consecutive nights every-other month. New captures received unique Monel fingerling eartags with the exception of *Acomys, Crocidura* and *Mus* spp.; these species were marked with indelible ink upon first capture for individual identification within sampling bouts because they were too small or delicate for eartags to be applied. (Goheen et al., 2013; Seifert et al., 2012). Species identification, individual identification, weight, age, reproductive status and trap location were recorded. At first capture during a trapping bout, if there was no visible haircut from previous captures, hair samples were collected from the rump of the animal for stable isotope analysis.

I focused on eight species of small mammal: Hinde's bush rat (*Aethomys hindei*), African grass rat (*Arvicanthis niloticus*), rufous elephant shrew (*Elephantulus rufescens*), fringe-tailed gerbil (*Gerbilliscus robustus*), woodland thicket rat (*Grammomys dolichurus*), Kellen's small-eared dormouse (*Graphiurus kelleni*), East African pouched mouse (*Saccostomus mearnsi*), and Harrington's tateril (*Taterillus harringtoni*). These species were selected because they vary widely in abundance and occupancy, can be detected with regularity (probability of detection given presence was >0.80 for all species) and are large enough to be uniquely marked for subsequent identification. With the exception of *E. rufescens* that consumes primarily arthropods and feeds occasionally on plants (Rathbun, 1979), all of these species are primary consumers and are reported to rely on understory vegetation (Bergstrom, 2013; Kingdon et al., 2013; Metz and Keesing, 2001; Neal, 1984; Rabiu and Rose, 1997; Smithers, 1971); however, they may also opportunistically consume arthropods (Kingdon et al., 2013).

Plant Surveys: I quantified biomass and composition of understory vegetation at the height of the dry season (Feb–Mar), and again during Sep–Oct when plants were green and productive. A 0.25 m^2 quadrat was placed on the north side of each stake in the trapping grid and presence/absence for all grasses and forbs within the quadrat was recorded. A 10-point pin frame was placed centrally within the smaller quadrat and the total number of live understory and bare-ground pin hits was recorded. At my sites, the number of pin hits is strongly correlated with understory biomass (Augustine, 2002).

Biomass of understory vegetation was used as a proxy for food availability because the majority of the small mammal species rely primarily on plant dietary resources. I did not incorporate overstory biomass into estimates of food availability for two reasons. First, any consumption of overstory plants likely would be restricted to seeds, which are sporadically available throughout the year; it is difficult to estimate access by ground-dwelling herbivores to ephemeral seed crops in the canopy. More importantly, from published natural histories of each species (described above), most diets within this guild are comprised of leaves and seeds of understory plants. This expectation is supported by fecal DNA metabarcoding data on diet composition (Goheen and Kartzinel unpublished data; see also Kartzinel et al., 2015).

From October 2009 to March 2013, I estimated food availability within individual plots. Home ranges of small mammals are sufficiently small that inter-plot movements are very rare (Young et al., 2015). The number of green vegetation pin hits for each species of forb and grass at each stake was summed across all stakes in each plot to estimate species-specific biomass (food availability). I then calculated the percent of the biomass that was grass to estimate the C_4 plant resources available in that plot. I estimated food availability for each individual based on the plot and sampling bout in which an individual was trapped, such that individuals sampled Jan–Jun were assigned estimates of food availability from March, and individuals sampled Jul–Dec were assigned estimates of food availability from September. I also calculated the average proportion of C_3 and C_4 plants by genus in each plot to determine the most likely diet items within each plant photosynthetic type.

Stable Isotope Analysis: My study sites are characterized by a mosaic of plants that use either the C_3 (trees, shrubs and forbs) or C_4 (most grasses) photosynthetic pathway (Bergstrom, 2013; Sponheimer et al., 2003), which can be readily distinguished via carbon isotope ($\delta^{13}C$) analysis. The nitrogen isotope ($\delta^{15}N$) composition of a consumer's tissue indicates trophic level (Ben-David and Flaherty, 2012) when spatial or temporal (baseline) shifts in the $\delta^{15}N$ of plants can be accounted for via analysis of dominant primary producers. The $\delta^{13}C$ and $\delta^{15}N$ composition of a consumer mirrors that of its food resources, but is offset by predictable amounts due to isotopic discrimination that occurs during resource assimilation and tissue synthesis. Trophic discrimination factors vary between 0–3‰ for $\delta^{13}C$ (Post, 2002) and 3–5‰ for $\delta^{15}N$ (DeNiro and Epstein, 1981) depending on the tissue type, diet quality (protein content), and nitrogen excretionary pathway (Bearhop et al., 2002; Kurle, 2002; Pearson et al., 2003; Vanderklift and Ponsard, 2003). The isotopic composition of consumer tissues reflects that of their diet at the time of the tissue formation (Martinez del Rio et al. 2009). Tropical mammals molt continuously (Mares et al., 1982), so hair samples reflect diet consumed over the 3–4 months (Bergstrom, 2013; Priestley, 1966; Tieszen et al., 1983).

From March 2016–June 2016, I collected leaves of the 20 most abundant species of understory plants at all three rainfall levels. I pressed or dried plant samples at ~45°C. Dried plant leaves were weighed (~2.5 mg) into tin capsules. Hair samples were cleaned with chloroform methanol, dried, and weighed (~0.5 mg) into tin capsules. All plant and hair samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ using a Costech 4010 Elemental Analyzer (Valencia, CA) coupled to a Thermo Scientific Delta V isotope ratio mass spectrometer (Bremen, Germany) at either the University of Wyoming Stable Isotope Facility (Laramie, WY) or the University of New Mexico Center for Stable Isotopes (Albuquerque, NM). Isotopic data are reported in δ notation, as $\delta^{13}C = 1{,}000 \times [(R_{sample}/R_{standard}) - 1]$, where R_{sample} and $R_{standard}$ represent the $^{13}C/^{12}C$ ratio of samples and standards, respectively. δ values are reported in units of per mil (‰) and are calibrated to international standards of Vienna Pee Dee Belemnite limestone (V-PDB) for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$. The within-run standard deviation of internal reference materials that were calibrated to these international standards was ±0.2‰.

Data Analysis: To quantify the shape of the AOR, I determined abundance for species with small sample size (*A.* niloticus, *G. dolichurus*, *G. kelleni*, and *T. harringtoni*) by number of unique individuals captured across all plots for each species in each trapping period, then divided that number by the number of plots in which each species occurred. The resulting values were averaged for each species across all trapping periods in which the species was captured (Borregaard and Rahbek, 2010; He et al., 2002). For the most common species (*A. hindei*, *E. rufescens*, *G. robustus*, and *S. mearnsi*), abundances were calculated by rainfall level using a robust design Huggins model with full heterogeneity. I used the R package RMark (Laake, 2013) to construct models for Program MARK (Huggins, 1989; White and Burnham, 1999). Models were ranked based on Akaike's Information Criterion and abundance estimates were obtained from the highest ranking model. For species for which I was able to employ robust design models, abundance values were summed across each period and divided by the number of plots in which the species was sampled (Goguen et al., 2015); that value was averaged across periods in which individuals were caught to obtain an abundance value comparable to the other species. Occupancy was determined by counting the number of plots in which a species was present during a given trapping period. These values were then averaged across all trapping periods.

For each species, I estimated the relative proportion of C_3 versus C_4 resources consumed by each individual and tested if food availability drove resource use. I used a Bayesian mixing model Stable Isotope Analysis in R (Parnell et al., 2010) to estimate the relative proportions of C_3 versus C_4 resources consumed by each individual, which I report as $\%C_{4;}$ assuming that $\%C_3 + \%C_4$ sums to 100%. In the mixing model I used mean (±SD) $\delta^{13}C$ values of C_3 and C_4 plants collected from each rainfall level (Table 1) for individuals from that level. I applied a mean (±SD) trophic discrimination factor of 1.0 ± 0.5‰ to $\delta^{13}C$ values from small mammal hair (Post, 2002). I regressed the %C_4 biomass in the plot during an individual's capture (food availability) and %C_4 of the individual's diet (resource use) and calculated slopes, intercepts, p-values and R^2 values for each species in R.

I used the package Stable Isotope Bayesian Ellipses in R (Jackson et al., 2011) to calculate the $\delta^{13}C$ versus $\delta^{15}N$ standard ellipse area of each species, which I used as a metric of isotopic niche width. I calculated 40% Bayesian standard ellipse areas (SEA) estimates for all species, which is approximately equal to one standard deviation around the mean (centroid) of each ellipse. The SEA quantifies variation in a population's isotopic composition, a proxy for species-level diet breadth, and is robust to sample size (Jackson et al., 2011). I then calculated the proportion of Bayesian ellipses of one species that were larger than those of another species for all possible pairwise combinations of species' ellipses. I consider species in which ≥95% of the ellipses exceed those of another species as significantly larger. Occupancy and abundance were regressed against SEA separately and together to determine any relationships with isotopic niche width.

RESULTS

Stable isotopes analysis distinguished between the $\delta^{13}C$ values of C_3 and C_4 plants; isotope values did not vary significantly by rainfall level for any of the 20 most common species of understory plants. The average $\delta^{13}C$ value of C_3 plants was -27.0 ± 1.8 and the average $\delta^{13}C$ value of C_4 plants was -13.9 ± 1.1 (Table 1). The range of $\delta^{13}C$

values across all food sources—plant and arthropod—was 19.0‰. The range of $\delta^{15}N$ values across all food sources was 17.1‰. Average $\delta^{13}C$ and $\delta^{15}N$ for each species can be found in Table 2.

The distribution of C_3 and C_4 biomass was highly skewed across genera (Appendices B and C). Relatively few genera accounted for most of the biomass in the plots so small mammals that specialize on C_3 or C_4 are likely utilizing a very narrow selection of plants. Among C_3 plants ≥50% of the biomass was accounted for by 4 or less genera, though the dominant genera varied between plots. *Barleria*, *Commelina*, and *Indigofera* species were often among the dominant forbs. Among C_4 plants ≥50% of the biomass was accounted for by 3 or less genera with *Cynodon* and *Pennisetum* species comprising the top two in almost 80% of the plots.

Abundance and occupancy were linearly related ($R^2 = 0.62$, $P < 0.01$; Fig. 2). For two of the eight focal species (*A. hindei* [$R^2 = 0.07$, $P = 0.02$] and *A. niloticus* [$R^2 = 0.19$, $P = 0.01$]), food use mirrored food availability, although the amount of variation in food use explained by food availability was low (Fig. 3). Food use was unrelated to food availability for the remaining six species ($P > 0.05$; Table 3).

Standard ellipse area varied significantly between most pairs of species (Fig. 4). The species are ordered by SEA from smallest to largest with abundance and occupancy rank, respectively, as follows: *E. rufescens* (4, 7), *S. mearnsi* (7, 5), *A. hindei* (8, 6), *G. dolichurus* (1, 2), *G. kelleni* (3, 1), *A. niloticus* (5, 4), *G. robustus* (6, 8), *T. harringtoni* (2, 3).Neither occupancy ($P = 0.95$) nor abundance ($P = 0.55$) were related to the area of standard ellipses (Fig. 5).

DISCUSSION

I found limited support for the resource breadth hypothesis. Population-level diet breadth was related neither to abundance nor occupancy. Further, diets of abundant, widespread species (*A. hindei*, *G. robustus,* and *S. mearnsi*) were related to food availability no more than those of rare, restricted species (*Grammomys dolichurus*, *Graphiurus kelleni*, and *T. harringtoni*). Only two species (*Aethomys hindei*, *Arvicanthis niloticus*) exhibited relationships between diet and food availability, and the relationship between diet and food availability for *A. hindei* was negative, which is opposite that predicted for an abundant, widespread species. Independence between diet and food availability could be explained by optimal foraging theory, in which abundant resources are ignored when more energetically profitable options are available (Charnov, 1976; Kotler and Brown, 1988; St. Juliana and Mitchell, 2016).

Counter to conventional wisdom surrounding ecological specialization and fitness trade-offs (Berumen and Pratchett, 2008; Futuyma and Moreno, 1988; Østman et al., 2014; Pelegrin et al., 2017), the resource breadth hypothesis posits that species pay no penalty for generalizing: to the extent that high abundances and widespread distributions are indicative of fitness benefits. In other words, the jack-of-all trades may also be the master of all (Brown, 1995; MacArthur, 1972). In this system, neither metric of diet generalism (diet vs. food availability, population-level diet breadth) was related to abundance or occupancy. This finding implies that neither dietary specialization nor dietary generalism confers a fitness advantage over the other, and that trade-offs likely are associated with each strategy or a neutral model for specialization exists (Forister and Jenkins, 2017; Hubbell, 2005).

Traditionally, dietary niche width has been evaluated by counting the number of species an animal eats using a metric such as gut content analysis (Kerley, 1989; Roughgarden, 1979). While stable isotopes do not use a taxonomic approach to define niche width, they instead provide a very good estimate of functional dietary niche width (i.e. C_3 browser vs. C_4 grazer, herbivore vs. insectivore). Small mammals select diet items not because of their taxonomic designation but because of characteristics such as nutritional content or size (Cole, 2017; Kotler and Brown, 1988; St. Juliana and Mitchell, 2016), making a functional approach to niche width perhaps even more informative than a taxonomical approach. Furthermore, plant biomass estimates in this study have demonstrated that within the functional groups of C_3 forbs or C_4 grasses relatively few taxa comprise the majority of the biomass; therefore a specialist on one of these groups of plants is probably also taxonomically restricted in diet.

An additional benefit to using stable isotopes is that they incorporate dietary information over time, allowing the researcher to determine what an individual has eaten over the past few months as opposed to a 24 hour snapshot in time that would be provided by fecal or gut analyses. Many studies have explored the benefits of combining stable isotope analysis with other types of analyses such as gut contents analysis (Grey et al., 2002; Scharnweber et al., 2016) and DNA metabarcoding of feces (Hardy et al., 2010; Kartzinel et al., 2015). Because isotopes and fecal or gut contents incorporate diet information over different time scales (i.e. months vs. days) and taxonomical scales, these methods have been shown to complement each other and may be a valuable next step if one were to revisit the resource breadth hypothesis as a mechanism for the AOR. Fecal or gut analyses would allow us to determine the diversity of plant species that comprise the diet at a fine temporal scale. Combined with stable isotopes, which shows coarse diet composition over time, one could develop a robust diet profile for each species across multiple temporal and taxonomic scales. By incorporating a fine-scale approach it might be found necessary to redefine species along the specialization spectrum and under this altered scenario a correlation between abundance, occupancy and diet breadth may be discovered.

