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Spatial patterns, availability and cultural preferences for edible plants in southern Africa

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Abstract

Aim: We investigated whether cross-cultural food plant selection in southern Africa is best explained by language ancestry, floristic environment or subsistence strategy.

Location: The flora of southern Africa region.

Taxa: All 1,740 edible plant taxa of southern Africa, representing 711 genera in 156 families.

Methods: Distribution data of plants were overlapped in ArcMap with 19 language maps, eight biomes and all taxa with nutritional data. Six correlations were estimated between five pairwise distance matrices (language ancestry, geographical proximity, floristic and edible environments and utilized species) with Mantel tests using the 'vegan' package in R. Regression analyses were used to identify floristic and cultural preferences in food plant selection.

Results: Spatial autocorrelation did not influence the selection of edible plants by the 19 language groups of southern Africa ($r = -.078$). The floristic and edible environments had a strong correlation ($r = .9743$) while the distance matrices of the edible and actually utilized plants had a low correlation for 13 of the language groups ($r = .2174$). Regression analyses between the floristic and edible environments for the FSA region and three languages, representing hunter-gatherers (Ju|'hoan), pastoralists (Khoekhoe) and agrarians (Venda) were all significant ($p < .001$) with high R^2 values (respectively .6181, .7702, .6654 and .7900), as were the relationship ($p < .001$) between what is edible and what was actually utilized. Surprisingly, the Apocynaceae had a much higher residual value than globally important food plant families. Vitamin C of fruits seems to have higher levels along the coastal regions, and carbohydrates in underground storage organs have higher levels in the summer-arid western region.

Main conclusions: There is an apparent preference for certain food plant families in southern Africa. This selection appears to be driven by subsistence strategy, based on the categories of plants preferred by the three representative language groups.

KEYWORDS

Apocynaceae, carbohydrates, edible plants, Fabaceae, Flora of southern African region, Galton's problem, indigenous cultures, regression analysis, subsistence strategy, underground storage organs

1 | INTRODUCTION

A study of the patterns of edible plant use in the Flora of southern Africa region (FSA, here also referred to as southern Africa), by Welcome and Van Wyk (2019), revealed how unique this region is compared to the rest of the world. This comprehensive checklist of edible plants in the FSA region revealed that the Apocynaceae and Fabaceae are the most species-rich edible plant families. Underground storage organs, fruits and leaves were found to be the most important plant parts used and foods are mostly eaten raw as snacks (or cooked, in the case of vegetables).

It is not only the plant diversity that makes southern Africa unique, but also the cultural diversity. Van Wyk, Van den Berg, Palgrave, and Jordaan (2011) provided geographical and linguistic information for all 22 indigenous language groups of southern Africa. These are (the name in the source language in brackets) the Bantu languages [Herero (*Otjiherero*), Kalanga (*ChiKalanga*), Kwangali (*Rukwangali*), Lozi (*Silozi*), Manyo (*Rumanyo*), Mbukushu (*Thimbukushu*), Southern Ndebele (*isiNdebele*), Northern Sotho (*Sepedi*), Ronga (*Xironga*), Southern Sotho (*Sesotho*), Swati (*siSwati*), Tsonga (*Xitsonga*), Tswana (*Setswana*), Venda (*Tshivenda*), Wambo (*Oshiwambo*), Xhosa (*isiXhosa*) and Zulu (*isiZulu*)], the Khoesaan languages [Ju|'hoan (*Ju|'hoan*), Khoekhoe (*Khoekhoegowab*, often called Nama), Kxoe (*Kxoe*) and !Xóõ (*!Xóõ*)] and one classified as Indo-European [Afrikaans (*Afrikaans*)]. Distribution maps of 19 of these languages are presented in Figure 1. The ethnobotanical reviews by Liengme (1983) and Van Wyk (2002) as well as the work done by Van Wyk et al. (2011) summarized the available ethnobotanical information on each of these cultural groups as well as the gaps in our knowledge. Many of the cultural groups have been well documented, such

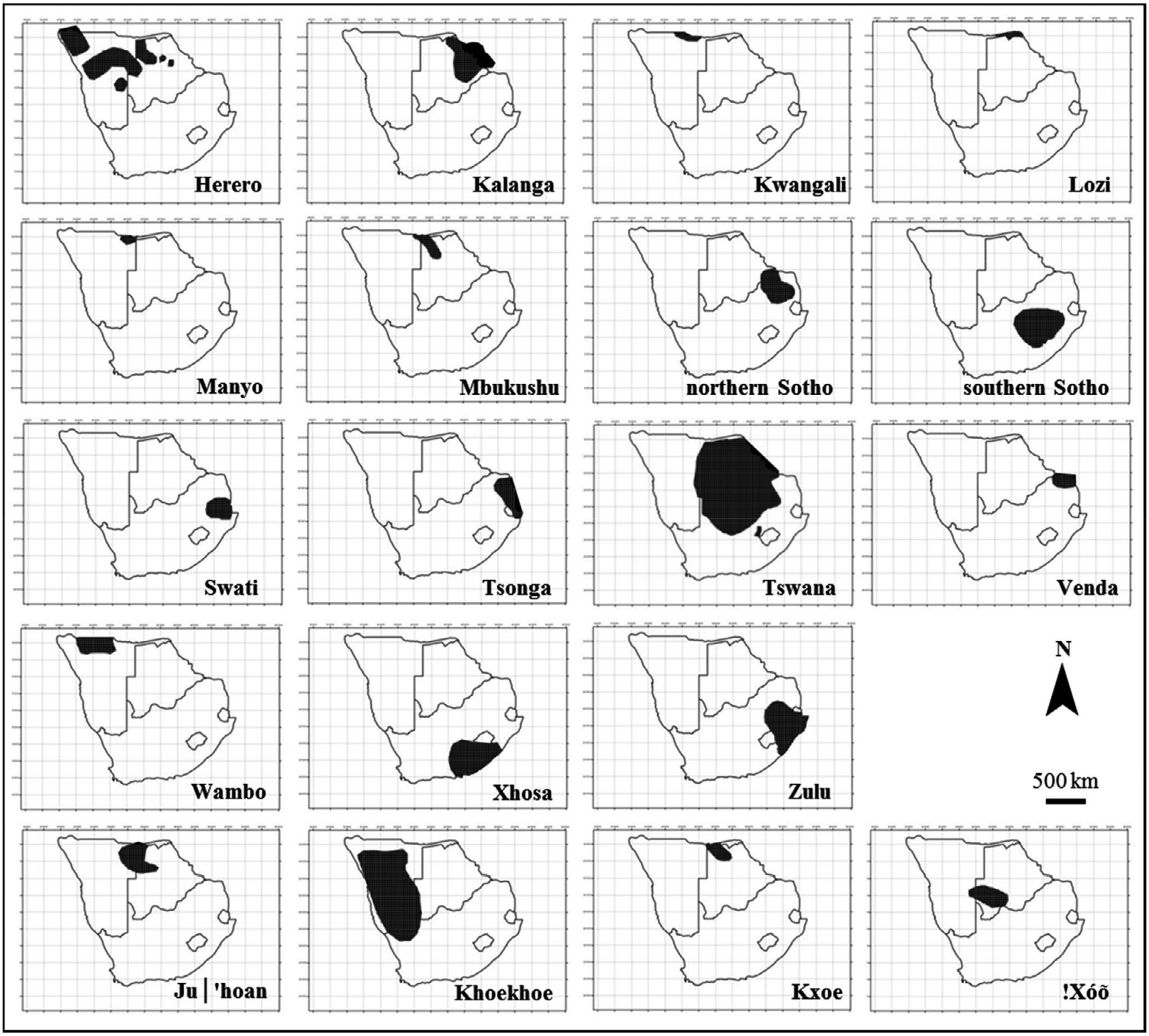

FIGURE 1 Historical and/or contemporary distribution ranges of the Bantu and Khoesaan cultural groups in the Flora of southern Africa region, based on the language maps provided by Van Wyk et al. (2011)

as the Herero (Malan & Owen Smith, 1974), the Kwangali and Manyo (Roodt, 1992, 1998), the Northern Sotho (Quin, 1959), the Southern Sotho (Moteetee & Van Wyk, 2006), the Swati (Dlamini, 1981), the Tsonga (Liengme, 1981), the Venda (Magwede, Van Wyk, & Van Wyk, 2018), the Wambo (Rodin, 1985), the Xhosa (Dold & Cocks, 2000), the Zulu (Gerstner, 1938, 1939, 1941), the Ju|'hoan (Leffers, 2003) and the Cape Khoekhoe (Archer, 1982, 1994). Despite the available ethnobotanical information, there have been no broad-scale comparisons amongst these groups to determine the patterns of plant use across cultures and how these patterns of use relate to the availability of, as well as the preferences for, certain plants.

According to the Database of Places, Language, Culture, and Environment (D-place), there are three types of subsistence strategies in the FSA region, namely gathering, pastoralism and agriculture (Kirby et al., 2016; Murdock et al., 1999) . Table 1 is a summary extracted from D-place which presents a comparison between three cultural groups, representing each of the subsistence strategies in southern Africa, namely a hunter-gatherer culture (Ju|'hoan), a nomadic pastoralist culture (Khoekhoe) and a sedentary agrarian culture (Venda). The subsistence strategy of each group is based on their dependence (shown in percentage, Table 1) on different activities to acquire food.

