

Ecosystem-scale impacts of non-timber forest product harvesting: effects on soil nutrients

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Summary

1. The harvesting of non-timber forest products (NTFPs) is a global phenomenon, the sustainability of which has been studied for many species at the individual and population level. However, the broader scale impacts of NTFP harvesting have been acknowledged but rarely examined.

2. We assessed plant size and the soil attributes undercanopy and in the open, in replicate, paired harvested and non-harvested sites for three NTFPs differing in the extent of biomass removed, i.e. timber for firewood from a tree (*Acacia karroo*), fruits from a cactus (*Opunita ficus-indica*) and flowering culms from a grass (*Cymbopogon marginatus*). Soil variables tested included pH, resistivity, P, total N, nitrate nitrogen, ammonium nitrogen, K, Na, Ca and Mg. 3. The extent of loss of soil nutrients decreased across the three NTFPs relative to the proportion of biomass removed. Thus, significant differences in more soil variables were evident for the firewood species, least for the fruit species and intermediate for the grass species. Lower soil pH, P, C and K were evident in soils collected underneath *A. karroo*, while losses in cations of Na, Ca and Mg were reported in soils underneath *C. marginatus*, and only NO₃N losses were recorded underneath *O. ficus-indica*.

4. Synthesis and applications. Our study reveals that while non-timber forest product (NTFP) harvesting may affect soil nutrients, this is not uniform between species and is likely to be a function of the extent of biomass removed and harvesting frequency. This indicates the need for caution in generalisations about the ecosystem-level impacts of NTFP harvesting as well as a concerted effort to better understand impacts at a greater range of scales than has been the case to date.

Key-words: biomass, cations, nitrogen, non-timber forest product, phosphorus, plant size, seasonality, South Africa

Introduction

Non-timber forest products (NTFPs) include an amazing array of species and biological products that are harvested from natural, partially and wholly transformed landscapes for a range of uses by local communities (Belcher 2003; Shackleton *et al.* 2011). Common uses are for household consumption, cash saving, income generation, buffering in times of household shock and for cultural purposes (Shackleton 2015). Use of NTFPs is both geographically widespread and intense in terms of the frequency of use and amounts harvested. There is also growing evidence that NTFP use is not restricted to developing nations (although it might be more widespread and intense in such settings) nor to rural communities. For example, use of NTFPs by urban communities has been reported in both developing (Kaoma & Shackleton 2015; Schlesinger, Drescher & Shackleton 2015) and developed countries (Hurley *et al.* 2008; McLain *et al.* 2014).

Two core debates germane to the use and management of NTFPs relate firstly to the potential of NTFPs to alleviate poverty and secondly the extent to which they can be sustainably harvested. Whether use of NTFPs can alleviate poverty has been the subject of multiple studies internationally over the last decade or so (e.g. Babulo *et al.* 2009; Kar & Jacobson 2012; Angelsen *et al.* 2014). There is perhaps an evolving perspective that use of NTFPs can alleviate poverty for some in specific settings, but for most they play a more poverty easing role (Shackleton *et al.* 2008; Angelsen *et al.* 2014). Irrespective, this debate has revealed the tremendous value attached to NTFPs, in consumptive, monetary and cultural terms, which in turn, has served to illustrate the real or potential

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value lost, in monetary terms or to livelihoods, when they are degraded or lost. Such reductions or loss may be the result of heavy use of the NTFPs by local communities, traders, a variety of other drivers (such as fire, alien invasive species, herbivory or pests), land transformation or synergies between any combinations of these (McGraw & Furedi 2005; Mandle & Ticktin 2012; Ticktin 2015). Consequently, the valuation of NTFPs has contributed to debates and advocacy for sustainable land and resource use, thereby linking into the second debate on the sustainable use of NTFPs.

Determination of the conditions that foster ecological sustainability during the use of NTFPs has not received as much attention as the debates about their poverty alleviation potential, even though ecological sustainability is a core tenet if any degree of poverty alleviation were to be achieved (Ticktin 2004). This is partially a result of the vast diversity of NTFP species, products, uses and settings which mean that only a small proportion have been examined in detail (Ticktin & Shackleton 2011). Moreover, realistic framings of sustainability require exploration along temporal and spatial scales that very few studies can afford or sustain (Ticktin 2004, 2015). Consequently, modelling temporal and spatial variations in the ecological conditions in which the NTFP species occur, as well as variabilities in harvest patterns is important in understanding ecological sustainability (Gaoue, Horvitz & Ticktin 2011; Groenendijk et al. 2012; van Andel et al. 2015). Spatially, the effects of harvest or other drivers on NTFPs abundance and viability should, ideally, be examined from the genetic level, through population and species levels, to community and landscape levels (and even country and international scales for highly traded NTFPs). Regards examining the effects of NTFP harvesting on genetic diversity, results have been mixed with some studies showing that harvesting can have a negative impact on the genetic diversity and structure of harvested populations (Cruse-Sanders, Hamrick & Ahumada 2005), while other studies have shown that harvesting has no effect on genetic diversity and structure (Gaoue et al. 2014). With respect to NTFP examination at landscape levels, this has rarely been achieved, and the majority of studies focus on the population or species levels (Ticktin 2004, 2015; Stanley, Voeks & Short 2012). The same restriction characterises the temporal scale of examinations, with most studies limited to single determinations, with a few spanning a few seasons, and a handful incorporating long-term monitoring of harvesting impacts beyond 5-6 years (Stanley, Voeks & Short 2012), usually at a single spatial scale as already observed. This means that many studies will not have been able to gather empirical data covering the wide range of single or interactive factors that drive fluctuations in many NTFP populations, such as fires, pests, droughts, alien species, land use change or herbivory, which may interact with the effects of harvesting, increasing the uncertainty underlying modelling projections or management guidelines. These shortfalls are of concern given the value of NTFPs to user households and local and more distant markets, and increasing commercialisation in many regions (Campbell *et al.* 2002; Ticktin 2004; Cunningham 2011).