Although the niche is widely accepted as a n-dimensional hypervolume (Hutchinson, 1957), for practical purposes it is impossible to quantify all niche axes. Food, time, and space are generally considered the primary axes explaining species' requirements and behavior (Pelegrin et al., 2017; Pianka, 1973; Schoener, 1974). This study focused on food, a key driver of small mammal abundance, over a spatial scale spanning a large environmental gradient, but did not address microhabitat use by small mammals or patterns of aggregation in resources. Microhabitat studies have illustrated the importance of space on small mammals' fitness especially as it relates to predator avoidance (Ceradini and Chalfoun, 2017; Kerley et al., 1990). Further studies focusing on fine-scale movement and resource distribution could enhance our understanding of the drivers behind abundance and occupancy.

I investigated one mechanism for the AOR – the resource breadth hypothesis – however there are many more explanations for the AOR that warrant investigation; one such explanation is metapopulation dynamics. Local abundance and regional distribution are created and maintained through immigration to and emigration from habitat patches. It predicts that higher abundance will lead to less extinction through the rescue effect, more dispersers and thus higher occupancy. Higher occupancy strengthens the AOR by providing more patches from which individuals can be recruited (Cowley et al., 2001; Hanski and Gyllenberg, 1993; Hanski et al., 1993).

My study suggests, contrary to the resource breadth hypothesis, that specialist species are not inherently at higher risk of extinction than generalist species in systems where population dynamics are driven by food availability; specialists can have abundance and occupancy comparable to that of generalist species (see also Williams et al., 2009). As long as a reserve is designed to encompass suitable sites for a specialist, it is not necessarily in “double jeopardy” as specialists are capable of having high abundance and occupancy (Gaston et al., 2000). There are many studies predicting specialist species to be more at risk with climate change (Davies et al., 2004; Munday, 2004), but this study gives us hope that this may not be the case.

Figure 1. Schematic A) represents predictions of the resource breadth hypothesis. Species that are more abundant and widespread are diet generalists, while species that are less abundant and within a constrained distribution are diet specialists. In schematic B), i) depicts a diet generalist, ii) depicts a C_4 specialist, and iii) depicts a C_3 specialist.

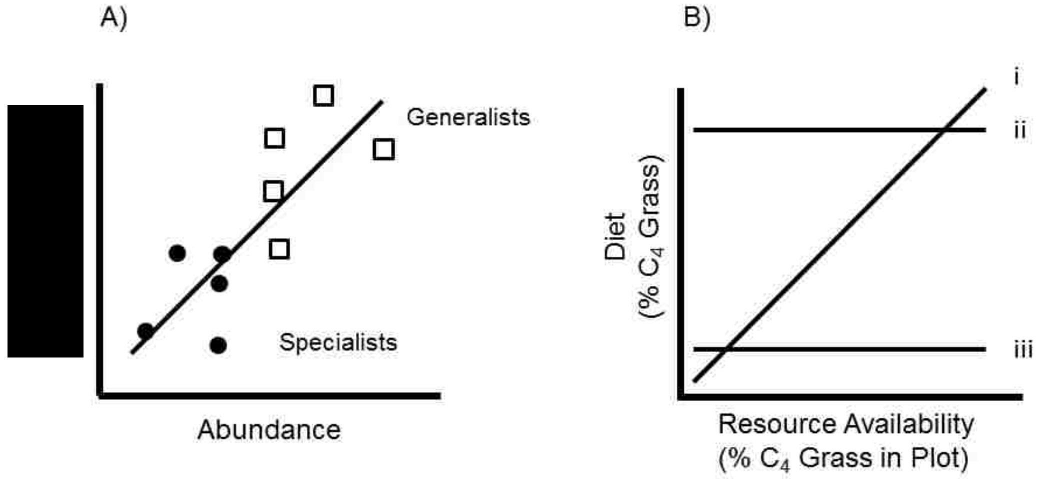


Figure 2. The abundance-occupancy relationship for small mammals in the UHURU experiment. Species names are abbreviated as follows: AEHI (*Aethomys. hindei*), ARNI (*Arvicanthis niloticus*), ELRU (*E. rufescens*), GERO (*Gerbilliscus robustus*), GRDO (*Grammomys dolichurus*), GRKE (*Graphiurus kelleni*), SAME (*S. mearnsi*), and TAHA (*T. harringtoni*). Hollow data points represent species for which carbon and nitrogen isotope values were not quantified.

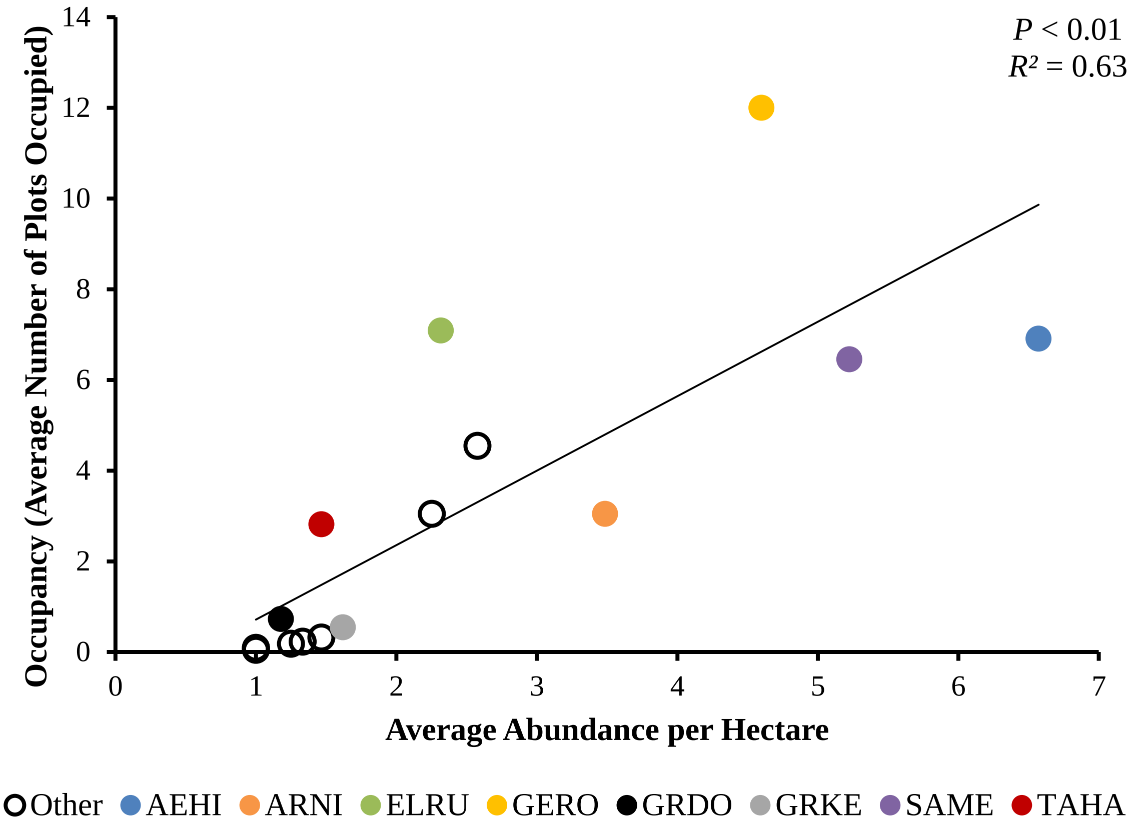
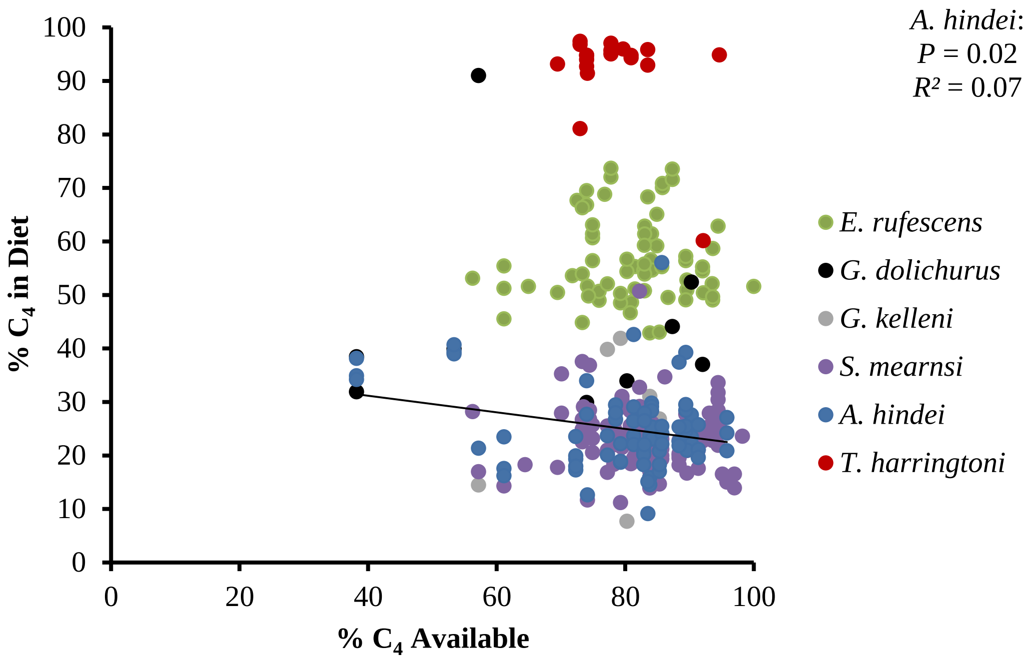


Figure 3. A) *A. hindei*'s diet is negatively correlated with food available. B) *A. niloticus*' diet is positively correlated with food available. While significant, neither relationship sufficiently explains the variability in the data.

A)



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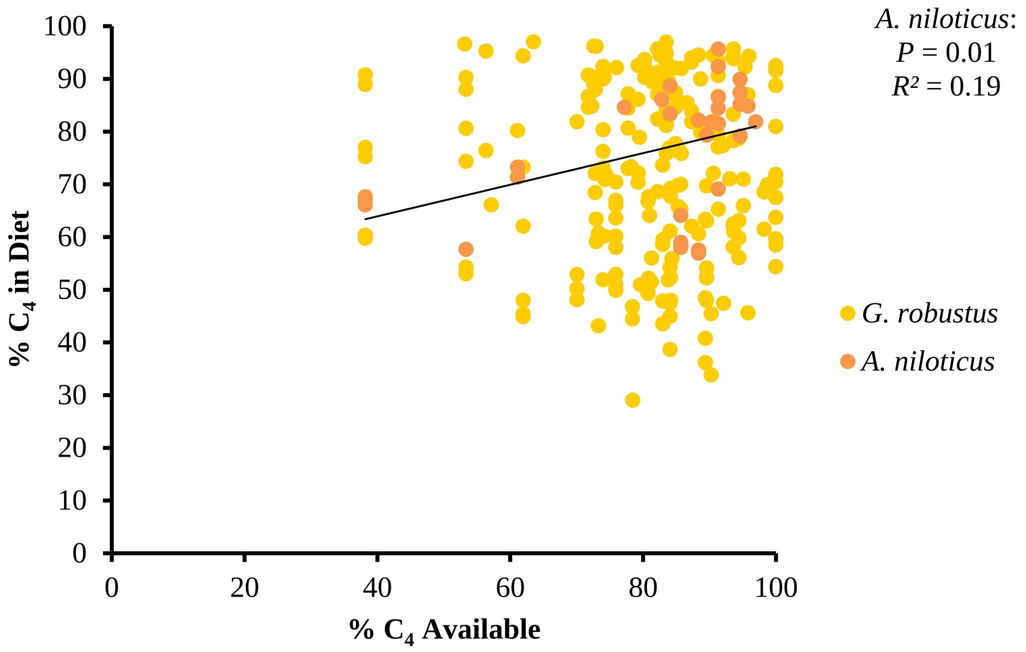


Figure 4. Bayesian standard ellipse areas (SEA, black dots) for each species. The telescoping steps indicate credible intervals of 50%, 75% and 95%. Species names are abbreviated as follows: AEHI (*A. hindei*), ARNI (*A. niloticus*), ELRU (*E. rufescens*), GERO (*G. robustus*), GRDO (*G. dolichurus*), GRKE (*G. kelleni*), SAME (*S. mearnsi*), and TAHA (*T. harringtoni*).