The selection of useful plants is based on what species are available in the surrounding environment, and this is determined by the vegetation type. There are 440 vegetation types described thus far for South Africa, Lesotho and Swaziland (SANBI, 2012, based on Mucina & Rutherford, 2006) which make up nine biomes (Figure 2). These are Albany Thicket—an evergreen, somewhat impenetrable and thorny, shrubland to low forest; Desert—with mostly annual plants in very harsh conditions (summer rainfall, but high levels of summer aridity); Forest—made up of evergreen trees with multi-layered vegetation below in frost-free areas; Fynbos—characterized by the presence of three components (ericoid, restioid and proteoid elements) usually on infertile soils; Grassland—dominated by grasses; Indian Ocean Coastal Belt—with a dominant forest cover; Nama-Karoo—with grassy, dwarf shrubland vegetation; Savanna—made up of a grassy ground layer with an upper layer of woody plants; and Succulent Karoo—dominated by dwarf, succulent shrubs. The Desert, Nama Karoo, Savanna and Succulent Karoo also extend into Namibia and Botswana (Low & Rebelo, 1996; Van Wyk & Van Wyk, 2013; White, 1983).

A comparison of Figures 1 and 2 shows the degrees of overlap between the biomes and the geographical ranges of the language groups. Albany thicket overlaps almost exclusively with the Xhosa language area, Desert with Khoekhoe and Herero, Fynbos historically with Khoekhoe, Grassland with southern and northern Sotho, Indian Coastal Belt with Zulu, Nama Karoo with Khoekhoe and Savanna with practically all Bantu language groups except Sotho, as well as the San languages (Ju|'hoan, Kxoe and !Xóõ). Because of this overlap between biomes and cultural groups, it can be expected that the preferred food plant taxa are not uniformly distributed. A detailed study of the locally available edible plants and those that are actually used may reveal new insights into the historical and contemporary human food ecology of southern Africa. Due to the close geographic proximity between different cultural groups, it is possible that they can influence each other's selection of useful plants. This is known as spatial autocorrelation or Galton's problem. In a study in Nepal, Saslis-Lagoudakis et al. (2014) showed that

TABLE 1 The subsistence variables (with descriptions) for three cultural groups in the southern African region which represent each of three subsistence strategies, namely a hunter-gatherer culture (Ju|'hoan/!Kung), a nomadic pastoralist culture (Khoekhoe/Nama) and a sedentary agrarian culture (Venda)

Variable	Description	Ju|'hoan	Khoekhoe	Venda
Subsistence economy: dominant activity	Dominant mode of subsistence.	Gathering	Pastoralism	Agriculture
Agriculture: intensity	Intensity of cultivation.	No agriculture	No agriculture	Intensive
Agriculture: major crop type	Principal type of crop cultivated.	No agriculture	No agriculture	Cereals
Subsistence economy: gathering	Dependence on the gathering of wild plants and small land fauna, relative to other subsistence activities.	76%–85%	6%–15%	6%–15%
Subsistence economy: hunting	Dependence on hunting, including trapping and fowling, relative to other subsistence activities.	16%–25%	26%–35%	6%–15%
Subsistence economy: fishing	Dependence on fishing, including shell fishing and the pursuit of large aquatic animals, relative to other subsistence activities.	0%–5%	6%–15%	0%–5%
Subsistence economy: animal husbandry	Dependence on animal husbandry, relative to other subsistence activities.	0%–5%	46%–55%	16%–25%
Subsistence economy: agriculture	Dependence on agriculture, relative to other subsistence activities.	0%–5%	0%–5%	56%–65%

Note: Data cited from Murdock et al. (1999) and Kirby et al. (2016).

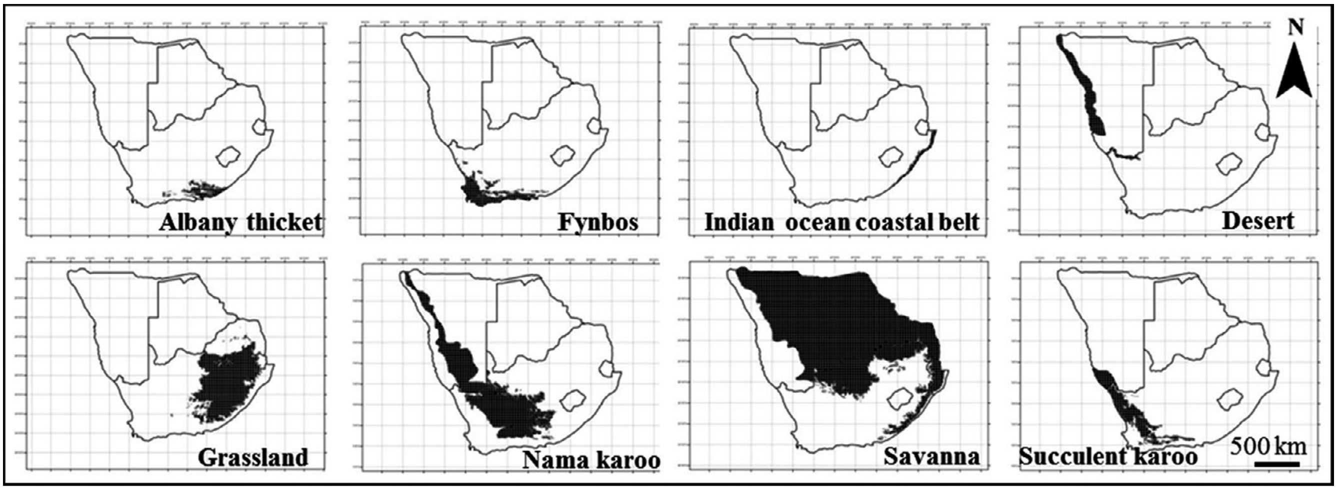

FIGURE 2 Distribution ranges of the biomes of the Flora of southern Africa region, based on SANBI (2012) and Van Wyk and Van Wyk (2013)

spatial autocorrelation was not significant and that the floristic environment had the strongest influence on the selection of medicinal plants by the local cultures.

Amongst the many ethnobotanical hypotheses and theories (reviewed by Gaoue et al., 2017), non-random (intentional) plant selection as proposed by Moerman (1979, 1991) provides a methodology to identify families that are preferentially selected or avoided. Moerman (1979, 1991) argued that if plant selection is random (not intentional), then there will be a linear relationship between the total number of species in a given plant family and the number of species selected for medicinal use. Intentional selection is evident in those families where the residual number of species exceeds the standard error of the regression.

With the availability of distribution maps for all language groups (Van Wyk et al., 2011) and biomes (SANBI, 2012), as well as distribution data for the taxa of southern Africa (Botanical Database of Southern Africa—BODATSA, SANBI, 2016), it has become possible to analyse patterns of plant use across cultures using regression analysis (Moerman, 1979, 1991), as well as a multi-layered map and GIS software. This multi-layered approach is known as deep mapping (Roberts, 2016) which is part of an emerging field known as Digital humanities or geolinguistics (if linguistic data are involved) (Lock & Pouncett, 2017). Languages are considered to be fluid in their distribution which makes it difficult to represent them spatially (Earley-Spadoni, 2017; Lock & Pouncett, 2017). However, plant use is usually based on historical data and is therefore linked to a historical distribution range. This use of historical data is much like the work done by Trifkovic (2006) who discusses the interaction between people and their landscape to determine prehistoric food resources and exploitation practices in the Iron Gates Gorge, Serbia. There has also been considerable interest in the underground storage organs which were potentially used as food resources in prehistoric times and how these resources influenced the evolution of modern humans along the south coast of South Africa (De Vynck, Van Wyk, & Cowling, 2016; Marean, 2010; Singels et al., 2016). With nutritional data available on these edible underground storage organs, it is possible to determine if those species with high carbohydrate values are concentrated within the Cape region where they seem to have been heavily relied upon in the past.

The aim of this paper was to do the first broad scale comparison of all plants available to the cultural groups of the FSA region as well as the availability, and in some cases the use, of edible taxa. Another aim was to determine if food plant selection preferences are based on cultural ancestry (language groups), plant families (floristic environment), or subsistence strategy (hunter-gatherers versus pastoralists versus agrarians).

2 | MATERIALS AND METHODS

The methodology followed here used ArcMap 10.3.1 (ESRI) and the GCS_WGS_1984 geographic coordinate system. It is based on the "overlapping" of four datasets: the distribution of (a) languages (also referred to as cultural groups), (b) biomes, (c) all taxa and (d) taxa with nutritional data.

In order to test for spatial autocorrelation (Galton's problem), a similar method was used as the one by Saslis-Lagoudakis et al. (2014) for the study of cultural groups in Nepal. A distance matrix of ancestral relatedness between cultural groups (Table S1 in Appendix S1) was produced using the hierarchical levels between each language according to the Ethnologue website (Lewis, 2009). A distance matrix of geographical proximity between all cultural groups (Table S2 in Appendix S1) was made using an online calculator that uses the Haversine formulae (Veness, n.d.). There is no complete phylogeny available for the FSA region and therefore the Sorensen Index (Sorensen, 1948) was used to produce distance matrices of the similarity between all available taxa (Table S3 in Appendix S1) and the available edible taxa (Table S4 and S5 in Appendix S1) between the cultural groups (based on the data in Appendix S2—see below). The Sorensen Index was also used to produce a distance matrix (Table

S6 in Appendix S1) of the edible plants utilized by 13 cultural groups with adequate ethnobotanical data [Herero (Malan & Owen Smith, 1974), the Kwangali and Manyo (Roodt, 1992, 1998), the Northern Sotho (Quin, 1959), the Southern Sotho (Moteetee & Van Wyk, 2006), the Swati (Dlamini,), the Tsonga (Liengme, 1981), the Venda (Magwede et al., 2018), the Wambo (Rodin, 1985), the Xhosa (Dold & Cocks, 2000), the Zulu (Gerstner, 1938, 1939, 1941), the Ju|'hoan (Leffers, 2003) and the Cape Khoekhoe (Archer, 1982, 1994)]. To calculate the Pearson product-moment coefficient (*r*) along with the significance values (*p*), six correlations between the distance matrices were done (culture versus geography, available taxa versus edible taxa, geography versus available taxa, geography versus edible taxa, culture versus available edible taxa and edible taxa versus utilized taxa). These correlations were determined with Mantel tests (Mantel, 1967) using the vegan package in R (Oksanen et al., 2009).

