TOWARDS AN UNDERSTANDING OF PLANT RARITY IN KWAZULU-NATAL, SOUTH AFRICA

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DECLARATION

This thesis is submitted, in accordance with the regulations of the University of the Witwatersrand, Johannesburg in fulfilment of the requirements for the degree of Master of Science. The work described in this thesis was carried out by me, except where otherwise acknowledged, and has not been submitted for any degree or examination to any other university or institution.

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ABSTRACT

The persistence of rare plants is an important dimension in the conservation of biodiversity. Consequently an improved understanding of the nature and determinants of plant rarity and its relation with vulnerability to extinction could provide a basis for “proactive conservation” instead of the present day tendency for conservation actions to be “reactive”.

In this dissertation I explore the relation between plant rarity and anthropogenic pressures (land transformation and use), biophysical factors, and plant traits in KwaZulu-Natal Province. Rarity was defined as the product of plant species abundance (population size) and its distribution (extent of occurrence). A number of *a priori* hypotheses regarding plant rarity were developed from the literature and these were then tested on a sample of plant species from KwaZulu-Natal. Species were selected in a stratified random manner to include species from different levels of threat and rarity or commonness. As the interest of this study was KwaZulu-Natal, only KwaZulu-Natal records were used for the analysis. Although the study suffered from a paucity of data particularly on the biological traits and behaviour of each species I was able to explore rarity in terms of seed dispersal distance, stress tolerance, habitat specificity and ecological niche width. I also explored potential island effects based on a species affinity to isolated erosional land surfaces and the anthropogenic effects of utilization and land transformation.

To get an initial insight into relations, rarity was compared with each explanatory variable independently prior to using a multiple regression analysis approach aimed at understanding the potential interactive effects of suitable variables on rarity. Three different analytical techniques were used to provide a more robust understanding of the variable associations. These included Regression tree analysis (CART Salford Systems Inc., USA) and two generalized linear regression approaches; Generalized Linear Modelling (GLM) and Generalized Additive Modelling (GAM).

All three multiple regression methods indicated that niche width had the strongest influence on rarity. Although Land Surface was shown to be the second strongest variable this, according to the GLM and GAM analyses, was due to a positive correlation between species with no affinity to land surface and species commonness. Visual representation of the regression tree analysis showed inconsistent partitioning of this variable throughout the tree indicating that land surfaces are not good predictors of rarity.

Although the relation between Rarity Index and Habitat Transformation is not linear it was shown to be significant ($p < 0.1 (p = 0.0549)$) after “smoothing” in GAM analysis. A smoothing curve on the bivariate analysis and the regression tree analysis indicated that species start to become rare after approximately 36% of their habitat is transformed.

While GLM and GAM showed little or no relation between life history, dispersal distance, habitat specificity and rarity, the regression tree selected habitat specificity as the third most important splitter in the tree and dispersal distance was selected as a primary splitter for species with a niche width of greater than four. These differences observed in the three multiple regression analyses highlight the value of using more than one method to explore relations in ecological data.

Considering all three analyses Niche Width is the strongest determinant of Rarity in KwaZulu-Natal, followed by Habitat Transformation and then Habitat Specificity. This improved understanding of the determinants of rarity will enhance our ability to prioritise plant species for conservation action.

Key Words: ecological niche width, habitat specificity, habitat transformation, rarity, seed dispersal distance, stress tolerance, human use.

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Contents

List of Figures

List of Tables

1. **Introduction**

The continued decline in the world's biodiversity and loss of species due to human actions have been widely documented with the rate of species extinctions being reported as comparable to past extinction events such as the Cretaceous Tertiary mass extinction 65 million years ago (Sodhi & Ehrlich, 2010). Attempts by the global community to reduce the rate of extinction have included the development of global treaties, protocols, conventions and legislation. In addition to this the conservation community has developed a number of tools to understand and manage biodiversity loss. These tools vary from the development of categorization systems that list biodiversity elements (e.g. species and vegetation types) according to their extinction risk, to tools that assist in the selection of priority areas for conservation (Margules & Pressey, 2000). The lack of sufficient financial resources available for the conservation of biodiversity has forced conservationists to be systematic, objective and transparent in their prioritization of conservation efforts. Decisions on which species to spend resources on and which ones to "Let go" (Marris, 2009) therefore must be logical, explicit and transparent.

A number of systems or approaches have been used to prioritize species for conservation action including Red Listing (Possingham et al., 2002a), surrogate and indicator species (Lambeck, 1997; Loyola & Kubota, 2007; Reyers & McGeoch, 2007; Wiens et al., 2008; Arponen, 2009; Larsen et al., 2009), multiple species approaches, systems that use threats and drivers (Possingham et al., 2002b; Regan et al., 2008) and triage to direct prioritization. Triage for nature conservation has been adapted from medical crisis management to manage the conservation crisis of today and it is implicit that with "finite" conservation funds extinction of some species is a possibility (Bottrill *et al.,* 2008; Joseph *et al.*, 2008; Bottrill *et al,* 2009). Bottrill et al. (2008) defined conservation triage as the "process of prioritizing the allocation of limited resources to maximize conservation returns by accounting for the value, costs, benefits and likelihood of success of alternative conservation actions". Conservation triage and resource allocation species prioritization methods distinguish themselves from conservation risk methods by accepting potential loss of species, but attempt to maximize retention of biodiversity with the limited resources available for conservation action.

Although these approaches are different, a common selection criterion often used is the level of rarity or ‘uncommonness’ of a species. The IUCN Red listing process, which is designed to determine the probability of a species becoming extinct under the current circumstances, incorporates the demographic rarity (population size) and geographic rarity (the area of occurrence and area of extent) of a species as criteria to list species (IUCN, 2008; Mace et al., 2008). In order to engage in conservation triage, a ‘relative value’ needs to be placed on each species and rarity (Keith et al., 2007) is often included as one of the criteria used to quantify this.

Rare species are not necessarily threatened and not all threatened species are rare (Oredsson, 1997). Therefore an improved understanding of the nature and determinants of a species’ rarity and its vulnerability to extinction could assist in providing a mechanism for prioritizing rare species for conservation action. Conservation measures applied to rare species are often dependent on the type and causes of rarity. ‘Naturally rare’ species are distinguished from those species that are driven to rarity by known human impacts which are termed ‘anthropogenically rare’. Species that are ‘anthropogenically rare’ might require different management prescriptions from those that are ‘naturally rare’ (Pärtel et al., 2005). Where preservation might be the only action necessary for the conservation of species that are rare due to biogeographic reasons (Witkowski & Lamont, 1997), other management prescriptions such as a change in fire regime, protection from use, restoration and re-establishment may be applicable to ‘anthropogenically rare’ species depending on the causes of rarity (Pärtel et al., 2005).

The province of KZN (KZN) in South Africa has more than 6000 species of plants (Scott-Shaw, 1999), of which 205 have been listed in the 2009 Red List of South African Plants (SANBI, 2013) as threatened, i.e. Critically Endangered, Endangered or Vulnerable, and a further 242 have been listed as species of conservation concern which “include all species that have a high conservation importance in terms of preserving South Africa's high floristic diversity and include not only threatened species, but also those classified in the categories

Extinct in the Wild (EW), Regionally Extinct (RE), Near Threatened (NT), Critically Rare, Rare, Declining and Data Deficient (Species with insufficient information (DDD))” (http://redlist.sanbi.org/). A total of 5158 plant species from KZN were assessed in the 2009 national red listing process, of which 400 are endemic to the province. In addition to this 166 species are near endemics with localized distributions on the borders of South Africa and Lesotho, Swaziland and Mozambique.

Ezemvelo KZN Wildlife is a statutory body mandated to conserve representative samples of the biodiversity of the province of KZN. In reality, the resources given to the organization are not adequate to do this without some loss. To be effective the organization must prioritize actions that are going to yield the best result for resource expenditure. All components of biodiversity need to be considered in this prioritization process but it is my role as the Threatened Species Scientist for plants to advise the organization on plant conservation. My overall focus is to develop a mechanism to prioritize plant species for conservation action. As the level of a species rarity is an important criterion to consider in this endeavour, this research seeks to improve our understanding of the determinants of plant rarity in KZN.

1.1. **Defining Plant Rarity**

Rare is defined in the Oxford dictionary as “(of a thing) not found in large numbers and so of interest or value” or “not done, seen, happening, etc. very often”. In conservation ecology rarity has not been defined as simply as this, but rather with a number of different components and thresholds being used to determine whether a species is rare or not (Gaston, 1994; Hartley & Kunin, 2003; Reilly, 2010). These include geographic range, abundance, habitat specificity, habitat occupancy, taxon age or persistence, threatened status, gene flow, genetic diversity and endemism (Gaston, 1997; Hartley & Kunin, 2003; Reilly, 2010), which have been used independently (Nathan et al., 1996; Murray et al., 2002; Ohlemüller et al., 2008) or in a matrix combined to form a number of types of rarity (Rabinowitz, 1981; Fiedler & Ahouse, 1992; Benayas et al., 1999; Reilly, 2010).

Possibly the most well-known framework characterizing rarity is Rabinowitz's (1981) seven forms of rarity, in which three components; geographic range, abundance and habitat specificity are combined in a matrix to classify species into forms of rarity. Other more recent frameworks were developed by Fiedler and Ahouse (1992) in which spatial distribution and longevity were used as components, and Benayas et al. (1999) who added habitat occupancy or the ability of a species to occupy a larger or smaller fraction of its potential suitable habitats, to Rabinowitz's three components. These frameworks include both pattern (geographic range and abundance) and process or causes of rarity (longevity, habitat specificity and habitat occupancy) to describe different forms of rarity (Reilly, 2010). The inclusion of certain processes in the definition of rarity could be considered as "putting the cart before the horse" as it presupposes the causes of rarity (Gaston, 1997).

The general consensus is that species with "a low abundance and small range" are rare (Gaston, 1994; Fiedler et al., 2007). Abundance is sometimes measured as density, percentage canopy cover, biomass, number of populations or number of individuals and range is measured as extent of occurrence or area of occupancy (Murray et al., 2002). Regardless of this, both these measures of rarity (or commonness) are quantifiable and in reality all species fall somewhere along a continuum from low range or abundance to high range or abundance (Gaston, 1994). Research has shown that in an assemblage of species a very small percentage of species are in fact common, the majority are rare (Gaston, 2011; Verberk, 2012). This distribution of rare to common species varies with ecosystem. For example Verbeck (2012) showed that saltmarshes have a very skew species abundance distribution compared with a wetland system (Fig. 1).

In order to select species for conservation effort, a number of different thresholds have been used to designate a species to a rarity category. These cut-offs or thresholds are often related to the spatial scale of the study area (Gaston, 1994; Hartley & Kunin, 2003) and consequently rarity is considered as a "scale-dependent concept" (Abarca & Allison, 2000). Gaston (1994) recommended using a 'relative' cut-off of 25% of species with the smallest abundance or range size in the assemblage. Although he acknowledged that this figure was somewhat arbitrary, his justification for its use was that it is "practical, convenient and comparative". Alternatively cut-off points have been developed by natural resource and conservation agencies to derive at risk species statuses. The Nature Conservancy/Saskatchewan Conservation Data Centre ranking uses thresholds of 5 or fewer occurrences or less than 1000 plants for a critically imperilled species and 6 to 20 occurrences or 1000 to 3000 plants for imperilled species (Herbarium of the University of Saskatchewan, 2013). The IUCN Red listing process uses thresholds of area of occurrence (AOO), extent of occurrence (EOO) and the number of individuals as a measure of rarity and threatened status (IUCN, 2008). One of the criticisms of the IUCN red listing system is that there are discrepancies in the scale at which these measurements are taken. EOO is a measure of range size and is usually measured as the minimum convex polygon that encompasses all known records of the species, the scale of this is dependent on the region of interest. The AOO of a species is often measured as the number of grid squares containing that species but the size of these grid squares can vary from small units that correlate well with population size to large units that produce high values of AOO. This could result in a species being placed in the incorrect threat or rarity category. The cause of these discrepancies is most often related to a lack of data (Hartley & Kunin, 2003). This is also the case for population size and in most instances estimates, based on the most up to date information are used to determine a species rarity and threatened status.

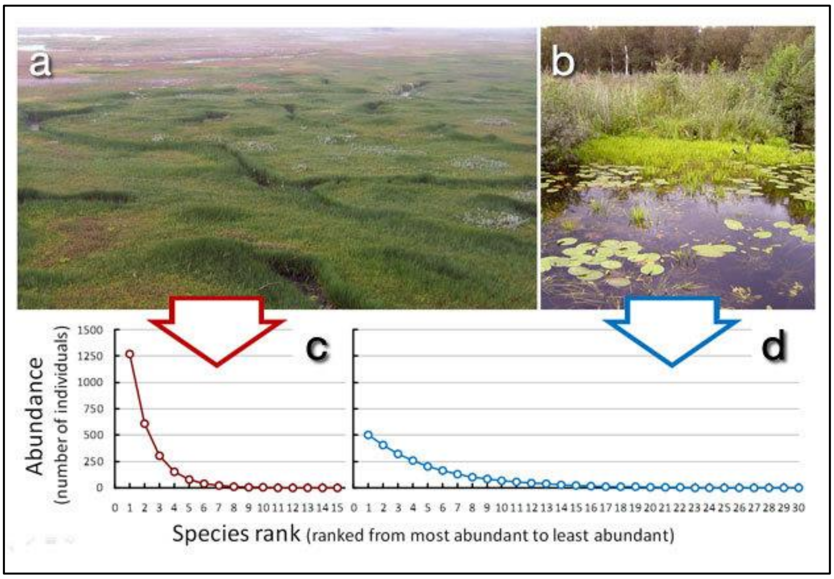

Figure 1: Differences between species abundances (using rank abundance curves) in two communities, (A & C) salt marshes and (B & D) wetlands or fens (from Verberk, 2012).

A ‘cut-off’ may be useful for prioritizing species for conservation effort but it does little to assist in the understanding of the drivers of a species distribution range and population size. As no natural disjunctions have been found, thresholds are either arbitrary or related to perceived threat to small populations with small ranges (Gaston, 1997). These inconsistent measures of rarity make it very difficult to draw conclusions from the numerous studies on the biology of rarity.

1.2. **Drivers of Rarity**

The complexity in understanding rarity was highlighted in the 1800s by renowned scientific theorist Charles Darwin in his statement “*If we ask ourselves why this or that species is rare, we answer that something is unfavourable in its conditions of life; but what that something is we can hardly ever tell.*” Many years later this perception was reiterated by Stebbins (1980) who stated “*For more than a century, botanists have theorized and argued about the reasons why some species of plants are rare or local, but no theory has proved altogether satisfactory. This is because the factors involved are numerous and complex.*” Stebbins went on to give examples of species that either proved or discounted theories on the drivers of localized plant distribution patterns. These included plant history, age, genetics and some ecological theories. He did however state that, ecological factors accounted for most occurrences of rare and localized species but that they cannot be considered in isolation from other factors. He proposed the gene pool-niche interaction theory in which he advocated three major determinants of species rarity; the inherent mosaic of the environment in which it grows; the complex genetic structure of a species population and its expressed traits; and the history of the population.

Unfortunately information on the history of species populations from origin to present day has not been well documented, possibly because of the difficulty in determining the point and time of origin. Without this information it is difficult to establish whether a species is a relic of a previously wide spread species (Paleoendemic) or a newly formed neoendemic species (Kruckeberg & Rabinowitz, 1985). A number of phylogeographic studies have examined the history of genetic exchange to gain insights into plant evolution and geographical distribution (Schaal et al., 1998; Collevatti et al., 2009; Zhang et al., 2012). Although these are insightful they do not conclusively predict the historical sequence of expansion and contraction of a species population and its range. It is also difficult to identify DNA sequences with appropriate levels of order within the DNA of some species and therefore current methods are not universal (Schaal & Olsen, 2000).

A species adaptation to a particular habitat or niche has an influence on its ability to disperse in a heterogeneous landscape. Without the ability to move, plants rely on dispersal vectors to aid dispersal and exploitation of new habitats. Propagules are adapted for movement by environmental dispersal vectors or by other organisms. The extent of dispersal is linked to the mode of dispersal and physical barriers or areas of unsuitable habitat (Wiens, 2011) that may impede movement or establishment (Croteau, 2010). Long distance dispersal which is thought to be a rare phenomenon allows species to transcend barriers and can result in disjunct distributions. Successful colonization by a species is dependent both on ecological factors and on the species ability to compete with other organisms for resources (Mott, 2010). Species will colonize areas within their range limit, which is defined by a combination of abiotic and biotic factors (Cain et al., 2000; Wiens, 2011).

1.2.1. **Abiotic Factors**

Climatic variables including temperature, precipitation, sunlight and wind have long been associated with plant distributions (Woodward, 1987). The existence of vegetation biomes gives clear evidence of the effect of climate on plant distribution and range. Five major global biomes; aquatic, deserts, forests, grasslands and tundra, have been recognized and a number of regional biomes, ecosystems and habitat types have been described based on the regional variation of dominant plant types (Olsen et al., 2001; Mucina & Rutherford, 2006). Physiogeographic factors including topography, elevation, slope and aspect influence climate on a more localized scale (Dobrowski, 2011). Further evidence of the role of climate in determining range limits for species has been shown in gradient analyses (Tuomisto et al., 2003; Lutz et al., 2010) and in species distribution modelling (Gelfand et al., 2006; Wiens, 2011). In KZN both temperature and precipitation have been shown to have a strong influence on floristic composition (Jewitt et al., 2014).

Another major abiotic determinant of plant distribution is the substrate on which it occurs (Rajakaruna, 2004). Geological processes have resulted in discontinuous topographic, lithological and pedological land forms. In a comparison between geomorphological heterogeneity and biotic diversity, Burnett et al. (1998) found that richness and diversity of both trees and shrubs were significantly higher in sites with high geomorphological heterogeneity than in sites that exhibited little change in terrain or soil conditions. The adaptation of species to specific edaphic conditions has been widely documented (Rajakaruna, 2004; Flather & Sieg, 2007). Examples of these include; endemics of the Cape Floristic Region in South Africa which are thought to be linked to nutrient-poor soils (Cowling & Holmes, 1992; Cowling et al., 1994; Schnitzler et al., 2011) and California's serpentine flora adapted to toxic minerals (Fiedler, 2001; Kruckeberg, 2002).

The relation between plants and geomorphology is encapsulated by Kruckeberg's (2002) statement, "All landforms can be expected to influence flora and vegetation in diverse ways – hence any classification scheme of geomorphological features has relevance for the explanation of plant distribution". In a fascinating account of the influence of the assembly and breakup of the Southern Hemisphere supercontinent Gondwana on floral history, McCloughlin (2001) confirms the significance in considering earth's history in any attempt to understand plant biogeography. Latitudinal orientation and the associated climatic effect have been proposed to have strongly influenced the Southern Hemisphere flora (McLoughlin, 2001). Fragmentation of habitats through mass movement of continents, change in climate, uplifting and degradation of geomorphology has resulted in 'terrestrial Islands' that act as refugia for formally contiguous species. This has been affirmed by genetic studies of disjunct species (Collevatti et al., 2009; Collevatti et al., 2012).

In KZN geomorphology is relevant when considering the landscape. The break up and dispersal of the single landmass Pangea and its subsidiary land masses Gondwana and Laurasia had a profound effect on the current surface topography of the continents of the earth (McCarthy & Rubidge, 2005). In KZN there are remnants of what is thought to be the oldest major erosion surface remaining on the African continent. This surface was referred to by L.C. King as the African surface. In the early Oligocene this surface was a low-elevation, low relief land surface, mantled by deeply weathered rock. Later the surface experienced upward flexing and became buried by sediment (Burke & Gunnell, 2008). Further uplift and tilting of the continental surface created from two periods of uplift, 20 million years ago and 5 million years ago, resulted in further erosion particularly on the east coast where the increase in slopes of the rivers caused deep valleys to be incised. The removal of the deep weathering mantles of the African surface after these two periods of uplift formed the Post African I and II erosional surfaces (Partridge & Maud, 2000).

Despite these degradational processes some remnants of the African surface remain today. Preservation of these is thought to be linked to bedrock control, aridity, an ineffective drainage network or thick sediment cover (Botha, 2000). Some of these old land surfaces potentially form “islands” within the Post-African erosional surfaces and other dissected areas because of their variation in altitude and structure. Other altitudinal or structural ”islands” created by geomorphological events include the Escarpment and large mountain massifs, which lie above the African surface, and the Neogene and Aeolian sediments of the Northern KZN and Mozambique coastal areas. The latter area of sedimentation was created through marine deposition, changes in sea level and aeolian movement of sand deposits (Fig. 2). The island nature of the African surface and mountainous areas of KZN is proposed to be something that could have led to the development of rarity amongst species that were more widely distributed over a more uniform landscape such as the African surface.

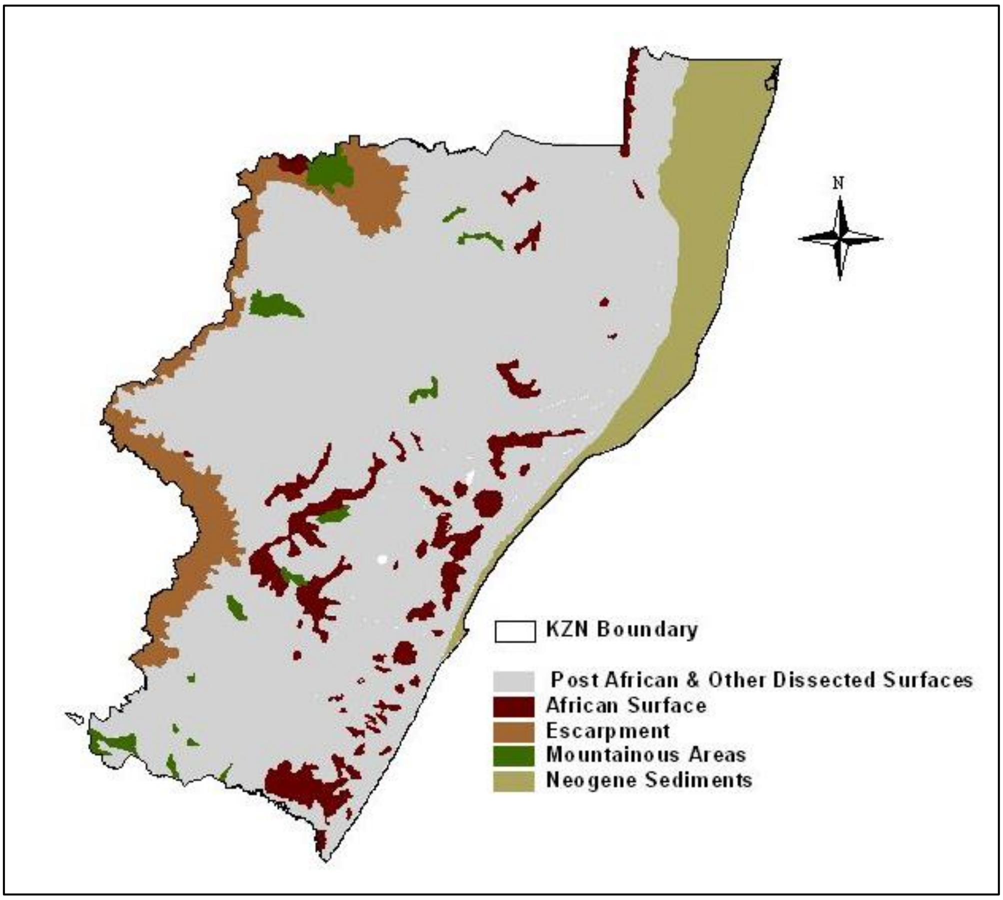

Figure 2: Map of erosional land surfaces of KwaZulu-Natal (KZN) Province (after Partridge & Maud, 2000).

1.2.2. **Plant Traits**

Species become rare when there is a constraint on the rate at which their population can increase (Greig-Smith and Sagar (1981) in Gaston, 1994). The life history of individual plant species and their functional traits are a consequence of evolutionary and environmental processes. The ability of populations to adapt to environmental change is dependent on the plasticity of their life history (Stearns, 1992; Krebs & Davies, 1997 in Norris, 2008).

Grime (1977) proposed that functional trait development was primarily related to a response to stress and disturbance. Stress was defined as those environmental factors that restrict photosynthetic production and therefore limit the rate of dry matter production. Disturbance was considered to be associated with the partial or total destruction of plant biomass. Grime (1977) described three strategies that have evolved in plants from varying intensities of these two factors; *competitors (C)* which exploit conditions of low stress and low disturbance, *stress-tolerators (S)* which exploit conditions of high stress and low disturbance and *ruderals (R)* which exploit conditions of high disturbance and low stress.

Plant species that have high competitive ability depend on characteristics which maximize the capture of resources in productive, relatively undisturbed conditions while those that tolerate stress have reduced vegetative and reproductive vigour to survive in harsh unproductive environments. Ruderals that have evolved in severely disturbed but potentially productive environments have developed short lifespans and high seed production (Grime, 1979). A triangular model (Fig. 3) of the relation between these three strategies represents their relative importance spatially. As there are varying intensities of competition, stress and disturbance Grime (1977) also described four secondary strategies. These are: (1) competitive ruderals (C-R) which are adapted to circumstances in which there is low stress and competition is restricted to a moderate intensity by disturbance; (2) stress tolerant competitors (C-S) which are adapted to undisturbed conditions with moderate intensities of stress; (3) Stress tolerant ruderals (S-R) which are adapted to lightly disturbed unproductive habitats; (4) “C-S-R” plants which are confined to habitats in which competition is restricted to moderate intensities by the combined effects of stress and disturbance. The location of these can be determined by using C, S, R triple co-ordinates (Hodgson et al., 1999) on the triangular C-S-R- model. The C-S-R co-ordinates for each species are determined by using selected criteria for attributes of morphology, life history and physiology (Grime, 1979).

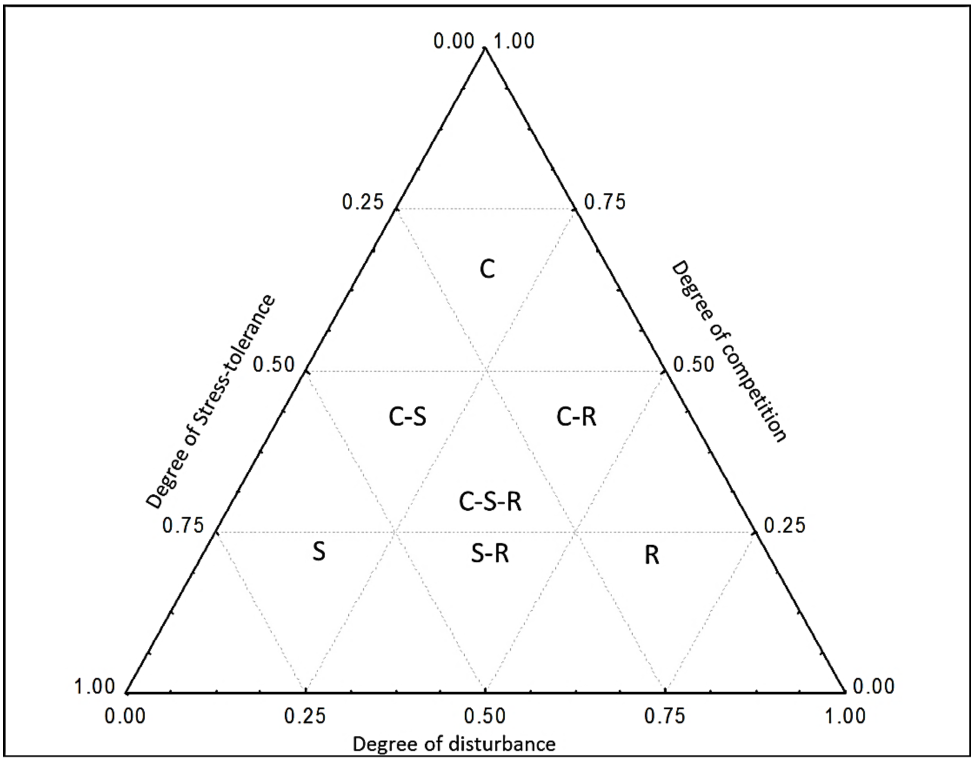

Figure 3: Model illustrating the interplay between competition, stress and disturbance and the location of primary (C = competitors, S = stress-tolerators, R = ruderal species) and secondary plant strategies (C-R = competitive ruderals, C-S = stress-tolerant competitors, S-R = stress-tolerant ruderals and C-S-R = stress and disturbance restricts competition) (from Grime 1977).

Studies into the C-S-R strategies of endemic plants have shown a predominance of stress tolerant taxa amongst them as they are able to colonize harsh environments with low competition and low disturbance (Medail & Verlaque, 1997; Casazza et al., 2005; Brofas et al., 2007). Although not all endemics are rare it is proposed that this would also be the case with rare plants.

Autecological studies of individual species are required to fully understand the biological causes of rarity (Murray et al., 2002) but due to the large number of rare species that require conservation strategies, a number of researchers have attempted to use comparative studies between common and rare species to gain an understanding of the characteristics of rare species (Witkowski & Lamont, 1997; Bevill & Louda, 1999; Hedge & Ellstrand, 1999; Murray et al., 2002; Pocock et al., 2006; Farnsworth, 2007; Farnsworth & Ogurcak, 2008). This approach is based on the assumption that plants with similar ecological traits respond to environmental factors and the changes in environment in similar ways (Bernhardt-Romermann et al., 2008). A wide variety of plant traits relating growth, reproduction, competitive ability and habitat specialization, to abundance and distribution patterns have been studied but with little replication. Some traits have shown significant differences between rare and common species i.e. clonality (Kelly et al., 1996), seed production (Eriksson & Jakobsson, 1998), pollination (Rymer et al., 2005), dispersal investment (Edwards & Westoby, 1996) and flowering time (Lahti et al., 1991). In a review of a large body of work examining the relation between traits and rarity in plants, Murray et al. (2002) found it difficult to demonstrate robust generalizations between individual plant traits and species rarity. The relation between rarity and the majority of traits examined appeared to differ from one study to the next and therefore work from one study site cannot be easily extrapolated to another.

This considered, plant traits that enhance the dispersal and colonization of suitable habitat have an influence on population size and distribution (Harper, 1977). Seed dispersal is determined by the spatial pattern of reproductive adults, the number of seeds produced and the mechanism by which it is able to disperse, while recruitment depends on the probability of a seed arriving in a suitable habitat (Jersáková & Malinová, 2007). In a study on dispersal limitation in montane grasslands in central Germany, Stein et al. (2008) showed, in a seed addition experiment, that species distribution can be constrained by short distance dispersal. Although plants have adapted morphological traits to effect dispersal over a range of specific distances (Soons & Ozinga, 2005), dispersal distance is often reported as very limited (Cain et al., 2000). This is because the majority of seeds produced by a plant are distributed very close to the mother plant (Jacquemyn et al., 2007; Corlett, 2009). Longer distance dispersal is reliant on the plant attributes (e.g. plant height), seed attributes and mechanism by which they are transported. In determining potential dispersal distance for seeds in East Asia, Corlett (2009) estimated that seeds dispersed mechanically or by ants would fall within 10m of the parent plant, large winged seeds or those dispersed by rodents, primates (not swallowed) or fruit bats would fall within

100m and wind, water, large mammals and bird dispersed seed had potential to be transported more than 100m. Nogales et al. (2012) concurred with this. The actual dispersal distance is dependent on the circumstance under which it is dispersed (Nogales et al., 2012). For example in wind dispersed seeds, wind velocity and surface heat are important factors in determining realized dispersal distance (Soons et al., 2012). Long distance dispersal i.e. greater than 100m, may therefore occur relatively rarely but when it does occur it makes a significant contribution to a species range size and is particularly important in fragmented landscapes (Cain et al., 2000). Long distance dispersal of orchids to volcanic islands demonstrates the extensive distances travelled by these minute seeds (Jersáková & Malinová, 2007). With respect to rarity it is expected that species with the ability to disperse long distances should overtime be more widespread than those with little ability to disperse (Farnsworth, 2007).

1.2.3. **Anthropogenic Factors**

Human impact on biodiversity is extensive and ranges from total destruction of organisms and their habitat to modification and fragmentation of habitats (Pimm, 1996; Lavergne et al., 2005; Helm et al., 2006; Grobler et al., 2006). There is unfortunately little before and after land transformation data on individual species population sizes and range size but GIS mapping tools have enabled the quantification of land surface and habitat transformation (Coetzer et al. 2010; Amin & Fazal, 2012; Fichera et al., 2012). Land transformation and the resultant fragmentation of natural habitats are serious threats to biodiversity in KZN with almost 50% of the land surface completely transformed (KZN land cover, 2008) (Fig.4).

The utilization of plants for medicinal purposes and for household use has caused extirpation of subpopulations at many localities (Williams et al., 2013). In Africa 70 to 80 percent of people use traditional medicines and most medicinal plants are collected from the wild (Cunningham, 1993). The medicinal use of *Warburgia salutaris* has caused a population decline throughout Southern Africa (Botha et al., 2004). In KZN the subpopulations outside protected areas have been decimated and only the populations in protected areas are extant (pers. obs.). The decreasing size of bulbs found in medicinal markets and the reference by collectors to increasing distance from collection areas to the markets is suggestive that populations of these species are declining (Williams et al., 2007). The extent of decline is difficult to assess as qualitative data on the historical distribution of most utilized plant species is not available (Williams et al., 2013) but high utilization of species could result in rarity.