The many relatively short-term studies at the population or species levels reveal an assortment of sustainability determinations, reflecting the wide range in contexts, species and parts used, harvesting frequencies, seasons and intensity, and interactions with other land use activities. Some of the broad characteristics of the settings and species and parts that contribute to a higher probability of sustainable use have been summarised and help in initial considerations for a new setting or product (e.g. Ticktin & Shackleton 2011; Ticktin 2015). Stanley, Voeks & Short (2012) systematically reviewed 101 published studies and concluded that almost two-thirds, on the basis of the information provided, were likely to be ecologically sustainable, although nearly all were short-term assessments at only the population level, and the degree of variance in the main response variables between studies was high, limiting the study's conclusions. Matrix modelling is increasingly used as a useful tool to extrapolate such studies over longer time frames (e.g. Ticktin et al. 2012; Vallejo et al. 2014). In a meta-analysis of matrix model use in 46 NTFP studies, Schmidt et al. (2011) concluded that leaf and fruit harvest of some plants (e.g. palms) and bark harvest of some trees (e.g. Garcinia lucida) is sustainable; however, whole-plant harvest of many herbs (e.g. Echinacea angustifolia) is potentially unsustainable.

Empirical studies and knowledge of the impacts and sustainability of NTFP harvesting at other scales is limited (Stanley, Voeks & Short 2012) and understudied (Ticktin 2015). At the ecosystem level, only the oft-cited study of Witkowski & Lamont (1996) has considered the export of soil nutrients during NTFP harvesting. They reported that a 29% harvest of Banksia hookeriana flowers over a 9-year period resulted in an approximately 30% reduction of N and P in the plant tissues and small, albeit significant, reductions in soil organic C, NH₄, NO₃, Mg and Ca in nutrient-poor, sandy soils in southwest Australia. How applicable their findings and recommendations are to other NTFPs and to other settings remains unknown, and thus requires a suit of empirical studies to help address this lack of understanding. Siebert (2001) quantified potential nutrient exports associated with harvesting of rattans in Sulawesi (Indonesia) and espoused that it was unlikely to affect soil nutrients. The meta-analysis of Johnson & Curtis (2001) for forest tree harvesting concluded that impacts on topsoil carbon and nitrogen stocks were generally not significant, but did differ between coniferous and hardwood species and how much of the tree biomass was removed. It is likely that the extent of nutrient losses attributable to NTFP harvesting will be a function of (i) the intensity of harvesting, (ii) the contribution of the NTFP species to the above- and below-ground biomass, (iii) the existing nutrient pools in biomass and the soil and (iv) the rate of nutrient

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replenishment from weathering, fixation and wet and dry deposition. To this end this paper reports on a study of which the objective was to determine the effects of harvesting of NTFPs on soil nutrient pools by contrasting harvested and unharvested populations. Three different NTFPs were selected to provide a range in biomass removed through harvesting, namely culms of a grass (*Cymbopogon marginatus* (Steud) Stapf ex Burtt Davy), the fruits of a cactus (*Opuntia ficus-indica* (L.) Miller) and firewood from a tree species (*Acacia karroo* Hayne).

Materials and methods

STUDY NTFP SPECIES

The three species were selected to contrast relative biomass removed during the harvesting process and thus cover a greater range of possible effects and harvesting regimes (Table 1).

Acacia karroo Hayne (Fabaceae) is a widespread native tree (3–15 m tall). The tree has a variety of uses that include food (gum is eaten by children and herders as a confection), fodder (foliage, flowers and green pods are important browse for livestock), apiculture, firewood (it burns brightly, with little smoke and no odour), timber, tannin and traditional medicines (Barnes, Filer & Milton 1996). It is a favoured firewood species throughout much of its range.

Opuntia ficus-indica (Cactaceae) is commonly a multi-stemmed tree cactus (up to 5 m tall). The species is native to Mexico, but has been present in semi-arid regions of South Africa for over two centuries (Zimmermann & Moran 1991). Once considered a noxious invasive, it is now naturalised and invasions have been severely limited by biological control agents. The plant is comprised of large spinescent cladodes (20–30 cm long). The apical cladodes produce several spiny, egg-sized fruits in mid- to late summer (December–March), which are collected directly from the plant and consumed by the household or sold locally (Shackleton, Kirby & Gambiza 2011; Wotshela & Beinert 2011).

Cymbopogon marginatus (Poaceae) is a perennial, densely tufted, clump-forming grass, the culms of which can grow to more than 2 m tall. The stems are cane-like and the narrow-bladed leaves are approximately 1 m long. It grows on all types of soils, but prefers heavy soils where it dominates. The grass is rarely grazed by herbviores, except immediately after a fire. The culms are widely used for thatching of roofs in rural villages.

STUDY SITES

To contrast harvested with non-harvested sites, we identified two protected areas that share boundaries with villages that are harvesting NTFPs. Fieldwork for *A. karroo* and *C. marginatus* was conducted adjacent to the protected Ngcizele forest and the neighbouring Qhora village (32°25.6′S; 28°39.6′E), whereas that of *O. ficus-indica* was conducted in the Great Fish River Nature Reserve and the adjacent Nomtayi village (32°56.6′S; 26°49.1′E) (Fig. 1). Both Ngcizele forest and Great Fish River Nature Reserve have been protected for decades by what is now the Eastern Cape Parks and Tourism Agency who restrict entrance. The Ngcizele forest is not fenced but has forest guards who patrol the area. The Great Fish River Nature Reserve is fenced as it houses large herbivores, such as rhinoceros, zebra and buffalo. The harvested sites have been subjected to harvesting for at least four decades.

The vegetation in the Ngcizele forest is Scarp Forest (Mucina & Rutherford 2006) with a well-developed canopy and understorey layers, but a poorly developed herb layer. Dominant tree species include Buxus macowanii, Harpephyllum caffrum, A. karroo, Drypetes gerrardii and Englerophytum natalense. The forest patch is surrounded by grasslands dominated by Aristida junciformis subsp. galpinii, Stenotaphrum secundatum, Ehrharta erecta and C. marginatus. The vegetation in the adjacent Qhora village is more open with a mosaic of grasslands (dominated by the same species) on rolling hills with small patches of forest in the valleys (e.g. Ngcizele forest). The grasslands in the protected area and around the village are burnt regularly, and are also grazed by livestock, although to a lesser extent in the forest reserve. The soils are generally sandy and clay loams and derived from the Karoo Supergroup, consisting of mudstones of the Adelaide Subgroup and shales, mudstones and sandstones of the Ecca Group (Mucina & Rutherford 2006). The mean annual rainfall is approximately 800-1000 mm per year, falling mostly in summer (October-April), although winter rainfall is common. Mean temperature ranges from 27 °C in summer to 3 °C in winter (Mucina & Rutherford 2006).