The shape file of African countries (Ruth, 2016), downloaded from ArcGIS.com, was the base map for the project, which was clipped onto a map of the Flora of Southern Africa (FSA) region. Collection data for all taxa for South Africa were downloaded from the SANBI newposa website (SANBI, 2016). Collection data for taxa in Namibia, Botswana, Lesotho and Swaziland were extracted from the BODATSA database provided by the South African National Biodiversity Institute. Distribution maps for the 19 southern African language groups (Van Wyk et al., 2011) were geoprocessed to fit onto the FSA map, and digitized into layers on the GIS platform (Figure 1).

The biome map shapefile was accessed from the BGIS website (SANBI, 2012), which represents an updated version of the original map by Mucina and Rutherford (2006). The layers were activated in the symbology tab of the properties. The forest biome was excluded due to its small size (less than 0.25% of the surface area of South Africa, and almost invisible at the scale used in Figure 2). The Nama Karoo, Desert, Savanna and Succulent Karoo biomes were extended into Namibia and Botswana using a geoprocessed and digitized map of the biomes from Van Wyk and Van Wyk (2013), which is partly based on the maps of White (1983) and Low and Rebelo (1996) (Figure 2).

Attribute tables of all taxa available in the distribution ranges of each language group and biome were extracted after clipping (using the GIS clipping tool) the distribution data onto each of these layers. These attribute tables were all combined into one dataset of all taxa within the distribution ranges of the biomes and cultural ranges (Excel spreadsheet, Appendix S2). Author citations are given in Appendix S2 and are not repeated elsewhere. The tables were combined using the "VLOOKUP" formula to repeat the relevant taxa names underneath each relevant cultural group and also to repeat the edible taxa names in a separate column. In order to filter out all taxa and all edible taxa, and to determine taxa-rich families, the names were replaced with a “1” in the Excel spreadsheet. Using the "COUNTIF" formulae, the number of taxa available for each family in the distribution ranges of all biomes and all 19 cultural groups for the FSA region as a whole, as well as each individual FSA country, were counted. Only 13 cultural groups had adequate data available for further comparisons based on what they actually use, namely the Herero (Malan & Owen Smith, 1974), the Kwangali and Manyo (Roodt, 1992, 1998), the Northern Sotho (Quin, 1959), the Southern Sotho (Moteetee & Van Wyk, 2006), the Swati (Dlamini,), the Tsonga (Liengme, 1981), the Venda (Magwede et al., 2018), the Wambo (Rodin, 1985), the Xhosa (Dold & Cocks, 2000), the Zulu (Gerstner, 1938, 1939, 1941), the Ju|'hoan (Leffers, 2003) and the Cape Khoekhoe (Archer, 1982, 1994).

Regression analysis was used to study if plant selection is intentional or not (Moerman, 1979, 1991), following the method described by Bennet and Husby (2008)—they simply used the LINEST regression function of Microsoft Excel. We used not only the total number of available taxa per family as an independent variable, but also the number of edible taxa. This resulted in two regression analyses for each of the four study regions (entire FSA, Ju|'hoan, Khoekhoe and Venda). The corresponding data on edible taxa came from our comprehensive data for the FSA region (Welcome & Van Wyk, 2019), Leffers (2003) for the Ju|'hoan, Archer (1982, 1994) for the Khoekhoe and Magwede et al. (2018) for the Venda. The entire FSA region was chosen because we now have, for the first time, a comprehensive checklist of edible taxa. These three cultural regions were selected because they represent the most complete survey data of food plants for the three subsistence strategies (respectively hunter-gatherers, pastoralists and agrarians).

The data of Wehmeyer (1986) were explored to compare the geographical distributions of underground storage organs with high and low levels of carbohydrates, as well as fruits with high and low levels of energy and vitamin C. The comparison was expanded using a dataset of all nutritional values for 413 species, compiled from the Food and Agriculture Organization of the United Nations & US Department of Health Education and Welfare (FAO, 1968), Wehmeyer (1986), Archer (1994) and Odhav, Beekrum, Akula, and Baijnath (2007). Comparisons were made for moisture, ash, protein, fat, fibre, carbohydrates, energy, Ca, Mg, Fe, Na, K, Cu, Zn, Mn, P, thiamin, riboflavin, niacin, vitamin C and carotene. The carbohydrate values for 81 species with edible underground storage organs were extracted and a comparison was made between species with carbohydrate values below (57 spp.) or above (24 spp.) the average value of 29.6 g/100 g.

The inventory data of Welcome and Van Wyk (2019) were used to summarize the relationships between plant parts and subsistence strategy, as well as the pattern of utilized plant parts in the most taxa-rich food plant families.

3 | RESULTS

Table 2 presents the Pearson product-moment correlation coefficient (*r*) and significance (*p*) of six correlations done between six different distance matrices. Table 3 presents the statistics of regression analyses done of all available versus edible versus utilized taxa of the southern African food plant families and Tables 3–6 and Figure 3 list and illustrate the results of these regression analyses. The patterns

TABLE 2 The Pearson product-moment correlation coefficient (*r*) and significance (*p*) of six correlations done between five different distance matrices

Distance matrix 1	Distance matrix 2	Correlation coefficient (*r*)	Significance (*p* value)
available	edible	.9743	.001
culture	geography	−.07802	N.S.
geography	edible	−.606	N.S.
geography	available	−.6395	N.S.
culture	edible	−.1098	N.S.
edible	utilized	.2174	N.S.

Note: Available refers to the similarity between the available taxa in each distribution range. Edible refers to the similarity between the edible taxa in each distribution range. Culture refers to the hierarchical levels between language groups and geography refers to the geographical distance between language groups. Utilized refers to the similarity between the utilized species of 13 cultural groups.

TABLE 3 Statistics of regression analyses of the available versus edible taxa within the FSA region, as well as the available versus edible, and edible versus used taxa within the Ju|'hoan, Khoekhoe and Venda regions

Region	Regression	R^2	Standard error	Significance (*p* value)
FSA	available versus edible	.6181	12	<.001
Ju|'hoan	available versus edible	.7702	2	<.001
Ju|'hoan	edible versus used	.5582	1	<.001
Khoekhoe	available versus edible	.6654	4	<.001
Khoekhoe	edible versus used	.3347	1	<.001
Venda	available versus edible	.7900	3	<.001
Venda	edible versus used	.6948	1	<.001

for all language groups are presented in Figure S1 in Appendix S1. This data were used to determine family patterns for all available, available edible and utilized food plant taxa for the Ju|'hoan, Khoekhoe and Venda cultures (Figure 4). In Figure S2 in Appendix S1, all the biome patterns are shown. The data were also used to study the relationships between available and available edible taxa in the Nama Karoo and Savanna biomes (Figure 5). The combination of all attribute tables provided a base dataset (Appendix S2) which is compatible with any plant use category if there is a checklist available. Differences in the plant parts that are used by the Ju|'hoan, Khoekhoe and Venda cultures are shown in Figure 7, together with a summary of the available edible plant parts of the ethnobotanically most relevant plant families. Figure 7 shows the spatial distribution of taxa with high and low values for Vitamin C in their fruits and taxa with high and low carbohydrates in their underground storage organs.

4 | DISCUSSION

Spatial autocorrelation (Galton's problem) implies that cross-cultural similarities may occur if cultural groups are ancestrally as well as geographically close to each other. This close proximity could influence similarity in the different cultural groups selection of edible plants (Saslis-Lagoudakis et al., 2014). Table 2 shows that the correlation coefficient between the geographic proximity and the language ancestry distance matrices is very low (*r* = −.07802), with no significance between the two datasets. Spatial autocorrelation therefore does not influence the edible plant selection by different cultural groups in the FSA region. Similarly, according to Saslis-Lagoudakis et al. (2014), the geographical proximity between the cultural groups in Nepal also did not influence their selection of medicinal plants. Saslis-Lagoudakis et al. (2014) rather found that the floristic environment was the main driver of medicinal plant selection by Nepalese cultural groups. The high correlation (*r* = .9743; *p* = .001) between the available and edible taxa (Table 2) shows that edible plant availability for the cultural groups in the FSA region is influenced by the floristic environment. This high correlation between the floristic and edible environments is expected. There is a very low correlation between cultural ancestry and available edible taxa (*r* = −.1098). There is also a low correlation between the geographical proximity of cultural groups and their floristic environments (available taxa), as well as their edible environments (*r* = −.6395 and *r* = −.606). This implies that all of the cultural groups, even closely related ones, have unique floristic and edible environments that they can respond to without being influenced by their language ancestry or the practices