The horticultural industry has also placed pressure on wild populations of plants, as people's desire to have rare, unusual and Jurassic (cycads) plants have caused extinction of wild plant populations (Donaldson, 2003). In South Africa only one of the thirty seven species of *Encephalartos* is categorized as least concern and does not qualify for any Red listing category (SANBI, 2013). All other species are threatened due to the collection of wild plants (e.g. Cousins et al., 2012). Other plant species threatened by unscrupulous collection by hobbyists include orchids (Kurzwril & Archer, 2010) and succulent species such as Aloes and Haworthias (Cousins & Witkowski, 2012; SANBI, 2013).

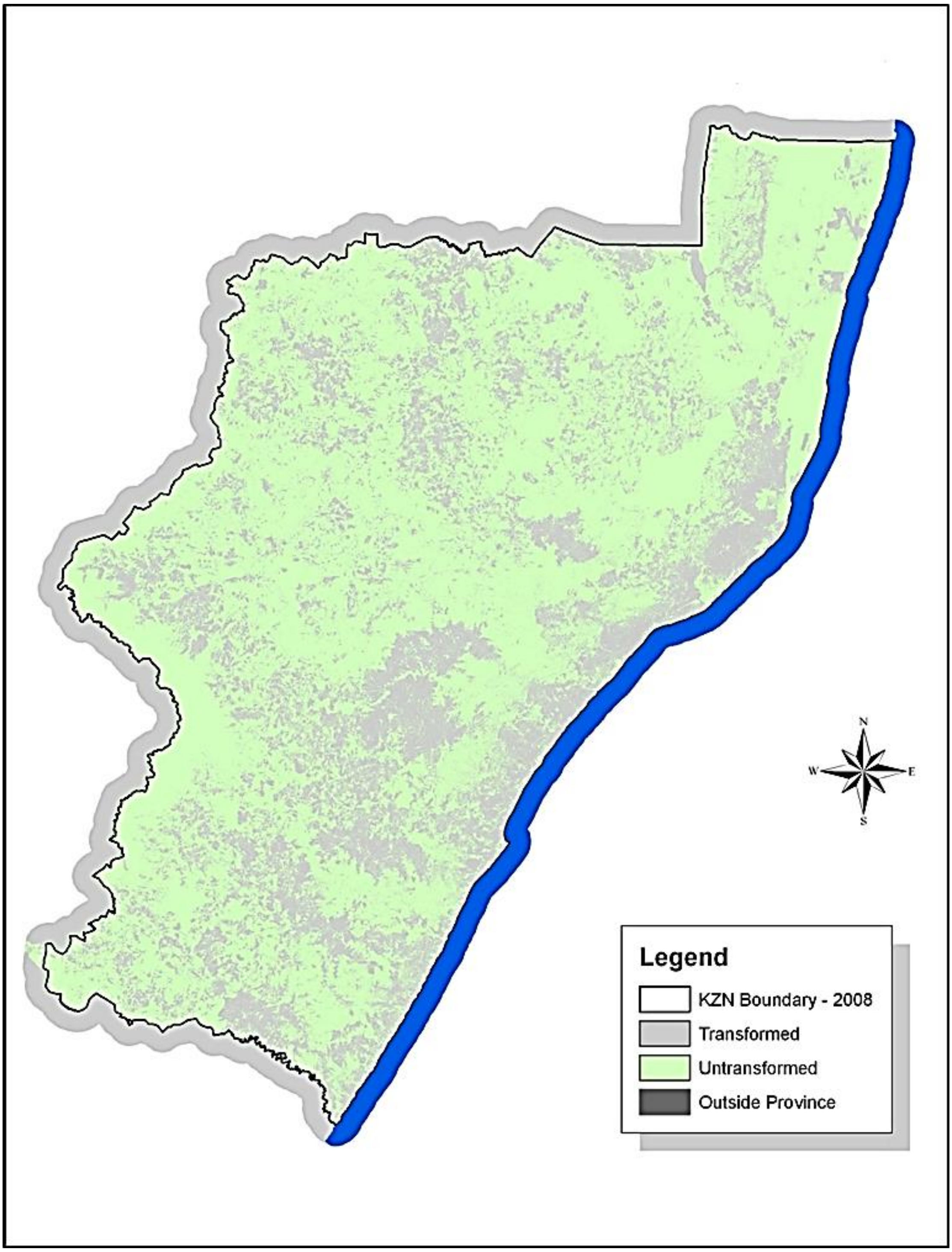

Figure 4: Map of the transformed areas (grey) of KwaZulu-Natal (KZN) (Ezemvelo KZN Wildlife, 2011).

1.2.4. Overall objective of the study and hypotheses to be tested on causes of rarity in KwaZulu-Natal

The overall objective of this investigation is to explore the relations between the rarity of plant species and the potential determinants of this namely; plant traits, biophysical factors and anthropogenic pressures in KZN. For this purpose I define rarity as the product of the abundance (population size) and distribution of a plant species. This definition differs from Rabinowitz's (1981) definition, which included habitat specificity in the definition of rarity. I include habitat specificity in this analysis as one of the potential determinants of rarity.

The broad approach implemented is to first examine the relations between rarity and individual traits and factors independently, then to explore these in combination. The investigation revolves around the following hypotheses:

- *Plants are expected to be rarer the smaller their ecological niche* - plants with small ranges in temperature, precipitation (Slik et al., 2003; Jewitt et al., 2014) and soil fertility (Burnett et al., 1998; Cron et al., 2009) are expected to be rarer than those with wide ranges of these variables.
- *Plants are expected to be rarer if they have high habitat specificity* – thus plants that are adapted to specific conditions such as specific substrates, light intensity and soil moisture content may be restricted to specific habitats and hence be rare (Rabinowitz, 1981) whereas species that are habitat generalists are expected to be common (Benayas et al., 1999).
- *Plants are expected to be rarer the shorter their dispersal distance* - Long distance dispersal of seeds promotes range expansion and enables species to colonize patches of suitable available habitat thereby allowing the species to increase in both population size and extent (Cain et al., 2000; Corlett, 2009). Species that are not equipped to disperse far from parent plants are expected to have smaller ranges than those that have the potential to disperse far (Farnsworth & Ogurcak, 2008).
- *Plants are expected to be rarer if they have a stress tolerant survival strategy* - The adaptation of plants to particular environments relates to their ability to overcome stress and/or competition (Grime, 1979). Plants that are able to survive harsh climates have adapted traits to survive suboptimal temperatures or shortages of resources (Bornhofena et al., 2011). Many harsh habitats have been found to have a strong link with endemism and it is

expected that this would also be the case with rare plants (Brofas et al., 2007).

- *Plants that occur on land surfaces that are islands of former much larger land surfaces are expected to be rarer than those that occur on more extensive or contiguous land surfaces* - Paleoendemic species that have survived and remained in refugia resulting from changes in the earth’s physical profile and the accompanying climatic changes are expected to be rare (Collevatti et al., 2009).
- *Plants are expected to be rarer if they are selectively and intensively utilized by humans* - Over utilization of plant species for household and commercial purposes has a direct impact on population size and range. Species that are slow growing, have limited reproduction potential and occur in limited habitats are particularly vulnerable (Cunningham, 2009).
- *Plants are expected to be rarer the greater their habitat has been transformed* - Habitat transformation has a direct impact on species population sizes (Helm et al., 2006). In addition to this fragmentation of habitat as a result of transformation can affect the reproductive process of plants, particularly those species that require other organisms for pollination and seed distribution. The response of these organisms to transformation cascades to plants (Kearns et al., 1998).

2. Methods

2.1. Study Area

KZN is a small province situated in the south east of South Africa. It is only 92,100 km² but is home to 10 819 130 people at a density of 117 people per km² (based on the July 2011 national census, Statistics South Africa, 2011). Despite this it is well known for its rich diversity of plants. The province varies geographically from sub–tropical coastal lowlands along the Indian Ocean, to undulating mid-altitude plateau's deeply dissected by eastward flowing rivers in the centre and the high lying Drakensberg Mountains (up to 3425m above sea level) in the west on the Lesotho border.

Temperatures in the province are related to altitude, with the mean annual temperature ranging from less than 10˚C in the Drakensberg to more than 22˚C on the coastal plain in Maputaland. The mean annual rainfall in the province ranges between 400mm and 1900mm (Schulze, 1997). This diverse physical environment and its position on the tropical-temperate gradient have resulted in KZN's rich biodiversity. Two centres of endemism are recognized in the province, the Drakensberg Centre and the Albany Maputaland Centre (Van Wyk & Smith, 2001). These "hot spots" for plant diversity are recognized internationally as areas of global botanical importance (Pooley, 1998). The province also falls within a transitional zone of subtropical biota in the south and tropical biota in the north (Goodman, 2003), resulting in the occurrence of a number of species at the ends of their distribution range.

2.2. Data Collection

One hundred plant species were selected in a stratified random manner from a compilation of rare and threatened species for KZN. The stratification was based on the IUCN threatened species categories, with the objective of getting at least nine species from each group. Although there was no attempt to select from the declining group as this is a category used exclusively in the South African listing process, selected species that are categorized as declining were not excluded (see Table 2.1). Species, for which there were little or no data, were removed from the selection and replaced by a further random selection from the remaining species on the list. This process resulted in a list of 80 rare or threatened species with enough data for investigation. In order to be able to explore relations across the rare to common gradient, a further 17 species considered to be common and/or not threatened were selected (Appendix 1). The plant species selected included 42 families with a minimum of 9 species from each of the following IUCN conservation status categories: (i) Critically Endangered (CR), (ii) Endangered (EN) (iii) Vulnerable (VU) (iv) Near Threatened (NT), (v) Least Concern (LC), (vi) and rare in KZN (Table 2.1).

Table 2.1: The number of species per threat and rarity category in the sample of KwaZulu-Natal (KZN) plants and the breakdown of species that are endemic to KwaZulu-Natal.

	CR	**EN**	**VU**	**NT**	**Declining**	**Rare**	**LC**	**Total**
# KZN endemics	14	11	11	0	0	6	1	43
# Total species	15	19	24	11	2	9	17	97

The data collated on each species were obtained from the Ezemvelo KZN Wildlife Biodiversity Database, the Threatened Species Database (SANBI), JSTOR herbarium data, and literature including Pooley (1994) and Boon (2010). While it is recognized that there is a general lack of data on individual plant species in KZN, the data used were the best available.

2.3. Derivation of Variables

2.3.1. Rarity Index

For each species a measure or index of its rarity was determined as the product of the estimated population size and extent of its occurrence (Appendix 2):

$$\mathbf{Ra_i = N_i \times EOO_i}$$

Where:

$\mathbf{Ra_i}$ - rarity estimate for species i

$\mathbf{N_i}$ - estimated population size for species i

$\mathbf{EOO_i}$ – estimated extent of occurrence for species i

The population size of each species was estimated from the available data and placed into the following size classes: 0- ≤10; >10 - ≤100; >100 - ≤1 000; >1 000 - ≤ 5000; >5000-≤ 10000; >10000 - ≤100000. The midpoint of each class was used as the abundance estimate for each species (Appendix 2).

The estimated extent of occurrence (EOO) was calculated using the convex hull method (Jenness, 2008) on all the locality data available for the species. As the focus of this study is KZN, only KZN localities were used to derive EOO (Appendix 2).

2.3.2. Ecological Niche Width Measurement

The estimate of each species' ecological niche width was derived as a function of its known range in temperature, precipitation and soil fertility tolerance (Appendix 2). Temperature and precipitation ranges were derived through a point to raster query on the appropriate temperature and precipitation layers (Schulze, 1997). The soil fertility range was derived via a similar method but using the KZN soil fertility layer (van den Berg et al., 2009), more specifically:

$$\mathbf{Nw_i = Temp(max\text{-}min)_i \times Precip(max\text{-}min)_i \times SF(range)_i}$$

Where:

Nw_i – niche width for species i

$Temp(max\text{-}min)_i$ – The difference in the absolute mean maximum (as ^oC) and the absolute mean minimum temperatures recorded across all records of species i

$Precip(max\text{-}min)_i$ - The difference in the absolute mean maximum and the absolute mean minimum annual precipitation (mm/annum) recorded across all records of species i

$SF(range)_i$ – The range (number) of soil fertility classes recorded for all records of species i.

Since the range in precipitation exceeds the range in temperature, which in turn exceeds the soil fertility range, this measure will be weighted Precipitation > Temperature > Soil fertility. Few investigations have been undertaken on impacts of standardization on the biological interpretation of physical variables (see Cao et al (1999)) and since two of the variables used to derive niche width are quantitative and one is ordinal I have chosen not to standardize them prior to calculating Niche Width.

2.3.3. **Habitat Specificity**

Habitat Specificity was determined by assessing a species' fidelity to a non-matrix habitat. Non-matrix habitats were defined as those which included wetlands, forests and rocky outcrops. All other habitats were considered to be matrix. Each species was coded as either M for matrix or Hs for habitat specific, based on general habitat descriptions in the literature. In addition, species that were referred to as habitat specific in the literature were coded as such (Appendix 3).

2.3.4. **Dispersal Distance**

Species were categorized according to their capacity for dispersal. This was based on information from Pooley (1998) and Boon (2010) on the size, morphology and mode of dispersal of seed. Seeds with morphological features that gave them the capacity to disperse a distance of > 100m from the parent plant were considered to be long distance dispersers. Seeds without features known to enhance longer-distance dispersal (i.e. those that rely primarily on gravity) were considered localized dispersers (i.e. up to 10m) whereas seeds that had morphological features that allowed them to disperse away from the parent plant to a distance <100m were considered medium dispersers (Farnsworth's, 2007) (Appendix 4). The categories and codes used are described in Table 2.2.

Table 2.2: Criteria for the three dispersal distance categories used for the sampled species.

Code	Description	Approximate dispersal distance	Possible Dispersal Vectors
1	*Localized dispersal*	0-10m	Large seeds, gravity, mechanical (e.g. ballistic), ants
2	*Medium dispersal*	10-100m	Large winged seed dispersed by wind, rodents, monkeys and baboons (not swallowed), water (drip lines)
3	*Far (Long distance) dispersal*	> 100m	Light, small wind dispersed seed, animals, birds, bats, water (river and sea)

2.3.5. **Life History Strategy**

In this analysis Grime's (1977) characteristics of Competitive (C), Stress-Tolerant (S) and Ruderal (R) plants were used to determine the survival strategy of each of the sampled species. Grime (1979) described 18 traits that allow one to categorize species as C, S or R strategists. Each species was scored for each of the traits where information was available on the species. A trait for a plant was scored as C, S, or R if the plant fell clearly into the category description. In some cases more than one category was assigned to a trait as the characteristics derived by Grime are sometimes the same for the different strategies. For example, the proportion of annual production devoted to seeds is small for both Competitive and Stress-tolerant species but large for Ruderal species. Therefore species, such as *Encephalartos aemulans,* in which plants do not produce seed every year, would fit into both competitive and stress-tolerant categories for this trait and therefore both strategies would be allocated to this trait.

After this scoring process, traits and species were retained for the analysis based on the following

- Traits – only traits for which information for at least 60% of the sampled species was available were retained. This resulted in 9 of Grimes 18 traits being included in the analysis (Appendix 5).

- Species – only species for which information was available on more than six of the nine remaining traits were included in the analysis (Appendix 5).

In order to position a species in the 2 dimensional C-S-R plane, the position on each axis was calculated as a proportion by summing the number of like strategy scores allocated to each trait, and then dividing by the total number of strategy scores allocated to a species. If two strategy scores were allocated to a particular trait, i.e. C and S then both were added and therefore the total score could be greater than the number of traits i.e. 9. For example, if a species was allocated 10 strategy scores across all nine groups and four of those were the C strategy, and six were S strategy, the proportions allocated to C:S:R would be 0.4 : 0.6 : 0 as in the case of *Acalypha entumenica.* These values were then plotted using a ternary 2D scatterplot. The species were then assigned a life history strategy based on where they were positioned on the ternary C:S:R plot.

2.3.6. **Geological Land Surfaces**

Partridge and Maud's (1987) map of erosional surfaces was captured digitally (Fig.2). The land surfaces that were digitized and used in this analysis comprised:

- Mountainous areas above the African Surface,
- The African Surface itself, emanating from the early Cretaceous,
- Post African surfaces and other Dissected Areas from the early Miocene,
- The Escarpment and
- Neogene marine and coastal aeolian sediments.

This layer was queried with each species' point distribution coverage and the proportion of points occurring on each land surface was extracted. From these queries, a data matrix of species versus land surface was developed and populated by the proportion of each species' occurrences on each Land surface (Appendix 6).

In order to objectively understand a species' fidelity with a single land surface, the matrix was subjected to a principal component analysis (PCA) to explore the likelihood of distinct groups. These data were then subjected to a k-means cluster analysis (STATISTICA data analysis software system, version 7.1.

www.statsoft.com) which confirmed the groups formed in the PCA and allocated membership of individual plants to viable clusters. The k means cluster analysis also identified species that showed no affinity to any of the surfaces.

2.3.7. **Human Use**

Data on the human utilization of species was collected from Pooley (1998), Boon (1998), Manders, (2006) and from the South African National Biodiversity Institute (SANBI) Threatened plant database. Species categorized as highly utilized included those listed as such in reports and those that have utilization listed as a threat in the SANBI threatened plant database (Appendix 7). Many plant species are reported as being utilized in KZN but not all utilization is considered to be severe. Species were categorized as follows:

Code	**Description**
0	No known utilization
1	Some utilization
2	Intense utilization

2.3.8. **Range Transformation**

The degree of habitat transformation within the species' range was determined by subtracting the untransformed habitat (Ezemvelo KZN Wildlife, 2011) from the range (EOO) of the species and dividing this by the species EOO. More precisely:

$$\mathbf{Ht_i = (EOO_i - T_i)/EOO_i}$$

Where: **Ht_i** = Degree of habitat transformation for species i

EOO_i = Extent of occurrence of species i

T_i = Extent of untransformed habitat within the EOO of species i (ha)

The calculation produced a metric that indexed transformed area of the range which had high values (close to 1) for EOO's with high levels of transformation and low values for EOO's with low levels of transformation (Appendix 8).

For species with only one locality record in the database, neither EOO nor the extent of transformation could be calculated and so these were excluded from the analysis. There were six species with only one known locality and therefore only 91 species were used.

2.4. Data Exploration

2.4.1. Rarity Index

The rarity scores or index derived as described above are dimensionless and, range from a minimum of 244 (2.44×10^2) for *Cyrtanthus brachysiphon*, a localized endemic, to 548170873415 (5.48×10^{11}) for *Ziziphus mucronata* a species known to be wide spread and "common". The frequency distribution of species across the rarity range was biased towards the rarer classes (Fig.5a). This was expected since the majority of plants were selected from the list of rare and threatened species of KZN.

Since the distribution of plant species across the range of rarity was skewed towards the very rare end of the scale $\log_{10}$ Rarity Index (Fig. 5b) was used in all comparisons with independent variables.

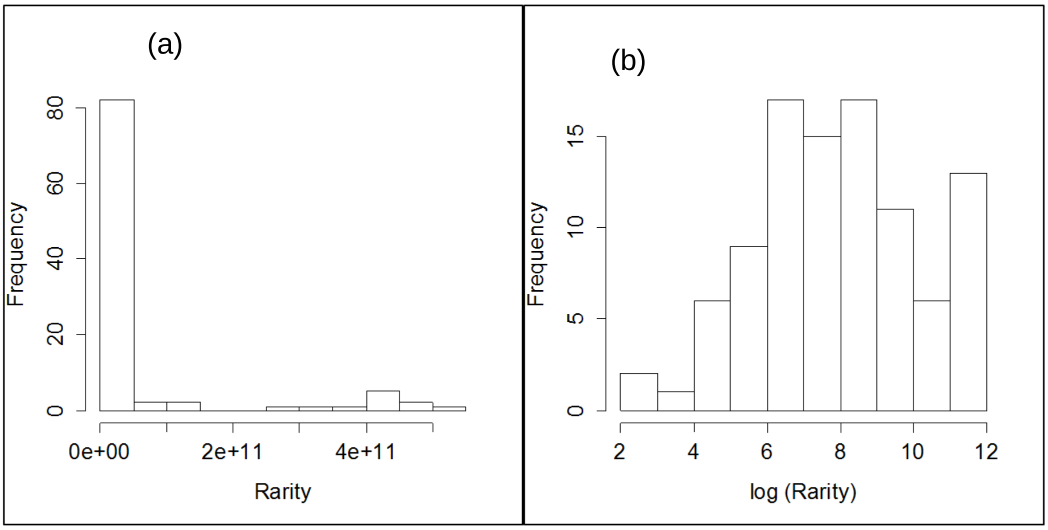

Figure 5: The frequency distribution of the values of rarity (a) and $\log_{10}$ Rarity Index (b) of the 97 sampled plant species.

2.4.2. **Ecological Niche Width**

The Niche Width ranged from a value of 17 to a value of 219625, and the distribution of Niche Width from the sample species selected was skewed in favour of species with narrow Niche Width (Fig. 6a).

Since the distribution of species across the range of Niche Width was skewed towards the very rare end of the scale the $\log_{10}$ of Niche Width (Fig. 6b) was used in all analyses.

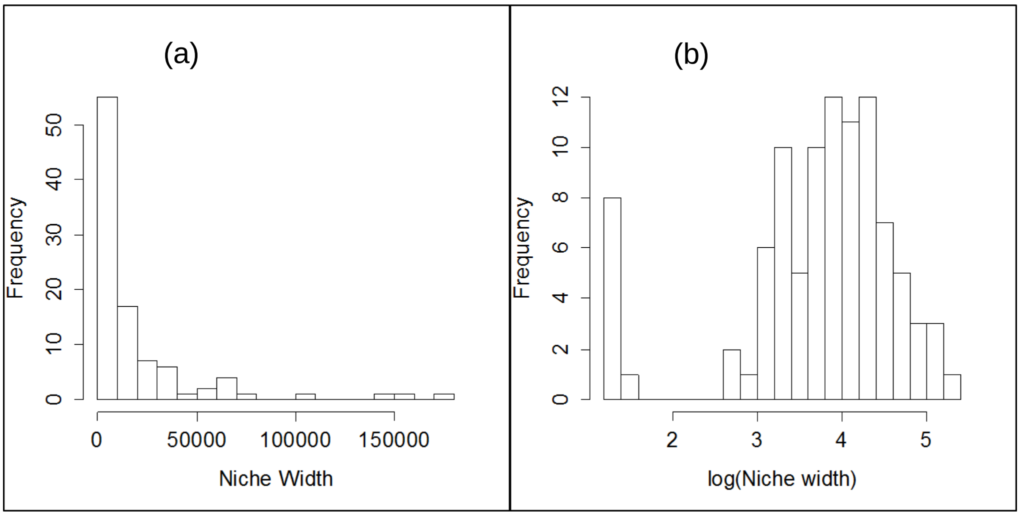

Figure 6: The frequency distribution of values of Niche Width (a) and $\log_{10}$ Niche Width (b) from the 97 sampled plant species.

2.4.3. Habitat Specificity

Of the 97 species (Appendix 1) in the sample, 50 were found to be habitat specific while 47 were considered to be matrix species (Fig. 7).

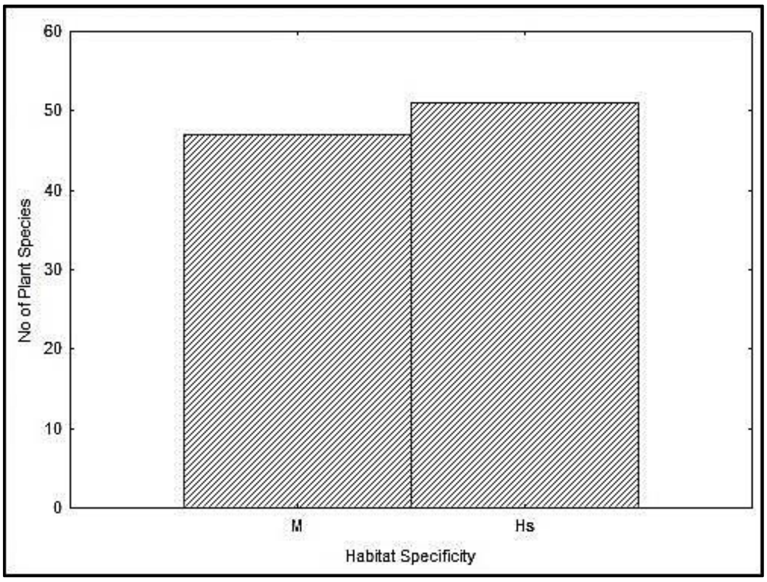

Figure 7: Frequency distribution of the 97 sampled plant species within two habitat specificity classes (M = matrix species and Hs = habitat specific species).

2.4.4. Dispersal Distance

Eleven species were not included in the analysis as there was not enough information available to place them in a dispersal distance category. Of the 86 species included in the analysis, 24 were categorized as localized dispersers, 27 were categorized as medium dispersers and 35 species were considered to be long distance or far dispersers (Fig.8).

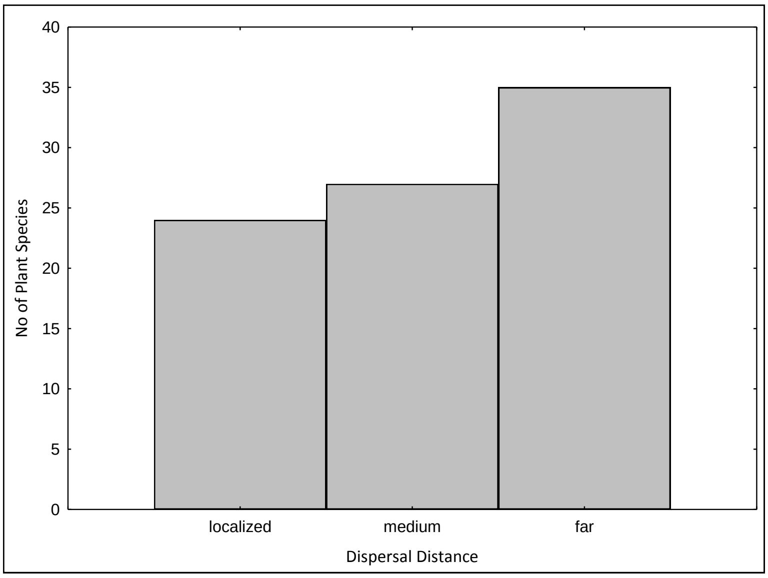

Figure 8: Frequency distribution of 86 sampled plant species according to three dispersal distances.

2.4.5. **Life History Strategy**

The spatial distribution of species in the ternary plot was found to be primarily along the S-C axis with a few species distributed in the C-S-R space (Fig.9). The highest number of species (38) fell within the stress-tolerant (S) space while no species fell within the ruderal life history space. A small number of species was found to have mixed life histories with traits adapted to competition, stress and ruderal life histories (Fig. 9 and 10).

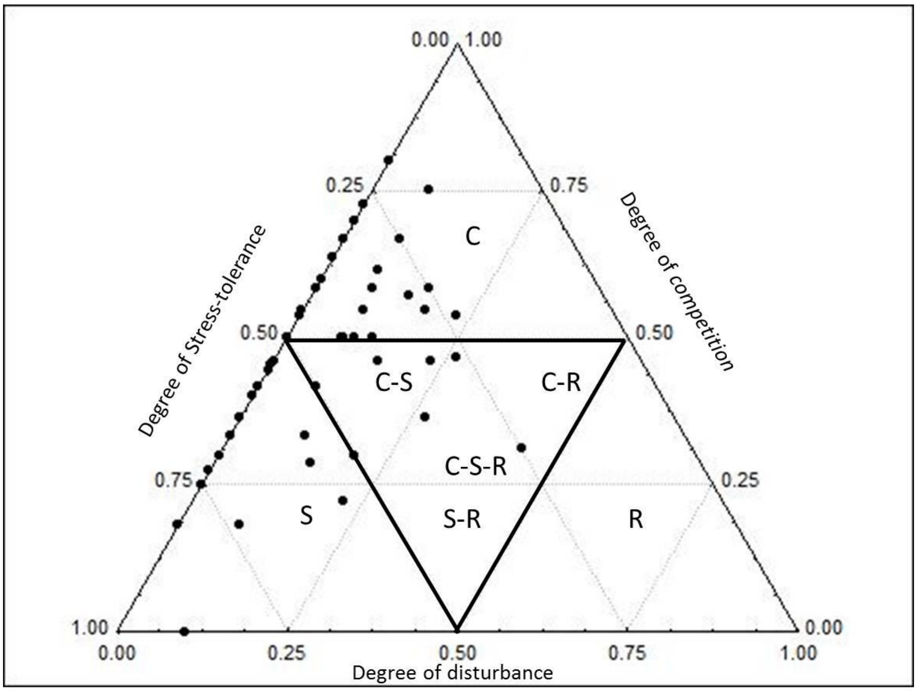

Figure 9: The positions of the 97 sampled species in C-S-R space where, C = competitors, S = stress-tolerators, R = ruderal species, C-R = competitive ruderals, C-S = stress-tolerant competitors, S-R = stress-tolerant ruderals and C-S-R = stress and disturbance restricts competition.

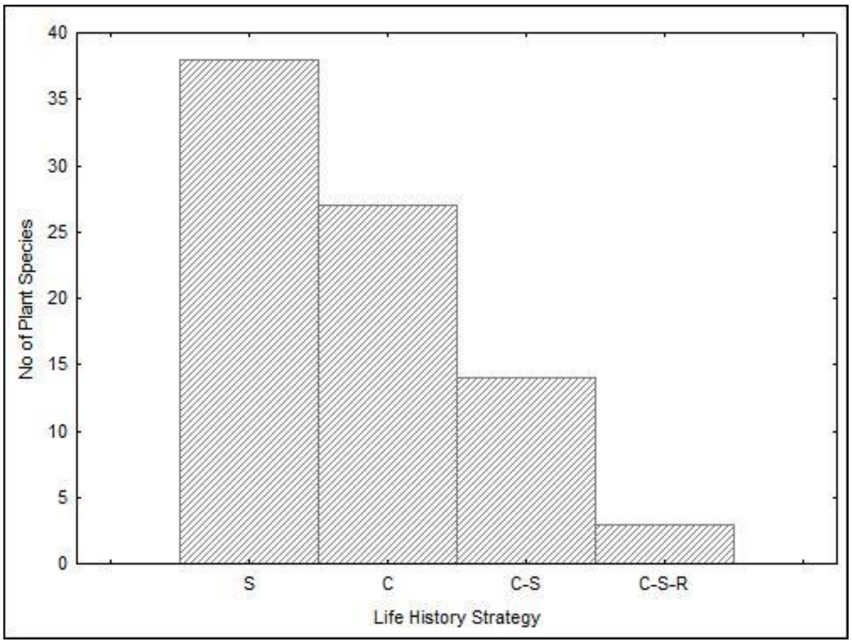

Figure 10: Frequency distribution of the 97 sampled plant species that fell within life history categories of S = stress-tolerant, C = competitive; C-S = competitive and stress tolerant; C-S-R = competitive, stress tolerant and ruderal.

2.4.6. **Geological Land Surfaces**

In the principal component analysis (PCA) 99.19 % of the variance was accounted for in the first three axes (Table 2.3). A projection of the land surfaces onto a 2 dimensional component plane, using a biplot (Multivariate Statistical Package 3.1 (MVSP 3.1)), shows well defined regions for 'Old African', 'Neogene', 'Escarpment' and 'Post African and Other Dissected Surfaces' while 'Mountain Surfaces' falls at the centre of the clusters and does not emerge as a grouping on its own (Fig. 11). The biplot also gives an indication of the association between species and the land surface vectors (Fig. 11). The direction of the vectors indicates an increase in the value of the vector in that direction (Quinn & Keough, 2002). Species such as *Brachystelma natalensis* and *Manilkara nicholsonii* are shown to have a strong affiliation with the African surface whereas *Searsia rudatisii* and *Eriosemopsis subanisophylla* have much weaker affiliations with this surface. Likewise *Aloe saundersiae* and *Asclepias schlechteri* are strongly associated with Post African and Other Dissected Surfaces. The single plane of this biplot makes it difficult to distinguish between species that are affiliated to Neogene land surfaces and those affiliated to the Escarpment.

Table 2.3: The eigenvalues and the percentage variance of first four axes in the principal component analysis (PCA) of the Land surfaces of KwaZulu-Natal (after Partridge and Maud, 2000).