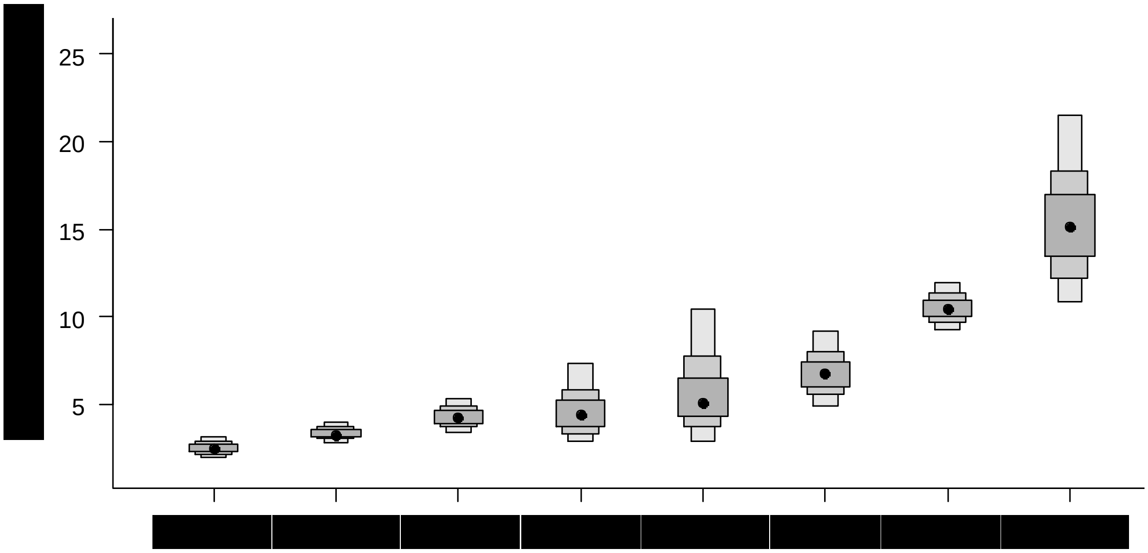
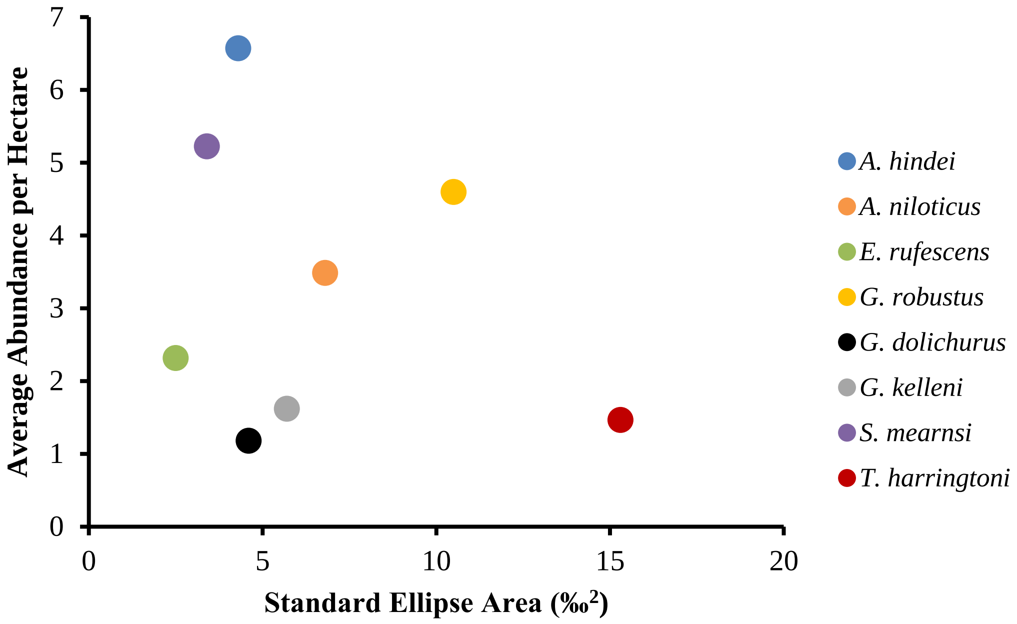


Figure 5. A) Regression between SEA and abundance. B) Regression between SEA and occupancy. Neither of these relationships are significant ($P > 0.05$).

A)



B)

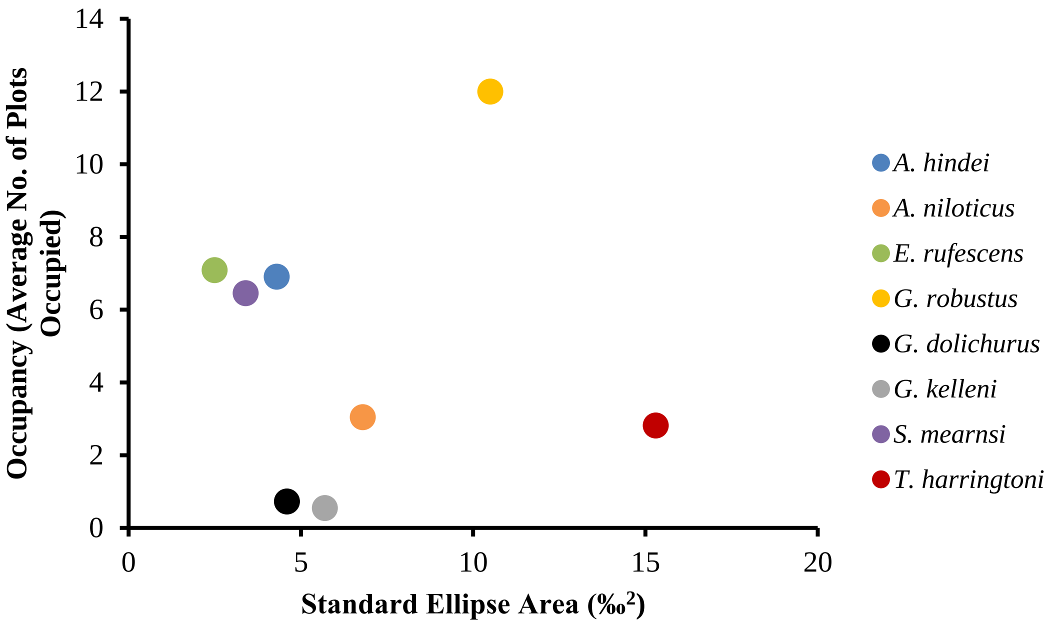


Table 1. Summary of carbon and nitrogen isotopic values and sample size for C_3 and C_4 plants sampled across north (arid), central (intermediate), and south (mesic) plots.

	C_3			**C_4**		
	Mean $\delta^{13}C$	**Mean $\delta^{15}N$**	**n**	**Mean $\delta^{13}C$**	**Mean $\delta^{15}N$**	**n**
N	-27.7 ± 1.2	6.6 ± 1.5	45	-13.6 ± 1.1	5.1 ± 2.0	54
C	-26.2 ± 1.4	6.4 ± 2.1	45	-14.1 ± 1.1	4.2 ± 1.4	63
S	-26.8 ± 2.2	6.2 ± 3.0	48	-13.7 ± 1.2	5.4 ± 3.1	60
All	-27.0 ± 1.8	6.5 ± 2.4	141	-13.9 ± 1.1	4.8 ± 2.1	178

Table 2. Summary of sample size (n), and carbon and nitrogen isotopic values from hair samples of each species across north (arid), central (intermediate) and south (mesic) plots.

Species	**Level**	**Mean $\delta^{13}C$**	**Mean $\delta^{15}N$**	**n**
A. hindei	**N**	-22.3 ± 0.8	9.4 ± 0.8	17
	C	-23.3 ± 0.6	8.9 ± 0.8	23
	S	-22.9 ±1.2	7.1 ± 1.1	37
	All	-22.9 ± 1.0	8.1 ± 1.4	77
A. niloticus	**N**	-15.3 ± 1.6	9.1 ± 0.7	15
	C	-16.3 ± 0.1	7.7 ± 0.2	2
	S	-15.6 ± 2.0	7.1 ± 0.5	15
	All	-15.5 ± 1.8	8.1 ± 1.1	32
E. rufescens	**N**	-17 ± 0.6	10.8 ± 0.5	14
	C	-18.6 ± 0.6	10.7 ± 0.5	21
	S	-18.3 ± 0.8	9.5 ± 0.9	34
	All	-18.1 ± 0.9	10.1 ± 1.0	69
G. robustus	**N**	-15.5 ± 2.8	10.5 ± 1.1	72
	C	-15.5 ± 1.9	10.3 ± 0.9	58
	S	-16.8 ± 2.3	9.0 ± 1.6	81
	All	-16 ± 2.5	9.8 ± 1.4	211
G. dolichurus	**N**	-21.2 ± 1.2	10.2 ± 0.5	6
	C	-17.3 ± 5.4	9.8 ± 0.5	2
	S	-21.1	10.2	1
	All	-20.3 ± 9	10.2 ± 0.4	9
G. kelleni	**N**	NA	NA	0
	C	-22.5 ± 1.9	11.0 ± 0.7	7
	S	-20.7	9.5	1
	All	-22.3 ± 1.9	10.8 ± 0.9	8
S. mearnsi	**N**	NA	NA	0
	C	-23.4 ± 0.8	8.3 ± 0.7	21
	S	-23.2 ± 0.8	7.8 ± 1.6	115
	All	-23.2 ± 0.8	7.9 ± 1.5	136
T. harringtoni	**N**	-12.1 ± 1.2	11.5 ± 1.2	16
	C	-14.3 ± 2.1	11.6 ± 2.0	3
	S	-15.3 ± 4.2	9.8 ± 1.1	3
	All	-12.8 ± 2.2	11.3 ± 1.4	22

Table 3. A summary of the linear regression statistics derived from the data presented in Figure 3. The x-variable is the percent C_4 available to the individual in the plot by biomass and the y-variable is the percent C_4 in the diet of an individual.

Species	**Slope**	**Intercept**	***P*-value**	**R^2**	**Residual Standard Error**
A. hindei	-0.155	37.376	**0.023**	0.067	7.359
A. niloticus	0.300	51.923	**0.012**	0.193	10.920
E. rufescens	0.026	54.298	0.814	0.001	7.882
G. robustus	-0.054	76.685	0.544	0.002	16.710
G. dolichurus	-0.029	46.265	0.931	0.001	20.060
G. kelleni	0.272	3.522	0.618	0.044	12.740
S. mearnsi	-0.031	26.025	0.599	0.002	5.409
T. harringtoni	-0.506	131.827	0.097	0.153	8.070

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LIST OF APPENDICES

Appendix A: Supplementary Figure 1. Percent of biomass comprised of each genus of C_4 plant, averaged across understory surveys 2009 – 2013 by plot. Mesic south (A-F), intermediate central (G-L) and arid north (M-R).

Appendix B: Supplementary Figure 2. Percent of biomass comprised of each genus of C_3 plant, averaged across understory surveys 2009 – 2013 by plot. Mesic south (A-F), intermediate central (G-L) and arid north (M-R).

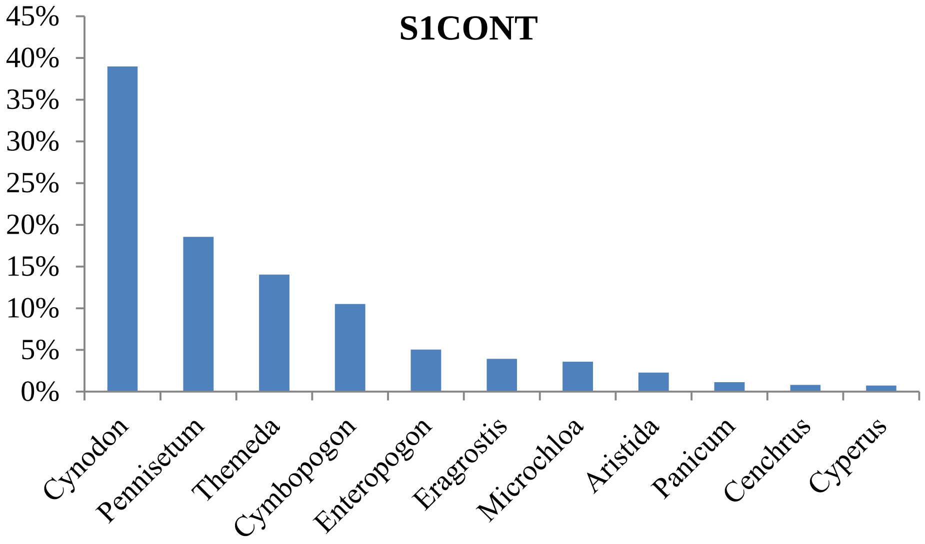
Appendix C: Supplementary Figure 3. SEA for each small mammal species. Ellipses encircle 40% of the data points for each species.

Appendix D: Supplementary Table 1. Carbon and nitrogen isotope data and sample size for the most prevalent plant species across south (mesic), central (intermediate) and north (arid) plots.

Appendix E: Supplementary Table 2. Summary of carbon and nitrogen stable isotope data and sample size for main arthropod orders across south (mesic), central (intermediate) and north (arid) plots.

Appendix A: Supplementary Figure 1. Percent of biomass comprised of each genus of C_4 plant, averaged across understory surveys 2009 – 2013 by plot. Mesic south (A-F), intermediate central (G-L) and arid north (M-R).

A)



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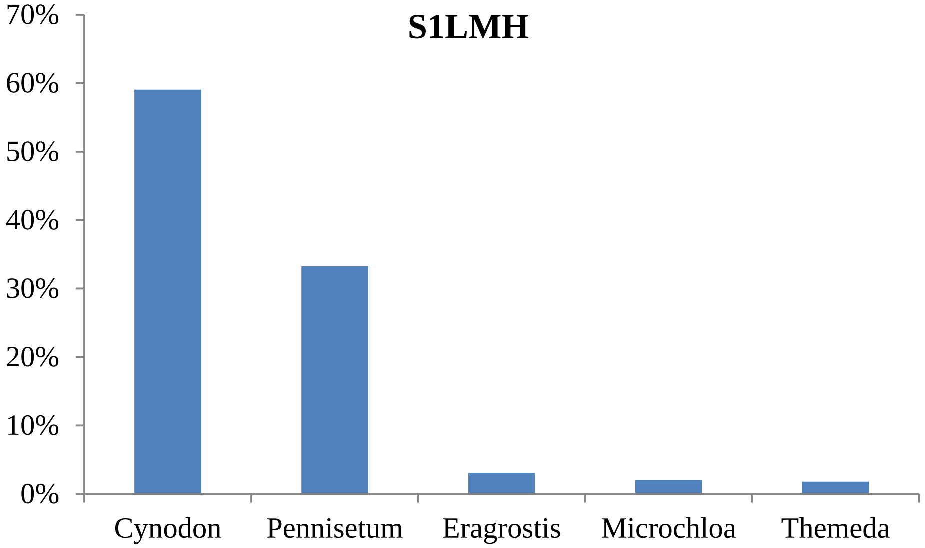