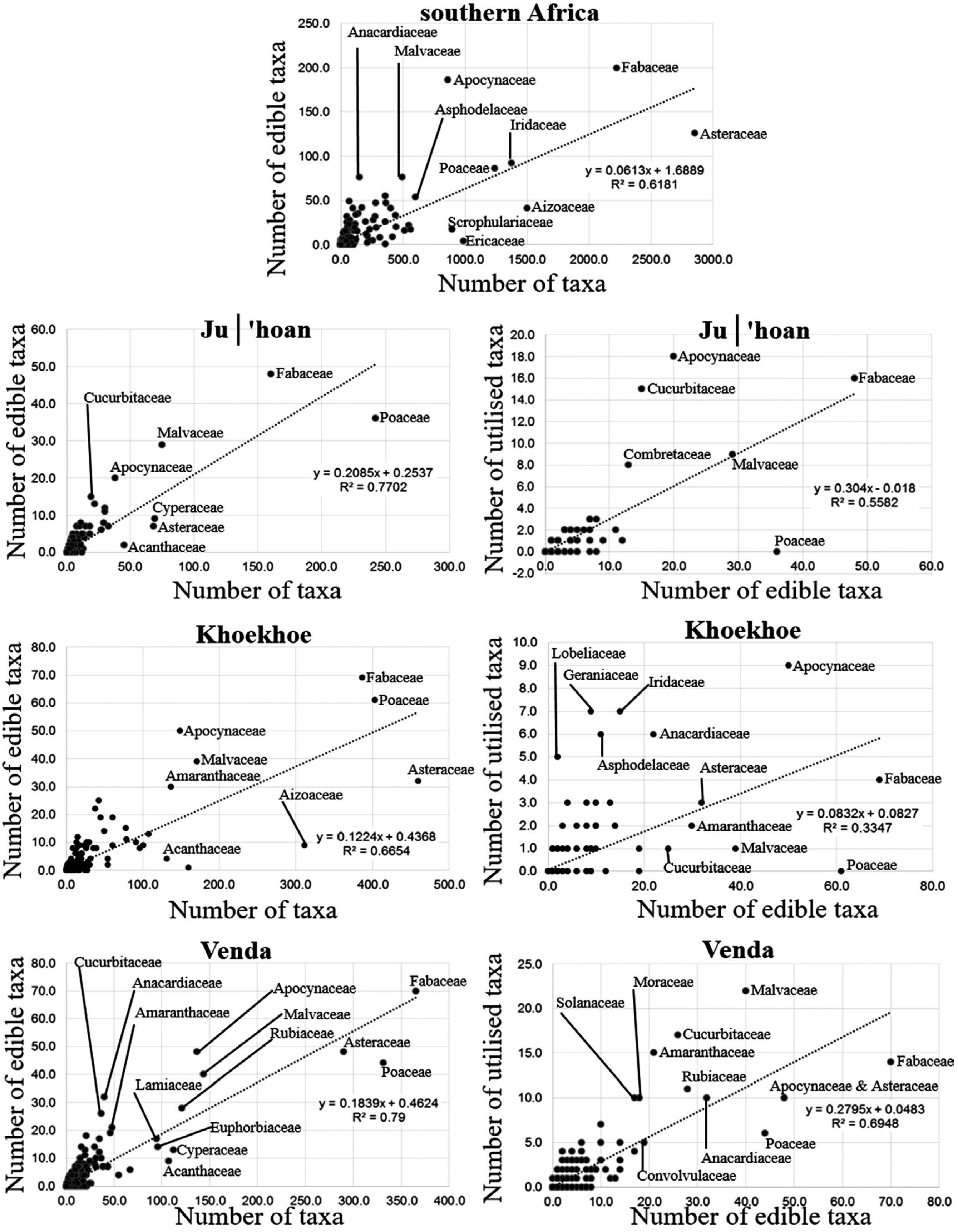

FIGURE 3 Scatter plots showing the regression values of all taxa versus edible taxa for the Flora of southern African region, as well as for examples of a hunter-gatherer culture (Ju|'hoan), a nomadic pastoralist culture (Khoekhoe) and a sedentary agrarian culture (Venda). For the Ju|'hoan, Khoekhoe and Venda cultures, the results of an additional regression analysis of edible taxa versus utilized taxa are also shown

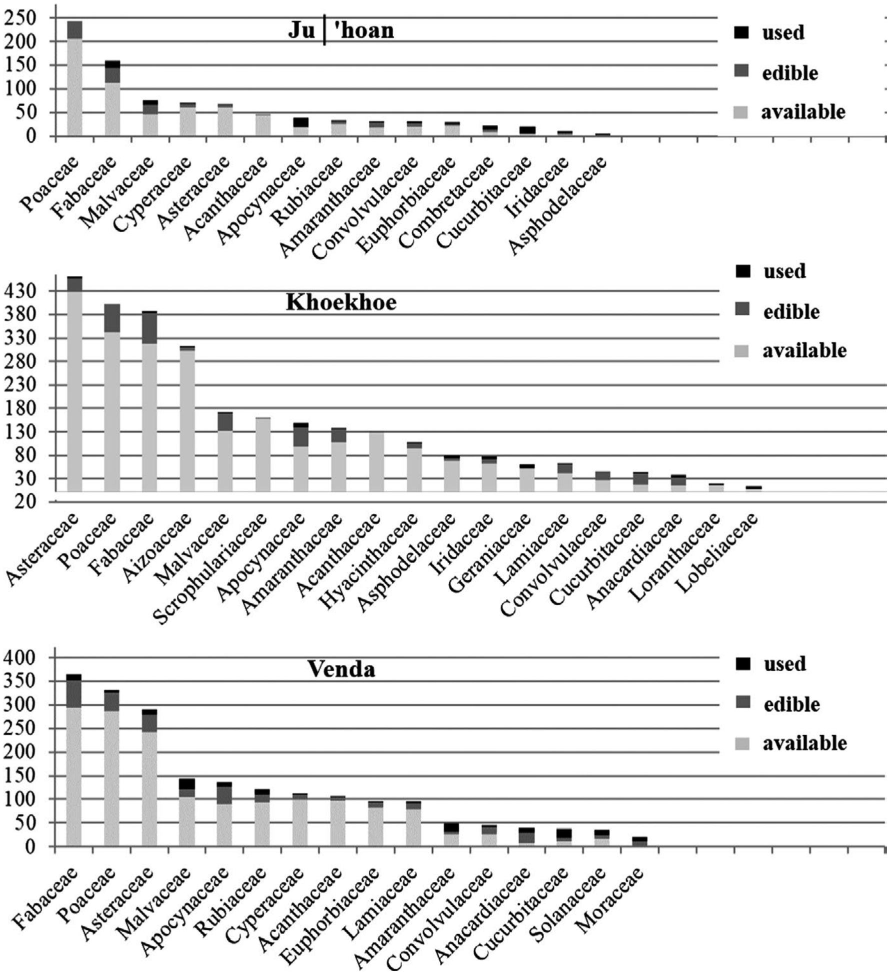

FIGURE 4 Comparisons of the most taxa-rich food plant families in the Flora of southern African region, according to the numbers of available taxa, the numbers of edible taxa and the numbers of taxa that are actually used by the Ju|'hoan, Khoekhoe and Venda cultures

of geographically nearby cultures. This corresponds to the study by Saslis-Lagoudakis et al. (2014), who concluded that closely related cultures do not use the same edible species or even close relatives of those species. Of the six correlations shown in Table 2, it is apparent that ancestral and geographic relationships between cultural groups have no influence on their edible plant selection and only what is available to each culture should have an influence. There is however a low correlation ($r = .2174$) between the edible plants available and those actually utilized by the 13 language groups with adequate ethnobotanical data. This low correlation indicates that even if language groups in southern Africa have the same edible plants available to them, they are not utilizing the same plants and are therefore displaying preference for certain plants. Regression analyses were done to further explore the patterns of plant selection at family level. These analyses were done for the FSA region and three cultural groups who historically represent three different food cultures: nomadic hunter-gatherers (Ju|'hoan), nomadic pastoralists (Khoekhoe) and sedentary pastoralists (Venda).

Table 3 shows the statistics of all regression analyses done. The R^2 values between the floristic and edible environments in all of the four regions (FSA, Ju|'hoan, Khoekhoe and Venda) are all high, namely .6181 for FSA, .7702 for Ju|'hoan, .6654 for Khoekhoe and .7900 for Venda, all with p values below .001. This agrees with the significant relationship shown for the correlation between the floristic and edible distance matrices in Table 2. The R^2 values between the edible environments and the utilized species are much lower for all three cultural groups, .5582 for Ju|'hoan, .3347 for Khoekhoe and .6948 for Venda, all with p values below .001. This result agrees with the low correlation found between edible and utilized species for the 13 cultural groups (Table 2). Table 4 shows that all 20 families listed for the FSA region have residual values that exceed the standard error of 12 (given in Table 3) and that all of them include many more or many less taxa than the regression equation predicts. The residual values for the Ju|'hoan, Khoekhoe and Venda regression analyses are given in Tables 4–6 (with standard errors listed in Table 3). Here, the pattern is similar, namely that almost all families in the available versus edible regression analyses have residual values that exceed the standard errors, while fewer families have residuals that exceed the standard errors in the edible versus utilized analyses. All regression analyses showed statistically significant relationships between the dependent and independent variables (Table 3, Figure 3). For southern Africa as a whole, the Apocynaceae are clearly over-represented, as are the Anacardiaceae, Fabaceae and Malvaceae; in contrast, the Ericaceae, Scrophulariaceae, Aizoaceae and Asteraceae are under-represented. As expected, Tables 4–6 show that the representation of families is not uniform for the three different cultures, with several of the top and bottom families remarkably different. This trend is also displayed in Figure 4 for the three cultures (these