	Eigenvalue	**Total variance explained (%)**	**Cumulative**	**Cumulative %**
1	1787.118	52.16	1787.118	52.1550
2	930.757	27.16	2717.875	79.3181
3	681.012	19.87	3398.887	99.1927
4	27.664	0.81	3426.551	100.0000

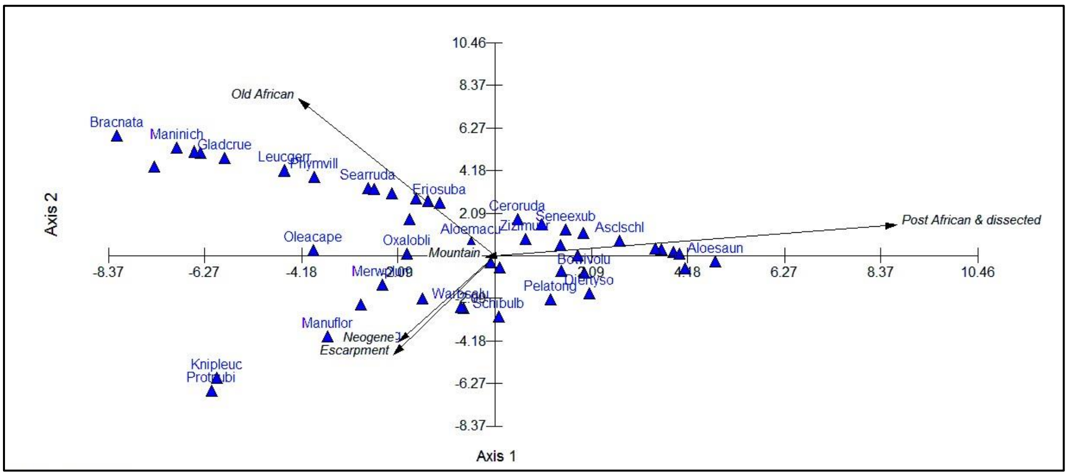

Figure 11: The projection of five land surface types (vectors from the origin) and species (triangles) on a principle component plane (1 x 2) derived from a Principle Components Analysis of the matrix of the 97 sampled species versus the proportion of each species' occurrences on each land surface type. The axes are scaled in proportion to the variance explained. Only some species are labelled with their respective codes as labelling of all species makes it difficult to read (MVSP 3.1).

The k means cluster analysis produced 5 distinct clusters (Table 2.4). These clusters confirmed the PCA grouping of species in four Land surface types but included an additional cluster where species with no affinity for any particular Land surface were grouped.

The clusters are aligned to the following land surface:

- Cluster 1 - Neogene Surface as this surface contributes 100 percent to this cluster mean;
- Cluster 2 - Escarpment species with an 88.14 percent contribution to the mean;
- Cluster 3 - No special affinity to a surface as this cluster is clearly a mixture of Old African (33.70%), Escarpment (9.8%) and Post African and other dissected surfaces (52.88%)
- Cluster 4 - Post African and other Dissected surface species (94.81%);
- Cluster 5 - Old African surface species (84.64%)

Table 2.4: The contribution of the five land surfaces to the means of 5 clusters using k means cluster analysis.

Land Surfaces	**Cluster Means**				
	Cluster 1	**Cluster 2**	**Cluster 3**	**Cluster 4**	**Cluster 5**
Mountain	0	4.714	1.891	0.643	1.819
Old African	0	0	33.703	2.286	84.637
Escarpment	0	88.14286	9.813	1.262	0
Neogene	100	0	1.719	1	0
Post African and other Dissected surfaces	0	7.145	52.875	94.81	13.545

The k means cluster analysis resulted in 41 species being assigned to the Post African and other dissected surfaces, 11 species were assigned to the Old African surface, 7 species to the Escarpment, 6 species to Neogene marine and coastal aeolian sediments and 32 species were found to have no fidelity to a particular surface (Fig. 12).

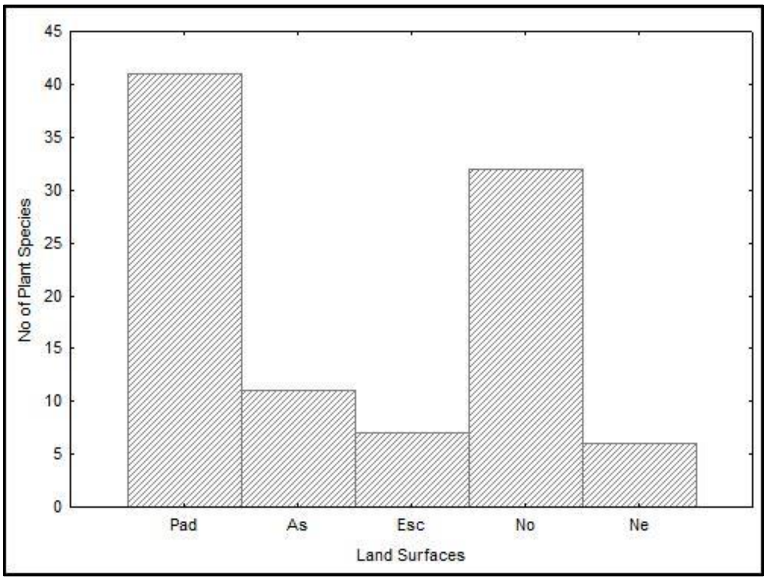

Figure 12: Frequency distribution of species in the five land surfaces (Pad = Other dissected areas and Post African surfaces; As = African Surfaces; Esc = Escarpment; No = no fidelity to a surface; Ne = Neogene Marine and Coastal Sediments).

2.4.7. **Human Use**

Of the 97 species in the sample, 68 are not known to be utilized (None), 16 are utilized but not extensively (Some) and 13 are utilized intensively (Intense) (Fig. 13).

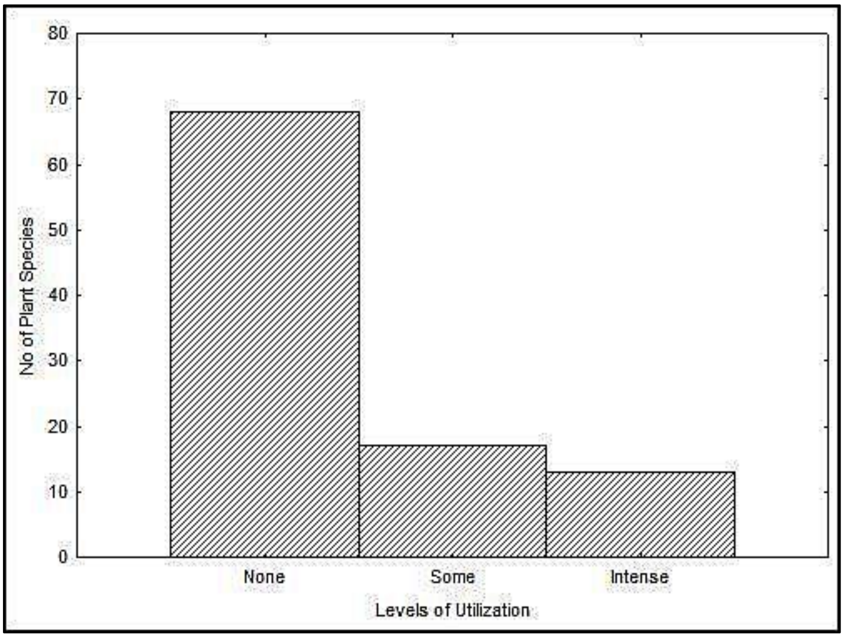

Figure 13: Frequency distribution of 97 sampled species in three categories of human utilization.

2.4.8. **Range Transformation**

The proportion of habitat transformation found in the range (EOO) of the 91 species included in this analysis ranged from 0 or no transformation, to 1 where the entire species range has been transformed (Fig. 14).

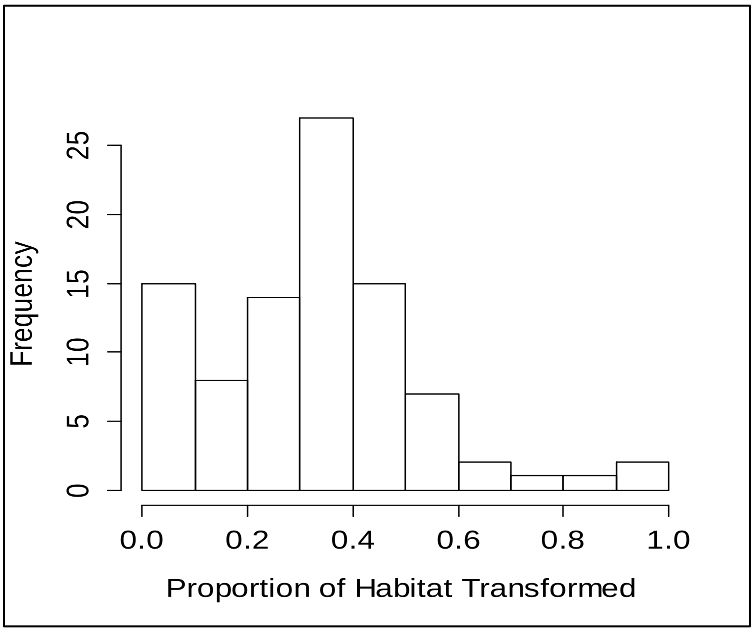

Figure 14: The frequency distribution of the proportion of habitat transformed of the 91 sampled plant species used in this analysis.

2.5. Data Analyses Approach

2.5.1. Bivariate Analysis

Clearly there is unlikely to be a single explanation for rarity in plants, but in order to understand the individual relations, each variable was compared independently with the response variable Rarity. Two variables (Ecological Niche Width and Habitat Transformation) were continuous and the other five variables were categorical (Table 2.5). STATISTICA version 7.1. (www.statsoft.com) was used for the individual statistical analyses. The analyses used are summarized in Table 2.5.

Based on these bivariate analyses, those variables that were suitable (refer to section 3.1.6 for explanation for the exclusion of Human Use from the multiple regression analysis) were then analysed using a multiple regression analysis approach of Rarity Index and the explanatory variables. The basic formulae used for the multiple regression analysis was:

$\log_{10}$(Rarity Index) = f($\log_{10}$(Niche Width); Habitat Transformation; Dispersal Distance; Habitat Specificity; Land Surface; Life History)

This was aimed at gaining a better understanding of the contribution and/or roles of the different explanatory variables with respect to rarity, and the interaction between them. Three different analytical techniques were used in a complementary and comparative way to provide a more robust understanding of the variable associations (Levins, 1966). The techniques used were Regression Tree Analysis, Generalized Linear Modelling (GLM) and Generalized Additive Modelling (GAM).

Table 2.5: Summary of the variables used, data type and analysis approach in the pairwise data analysis. In each of these analyses, $\log_{10}$ Rarity Index was the response variable.

Variables	Type	Analysis Approach
Rarity Index (response)	Continuous	
Ecological Niche Width (explanatory)	Continuous	Pearson Product Moment Correlation (*r*) of $\log_{10}$ Niche Width vs. $\log_{10}$ Rarity Index based on the hypothesis that plants are expected to be rarer the smaller their ecological niche
Habitat Specificity (explanatory)	Categorical	A one tailed t-test for independent samples on $\log_{10}$ Rarity Index based on the hypothesis that Habitat Specific species are expected to be rarer than Matrix species.
Dispersal Distance (explanatory)	Rank	Spearman's Rank Correlation (r_s) test based on the hypothesis that plants are expected to be rarer the shorter their dispersal distance
Life History Strategy (explanatory)	Categorical	One tailed t-tests on independent samples were conducted on $\log_{10}$ transformed Rarity Index, based on the hypothesis that plants are expected to be rarer if they have a stress tolerant survival strategy
Land surfaces (explanatory)	Categorical	One tailed t-tests on independent samples were conducted on $\log_{10}$ transformed Rarity Index based on the hypothesis that plants that occur on land surfaces that are islands of former much larger land surfaces are expected to be rarer than those that occur on more extensive or contiguous land surfaces.
Utilization by humans (explanatory)	Rank	Graphical based on the hypothesis that plants are expected to be rarer if they are selectively and intensively utilized by humans
Range Transformation (explanatory)	Continuous	Pearson Product Moment Correlation (*r*) of degree of habitat transformation vs. $\log_{10}$ Rarity Index based on the hypothesis that plants are expected to be rarer the greater their habitat has been transformed.

2.5.2. **Regression Tree Analysis**

Classification and Regression Tree analysis (CART, 2012 Salford Systems Inc., USA) was initially used to explore the structure of the rarity data and its relation to the explanatory variables. Classification and regression trees are useful tools for the exploration, description and predictions of patterns and processes. They are particularly suited to ecological data as they are flexible enough to handle a broad range of data types, are invariant to monotone transformations of data and can handle missing values and outliers (De'ath & Fabricius, 1999; Timofeev, 2004).

Classification and regression trees explain the variation of a single response variable by one or more explanatory variables with the objective of dividing the subjects of analysis (species) into homogenous groups. A tree is grown through a process of binary recursive partitioning where parent nodes are split into two more homogenous groups (Moisen, 2008, Timofeev, 2004) based on one of the explanatory variables. Partitioning at each node considers all possible splits using the case data for all variables (no. of cases x no. of variables) with the aim of minimizing the impurity of the node at that point. The actual split at each node is based on a single explanatory variable and results in two mutually exclusive groups. Splitting of groups continues in the tree until no further splitting is possible. Regression tree analysis is used for a continuous response (dependent) variable while classification tree analysis is appropriate where the response falls into a class (Moisen, 2008, De’ath and Fabricus, 2000, Timofeev, 2004).

For regression trees there are two commonly used splitting rules, these are:

- *Least squares* – in which splits are chosen to minimize the sum of squared error between the observation and the mean in each node and

- *Least absolute deviation* - which minimizes the mean absolute deviation from the median within a node (Moisen, 2008).

In a regression tree analysis the splitting of each node continues until a maximum size tree is developed (Timofeev, 2004). In CART, trees are developed in a sequence of nested trees of decreasing size, each of which is the perfect tree for its terminal node size. The model selects the best tree as the tree with minimum cost regardless of the tree size. The selection of the final tree is then based on balancing complexity, in terms of the number of terminal nodes with relative error.

In this analysis CART (Salford Systems, 2012) was used to explore the relation between $\log_{10}$ Rarity Index as the response variable and Niche Width, Habitat Transformation, seed Dispersal Distance, Life History Strategy, Land Surface and Habitat Specificity as the explanatory variables. The default settings were used for the model with the exception of the testing method. This was set on exploratory mode instead of the default V fold Cross Validation because the number of cross validation folds (CV folds) cannot be set higher than the least number of cases in a target class which in these data is three for the class C-S-R in the variable Life History. A CV fold of three is not recommended as it will not give an accurate assessment of the models predictive power. Breiman et al. (1984) do not recommend a CV fold of less than 10 as the results become less reliable below this (Appendix 9).

Bootstrapping, which generates a set of trees by resampling the data and averaging the output, was used to improve the estimate of error and in all analyses the bootstrap model with the least relative error was selected. Selection of the final tree within this model was determined by successive pruning of the optimum tree to decrease the complexity or number of terminal nodes and to improve the biological significance of the tree.

A battery run (which automates a number of comparative runs to compare parameter values and determine the optimal values for an analysis) termed “Shaving” in CART was used to determine the effect of removing variables sequentially from the least important variable to the most important variable. A regression tree using only the variables shown as important in the shaving battery run, was developed and compared with the tree developed using all six variables.

2.5.3. **Generalized Linear Regression**

As the Rarity Index for plants is a gradient from very rare (low value of the index) to common (high value of the index) it would seem to be pragmatic to explore a linear relation between rarity (Y) and the independent variables (X). However, linear regression is only useful if the following assumptions are met:

I. The errors are assumed to be identically and independently distributed; this includes the assumption that the variance of Y is constant across observations.
II. The errors are assumed to follow a normal (Gaussian) distribution.
III. The regression function is linear in the predictors (Guisan et al. 2002).

Initial tests using the Breusch-Pagan test in R 2.14.0 (R Development Core Team, 2008) of the multiple linear regression model with Rarity Index as the response variable and the explanatory variables, Niche Width, Habitat Transformation, Dispersal Distance, Life History Strategy, Land Surface and Habitat Specificity was found to be heteroscedastic (Chi Squared = 22.1042, p = 2.5824e-06). The Breusch-Pagan Test, tests the null hypothesis that the error variances are all equal. High Chi Square values and very low p values in the test rejects the Null hypothesis. Residual plots of this model also indicated problems with non-variance of data and data normality (Appendix 10). Use of the $\log_{10}$ of Rarity Index and $\log_{10}$ of Niche Width in the linear regression improved this substantially (Chi Square value = 0.9767, p = 0.32299) but the residual plots of the predictors still indicate that a linear model may not be the best model to describe this data (Appendix 10). Therefore a choice of model that allows for non-linearity and non-constant variance is more likely to be realistic for this data. Two such models, Generalized Linear Models (GLM) and Generalized Additive Models (GAM) have been widely recommended for use with ecological data (Friedlander et al., 2012; Guisan et al., 2002; Guisan et al., 1999; Edwards, Jr. et al., 2002; Guisan & Zimmermann, 2000; Simpson, 2012; Arroyo-Rodriguez et al., 2007).

Generalized linear models (GLM) are extensions of linear models that cater for non-normal errors by allowing the specification of error distributions i.e. Poisson, binomial, gamma and exponential. The model relates each observed value of the response variable to a predicted value which is obtained by transformation of the value emerging from the linear combination of the explanatory variables (Guisan et al., 2002). The "fit" of the model is determined by a comparison of the linear predictor (the combination of explanatory variables) for each value of the response variable (y) and the transformed value of y. GLMs are fit to data by optimization of the maximum likelihood estimate by an iteratively reweighted least squares mechanism (Abeare, 2009). The transformation is specified by a link function (Crawley, 2008; Hastie & Tibshirani, 1986) which describes how the mean depends on the linear predictor (Turner, 2008).

Generalized additive models (GAM) are similar to GLMs in that they allow for non-linearity and non-constant variance in that they do not assume any form of parametric relationship between variables, but allow the data to determine the nature of relationship between the response variable and the set of explanatory variables (Guisan et al., 2002). This is achieved via a smoothing function in which smoothers can be applied independently to each explanatory variable (Guisan & Zimmermann, 2000) in an attempt to achieve the best possible compromise between goodness of fit and parsimony (lowest possible degrees of freedom) in the final curve (Crawley, 2008). In GAM an additive predictor replaces the linear predictor used in GLM (Hastie & Tibshirani, 1986). Similar to GLMs, GAMs operate on deviance, rather than variance, and attempt to achieve the minimal residual deviance with the fewest degrees of freedom. In GAM this is done by approximating the appropriate number of degrees of freedom, which often results in the number of degrees of freedom being a real number with some fractional component (Hastie & Tibshirani, 1986). The GLM and GAM models explored were:

$\log_{10}$(Rarity Index) = f($\log_{10}$(Niche Width); Habitat Transformation; Dispersal Distance; Habitat Specificity; Land Surface; Life History)

To determine the relative importance of the explanatory variables for association with rarity the models were initially run in R 2.14.0 (R Development Core Team, 2008) using the R package “mgcv” (Wood, 2011) and included all the variables. Then a backward selection approach was used to find the optimal model. This approach starts with a complicated model and removes the term with the largest non-significant p-value. This backward selection approach continues until all explanatory variables significantly improve the fit of the model (Crawley, 2008; R Development Core Team, 2008; Zuur et al., 2009).

The initial and final models were checked for homogeneity of variance and normality using residual and Q-Q plots. Residuals are the difference between the observed and the fitted values and residual plots are scatterplots of the residuals versus the fitted values. Residual plots that show no trend or pattern indicate homoscedasticity. Q-Q plots test the assumption of normality and are plots of the quantiles of the data versus the quantiles of a distribution. A Q-Q plot that is a straight line indicates normality (Zuur et al., 2009; Zuur et al., 2010; Rodriguez, 2007). In order to select a model that would best approximate reality, given the available data for this analysis, a quantitative comparison was made between GAM and GLM models using both the deviance produced (Chi-squared) and the Akaike Information Criterion (AIC). Akaike Information Criterion (Akaike, 1974) quantifies the discrepancy between the unknown true model and the approximate model (Anderson et al., 1994). The formulae for AIC is:

AIC = $-2 \times \log(\text{maximized likelihood for model}) + 2 \times (\text{no. of fitted parameters})$

The AIC has no value to a model in itself, but allows for model comparisons provided the same data set is used for each model. The model with a lower value of AIC is a better model (Mazerolle, 2012).

In fitting both GLM and GAM the distribution used was “Gaussian” and the link function used was “identity” as the errors were normally distributed after Rarity Index and Niche Width were $\log_{10}$ transformed (Appendix 10). The default link function for the selection of a Gaussian family in both GLM and GAM is “identity”. All the models were run using the $\log_{10}$ of both Rarity Index and Niche Width as with all other investigations. A notable difference in the analysis using CART compared with GLM and GAM is that in the former missing values are interpolated and substituted by CART whereas in GLM and GAM the species with missing data are removed from the analysis.

3. **Results**

3.1. **Results of Bivariate Analyses**

3.1.1. **Ecological Niche Width**

A Pearson product moment correlation coefficient was computed to assess the relation between Niche Width and the Rarity Index. There was a positive correlation between the $\log_{10}$ Niche Width and $\log_{10}$ Rarity Index (Pearsons *r*(97) = 0.71, *p*<0.001), which supports the hypothesis that rare species tend to have smaller Niche Widths than common species. Whilst 51% of the variance ($r^2(97) = 0.51$) is accounted for by a linear relation between $\log_{10}$ Niche Width and $\log_{10}$ Rarity Index there is a fair degree of variation around this relation with some species with a medium Rarity Index value (i.e. more common species) having similar sized Niche Widths to some very rare species with low Rarity Indexes (Fig. 15).

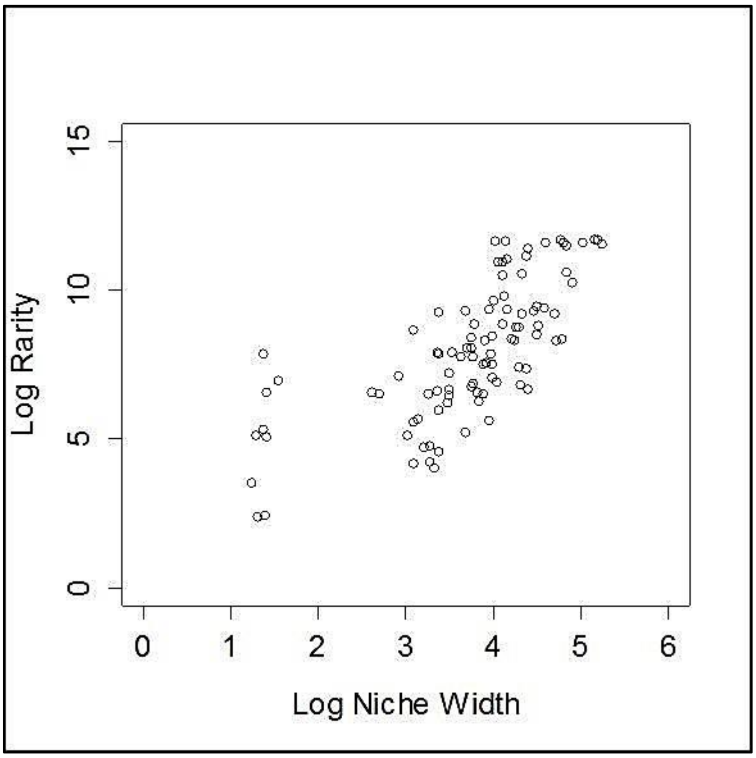

Figure 15: Relation between $\log_{10}$ Niche Width (log Niche Width) and $\log_{10}$ the Rarity Index (log Rarity) of a sample of n = 97 plant species from KwaZulu-Natal. (Pearson $r^2 = 0.5101$; $p < 0.001$).

3.1.2. **Habitat Specificity**

An independent one tailed t-test was conducted to evaluate the hypothesis that plants that have high habitat specificity are rarer than those that occur in matrix habitats. There was a significant difference in the means of $\log_{10}$ Rarity Index for Habitat Specific species ($\bar{x}$ = 7.5417, SD= 2.1745) and Matrix species ($\bar{x}$ = 8.4236, SD= 2.2908) in the specified direction ($t(95) = -1.944$, $p = 0.027$). These results suggest that habitat specific plants tend to be rarer than matrix plant species but there are some exceptions in which rare plants occur in matrix habitats. However, very rare plants ($\log_{10}$ Rarity Index ≤ 4) are always habitat specific (Fig.16).

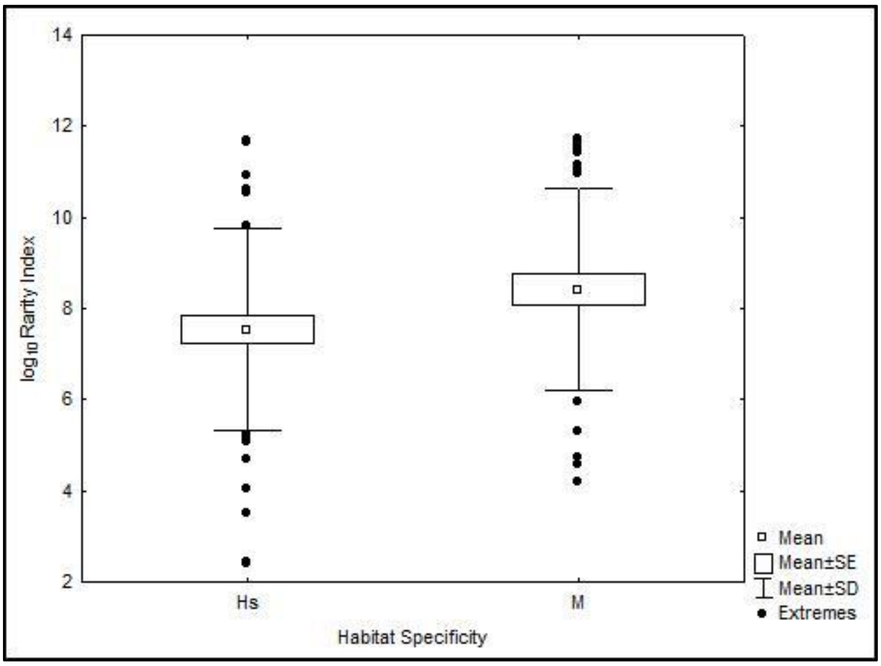

Figure 16: The relation between the two habitat specificity classes (Hs = Habitat Specific, M = Matrix) and $\log_{10}$ Rarity Index of a sample of 97 plant species from KwaZulu-Natal. Box plots show the mean and standard errors and the whiskers are the standard deviations of the means. The black dots represent species with the highest and lowest Rarity Index ($\log_{10}$ Rarity Index).

3.1.3. **Dispersal Distance**

The relation between Dispersal Distance and $\log_{10}$ Rarity Index was investigated using Spearman's rank correlation. There was a positive correlation between $\log_{10}$ Rarity Index and Dispersal Distance but this was not statistically significant ($r_s = 0.129$, $p = 0.236$). This trend (Fig. 17) indicates that seed dispersal distance tends to increase with an increase in the value of the Rarity Index.

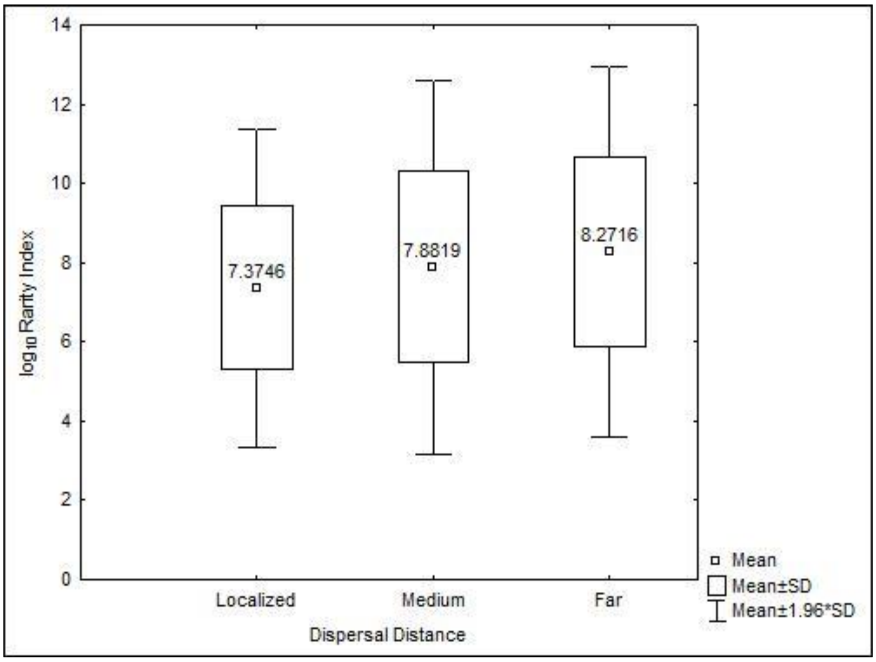

Figure 17: The relation between $\log_{10}$ the Rarity Index and Seed Dispersal Distance in a sample of plant species from KwaZulu-Natal. Box plots show the mean and standard errors and the whiskers are the standard deviations of the means.

3.1.4. **Life History Strategy**

As plants are expected to be rarer if they have a stress tolerant survival strategy the mean of $\log_{10}$ of the Rarity Index of Stress Tolerant Plants (S) was compared with the means of $\log_{10}$ of the Rarity Index of each other Life History Group using a one tailed t-test for independent groups. No statistical difference ($p > 0.05$) was found between the means (Table 3.1). The difference between the mean of the Rarity Index of species with a stress-tolerant survival strategy (S) and species with a competitive survival strategy (C) was the greatest (Fig. 18) but this was not significant (t (df 63) = -1.50, $p = 0.069$). As the p-value is close to the 0.05 cut-off point further investigation may be necessary before rejecting the hypothesis that stress tolerant plants are rarer than Competitive or Ruderal species.

Table 3.1: Means (SD) of $\log_{10}$ Rarity Index of plants with a Stress Tolerant (S) and, Competitive (C) survival strategy and a mixture of C and S (C-S) and C, S and Ruderal (R) survival strategy (C-S-R). *p* values are derived from one tail t-tests testing the hypothesis that S plants have a lower Rarity Index than plants with other survival strategies

Grimes Survival Strategy	**Mean (SD)**	**Number of species (N)**	**p value for comparison with Stress tolerant species**
Stress Tolerant (S)	7.675 (2.366)	38	
Competitive (C)	8.600 (2.566)	27	0.069299
mixture of C and S strategy	8.355 (1.751)	14	0.166003
mixture of C, S and ruderal strategy R	9.258 (3.333)	3	0.184153

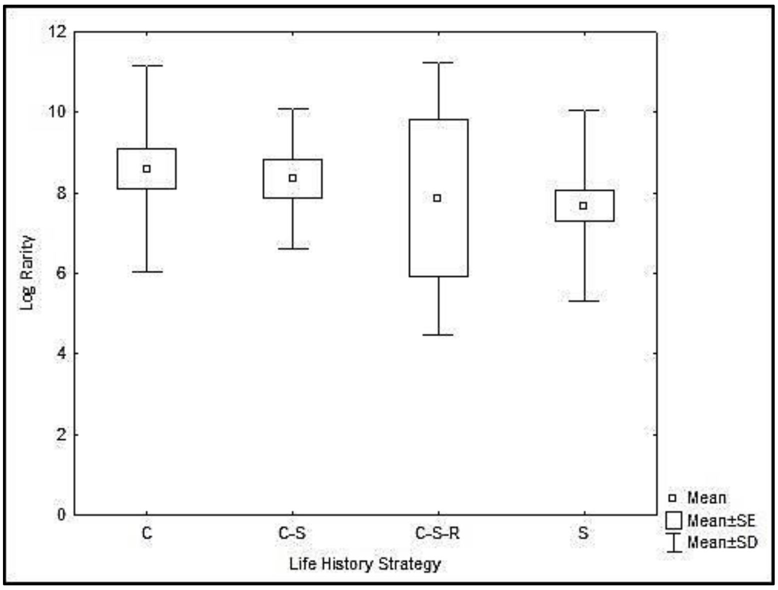

Figure 18: The relation between Grime's life history strategies and $\log_{10}$ the Rarity Index (Log Rarity) where C = competitive strategy, C-S = a mixture of C and S strategy, C-S-R = a mixture of C, S and ruderal strategy R and S = Stress-tolerant strategy. Box plots show the mean and standard errors and the whiskers are the standard deviations of the means.

3.1.5. **Geological Land Surfaces**

To test the hypothesis that plant species that are associated with ‘Islands’ of former large land surfaces are rarer than those that occur on more extensive or contiguous land surfaces, comparisons between the mean $\log_{10}$ Rarity Index of plants associated with the Post African and other dissected areas surface (PAD) and those associated with “island” land surfaces were made using t-tests for independent groups. No statistically significant (p>0.05) difference in the means (Table 3.2) of $\log_{10}$ Rarity Index was found between “island” species and those that have an affinity for the more contiguous Post African and other dissected areas surfaces. There is a notable degree of variation in the $\log_{10}$ Rarity Index values for species associated with the Post African and other dissected areas surface with values falling on both extremities of the axis. From this it appears that there is no association between plant species that are associated with ‘Islands’ of former large land surfaces and rarity.

However comparison between the means of $\log_{10}$ Rarity Index of species with ‘No Affinity’ to a particular land surface and those with an affinity to a land surface using a two tailed t-test showed statistical differences (p<0.001) for all comparisons (Table 3.2). Species with ‘No Affinity’ to a land surface were found to have a higher mean $\log_{10}$ Rarity Index i.e. are more common than those associated with specific land surfaces (Fig. 19).

Table 3.2: Means (SD) of $\log_{10}$ Rarity Index of plants with an affinity to Post African and other dissected areas surface (Pad), African Surfaces (As), Escarpment (Esc) Neogene (Ne) and those with no affinity to a land surfaces (No). *p* values are derived from one tail t-tests testing the hypothesis that plant species with an affinity to "Island" land surfaces have a lower Rarity Index than plants that occur on more contiguous surfaces and two tailed t-tests testing the difference between species that have an affinity to a land surface and those that don't.