The sampled area of the Great Fish River Nature Reserve is classified as Southern Mistbelt Forest, dominated by a layer of trees, a dense shrub layer and a well-developed herb layer (Mucina & Rutherford 2006). Dominant tree species include *Afrocarpus falcatus, Celtis africana, Calodendrum capense* and *Zanthoxylum davyi.* The soils are generally deep and loamy, developed from weathered dolerite intrusions or mudstones,

Table 1. Characteristics of the three non-timber forest	products (NTFP) sp	becies and the nature of the l	harvesting regimen
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	NTFP species		
Attribute of NTFP species and harvest system	Acacia karroo	Opuntia ficus-indica	Cymbopgon marginatus
Life form	Tree	Cactus	Grass
Part harvested	Branches or whole tree	Fruits	Dried flower culms
Use	Firewood	Direct consumption	Thatching for roofs
Continuous or seasonal harvest	Continuous	Seasonal (mid-summer)	Seasonal (late summer/autumn)
Relative proportion of the individual plant biomass typically removed	Variable (low to very high)	Low	Medium
Nutrient richness of biomass removed	Medium	High	Low
Relative proportion of the community biomass removed	High	Low	Medium

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Fig. 1. The location of the study sites (indicated in asterisk) in the Eastern Cape province of South Africa.

shales and sandstones of the Karoo Supergroup (Mucina & Rutherford 2006). Vegetation in the adjacent Nomtayi village is classified as Bhisho Thornveld (Mucina & Rutherford 2006). It is characterised by open savanna that is dominated by *A. karroo* and *Acacia natalitia* and short-to-medium grasses, notably *Themeda triandra* (Mucina & Rutherford 2006). Fire is uncommon in this area. The mean annual rainfall is approximately 750 mm, concentrated in summer (October–April) although some winter rainfall occurs. Mean temperatures range from 28 °C in summer to 3 °C in winter (Mucina & Rutherford 2006).

FIELD METHODS

Two focus group discussions (FGDs) per village were held with five harvesters from each village. Members of the focus groups helped with the identification of selected harvested sites. The FGDs considered the harvesting sites, harvesting techniques, seasons and benefits.

For each species, three paired (harvested and unharvested) sites were identified. Harvested and unharvested areas were approximately 2.5 km apart, whereas the distance between individual sites within each harvesting treatment was approximately 1 km apart. At each site, five individual plants, approximately 10 m apart, were selected for sampling. The height of each plant was estimated using a height rod and diameter at breast (for tree species only) was measured using callipers. The number of *C. marginatus* inflorescences was counted per plant.

To ascertain that changes in soil properties are a result of NTFP harvesting rather than other drivers like fire or nearby plants, soil sampling was conducted at two different sampling positions (underneath the plants and on adjacent open areas) within each harvest treatment. Underneath the plant canopy, soil samples were collected midway between the stem and the edge of the crown. Adjacent to the plants, soil samples were collected on

open areas between the plants. The location of soil samples underneath or adjacent open areas is hereafter referred to as the sampling position. A total of 60 soil samples were collected for each plant species [(5 samples underneath plant + 5 samples from open areas) \times 3 harvested \times 3 unharvested sites]. Sixty samples were deemed a sufficient balance between the financial costs of analysis and the expected variation in the measured variables. We did not expect marked differences in soil physico-chemical status with either an increase in soil samples or a repeat in measurements since soil sampling within each site was close (trees were approximately 10 m apart), thereby ensuring that the sampled trees were in a similar environmental space (e.g. water, sunlight and temperature availability) except plant harvesting. Soils were collected at a depth of 10 cm and diameter of 10 cm using a soil corer, after first removing overlaying debris. Debris removal was meant to reduce soil nutrient biases that are likely to be caused by litter, as well as standardise soil collecting since some soils were collected on open areas where there is little or no litter.

LABORATORY METHODS

After collection, the soils were sieved using a 2-mm sieve to remove stones and plant debris before being assessed for soil pH, soil resistivity, P, total nutrient concentrations of N and C, available N in the form of NO₃N and NH₄N as well as exchangeable cations (K, Na, Ca and Mg). Soil pH was measured in 1 : 5 soil-KCl extract (Rhoades 1982). Soil resistivity was measured using a resistivity meter. Soil phosphorus was analysed using a Bray II extract method as described by Bray & Krutz (1945). Total nitrogen was determined by complete combustion using a Eurovector Euro EA Elemental Analyser, while nitrate and ammonium were determined using an auto analyser. Total carbon was determined using a modified Walkley–Black method (Chan, Bowman & Oates 2001). Cations were extracted in a 1 : 10 ammonium acetate solution using the centrifuge procedure (Thomas 1982), filtered and analysed by atomic absorption spectrometry (SP428, LECO Corporation, St. Joseph, MI, USA).

DATA ANALYSIS

Data for all measured plant parameters (height, diameter and inflorescence count) and soil properties were normally distributed following testing via a Kolmogorov–Smirnov test and Levene's test for homogeneity of variances. To compare differences in plant morphology (plant height, diameter and inflorescence counts) between harvested and unharvested sites (harvesting treatments), data were analysed using a *t*-test.

To determine the effect of harvesting on all measured soil properties, we used the mixed-design analysis of variance (splitplot ANOVA) in R (R Development Core Team, 2015) using the library *MASS*. Use of the split-plot ANOVA was because the experimental design was a mixed-design with two independent groups, namely harvesting treatment and sampling position. The split-plot ANOVA allowed comparisons between harvesting treatment (harvested and unharvested sites) and sampling positions (under plants and open areas) being nested in harvesting treatments to be conducted.

Results

EFFECTS OF A. KARROO HARVESTING ON SOILS

Both height and diameter of *A. karroo* trees were significantly (P < 0.01) greater in unharvested compared to harvested sites (Table 1). The average tree height and diameter in unharvested sites were 2.70 ± 0.14 m and 49.1 ± 2.41 cm compared to 2.08 ± 0.12 m and 37.5 ± 2.40 cm in harvested sites (Table 2). The FGDs revealed that harvesting for firewood occurs throughout the year. Most is harvested for domestic use, but some people do harvest to sell firewood. Harvesting is relatively frequent, using an axe, because there is no electricity in the village and thus firewood is the primary energy source.