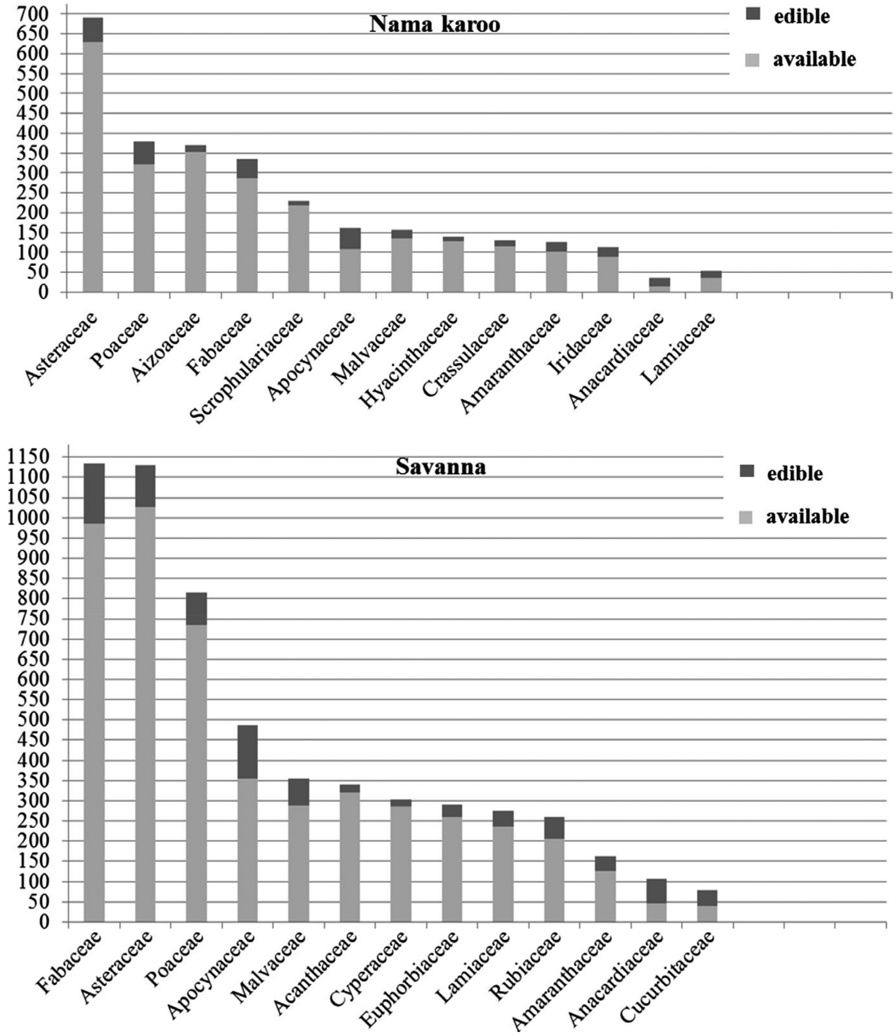

FIGURE 5 Comparisons of the most taxa-rich, available and edible, food plant families within the distribution ranges of the Nama Karoo and Savanna biomes

relative proportions are also shown for all the cultures in Figure S1 in Appendix S1) with families with more available edible species not having the most utilized species for the different cultural groups.

The numbers and ratios of available and edible taxa in the 13 most diverse families of the home biomes of the Ju|'hoan (Savanna), Khoekhoe (Nama Karoo) and Venda (Savanna) are shown in Figure 5. These relative proportions are also shown for all the biomes in Figure S2 in Appendix S1. The four most diverse families in the Nama Karoo are also the four most diverse families available to the Khoekhoe. Similarly, the five most diverse families of the Savanna biome are also the five most diverse families available to the Venda (and four out of five for the Ju|'hoan). The Asteraceae dominates in the Nama Karoo biome (with high numbers of available taxa also in the Poaceae, Aizoaceae and Fabaceae). The Fabaceae and Asteraceae are both dominant in the Savanna biome (with high numbers of available taxa also in Poaceae and Apocynaceae). The numbers of edible taxa are similar in the sense that three of the four most diverse families in the Nama Karoo have high numbers of edible taxa, to which the Apocynaceae should be added. It is noteworthy that the Aizoaceae have a low number of edible taxa. In the Savanna biome, all four of the most diverse families have the highest numbers of edible taxa, to which the Malvaceae and perhaps also the Rubiaceae and Anacardiaceae can be added. While similar taxa-rich food plant families are available to the Ju|'hoan and Venda (both predominantly in the Savanna biome), especially the Fabaceae, Poaceae, Malvaceae and Apocynaceae, the families available to the Khoekhoe are typical of the greater Cape and reflect the summer-aridity of the region with large numbers of geophytes.

These results seem to indicate that the food ecology and food preferences of the three lifestyles (nomadic hunter-gatherer, nomadic pastoralists and sedentary agrarians) differ considerably as far as the choice of food plants is concerned. Figure 6 summarizes the preferred plant parts of the three cultures as well as the number of edible plant parts for each of the most diverse food plant families. There is a direct relationship between the apparently preferred food plant families and the preferred plant parts for each of the three cultures. The Ju|'hoan show a high preference for fruits, followed by roots and then other plant parts. The almost exclusive use of several edible gum exudates by this culture is noteworthy. According to Table 5 and Figure 3, the Ju|'hoan have Apocynaceae, Fabaceae and Cucurbitaceae as the top utilized families, with Malvaceae at a level predicted by the regression and with Poaceae far below the predicted level. In terms of species diversity, the Apocynaceae are the most diverse food plant

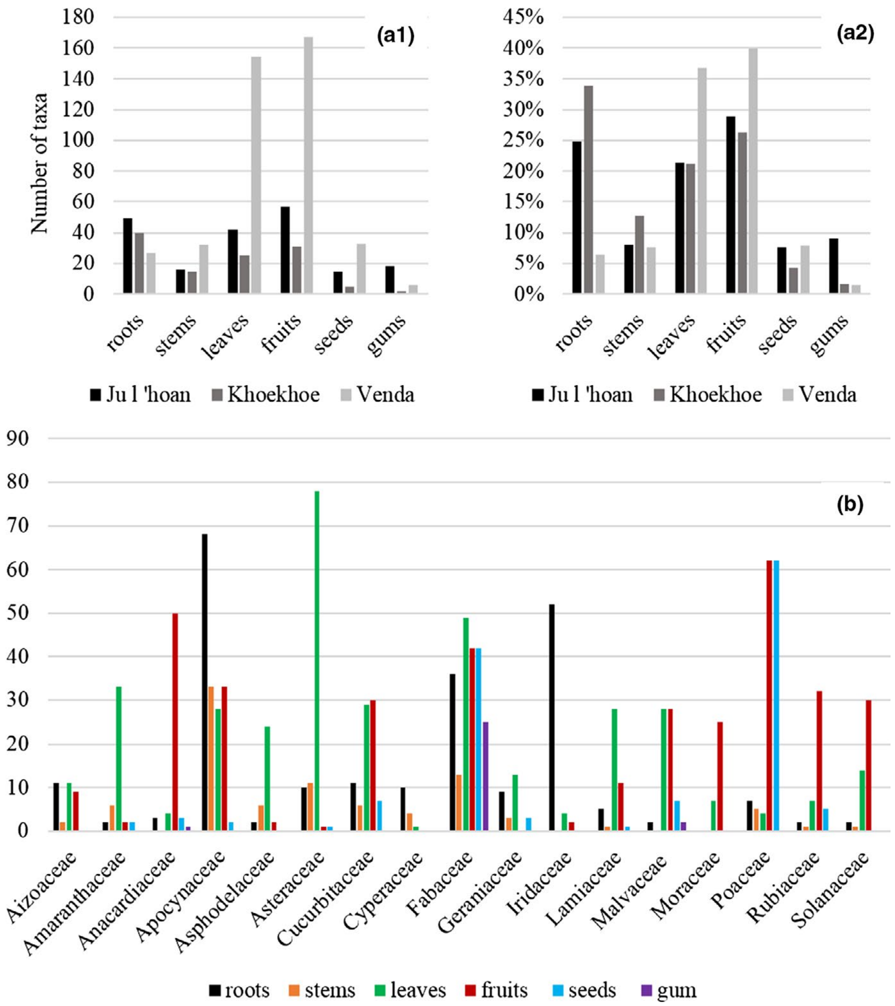

FIGURE 6 Comparison of plant parts used by the Ju|'hoan, Khoekhoe and Venda cultures (a1, numbers of taxa; a2, % of all taxa) and b, comparison of edible plant parts per family for a selection of the most diverse food plant families used by the Ju|'hoan, Khoekhoe and Venda cultures (see Figure 4)

family (Welcome & Van Wyk, 2019), which accounts for most of the edible roots and fruits used by the Ju|'hoan. The rest of the edible fruits used come from Fabaceae and Cucurbitaceae, which both have a high number of edible fruits. Figure 6 shows that the Apocynaceae and Fabaceae stand out among the top food plant families by the diversity of plant parts that are used as food items. This may also partly explain the prominence and importance of these two plant families in the analyses and results reported here.

The Khoekhoe show a preference for roots, followed by fruits and leaves (Figure 6). They have Fabaceae, Poaceae and Apocynaceae as the top available edible families but mostly utilize the Apocynaceae, Geraniaceae, Iridaceae, Asphodelaceae and Lobeliaceae, i.e. families with a large proportion of geophytes. The Fabaceae, Poaceae, Cucurbitaceae and Malvaceae are well below the levels predicted by the regression analysis. The Cape Khoekhoe group has a distribution range extending into the Fynbos region (Figure 1) and this is the only cultural group that has underground storage organs (mainly from Iridaceae and Apocynaceae) as the most popular plant part used (Welcome & Van Wyk, 2019). These edible underground storage organs are usually eaten raw or roasted (Archer, 1982, 1994). With regards to edible taxa, there are more Fabaceae (69 taxa) and Poaceae (61 taxa) than Apocynaceae (50 taxa) and Iridaceae (15 taxa). However, the most important families used by the Cape Khoekhoe, according to Archer (1982, 1994) are the Apocynaceae (nine species), and Geraniaceae and Iridaceae (both seven species). The importance of underground storage organs for the Cape Khoekhoe is apparently not due to the dominance of these taxa within the distribution range but rather due to a preference for underground storage organs. There is much archaeological evidence for the use of underground storage organs in the diets of the Khoe and San peoples. These underground storage organs are considered to have been a valuable source of carbohydrates (Singels et al., 2016).