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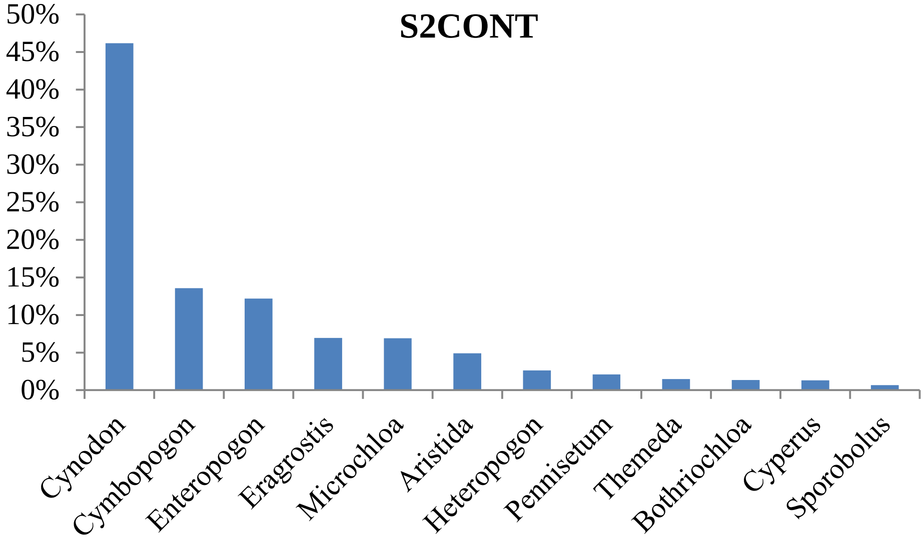
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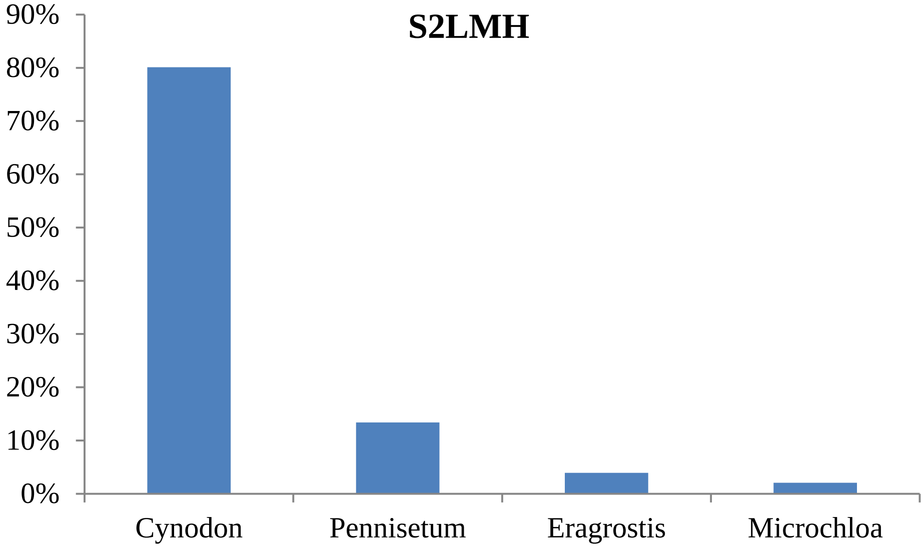
40%
35%
30%
25%
20%
15%
10%
5%
0%
Cynodon
Cymbopogon
Enteropogon
Eragrostis
Microchloa
Aristida
Heteropogon
Pennisetum
Themeda
Bothriochloa
Cyperus
Sporobolus

D)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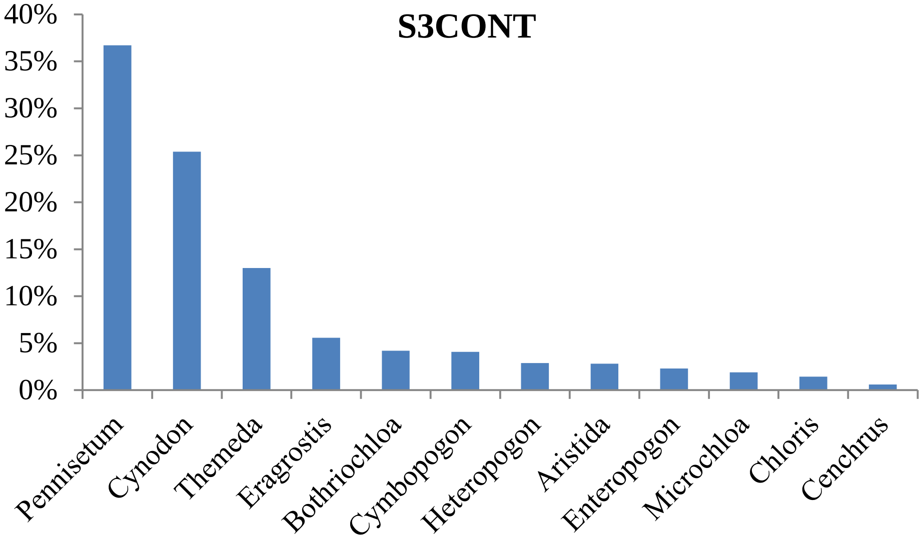
Pennisetum
Eragrostis
Microchloa

E)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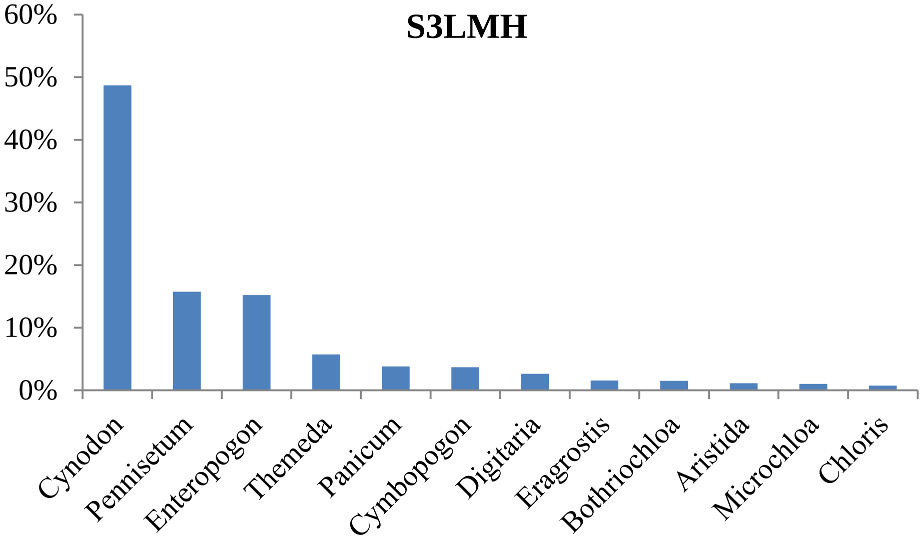
Pennisetum
Cynodon
Themeda
Eragrostis
Bothriochloa
Cymbopogon
Heteropogon
Aristida
Enteropogon
Microchloa
Chloris
Cenchrus

F)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Cymbopogon
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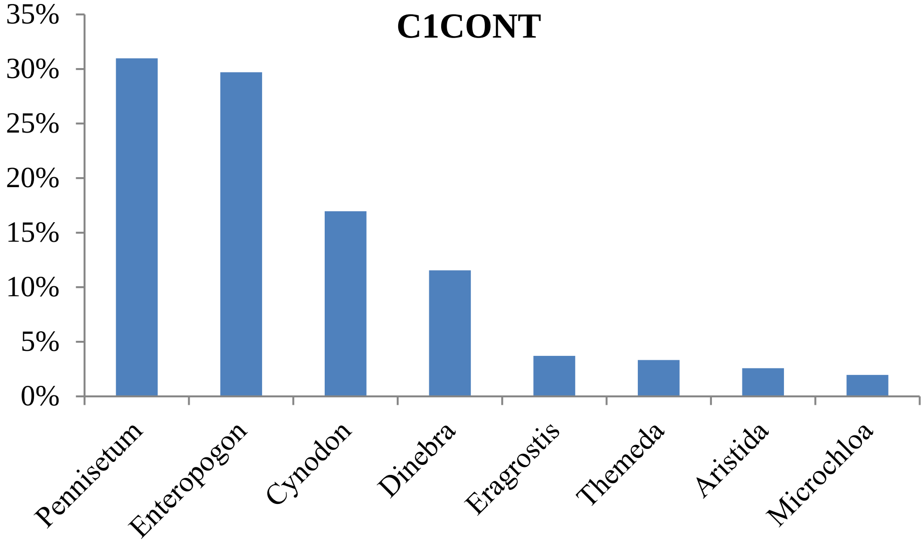
Bothriochloa
Aristida
Microchloa
Chloris

G)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Eragrostis
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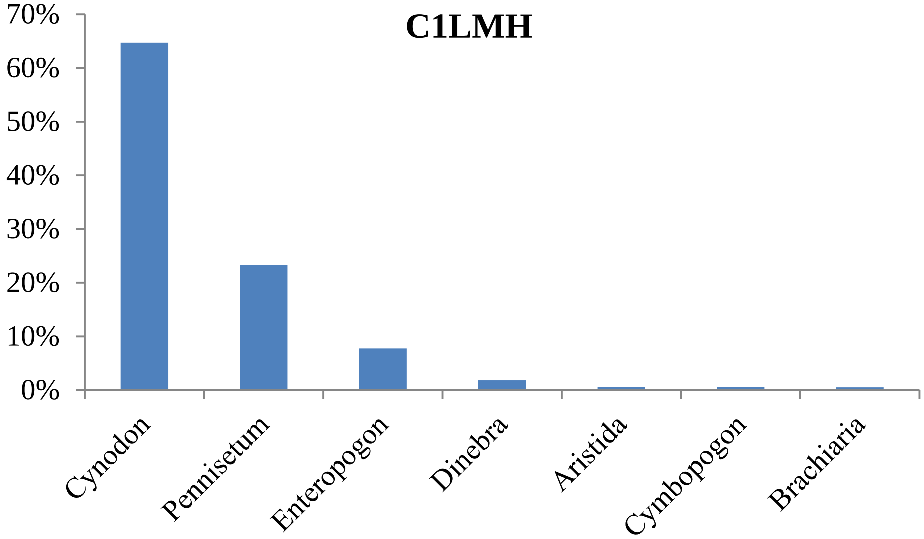
Aristida
Microchloa

H)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Cymbopogon
Brachiaria

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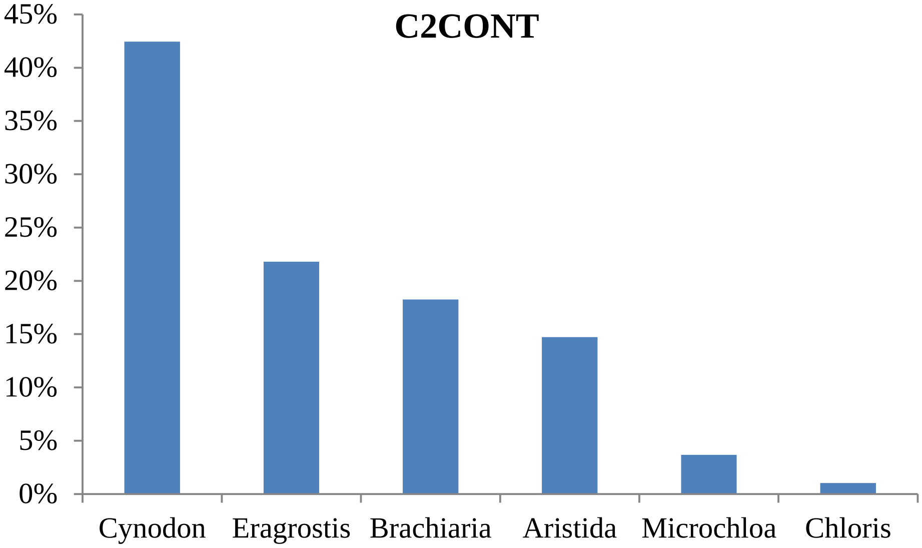
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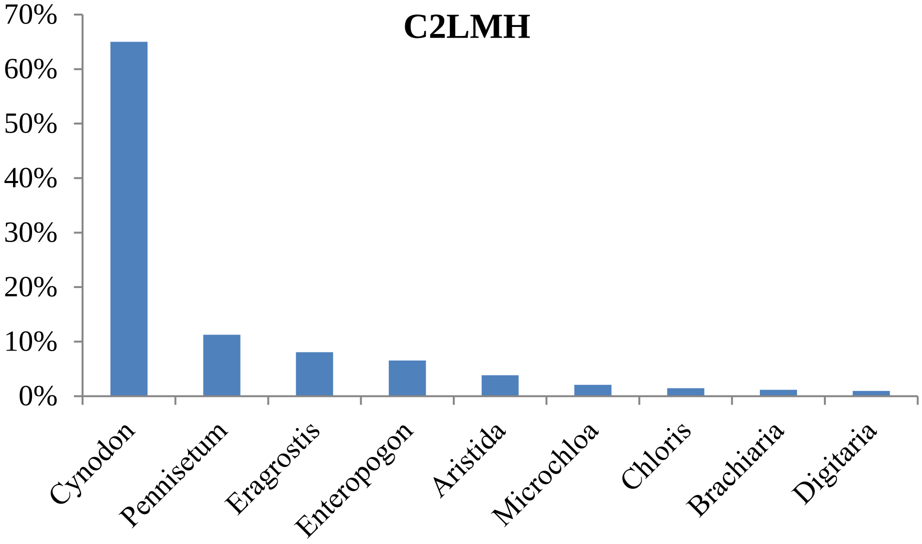
Chloris

J)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Microchloa
Chloris
Brachiaria
Digitaria

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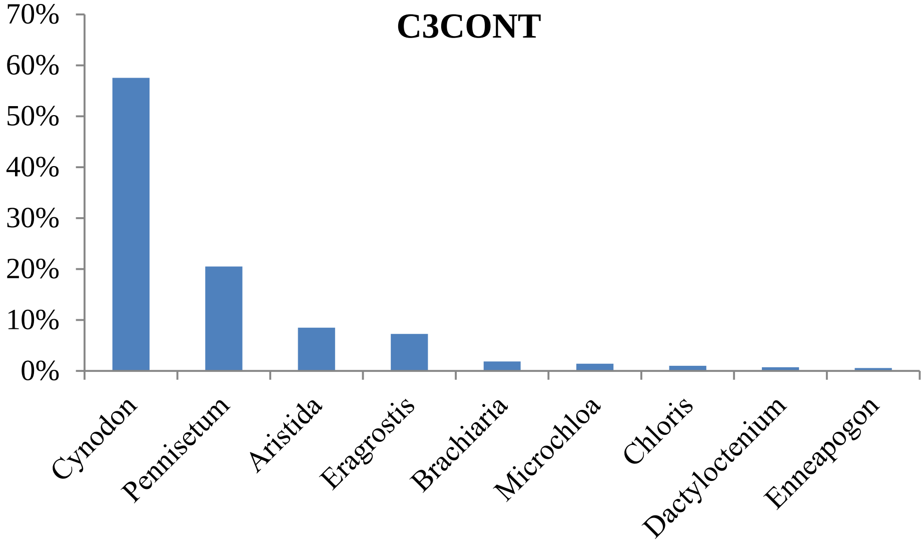

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Eragrostis
Brachiaria
Microchloa
Chloris
Dactyloctenium
Enneapogon