With regard to harvesting treatment, soil pH, resistivity, P, total C and K were significantly (P < 0.05) higher in unharvested compared to harvested sites (Table 3). Contrary, Na, Ca and Mg were substantially (P < 0.01) lower in the unharvested sites compared to the harvested ones (Table 3). Nitrogen (total, NO₃N and NH₄N) showed no

significant (P > 0.05) differences between harvesting treatments (Figs 2 and 3).

When sampling was nested in harvest treatments, soil pH, total N, total C, K, Na and Ca were significantly (P < 0.001) higher in soils underneath the trees compared to soils from open areas. Only resistivity was significantly (P < 0.001) higher in soil from open areas compared to soils from underneath the trees (Table 3). NH₄N showed no significant (P > 0.05) differences between sampling positions, whereas NO₃N was significantly (P < 0.01) higher in open areas (7.20 ± 1.26) than underneath the trees (2.86 ± 0.63).

EFFECTS OF O. FICUS-INDICA HARVESTING ON SOILS

The FGDs revealed that harvesting of *O. ficus-indica* fruits is done in summer (December–March) when the fruits are ripe. Harvesters remove the fruits using a wire rod and remove the spines before consuming or selling the fruits. The height and diameter of the sampled *O. ficus-indica* trees was significantly (P < 0.05) higher in harvested (1.74 ± 0.13 m and 53.2 ± 3.15 cm respectively) than unharvested (1.26 ± 0.16 m and 35.0 ± 2.32 cm respectively) sites (Table 2).

Almost all measured soil properties showed no significant (P > 0.05) differences between harvesting treatments, other than NO₃N and P (Table 3). The former was 30% higher in unharvested than harvested sites (13.71 ± 1.31 and 9.69 ± 1.60 respectively), while P was the opposite, being higher in harvested (50.83 ± 7.47) than unharvested (12.63 ± 1.28) sites (Table 3).

Similarly, when sampling positions were nested in harvest treatments, significant (P < 0.05) differences were only measured in NO₃N and Na (Table 3). Open sites (14.33 ± 1.76) had higher levels of NO₃N than undercanopy sites (9.07 ± 0.99). The opposite applied for Na with mean amounts 40.56 ± 2.37 underneath *O. ficusindica* and 28.06 ± 1.68 in open areas (Fig. 2).

EFFECTS OF C. MARGINATUS HARVESTING ON SOILS

Harvesting of *C. marginatus* culms for thatching occurs in autumn (March-May) after the culms have shed seed and

Table 2. Plant height, plant diameter and inflorescence count of three non-timber forest products from harvested and unharvested sites. Data are means \pm SE and *t*-test results are shown

				Statistics	
Species	Measure	Harvested	Unharvested	t	Р
Acacia karroo	Plant height (m)	2.08 ± 0.12	2.70 ± 0.14	3.33	0.002
	Plant diameter (cm)	37.47 ± 2.40	49.07 ± 2.41	3.41	0.002
Opuntia ficus-indica	Plant height (m)	1.74 ± 0.13	1.26 ± 0.16	2.30	0.030
X V	Plant diameter (cm)	53.20 ± 3.15	35.00 ± 2.32	4.56	0.001
Cymbopogon marginatus	Height (m)	0.87 ± 0.07	2.39 ± 0.15	9.26	0.001
	Inflorescence count	3.40 ± 0.64	$15{\cdot}27\pm1{\cdot}08$	9.46	0.001

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positions nested in harve	st treatments are	shown. All units are r	ng kg ⁻¹ other than _F	H and resistivity (oh	ums). Significant diffe	rent results hig	hlighted ir	bold			0
		Harvest treatments		Sampling positions		ANOVA - tr	eatment		ANOVA – sa nested in harv	npling pc est treatn	sitions tents
Species	Soil measure	Harvested sites	Unharvested sites	Under plants	Open areas	MS	$F_{(1 : 56)}$	<i>P</i> -values	MS	$F_{(2}:56)$	P-values
Acacia karroo	Soil pH	4.8 ± 0.03	4.9 ± 0.04	4.9 ± 0.04	4.7 ± 0.02	0.14	4.94	0.03	0.42	14.96	<0.001
	Soil resistivity	908.3 ± 25.2	1052.7 ± 34.7	897.7 ± 21.9	1063.3 ± 35.3	312 482	15.44	<0.001	23 3748	11.55	<0.001
	P Bray II	2.9 ± 0.1	4.1 ± 0.3	3.7 ± 0.3	3.3 ± 0.2	22.82	12.71	<0.001	2.82	1.57	0.22
	Total N	1246.7 ± 40.0	1266.7 ± 31.9	1346.7 ± 33.8	1166.7 ± 30.5	6000	0.19	0.66	270 000	8.68	<0.001
	Total C	$32\ 703.3\pm1221.4$	$35 \ 753.3 \pm 924.4$	$36\ 126.7 \pm 1137.9$	$32 \ 330.0 \pm 981.5$	139 537 500	4.36	0.04	124 024 167	3.87	0.03
	K	166.4 ± 6.4	238.6 ± 16.0	234.6 ± 16.9	170.5 ± 5.8	78 203	39.17	<0.001	73 993	37.06	<0.001
	Na	150.7 ± 4.3	125.4 ± 6.3	146.6 ± 6.3	129.5 ± 5.0	9660	14.03	<0.001	6081	8.83	<0.001
	Ca	1487.9 ± 47.7	1343.9 ± 49.0	1567.4 ± 47.7	1264.3 ± 34.3	31 1040	6.48	0.01	689 117	14.35	<0.001
	Mg	777.8 ± 24.7	632.1 ± 17.4	715.7 ± 24.6	694.2 ± 25.9	31 8340	22.58	<0.001	3484	0.25	0.78
Opuntia ficus-indica	Soil pH	5.1 ± 0.1	4.9 ± 0.1	4.9 ± 0.1	5.1 ± 0.1	0.40	1.04	0.31	0.14	0.36	0.70
	Soil resistivity	1064.3 ± 82.3	1210.3 ± 65.6	1103.3 ± 78.5	1171.3 ± 72.1	31 9740	1.99	0.06	320 843	2.00	0.15
	P Bray II	50.8 ± 7.5	12.6 ± 1.3	34.6 ± 7.1	29.0 ± 5.6	21 889	24.83	<0.001	305	0.35	0.71
	Total N	913.3 ± 27.4	910.0 ± 25.1	930.3 ± 25.0	893.3 ± 27.1	167	0.01	0.93	10 833	0.51	0.60
	Total C	$20\ 763.3 \pm 1118.3$	$19\ 613.3\ \pm\ 793.2$	$20\ 910.0\pm974.0$	$19\ 466.7\ \pm\ 950.0$	19 837 500	0.70	0.41	25 890 833	0.92	0.41
	К	432.6 ± 48.7	340.7 ± 25.3	380.6 ± 50.7	392.7 ± 24.1	12 6643	2.72	0.11	2967	0.06	0.94
	Na	32.8 ± 2.3	35.8 ± 2.4	40.6 ± 2.4	$28 \cdot 1 \pm 1 \cdot 7$	134.1	1.05	0.31	1203.4	9.43	<0.001
	Ca	1128.4 ± 82.4	993.4 ± 61.0	1111.8 ± 78.0	1010.0 ± 67.5	273 375	1.71	0.20	115 390	0.73	0.49
	Mg	233.0 ± 22.2	188.6 ± 10.5	223.2 ± 22.5	198.4 ± 11.0	29 464	3.21	0.08	6419	0.70	0.50
Cymbopogon marginatus	Soil pH	4.4 ± 0.03	4.7 ± 0.04	4.5 ± 0.05	4.5 ± 0.04	1.23	34.04	<0.001	0.03	0.78	0.46
	Soil Resistivity	1310.7 ± 50.2	1394.7 ± 63.0	1409.3 ± 52.5	1296.0 ± 60.3	105840	1.16	0.29	266 587	2.92	0.06
	P Bray II	3.13 ± 0.4	4.2 ± 0.5	3.4 ± 0.3	4.0 ± 1.6	18.15	3.12	0.08	2.42	0.42	0.66
	Total N	1043.3 ± 49.9	1086.7 ± 27.0	1083.3 ± 37.5	1046.7 ± 42.8	28 167	0.57	0.45	14 167	0.29	0.75
	Total C	$31 \ 020.0 \pm 1739.3$	$28 \ 616.7 \pm 1219.9$	$29\ 813.3 \pm 1512.2$	$29\ 823.3 \pm 1525.3$	86 640 167	1.25	0.27	19 441 500	0.28	0.76
	K	155.8 ± 25.1	161.0 ± 9.4	165.9 ± 16.7	150.8 ± 20.8	408	0.04	0.84	18 409	1.76	0.18
	Na	93.9 ± 2.9	106.9 ± 6.9	88.9 ± 4.2	111.9 ± 5.7	2518	5.24	0.03	11 172	23.23	<0.001
	Ca	582.4 ± 36.3	1001.8 ± 36.0	$779 \cdot 1 \pm 44 \cdot 6$	805.1 ± 60.3	2 638 445	65.70	<0.001	12 366	0.31	0.74
	Mg	354.1 ± 23.2	550.8 ± 17.0	416.5 ± 18.1	$488\cdot4~\pm~32\cdot8$	580 245	56.13	<0.001	69 749	6.75	0.002