The apparent preference for underground storage organs could also be due to their availability in the dry summer months, when food may be scarce. However, it is noteworthy that the carbohydrate content of utilized geophytes (Figures 7, a1) appears to be higher within the distribution range of this cultural group (Figures 7, a2 and b2) than in the rest of the FSA region (Figures 7, a3 and b3). The diversity of underground storage organs in the Cape flora is well-known (Procheş, Cowling, & du Preez, 2005). Of the 24 species which have edible underground storage organs high in carbohydrate values, eight of them are from the Iridaceae (*Babiana curviscapa* G.J.Lewis, *B. dregei* Baker, *B. pubescens* (Lam.) G.J.Lewis, *Moraea fugax* (D.Delaroche) Jacq., *M. longifolia* (Jacq.) Pers., *M. serpentina* Baker and *M. unguiculata* Ker Gawl.) and four are from the Geraniaceae family (*Pelargonium antidysentericum*

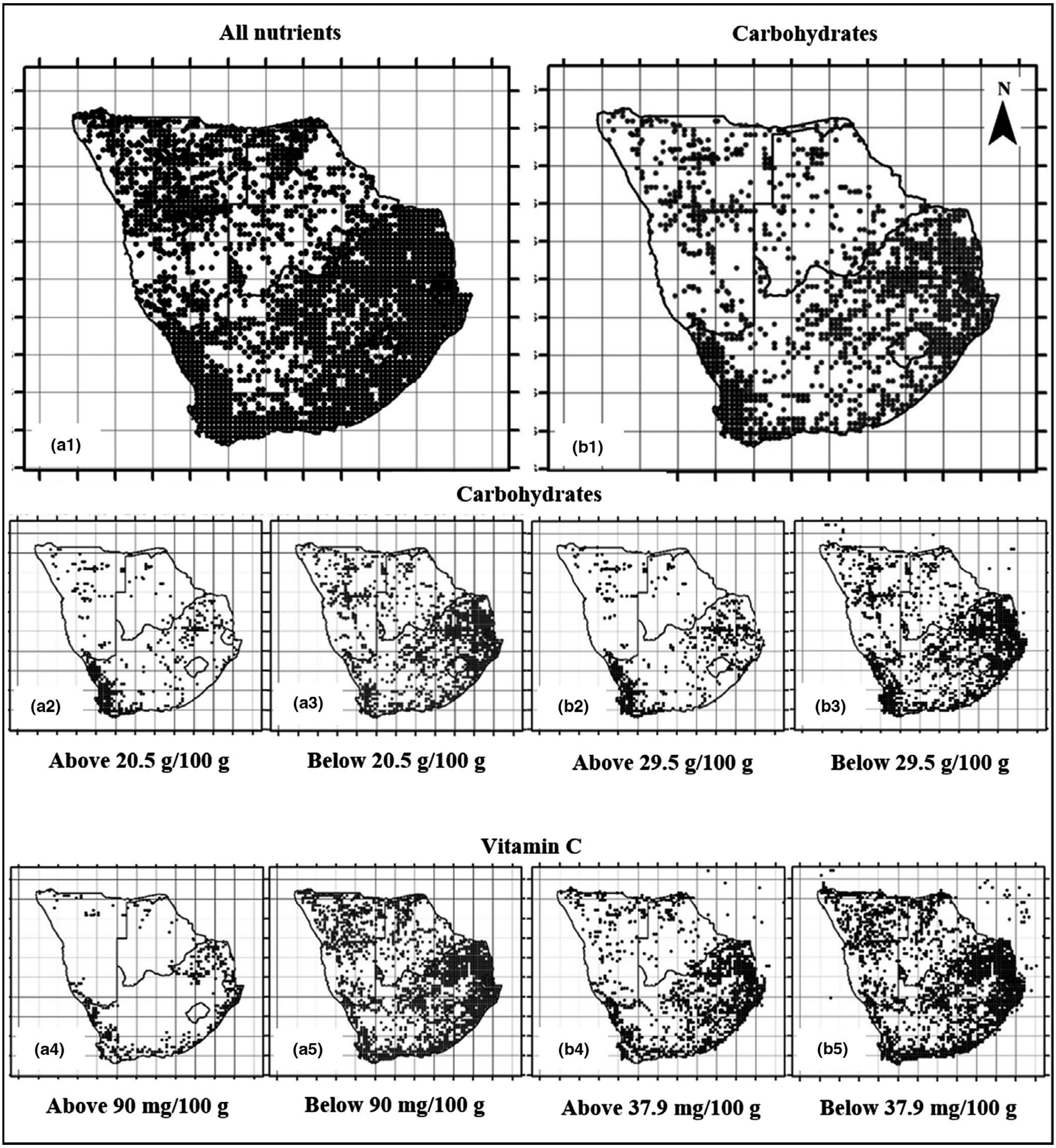

FIGURE 7 The spatial distribution of southern African plant taxa with available nutritional data for all nutrients (a1), carbohydrates (a2–a3, b2–b3) and vitamin C (a4–a5, b4–b5). Maps a1–a5 are based on Wehmeyer (1986), with a2–a5 showing distributions of taxa above and below arbitrary cut-off values; b1–b5 based on FAO (1968), Wehmeyer (1986), Archer (1994) and Odhav et al. (2007), with b2–b5 showing distributions of taxa above and below average values

(Eckl. & Zeyh.) Kostel., *P. triste* (L.) L'Hér., *P. incrassatum* (Andrews) Sims, and *P. rapaceum* (L.) L'Hér.) and only one from Apocynaceae (*Stenostelma capense* Schltr.). Three of the six underground storage organs studied by Singels et al. (2016) as part of a foraging study in the southern Cape, have above average carbohydrate values and are from the Iridaceae. These are *Chasmanthe aethiopica* (L.) N.E.Br., *Ferraria crispa* Burm. and *Watsonia meriana* (L.) Mill. This brings the total of species with underground storage organs with high carbohydrate values in the Western Cape region from the Iridaceae family to 11. The spatial distribution of plants

TABLE 4 Results of a regression analysis of the food plant families of the Flora of Southern Africa region (available versus edible taxa)

Family	All taxa	Edible taxa	Predicted	Residual
Apocynaceae	860	186	54	132
Anacardiaceae	152	76	11	65
Fabaceae	2,221	199	138	61
Malvaceae	492	76	32	44
Ebenaceae	65	49	6	43
Cucurbitaceae	94	41	7	34
Rubiaceae	360	55	24	31
Lobeliaceae	168	42	12	30
Amaranthaceae	280	47	19	28
Moraceae	47	32	5	27
Thymelaeaceae	215	2	15	−13
Cyperaceae	547	22	35	−13
Hyacinthaceae	512	16	33	−17
Proteaceae	415	9	27	−18
Orchidaceae	560	17	36	−19
Restionaceae	356	1	24	−23
Scrophulariaceae	895	17	57	−40
Asteraceae	2,854	126	177	−51
Aizoaceae	1,502	41	94	−53
Ericaceae	988	4	62	−58

Note: A selection of the 10 highest and 10 lowest residuals is shown.

TABLE 5 Results of two regression analyses of food plant families in the Ju|'hoan language region (available taxa [A] versus edible taxa [E], and edible taxa [E] versus taxa actually utilized [U])

Family	A	E	P	R	Family	E	U	P	R
Fabaceae	160	48	34	14	**Apocynaceae**	20	18	6	12
Malvaceae	75	29	16	13	**Cucurbitaceae**	15	15	5	10
Apocynaceae	38	20	8	12	**Combretaceae**	13	8	4	4
Cucurbitaceae	19	15	4	11	Fabaceae	48	16	15	1
Combretaceae	22	13	5	8	Asphodelaceae	3	2	1	1
Amaranthaceae	30	12	7	5	Loganiaceae	3	2	1	1
Pedaliaceae	11	8	3	5	Orchidaceae	3	2	1	1
Ebenaceae	8	7	2	5	Iridaceae	7	3	2	1
Iridaceae	10	7	2	5	Rubiaceae	7	3	2	1
Convolvulaceae	30	11	7	4	Olacaceae	4	2	1	1
Molluginaceae	7	0	2	−2	Burseraceae	4	0	1	−1
Polygalaceae	7	0	2	−2	Convolvulaceae	11	2	3	−1
Hydrocharitaceae	8	0	2	−2	Commelinaceae	5	0	2	−2
Lythraceae	13	1	3	−2	Moraceae	5	0	2	−2
Orobanchaceae	12	0	3	−3	Phyllanthaceae	5	0	2	−2
Scrophulariaceae	12	0	3	−3	Cyperaceae	9	1	3	−2
Cyperaceae	69	9	15	−6	Asteraceae	7	0	2	−2
Asteraceae	68	7	14	−7	Pedaliaceae	8	0	2	−2
Acanthaceae	45	2	10	−8	Amaranthaceae	12	1	4	−3
Poaceae	242	36	51	−15	Poaceae	36	0	11	−11

Note: P = predicted values, R = residuals (E − P and U − P). A selection of the 10 highest and 10 lowest residuals is shown. The most important families that are apparently selected for food are given in bold; those apparently avoided are underlined.