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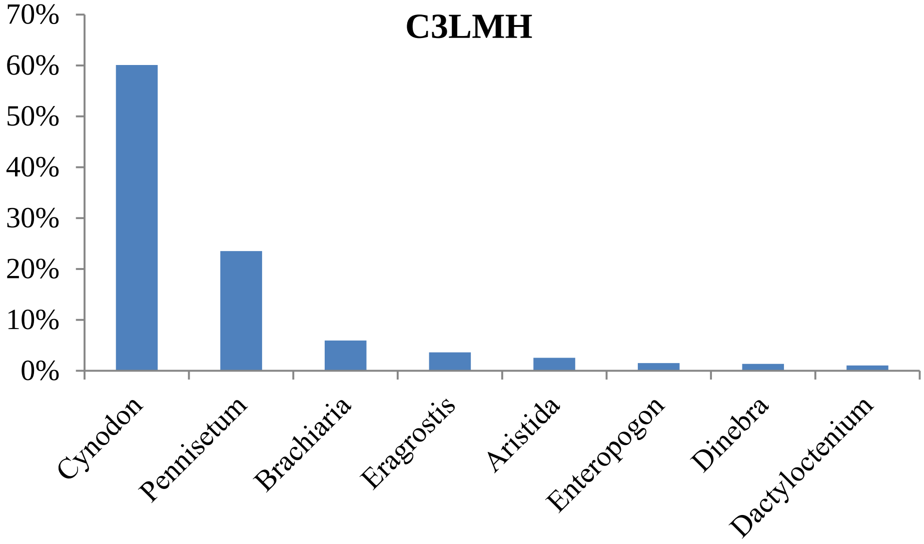

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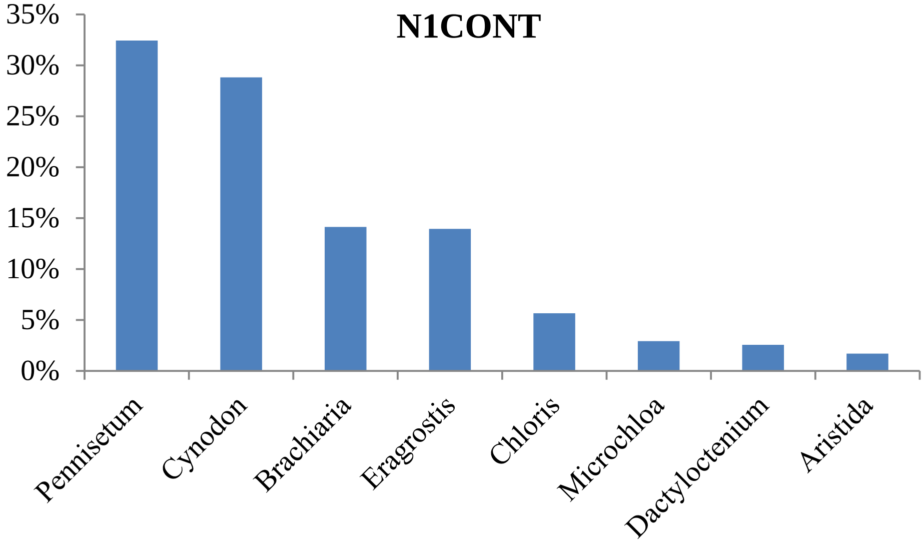
Aristida
Enteropogon
Dinebra
Dactyloctenium

M)



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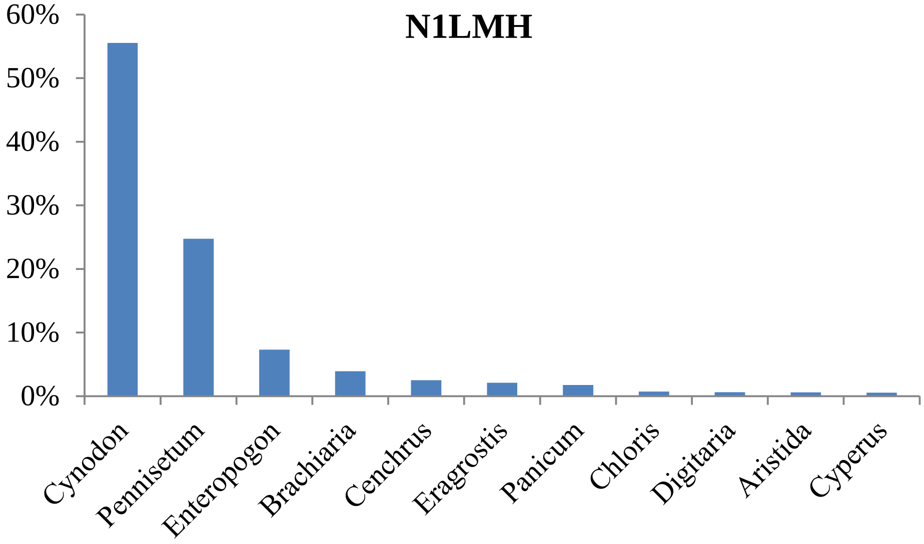
Chloris
Microchloa
Dactyloctenium
Aristida

N)



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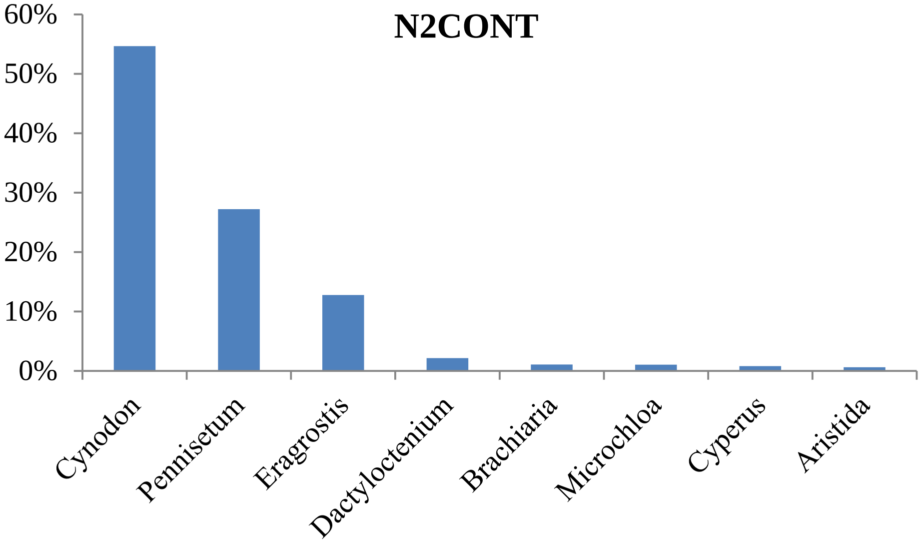
Eragrostis
Panicum
Chloris
Digitaria
Aristida
Cyperus

O)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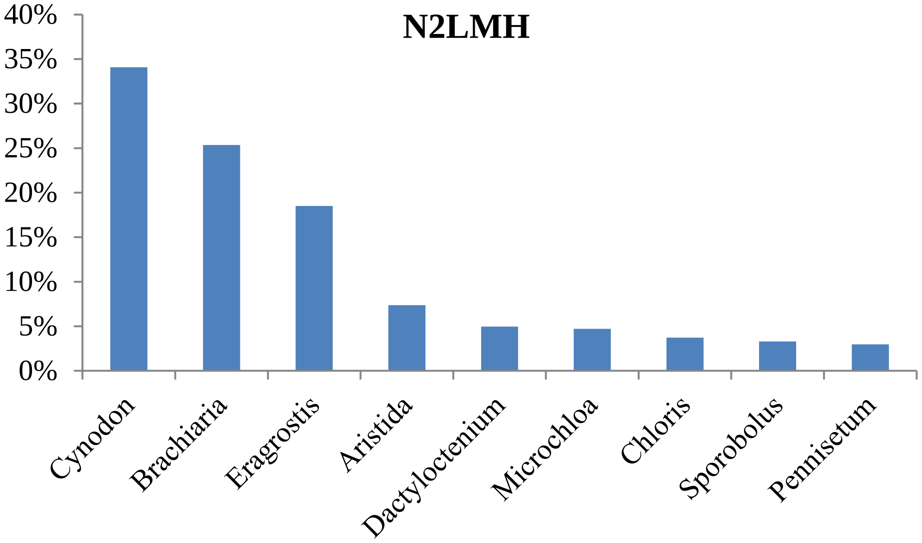
Brachiaria
Microchloa
Cyperus
Aristida

P)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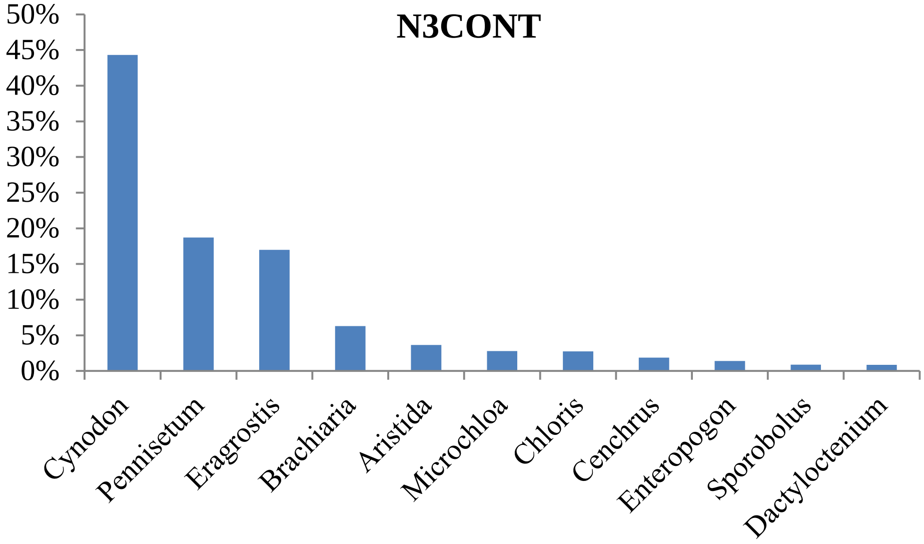
Aristida
Dactyloctenium
Microchloa
Chloris
Sporobolus
Pennisetum

Q)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Aristida
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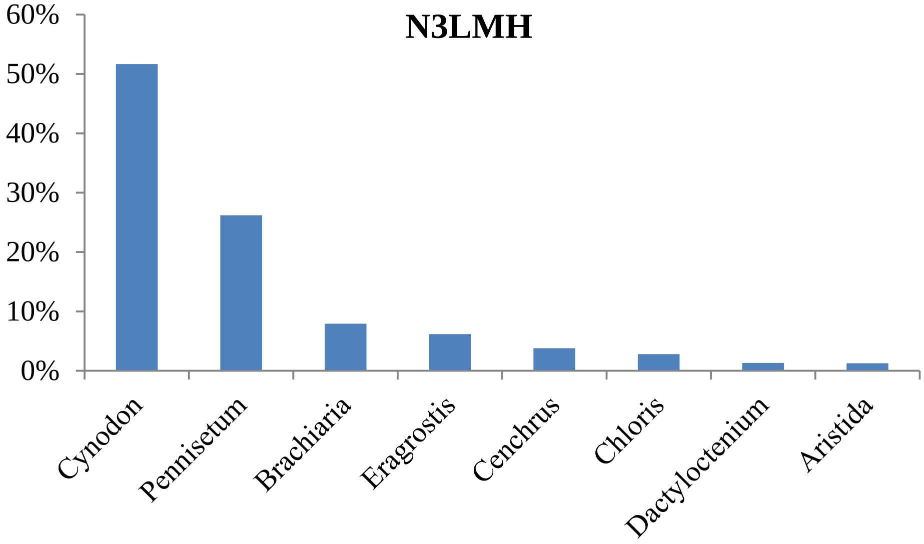
Chloris
Cenchrus
Enteropogon
Sporobolus
Dactyloctenium

R)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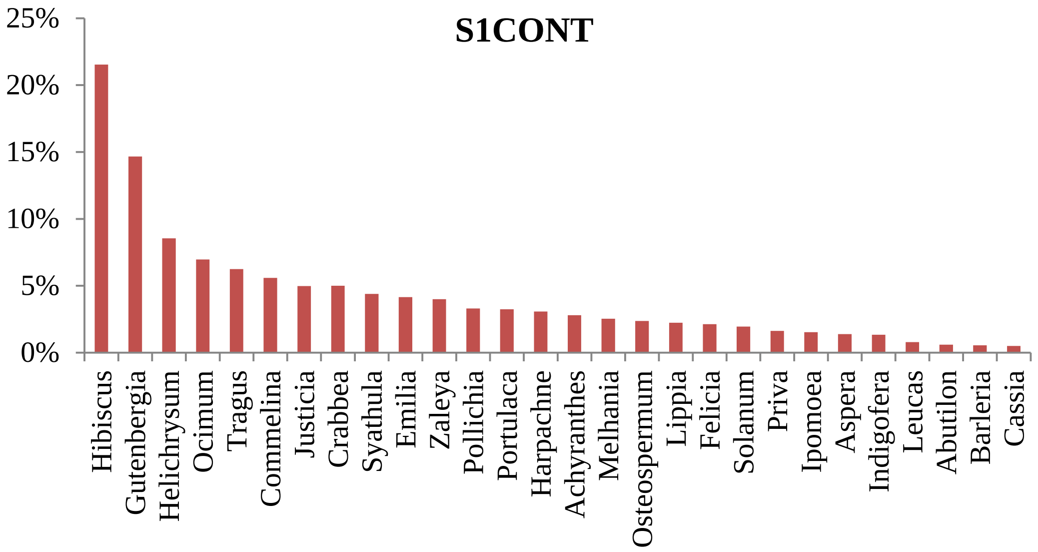
Brachiaria
Eragrostis
Cenchrus
Chloris
Dactyloctenium
Aristida

Appendix B: Supplementary Figure 2. Percent of biomass comprised of each genus of C_3 plant, averaged across understory surveys 2009 – 2013 by plot. Mesic south (A-F), intermediate central (G-L) and arid north (M-R).