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Fig. 2. Soil NO₃N results of three non-timber forest products (a) *Acacia karroo*, (b) *Opuntia ficus-indica* and (c) *Cymbopogon marginatus* from harvested and unharvested sites. Bars are means \pm SE and ANOVA with harvest treatments and sampling positions nested in harvest treatments are shown.

dried, but before the grasslands are too dry and burnt. Harvesters cut the entire crop of flowering culms per plant (at about 30 cm above-ground level) and then discard on site those that are too short along with any leaves or leaf tips that were cut with the culms. Harvesting reduced the height and number of culms per plant (Table 2). Mean height of plants in the unharvested site was $2 \cdot 39 \pm 1 \cdot 05$ m, while in the harvested site it was 0.87 ± 0.07 m. Corresponding figures for the number of flowering culms per plant were $15 \cdot 3 \pm 1 \cdot 08$ and $3 \cdot 4 \pm 0.64$ respectively.

The soils at the unharvested sites were significantly (P < 0.05) higher in pH and the cations of Na, Ca and Mg than the harvested site (Table 3). However, NH₄N was the opposite, being significantly (P < 0.001) higher in the harvested site (Fig. 2).

When sampling position was nested in harvesting treatment, there were relatively few differences between under grass 'canopy' and in the open, other than for NH₄N (Fig. 3), Na and Mg (Table 3) which were significantly (P < 0.05) higher in the open than under the grass.

Discussion

The impacts of harvesting on plant size were readily observable on all three NTFP species. Plants were smaller in the harvested sites than their corresponding protected sites for A. karroo and C. marginatus. The opposite applied for O. ficus-indica, but we interpret that to be a consequence of active strategies to clear it in the protected site because it is regarded as an invasive alien species. Large, mature O. ficus-indica trees are more visible and are therefore more easily targeted for removal, meaning that the population in the protected site is dominated by smaller individuals. A reduction in plant stature is a common response to frequent loss of above-ground biomass through processes such as herbivory (Pfab & Witkowski 1999; Kettenring, Weekely & Menges 2009), fire (Grady & Hoffmann 2012), harvesting by humans (Botha, Witkowski & Shackleton 2003; Ghimire et al. 2008) or some combination of such pressures. This is a result of either genetic selection for smaller individuals under such pressures or because larger individuals are removed first and there is limited opportunity or time for their replacement.

If the stature of plants in the population is diminished, then it is probable that soil nutrient stocks may also be reduced because of the lower above-ground biomass, unless the magnitude of the below-ground biomass compensates in some way. However, at first glance, the results were equivocal in two respects. Firstly, differences in various soil variables were not uniform between harvested and unharvested populations of the three study species.

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Fig. 3. Soil NH₄N results of three non-timber forest products (a) *Acacia karroo*, (b) *Opuntia ficus-indica* and (c) *Cymbopogon marginatus* from harvested and unharvested sites. Bars are means \pm SE and ANOVA with harvest treatments and sampling positions nested in harvest treatments are shown.

For *A. karroo* most of the soil variables displayed a significant difference between the harvested and unharvested treatments, only a few did for *C. marginatus* and only two for *O. ficus-indica*. Secondly, the direction of the difference was not uniform within and between NTFP species. For example, for *A. karroo* five of the soil variables were significantly higher in the unharvested sites, but three were significantly lower. Thus, the direction of the differences for this species, as well as the other two, was not uniformly in favour of the unharvested treatment. Thirdly, for specific soil attributes, the direction of significant differences was in favour of the unharvested site for one of the NTFP species, but the harvested site for another; for example, P for *A. karroo* and *O. ficus-indica* or Na, Ca and Mg for *A. karroo* and *C. marginatus*.