TABLE 6 Results of two regression analyses of food plant families in the Khoekhoe language region [available taxa (A) versus edible taxa (E), and edible taxa (E) versus taxa actually utilized (U)]

Family	A	E	P	R	Family	E	U	P	R
Apocynaceae	149	50	19	31	**Geraniaceae**	9	7	1	6
Fabaceae	387	69	48	21	**Iridaceae**	15	7	1	6
Cucurbitaceae	43	25	6	19	**Asphodelaceae**	11	6	1	5
Malvaceae	171	39	21	18	**Apocynaceae**	50	9	4	5
Anacardiaceae	38	22	5	17	**Lobeliaceae**	2	5	0	5
Convolvulaceae	45	19	6	13	**Anacardiaceae**	22	6	2	4
Amaranthaceae	137	30	17	13	Loranthaceae	4	3	0	3
Poaceae	403	61	50	11	Crassulaceae	8	3	1	2
Lamiaceae	61	19	8	11	Oxalidaceae	10	3	1	2
Combretaceae	15	12	2	10	Hyacinthaceae	13	3	1	2
Zygophyllaceae	55	4	7	−3	Rubiaceae	8	0	1	−1
Pottiaceae	25	0	3	−3	Asparagaceae	9	0	1	−1
Euphorbiaceae	101	9	13	−4	Pedaliaceae	9	0	1	−1
Parmeliaceae	28	0	4	−4	Polygonaceae	9	0	1	−1
Crassulaceae	96	8	12	−4	Combretaceae	12	0	1	−1
Amaryllidaceae	55	2	7	−5	Cucurbitaceae	25	1	2	−1
Acanthaceae	132	4	17	−13	Convolvulaceae	19	0	2	−2
Scrophulariaceae	160	1	20	−19	Fabaceae	69	4	6	−2
Asteraceae	460	32	57	−25	Malvaceae	39	1	3	−2
Aizoaceae	312	9	39	−30	Poaceae	61	0	5	−5

Note: P = predicted values, R = residuals (E − P and U − P). A selection of the 10 highest and 10 lowest residuals is shown. The most important families that are apparently selected for food are given in bold; those apparently avoided are underlined.

TABLE 7 Results of two regression analyses of food plant families in the Venda language region [available taxa (A) versus edible taxa (E), and edible taxa (E) versus taxa actually utilized (U)]

Family	A	E	P	R	Family	E	U	P	R
Anacardiaceae	40	32	8	24	**Malvaceae**	40	22	11	11
Apocynaceae	137	48	26	22	**Cucurbitaceae**	26	17	7	10
Cucurbitaceae	37	26	7	19	**Amaranthaceae**	21	15	6	9
Moraceae	21	18	4	14	**Solanaceae**	17	10	5	5
Malvaceae	144	40	27	13	**Moraceae**	18	10	5	5
Amaranthaceae	48	21	9	12	**Myrtaceae**	10	7	3	4
Ebenaceae	16	14	3	11	Rutaceae	2	4	1	3
Solanaceae	35	17	7	10	Urticaceae	6	5	2	3
Convolvulaceae	46	19	9	10	Rubiaceae	28	11	8	3
Capparaceae	20	13	4	9	Rosaceae	4	4	1	3
Pottiaceae	19	0	4	−4	Iridaceae	7	0	2	−2
Euphorbiaceae	96	14	18	−4	Polygonaceae	7	0	2	−2
Pteridaceae	26	1	5	−4	Asparagaceae	8	0	2	−2
Orobanchaceae	22	0	5	−5	Asphodelaceae	12	1	3	−2
Asteraceae	290	48	54	−6	Capparaceae	13	1	4	−3
Scrophulariaceae	55	4	11	−7	Cyperaceae	13	1	4	−3
Orchidaceae	67	6	13	−7	Apocynaceae	48	10	13	−3
Cyperaceae	112	13	21	−8	Asteraceae	48	10	13	−3
Acanthaceae	107	9	20	−11	Fabaceae	70	14	20	−6
Poaceae	331	44	61	−17	Poaceae	44	6	12	−6

Note: P = predicted values, R = residuals (E − P and U − P). A selection of the 10 highest and 10 lowest residuals is shown. The most important families that are apparently selected for food are given in bold; those apparently avoided are underlined.

with exceptionally high levels of vitamin C also seem to show some pattern, with a higher concentration along the coastal regions of southern Africa (Figures 7, a4 and b4) than in the rest of the region (Figures 7, a5 and b5).

Venda people were mostly dependent on agriculture for their subsistence, therefore maize and other grains were an important component of their diet (Gilbert, 1995). These grains must have provided enough carbohydrates so that there was no need to depend on edible roots. Figure 6 shows that the Venda prefer edible fruits and leaves and these are mostly from the Malvaceae, Cucurbitaceae and Amaranthaceae (Figure 4 and Table 7). These three families have a large percentage of exotic edible species (Welcome & Van Wyk, 2019). The preference for ruderal weeds, which are usually cooked as spinach, by the Venda culture is apparent when comparing the survey done by Mabogo in 1990 and the one done by Magwede et al. in 2018. Of the 110 edible plants recorded by Mabogo (1990) as being used by the Venda people, 13 are exotic species. In Magwede et al. (2018), 265 edible plants are recorded, of which 79 are exotic, cultivated or invasive species. There is apparently a large increase of ruderal weeds in the Venda diet since 1990. Of the 15 species listed by Mabogo (1990) and not by Magwede et al. (2018), only one is an exotic species, *Melia azedarach* L., and the other 14 are indigenous. Archer (1982, 1994) recorded no exotic species being used by the Khoekhoe people and Leffers (2003) recorded two exotic, but not cultivated, species being used by the Ju|'hoan (*Corchorus tridens* L., which was only mentioned by one person during the survey, and *Ancylanthos rubiginosus* Desf., with edible fruits).

Recent studies (e.g. Magwede et al., 2018; Moffett, 2010; Moteetee & Van Wyk, 2006) have shown that food plant species have not yet been comprehensively recorded. Furthermore, Williams and Crouch (2017) suggested that available distribution data based on herbarium specimens are not always representative and therefore not considered to be completely accurate. The exploration of southern Africa has not yet been comprehensive, so that there are many under-collected areas, especially in remote places (and the identification of some taxa is problematic). Since the method uses GIS software, the results are reproducible and can be repeated once more accurate or complete data become available. Nevertheless, the currently available data, incomplete as it may be, show interesting trends suggesting intentional selection.

5 | CONCLUSIONS

Sufficient data appear to be available to dismiss cultural ancestry and the floristic environment as the main drivers of food plant selection and it appears that subsistence strategy is a more plausible explanation. For southern Africa as a whole, the Apocynaceae, Anacardiaceae, Fabaceae and Malvaceae showed high residual values in the regression analysis, indicating a preference for these families. The Ericaceae, Aizoaceae, Asteraceae and Scrophulariaceae have residual values far below the predicted.

No significant correlation was found between edible and utilized species. The regression analyses of the three chosen cultural groups (Ju|'hoan, Khoekhoe and Venda) showed remarkable differences in the choice of taxa which seem to not only be independent of the total availability of taxa but also independent of available *edible* taxa. The second regression analyses for the three cultures, where edible taxa were used as the independent variable, were all significant ($p < .001$) but showed relatively low R^2 values, suggesting that only a part of the variance is explained by the data, and that the relationship between what is edible and actually utilized reveals intentional selection. There are striking differences between the cultures that seem to give new perspectives on the development of human food ecology, from ancient hunting and gathering (represented by the nomadic Ju|'hoan) to pastoralists (represented by the nomadic Khoekhoe), to agrarians (represented by the sedentary Venda). The differences appear to be related to the specific plant parts that are used (e.g., leaves versus underground storage organs) or the way in which they are used (e.g., foraged fresh leaves versus cooked leaves; fresh and roasted roots and bulbs versus fresh roots and bulbs versus hardly any roots or bulbs). The Ju|'hoan and Khoekhoe show a preference for Apocynaceae, which have mostly edible underground storage organs, while the Venda culture shows a preference for ruderal vegetables of the Malvaceae and Amaranthaceae. The diversity of geophytes in the Khoekhoe culture is striking, and seems to reflect the summer-aridity of their habitat. Edible fruits high in Vitamin C content are mostly distributed along the coast of southern Africa and those taxa with underground storage organs high in carbohydrate content are mostly distributed in the summer-arid western region. Nutritional value may therefore have contributed to the intentional plant selection of the Khoekhoe culture for underground storage organs from the Apocynaceae and Iridaceae.

The results appear to reflect the extreme diversity of both the flora and the cultures of southern Africa. The data and analyses presented here are the first broad scale comparison of edible plant use for the cultural groups of southern Africa and has produced a dataset that is compatible with any use category checklist. Once more complete distributional and ethnobotanical data become available, more sophisticated analyses can be attempted by simply updating the detailed food plant dataset presented here as an open file. For example, the intriguing differences between hunter-gatherers, pastoralists and agrarians are of global significance and should be studied in more detail.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in DRYAD at https://doi.org/10.5061/dryad.cc2fqz62g.

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REFERENCES

Archer, F. M. (1982). 'n Voorstudie in verband met die eetbare plante van die Kamiesberge. *Journal of South African Botany*, *48*, 433–449.

Archer, F. M. (1994). *Ethnobotany of Namaqualand: The Richtersveld*. M.A. dissertation, University of Cape Town, Cape Town.

Bennet, B. C., & Husby, C. E. (2008). Patterns of medicinal plant use: An examination of the Ecuadorian Shuar medicinal flora using contingency table and bionomial analyses. *Journal of Ethnopharmacology*, *116*, 422–430.

De Vynck, J. C., Van Wyk, B.-E., & Cowling, R. M. (2016). Indigenous edible plant use by contemporary Khoe-San descendants of South Africa's Cape South Coast. *South African Journal of Botany*, *102*, 60–69. https://doi.org/10.1016/j.sajb.2015.09.002

Dlamini, B. (1981). *Swaziland flora: Their local names and uses*. Mbabane: Ministry of Agriculture and co-operatives – Forestry section.

Dold, A. P., & Cocks, M. L. (2000). Indigenous plant use of the amaXhosa people on the Eastern Border of the Great Fish River Reserve, Eastern Cape. *Annals of Eastern Cape Museum*, *1*, 26–53.

Earley-Spadoni, T. (2017). Spatial history, deep mapping and digital storytelling: Archaeology's future imagined through an engagement with the digital humanities. *Journal of Archaeological Science*, *84*, 95–102. https://doi.org/10.1016/j.jas.2017.05.003

Food and Agriculture Organization of the United Nations & US Department of Health Education and Welfare (FAO). (1968). *Food composition table for use in Africa*. Rome: FAO. Retrieved from https://www.fao.org/docrep/003/X6877E/X6877E00.htm

Gaoue, O. G., Coe, M. A., Bond, M., Hart, G., Seyler, B. C., & McMillen, H. (2017). Theories and major hypotheses in ethnobotany. *Economic Botany*, *71*, 269–287. https://doi.org/10.1007/s12231-017-9389-8

Gerstner, J. (1938). A preliminary checklist of Zulu names of plants with short notes. *Bantu Studies*, *12*, 215–236, 321–342.