A)



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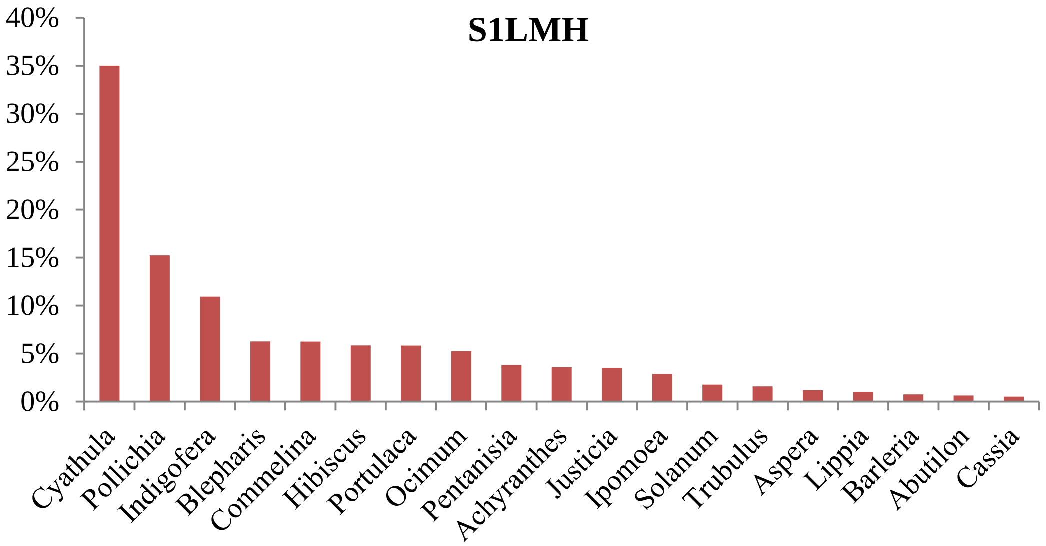

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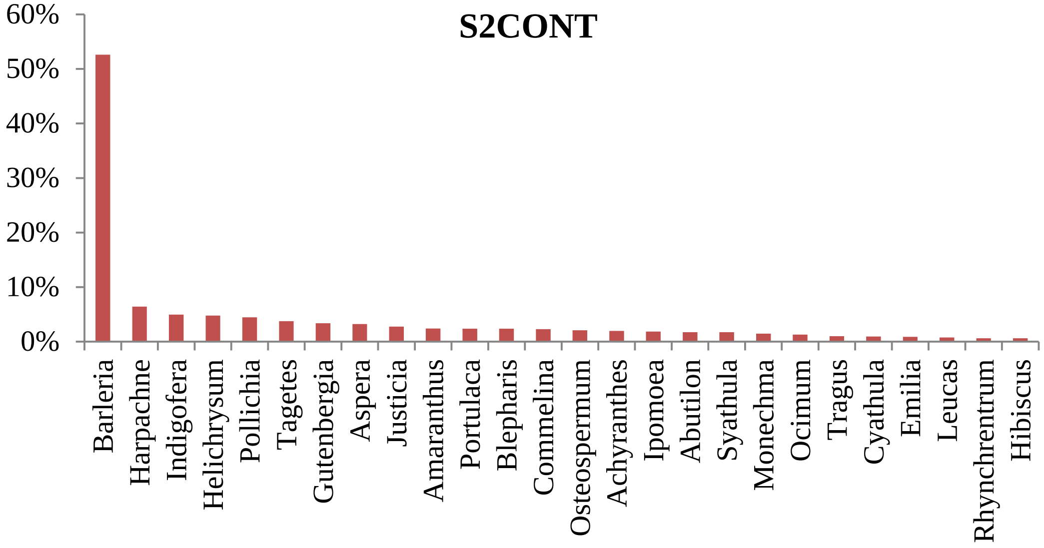
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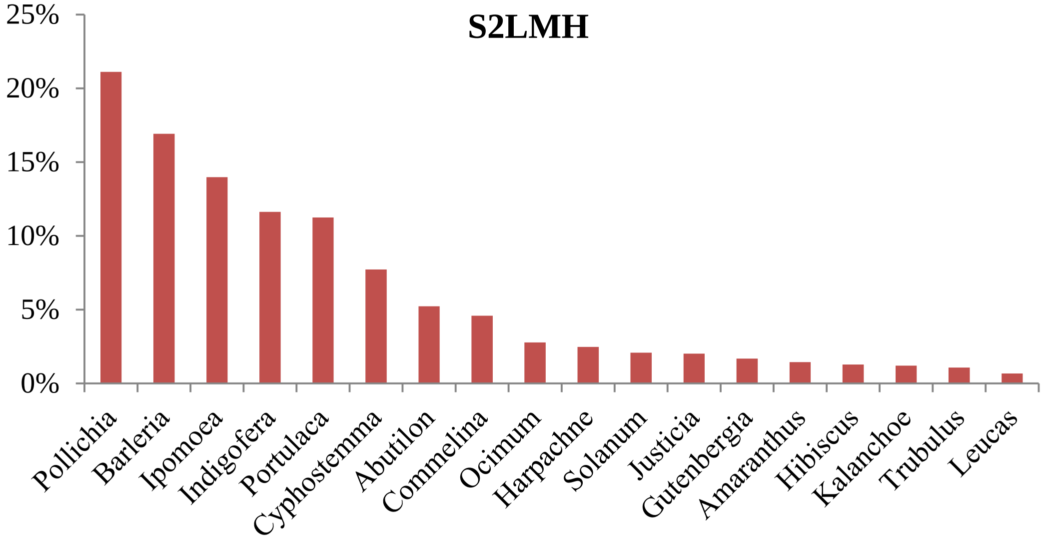
Indigofera
Helichrysum
Pollichia
Tagetes
Gutenbergia
Aspera
Justicia
Amaranthus
Portulaca
Blepharis
Commelina
Osteospermum
Achyranthes
Ipomoea
Abutilon
Syathula
Monechma
Ocimum
Tragus
Cyathula
Emilia
Leucas
Rhynchrentrum
Hibiscus

D)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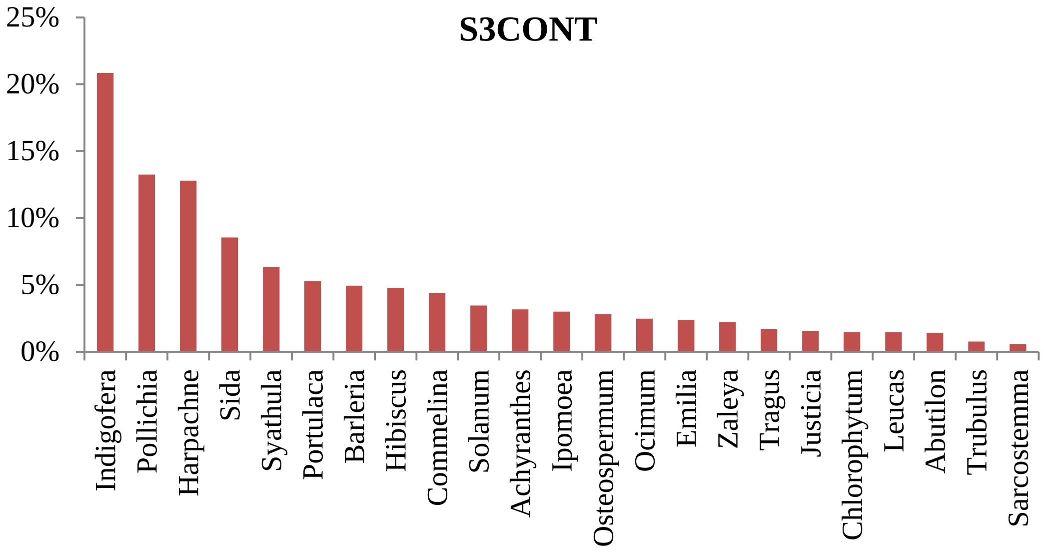
Ipomoea
Indigofera
Portulaca
Cyphostemma
Abutilon
Commelina
Ocimum
Harpachne
Solanum
Justicia
Gutenbergia
Amaranthus
Hibiscus
Kalanchoe
Trubulus
Leucas

E)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Hibiscus
Commelina
Solanum
Achyranthes
Ipomoea
Osteospermum
Ocimum
Emilia
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Tragus
Justicia
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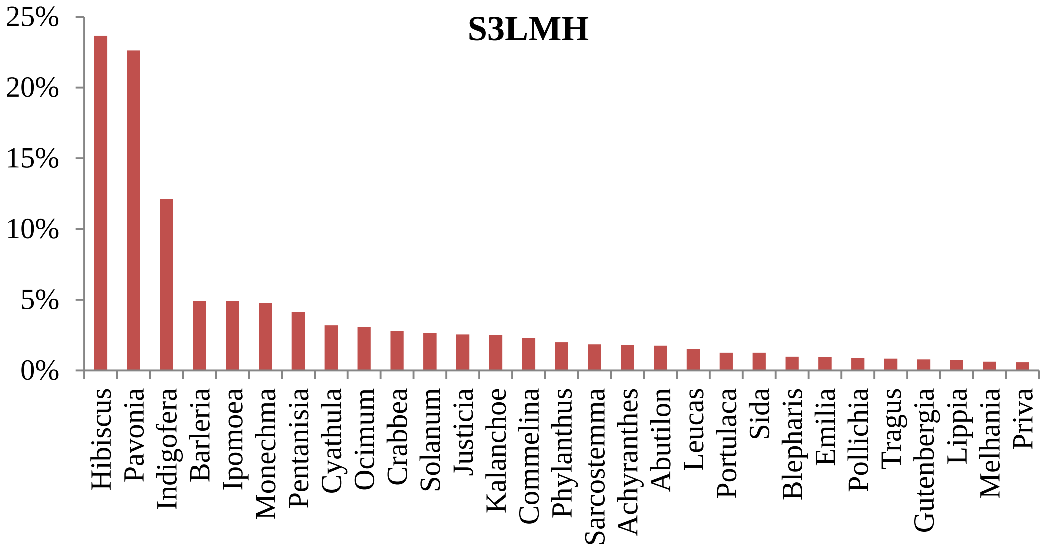
Abutilon
Trubulus
Sarcostemma

F)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Solanum
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Sarcostemma
Achyranthes
Abutilon
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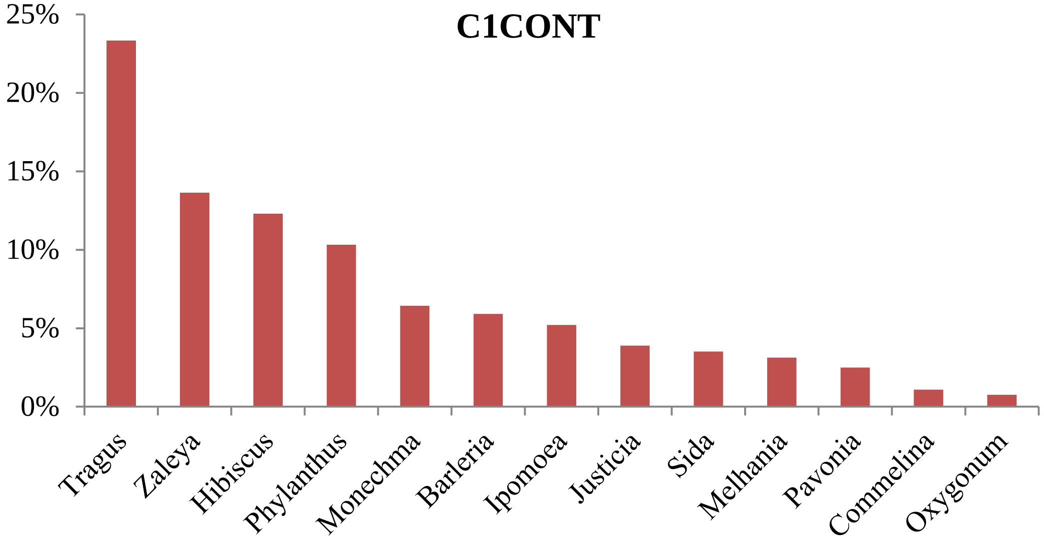
Emilia
Pollichia
Tragus
Gutenbergia
Lippia
Melhania
Priva

G)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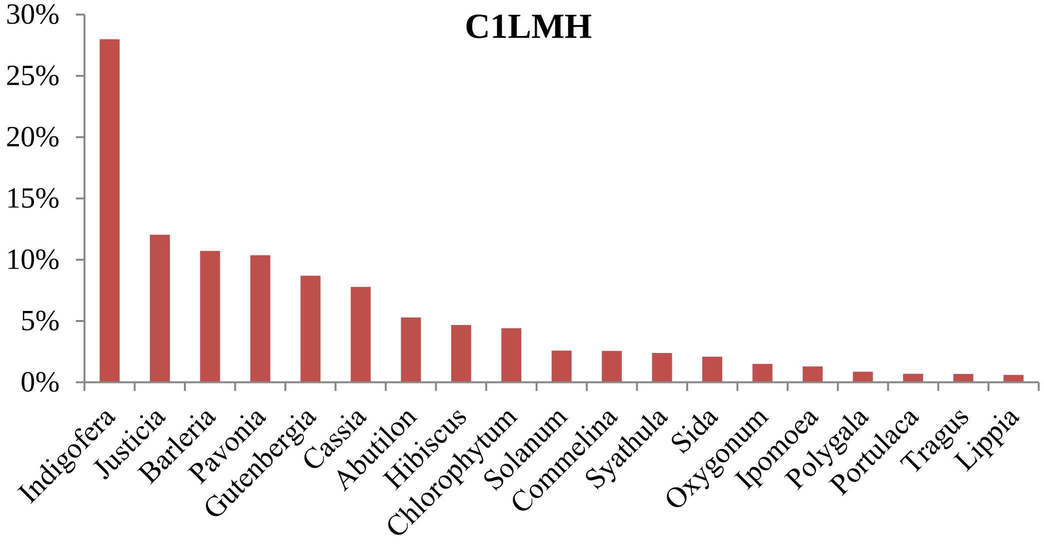
Justicia
Sida
Melhania
Pavonia
Commelina
Oxygonum