Affinity to land surface	**Mean (SD)**	**No. of Plant Species (N)**	**p value for comparison with Post African and other dissected areas surface (1 tailed t-test)**	**p value for comparison with No affinity to land surfaces (2 tailed t-test)**
Post African and other dissected areas surface (Pad)	7.297 (2.007)	41	_	0.000001***
African Surface (As)	6.706 (1.629)	11	0.187 (1 tailed)	0.00001***
Escarpment (Esc)	6.733 (2.164)	7	0.25 (1 tailed)	0.000338**
Neogene (Ne)	6.960 (2.670)	6	0.357 (1 tailed)	0.002357*
No affinity to land surfaces (No)	9.697 (1.719)	32		-

*** $p \leq 0.0001$; ** $p \leq 0.001$; * $p \leq 0.05$

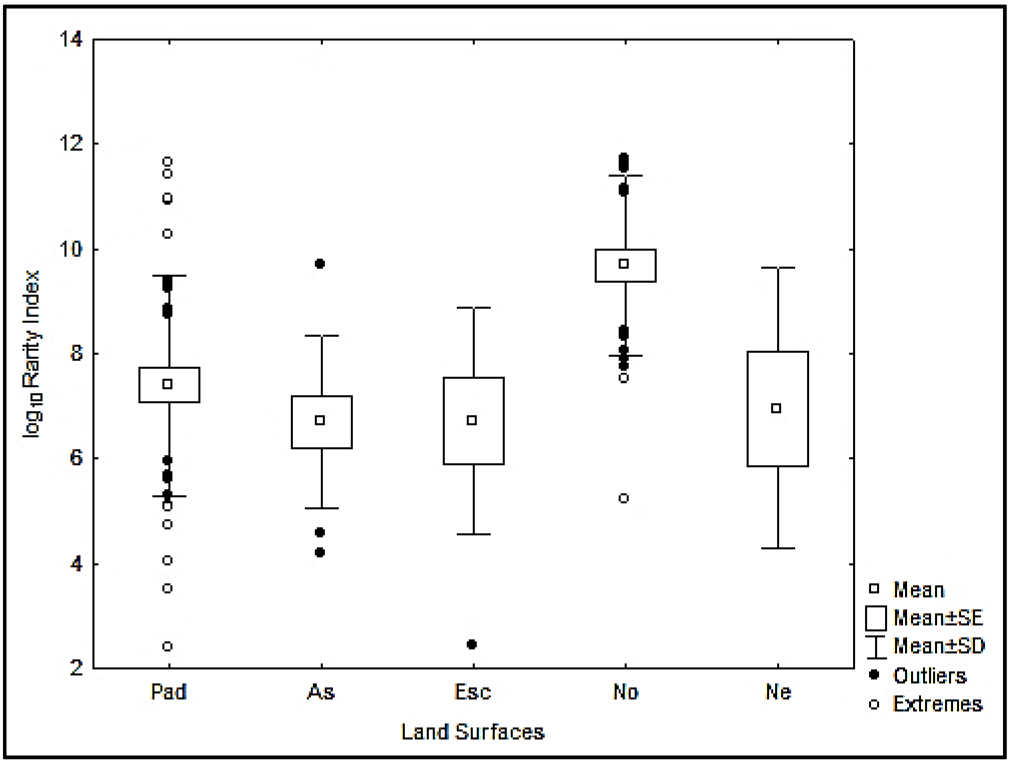

Figure 19: The relation between $\log_{10}$ Rarity Index and erosional land surface where As = African surface; Esc = Escarpment, Ne = Neogene marine and coastal aeolian sediments; No = No affinity to Land Surfaces and Pad = Post African surfaces and other Dissected Areas from the early Miocene. The clear circles represent outliers

3.1.6. Human Use

Here it was expected that high levels of use would cause plants to be rare. However the relation appeared to be more complex than this, with the vast majority of plants having no known use but also having the lowest mean rarity (Table 3.3). There are nevertheless some highly utilized species that are rare (Table 3.3, Fig. 20), but in general species that have intermediate or high levels of use are not rare. This is possibly because indices of use are derived from market studies and in most instances humans utilize species that are relatively common and widespread. As such, the impact of use has not yet affected their abundance or distribution range to the extent that it has made them rare.

Table 3.3: Mean (SD) of $\log_{10}$ Rarity Index of three utilization classes; no utilization, some utilization and intense utilization and the number of species in each class from the sampled plants.

Utilization level	**Mean (SD) of $\log_{10}$ Rarity Index**	**No of plant species (N)**
None	7.525 (0.526)	68
Some	9.280 (1.051)	17
Intense	8.790 (1.203)	13

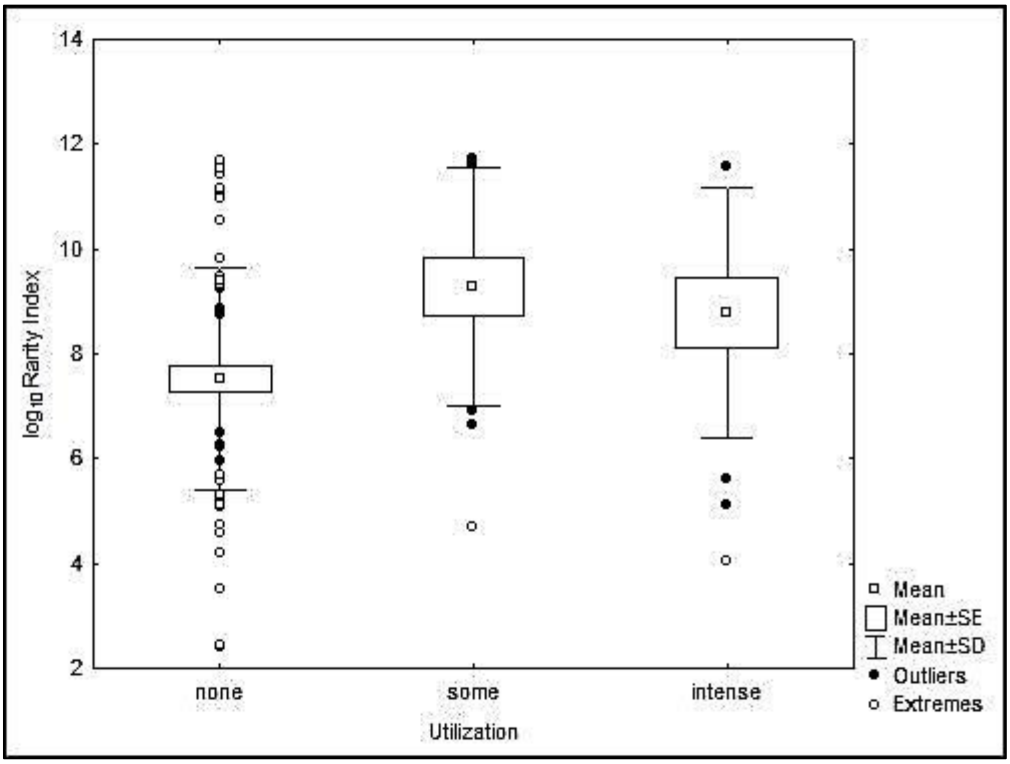

Figure 20: The relation between $\log_{10}$ Rarity Index and three utilization classes in the sample of plants from KwaZulu-Natal. Box plots show the mean and standard errors and the whiskers are the standard deviations of the means, the circles show (●) outliers and (○) extremes.

3.1.1. **Range Transformation**

In testing the relation between rarity and habitat transformation no statistical correlation was found between the degree of transformation and the $\log_{10}$ of Rarity Index (Pearsons *r*(91) = 0.0051, *p*=0.96). Rare species occur throughout the range of transformation levels but in this sample, all species with highly transformed habitats have a low Rarity Index ($\log_{10}$ Rarity Index) (Fig. 21). Although the hypothesis is not entirely supported by the results as some very rare plants are not affected by transformation, there appears to be a decline in Rarity Index (i.e. species become more rare) with habitat transformation of greater than 30%. This is well demonstrated using a loess smoothing curve (Fig. 21) in which a polynomial regression using weighted least squares is applied to each value of *x* in the regression function *y* = *f(x)* using the nearest neighbour observations. The fitted value for each focal *x* is plotted and joined to form the regression curve. This local approximation of the function *f* allows the non-linear relation between rarity and transformation to be visualized (Cleveland & Loader, 1996; Jacoby, 2005).

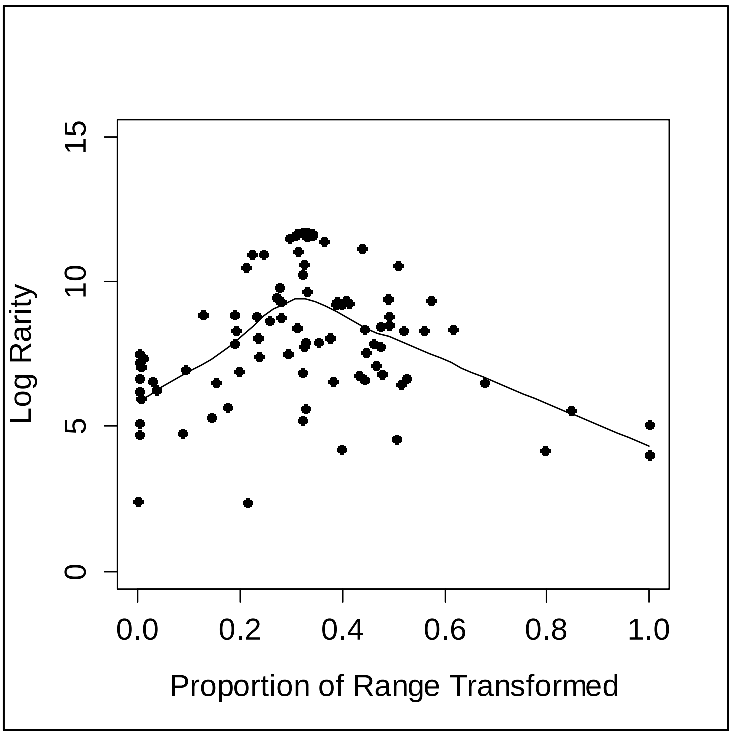

Figure 21: The relation between $\log_{10}$ Rarity Index and the proportion of habitat transformed. Fitted curve represents the Loess smoothing curve (R Development Core Team, 2008).

Some species with low values of Rarity Index are naturally rare and occur in single or isolated sites in habitat that is not conducive to transformation. For example *Protea nubigena* ($\log_{10}$ Rarity Index = 2.44) occurs at very high altitudes on top of the Drakensberg Mountains. *Holothrix majubensis* ($\log_{10}$ Rarity Index = 5.08) is only known from the type locality on the Amajuba Mountain near Newcastle and this site has not been affected by transformation as yet. On the other hand species such as *Kniphofia leucocephala* ($\log_{10}$ Rarity Index = 5.32) have been hugely impacted by transformation (84.7% of their known habitat) resulting in only one small remaining population.

3.2. **Regression Tree Analysis**

In the classification and regression tree programme, CART (Salford Systems Inc., USA) bootstrapping of the model using all six variables for the analysis resulted in an optimal tree of 22 nodes or groups with a relative error of 0.053 (Fig. 22).

Further investigation of this model shows that the tree with the lowest relative error (BSP_9 in Fig. 22) is not only the best tree with 22 nodes but has the lowest relative error for all node sizes (Fig. 23) which ensures any nested tree within this model will still be the perfect tree for its terminal node size.

To minimize complexity and retain a low relative error a tree with 10 nodes was selected from the best tree obtained by bootstrapping (BSP_9, with a relative error of 0.096; R^2 = 0.904) (Fig. 24).

According to the Variable Importance Score produced in the analysis, the most important splitter in this tree was $\log_{10}$ Niche Width, followed by Land Surface, Life History Strategy and Habitat Transformation (Table 3.4). Habitat Specificity and Dispersal Distance were of little importance overall. The Variable Importance Score in CART is a summary of a variables contribution to the overall tree when all nodes are examined. It reflects how good a splitter the variable is, as both a primary splitter and as a surrogate splitter (Steinberg & Golovnya, 2006)

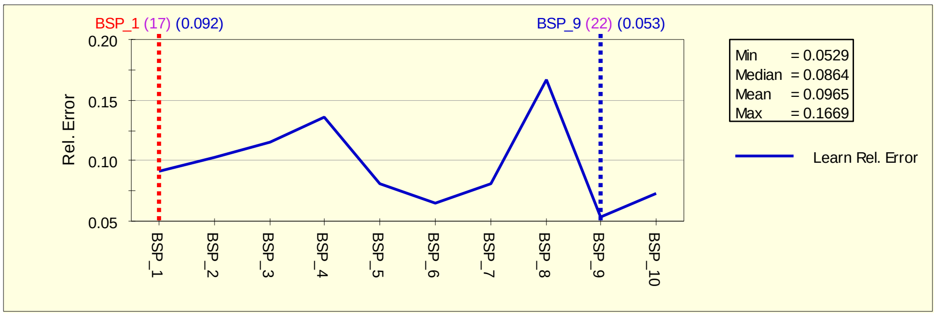

Figure 22: The relative error of models of regression trees (BSP_1 to 10) developed using bootstrapping. Regression tree BSP_9 has the lowest relative error

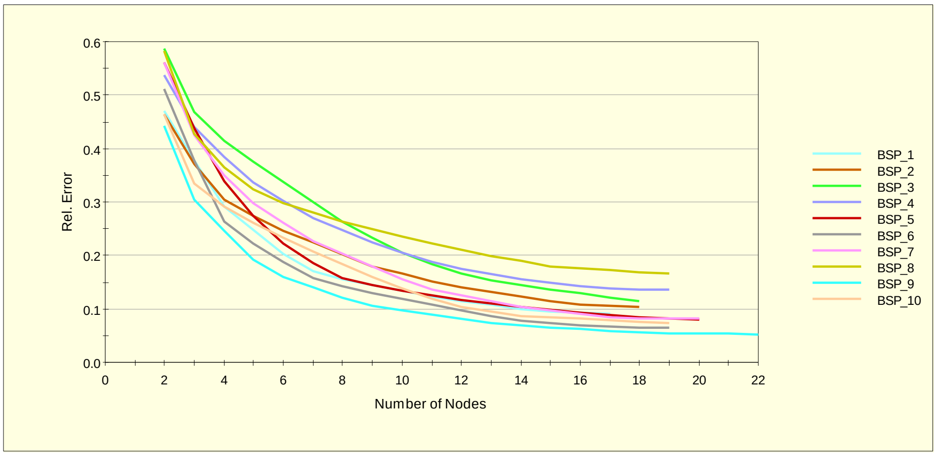

Figure 23: The relative error of bootstrap trees with increasing number of terminal nodes.

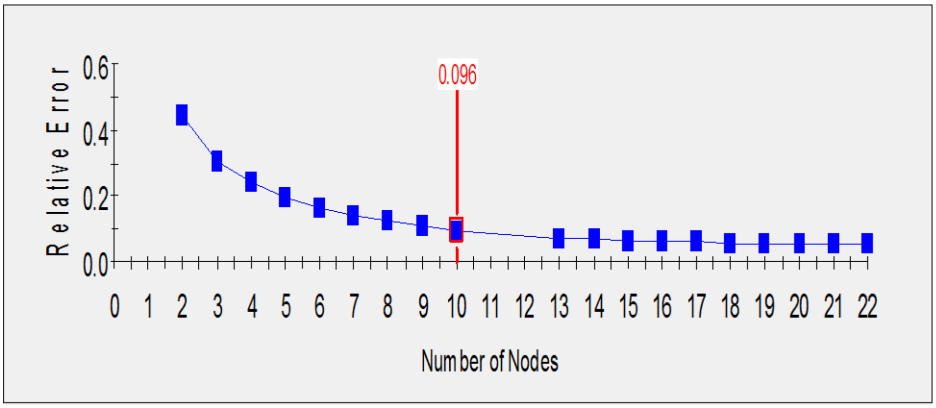

Figure 24: The change in relative error of the selected tree (BSP_9) with number of terminal nodes.

Table 3.4: Importance of plant trait variables in influencing the explanation of the response variable Rarity Index (CART)

Variable	**Importance score**
Log_{10} Niche Width	100
Land surface	66.59
Life history strategy	32.72
Habitat transformation	22.97
Habitat specificity	9.65
Dispersal distance	9.01

In the regression tree pruned to 10 terminal nodes (Fig. 25) the first split, based on $\log_{10}$ Niche Width, separated the sampled species into more common species (mean $\log_{10}$ Rarity Index = 10.130, SD=1.437) on the right hand side (group 2 in Fig. 25) and more rare species on the left hand side (group 1) (mean $\log_{10}$ Rarity Index = 6.449, SD=1.771). $\log_{10}$ Niche Width further split the more rare species, with lower values of $\log_{10}$ Niche Width being associated with lower values of $\log_{10}$ Rarity Index (groups 1.1 ($\bar{x}$ = 2.982, SD=0.543) and 1.2 ($\bar{x}$ = 6.882, SD=1.343). Group 1.2 was further split by $\log_{10}$ Niche Width (1.2.1 ($\bar{x}$ = 6.145, SD=1.050; 1.2.2 ($\bar{x}$ = 7.754, SD=1.108) but within these group the relations become slightly more complicated with the group containing the more common of the rare species (group 1.2.2) (i.e. with higher values of $\log_{10}$ Rarity Index) being further split by Land Surface and the group containing the rarer species (group 1.2.1) (i.e. with lower values of Rarity Index) being further split by a habitat transformation proportion of 92%. Species with a habitat transformation of greater than 92% are more rare ($\bar{x}$ =4.558, SD=0.519) than those with less than 92% transformed habitat ($\bar{x}$ = 6.277, SD=0.972). In the split based on land surfaces (group 1.2.2), Escarpment, Neogene and Post African and Other Dissected Surfaces were associated with a lower mean $\log_{10}$ Rarity Index ($\bar{x}$ = 6.912, SD=1.037) than old African surfaces and species with no affinity to a land surface ($\bar{x}$ = 8.336, SD=0.709)

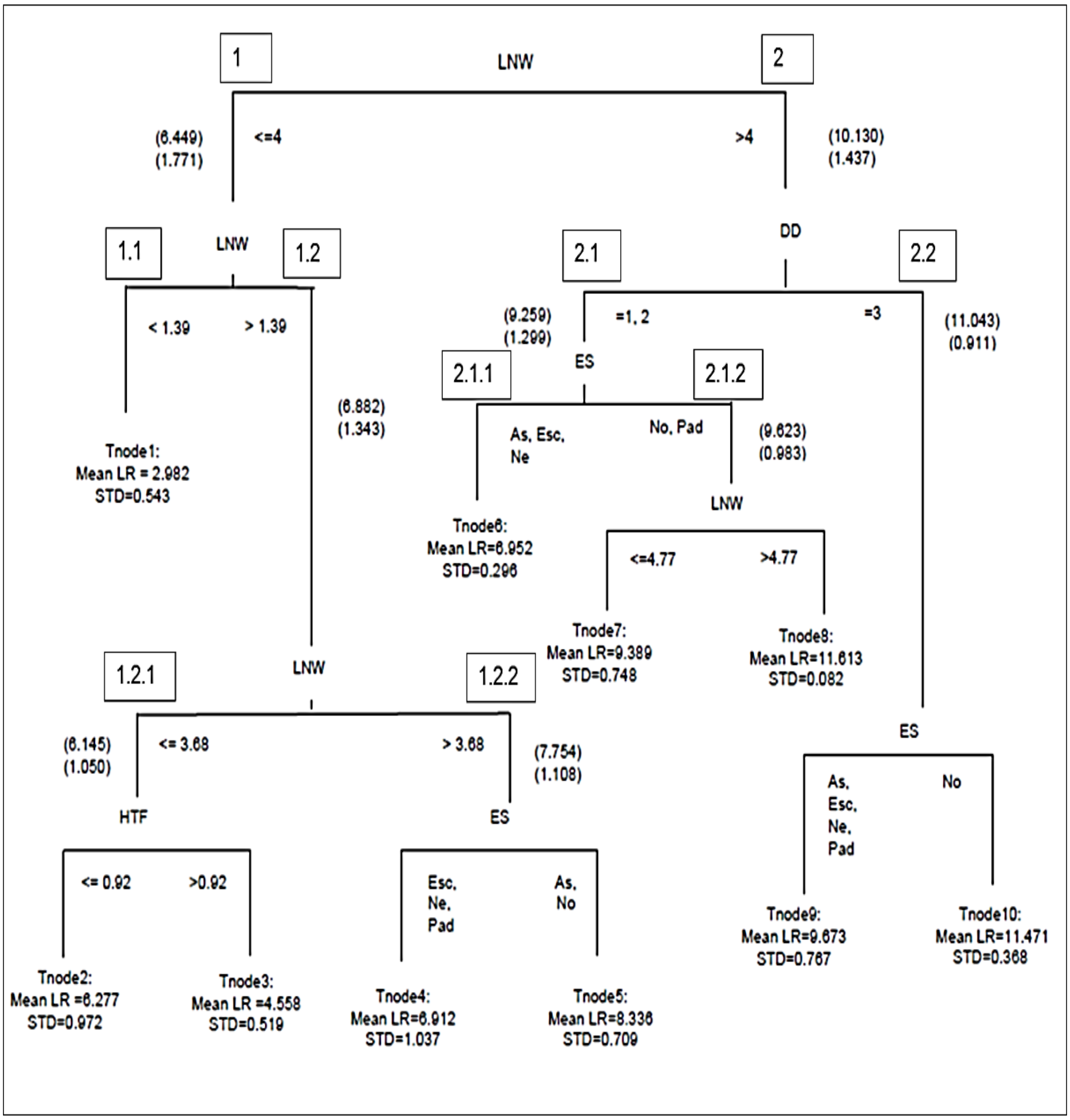

Figure 25: Regression tree for $\log_{10}$ Rarity Index (LR) and explanatory variables $\log_{10}$ Niche Width (LNW), Dispersal Distance (DD), Land Surface (ES), Life History strategy, Habitat Specificity and Habitat Transformation (HTF). The splitters are shown at each node and the splitting criteria are shown on the branches of each node. Each branch has been given a group code in a text box for interpretive purposes. Values in the terminal nodes are the mean and standard deviation (STD) of $\log_{10}$ Rarity Index for that node. The values on the outside of the branches are the mean $\log_{10}$ Rarity Index above and the STD (standard deviation) below for that split.

On the right hand side of the tree (group 2 of Fig. 25), longer Dispersal Distance (DD=3) is associated with a higher mean value of $\log_{10}$ Rarity Index ($\bar{x}$ =11.043, SD=1.437) i.e. more common species. Species in this group (group 2.2) are further split by land surfaces with the most common species being those with no affinity to a land surface ($\bar{x}$ =11.472, SD=0.368). The group with medium and localized dispersal (group 2.1) was further split by Land Surface with Escarpment, Old African surface and Neogene species having a lower mean $\log_{10}$ Rarity Index (group 2.1.1) ($\bar{x}$ =6.953, SD=0.296) than species associated with Post African and Other Dissected Surfaces and species with no affinity to a surface (group 2.12) ($\bar{x}$ =9.623, SD=0.983). Further splits to this group are based on $\log_{10}$ Niche Width. Throughout the tree $\log_{10}$ Niche Width is positively associated with $\log_{10}$ Rarity Index but the relation between Land Surface and $\log_{10}$ Rarity Index varies somewhat throughout the tree. The regression tree clearly indicates that the contribution of explanatory variables varies across their range and the range of the response variable Rarity Index.

The shaving battery used in CART to determine the effect of removing variables sequentially from the least important variable to the most important variable showed that the removal of the variables Dispersal Distance (Fig. 26) and Habitat Specificity decrease the relative error. For exploratory purposes a regression tree developed using the four most important variables was compared with the tree developed with all the variables. The regression tree produced when Dispersal Distance and Habitat Specificity were excluded (Fig. 27) produced similar results on the left hand side of the tree (group 1 in Fig. 27) to the regression tree that included all variables.

The right hand side of the tree which consists of more common species (group 2 in Fig. 27) (i.e. higher $\log_{10}$ Rarity Index) was somewhat different. Land Surface initially split the species into those with no affinity ($\bar{x}$ = 10.850, SD = 1.078) to a Land Surface (group 2.2) and those with an affinity to a Land Surface (group 2.1) ($\bar{x}$ = 9.029, SD = 1.199). Habitat transformation was associated with species with no affinity to Land Surfaces (No); those species with habitat transformation of greater than 36% having a lower mean value of $\log_{10}$ Rarity Index ($\bar{x}$ = 9.869, SD = 0.948) than those with habitat transformation of less than 36% ($\bar{x}$ = 11.369, SD = 0.723).

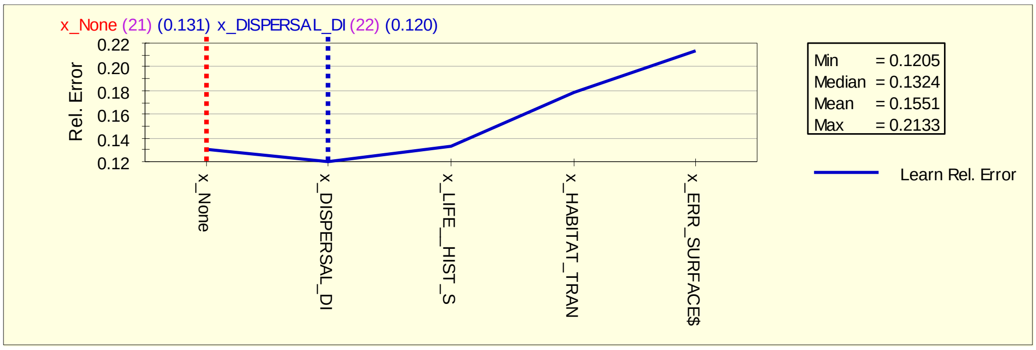

Figure 26: The effect on relative error (Rel. Error) of sequentially shaving variables from least important to most important. The blue line indicates the change in relative error from the removal of no variables (NONE) to the removal of Dispersal Distance (DISPERSAL_DI), Life History Strategy (LIFE_HIST_S), Habitat Transformation (HABITAT_TRAN) and Erosional Surfaces (ERR_SURFACES).

This supports the bivariate analysis result that showed a decrease in Rarity Index above 36% habitat transformation. Further splitting of the left hand side of this branch is contrary to the expected effect of habitat transformation with the more common species being associated with higher levels of transformation but as there is only one plant in the split this is not useful from an interpretive perspective. Species in group 2.1.1 with an affinity to African Surfaces and the Escarpment are not as common ($\bar{x}$ = 6.952, SD = 0.296) as those found on Neogene marine and coastal aeolian sediments and Post African surfaces and other Dissected Areas from the early Miocene (group 2.1.2) ($\bar{x}$ = 9.475, SD = 0.778).

Overall the regression tree analysis strongly supported the hypothesis that plants are expected to be rarer the smaller their ecological niche as Niche Width was the most important variable (Table 3.4). The species were initially split into two groups with a threshold value of 4 for Log_{10} Niche Width that determined the group of rarer species (Log_{10} Rarity Index $\bar{x}$ = 6.449, SD = 1.771) on the left hand side of the tree (group 1) and the more common species on the right hand side (group 2) ($\bar{x}$ = 10.130, SD = 1.437). Very rare species were very strongly associated with low Niche Width (group 1.1). Although Land Surfaces was the second most important predictor in this analysis the results were not entirely concurrent with the hypothesis. For rarer plants (group 1), species that have an affinity with Escarpments, Neogene marine and coastal aeolian sediments and Post African surfaces and other Dissected Areas, are more rare than those with an affinity for African surfaces and those with no affinity to a surface. On the right hand side of the tree the most common plants are those with an affinity to Post African surfaces and other Dissected Areas and those with no affinity to a Land Surface (terminal group 8). From this analysis it would appear that Land Surface was a poor and inconsistent predictor of rarity. The regression tree analysis strengthens the case that habitat transformation is related to rarity as species with a transformation of greater than 92% (Fig. 25 & 27) are rare and as shown in the second analysis when the two least important variables were removed a habitat transformation threshold of 36% (Fig. 27) is important in determining the commonness or rarity of a species. Although Dispersal Distance was one of the least important variables in the whole analysis and its removal actually decreased the relative error (Fig. 26) its selection as the most important splitter at the 2nd node on the right hand side indicated the relation between some common plants and long distance dispersal.

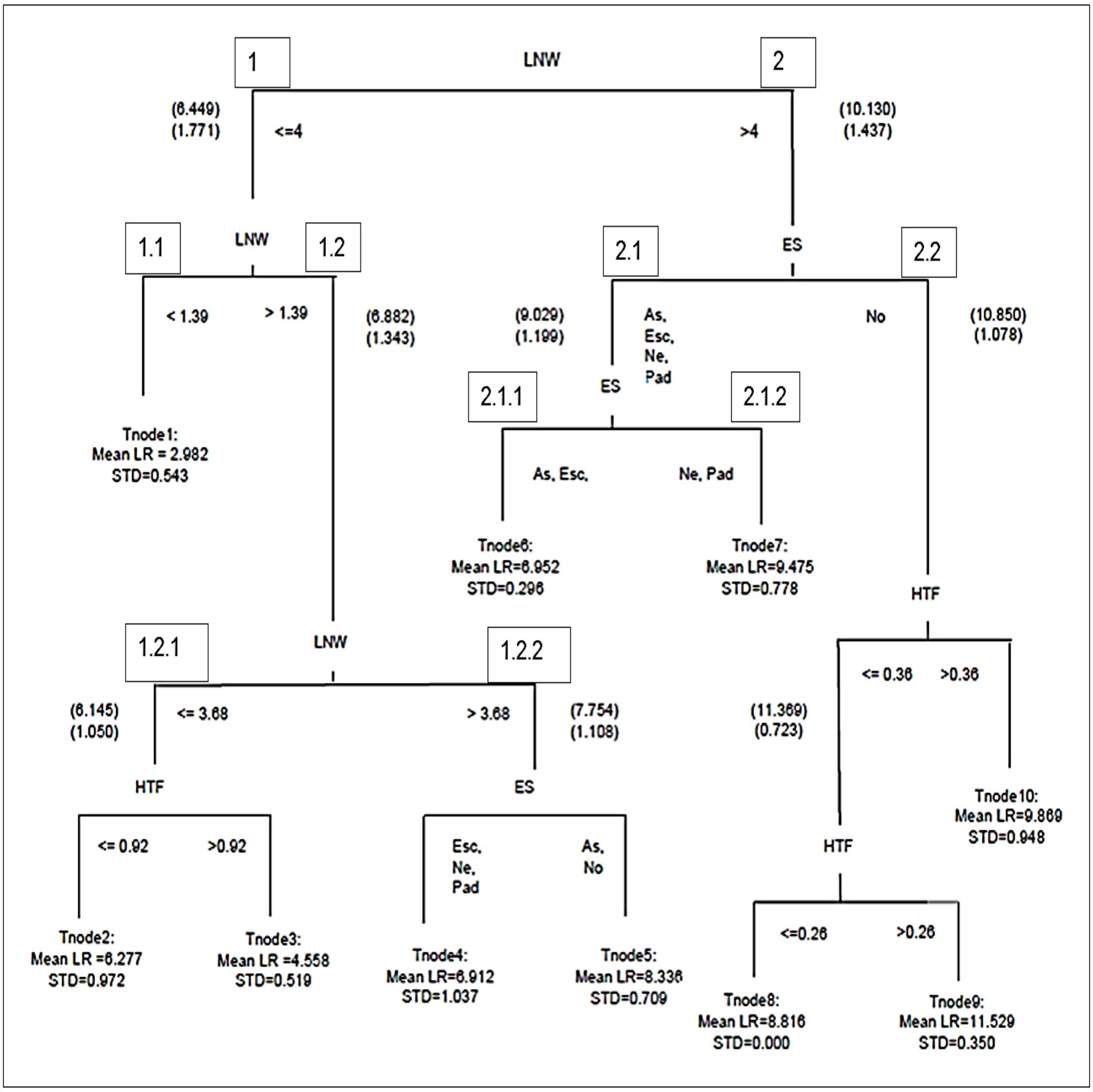

Figure 27: Regression tree for the $\log_{10}$ Rarity Index (LR) and explanatory variables $\log_{10}$ Niche Width (LNW), Land Surface (ES), Habitat Transformation (HTF) and Life History (LH). The splitting variables are shown at each node and the splitting criteria are shown on the branches of each node. Each branch has been given a group code in a text box for interpretive purposes. Values in the terminal nodes are the mean and standard deviation (STD) of $\log_{10}$ Rarity Index for that node. The values on the outside of the branches are the mean $\log_{10}$ Rarity Index above and the STD below for that split.

3.3. **Generalized Linear Regression (GLM)**

The generalized linear model which included all six explanatory variables used in the regression tree, explained 70.9% of the deviance in $\log_{10}$ Rarity Index. This value of deviance is analogous to R^2 and is termed pseudo R^2 (Dobson, 2002 in (Zuur et al., 2009) where:

$$\text{pseudo } R^2 = 1\text{-(residual deviance/null deviance)}$$

$\log_{10}$ Niche Width, Far Distance Dispersal and no affinity to land surface were significantly different from the null hypothesis (Table 3.5) in which the true value of each coefficient is 0 (Montana State University, 2012). Graphical investigation of the residuals versus the fitted values of this model (Fig. 28) shows no major violation of homoscedasticity but the Q-Q plot (Fig. 29) or standardized residual versus the theoretical quantile shows that there is a slight deviation from normality at the tails.

A backward selection approach (Appendix 11) in which non-significant terms were removed sequentially starting with the least significant variable resulted in a final generalized linear model that only included $\log_{10}$ of Niche Width and Land Surface (GLM5, Appendix 11). This model explained 60% of the deviance. The $\log_{10}$ of Niche Width was highly significant ($p< 0.00001$) as was No Affinity to any single land surface.