In terms of the first, i.e. variable impacts between NTFP species, we interpret that it is likely to be related, to some degree, to the *relative* proportion of biomass removed through harvesting. As indicated in Table 1, this can be at the scale of the individual plant, or also the community scale, which is a function of the dominance of the target species in the community. Removal of a high proportion of the biomass of a species in low abundance will represent only a small proportion of the community biomass (Siebert 2001). In contrast, a lower harvest of a dominant species could represent a noteworthy proportion of the community level above-ground biomass. With respect to the three

NTFP species examined, the harvesting of *A. karroo* represented a loss of significant above-ground biomass for both the individual trees as well as the community because it is a community dominant. This was consequently reflected in the higher number of soil attributes that showed differences between the harvested and unharvested sites. At the other extreme was *O. ficus-indica*, for which the harvesting of fruits represented only a small proportion of the plant and the community biomass, resulting in few soil attributes differing between the harvested and unharvested populations. *Cymbopogon marginatus* was intermediate between these two. It is a community dominant, but only the dead flowering culms were removed (along with a few leaves), representing 10–25% of plant biomass. Consequently, only a few soil variables showed any effects.

The picture is more complex than just the proportion of biomass removed. A second dimension of any harvesting regime is the frequency (Ticktin 2015). If harvests are infrequent, even if severe, there is opportunity for nutrient replenishment through wet and dry deposition and litter decomposition. Many NTFPs are seasonal resources, such as fruits, flowers, seeds, which imposes some limit on the proportion of the above-ground biomass that may be removed, which in turn, may limit impacts on soil nutrient stocks. Other NTFPs can be harvested all year round (such as firewood, leaves, bark), resulting in a continuous harvest which is likely to have greater impacts on soil nutrients than a seasonal harvest would. Our results conform to this, with *A. karroo* harvest, which is continuous, showing greater impacts on soil attributes than the seasonal harvest of the other two species, acknowledging that the proportion of biomass removed interacts with this. It is possible that the impacts on soil nutrients of seasonally harvested species will depend upon when any assessment is done in relation to the time of harvest, being highest immediately after harvest; this needs to be examined.

Thirdly, the impacts of NTFP harvest on soil nutrients may also be a function of the nutrient richness of the biomass harvested. In our study, the harvest of branches or the whole plant of A. karroo includes removal of nutrientrich leaves. Being a nitrogen-fixing species, the leaves and litter have high nutrient concentrations (Ndagurwa, Dube & Mlambo 2014). High leaf litter nutrient content has been associated with higher decomposition rates (Joanisse et al. 2007). Therefore, if A. karroo litter is associated with high nutrients as well as decay and decomposition rates, removal of most of the leaves could have a significant effect on the availability of litter, which will subsequently affect soil nutrients. Witkowski & Lamont (1996) argued that nutrient depletion (particularly N and C) in their study arose largely from the removal of the plant leaves during the harvest of the flowers. The same did not apply to O. ficus-indica as the fruits are borne on the tips of large, stout cladodes and there is no accidental harvest of these with the fruits. With respect to C. marginatus, the quality of the biomass removed was low because it was mostly dead and dried culms. There is usually some removal of the tips of some of the leaves but only a small proportion of the total leaf biomass.

The comparison of subcanopy and open locations indicated a similar trend. The largest NTFP, i.e. A. karroo showed significantly higher nutrient pools under the canopy than between trees, whereas there were relatively few differences for O. ficus-indica or C. marginatus. Such nutrient enrichment beneath trees in patchy environments is well documented, especially in drier ecosystems (Dohn et al. 2013). The few differences evident between subcanopy and open sites for C. marginatus indicated higher Na, Mg and ammonium nitrogen between plants than under them. We speculate that this may be related to the deposition of residual material (short culms and cut leaves) on the ground after cutting, but would require further investigation. The above suggestion has been reported for other NTFPs where leaving residuals on site resulted in increased soil C and N, whereas residual removal may result in a reduction in soil C and N, depending on species (Pennock & van Kessel 1997; Johnson & Curtis 2001).

An unanticipated finding was the significantly higher levels of several cations (Na, Ca and Mg) on the harvested *A. karroo* sites relative to the unharvested sites. The reasons for this are unclear and we recognise that it requires further investigation. One possibility relates back to the effect of the loss of nutrient-rich leaves when whole trees are harvested. As mentioned above, the removal of leaves could reduce decomposition and bacterial activity. In turn, reduced bacterial activity may result in lowered cation binding. Reduced cation binding causes less cation uptake and use by the plant which causes increased cation availability in the soil due to cations not being used (Oertli 2008). Elevated cations were also reported by Rutherford, Powrie & Husted (2014) in comparing heavily browsed sites with low above-ground vegetative biomass to less browsed sites with higher biomass. They suggested that it might have been a result of nutrient enrichment from livestock urine and dung. There is some livestock at the harvested site, but not in particularly high numbers.

Conclusions and management implications

In conclusion, the harvesting of the three NTFPs had variable impacts on soil nutrients. Most impacts were associated with the largest and most intensely harvested NTFP, i.e. *A. karroo*, and effects declined with lower biomass removal as illustrated by the other two species. Any sustained loss of soil nutrients could have a direct and indirect effect on ecosystems, e.g. nutrient cycling and availability, which will affect plant growth. Further studies are required to determine explicit relationships between actual volume and quality of biomass removed and changes in soil nutrient stocks, as well as the rate and sources of replenishment. This would provide insight into the proportion of biomass that could be removed at an ecosystem level without longterm depletion of soil nutrients.

Three management implications of this study are evident. First, in agreement with the recommendation of Witkowski & Lamont (1996), is the need to promote retention on site of harvested, but unused, residual biomass, such as twigs and leaves of A. karroo, and short culms and leaves of C. marginatus. Leaving unwanted residuals on site can trigger a temporary increase in soil nutrients (Johnson & Curtis 2001). Second is the promotion of rotational harvesting spatially and temporally to provide for periods of nutrient replenishment through litter decomposition and wet and dry deposition. The duration of non-harvest periods should be scaled in relation to the extent of biomass removal during harvesting. It would also be dependent on the capacities of local governance institutions to design and promote compliance. Third, is specific to O. ficus-indica, the results for which showed no reductions in soil nutrients in the harvested site. Consequently, we suggest that there would be no harm in permitting harvesters access to populations within the protected area, which would not only be of benefit to them but also help the management agency control the plant as an invasive species.