H)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Abutilon
Hibiscus
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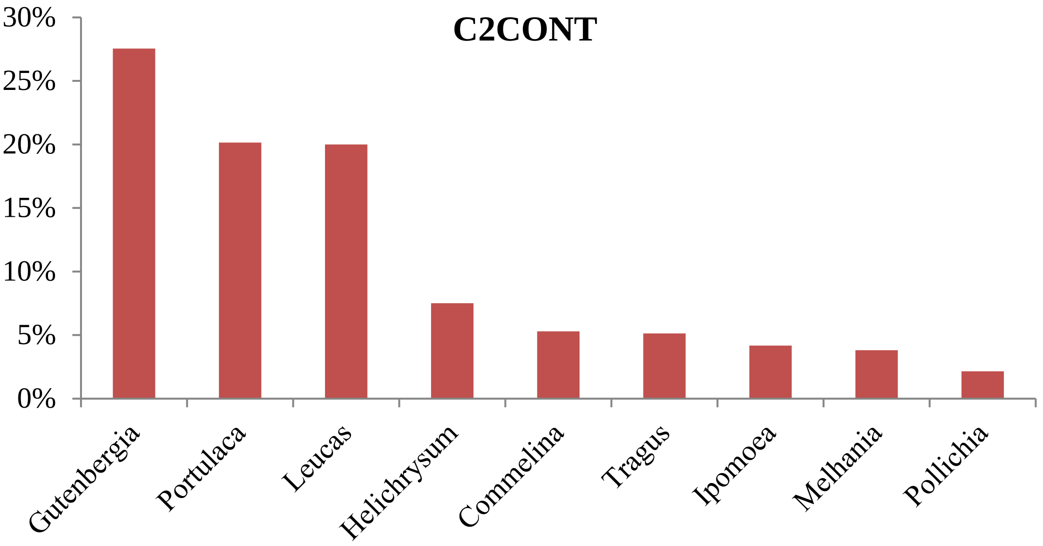
Commelina
Syathula
Sida
Oxygonum
Ipomoea
Polygala
Portulaca
Tragus
Lippia

I)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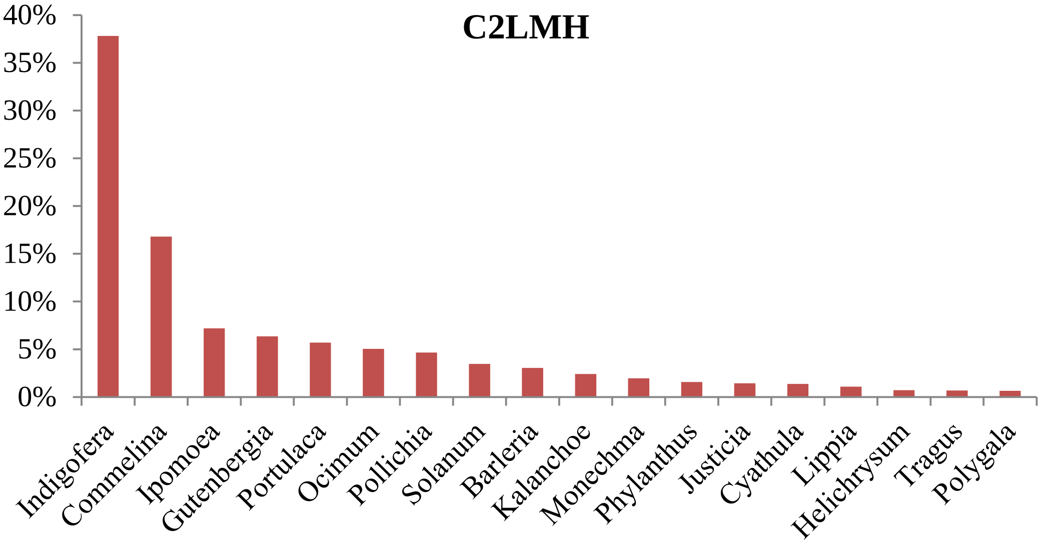
Ipomoea
Melhania
Pollichia

J)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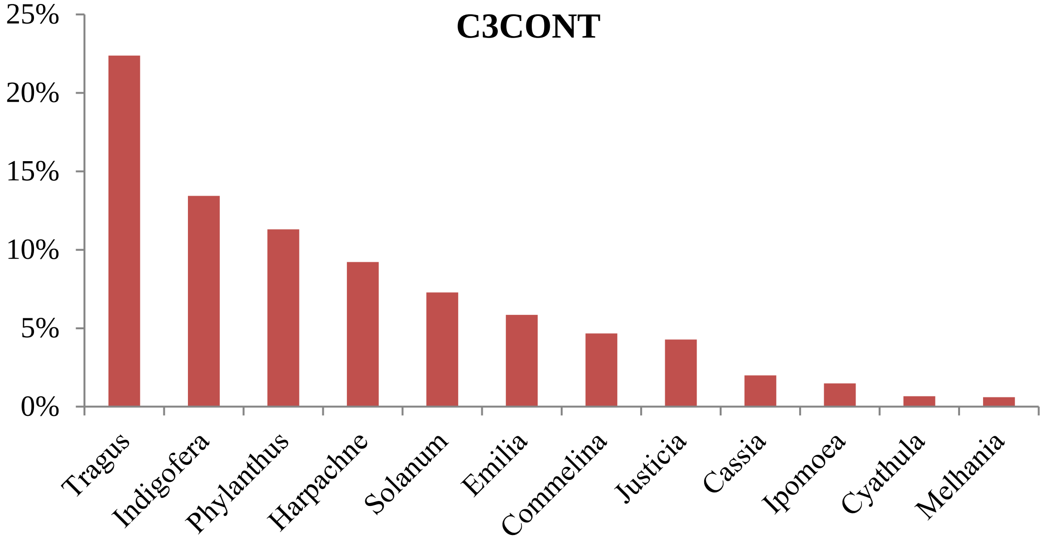
Tragus
Polygala

K)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Cassia
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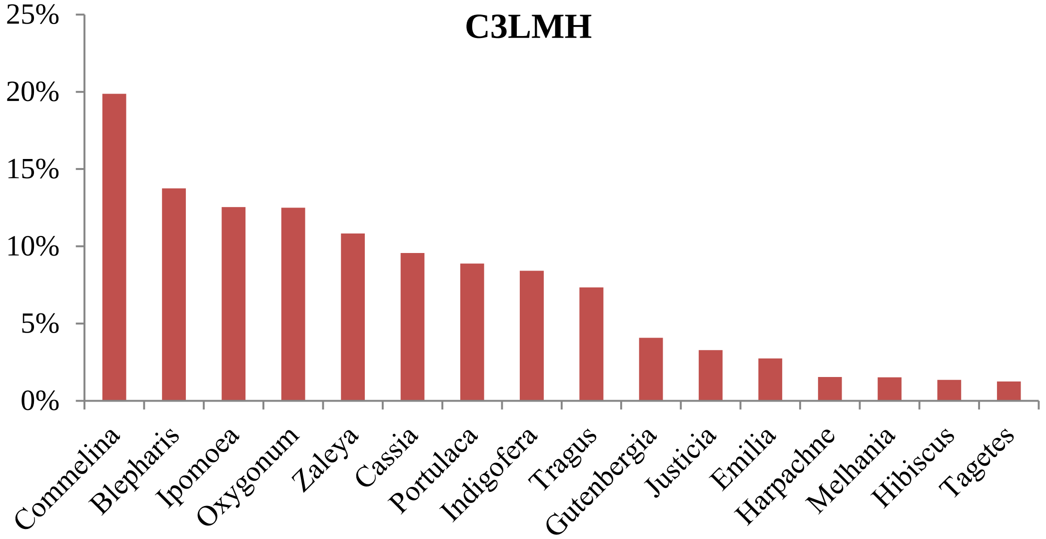
Melhania

L)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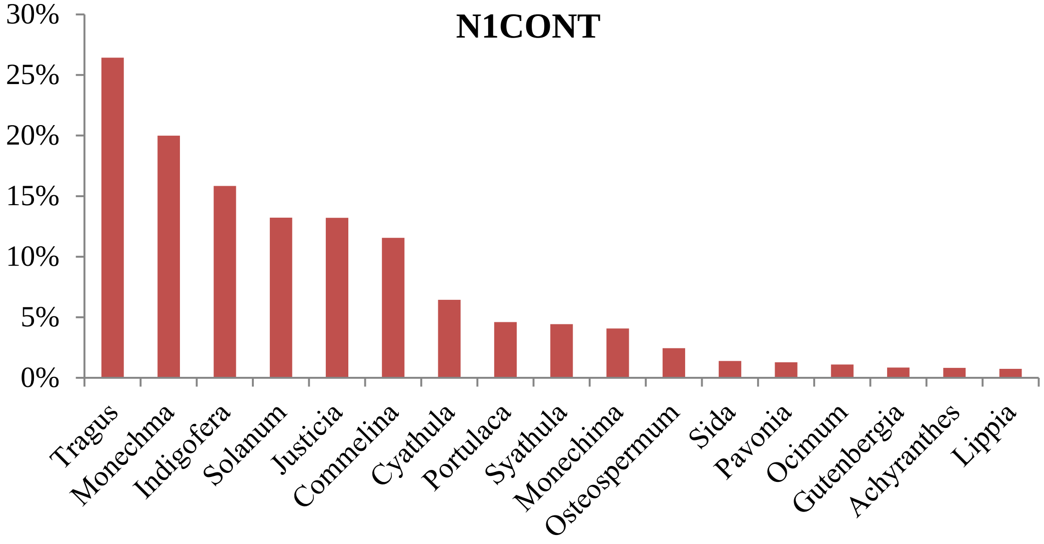
Melhania
Hibiscus
Tagetes

M)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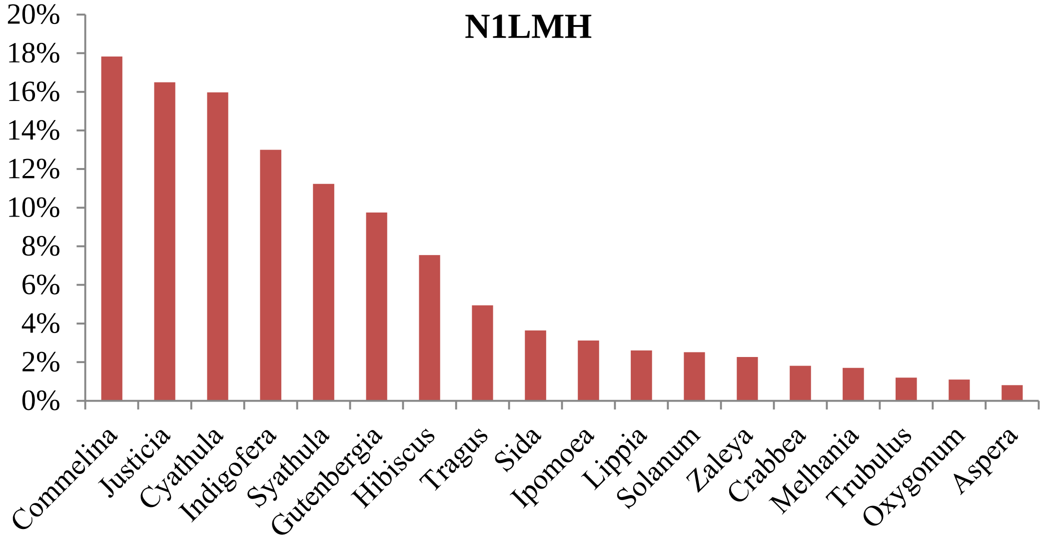
Achyranthes
Lippia

N)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Hibiscus
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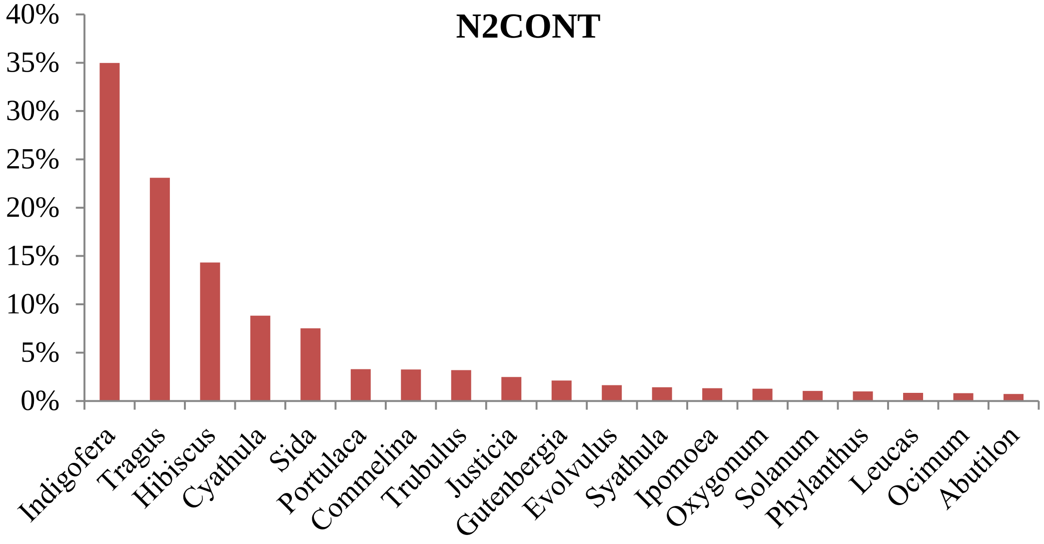
Lippia
Solanum
Zaleya
Crabbea
Melhania
Trubulus
Oxygonum
Aspera

O)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Solanum
Phylanthus
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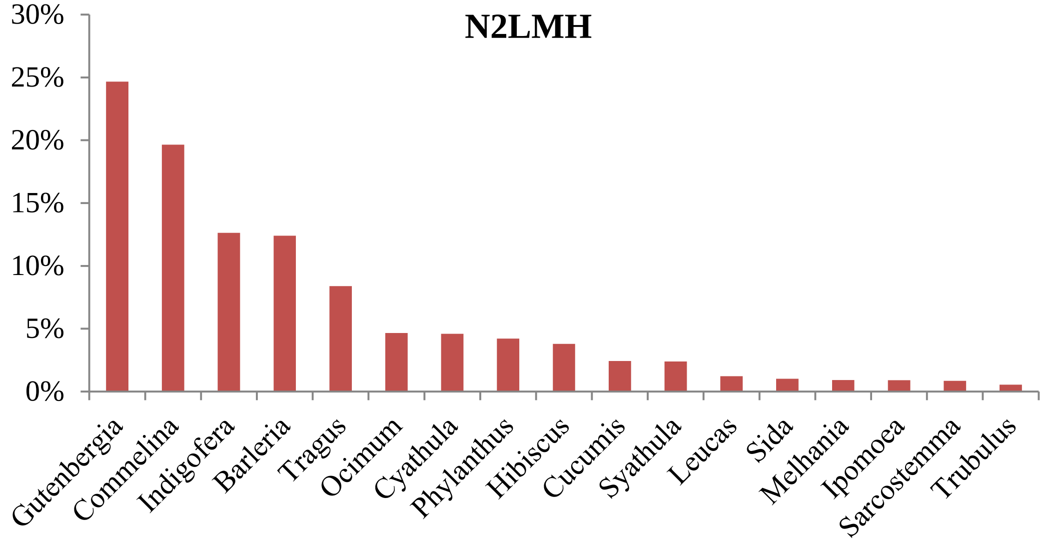
Ocimum
Abutilon