This final GLM model supports the notion of a positive correlation between Niche Width and Rarity and a positive correlation of species with no affinity to land surface and species commonness. The fourth model (GLM4, Appendix 11), which included Habitat Transformation, indicates that although not significant the relation between Rarity Index and Habitat Transformation is negative (Table 3.6) i.e. The Rarity Index decreases (species become more rare) with increasing Habitat Transformation.

Table 3.5: The coefficients of the generalized linear model (GLM1) of $\log_{10}$ Rarity Index on $\log_{10}$ Niche Width, Habitat Transformation, Life History, Land Surfaces, Habitat Specificity and Dispersal Distance.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	1.29025	1.10406	1.169	0.2474
Log_{10} Niche Width	1.58348	0.21599	7.331	8.92e-10 ***
Habitat Transf	-1.16789	0.88101	-1.326	0.1902
Dispersal (f)	1.03948	0.45554	2.282	0.0263 *
Dispersal (m)	-0.06618	0.46513	-0.142	0.8874
HSpec (Matrix)	0.56165	0.37579	1.495	0.1405
Land Surf (Esc)	-0.40909	0.91534	-0.447	0.6566
Land Surf (Ne)	-0,14709	0.84005	-0.175	0.8616
Land Surf (No)	1.69651	0.69886	2.428	0.0184 *
Land Surf (Pad)	0.77120	0.65741	1.173	0.2456
Life History (C-S)	-0.40596	0.49767	-0.816	0.4181
Life History (C-S-R)	-0.35003	0.92841	-0.377	0.7076
Life History (S)	-0.55722	0.40868	-1.363	0.1781

*** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$

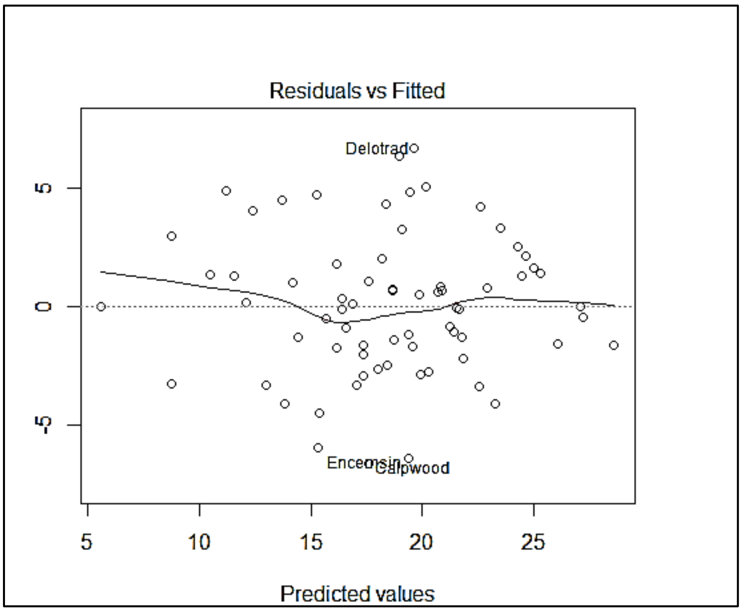

Figure 28: Residuals versus fitted values of the generalized linear regression of $\log_{10}$ Rarity Index on $\log_{10}$ Niche Width, Habitat Transformation, Life History Strategy, Land Surfaces, Habitat Specificity and Dispersal Distance. The plot also shows potential outliers including *Delosperma tradescantioides* (Delotrad), *Encephalartos msinganus* (Encemsin) and *Calpurnia woodii* (Calpwood).

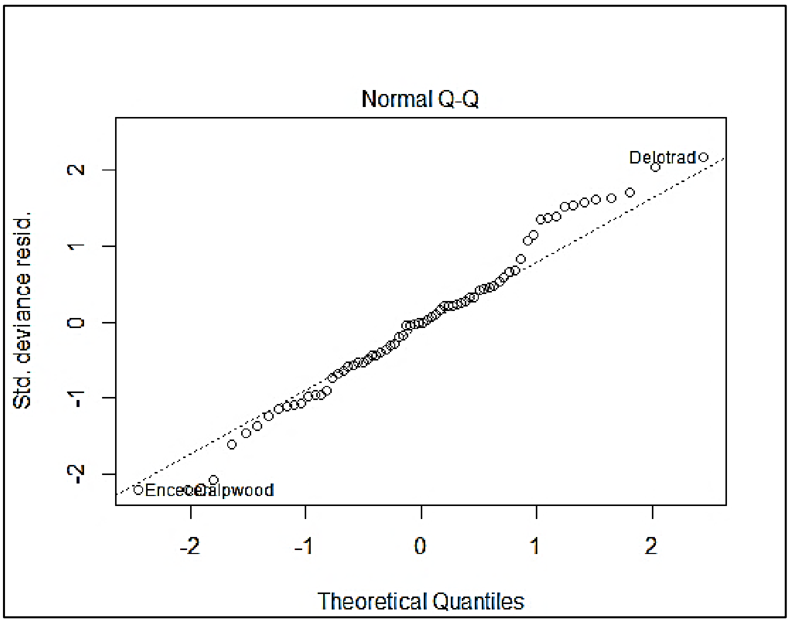

Figure 29: QQ plot of the generalized linear regression of $\log_{10}$ Rarity Index on $\log_{10}$ Niche Width, Habitat Transformation, Life History Strategy, Land Surfaces, Habitat Specificity and Dispersal Distance. The plot also shows potential outliers including *Delosperma tradescantioides* (Delotrad), *Encephalartos msinganus* (Encemsin) and *Calpurnia woodii* (Calpwood).

Table 3.6: The coefficients of the generalized linear model (GLM4) of $\log_{10}$ Rarity Index on $\log_{10}$ Niche Width, Habitat Transformation and Land Surface.

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	2.5057	2.0026	1.251	0.21428
$\mathbf{Log_{10}}$ NicheWidth	1.6659	0.1954	8.525	4.94e-13 ***
Habitat Transf	-1.8724	1.8179	-1.03	0.30594
Land Surf (Esc)	-0.8173	1.7018	-0.48	0.63229
Land Surf (Ne)	0.435	1.674	0.26	0.79562
Land Surf (No)	3.9881	1.2016	3.319	0.00133 **
Land Surf (Pad)	1.6139	1.1482	1.406	0.1635

*** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$

3.4. Generalized Additive Model (GAM)

The full generalized additive (GAM 1) model including all variables, explained 75.3% of the deviance. Both smoothed terms, $\log_{10}$ Niche Width ($p<0.001$) and Habitat Transformation ($p<0.05$) were significant as was the intercept ($p<0.001$), no affinity to land surfaces ($p<0.01$) and ‘far’ distance dispersal ($p<0.05$) (Table 3.7).

The smoothing curve for GAM 1 shows an almost linear relation between $\log_{10}$ Rarity Index and $\log_{10}$ Niche Width. The curve for Habitat Transformation is clearly nonlinear but shows a decline in the Rarity Index above about 30% habitat transformation (Fig.30)

Diagnostic plots of the model (Fig. 31) indicate normality (Q-Q plot) and homogeneity of variance (residual plots).

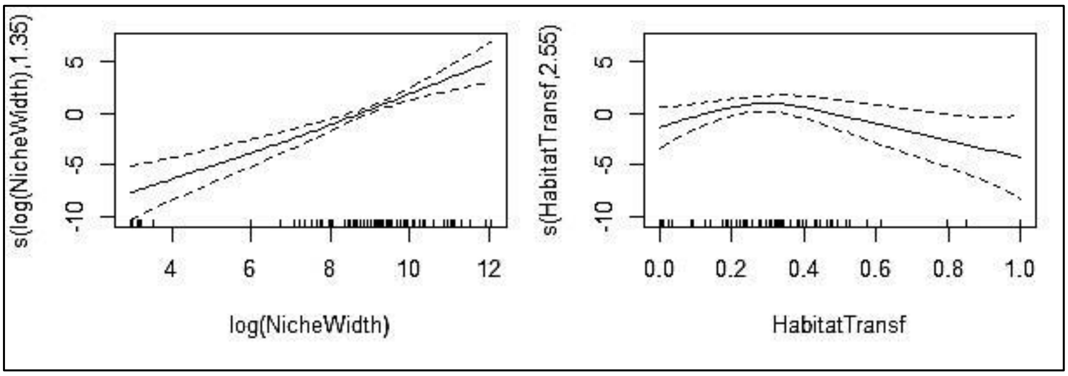

Figure 30: Smoothing curves for the generalized additive model GAM 1

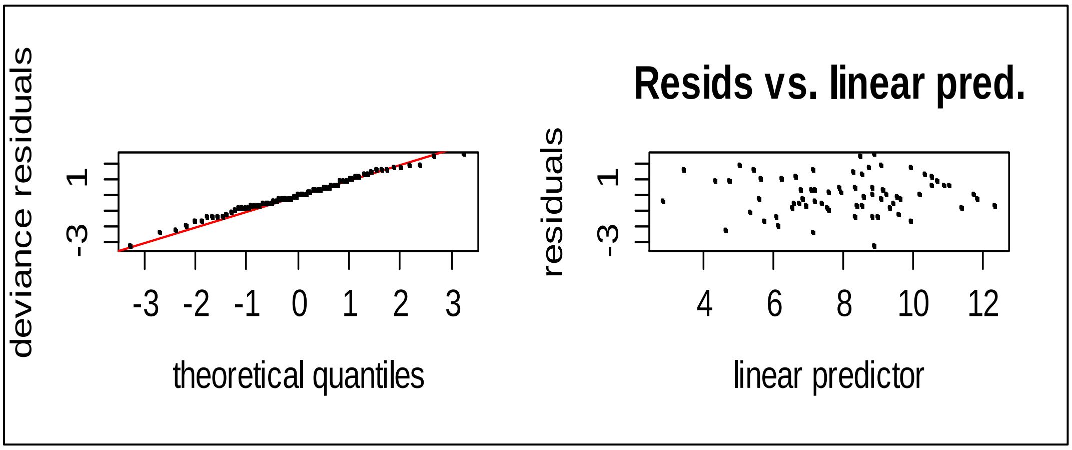

Figure 31: Q-Q and residuals versus the linear predictor plots of the generalized additive model of $\log_{10}$ Rarity Index on $\log_{10}$ Niche Width, Habitat Transformation, Life History, Land Surfaces, Habitat Specificity and Dispersal Distance.

Table 3.7: The parametric coefficients of the generalized additive model (GAM1) of $\log_{10}$ Rarity Index on Life history, Land Surfaces, Habitat Specificity and Dispersal Distance and the approximate significance of the smooth terms $\log_{10}$ Niche Width and Habitat Transformation.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	6.6345	0.6567	10.102	3.8e-14 ***
Dispersal (f)	0.9175	0.4339	2.115	0.0390 *
Dispersal (m)	-0.1353	0.4393	-0.308	0.7593
HSpec (Matrix)	0.4272	0.3597	1.188	0.2401
Land Surf (Esc)	0.6060	0.9752	0.621	0.5369
Land Surf (Ne)	0.4541	0.8584	0.529	0.5989
Land Surf (No)	1.8402	0.6775	2.716	0.0088 **
Land Surf (Pad)	1.1542	0.6709	1.72	0.0910 •
Life History (C-S)	-0.3483	0.4690	-0.743	0.4607
Life History (C-S-R)	-0.2564	0.8989	-0.285	0.7766
Life History (S)	-0.4587	0.3870	-1.185	0.2409

Approximate significance of smooth terms

	edf	**Ref.df**	**F**	***p*-value**
s($\log_{10}$(NicheWidth))	1.353	1.615	25.803	9.69e-08 ***
s(HabitatTransf)	2.554	3.178	2.762	0.0476 *

*** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; • $p \leq 0.1$

The backward selection approach in which non-significant terms were removed sequentially starting with the least significant variable (Appendix 12) resulted in a final generalized additive model that only included $\log_{10}$ Niche Width, Land Surface and Habitat Transformation (Table 3.8).

This model explained 66.6% of the deviance. The $\log_{10}$ Niche Width was highly significant ($p < 0.001$) as was the intercept while no affinity to land surfaces was significant ($p < 0.01$) and habitat transformation was almost significant at the 5% level ($p = 0.0549$).

Diagnostic plots of this final model also indicate normality (Q-Q plot) and homogeneity of variance (residual plots) (Fig. 32).

This final GAM model indicates that there is a strong relation between Niche Width and Rarity Index and it shows some relation between species with no affinity to a land surface and species commonness. It also indicates a positive relation between Rarity Index and Habitat Transformation.

Table 3.8: The parametric coefficients of the final generalized additive model (GAM4) of $\log_{10}$ Rarity Index on Land Surfaces and the approximate significance of the smoothed terms $\log_{10}$ Niche Width and Habitat Transformation.

	Estimate	**Std. Error**	**t value**	**Pr(>|t|)**
(Intercept)	7.22552	0.43638	16.558	< 2e-16 ***
Land Surf (Esc)	007917	0.75837	0.104	0.91711
Land SurfNe	0.50153	0.73246	0.685	0.49545
Land SurfNo	1.43557	0.51012	2.814	0.00612 **
Land SurfPad	0.68203	0.50011	1.364	0.17637

Approximate significance of smoothed terms

	edf	**Ref.df**	**F**	***p*-value**
s($\log_{10}$NicheWidth)	2.087	2.556	22.188	1.06e-09 ***
s(HabitatTransf)	2.781	3.458	2.527	0.0549 •

*** $p \leq 0.001$; ** $p \leq 0.01$; * $p \leq 0.05$; • $p \leq 0.1$

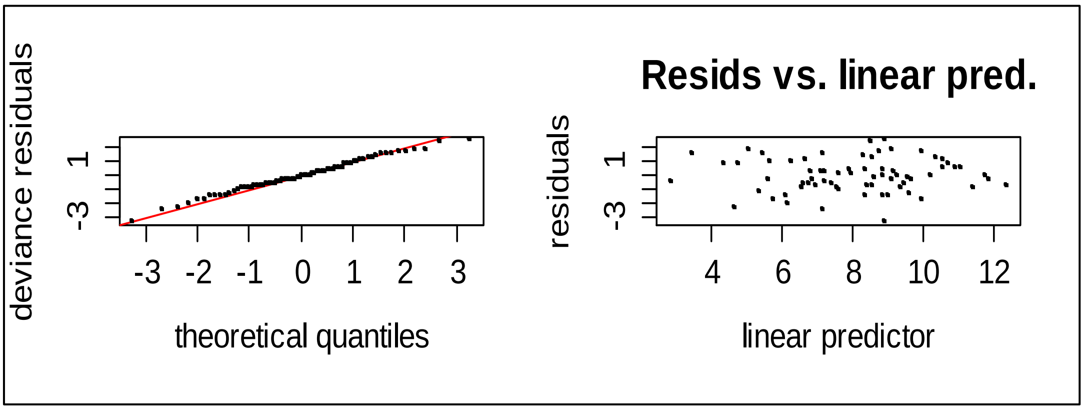

Figure 32: Q-Q and residuals versus the linear predictor plots of the generalized additive model of $\log_{10}$ Rarity Index on $\log_{10}$ Niche Width, Habitat Transformation and Land Surfaces.

3.5. **Comparison between GAM and GLM models**

The comparison between the final GLM and GAM models with the same explanatory variables (i.e. GLM 4 in Appendix 11 and GAM 4 in Appendix 12) indicated that the GAM model is the better model (AIC for GAM substantially lower than GLM) (Table 3.9). The deviance (Chi-squared) explained by the GAM model (68.8%) was higher than that explained by the comparable GLM model (62.63%). This was consistent in comparisons between all GAM and GLM models with the same data set in the backward selection process.

Table 3.9: Comparison of model diagnostics for GLM and GAM models of $\log_{10}$ Rarity Index versus $\log_{10}$ Niche Width, Land Surface and Habitat Transformation. AIC - Akaike Information Criterion, df - degrees of freedom, Deviance Explained (%).

Model	**AIC**	**df**	**Deviance Explained (%)**
GLM	489.38	8	62.63
GAM	478.42	8	68.8

Both these models indicate that $\log_{10}$ Niche Width was the most important variable and that $\log_{10}$ Niche Width was positively correlated with the $\log_{10}$ Rarity Index i.e. the greater the Niche Width the more common the species. Similarly species that showed no affinity to any land surface was positively correlated with

Rarity Index and in the GAM model an additional predictor of rarity was the extent to which the species area of extent had been transformed.

4. **Discussion**

The aim of this research was to generate a better understanding of the main drivers of plant rarity in KZN prior to developing methods of prioritizing plants for conservation action. One of the most significant messages coming out of the literature on rarity is that rare species are inherently vulnerable to extinction i.e. rarity and extinction proneness are co-related. This is supported by rare plants generally being placed into at least one of the IUCN red list categories and therefore being considered as important species for conservation action. Furthermore diagnosis of the cause of rarity and/or a decline in the population size and range extent is an important step in developing effective conservation actions for rare and threatened plants (Norris, 2008). In this study a correlative approach was adopted to test the primary driving variables of rarity in KZN. The definition and derivation of the rarity index used (estimated population size x EOO) is a quantifiable virtually continuous index of rarity from very rare to common. The advantage of this is that it emulates nature in which no “cut-offs” are evident (Gaston, 1997; Reilly, 2010) and it does not rely on the categorization of species into high and low categories of abundance and distribution based on expert opinion as used in many other studies of rarity (Rabinowitz, 1981; Kaye et al., 1997; Farnsworth, 2007; Farnsworth & Ogurcak, 2008; Cortês-Burns et al., 2009). This makes it a useful method as it enables the calculation of rarity indices for other plant species in KZN as part of the prioritization process.

The approach adopted was a province wide, broad scale study to identify the most important explanatory variable for rarity. The variables tested were niche width, habitat specificity, dispersal distance, life history strategy, land surface, human use and range transformation.

Niche Width

This study showed a strong positive relation between the index of rarity and ecological niche width. Species with the ability to tolerate a wide range of temperature, rainfall and soil fertility regimes are common species in KZN whereas those with narrow ranges of these environmental variables are generally rare. *Searsia dentata* is a widespread common small tree or shrub (Rarity Index = 11.699) that is adapted to tolerate a wide range of temperature, rainfall and soil fertility regimes ($\log_{10}$ Niche width = 5.185). In contrast to this *Cyrtanthus* *brachysiphon*, a rare endemic ($\log_{10}$ Rarity Index = 2.387) has a narrow niche width ($\log_{10}$ Niche width = 1.301). Although this result may not be entirely surprising because plant distribution has for many years been linked to environmental variables (Woodward, 1987) this direct association with rarity has not been reported in the literature. The definition and characterization of the term niche width or breadth used in rarity studies varies widely, but according to one study on the relation between niche breadth and geographical range size (Slatyer et al., 2013), habitat use, diet and environmental tolerance were the most commonly used classifications of niche breadth. Interestingly enough, results from the work of Slatyer et al. (2013), showed that niche width measured as either habitat breadth or environmental tolerance range was positively correlated with geographic range for a wide range of taxonomic groups including plants. This was despite a wide variety of measures used for both niche breadth and geographic range (Slatyer et al., 2013). In contrast to this Burgman (1989) concluded that scarcity in plants was not related to ”restricted environmental tolerances” however he only used physical and chemical soil parameters as a measure for environmental tolerance.

The extensive use of temperature, rainfall and to a lesser extent, soil in species distribution models (Ferrier, 2002; Thuiller et al., 2005; Kuper et al., 2006; Jewitt et al., 2014) is indicative of their importance in determining range limits for species. The strong positive relation between rarity and niche width in this study indicates that rare species in KZN are limited by eco-physiological barriers that prevent expansion (Mott, 2010). The shift in distribution of some species to higher altitudes with climate change demonstrates their propensity to occur within their niche boundary (Ackerly, 2003; Lenoir et al., 2008) as they preferentially occupy habitats that closely match conditions to which they are adapted (Ackerly, 2003; Kelly & Goulden, 2009).

Concerns on the effect of climate change on species have fuelled wide debate on the adaptability of species (Ackerly, 2003; Pearson & Dawson, 2003). Although species physiological barriers are believed to be a function of the adaptive response of species (Chust et al., 2006) to abiotic and biotic pressures, the mechanisms and processes that enabled some species to be widely spread and others to be rare are not well understood. Common topics include phylogenetic and physiological traits (Chown et al., 2004) with a number of hotly debated theories such as Niche Conservatism (Qian & Ricklefs, 2004; Holt & Barfield, 2008; Wiens et al., 2010) which is the tendency of a species niche to remain unchanged over time, and Unified Neutral theory which assumes that each species in a community has equal opportunity of success (Hubbell, 1997). Little proof is available as yet for the Unified Neutral theory (Gaston & Chown, 2005) but there appears to be some evidence of niche conservatism (Qian & Ricklefs, 2004; Crisp et al., 2009; Wiens et al., 2010) although it is a relatively new area of research. It has been suggested that it has potential to bridge the gap between two, often conflicting, perspectives on species patterns, evolution and ecology (Wiens et al., 2010). This could also give an improved understanding of the threats imposed by climate change.

Habitat Specificity

In many cases narrow environmental parameters are used synonymously with habitat specificity and are included in the classification of species into types of rarity (Rabinowitz, 1981; Kruckeberg & Rabinowitz, 1985b ; Kaye et al., 1997; Mills & Schwartz, 2005; Söderström et al., 2007; Cron et al., 2009;). In this study habitat specificity was investigated as a driver of rarity. As with niche width the derivation of habitat specificity varies from study to study (Benayas et al., 1999; Söderström et al., 2007; Oliver et al., 2009) and appears to be somewhat dependent on the scale of the investigation and the available information. In this investigation species affinity to a non-matrix habitat and documented information on a species' habitat specificity was used to categorize species as a habitat specialist or matrix species. Although this is a relatively coarse measure, the results showed that habitat specific plants tend to be rarer than matrix plant species and that very rare plant are always habitat specific. There were a number of exceptions to this in which habitat specific plants had quite high Rarity Indices (i.e. common), for example *Alberta magna* ($\log_{10}$ Rarity Index = 9.691) which occurs in scarp forest. Other species that occur in the grassland matrix like *Kniphofia pauciflora* ($\log_{10}$ Rarity Index = 4.193) have not been documented as being habitat specific but are quite rare. This is not totally unexpected for a number of reasons. Firstly there is a paucity of information on the microclimates of KZN plant species and data that are available is often anecdotal without empirical evidence. Secondly a species fundamental niche is not necessarily equivalent to its realized niche (Soberón & Peterson, 2005) due to the influence of biotic factors such as competition, predation and symbiosis (Pearson & Dawson, 2003). Effective dispersal is also an essential component of a species realization of the available suitable habitat (Jacquemyn et al., 2003; Rossetto et al., 2008; Wiens, 2011).

Dispersal Distance

Spatial distribution and abundance are inextricably related to the success of recruitment of plants. Plant recruitment is an intricate process that is dependent on a number of biotic and abiotic factors that interact at various stages in the life history of individuals. The process from pollination, seed production, seed dispersal, establishment and survival to adulthood is well illustrated by Nathan & Muller-Landau (2000) (Fig. 33). This illustration highlights the onerous challenge faced by an individual seed from source to new territory and on to adulthood. It also draws attention to the substantial information required to fully understand the spatial distribution of a species. An in-depth study such as this cannot be undertaken for all species, therefore a number of alternative methods have been used to determine traits that are correlated with distribution and abundance (Pocock et al., 2006).

The dispersal capacity of species has long been associated with spatial distribution and there are numerous studies on the efficiency of dispersal mechanisms in distributing species (Murray et al., 2002; Jacquemyn et al., 2007; Kunz & Linsenmair, 2008; Samansiri & Weerakoon, 2008; Corlett, 2009; Soons et al., 2012). The results of this study indicate that seed dispersal distance increases with an increase in the value of the Rarity Index (i.e. long distance dispersers are more common than narrow dispersers) but this was not validated statistically. As “there is nothing sacred about the 5% significant level” (Field et al., 2007), a lack of statistical corroboration at this level does not necessarily infer that there is no relation but previous studies on this subject are also not particularly helpful as results relating rarity or distribution to dispersal are inconsistent (Eriksson & Jakobsson, 1998; Murray et al., 2002; Chust et al., 2006; Pocock et al., 2006; Farnsworth, 2007).

Other studies that have looked at the effect of seed size on distribution and abundance also differ, from positive correlations being found between large seeds and narrow geographic range and abundance (Guo et al., 2000) to no correlation with geographical range (Edwards & Westoby, 1996). Seed addition trials have indicated that seed limitation is a potential cause of limited distribution (Witkowski & Lamont, 2006; Stein et al., 2008) however these trials do not take into consideration the effect of post germination mortality, establishment limitations (Turnbull et al., 2000) or seed source limitations which may also contribute to a lack of colonization of suitable habitat patches.

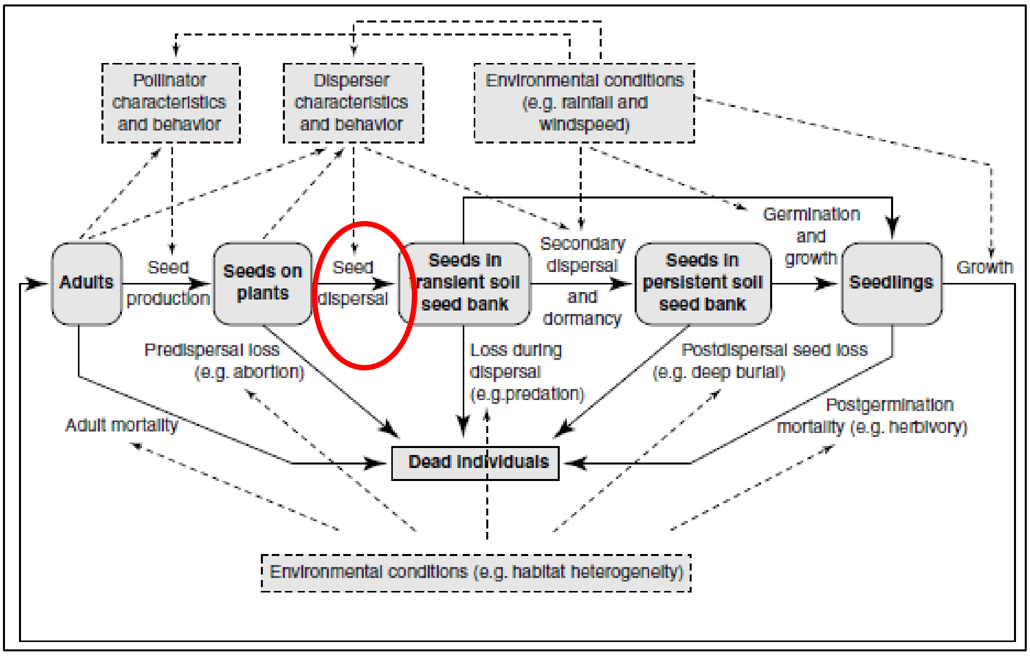

Figure 33:The processes (unbroken arrows) and influences (broken arrows) on seed dispersion (from Nathan & Muller-Landau, 2000) and the position of seed dispersal in this process (red oval).

Although long distance dispersal is considered to play a critical role in influencing metapopulation dynamics, sampling difficulties have limited the collection of empirical data (Nathan & Muller-Landau, 2000). Long distance dispersal is considered to be a rare event (Nathan & Muller-Landau, 2000; Soons & Ozinga, 2005; Nogales et al., 2012) with most seeds being distributed short distances from parent plants (Cain et al., 2000). Even terrestrial orchids that produce large quantities of extremely light seed, considered to be dispersed by wind, distribute most of their seed within 10m of parent plants (Jacquemyn et al., 2007). None the less the ability of species to disperse long distances is well demonstrated in island biogeography where species have managed to colonize areas that are separated by extensive barriers. Recent advances in genetic research (He et al., 2004; De Groot et al., 2012) and long distance model development (Davies et al., 2004; Soons & Ozinga, 2005) are playing an important role in improving our understanding of the dynamics of plant migration.

Although methodological progress has been made in the study of dispersal, results are contradictory and therefore cannot necessarily be used to validate theory (Harper, 1977; Howe & Smallwood, 1982). Indications are that studies on individual processes that contribute to spatial patterns are not sufficient. From the illustration by Nathan & Muller-Landau, (2000) we can see (Fig. 33) that seed dispersal is a vital but not independent process in the success of plant dispersion and is reliant on other factors for success. Improved understanding of these complicated dynamics requires interdisciplinary research (Nathan, 2005) that includes model development, genetic studies and empirical testing.

Life History Strategy

The life history strategy of plant species evolves through the process of natural selection in response to environmentally imposed stresses and constraints (processes). Their mechanism of survival is through the development of functional traits in response to pressures in the environment (Norris, 2008). For survival in a continuous unproductive system plants evolve traits that enable them to tolerate these conditions. This is well demonstrated in the xerophyte’s adaptation of succulent leaves in habitats that are limited by water availability. In productive environments where resources are readily available and disturbance is low trait development such as rapid height growth, large leaves or lateral spread that improves competitive ability for light is advantageous. Similarly in environments of continual disturbance where vegetation is subject to partial or complete destruction (e.g. fire prone areas or flood plains) species have developed traits such as short life cycles to enable them to exploit these habitats in between disturbances (Grime, 1979). This of course is an over simplified view of reality as the scale at which both evolutionary and environmental drivers operate varies widely (Reich et al., 2009) resulting in the development of species with unique combinations of traits and strategies for survival.

Although it has been found that endemic species have predominantly stress tolerant life history strategies (Brofas et al., 2007) the evidence for this was not convincing for rare species in KZN. The species used in this analysis were found to be primarily stress tolerant and competitive strategists and a combination of these (C-S) with only a few species being aligned to a mixture of all three strategies (C-S-R). None of the sampled species were found to be ruderals, possibly because other than in Poaceae there are relatively few annual species that occur in KZN.

Very little comparative work has been done on the relation between life history strategies and rarity and to the best of my knowledge no other study has used Grimes C-S-R strategy (Grime, 1977; Grime, 1979) in rarity studies. Trait based studies vary considerably both in traits used and in their objectives. Farnsworth (2007) found little difference between traits of rare and common species in the Coastal sand plain grasslands of North-eastern North America. Cornwell & Ackerly (2010) compared the traits of woody species in woody plant communities of the eastern foothills of the Santa Cruz Mountains, California and found a relation between species traits and abundance at a local level but not at a landscape level. Many trait based studies comparing species abundance, distribution and performance are confined to a particular habitat type (Subtropical forest in Eastern China (Yan et al., 2013); North American coastal sandplain grasslands (Farnsworth, 2007)) or a particular plant type (woody species (Cornwell & Ackerly, 2010)) where plants co-occur (Westoby et al., 2002).

In this analysis I was only able to include nine of the 18 characteristics used to determine the life history strategy of plant species by Grime (see page 48 Grime, 1979), due to a lack of data. Data paucity is an omnipresent problem in ecological research and to overcome this researchers need to “box smartly” both literally and figuratively by determining a minimum set of easily measurable traits that can be used universally and consistently to improve prediction of ecological behaviour (Westoby et al., 2002).

Geological land surface

No association was found between plant species that have an affinity to Island land surfaces and rarity. Species that have no affinity to a particular land surface were found to have a higher Rarity Index (i.e. tend to be more common) than those associated with a specific land surface, including those associated with the Post African and other dissected areas surface. Although it was expected that Island habitats would retain rare ancient paleoendemic or neoendemic species resulting from vicariance this was not evident in this study. Prior to 1970 vicariance was considered as the primary initiator of speciation and high endemicity in areas isolated through uplifting or land mass separation but more recently studies have found that in plants dispersal also plays an important role in isolated populations. The Island of Madagascar is a remnant of the great continents of Pangea and Gondwana and its separation from Africa preceded its separation from India and yet a number of endemic species have been shown to have close links with African taxa suggesting the importance of dispersal in the lineage of Malagasy endemics (Yoder & Nowak, 2006). In an investigation on the roles played by vicariance and dispersal in shaping the biotas of the Southern hemisphere Sanmartín & Ronquist (2004) found that plants did not appear to be influenced by the Gondwana breakup but by dispersal and extinction events. As speciation events span long periods of time (Zink et al., 2000) and dispersal and extinction play a large role in plant biogeography it would seem to be difficult to identify truly vicariant species without conducting phylogenetic studies on their families (Mao et al., 2012).

Human Use

The utilization of plants by humans is well documented with concerns of possible extinction of species being expressed on a number of fronts (CITES, TRAFFIC, IUCN red lists). In KZN a large proportion of the human population depend on indigenous plants for domestic and medicinal purposes. A visit to the Warwick Avenue market in Durban is an eye opener to the quantities that are collected from the wild and yet the results of this study show that utilization is not a primary driver of rarity in KZN. Human exploitation has certainly reduced the species Rarity Index for some highly utilized species to the point where the species can be considered as rare (for e.g. *Encephalartos msinganus*) but this does not appear to be the general trend with highly utilized species. A possible reason for this is that many highly utilized plant species are naturally widespread and abundant (Williams et al., 2013), and occur in sufficient numbers or have reproductive capacities which allow sustained use with little or no apparent impact on the species abundance. In addition not all harvesting is destructive as only leaves, flowers and fruit are used in some species making these species less vulnerable to losses through utilization (Dzerefos & Witkowski, 2001).