Authors' contributions

C.S. conceived the study and jointly planned it with S.R., who undertook the field sampling and data analysis. Both C.S. and S.R. co-wrote the paper.

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Data accessibility

Data are available from the Dryad Digital Repository https://doi.org/10. 5061/dryad.mp6d3 (Ruwanza & Shackleton 2017).

References

- van Andel, T.R., Croft, S., van Loon, E.E., Quiroz, D., Towns, A.M. & Raes, N. (2015) Prioritizing West African medicinal plants for conservation and sustainable extraction studies based on market surveys and species distribution models. *Biological Conservation*, **181**, 173–181.
- Angelsen, A., Jagger, P., Babigumira, R., Belcher, B., Hogarth, N.J., Bauch, S., Börner, J., Smith-Hall, C. & Wunder, S. (2014) Environmental income and rural livelihoods: a global comparative analysis. *World Development*, 64S, S12–S28.
- Babulo, B., Muys, B., Nega, F., Tollens, E., Nyssen, J., Deckers, J. & Mathijs, E. (2009) The economic contribution of forest resource use to rural livelihoods in Tigray, Northern Ethiopia. *Forest Policy & Economics*, **11**, 109–117.
- Barnes, R.D., Filer, D.L. & Milton, S.J. (1996) Acacia karroo: Monograph and Annotated Bibliography. Tropical forestry papers no. 32. Oxford Forestry Institute, Oxford University Press, Oxford, UK.
- Belcher, B.M. (2003) What isn't and NTFP? *International Forestry Review*, **5**, 161–168.
- Botha, J., Witkowski, E.T.F. & Shackleton, C.M. (2003) The impact of commercial harvesting on *Warburgia salutaris* ('pepper-bark tree') in Mpumalanga, South Africa. *Biodiversity & Conservation*, 13, 1675–1698.
- Bray, R.H. & Krutz, L.T. (1945) Determination of total, organic and available forms of phosphorus in soils. *Soil Science*, 59, 39–45.
- Campbell, B.M., Jeffrey, S., Kozanayi, W., Luckert, M., Mutamba, M. & Zindi, C. (2002) Household Livelihoods in Semi-Arid Regions: Options and Constraints. CIFOR, Bogor, Indonesia.
- Chan, K.Y., Bowman, A. & Oates, A. (2001) Oxidizible organic carbon fractions and soil quality changes in an Oxic Paleustalf under different pasture leys. *Soil Science Society of America Journal*, **166**, 61–67.
- Cruse-Sanders, J.M., Hamrick, J.L. & Ahumada, J.A. (2005) Consequences of harvesting for genetic diversity in American ginseng (*Panax quinquefolius* L.): a simulation study. *Biodiversity Conservation*, 14, 493– 504.
- Cunningham, A.B. (2011) Non-timber products and markets: lessons for export-orientated enterprise development from Africa. *Non-Timber Forest Products in the Global Context* (eds S.E. Shackleton, C.M. Shackleton & P. Shanley), pp. 83–106. Springer, Heidelberg, Germany.
- Dohn, J., Dembélé, F., Karembé, M., Moustakas, A., Amévor, K.A. & Hanan, N.P. (2013) Tree effects on grass growth in savannas: competition, facilitation and the stress-gradient hypothesis. *Journal of Ecology*, 101, 202–209.
- Gaoue, O.G., Horvitz, C.C. & Ticktin, T. (2011) Non-timber forest product harvest in variable environments: modelling the effect of harvesting as a stochastic sequence. *Ecological Applications*, 21, 1604–1616.
- Gaoue, O.G., Lemes, M.R., Ticktin, T., Sinsin, B. & Eyog-Matig, O. (2014) Non-timber forest product harvest does not affect the genetic diversity of a tropical tree despite negative effects on population fitness. *Biotropica*, 46, 756–762.
- Ghimire, S.K., Gimenez, O., Pradel, R., McKey, D. & Aumeeruddy-Thomas, Y. (2008) Demographic variation and population viability in a threatened Himalayan medicinal and aromatic herb Nardostachys grandiflora: matrix modelling of harvesting effects in two contrasting habitats. Journal of Applied Ecology, 45, 41–51.
- Grady, J.M. & Hoffmann, W.A. (2012) Caught in a fire trap: recurring fire creates stable size equilibria in woody resprouters. *Ecology*, **93**, 2052– 2060.
- Groenendijk, P., Eshete, A., Sterck, F.J., Zuidema, P.A. & Bongers, F. (2012) Limitations to sustainable frankincense production: blocked

regeneration, high adult mortality and declining populations. *Journal of Applied Ecology*, **49**, 164–173.