P)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Ocimum
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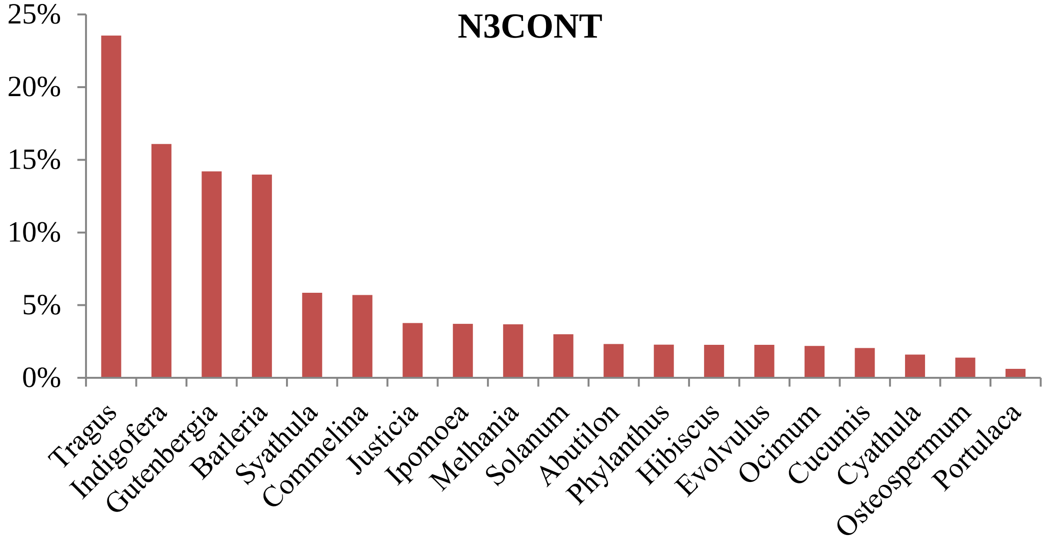
Leucas
Sida
Melhania
Ipomoea
Sarcostemma
Trubulus

Q)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Ocimum
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Osteospermum
Portulaca

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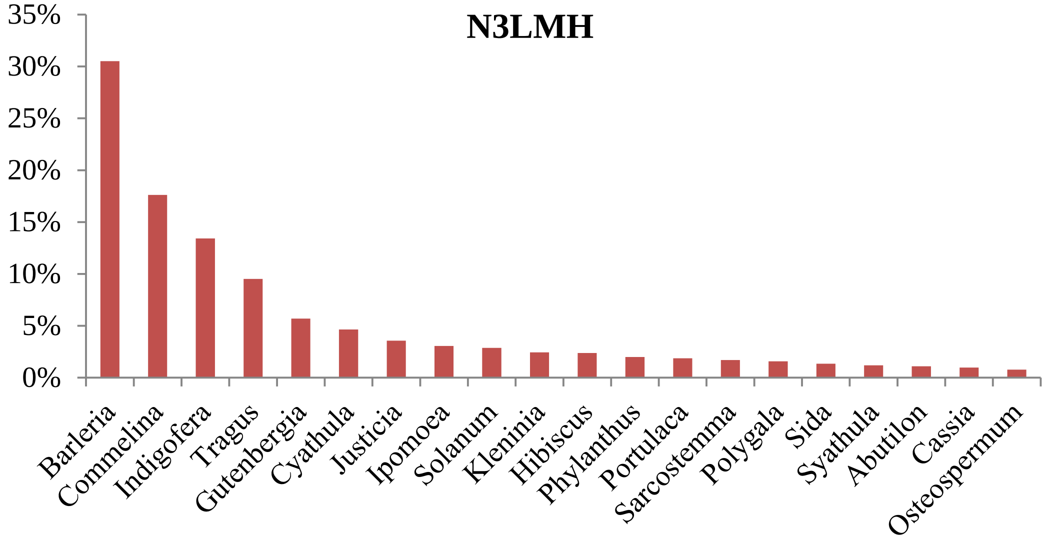
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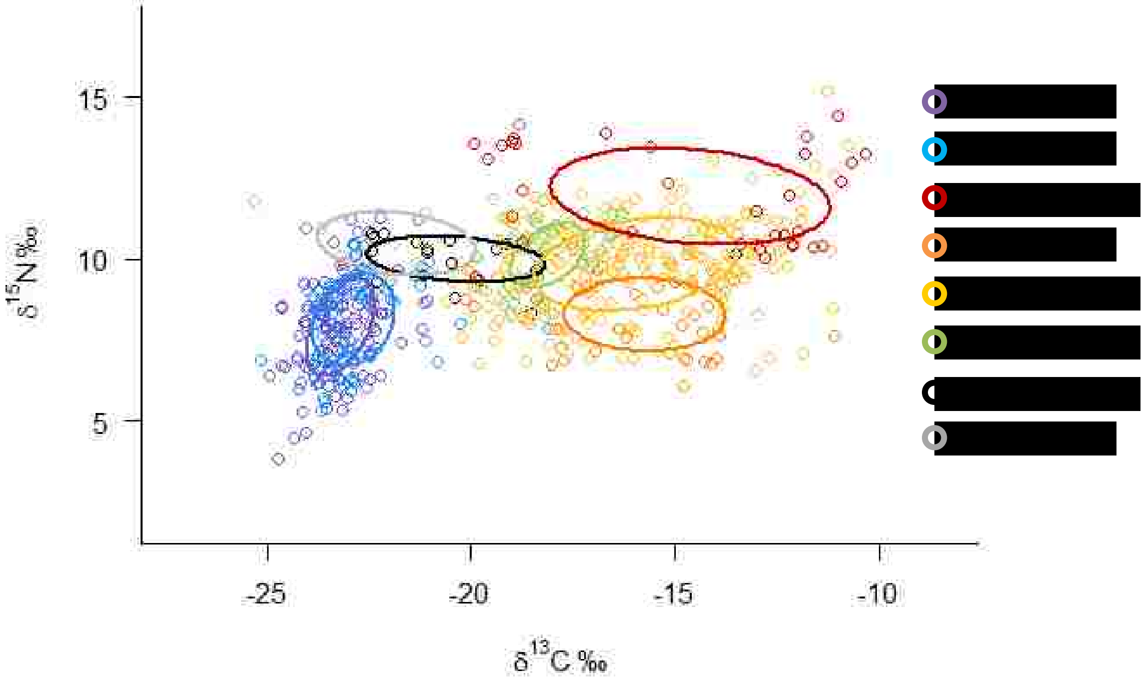
Solanum
Kleninia
Hibiscus
Phylanthus
Portulaca
Sarcostemma
Polygala
Sida
Syathula
Abutilon
Cassia
Osteospermum

Appendix C: Supplementary Figure 3. SEA for each small mammal species. Ellipses encircle 40% of the data points for each species.



Appendix D: Supplementary Table 1. Carbon and nitrogen isotope data and sample size for the most prevalent plant species across south (mesic), central (intermediate) and north (arid) plots.

	South			**Central**			**North**		
	Mean δ^{13}C	**Mean δ^{15}N**	**n**	**Mean δ^{13}C**	**Mean δ^{15}N**	**n**	**Mean δ^{13}C**	**Mean δ^{15}N**	**n**
Acacia brevispica	-27.2 ± 1.1	8.6 ± 1.3	5	-26.8 ± 0.5	7.1 ± 1.4	5	-29.7 ± 0.5	7.1 ± 2.4	5
Acacia etbaica	-26.0 ± 0.8	7.3 ± 4.8	5	-26.9 ± 0.8	9.0 ± 2.0	5	-26.8 ± 1.2	6.2 ± 0.7	5
Acacia mellifera	-26.6 ± 1.2	6.0 ± 0.8	5	-24.7 ± 0.8	6.2 ± 2.0	5	-26.8 ± 1.4	5.6 ± 2.1	5
Aristida congesta	-14.3 ± 0.7	5.1 ± 1.0	6	-14.1 ± 0.4	3.3 ± 0.07	5	NA	NA	NA
Aristida kenyensis	-13.7 ± 0.5	3.7 ± 0.6	5	-14.2 ± 0.9	3.6 ± 1.9	5	-14.0 ± 0.6	5.4 ± 4.1	5
Brachiaria leersoides	-12.6 ± 0.5	11.9 ± 1.8	5	-14.7 ± 0.4	5.8 ± 1.5	5	-14.1 ± 0.3	7.4 ± 1.3	5
Commelina africana	-26.6 ± 0.3	7.7 ± 0.8	5	-26.1 ± 0.7	8.7 ± 1.0	5	-28.0 ± 0.6	7.7 ± 1.6	5
Cyathula orthocantha	-27.9 ± 0.7	6.8 ± 0.5	6	-24.9 ± 0.3	5.8 ± 0.3	5	-27.9 ± 0.7	7.1 ± 1.3	5
Cymbopogon commutatus	-12.6 ± 0.5	2.4 ± 0.8	5	-13.5 ± 0.2	3.7 ± 0.7	6	NA	NA	NA
Cynodon dactylon	-12.9 ± 0.3	2.8 ± 0.4	5	-13.6 ± 0.6	4.8 ± 0.5	5	-12.9 ± 0.3	4.8 ± 0.9	5
Cynodon plectostachyus	-14.3 ± 0.7	7.2 ± 1.4	5	-14.3 ± 1.0	5.9 ± 1.0	5	-13.9 ± 0.6	4.0 ± 0.7	5
Enteropogon macrostachyus	-16.4 ± 0.6	2.8 ± 0.8	5	-16.5 ± 0.5	3.6 ± 1.7	5	-15.2 ± 0.7	4.0 ± 0.6	5
Eragrostis tenuifolia	-15.1 ± 0.3	4.9 ± 1.7	5	-15.1 ± 0.4	4.7 ± 0.9	6	-15.4 ± 0.4	4.5 ± 0.7	6
Gutenbergia cordifolia	-29.6 ± 1.0	4.4 ± 1.5	5	-25.2 ± 1.3	5.0 ± 1.6	5	-26.7 ± 0.8	6.4 ± 1.6	5
Indigofera brevicalyx	-27.6 ± 0.6	0.9 ± 0.3	5	-27.4 ± 1.0	3.8 ± 1.8	5	-27.4 ± 0.4	5.8 ± 0.8	5
Microchloa kunthii	-13.5 ± 0.2	4.7 ± 0.7	3	-13.6 ± 0.4	4.0 ± 0.5	5	-13.4 ± 0.2	4.7 ± 1.1	5
Pennisetum mezianum	-13.0 ± 0.5	6.7 ± 1.8	6	-13.9 ± 0.4	4.9 ± 0.4	5	-12.7 ± 0.6	6.4 ± 2.3	7
Pennisetum stramineum	-13.5 ± 0.4	7.0 ± 0.4	5	-13.6 ± 0.6	3.7 ± 1.3	5	-12.6 ± 0.3	4.8 ± 0.7	5
Plectranthus montanus	-17.3 ± 0.3	5.3 ± 2.2	5	-18.6 ± 0.9	6.5 ± 2.5	5	-23.6 ± 2.5	5.0 ± 1.5	5
Pollichia campestris	-23.6 ± 5.3	7.2 ± 2.6	5	-28.4 ± 0.3	5.1 ± 0.3	5	-28.2 ± 0.6	6.6 ± 0.8	5
Solanum incanum	-26.2 ± 1.2	7.7 ± 4.1	7	-25.6 ± 0.7	7.1 ± 0.9	5	-28.6 ± 1.0	7.5 ± 1.5	8
Themeda triandra	-12.9 ± 0.8	4.0 ± 1.1	5	-13.0 ± 0.5	3.0 ± 1.1	8	-12.5 ± 0.4	3.5 ± 0.8	5

Appendix E: Supplementary Table 2. Summary of carbon and nitrogen stable isotope data and sample size for main arthropod orders across south (mesic), central (intermediate) and north (arid) plots.

Level	Order	Mean $\delta^{13}C$	Mean $\delta^{15}N$	n
South	**Araneae**	-19.5 ± 3.1	8.7 ± 2.2	5
	Coleoptera	-22.9 ± 3.2	7.7 ± 1.1	5
	Diptera	-23.8 ± 1.5	6.3 ± 2.5	5
	Hemiptera	-18.6 ± 7.5	7.4 ± 2.7	5
	Hymenoptera	-22.0 ± 2.8	9.6 ± 5.3	5
	Lepidoptera	-20.3 ± 8.3	6.6 ± 2.4	5
	Orthoptera	-22.7 ± 5.2	7.1 ± 2.7	5
	All South	-21.4 ± 5.0	7.6 ± 2.9	35
Central	**Araneae**	-17.9 ± 2.1	11.2 ± 1.3	3
	Coleoptera	-24.5 ± 3.2	6.3 ± 3.7	5
	Diptera	-24.4 ± 1.2	10.0 ± 2.4	5
	Hemiptera	-21.3 ± 5.3	8.9 ± 2.7	5
	Hymenoptera	-20.4 ± 0.8	7.9 ± 2.5	5
	Lepidoptera	-24.4 ± 1.5	10.4 ± 1.0	5
	Orthoptera	-15.1 ± 3.8	8.4 ± 1.5	7
	All Central	-21.0 ± 4.6	8.8 ± 2.6	35
North	**Araneae**	-18.7 ± 2.3	10.8 ± 2.0	5
	Coleoptera	-17.8 ± 2.9	10.1 ± 1.9	4
	Diptera	-19.0 ± 2.8	10.1 ± 1.7	5
	Hemiptera	-25.1 ± 1.3	5.9 ± 1.4	5
	Hymenoptera	-20.1 ± 3.5	9.3 ± 1.9	5
	Lepidoptera	-18.4 ± 5.9	5.4 ± 1.6	5
	Orthoptera	-22.1 ± 4.8	6.3 ± 2.2	6
	All North	-20.3 ± 4.2	8.2 ± 2.7	35
All Levels	**All Orders**	-20.9 ± 4.6	8.2 ± 2.8	105