Unfortunately there is very little information on the effect of harvest on wild plant populations. The process of red listing of plants has used data from medicinal market information to infer decline of species (Cunningham, 1988; Dold & Cocks, 2002; Williams et al., 2007) and is used as a proxy for the state of wild populations (Williams et al., 2013). For the purpose of this study data have been categorized (no known utilization, some utilization, highly utilized) using a similar proxy but it would be more robust if they could be expressed as a relative measure i.e. the number or amount used per population size and potential growth rate. Such a measure would give a much better indication of likely impact on plant abundance.

Range Transformation

Loss of habitat is recognized as one of the greatest threats to species survival (Mace et al., 2010). This is highlighted in numerous papers on threatened species from all taxonomic groups (Hula et al., 2004; Githiru & Lens, 2007; Bruegmann, 2008; Norris, 2008; Regan et al., 2008). It is also evident from the large amount of effort placed on systematic conservation planning in an attempt to conserve viable habitats for species (Fjeldsa, 2007; Mikusinski et al., 2007; Carwardine et al., 2008a; Carwardine et al., 2008b; Tallis et al., 2008; Wiens et al., 2008). In KZN transformation levels have exceeded 50% of the land surface of the Province and continue to rise (Goodman et al., 2010; Jewitt et al., 2014). There is no doubt that this has caused the decrease in Rarity Index of numerous plant species, but to what extent? The results of this study show that there are a number of very rare species (i.e. with low Rarity Indices) that do not appear to be directly impacted by habitat transformation. This is possibly because they occur in very unproductive hostile habitats that are not favoured for human use. For example *Protea nubigena* occurs in extremely harsh conditions on the top of the Drakensberg escarpment at altitudes of around 2250m above sea level. The habitats of the most common species in this study (i.e. with high Rarity Index values) were only between 30-36% transformed but after this noticeable threshold, the species rarity index declined with further increase in habitat transformation. This threshold of 36% was confirmed in the regression tree analysis.

Although there is no doubt that habitat transformation causes a decrease in species range and population size, results such as those found in this study should be accepted with caution when considering conservation interventions for species. Data used in this analysis is based purely on current population size and extent but does not take into account a delayed population size reduction or extinction debt (Tilman et al., 1994). The theory of extinction debt is based on a time lag between the impact of habitat destruction and the local extinction of the species. There are numerous reasons for an extinction debt including reduced population size and population fragmentation, which affect dispersal and pollination ability, (Cagnolo et al., 2006) and decreases in genetic diversity (Aguilar et al., 2008). Extinction debts of specialized vascular plants have been shown to occur in grassland affected by rapid habitat loss in Europe (Krauss et al., 2010). This has important consequences for the conservation of species habitat and should be considered when setting area targets for rare species in systematic conservation planning.

Multiple regression analysis

Multiple regression analysis has been a useful way of exploring the relation between a response variable in this case rarity index (a combination of range size and population size) and a number of potential explanatory variables. It enables a certain amount of insight into the contribution and roles of the different explanatory variables (Guisan et al., 2002). A number of statistical models are being used today and there have been a number of comparative analyses to determine the “best” model for a particular set of data (Walsh & Kleiber, 2001; Miller & Franklin, 2002; Thuiller et al., 2003; Austin et al., 2006; Abeare, 2009). The three statistical methods used in this study have been recommended as suitable methods for exploring ecological data as they can handle missing data, both categorical and continuous variables and nonlinear relations (De'ath & Fabricius, 1999; Guisan & Zimmermann, 2000; Friedlander et al., 2012; Moisen, 2012). Using all three methods allowed a more robust interpretation of the relations between the Rarity Index and the explanatory variables. All three methods concurred that Niche Width was the strongest variable. They also indicated that Land Surface was the second strongest variable but the visual representation of the regression tree partitioning allowed insight into the nature of this relation. It showed that for plants with a Niche Width of less than four, within Post African and other dissected areas, Escarpment and Neogene land surfaces, species were rarer than those with an affinity to the African surface and those with no affinity to any one land surface. This was in contradiction to my hypothesis that plants that occurred on land surfaces that are islands of former much larger land surfaces are expected to be rarer than those that occur on more extensive or contiguous land surfaces. Another interesting result which is not easy to interpret is the importance given to Life History Strategy. Life History Strategy must be an important surrogate splitter in the regression tree for it to be listed as the third most important variable. However, neither the GLM nor GAM statistical analysis concurred with this.

The GLM and GAM analysis also differed slightly in the results of their final models (after the stepwise removal of non-significant terms). For GLM only $\log_{10}$ Niche Width and no affinity for any one land surface were significant but for GAM habitat transformation was also significant. Although the objective of this study was not to compare statistical methods *per se*, a comparison of GLM and GAM was done using deviance (Chi-squared) and Akaike Information Criterion (Akaike, 1974) to determine the model that better described the relation between Rarity Index and the explanatory variables. My results indicated that GAM produced a better model than GLM for this data set. The advantage of GAM in this analysis is possibly its ability to deal with non-linear data using smoothers that generalize data into smooth curves (Hastie & Tibshirani, 2011). Although the relation between Rarity Index and Habitat Transformation is not linear it is shown to be significant ($p < 0.1 (p=0.0549)$) after “smoothing”. The differences observed in the three multiple regression analyses highlight the value of using more than one method to explore relations in ecological data.

5. **Conclusion**

Extinction vulnerability is considered to be greatest for species with low population sizes and restricted ranges (Gaston, 1994). In the context of this study therefore, species with low rarity index should be considered extinction prone**.** At the scale of this study Niche Width is the strongest determinant of Rarity, followed by Habitat Transformation and then Habitat Specificity (Figure 34).

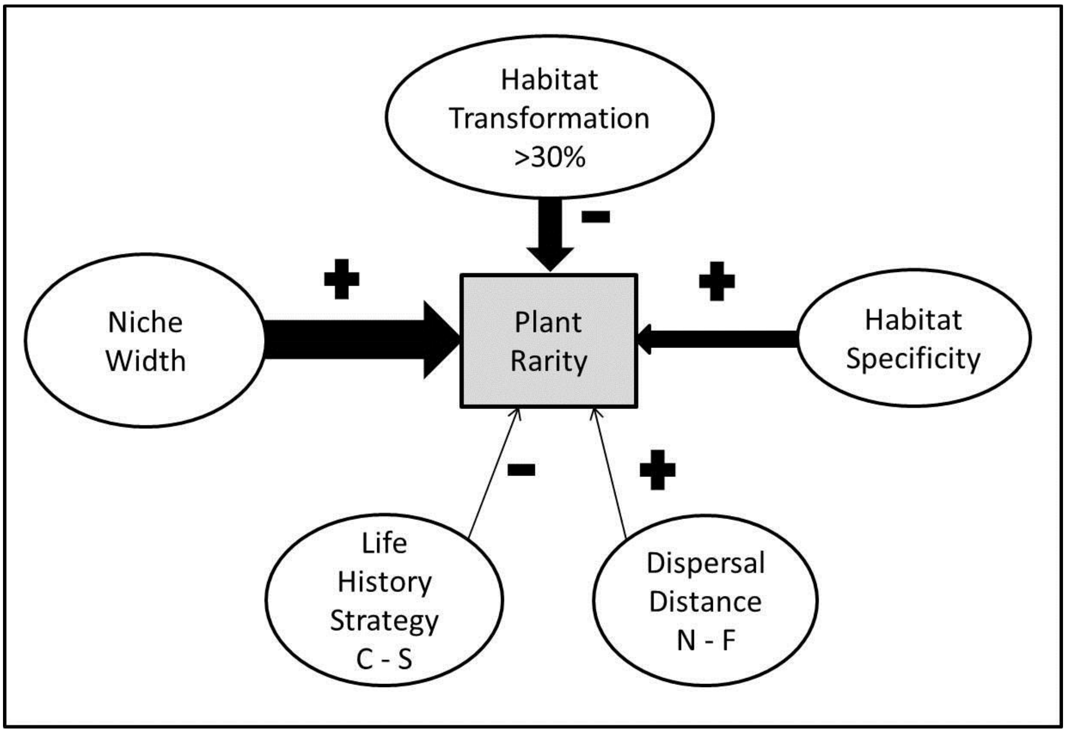

Figure 34: A conceptual model of the drivers of rarity in plants in KwaZulu-Natal. The thickness of arrows depicts the magnitude of importance of the explanatory variables. The '+' and '-'signs associated with each arrow indicate the direction of the influence of the explanatory variable in the relation Rarity Index ≈ f(Explanatory Variable).

The purpose of this study was to get a better understanding of the causes of rarity in plants in KZN. I hope to use this improved understanding to rationally improve the manner in which I would prioritise plant species for conservation action. Conservation action in this context includes surveillance, monitoring, research and management intervention to improve or maintain population persistence.

Firstly, while rarity is an important component of prioritization other criteria are also important. These criteria may include taxonomic distinctiveness or uniqueness (Faith, 1992; Williams et al., 1994; Joseph et al., 2008); endemism (Keith et al., 2007); societal and utilitarian value; and ecological functional value. These could be considered in combination with rarity in a prioritization framework. An understanding of the determinants of rarity allows one to use the most important determinants in combination with other criteria. For example, a priority score might be derived along the lines of

P score = *f (a x* Niche Width, b x Habitat Transformation, c x Habitat Specificity)

Where a, b and c are weighting factors.

The question "Do we have enough data to make good conservation decisions?" will always plague biological scientists and although improved scientific analytical methods and model development have advanced the ability to understand relations and allowed prediction based on minimum datasets or artificial data (Austin et al., 2006), this cannot replace the collection of empirical data. Unfortunately due to the high cost of data collection, limited data is available and these tools are proving to be extremely useful substitutes particularly for decision making at a regional level or higher. This is not the case at a more local level and there is an urgent need to improve our understanding of species survival at this scale. Important areas of research relate to survival mechanisms such as dispersal, niche conservatism and genetic plasticity and how this may create an extinction debt.

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Appendix 1: List of 97 sampled species including their IUCN Red Data category, endemism and the specific code used for each species in the analysis, which is the first four letters of the genus and then the first four letters of the species names.

Scientific name with authority	Family	Reference	Species Code	Red Data Cat.	Endemism
Acalypha entumenica Prain	Euphorbiaceae	Bull. Misc. Inform. Kew 1913, 22	Acalentu	EN	KZN
Alberta magna E.Mey.	Rubiaceae	Linnaea 12: 258. 1838	Albemagn	NT	
Albizia suluensis Gerstner	Leguminosae	J. S. African Bot. xiii. 62 (1947)	Albisulu	EN	KZN
Aloe gerstneri Reynolds	Aloaceae	J. S. African Bot. 1937, iii. 123	Aloegers	VU	KZN
Aloe maculata All.	Aloaceae	Auct. Syn. 13 1773.	Aloemacu	LC	
Aloe modesta Reynolds	Aloaceae	J. S. African Bot. xxii. 85 (1956)	Aloemode	VU	SA
Aloe saundersiae (Reynolds) Reynolds	Aloaceae	J. S. African Bot. xiii. 103 (1947)	Aloesaun	CR	KZN
Ansellia africana Lindl.	Orchidaceae	Edwards's Bot. Reg. 30: sub t. 12. 1844	Anseafri	NT	
Argyrolobium longifolium Walp.	Leguminosae	Repert. Bot. Syst. (Walpers) ii. 844	Argylong	VU	Midlands
Asclepias bicuspis N.E.Br.	Asclepiadaceae	Fl. Cap. (Harvey) 4(1,5): 675. 1908 [Mar 1908]	Asclbicu	CR	KZN midlands
Asclepias concinna Schltr.	Asclepiadaceae	J. Bot. 34: 456. 1896	Asclconc	VU	KZN midlands
Asclepias schlechteri N.E.Br.	Asclepiadaceae	Fl. Cap. (Harvey) 4(1,5): 714. 1908 [Mar 1908]	Asclschl	EN	S KZN
Asclepias woodii Schltr.	Asclepiadaceae	J. Bot. 34: 456. 1896	Asclwood	VU	KZN

Scientific name with authority	**Family**	**Reference**	**Species Code**	**Red Data Cat.**	**Endemism**
Barleria argillicola Oberm.	Acanthaceae	Bothalia 7: 444 1961.	Barlargi	CR	KZN(Tugela basin)
Barleria greenii M.Balkwill & K.Balkwill	Acanthaceae	S. African J. Bot. 56(5): 571 (1990)	Barlgree	CR	KZN (Tugela Basin)
Begonia dregei Otto & A.Dietr.	Begoniaceae	Allg. Gartenzeit. iv. (1836) 357	Begodreg	EN	SA
Berkheya draco Roessler	Asteraceae	Mitt. Bot. Staatssamml. München iii. 217 (1959).	Berkdrac	RARE	KZN Drakensberg
Bonatea lamprophylla J.Stewart	Orchidaceae	Amer. Orchid Soc. Bull. 47(11): 995. 1978	Bonalamp	VU	KZN Maputaland
Bowiea volubilis Harv. ex Hook.f.	Hyacinthaceae	Bot. Mag. 93: t. 5619. 1867 [1 Jan 1867]	Bowivolu	VU	
Brachystelma natalense N.E.Br.	Asclepiadaceae	Fl. Cap. (Harvey) 4(1,5): 850. 1908 [Mar 1908]	Bracnata	CR	KZN
Calpurnia woodii Schinz	Leguminosae	Bull. Herb. Boissier iv. 428.	Calpwood	VU	KZN Tugela basin
Ceropegia arenaria R.A.Dyer	Asclepiadaceae	Bothalia 12(3): 444 (1978)	Ceroaren	EN	KZN Maput.
Ceropegia rudatisii Schltr.	Asclepiadaceae	Bot. Jahrb. Syst. 40(1): 94. 1907 [21 May 1907]	Ceroruda	CR	KZN
Crinum moorei Hook.f.	Amaryllidaceae	Bot. Mag. 100: t. 6113. 1874	Crinmoor	VU	SA
Cryptolepis oblongifolia Schltr.	Asclepiadaceae	J. Bot. 34: 315. 1896	Crypoblo	LC	

Scientific name with authority	**Family**	**Reference**	**Species Code**	**Red Data Cat.**	**Endemism**
*Cryptocarya wylie*i Stapf	Lauraceae	Fl. Cap. 5(1): 498 1912.	Crypwyli	NT	SA
Curtisia dentata (Burm.f.) C.A.Sm.	Cornaceae	Journ. S. Afr. For. Assoc. No. 20, 34, in obs., 50 (1951)	Curtdent	NT	
Cyrtanthus brachysiphon Hilliard & B.L.Burtt	Amaryllidaceae	Notes Roy. Bot. Gard. Edinburgh 43(2): 189. 1986	Cyrtbrac	EN	SA
Cyrtanthus obliquus Aiton	Amaryllidaceae	Hortus Kew. (W. Aiton) 1: 414. 1789	Cyrtobli	Declining	SA
Delosperma tradescantioides (P.J.Bergius) L.Bolus	Aizoaceae	Fl. Pl. South Africa 7: t. 261 1927.	Delotrad	LC	
Dierama luteoalbidum I.Verd.	Iridaceae	Fl. Pl. South Africa xxii. t. 845 (1942)	Dierlute	VU	KZN midlands
Dierama pallidum Hilliard	Iridaceae	O.M. Hilliard & B.L. Burtt, Dierama: Harebells of Africa 143, 104 (1991)	Dierpall	VU	KZN Midlands
Dierama tysonii N.E.Br.	Iridaceae	Journ. Roy. Hort. Soc. liv. 200 (1929)	Diertyso	VU	E. grqualand
Diospyros glandulifera De Winter	Ebenaceae	Bothalia vii. 457 (1961)	Diosglan	LC	
Disa montana Sond.	Orchidaceae	Linnaea 19: 90. 1846	Disamont	VU	Drakensberg
Disa sanguinea Sond.	Orchidaceae	Linnaea 19: 97. 1846	Disasang	RARE	Drakensberg
Disa scullyi Bolus	Orchidaceae	J. Linn. Soc., Bot. 22: 70. 1885 [1887 publ. 24 Dec 1885]	Disascul	EN	SA
Dracosciadium italae Hilliard & B.L.Burtt	Apiaceae	Notes Roy. Bot. Gard. Edinburgh 43(2): 223. 1986	Dracital	EN	NKZN

Scientific name with authority	**Family**	**Reference**	**Species Code**	**Red Data Cat.**	**Endemism**
Encephalartos aemulans Vorster	Zamiaceae	S. African J. Bot. 56(2): 239 (1990)	Enceaemu	CR	KZN
Encephalartos cerinus Lavranos & D.L.Goode	Zamiaceae	Durban Mus. Novit. 14: 153 1989.	Encceri	CR	KZN
Encephalartos msinganus Vorster	Zamiaceae	S. African J. Bot. 62(2): 67 (1996)	Encemsin	CR	KZN Tugela basin
Encephalartos senticosus Vorster	Zamiaceae	S. African J. Bot. 62(2): 76 (1996)	Encesent	VU	
Eriosemopsis subanisophylla Robyns	Rubiaceae	Bull. Jard. Bot. État 11: 38 1928.	Eriosuba	VU	SA
Eriosema umtamvunense C.H.Stirt.	Leguminosae	Bothalia 16(1): 16 (1986)	Erioumta	VU	SA
*Felicia wrighti*i Hilliard & B.L.Burtt	Asteraceae	Notes Roy. Bot. Gard. Edinburgh 31(1): 7. 1971	Feliwrig	RARE	KZN Drakensberg
Gerbera aurantiaca Sch.Bip.	Asteraceae	Flora 27(2): 781. 1844	Gerbaura	EN	
Gladiolus cruentus T Moore	Iridaceae	Gard. Chron. (1868) 1138	Gladcrue	CR	KZN Midlands
Gnidia kraussiana Meisn.	Thymelaeaceae	London J. Bot. 2: 552 (err. typ. 452). 1843	Gnidkrau	LC	
Helichrysum citricephalum Hilliard & B.L.Burtt	Asteraceae	Notes Roy. Bot. Gard. Edinburgh 34(3): 259. 1976	Helicitr	CR	KZN
Holothrix majubensis C.Archer & R.H.Archer	Orchidaceae	S. African J. Bot. 62(4): 209 (1996)	Holomaju	VU	

Scientific name with authority	**Family**	**Reference**	**Species Code**	**Red Data Cat.**	**Endemism**
Kniphofia brachystachya (Zahlbr.) Codd	Asphodelaceae	Fl. Pl. Africa xxxvi. sub t. 1424 (1964), in adnot	Knipbrac	LC	
Kniphofia evansii Baker	Asphodelaceae	Fl. Cap. (Harvey) 6(2): 278. 1896 [Sep 1896]	Knipevan	RARE	KZN
Kniphofia latifolia Codd	Asphodelaceae	Bothalia ix. 484 (1968)	Kniplati	EN	KZN
Kniphofia leucocephala Baijnath	Asphodelaceae	S. African J. Bot. 58(6): 482 (1992)	Knipleuc	CR	KZN
Kniphofia pauciflora Baker	Asphodelaceae	J. Bot. 23: 280. 1885	Knippauc	CR	KZN
Leucospermum gerrardii Stapf	Proteaceae	Fl. Cap. (Harvey) 5(1.3): 619. 1912 [Jan 1912]	Leucgerr	NT	
Manilkara nicholsonii A.E.van Wyk	Sapotaceae	S. African J. Bot. 1: 33 1982.	Maninich	EN	Pondoland
Manulea florifera Hilliard & B.L.Burtt	Scrophulariaceae	Notes Roy. Bot. Gard. Edinburgh 40(2): 290. 1982	Manuflor	NT	SA
Maytenus abbottii A.E.van Wyk	Celastraceae	S. African J. Bot. 3(2): 115 (1984)	Maytabbo	EN	SA
Melhania didyma Eckl. & Zeyh.	Sterculiaceae	Enum. Pl. Afric. Austral. [Ecklon & Zeyher] 1: 52. [Dec 1834-Mar 1835]	Melhdidy	LC	
Melhania polygama I.Verd.	Sterculiaceae	Bothalia viii. 178 (1964)	Melhpoly	RARE	KZN
Merwilla plumbea (Lindl.) Speta	Hyacinthaceae	Phyton (Horn) 38(1): 109. 1998	Merwplum	NT	
Mystacidium aliceae Bolus	Orchidaceae	Icon. Orchid. Austro-Afric. 2: t. 6 1911	Mystalic	VU	SA

Scientific name with authority	**Family**	**Reference**	**Species Code**	**Red Data Cat.**	**Endemism**
Olea capensis L.	Oleaceae	Sp. Pl. 1: 8. 1753 [1 May 1753]	Oleacape	LC	
Olinia radiata Hofmeyr & E.Phillips	Oliniaceae	Bothalia i. 102 (1922)	Olinradi	LC	
Oxalis obliquifolia Steud. ex A.Rich.	Oxalidaceae	Tent. Fl. Abyss. 1: 123. 1847 [22 May 1847]	Oxalobli	LC	
Pelargonium tongaense Vorster	Geraniaceae	S. African J. Bot. 2(1): 76 (1983)	Pelatong	RARE	KZN
Peucedanum wilmsianum H.Wolff	Apiaceae	Bot. Jahrb. Syst. xlviii. 280 (1912)	Peucwilm	VU	
Phymaspermum villosum (Hilliard) Källersjö	Asteraceae	Nordic J. Bot. 5(6): 538. 1986 [1985 publ. 1986]	Phymvill	RARE	SA
Protea comptonii Beard	Proteaceae	Bothalia vii. 61 (1958)	Protcomp	NT	
Protea nubigena Rourke	Proteaceae	J. S. African Bot. 44(4): 373 (1978)	Protnubi	CR	KZN Drakensberg
Raspalia trigyna Dummer	Bruniaceae	J. Bot. 50(Suppl. 2): 21. 1912	Rasptrig	CR	SA
Restio zuluensis H.P.Linder	Restionaceae	Bothalia 15: 463 1985.	Restzulu	VU	
Salacia gerrardii Harv. ex Sprague	Celastraceae	Bull. Misc. Inform. Kew 1916, 176, descr	Salagerr	LC	
Sandersonia aurantiaca Hook.	Colchicaceae	Bot. Mag. 79: t. 4716. 1853	Sandaura	Declining	

Scientific name with authority	**Family**	**Reference**	**Species Code**	**Red Data Cat.**	**Endemism**
Scadoxus puniceus (L.) Friis & Nordal	Amaryllidaceae	Norweg. J. Bot. 23(2): 64 (1976)	Scadpuni	LC	
Schizochilus bulbinella (Rchb.f.) Bolus	Orchidaceae	J. Linn. Soc., Bot. xxv. 205 (1889)	Schibulb	RARE	
Schizochilus gerrardii Bolus	Orchidaceae	J. Linn. Soc., Bot. xxv. (1889) 205	Schigerr	EN	KZN
Scolopia mundii (Eckl. & Zeyh.) Warb.	Salicaceae	Germishuizen, G., Meyer, N.L., Steenkamp, Y. & Keith, M. (eds) 2006. A Checklist of South African plants. Southern African Botanical Diversity Network Report No. 41. SABONET, Pretoria.	Scolmund	LC	
Searsii dentata Thunb.	Anacardiaceae	Moffett, R.O. 2007. Name changes in the Old World Rhus and recognition of Searsia (Anacardiaceae). Bothalia 37(2):165-175	Seardent	LC	
Searsii rudatisii Engl.	Anacardiaceae	Engl. Pflanzenw. Afr. iii. II. (Engl. & Drude, Veg. der Erde, ix.), 217(1921); Schonland in Bothalia, iii. 36 (1930) Moffett, R.O. 2007. Name changes in the Old World Rhus and recognition of Searsia (Anacardiaceae). Bothalia 37(2):165-175	Searruda	EN	KZN
Selago longiflora Rolfe	Scrophulariaceae	Fl. Cap. (Harvey) 5(1.1): 159. 1901 [Jun 1901]	Selalong	EN	KZN midlands
Senecio exuberans R.A.Dyer	Compositae	J. S. African Bot. ix. 124 (1943). ix. 124 1943.	Seneexub	EN	KZN midlands
Stachys comosa Codd	Lamiaceae	Bothalia 16: 51 1986.	Staccomo	NT	SA
Streptocarpus floribundus Weigend & T.J.Edwards	Gesneriaceae	S. African J. Bot. 60: 168 1994.	Streflor	VU	KZN Midlands
Synaptolepis kirkii Oliv.	Thymelaeaceae	Hooker's Icon. Pl. 11: 59-60, pl. 1074 59 1870.	Synakirk	NT	

Scientific name with authority	**Family**	**Reference**	**Species Code**	**Red Data Cat.**	**Endemism**
Syncolostemon latidens (N.E.Br.) Codd	Lamiaceae	Bothalia 12: 26 1976.	Synclati	VU	KZN Midlands
Syncolostemon ramulosus Benth.	Lamiaceae	Comm. Pl. Afr. Austr. 230 1838.	Syncramu	VU	Pondoland sand stone
Tecoma capensis (Thunb.) Lindl.	Bignoniaceae	Bot. Reg. 13: t. 1117 1828.	Tecocape	LC	
Tephrosia pondoensis (Codd) Schrire	Fabiaceae	Bothalia 15: 552 1985.	Tephpond	EN	Pondoland
Triglochin bulbosa L.	Juncaginaceae.	Germishuizen, G., Meyer, N.L., Steenkamp, Y. & Keith, M. (eds) 2006. A Checklist of South African plants. Southern African Botanical Diversity Network Report No. 41. SABONET, Pretoria.	Trigbulb	LC	
*Vanilla roscher*i Rchb.f.	Orchidaceae	Linnaea 41: 65 1876.	Vanirosc	NT	
Vitellariopsis dispar (N.E.Br.) Aubrév.	Sapotaceae	Adansonia n.s., 3: 42 1963.	Vitedisp	RARE	KZN Tugela
Warburgia salutaris (G.Bertol.) Chiov.	Canellaceae	Nuovo Giorn. Bot. Ital. n.s., 44: 683 1937.	Warbsalu	EN	
Watsonia canaliculata Goldblatt	Iridaceae	Ann. Kirstenbosch Bot. Gard. 19: 83 1989.	Watscana	EN	KZN midlands
Woodia verruculosa Schltr.	Asclepiadaceae	Bot. Jahrb. Syst. 18(45): 31 1894.	Woodverr	VU	KZN midlands
Ziziphus mucronata Willd.	Rhamnaceae	Enum. Pl. 251 1809.	Zizimucr	LC	

Appendix 2: List of values used in the derivation of a Rarity Index and Niche Width for each selected species. See Appendix 1 for species codes.

Species Code	Estimated Population Size (EPS)	Extent of Occurrence (EOO) (ha)	Rarity Index (EPS x EOO)	Log_{10} Rarity	Rainfall range (mm)	Temp range (˚C)	Number of classes of soil fertility	Niche width (rainfall range X Temp range X No. of soil classes)	Log_{10} niche width
Acalentu	555	221392.5	122872852.5	8.0895	216	23	1	4968	3.6962
Albemagn	7500	654165.4	4906240500	9.6907	152	22	3	10032	4.0014
Albisulu	3000	10783.8	32351475	7.5099	127	20	3	7620	3.8820
Aloegers	7500	10112.4	75842775	7.8799	125	19	1	2375	3.3757
Aloemacu	55000	7632693.9	4.19798E+11	11.6230	399	33	3	39501	4.5966
Aloemode	555	141004.9	78257736.71	7.8935	1	23	1	23	1.3617
Aloesaun	3000	596.6	1789698	6.2528	298	23	1	6854	3.8359
Anseafri	55000	1600451.9	88024856150	10.9446	194	22	3	12804	4.1073
Argylong	555	69143.6	38374689.68	7.5840	126	22	3	8316	3.9199
Asclbicu	55	55959.2	3077754.075	6.4882	142	22	1	3124	3.4947
Asclconc	55	66958	3682688.9	6.5662	1	25	1	25	1.3979

Species Code	**Estimated Population Size (EPS)**	**Extent of Occurrence (EOO) (ha)**	**Rarity Index (EPS x EOO)**	**Log_{10} Rarity**	**Rainfall range (mm)**	**Temp range (˚C)**	**Number of classes of soil fertility**	**Niche width (rainfall range X Temp range X No. of soil classes)**	**Log_{10} niche width**
Asclschl	55	137222.7	7547246.08	6.8778	291	20	1	5820	3.7649
Asclwood	55	57195.4	3145748.43	6.4977	86	21	1	1806	3.2567
Barlargi	3000	1286.9	3860613	6.5867	8	25	2	400	2.6021
Barlgree	555	1609.6	893349.645	5.9510	44	27	2	2376	3.3758
Begodreg	3000	815920.9	2447762589	9.3888	250	19	3	14250	4.1538
Berkdrac	555	41539.7	23054537.94	7.3628	869	27	1	23463	4.3704
Bonalamp	55	144648.6	7955672.065	6.9007	490	22	1	10780	4.0326
Bowivolu	555	3060788.3	1698737479	9.2301	549	30	3	49410	4.6938
Bracnata	55	668.6	36774.485	4.5655	159	15	1	2385	3.3775
Calpwood	555	101.8	56524.752	4.7522	72	26	1	1872	3.2723
Ceroaren	555	16521.8	9169594.56	6.9624	1	17	2	34	1.5315
Ceroruda	5	35196.7	175983.265	5.2455	124	19	2	4712	3.6732
Crinmoor	555	3231741.6	1793616565	9.2537	65	18	2	2340	3.3692

Species Code	**Estimated Population Size (EPS)**	**Extent of Occurrence (EOO) (ha)**	**Rarity Index (EPS x EOO)**	**Log_{10} Rarity**	**Rainfall range (mm)**	**Temp range (˚C)**	**Number of classes of soil fertility**	**Niche width (rainfall range X Temp range X No. of soil classes)**	**Log_{10} niche width**
Crypoblo	55000	2118938.9	1.16542E+11	11.0665	248	28	2	13888	4.1426
Crypwyli	7500	300076.8	2250575753	9.3523	214	21	2	8988	3.9537
Curtdent	7500	5438088.2	40785661185	10.6105	694	33	3	68706	4.8370
Cyrtbrac	55	4.4	243.98	2.3874	1	20	1	20	1.3010
Cyrtobli	555	7980	4428900.555	6.6463	147	21	1	3087	3.4895
Delotrad	55000	4736025.9	2.60481E+11	11.4158	374	22	3	24684	4.3924
Dierlute	3000	77252.7	231758040	8.3650	642	25	1	16050	4.2055
Dierpall	555	103874.3	57650225.4	7.7608	255	23	1	5865	3.7683
Diertyso	55	462807.9	25454433.84	7.4058	343	28	2	19208	4.2835
Diosglan	7500	100011.2	750084337.5	8.8751	298	21	2	12516	4.0975
Disamont	55	3762	206909.23	5.3158	1	23	1	23	1.3617
Disasang	55	30951.5	1702333.215	6.2310	113	26	1	2938	3.4681
Disascul	555	369528.9	205088556.7	8.3119	333	26	2	17316	4.2384

Species Code	**Estimated Population Size (EPS)**	**Extent of Occurrence (EOO) (ha)**	**Rarity Index (EPS x EOO)**	**Log_{10} Rarity**	**Rainfall range (mm)**	**Temp range (˚C)**	**Number of classes of soil fertility**	**Niche width (rainfall range X Temp range X No. of soil classes)**	**Log_{10} niche width**
Dracital	555	108711.2	60334705.46	7.7806	184	23	1	4232	3.6265
Enceaemu	555	246.2	136647.105	5.1356	1	19	1	19	1.2788
Enceceri	55	199	10944.945	4.0392	92	23	1	2116	3.3255
Encemsin	55	7641.8	420300.375	5.6236	178	25	2	8900	3.9494
Encesent	7500	92993.8	697453530	8.8435	238	25	1	5950	3.7745
Eriosuba	555	420083.6	233146375.8	8.3676	654	23	4	60168	4.7794
Erioumta	7500	27473.4	206050192.5	8.3140	156	17	3	7956	3.9007
Feliwrig	555	20453.5	11351682.51	7.0551	366	26	1	9516	3.9785
Gerbaura	555	580372.6	322106799.1	8.5080	542	29	2	31436	4.4974
Gladcrue	55	70205.4	3861294.36	6.5867	295	22	1	6490	3.8122
Gnidkrau	55000	7990916.	4.395E+11	11.6430	382	27	1	10314	4.0134
Helicitr	55	63652.9	3500908.455	6.5442	21	23	1	483	2.6839
Holomaju	3000	39.9	119568	5.0776	1	25	1	25	1.3979

Species Code	Estimated Population Size (EPS)	Extent of Occurrence (EOO) (ha)	Rarity Index (EPS x EOO)	Log$_{10}$ Rarity	Rainfall range (mm)	Temp range (˚C)	Number of classes of soil fertility	Niche width (rainfall range X Temp range X No. of soil classes)	Log$_{10}$ niche width
Knipbrac	3000	686827.7	2060483079	9.3140	523	27	2	28242	4.4509
Knipevan	555	8529.8	4734021.795	6.6752	901	27	1	24327	4.3861
Kniplati	3000	228663.4	685990116	8.8363	435	25	3	32625	4.5136
Knipleuc	555	683.2	379173.225	5.5788	67	18	1	1206	3.0813
Knippauc	5	3120	15599.94	4.1931	33	18	2	1188	3.0748
Leucgerr	55	119751.6	6586339.265	6.8186	413	24	2	19824	4.2972
Maninich	555	11238	6237084.45	6.7950	170	16	2	5440	3.7356
Manuflor	3000	1021609.7	3064829034	9.4864	351	29	3	30537	4.4848
Maytabbo	555	23039.6	12786983	7.1068	26	16	2	832	2.9201
Melhdidy	55000	1652823.8	90905308230	10.9586	130	29	3	11310	4.0535
Melhpoly	55	57859.9	3182293.895	6.5027	182	21	2	7644	3.8833
Merwplum	55000	7027992.2	3.8654E+11	11.5872	1273	34	4	173128	5.2384
Mystalic	555	485738.6	269584949.6	8.4307	224	25	1	5600	3.7482

Species Code	**Estimated Population Size (EPS)**	**Extent of Occurrence (EOO) (ha)**	**Rarity Index (EPS x EOO)**	**Log_{10} Rarity**	**Rainfall range (mm)**	**Temp range (˚C)**	**Number of classes of soil fertility**	**Niche width (rainfall range X Temp range X No. of soil classes)**	**Log_{10} niche width**
Oleacape	55000	7961231.6	4.37868E+11	11.6413	356	19	2	13528	4.1312
Olinradi	555	3830193	2125757115	9.3275	88	27	2	4752	3.6769
Oxalobli	55000	6174531.3	3.39599E+11	11.5310	690	32	3	66240	4.8211
Pelatong	55000	10498.3	577404080	8.7615	294	22	3	19404	4.2879
Peucwilm	555	519846.7	288514918.5	8.4602	451	21	1	9471	3.9764
Phymvill	555	152145.2	84440581.01	7.9266	133	25	1	3325	3.5218
Protcomp	3000	5797.9	17393676	7.2404	70	22	2	3080	3.4886
Protnubi	55	5	275	2.4393	1	24	1	24	1.3802
Rasptrig	5	3216.7	16083.52	4.2064	62	15	2	1860	3.2695
Restzulu	7500	910514.1	6828855975	9.8343	502	26	1	13052	4.1157
Salagerr	55000	2575940.9	1.41677E+11	11.1513	347	23	3	23943	4.3792
Sandaura	3000	6166737.1	18500211240	10.2672	500	32	5	80000	4.9031
Scadpuni	55000	7490251.7	4.11964E+11	11.6149	998	34	3	101796	5.0077

Species Code	Estimated Population Size (EPS)	Extent of Occurrence (EOO) (ha)	Rarity Index (EPS x EOO)	Log_{10} Rarity	Rainfall range (mm)	Temp range (˚C)	Number of classes of soil fertility	Niche width (rainfall range X Temp range X No. of soil classes)	Log_{10} niche width
Schibulb	3000	573908.8	1721726337	9.2360	391	27	2	21114	4.3246
Schigerr	555	1096782.9	608714530.6	8.7844	739	24	1	17736	4.2489
Scolmund	55000	9023603.7	4.96298E+11	11.6957	1120	32	4	143360	5.1564
Seardent	55000	9082059.2	4.99513E+11	11.6985	1125	34	4	153000	5.1847
Searruda	555	141938.1	78775622.19	7.8964	109	21	1	2289	3.3596
Selalong	555	7713.1	4280783.82	6.6315	113	20	1	2260	3.3541
Seneexub	3000	26040.6	78121845	7.8928	401	23	1	9223	3.9649
Staccomo	555	199959.3	110977411.5	8.0452	279	20	1	5580	3.7466
Streflor	55	61	3352.58	3.5254	1	17	1	17	1.2304
Synakirk	55000	622601.2	34243067100	10.5346	224	19	3	12768	4.1061
Synclati	555	59563.3	33057617.63	7.5193	411	23	1	9453	3.9756
Syncramu	555	238.6	132425.22	5.1220	35	15	2	1050	3.0212
Tecocape	55000	7449520	4.09724E+11	11.6125	718	29	3	62466	4.7956
Tephpond	555	865.5	480350.835	5.6816	85	16	1	1360	3.1335
Trigbulb	55000	650197.7	35760875700	10.5534	406	26	2	21112	4.3245

Species Code	**Estimated Population Size (EPS)**	**Extent of Occurrence (EOO) (ha)**	**Rarity Index (EPS x EOO)**	**$\mathbf{Log_{10}}$ Rarity**	**Rainfall range (mm)**	**Temp range (˚C)**	**Number of classes of soil fertility**	**Niche width (rainfall range X Temp range X No. of soil classes)**	**$\mathbf{Log_{10}}$ niche width**
Vanirosc	55	947.7	52122.18	4.7170	87	18	1	1566	3.1948
Vitedisp	555	831444.6	461451747.5	8.6641	40	30	1	1200	3.0792
Warbsalu	555	1178845.2	654259101.5	8.8157	295	27	4	31860	4.5032
Watscana	555	369539.1	205094214.9	8.3120	686	25	3	51450	4.7114
Woodverr	3000	824891.7	2474675100	9.3935	364	26	4	37856	4.5781
Zizimucr	55000	9966743.2	5.48171E+11	11.7389	671	29	3	58377	4.7662

Appendix 3: List of species coded as matrix (M) or Habitat Specific (Hs) depending on their vegetation physiognomy and/or information on their habitat.