Gerstner, J. (1939). A preliminary checklist of Zulu names of plants with short notes. *Bantu Studies*, *13*, 49–64, 131–149, 307–326.

Gerstner, J. (1941). A preliminary checklist of Zulu names of plants with short notes. *Bantu Studies*, *15*, 277–301, 369–383.

Gilbert, C. L. (1995). *Diet and subsistence patterns in the Later Iron Age of South Africa: An analysis of stable carbon and nitrogen isotopes and the incidence of dental caries*. M.A. dissertation, University of Cape Town, Cape Town.

Kirby, K. R., Gray, R. D., Greenhill, S. J., Jordan, F. M., Gomes-Ng, S., Bibiko, H.-J., … Gavin, M. C. (2016). D-PLACE: A global database of cultural, linguistic and environmental diversity. *PLoS ONE*, *11*(7), 1–14. https://doi.org/10.1371/journal.pone.0158391

Leffers, A. (2003). *Gemsbok Bean and Kalahari Truffle. Traditional plant use by Jul'hoansi in north-eastern Namibia*. Namibia: Macmillan Education Namibia Publishers.

Lewis, M. P. (2009). *Ethnologue: Languages of the world* (16th ed.). Dallas, TX: SIL International.

Liengme, C. A. (1981). Plants used by the Tsonga people of Gazankulu. *Bothalia*, *13*, 501–518. https://doi.org/10.4102/abc.v13i3/4.1357

Liengme, C. A. (1983). A survey of ethnobotanical research in southern Africa. *Bothalia*, *14*, 621–629. https://doi.org/10.4102/abc.v14i3/4.1219

Lock, G., & Pouncett, J. (2017). Spatial thinking in archaeology: Is GIS the answer? *Journal of Archaeological Science*, *84*, 129–135. https://doi.org/10.1016/j.jas.2017.06.002

Low, A. B., & Rebelo, A. G. (Eds.) (1996). *Vegetation of South Africa, Lesotho and Swaziland*. Pretoria: Department of Environmental Affairs and Tourism.

Mabogo, D. E. N. (1990). *The ethnobotany of the Vhavenda*. MSc thesis, University of Pretoria. Pretoria.

Magwede, K., Van Wyk, B.-E., & Van Wyk, A. E. (2018). An inventory of Vhavenḓa useful plants. *South African Journal of Botany*, *122*, 57–89. https://doi.org/10.1016/j.sajb.2017.12.013

Malan, J. S., & Owen Smith, G. L. (1974). The ethnobotany of Kaokoland. *Cimbebasia Ser.B*, *2*(5), 131–178.

Mantel, N. (1967). The detection of disease clustering and a generalized regression approach. *Cancer Research*, *27*, 209–220.

Marean, C. W. (2010). Pinnacle Point Cave 13B (Western Cape Province, South Africa) in context: The Cape Floral Kingdom, shellfish, and modern human origins. *Journal of Human Evolution*, *59*, 425–443. https://doi.org/10.1016/j.jhevol.2010.07.011

Moerman, D. E. (1979). Symbols and selectivity: A statistical analysis of native American medical ethnobotany. *Journal of Ethnopharmacology*, *1*, 111–119. https://doi.org/10.1016/0378-8741(79)90002-3

Moerman, D. E. (1991). The medicinal flora of native North America: An analysis. *Journal of Ethnopharmacology*, *81*, 1–42. https://doi.org/10.1016/0378-8741(91)90141-Y

Moffett, R. (2010). *Sesotho plant and animal names and plants used by the Basotho*. Bloemfontein: Sun Press.

Moteetee, A., & Van Wyk, B.-E. (2006). Sesotho names for exotic and indigenous edible plants in southern Africa. *Bothalia*, *36*, 25–32. https://doi.org/10.4102/abc.v36i1.328

Mucina, L., & Rutherford, M. C. (Eds.). (2006). *The vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19*. Pretoria: South African National Biodiversity Institute.

Murdock, G. P., Textor, R., Barry III, H., White, D. R., Gray, J. P., & Divale, W. T. (1999). Ethnographic Atlas. *World Cultures*, *10*, 24–136 (codebook).

Odhav, B., Beekrum, S., Akula, U., & Baijnath, H. (2007). Preliminary assessment of nutritional value of traditional leafy vegetables in KwaZulu-Natal, South Africa. *Journal of Food Composition and Analysis*, *20*, 430–435. https://doi.org/10.1016/j.jfca.2006.04.015

Oksanen, J., Kindt, R., Legendre, P., O'Hara, B., Simpson, G. L., Solymos, P., …Wagner, H. (2009). *Vegan: community ecology package*. R package version 1.15–4. Retrieved from https://cran.r-project.orghttps://vegan.r-forge.r-project.org/

Procheş, S., Cowling, R. M., & du Preez, D. R. (2005). Patterns of geophyte diversity and storage organ size in the winter-rainfall region of southern Africa. *Diversity and Distributions*, *11*, 101–109. https://doi.org/10.1111/j.1366-9516.2005.00132.x

Quin, P. J. (1959). *Food and feeding habits of the Pedi*. Johannesburg: Witwatersrand University Press.

Roberts, L. (2016). Deep mapping and spatial anthropology. *Humanities*, *5*(5), 1–7. https://doi.org/10.3390/h5010005

Rodin, R. J. (1985). The ethnobotany of the Kwanyama Ovambos. *Monographs in Systematic Botany from the Missouri Botanical Garden*, *9*, 1–161.

Roodt, V. (1992). *The shell field guide to the common trees of the Okavango Delta and Moremi Game Reserve*. Botswana: Shell Oil.

Roodt, V. (1998). *Common wild flowers of the Okavango Delta: Medicinal uses and nutritional value*, Part 2 of Shell field guide series. Botswana: Shell Oil.

Ruth, M. (2016). *Map of National Boundaries for Africa* [vector geospatial dataset] 2016. Retrieved from ArcGIS website. Downloaded on 22 April 2017.

Saslis-Lagoudakis, C. H., Hawkins, J. A., Greenhill, S. J., Pendry, C. A., Watson, M. F., Tuladhar-Douglas, W., … Savolainen, V. (2014). The evolution of traditional knowledge: environment shapes medicinal plant use in Nepal. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 1–7.

Singels, E., Potts, A. J., Cowling, R. M., Marean, C. W., De Vynck, J., & Esler, K. J. (2016). Foraging potential of underground storage organ plants in the southern Cape, South Africa. *Journal of Human Evolution*, *101*, 79–89. https://doi.org/10.1016/j.jhevol.2016.09.008

Sorensen, T. (1948). A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish Commons. *Biologiske Skrifter/Kongelige Danske Videnskabernes Selskab*, *5*, 1–34.

South African National Biodiversity Institute (SANBI). (2012). Vegetation Map of South Africa, Lesotho and Swaziland [vector geospatial dataset] 2012. Retrieved from Biodiversity GIS website, downloaded on 22 April 2017.

South African National Biodiversity Institute (SANBI). (2016). Botanical Database of Southern Africa (BODATSA) [dataset].

Trifkovic, V. (2006). Persons and landscapes: Shifting scales of landscape archaeology. In G. Lock, & B. Molyneaux (Eds.), *Confronting scale in archaeology: Issues of theory and practice* (pp. 257–271). New York: Springer.

Van Wyk, B.-E. (2002). A review of ethnobotanical research in southern Africa. *South African Journal of Botany*, *68*, 1–13. https://doi.org/10.1016/S0254-6299(15)30433-6

Van Wyk, B., Van den Berg, E., Palgrave, M. C., & Jordaan, M. (2011). *Dictionary of names for southern African trees*. Pretoria: Briza Publications.

Van Wyk, B., & Van Wyk, P. (2013). *Field guide to trees of southern Africa*. Cape Town: Struik Nature.

Veness, C. (n.d.). *Moveable type: Distance between pair of latitude/longitude points*. Retrieved from https://www.movable-type.co.uk/scripts/latlong.html

Wehmeyer, A. S. (1986). *Edible wild plants of southern Africa: data on the nutrient contents of over 300 species*. Unpublished report, CSIR (August 1986).

Welcome, A. K., & Van Wyk, B.-E. (2019). An inventory and analysis of the food plants of southern Africa. *South African Journal of Botany*, *122*, 136–179. https://doi.org/10.1016/j.sajb.2018.11.003

White, F. (1983). *The vegetation of Africa: A descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa*. Michigan: Unesco.

Williams, V. L., & Crouch, N. R. (2017). Locating sufficient plant distribution data for accurate estimation of geographic range: The relative value of herbaria and other sources. *South African Journal of Botany*, *109*, 116–127. https://doi.org/10.1016/j.sajb.2016.12.015

BIOSKETCHES

Ashton K. Welcome: My research interests include taxonomy (especially in the Malvaceae plant family) and ethnobotany (especially relating to food plants) as well as investigating tools and software that can be used to advance research and the passing down of knowledge in the future.

Ben-Erik Van Wyk: The focus of my research has broadened from highly specialized plant taxonomy and chemosystematics/molecular systematics (mainly Fabaceae and Apiaceae) to more generalized and interdisciplinary research into useful plants and economic botany. My aim has always been to generate practical and useful research publications in plant taxonomy and economic botany.

Author contributions: A.W. collected the data, did all the analyses and wrote the first rough draft; B.-E.VW conceptualized the study and wrote the final draft manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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