- Hurley, P.T., Halfacre, A.C., Levine, N.S. & Burke, M.K. (2008) Finding a "disappearing" nontimber forest resource: using grounded visualization to explore urbanization impacts on sweetgrass basket making in Greater Mt. Pleasant, South Carolina. *The Professional Geographer*, 60, 556–578.
- Joanisse, G.D., Bradley, R.L., Preston, C.M. & Munson, A.D. (2007) Soil enzyme inhibition by condensed litter tannins may drive ecosystem structure and processes: the case of *Kalmia angustifolia*. *New Phytologist*, **175**, 535–546.
- Johnson, D.W. & Curtis, P.S. (2001) Effects of forest management on soil C and N storage: meta analysis. *Forest Ecology & Management*, 140, 227–238.
- Kaoma, H. & Shackleton, C.M. (2015) The direct use value of urban tree non-timber forest products to household income in poorer suburbs in South African towns. *Forest Policy & Economics*, **61**, 104–112.
- Kar, S.P. & Jacobson, M.G. (2012) NTFP income contribution to household economy and related socio-economic factors: lessons from Bangladesh. *Forest Policy & Economics*, 14, 136–142.
- Kettenring, K.M., Weekely, C.W. & Menges, E.S. (2009) Herbivory delays flowering and reduces fecundity of *Liatris ohlingerae* (Asteraceae) an endangered, endemic plant of the Florida scrub. *Journal of Torrey Botanical Society*, **136**, 350–362.
- Mandle, L. & Ticktin, T. (2012) Interactions amongst harvest, grazing, fire and abiotic conditions shape palm demographic responses to disturbance. *Journal of Ecology*, **100**, 997–1008.
- McGraw, J.B. & Furedi, M.A. (2005) Deer browsing and population viability of an understory plant. Science, 307, 920–922.
- McLain, R.J., Hurley, P.T., Emery, M.R. & Poe, M.R. (2014) Gathering "wild" food in the city: rethinking the role of foraging in urban ecosystem planning and management. *Local Environment*, 19, 220–240.
- Mucina, L. & Rutherford, M.C. (2006) The Vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, South African National Biodiversity Institute, Pretoria, South Africa.
- Ndagurwa, H.G.T., Dube, J.S. & Mlambo, D. (2014) Decomposition and nutrient release patterns of mistletoe litters in a semi-arid savanna, southwest Zimbabwe. *Austral Ecology*, **40**, 178–185.
- Oertli, J.J. (2008) Soil fertility. *Encyclopaedia of Soil Science* (ed W. Chesworth), pp. 656–668. Springer, Dordrecht, The Netherlands.
- Pennock, D.J. & van Kessel, C. (1997) Clear-cut forest harvest impacts on soil quality indicators in the mixedwood forest of Saskatchewan, Canada. *Geoderma*, **75**, 13–32.
- Pfab, M.F. & Witkowski, E.T. (1999) Contrasting effects of herbivory on plant size and reproductive performance in two populations of the critically endangered species, *Euphorbia clivicola* R.A. Dyer. *Plant Ecology*, 145, 317–325.
- R Development Core Team (2015) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Rhoades, J.D. (1982) Cation exchanger capacity. *Methods of Soil Analysis*, 2nd edn (eds L. Page, A.L. Miller & R.H. Keeney), American Society of Agronomy, Madison, WI, USA.
- Rutherford, M.C., Powrie, L.W. & Husted, L.B. (2014) Herbivore-driven land degradation: consequences for plant diversity and soil in arid subtropical thicket in south-eastern Africa. *Land Degradation & Development*, 25, 541–553.
- Ruwanza, S. & Shackleton, C.M. (2017) Data from: Ecosystem-scale impacts of non-timber forest product harvesting: effects on soil nutrients. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.mp6d3.
- Schlesinger, J., Drescher, A. & Shackleton, C.M. (2015) Socio-spatial dynamics in the use of wild natural resources: evidence from six rapidly growing medium-sized cities in Africa. *Applied Geography*, 56, 107–115.
- Schmidt, I.B., Mandle, L., Ticktin, T. & Gaoue, O.G. (2011) What do matrix population models reveal about the sustainability of non-timber forest product harvest? *Journal of Applied Ecology*, 48, 815–826.
- Shackleton, C.M. (2015) Multiple roles of non-timber forest products in ecologies, economies and livelihoods. *Routledge Handbook of Forest Ecology* (eds K. Peh, R. Corlett & Y. Bergeron), pp. 559–570. Routledge, Abingdon, UK.
- Shackleton, S.E., Kirby, D. & Gambiza, J. (2011) Invasive plants friends or foes? The contribution of prickly-pear (*Opuntia ficus-indica*) to livelihoods in Makana Municipality, Eastern Cape, South Africa. *Development Southern Africa*, 28, 177–193.
- Shackleton, S.E., Campbell, B., Lotz-Sisitka, H. & Shackleton, C.M. (2008) Links between the local trade in natural products, livelihoods

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and poverty alleviation in a semi-arid region of South Africa. World Development, 36, 505-526.

- Shackleton, C.M., Delang, C., Shackleton, S.E. & Shanley, P. (2011) Nontimber forest products: concept and definition. *Non-Timber Forest Products in the Global Context* (eds S.E. Shackleton, C.M. Shackleton & P. Shanley), pp. 3–21. Springer, Heidelberg, Germany.
- Siebert, S.F. (2001) Nutrient levels in Rattan foliage and cane, and implications for harvesting. *Biotropica*, 33, 361–363.
- Stanley, D., Voeks, R. & Short, L. (2012) Is non-timber forest product harvest sustainable in the less developed World? A systematic review of the recent economic and ecological literature. *Ethnobiology & Conservation*, 1. Available at: http://ethnobioconservation.com/index.10 9 php/ ebc/article/view/19
- Thomas, G.W. (1982) Exchangeable cations. *Methods of Soil Analysis*, 2nd edn (eds A.L. Page, A.L. Miller & R.H. Keeney), pp. 159–166. American Society of Agronomy, Madison, WI, USA.
- Ticktin, T. (2004) The ecological implications of harvesting non-timber forest products. *Journal of Applied Ecology*, **41**, 11–21.
- Ticktin, T. (2015) The ecological sustainability of non-timber forest product harvest: principles and methods. *Ecological Sustainability for Non-timber Forest Products: Dynamics and Case-studies of Harvesting* (eds C.M. Shackleton, A. Pandey & T. Ticktin), pp. 31–52. Earthscan, London, UK.

- Ticktin, T. & Shackleton, C.M. (2011) Harvesting non-timber forest products sustainably: opportunities and challenges. *Non-Timber Forest Products in the Global Context* (eds S.E. Shackleton, C.M. Shackleton & P. Shanley), pp. 149–170. Springer, Heidelberg, Germany.
- Ticktin, T., Ganesan, R., Paramesha, M. & Setty, S. (2012) Disentangling the effects of multiple anthropogenic drivers on the decline of two tropical dry forest trees. *Journal of Applied Ecology*, 49, 744–784.
- Vallejo, M.I., Galeano, G., Bernal, R. & Zuidema, P.A. (2014) The fate of populations of *Euterpe oleracea* harvested for palm heart in Colombia. *Forest Ecology & Management*, **318**, 274–284.
- Witkowski, E.T.F. & Lamont, B.B. (1996) Nutrient losses from commercial picking and cockatoo removal of *Banksia hookeriana* blooms at the organ, plant and site levels. *Journal of Applied Ecology*, 33, 131–140.
- Wotshela, L.E & Beinert, W. (2011) Prickly Pear: The Social History of a Plant in the Eastern Cape. Wits University Press, Johannesburg, South Africa.
- Zimmermann, H.G. & Moran, V.C. (1991) Biological control of prickly pear, *Opuntia ficus-indica* (Cactaceae), in South Africa. *Agriculture*, *Ecosystems & Environment*, 37, 29–35.

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