Scientific name with authority	Species Code	Matrix (M) or Habitat Specific (Hs)	Vegetation Physionomy	Additional information used to classify species (from Pooley (1998), Scott-Shaw (1999), SANBI (2009) Coates Palgrave (1983); Boon (2010))
Acalypha entumenica Prain	Acalentu	M	grassland	Mistbelt and Ngongoni Grassland, dolerite, 850-1600 m
Alberta magna E.Mey.	Albemagn	Hs	scarp forest	
Albizia suluensis Gerstner	Albisulu	Hs	scarp forest/woodland	Scarp forest, riverine thicket and open woodland (Pooley 1993), often along streams (Ross 1975), usually along the upper altitudinal perimeter and on steep slopes (Scott-Shaw 1999).
Aloe gerstneri Reynolds	Aloegers	M	savanna	
Aloe maculata All.	Aloemacu	M	grassland	
Aloe modesta Reynolds	Aloemode	Hs	grassland	in rocky area & seasonal seepages
Aloe saundersiae (Reynolds) Reynolds	Aloesaun	Hs	grassland	in rocky areas, in moist moss (pers. obs.)
Ansellia africana Lindl.	Anseafri	Hs	savanna	Epiphytic in trees
Argyrolobium longifolium Walp.	Argylong	M	grassland	Mistbelt and Ngongoni grassland
Asclepias bicuspis N.E.Br.	Asclbicu	M	grassland	Mistbelt grassland
Asclepias concinna Schltr.	Asclconc	M	grassland	Montane grassland. Can be found in annually burnt midlands grasslands, (Nicholas 1999).

Scientific name with authority	**Species Code**	**Matrix (M) or Habitat Specific (Hs)**	**Vegetation Physionomy**	**Additional information used to classify species (from Pooley (1998), Scott-Shaw (1999), SANBI (2009) Coates Palgrave (1983); Boon (2010))**
Asclepias schlechteri N.E.Br.	Asclschl	M	grassland	
Asclepias woodii Schltr.	Asclwood	M	grassland	Mistbelt grassland, grows and flowers in unburnt grasslands. (Nicholas 1999).
Barleria argillicola Oberm.	Barlargi	M	savanna	Savanna, valley thicket
Barleria greenii M.Balkwill & K.Balkwill	Barlgree	M	savanna	Savanna, open rocky areas,on moderately sloping north-facing aspects in open, rocky areas
Begonia dregei Otto & A.Dietr.	Begodreg	Hs	scarp forest	Scarp forest. In Kloofs on rocky cliffs, steep banks and rock falls
Berkheya draco Roessler	Berkdrac	Hs	grassland	occurs in a specific habitat in steep gullies (SANBI)
Bonatea lamprophylla J.Stewart	Bonalamp	Hs	forest	occurs in few patches in shade/forest (pers. obs)
Bowiea volubilis Harv. ex Hook.f.	Bowivolu	M	savanna	Savanna and grassland
Brachystelma natalense N.E.Br.	Bracnata	M	grassland	
Calpurnia woodii Schinz	Calpwood	M	grassland	
Ceropegia arenaria R.A.Dyer	Ceroaren	Hs	forest	Coastal forest, sandy soils near dune forest
Ceropegia rudatisii Schltr.	Ceroruda	Hs	grassland	rock outcrops and bush clump margins (Scott-Shaw 1999)
Crinum moorei Hook.f.	Crinmoor	Hs	forest	Scarp Forest, Coastal and riverine forests, scarp forest, in damp or marshy places along rivers and rivulets (SANBI).

Scientific name with authority	**Species Code**	**Matrix (M) or Habitat Specific (Hs)**	**Vegetation Physionomy**	**Additional information used to classify species (from Pooley (1998), Scott-Shaw (1999), SANBI (2009) Coates Palgrave (1983); Boon (2010))**
Cryptolepis oblongifolia Schltr.	Crypoblo	M	grassland	
Cryptocarya wyliei Stapf	Crypwyli	Hs	coastal forest	
Curtisia dentata (Burm.f.) C.A.Sm.	Curtdent	Hs	forest	Mistbelt and Montane forest; Evergreen forest
Cyrtanthus brachysiphon Hilliard & B.L.Burtt	Cyrtbrac	Hs	wooded watercourses	occurring on moist cliffs and ledges along watercourses (SANBI)
Cyrtanthus obliquus Aiton	Cyrtobli	M	grassland	Ngongoni grassland
Delosperma tradescantioides (P.J.Bergius) L.Bolus	Delotrad	M	thicket/grassland	
Dierama luteoalbidum I.Verd.	Dierlute	M	grasslands	
Dierama pallidum Hilliard	Dierpall	M	grassland	
Dierama tysonii N.E.Br.	Diertyso	M	grassland	
Diospyros glandulifera De Winter	Diosglan	M	bushveld	
Disa montana Sond.	Disamont	M	grassland	
Disa sanguinea Sond.	Disasang	Hs	grassland	seasonally damp sites in Montane grassland
Disa scullyi Bolus	Disascul	Hs	wetland	

Scientific name with authority	**Species Code**	**Matrix (M) or Habitat Specific (Hs)**	**Vegetation Physionomy**	**Additional information used to classify species (from Pooley (1998), Scott-Shaw (1999), SANBI (2009) Coates Palgrave (1983); Boon (2010))**
Dracosciadium italae Hilliard & B.L.Burtt	Dracital	Hs	grassland	rocky outcrops
E*ncephalartos aemulans* Vorster	Enceaemu	Hs	savanna	on cliff faces
Encephalartos cerinus Lavranos & D.L.Goode	Enceceri	Hs	thicket	Valley thicket, scrub on cliffs
Encephalartos msinganus Vorster	Encemsin	Hs	savanna	Savanna wooded escarpment edge
Encephalartos senticosus Vorster	Encesent	Hs	scrub/forest	dry exposed cliffs, rocky forest ravines
Eriosemopsis subanisophylla Robyns	Eriosuba	Hs	grassland	on plateaux or gentle slope
Eriosema umtamvunense C.H.Stirt.	Erioumta	Hs	grassland	restricted to plateaux
F*elicia wrighti*i Hilliard & B.L.Burtt	Feliwrig	Hs	grassland	Only known from one locality, occurs on mountain slopes on damp earth banks
Gerbera aurantiaca Sch.Bip.	Gerbaura	M	grassland	
Gladiolus cruentus T Moore	Gladcrue	Hs	scarp forest	Scarp forest, edges of waterfalls
Gnidia kraussiana Meisn.	Gnidkrau	M	grassland	

Scientific name with authority	**Species Code**	**Matrix (M) or Habitat Specific (Hs)**	**Vegetation Physionomy**	**Additional information used to classify species (from Pooley (1998), Scott-Shaw (1999), SANBI (2009) Coates Palgrave (1983); Boon (2010))**
Helichrysum citricephalum Hilliard & B.L.Burtt	Helicitr	M	grassland	
Holothrix majubensis C.Archer & R.H.Archer	Holomaju	Hs	grassland	Montane grassland, Sandstone cliffs; Montane grassland, sandstone cliffs, 2200m, cracks in verticle sandstone cliffs; A high altitude habitat specialist
Kniphofia brachystachya (Zahlbr.) Codd	Knipbrac	M	grasslands	
Kniphofia evansii Baker	Knipevan	Hs	grassland	Montane grassland, moist ledges, seepage lines and stream banks; moist ledges, seepage lines, stream banks
Kniphofia latifolia Codd	Kniplati	Hs	wetland	
Kniphofia leucocephala Baijnath	Knipleuc	Hs	wetland	
Kniphofia pauciflora Baker	Knippauc	M	grassland	
Leucospermum gerrardii Stapf	Leucgerr	M	grassland	
Manilkara nicholsonii A.E.van Wyk	Maninich	Hs	forest	Scarp forest, margins, among rocks, along escarpment edges and ravines
Manulea florifera Hilliard & B.L.Burtt	Manuflor	Hs	grassland	Montane grassland Damp or marshy grassland
Maytenus abbottii A.E.van Wyk	Maytabbo	Hs	forest	
Melhania didyma Eckl. & Zeyh.	Melhdidy	M	grassland/woodland	

Scientific name with authority	**Species Code**	**Matrix (M) or Habitat Specific (Hs)**	**Vegetation Physionomy**	**Additional information used to classify species (from Pooley (1998), Scott-Shaw (1999), SANBI (2009) Coates Palgrave (1983); Boon (2010))**
Melhania polygama I.Verd.	Melhpoly	M	grassland	
Merwilla plumbea (Lindl.) Speta	Merwplum	M	grassland	
Mystacidium aliceae Bolus	Mystalic	Hs	Forest	Occurs in thick scrub in hilly regions as a low level epiphyte in shady conditions
Olea capensis L.	Oleacape	Hs	forest/forestmargins	
Olinia radiata Hofmeyr & E.Phillips	Olinradi	Hs	forest	
Oxalis obliquifolia Steud. ex A.Rich.	Oxalobli	M	grassland	
Pelargonium tongaense Vorster	Pelatong	Hs	forests	
Peucedanum wilmsianum H.Wolff	Peucwilm	M	grassland	
Phymaspermum villosum (Hilliard) Källersjö	Phymvill	Hs	grassland	Grassland, rock outcrops or stony slopes
Protea comptonii Beard	Protcomp	Hs	savanna	on steep cool south-facing slopes; Steep rocky mountain slopes (Coates P)
Protea nubigena Rourke	Protnubi	Hs	grassland	Subalpine grassland, low scrub communities. Near precipitous south-facing slopes, in shade most year
Raspalia trigyna Dummer	Rasptrig	M	grassland	
Restio zuluensis H.P.Linder	Restzulu	Hs	wetland	

Scientific name with authority	**Species Code**	**Matrix (M) or Habitat Specific (Hs)**	**Vegetation Physionomy**	**Additional information used to classify species (from Pooley (1998), Scott-Shaw (1999), SANBI (2009) Coates Palgrave (1983); Boon (2010))**
Salacia gerrardii Harv. ex Sprague	Salagerr	M	grassland/open woodland	
Sandersonia aurantiaca Hook.	Sandaura	M	grassland	
Scadoxus puniceus (L.) Friis & Nordal	Scadpuni	M	grassland/forest	
Schizochilus bulbinella (Rchb.f.) Bolus	Schibulb	Hs	grassland	Montane grassland and alpine grassland, on shallow soil over rock
Schizochilus gerrardii Bolus	Schigerr	Hs	grassland	rock outcrops, shallow soil, seepages
Scolopia mundii (Eckl. & Zeyh.) Warb.	Scolmund	Hs	forest	
Searsii dentata Thunb.	Seardent	M	scrub/forest	
Searsii rudatisii Engl.	Searruda	M	grassland	
Selago longiflora Rolfe	Selalong	Hs	grassland	scrub on forest margins
Senecio exuberans R.A.Dyer	Seneexub	M	grassland	
Stachys comosa Codd	Staccomo	M	grassland	grassy slopes among rocks
Streptocarpus floribundus Weigend & T.J.Edwards	Streflor	Hs	forest	Scarp forest; grow on doleritic cliffs overlooking the Tugela Valley.
Synaptolepis kirkii Oliv.	Synakirk	M	grassland	

Scientific name with authority	**Species Code**	**Matrix (M) or Habitat Specific (Hs)**	**Vegetation Physionomy**	**Additional information used to classify species (from Pooley (1998), Scott-Shaw (1999), SANBI (2009) Coates Palgrave (1983); Boon (2010))**
Syncolostemon latidens (N.E.Br.) Codd	Synclati	M	grassland	highly habitat specific
Syncolostemon ramulosus Benth.	Syncramu	Hs	grassland	rocky outcrops on rock sheets, forest margins
Tecoma capensis (Thunb.) Lindl.	Tecocape	M	scrub	
Tephrosia pondoensis (Codd) Schrire	Tephpond	Hs	grassland	rocky outcrops, drainage lines, forest margin
Triglochin bulbosa L.	Trigbulb	Hs	wetland	
*Vanilla roscher*i Rchb.f.	Vanirosc	Hs	forest	forest margins at the edge of water
Vitellariopsis dispar (N.E.Br.) Aubrév.	Vitedisp	Hs	savanna	closed woodland, dry riverine forest
Warburgia salutaris (G.Bertol.) Chiov.	Warbsalu	Hs	woodland	
Watsonia canaliculata Goldblatt	Watscana	M	grassland	
Woodia verruculosa Schltr.	Woodverr	M	grassland	
Ziziphus mucronata Willd.	Zizimucr	M	bushveld	

Appendix 4: List of species coded for dispersal distance as localized (dispersal of up to 10m), medium (dispersal distance between 10m and 100m) and far (dispersal distance of greater than 100m)

Scientific name with authority	**Species Code**	**Dispersal Distance**	**Seed characteristics**	**Dispersal Vector**
Acalypha entumenica Prain	Acalentu	localized		
Alberta magna E.Mey.	Albemagn	far	small seed with papery wings	Seeds are wind dispersed, and can be dispersed quite effectively over large distances by strong winds (T. Abbott pers. obs)
Albizia suluensis Gerstner	Albisulu	medium	dehiscent pod	expulsion and gravity
Aloe gerstneri Reynolds	Aloegers	medium	winged seeds	Wind
Aloe maculata All.	Aloemacu	medium	Aloe seed capsules split open and the seeds are light and winged which aids dispersal by wind	wind
Aloe modesta Reynolds	Aloemode	medium	Aloe seeds light	winged so probably wind
Aloe saundersiae Reynolds	Aloesaun	localized		seeds transported down drip lines
Ansellia africana Lindl.	Anseafri	far	Extremely small seeds are able to wind-disperse over large distances.	wind
Argyrolobium longifolium Walp.	Argylong	far		
Asclepias bicuspis N.E.Br.	Asclbicu	far		wind, seeds compressed with a basal tuft of silky hairs
Asclepias concinna Schltr.	Asclconc	far		wind, seeds compressed with a basal tuft of silky hairs
Asclepias schlechteri N.E.Br.	Asclschl	far		wind, seeds compressed with a basal tuft of

Scientific name with authority	Species Code	Dispersal Distance	Seed characteristics	Dispersal Vector
				silky hairs
Asclepias woodii Schltr.	Asclwood	far		wind, seeds compressed with a basal tuft of silky hairs
Barleria argillicola Oberm.	Barlargi	localized		Barleria argillicola is only capable of very short distance dispersal by means of explosive seed capsules (Makholela et al. 2004).
Barleria greenii M.Balkwill & K.Balkwill	Barlgree	localized		short distance dispersal by means of explosive seed capsules
Begonia dregei Otto & A.Dietr.	Begodreg	medium	similar sp seed size 10-20mm across wings	
Berkheya draco Roessler	Berkdrac	medium	Seeds are small and light with a ring of scale-like bristles on the upper end and stiff hairs covering the surface assisting in the dispersal by wind.	
Bonatea lamprophylla J.Stewart	Bonalamp	far	minute seeds	wind
Bowiea volubilis Harv. ex Hook.f.	Bowivolu	medium	Fruits are in the form of a brownish oval capsule, about 25 mm in diameter.	
Brachystelma natalense N.E.Br.	Bracnata	medium	seeds compressed with a basal tuft of silky hairs	
Calpurnia woodii Schinz	Calpwood	medium	thin papery pods	
Ceropegia arenaria R.A.Dyer	Ceroaren	far	seeds compressed with a basal tuft of silky hairs	Wind
Ceropegia rudatisii Schltr.	Ceroruda	far	seeds compressed with a basal tuft of silky hairs	Wind
Crinum moorei Hook.f.	Crinmoor	localized	large seeds	gravity

Scientific name with authority	**Species Code**	**Dispersal Distance**	**Seed characteristics**	**Dispersal Vector**
Cryptolepis oblongifolia Schltr.	Crypoblo			
*Cryptocarya wylie*i Stapf	Crypwyli	far	bright red fruit	birds
Curtisia dentata (Burm.f.) C.A.Sm.	Curtdent	far	Fruit drupaceous, 5–7 × 3–5 mm., fruit small, round, fleshy berry with 4 seeds; dispersed by lourie and bats mainly but also eaten by other mammals.	Birds/ animals
Cyrtanthus brachysiphon Hilliard & B.L.Burtt	Cyrtbrac	medium		water as they occur on the edge of streams
Cyrtanthus obliquus Aiton	Cyrtobli	localized	The seeds are papery and black.	gravity
Delosperma tradescantioides (P.J.Bergius) L.Bolus	Delotrad	medium	fruit capsules, which have four to six locules and wings	
Dierama luteoalbidum I.Verd.	Dierlute	medium	rounded capsule bearing angular seeds	wind
Dierama pallidum Hilliard	Dierpall	medium	rounded capsule bearing angular seeds	wind
Dierama tysonii N.E.Br.	Diertyso	medium	rounded capsule bearing angular seeds	wind
Diospyros glandulifera De Winter	Diosglan	far		fruit eaten by birds and animals
Disa montana Sond.	Disamont	far		Wind
Disa sanguinea Sond.	Disasang	far		Wind
Disa scullyi Bolus	Disascul	far		Wind
Dracosciadium italae Hilliard & B.L.Burtt	Dracital	localized		
E*ncephalartos aemulans* Vorster	Enceaemu	far		fleshy fruit ; birds/animals

Scientific name with authority	**Species Code**	**Dispersal Distance**	**Seed characteristics**	**Dispersal Vector**
Encephalartos cerinus Lavranos & D.L.Goode	Enceceri	far		fleshy fruit ; birds/animals
Encephalartos msinganus Vorster	Encemsin	far	large	fleshy fruit ; birds/animals
Encephalartos senticosus Vorster	Encesent	far		fleshy fruit ; birds/animals
Eriosemopsis subanisophylla Robyns	Eriosuba			
Eriosema umtamvunense C.H.Stirt.	Erioumta			
F*elicia wright*ii Hilliard & B.L.Burtt	Feliwrig	medium	Large winged seeds	
Gerbera aurantiaca Sch.Bip.	Gerbaura	medium	Large winged seeds	
Gladiolus cruentus T Moore	Gladcrue	medium		gravity as seeds occur on cliff faces
Gnidia kraussiana Meisn.	Gnidkrau	far	The fruit is a 1-seeded berry	birds
Helichrysum citricephalum Hilliard & B.L.Burtt	Helicitr	medium	Pappus bristles	Wind
Holothrix majubensis C.Archer & R.H.Archer	Holomaju	far	minute seeds	Wind
Kniphofia brachystachya (Zahlbr.) Codd	Knipbrac	localized	small flat seeds	
Kniphofia evansii Baker	Knipevan	localized	small flat seeds	
Kniphofia latifolia Codd	Kniplati	localized	small flat seeds	
Kniphofia leucocephala Baijnath	Knipleuc	localized	small dark flat seeds	
Kniphofia pauciflora Baker	Knippauc	localized	small flat seeds	

Scientific name with authority	**Species Code**	**Dispersal Distance**	**Seed characteristics**	**Dispersal Vector**
Leucospermum gerrardii Stapf	Leucgerr	localized	small nuts covered by a soft, fleshy, white skin	
Manilkara nicholsonii A.E.van Wyk	Maninich	far	Mode of dispersal is unknown, but fruit set is extremely poor due to parasitizing of flowers, and dispersal betwee isolated forest fragments is highly unlikely.	
Manulea florifera Hilliard & B.L.Burtt	Manuflor			
Maytenus abbottii A.E.van Wyk	Maytabbo	localized	seeds round, glossy with white minute hairy aril, fruit dehiscent 2-4 lobed capsule	expulsion
Melhania didyma Eckl. & Zeyh.	Melhdidy	localized	Fruit a loculicidal capsule or a schizocarp, separating into individual mericarps, rarely berrylike when mature (Malvaviscus) ; carpels sometimes with an endoglossum (a crosswise projection from back wall of carpel to make it almost completely septate . Seeds often reniform , glabrous or hairy , sometimes conspicuously so.	gravity
Melhania polygama I.Verd.	Melhpoly	localized	dry fruit of Sterculiaceae splits into carpels when ripe	
Merwilla plumbea (Lindl.) Speta	Merwplum	medium	The seed, which is formed in capsules that split when mature, does not look much like seed.	Wind dispersed
Mystacidium aliceae Bolus	Mystalic	far		wind, minute seeds
Olea capensis L.	Oleacape	far		fruit of Olea sp eaten by birds and mammals
Olinia radiata Hofmeyr & E.Phillips	Olinradi	far		Fruit eaten by birds

Scientific name with authority	**Species Code**	**Dispersal Distance**	**Seed characteristics**	**Dispersal Vector**
Oxalis obliquifolia Steud. ex A.Rich.	Oxalobli	localized	Ovary 5 locular with one or more ovules in each locule. Often heterostylous (in some European species); Fruit capsular; Seeds with an elastic testa.	
Pelargonium tongaense Vorster	Pelatong	medium	Large wind propelled seeds	
Peucedanum wilmsianum H.Wolff	Peucwilm	medium	seeds flattened, ribbed or winged	Wind dispersed
Phymaspermum villosum (Hilliard) Källersjö	Phymvill	far		"It has good seed dispersal abilities " (Scott-Shaw)
Protea comptonii Beard	Protcomp	medium		seeds have been found to be distributed further than 10m from parent plants
Protea nubigena Rourke	Protnubi	medium		Assumed to be similar as has similar seed
Raspalia trigyna Dummer	Rasptrig	localized	very limited seed dispersal observed	
Restio zuluensis H.P.Linder	Restzulu	far		Wind
Salacia gerrardii Harv. ex Sprague	Salagerr	far	Fruit	eaten by people, animals
Sandersonia aurantiaca Hook.	Sandaura	medium	The fruit is a capsule containing many small, hard brown seeds, without a papery seed coat,	
Scadoxus puniceus (L.) Friis & Nordal	Scadpuni	far	Berry	birds, monkeys
Schizochilus bulbinella (Rchb.f.) Bolus	Schibulb	localized		
Schizochilus gerrardii Bolus	Schigerr	localized		
Scolopia mundii (Eckl. & Zeyh.) Warb.	Scolmund			

Scientific name with authority	**Species Code**	**Dispersal Distance**	**Seed characteristics**	**Dispersal Vector**
Searsii dentata Thunb.	Seardent	far		fruit eaten by birds
Searsii rudatisii Engl.	Searruda	medium		
Selago longiflora Rolfe	Selalong			
Senecio exuberans R.A.Dyer	Seneexub	far	seed has bristles or pappus to aid dispersal	wind, seeds can be carried long distances becaise of pappus
Stachys comosa Codd	Staccomo			
Streptocarpus floribundus Weigend & T.J.Edwards	Streflor	localized	Fruit capsules will twist open in a spiral when dry, releasing a large amount of very small, light seeds.	gravity
Synaptolepis kirkii Oliv.	Synakirk	far	Fruit bright red or orange-coloured.	birds
Syncolostemon latidens (N.E.Br.) Codd	Synclati			
Syncolostemon ramulosus Benth.	Syncramu			
Tecoma capensis (Thunb.) Lindl.	Tecocape	medium		
Tephrosia pondoensis (Codd) Schrire	Tephpond	localized	dehiscent pod	
Triglochin bulbosa L.	Trigbulb			
*Vanilla roscher*i Rchb.f.	Vanirosc	far	minute seeds	wind
Vitellariopsis dispar (N.E.Br.) Aubrév.	Vitedisp	localized		
Warburgia salutaris (G.Bertol.) Chiov.	Warbsalu	localized		

Scientific name with authority	**Species Code**	**Dispersal Distance**	**Seed characteristics**	**Dispersal Vector**
Watsonia canaliculata Goldblatt	Watscana	medium	The fruit is an oblong capsule, more or less woody, sometimes widening at the apex, splitting to release winged seeds	wind
Woodia verruculosa Schltr.	Woodverr			
Ziziphus mucronata Willd.	Zizimucr	far		birds and animals

Appendix 5: Grime’s (1977) Competitive (C), Stress-Tolerant (S) and Ruderal (R) survival strategies allocated to each species of plant. Only nine of the possible 18 plant traits were scored as only traits for which information for at least 60% of the sampled species was available were included. Species for which information was available on more than six of the nine remaining traits were retained for this analysis. A trait for a plant was scored as C, S, or R if the plant fell clearly into the category description. In some cases more than one category was assigned to a trait as the characteristics derived by Grime are sometimes the same for the different strategies. The proportion of C, S and R strategies for each species was derived by summing the number of like strategy scores allocated to each trait, and then dividing by the total number of strategy scores allocated to a species. The life history strategy allocated to each species was then based on the position of each species on a ternary C:S:R plot. See Appendix 1 for species codes.

Species Code	Shoot Morphology	Leaf Form	Litter	Relative Growth Rate	Life Form	Leaf Long-evity	Phenology		Seed Production	Total Strategy Score	C	S	R	Life History strategy derived from ternary graph
							Leaf Production	Flowering						
Acalentu	S	S	S	S	C; S		C	C	C; S	10	0.40	0.60	0.00	S
Albemagn	C; S	C	S	S	C; S	C	C	C	C; S	12	0.58	0.42	0.00	C
Albisulu	C	C	S	S	C; S	C	C	C	C; S	11	0.64	0.36	0.00	C
Aloegers	S	S	S	S	C; S	S	S	C	C; S	11	0.27	0.73	0.00	S
Aloemacu	S	S	S	S	C; S	S	S	S	C; S	11	0.18	0.82	0.00	S
Aloemode	S	S	S	S	C; S	S	S	C	C; S	11	0.18	0.82	0.00	S
Aloesaun	S	S	S	S	C; S	S	S	C	C; S	11	0.18	0.82	0.00	S
Anseafri	S	S	S	S	S	S	S	S	C; S	10	0.00	0.90	0.10	S
Argylong	S; R	R	S		C; S		S	C	C; S	10	0.30	0.50	0.20	S
Asclbicu														

Species Code	Shoot Morphology	Leaf Form	Litter	Relative Growth Rate	Life Form	Leaf Long-evity	Phenology		Seed Production	Total Strategy Score	C	S	R	Life History strategy derived from ternary graph
							Leaf Production	Flowering						
Asclconc														
Asclschl	R	S; R	S	C; R	C; S									
Asclwood	S; R	S	S	C; R	C; S									
Barlargi	S	S	S	C	C; S	S	S	C	C; S	11	0.36	0.64	0.00	S
Barlgree	S	S	S	C	C; S	S	S	C	C; S	11	0.36	0.64	0.00	S
Begodreg	S	C; R	S	C	C; S	C		C	C; S	11	0.55	0.36	0.09	C
Berkdrac	S	S	S	C	C; S	C		C	C; S	10	0.50	0.50	0.00	C-S
Bonalamp	S; R	C; R	S	C	C; S	C; R	C-R	C	C; S	15	0.47	0.27	0.27	C-S-R
Bowivolu	S	S	S	C	C; S	C	S	C	C; S	11	0.45	0.55	0.00	C-S
Bracnata	S; R	S	S	C	C; S	C; R	C	C	C; S	13	0.46	0.38	0.15	C-S
Calpwood	C	C	S		C; S	C	C	C	C; S	10	0.70	0.30	0.00	C
Ceroaren	S; R	S	S	S	C; S	S	S		C; S	11	0.18	0.73	0.09	S
Ceroruda			S						C; S					
Crinmoor	S	C	S	S	C; S	C	C	C	R	10	0.50	0.40	0.10	C-S
Crypoblo	C	C	S	C	C; S	C		C	C; S	10	0.70	0.30	0.00	C
Crypwyli	S	S	S	S	C; S	C		C	C; S	10	0.40	0.60	0.00	S
Curtdent	C	S	S	C	C; S	C	C	C	C; S	11	0.64	0.36	0.00	C

Species Code	Shoot Morphology	Leaf Form	Litter	Relative Growth Rate	Life Form	Leaf Long-evity	Phenology		Seed Production	Total Strategy Score	C	S	R	Life History strategy derived from ternary graph
							Leaf Production	Flowering						
Cyrtbrac	R	C; R	S	C; R	C; S	C	C	C	C; S	13	0.54	0.23	0.23	C
Cyrtobli	C; S	C; R	S	C; R	C; S	C	C	C	C; S	14	0.57	0.29	0.14	C
Delotrad	C; S	S	S		C; S	S	S	S	C; S	11	0.27	0.73	0.00	S
Dierlute	S	S	S	C; R	C; S	C	C	C	C; S	12	0.50	0.42	0.08	C-S
Dierpall	S	S	S	C; R	C; S	C	C	C	C; S	12	0.50	0.42	0.08	C-S
Diertyso	S	S	S	C; R	C; S	C	C	C	C; S	12	0.50	0.42	0.08	C-S
Diosglan	C	S	S	S	C; S			C	C; S	9	0.44	0.56	0.00	S
Disamont	S; R	R	S	C; R	C; S	C	C	C	C; S	13	0.46	0.31	0.23	C-S
Disasang	S; R	R	S	C; R	C; S	C	C	C	C; S	13	0.46	0.31	0.23	C-S
Disascul	S; R	R	S	C; R	C; S	C	C	C	C; S	13	0.46	0.31	0.23	C-S
Dracital	S	C	S	C; R	C; S			C	C; S	10	0.50	0.40	0.10	C-S
Enceaemu	S	S	S	S	C; S	S	S	S	C; S	11	0.18	0.82	0.00	S
Enceceri	S	S	S	S	C; S	S	S	S	C; S	11	0.18	0.82	0.00	S
Encemsin	S	S	S	S	C; S	S	S	S	C; S	11	0.18	0.82	0.00	S
Encesent	S	S	S	S	C; S	S	S	S	C; S	11	0.18	0.82	0.00	S
Eriosuba	S; R	S	S		C; S			C	C; S	9	0.33	0.56	0.11	S
Erioumta	C	C	S	S	C; S	S	S	C	C; S	11	0.45	0.55	0.00	S

Species Code	Shoot Morphology	Leaf Form	Litter	Relative Growth Rate	Life Form	Leaf Long-evity	Phenology		Seed Production	Total Strategy Score	C	S	R	Life History strategy derived from ternary graph
							Leaf Production	Flowering						
Feliwrig	C	C	S	C	C; S	C	C	C	C; S	11	0.73	0.27	0.00	C
Gerbaura	S	S	S	S	C; S	C	C	C	C; S	11	0.45	0.55	0.00	S
Gladcrue	S	C; R	S	C	C; S	C	C	C	C; S	12	0.58	0.33	0.08	C
Gnidkrau	C	S	S	S	C; S	C	C	C	C; S	11	0.55	0.45	0.00	C
Helicitr	S	S	S	S	C; S		S	C	C; S	10	0.30	0.70	0.00	S
Holomaju	S; R	S; R	S; R	C; R	C; S	C; R	C; R	C	R	16	0.31	0.25	0.44	C-S-R
Knipbrac	S	C	S	C; R	C; S	C	C	C	R	11	0.55	0.27	0.18	C
Knipevan	S	C; S	S	C	C; S	C	C	C	C; S	12	0.58	0.42	0.00	C
Kniplati	C	C	C	C; R	C; S	C	C	C	C; S	12	0.75	0.17	0.08	C
Knipleuc	S	C; S	C	C; R	C; S	C	C	C	C; S	13	0.62	0.31	0.08	C
Knippauc	S	C; S	C	C; R	C; S	C	C	C	C; S	13	0.62	0.31	0.08	C
Leucgerr	S	S	S	S	C; S	S	S	C	C; S	11	0.27	0.73	0.00	S
Maninich	S	C; S	S	S	C; S	S	S	S	C; S	12	0.25	0.75	0.00	S
Manuflor	S	S	S		C; S			C	R	7	0.29	0.57	0.14	S
Maytabbo	C	C	S	C	C; S	C		S	C; S	10	0.60	0.40	0.00	C
Melhdidy	S; R	S	S	C; R	C; S	S				9	0.22	0.56	0.22	S
Melhpoly	S; R	S	S		C; S				C; S					

Species Code	Shoot Morphology	Leaf Form	Litter	Relative Growth Rate	Life Form	Leaf Long-evity	Phenology		Seed Production	Total Strategy Score	C	S	R	Life History strategy derived from ternary graph
							Leaf Production	Flowering						
Merwplum	S	C; S	S	S	C; S	C	C	C	C; S	12	0.50	0.50	0.00	C-S
Mystalic	S	S	S	S	C; S	S	S	C	C; S	11	0.27	0.73	0.00	S
Oleacape	C	C		C	C; S	C	C	C	C; S	10	0.80	0.20	0.00	C
Olinradi	C	C	S	S	C; S	C	C	S	C; S	11	0.55	0.45	0.00	C
Oxalobli	C	R	S; R	C	C; S	C	C	C; R	C; S	13	0.54	0.23	0.23	C
Pelatong	S	S	S	S	C; S	C	S	S	C; S	11	0.27	0.73	0.00	S
Peucwilm	C	S; R	S		C; S									
Phymvill	S	S	S		C; S			C	C; S					
Protcomp	C; S	C	S	S	C; S	C	C	S	C; S	12	0.50	0.50	0.00	C-S
Protnubi	S	S	S	S	C; S	C	C	S	C; S	11	0.36	0.64	0.00	S
Rasptrig	S	S	S	S	C; S	S	S	C	C; S	11	0.27	0.73	0.00	S
Restzulu	C	S	S		C; S	C		C	R	8	0.50	0.38	0.13	C-S
Seardent	C	S	C	C	C; S	C	C	C	C; S	11	0.73	0.27	0.00	C
Salagerr	C; S	C	C	S	C; S	S	S	C	C; S	12	0.50	0.50	0.00	C-S
Sandaura	S	C	S	C; R	C; S	C	C	C	C; S	12	0.58	0.33	0.08	C
Scadpuni	S	C	S; R	C; R	C; S	C		S	R	11	0.36	0.36	0.27	C-S-R
Schibulb	S	S	S	C; R	C; S	C	C	C	C; S	12	0.50	0.42	0.08	C-S

Species Code	Shoot Morphology	Leaf Form	Litter	Relative Growth Rate	Life Form	Leaf Long-evity	Phenology		Seed Production	Total Strategy Score	C	S	R	Life History strategy derived from ternary graph
							Leaf Production	Flowering						
Schigerr	C	C	S	C; R	C; S	C	C	C	C; S	12	0.67	0.25	0.08	C
Scolmund	C	S	S	S	C; S	S	S	S	C; S	11	0.27	0.73	0.00	S
Searruda	S	C	C	C; S	C; S	C	C	C	C; S	12	0.67	0.33	0.00	C
Selalong														
Seneexub					C; S									
Staccomo	S			C; R	R				C; S					
Streflor	S	C; S	C	S	C; S	S	S	C	C; S	12	0.42	0.58	0.00	S
Synakirk	C; S	S	S	S	C; S	C	S	C	C; S	12	0.42	0.58	0.00	S
Synclati														
Syncramu	C; S	S	S	S	C; S	S	S	C	C; S	12	0.33	0.67	0.00	S
Tecocape	C	C	C	C	C; S	C	S	S	C; S	11	0.64	0.36	0.00	C
Tephpond	S	C; S	C; S	C; S	C; S		S	C	C; S	13	0.46	0.54	0.00	S
Trigbulb	S	C	S	S	C; S	C	C	C	C; S	11	0.55	0.45	0.00	C
Vanirosc	S	S	S	C	C; S			C	C; S	9	0.44	0.56	0.00	S
Vitedisp	C	C; S	S	S	C; S	C	C	C	C; S	12	0.58	0.42	0.00	C
Warbsalu	S	S	S	S	C; S	S	S	C	C; S	11	0.27	0.73	0.00	S
Watscana	C; S	C; S	S	S	C; S	C	C	C	C; S	13	0.54	0.46	0.00	C

Species Code	Shoot Morphology	Leaf Form	Litter	Relative Growth Rate	Life Form	Leaf Long-evity	Phenology		Seed Production	Total Strategy Score	C	S	R	Life History strategy derived from ternary graph
							Leaf Production	Flowering						
Woodverr	S	R	S		C; S	C	C	C	C; S	10	0.50	0.40	0.10	C-S
Zizimucr	C	R	R	C; S	C; S	C	C	C	C; S	12	0.58	0.25	0.17	C

Appendix 6: The percentage of each species' occurrences on each land surface and the land surface that the species was assigned to using K means cluster analysis. See Appendix 1 for species codes.

Species Code	Mountainous areas above the African Surface	Old African	Escarpment	Neogene	Post African & dissected	Number of records	Affinity to surface derived by K means cluster
Acalentu	0	9	0	0	91	11	Post African and other dissected areas
Albemagn	0	86	0	0	14		African Surface
Albisulu	0	0	0	0	100	22	Post African and other dissected areas
Aloegers	0	0	100	0	0	4	Escarpment
Aloemacu	0	29	14	0	57	14	no affinity for a particular land surface
Aloemode	0	0	0	0	100	1	Post African and other dissected areas
Aloesaun	0	0	0	0	100	35	Post African and other dissected areas
Anseafri	0	0	0	0	100	186	Post African and other dissected areas
Argylong	0	0	0	0	100	12	Post African and other dissected areas
Asclbicu	0	0	0	0	100	8	Post African and other dissected areas
Asclconc	0	0	0	0	100	1	Post African and other dissected areas
Asclschl	0	16	0	0	84	6	Post African and other dissected areas
Asclwood	0	0	0	0	100	2	Post African and other dissected areas
Barlargi	0	0	0	0	100	3	Post African and other dissected areas

Species Code	Mountainous areas above the African Surface	Old African	Escarpment	Neogene	Post African & dissected	Number of records	Affinity to surface derived by K means cluster
Barlgree	0	0	0	0	100	10	Post African and other dissected areas
Begodreg	0	50	0	0	50	8	no affinity for a particular land surface
Berkdrac	0	0	100	0	0	12	Escarpment
Bonalamp	0	0	0	100	0	44	Neogene marine and coastal aeolian sediments
Bowivolu	15	4	9	0	72	47	Post African and other dissected areas
Bracnata	0	100	0	0	0	39	African Surface
Calpwood	0	0	0	0	100	14	Post African and other dissected areas
Ceroaren	0	0	0	0	100	1	Post African and other dissected areas
Ceroruda	0	33	0	0	67	3	no affinity for a particular land surface
Crinmoor	0	50	0	0	50	6	no affinity for a particular land surface
Crypoblo	0	29	0	0	71	14	no affinity for a particular land surface
Crypwyli	0	54	0	0	46	26	no affinity for a particular land surface
Curtdent	5	5	40	0	50	40	no affinity for a particular land surface
Cyrtbrac	0	0	0	0	100	5	Post African and other dissected areas
Cyrtobli	0	0	0	0	100	379	Post African and other dissected areas

Species Code	Mountainous areas above the African Surface	Old African	Escarpment	Neogene	Post African & dissected	Number of records	Affinity to surface derived by K means cluster
Delotrad	0	10	0	0	90	8	Post African and other dissected areas
Dierlute	0	7	0	0	93	17	Post African and other dissected areas
Dierpall	0	46	0	0	54	13	no affinity for a particular land surface
Diertyso	0	0	25	0	75	12	Post African and other dissected areas
Diosglan	0	0	0	6	94	16	Post African and other dissected areas
Disamont	0	0	0	0	100	2	Post African and other dissected areas
Disasang	0	0	100	0	0	6	Escarpment
Disascul	1	20	20	0	59	20	no affinity for a particular land surface
Dracital	0	0	0	0	100	6	Post African and other dissected areas
Enceaemu	0	0	0	0	100	33	Post African and other dissected areas
Enceceri	0	0	0	0	100	9	Post African and other dissected areas
Encemsin	0	0	0	0	100	23	Post African and other dissected areas
Encesent	0	50	0	0	50	92	no affinity for a particular land surface
Eriosuba	0	46	0	0	54	35	no affinity for a particular land surface
Erioumta	0	67	0	0	33	15	African Surface

Species Code	**Mountainous areas above the African Surface**	**Old African**	**Escarpment**	**Neogene**	**Post African & dissected**	**Number of records**	**Affinity to surface derived by K means cluster**
Feliwrig	0	0	67	0	33	6	Escarpment
Gerbaura	0	48	0	0	52	48	no affinity for a particular land surface
Gladcrue	0	82	0	0	18	17	African Surface
Gnidkrau	0	50	0	0	50	4	no affinity for a paicular land surface
Helicitr	0	0	0	0	100	2	Post African and other dissected areas
Holomaju	0	0	0	0	100	2	Post African and other dissected areas
Knipbrac	0	0	0	0	100	12	Post African and other dissected areas
Knipevan	0	0	100	0	0	9	Escarpment
Kniplati	0	6	0	0	94	33	Post African and other dissected areas
Knipleuc	0	0	0	100	0	233	Neogene marine and coastal aeolian sediments
Knippauc	0	0	0	100	0	4	Neogene marine and coastal aeolian sediments
Leucgerr	0	72	0	0	28	11	African Surface
Maninich	0	90	0	0	10	42	African Surface
Manuflor	33	0	50	0	17	12	Escarpment
Maytabbo	0	87	0	0	13	30	African Surface

Species Code	**Mountainous areas above the African Surface**	**Old African**	**Escarpment**	**Neogene**	**Post African & dissected**	**Number of records**	**Affinity to surface derived by K means cluster**
Melhdidy	0	0	0	0	100	11	Post African and other dissected areas
Melhpoly	0	0	0	0	100	6	Post African and other dissected areas
Merwplum	0	22	38	2	38	58	no affinity for a particular land surface
Mystalic	0	0	0	0	100	3	Post African and other dissected areas
Oleacape	12.5	37.5	25	0	25	8	no affinity for a particular land surface
Olinradi	0	25	0	0	75	4	no affinity for a particular land surface
Oxalobli	7	29	21	0	43	14	no affinity for a particular land surface
Pelatong	0	0	0	33	67	6	Post African and other dissected areas
Peucwilm	0	50	0	0	50	2	no affinity for a particular land surface
Phymvill	0	67	0	0	33	3	African Surface
Protcomp	0	0	0	0	100	612	Post African and other dissected areas
Protnubi	0	0	100	0	0	2	Escarpment
Rasptrig	0	100	0	0	0	7	African Surface
Restzulu	0	0	0	100	0	19	Neogene marine and coastal aeolian sediments
Salagerr	0	50	0	0	50	8	no affinity for a particular land surface

Species Code	**Mountainous areas above the African Surface**	**Old African**	**Escarpment**	**Neogene**	**Post African & dissected**	**Number of records**	**Affinity to surface derived by K means cluster**
Sandaura	6	9	12	3	70	33	Post African and other dissected areas
Scadpuni	8	15	46	0	31	13	no affinity for a particular land surface
Schibulb	0	0	43	0	57	7	no affinity for a particular land surface
Schigerr	0	0	0	0	100	12	Post African and other dissected areas
Scolmund	6	12	39	0	43	49	no affinity for a particular land surface
Seardent	2	17	21	0	60	129	no affinity for a particular land surface
Searruda	0	58	0	0	42	38	no affinity for a particular land surface
Selalong	20	80	0	0	0	5	African Surface
Seneexub	0	25	0	0	75	16	no affinity for a particular land surface
Staccomo	0	50	0	0	50	6	no affinity for a particular land surface
Streflor	0	0	0	0	100	1	Post African and other dissected areas
Synakirk	0	0	0	100	0	12	Neogene marine and coastal aeolian sediments
Synclati	0	57	0	0	43	14	no affinity for a particular land surface
Syncramu	0	100	0	0	0	22	African Surface
Tecocape	0	20	7	0	73	45	no affinity for a particular land surface

Species Code	Mountainous areas above the African Surface	Old African	Escarpment	Neogene	Post African & dissected	Number of records	Affinity to surface derived by K means cluster
Tephpond	0	22	0	0	78	9	Post African and other dissected areas
Trigbulb	0	33	0	0	67	24	no affinity for a particular land surface
Vanirosc	0	0	0	100	0	61	Neogene marine and coastal aeolian sediments
Vitedisp	0	0	0	0	100	14	Post African and other dissected areas
Warbsalu	0	5	0	45	50	22	no affinity for a particular land surface
Watscana	19	38	0	0	43	16	no affinity for a particular land surface
Woodverr	0	0	0	0	100	10	Post African and other dissected areas
Zizimucr	0	25	0	8	67	24	no affinity for a particular land surface

Appendix 7: List of species categorized according to their extent of utilization. Categorization is based on the literature and the SANBI threatened plant database. See Appendix 1 for species codes.

Species Code	Utilization	Species Code	Utilization	Species Code	Utilization
Acalentu	none	Encesent	intense	Seneexub	none
Albemagn	some	Eriosuba	none	Staccomo	none
Albisulu	some	Erioumta	none	Streflor	none
Aloegers	none	Feliwrig	none	Synakirk	intense
Aloemacu	none	Gerbaura	some	Synclati	none
Aloemode	none	Gladcrue	none	Syncramu	none
Aloesaun	none	Gnidkrau	some	Tecocape	some
Anseafri	intense	Helicitr	none	Tephpond	none
Argylong	none	Holomaju	none	Trigbulb	none
Asclbicu	none	Knipbrac	none	Vanirosc	some
Asclconc	none	Knipevan	none	Vitedisp	some
Asclschl	none	Kniplati	none	Warbsalu	intense
Asclwood	none	Knipleuc	none	Watscana	none
Barlargi	none	Knippauc	none	Woodverr	none
Barlgree	none	Leucgerr	none	Zizimucr	some
Begodreg	intense	Maninich	none		
Berkdrac	none	Manuflor	none		
Bonalamp	some	Maytabbo	none		
Bowivolu	intense	Melhdidy	none		
Bracnata	none	Melhpoly	none		
Calpwood	none	Merwplum	intense		
Ceroaren	none	Mystalic	none		
Ceroruda	none	Oleacape	some		
Crinmoor	intense	Olinradi	none		
Crypoblo	none	Oxalobli	none		
Crypwyli	none	Pelatong	none		
Curtdent	intense	Peucwilm	none		
Cyrtbrac	none	Phymvill	none		

Species Code	Utilization	Species Code	Utilization	Species Code	Utilization
Cyrtobli	**some**	**Protcomp**	**none**		
Delotrad	none	Protnubi	none		
Dierlute	some	Rasptrig	none		
Dierpall	some	Restzulu	none		
Diertyso	some	Salagerr	none		
Diosglan	none	Sandaura	intense		
Disamont	none	Scadpuni	some		
Disasang	none	Schibulb	none		
Disascul	none	Schigerr	none		
Dracital	none	Scolmund	some		
Enceaemu	intense	Seardent	none		
Enceceri	intense	Searruda	none		
Encemsin	intense	Selalong	none		

Appendix 8: The proportion of habitat of each sampled species transformed - derived from the untransformed area and the area of extent of each species. See Appendix 1 for species codes.

Species Code	Area Transformed (ha)	Total habitat EOO(ha)	Proportion transformed
Acalentu	51986.4	221392.6	0.235
Albemagn	214959.2	654165.52	0.329
Albisulu	33.56	10784.04	0.003
Aloegers	1896.44	10112.36	0.188
Aloemacu	2466898	7221327.24	0.342
Aloemode	1 known site	14.1004931	
Aloesaun	21.28	596.4	0.036
Anseafri	388792.36	1593124.92	0.244
Argylong	30877.04	69143.8	0.447
Asclbicu	28688.12	55959.44	0.513
Asclconc	1 known site	6.695798	
Asclschl	43937.32	137081.24	0.321
Asclwood	38687.8	57195.84	0.676
Barlargi	36.48	1286.52	0.028
Barlgree	9.04	1609.44	0.006
Begodreg	325369.08	802571.32	0.405
Berkdrac	370.16	37408.44	0.010
Bonalamp	28507.8	144485.68	0.197
Bowivolu	1217276.2	3054273.12	0.399
Bracnata	336.88	668.68	0.504
Calpwood	8.96	102	0.088
Ceroaren	1537.64	16521.44	0.093
Ceroruda	11311.8	35196.68	0.321
Crinmoor	1300466.36	3148650.96	0.413
Crypoblo	662283.44	2118938.88	0.313
Crypwyli	171158.08	298686.32	0.573
Curtdent	1686286.52	5220769.76	0.323
Cyrtbrac	0.96	4.48	0.214
Cyrtobli	4193.24	7979.68	0.525
Delotrad	1622408.2	4446797.56	0.365

Species Code	Area Transformed (ha)	Total habitat EOO(ha)	Proportion transformed
Dierlute	47573.8	77252.8	0.616
Dierpall	49115.24	103874.68	0.473
Diertyso	108359.92	456408.48	0.237
Diosglan	12498.04	100011.2	0.125
Disamont	539.4	3762.08	0.143
Disasang	96.12	29707.36	0.003
Disascul	69789.48	364956.32	0.191
Dracital	35255.32	108711.36	0.324
Enceaemu	0.68	246.24	0.003
Enceceri	198.84	198.84	1.000
Encemsin	2496.44	7641.72	0.327
Encesent	17517.76	92989.44	0.188
Eriosuba	185580.52	418476.4	0.443
Erioumta	15388.44	27473.16	0.560
Feliwrig	106.64	20453.44	0.005
Gerbaura	284902.04	580372.68	0.491
Gladcrue	26724.92	70206.16	0.381
Gnidkrau	2588991	7590076.56	0.341
Helicitr	1 known site	0	
Holomaju	0	39.76	1.000
Knipbrac	189056.52	676109.92	0.280
Knipevan	8.16	8530.12	0.001
Kniplati	112501.68	228664.2	0.492
Knipleuc	578.96	683.36	0.847
Knippauc	248.72	312.28	0.796
Leucgerr	57210.68	119751.8	0.478
Maninich	4817	11193.96	0.430
Manuflor	259325.68	955596.36	0.271
Maytabbo	10702	23039.64	0.465
Melhdidy	369601.68	1652823.76	0.224
Melhpoly	8820.04	57859.92	0.152
Merwplum	2118772.76	6434945.72	0.329

Species Code	Area Transformed (ha)	Total habitat EOO(ha)	Proportion transformed
Mystalic	150957.96	485739.44	0.311
Oleacape	2307365.64	7465367.72	0.309
Olinradi	1431233.44	3685602.24	0.388
Oxalobli	1710408.36	5799050.48	0.295
Pelatong	2920.84	10498.2	0.278
Peucwilm	245849	519846.76	0.473
Phymvill	53385.28	152105.8	0.351
Protcomp	9.08	5797.72	0.002
Protnubi	1 known site	0.0005	
Rasptrig	1277.68	3216.56	0.397
Restzulu	251040	907479.6	0.277
Salagerr	1125490.8	2573906.64	0.437
Sandaura	1971875.68	6157256.96	0.320
Scadpuni	2229380.12	7259852.32	0.307
Schibulb	222170.68	573908.92	0.387
Schigerr	1 known site	109.68	
Scolmund	2665070.56	8315316.84	0.321
Seardent	2792871.68	8436468.96	0.331
Searruda	46242.92	141938.24	0.326
Selalong	3419.6	7713.4	0.443
Seneexub	11989.44	26040.48	0.460
Staccomo	74987.88	199959.28	0.375
Streflor	1 known site	0.0060956	
Synakirk	131954.6	622248.88	0.212
Synclati	17506.32	59563.28	0.294
Syncramu	0.12	238.84	0.001
Tecocape	2372019.16	7131215.08	0.333
Tephpond	148.44	855.68	0.173
Trigbulb	330808.28	650197.84	0.509
Vanirosc	1.56	947.8	0.002
Vitedisp	213432.2	831444.68	0.257
Warbsalu	259647.8	1121103.04	0.232

Species Code	Area Transformed (ha)	Total habitat EOO(ha)	Proportion transformed
Watscana	191766	369540.16	0.519
Woodverr	402893.04	824891.64	0.488
Zizimucr	2920196.32	9016144.92	0.324

Appendix 9: Parameters used for Regression Tree Analysis in CART (CART, 2012 Salford Systems Inc, USA).

In the regression tree analysis CART (Salford Systems 2012) was used to explore the relation between $\log_{10}$ Rarity Index as the response variable and niche width, habitat transformation, seed dispersal distance, life history strategy, erosional land surface and habitat specificity as the explanatory variables. The default settings were used for the model with the exception of the testing method. This was set on exploratory mode instead of the default V fold Cross Validation. The following model was used

- No weights were applied to any of the explanatory variables.
- No independent testing was conducted.
- The minimum cost tree is selected as the best tree.
- Five surrogates were used to construct the tree and all surrogates count equally in determining variable importance
- The least squares splitting criterion was used.
- No penalties were applied to the variables. Penalties can be applied to variables to make them less likely to be selected as a splitter
- The minimum parent node size for splitting was set to 10 and minimum number of observations that could be separated into a child node was set at 1
- The threshold level for intelligent categorical split search was set at the default 15. This means that for categorical predictors with 15 or fewer levels, CART will search for all possible splits and is guaranteed to find the best possible partition.
- The default method of handling missing values was used, which entailed developing surrogate splits which redistribute the missing data between the left and right part of the tree based on an alternative split that most resembles the local split.

Appendix 10: Diagnostic tests for the linear regression model of the response variable Rarity Index and the explanatory variables, Niche Width, Habitat Transformation, seed Dispersal Distance, Life history Strategy, Land Surface and Habitat Specificity.

To assess the assumptions of linear regression, residual plots of residuals versus fitted values against each of the predictors were produced using the R 2.14.0 package Car (R Development Core Team, 2008). If the linear model adequately fits the data and the assumptions of homogeneity are met then the Pearsons residuals will be independent of the fitted values and the predictors and the residual plots will be null plots with y=0 (http://www.sagepub.com/upm-data/38503_Chapter6.pdf downloaded on 2 August 2012). Normality was tested using Normal Probability plots (QQ Plots) which compare the quantiles of the data versus the quantiles of a distribution. A Q-Q plot that is a straight line indicates normality (Zuur et al., 2009; Zuur et al., 2010).

In the plot of residual versus the fitted values for the linear model of the Rarity Index and the response variables, the residuals do not appear to be randomly scattered indicating that a linear model is not the best model for this data. (Fig. 35a) In addition to this the plot of residuals versus niche width shows decreasing residuals with an increase in niche width which indicates heterogeneity or non-constant variance (36a). Similarly in the plot of residuals versus habitat transformation the spread of residuals is not the same across the habitat transformation levels (Fig. 36b). The residuals for Habitat Specificity (Fig. 36d) do not appear to be problematic i.e. they have the same centre and similar spread, but for Dispersal Distance (Fig. 36c), Land Surface (Geolsurf in Fig. 36e) and Life History (Fig. 36f), the residuals are not evenly spread across the different levels of the variables. The QQ plot (Fig. 35) shows that the distribution of residuals is close to normal distribution in the median but the residuals diverge from the normal distribution at the extremes. To improve this Rarity Index and Niche Width were Log_{10} transformed and then the assumptions for the linear regression model of the Log_{10} Rarity Index and the response variables were tested again.

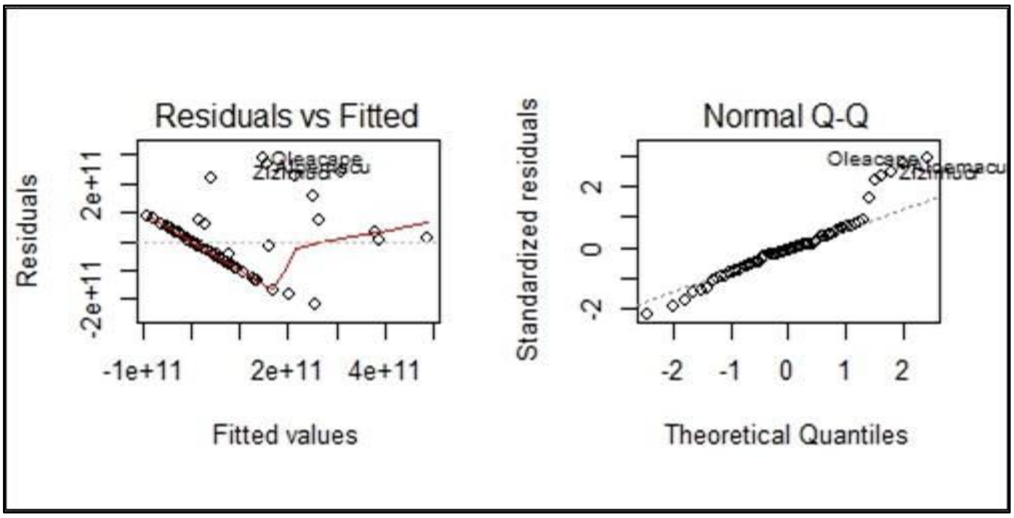

Figure 35: Residual versus fitted (left hand side) and theoretical quantile model (right hand side) validation graphs for the linear regression model of Rarity Index and the response variables Niche Width, Habitat Transformation, seed Dispersal Distance, Life History Strategy, Land Surface and Habitat Specificity. Outliers are shown with species code names.

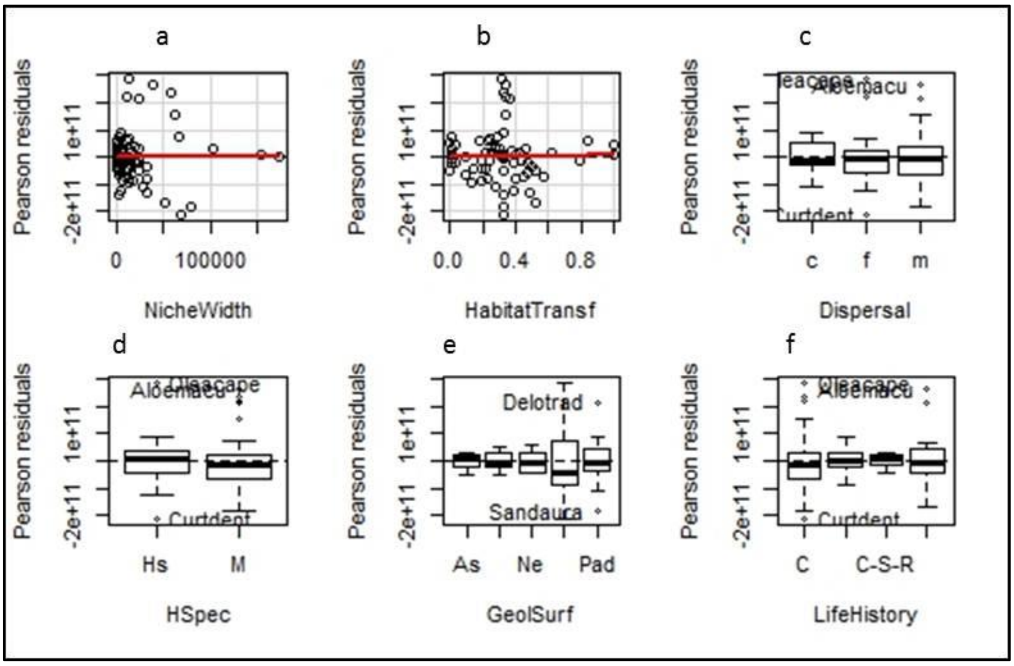

Figure 36: Model validation graphs for the linear regression model of Rarity index and the response variables Niche Width, Habitat Transformation, seed Dispersal Distance, Life history Strategy, Geological Land Surface and Habitat Specificity. Pearsons residuals versus a) Niche width; b) Habitat Transformation, c) Dispersal Distance d) Habitat Specificity e) Land Surface and f) Life History Strategy. Outliers are shown with species code names.

The Log_{10} transformation of Rarity Index and Niche Width improved the model, as shown by a fairly even distribution of the residuals across all fitted values. The variance is quite constant across X but indicates a slight under estimation of the model at low values of X and a slight over estimation by the model in the central values of X. (Fig. 37). The QQ plot (Fig. 37) shows that the distribution of residuals is close to normal distribution. The Residual plot of Log_{10} Niche Width (Fig. 38a) shows a slightly curved general trend and the plot of transformation (Fig. 38b) shows quite a strong curve which indicates that a linear model is not perfect for this data. The plots for Dispersal Distance(Fig. 38c, Geological Surface (Fig. 38e) and Life History Strategy(Fig. 38f) still show some variation in the spread of residuals indicating that an alternative model might be preferable for this data.

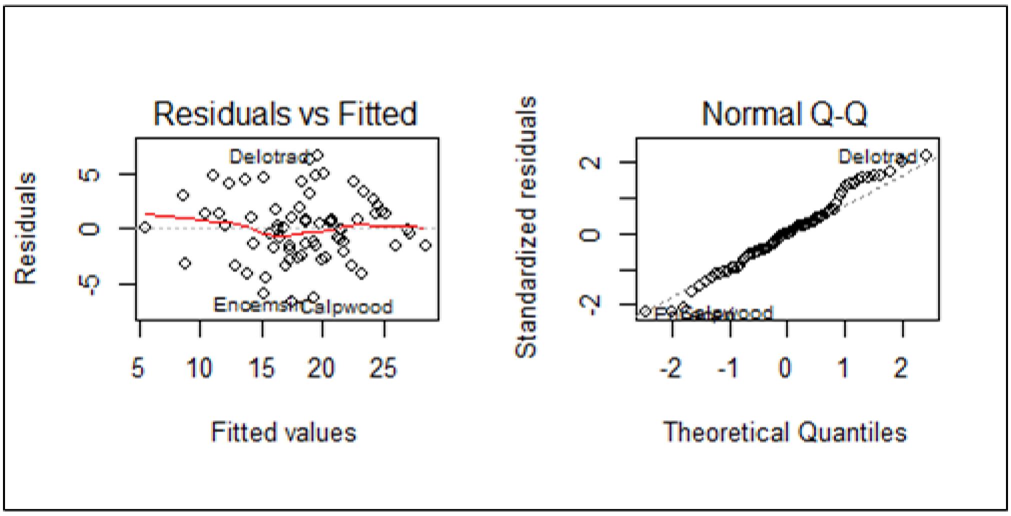

Figure 37: Residual versus fitted (left hand side) and theoretical quantile (right hand side) model validation graphs for the linear regression model of log_{10} Rarity Index and the response variables log_{10} Niche Width, Habitat Transformation, seed Dispersal Distance, Life History Strategy, Land Surface and Habitat Specificity. Outliers are shown with species code names.

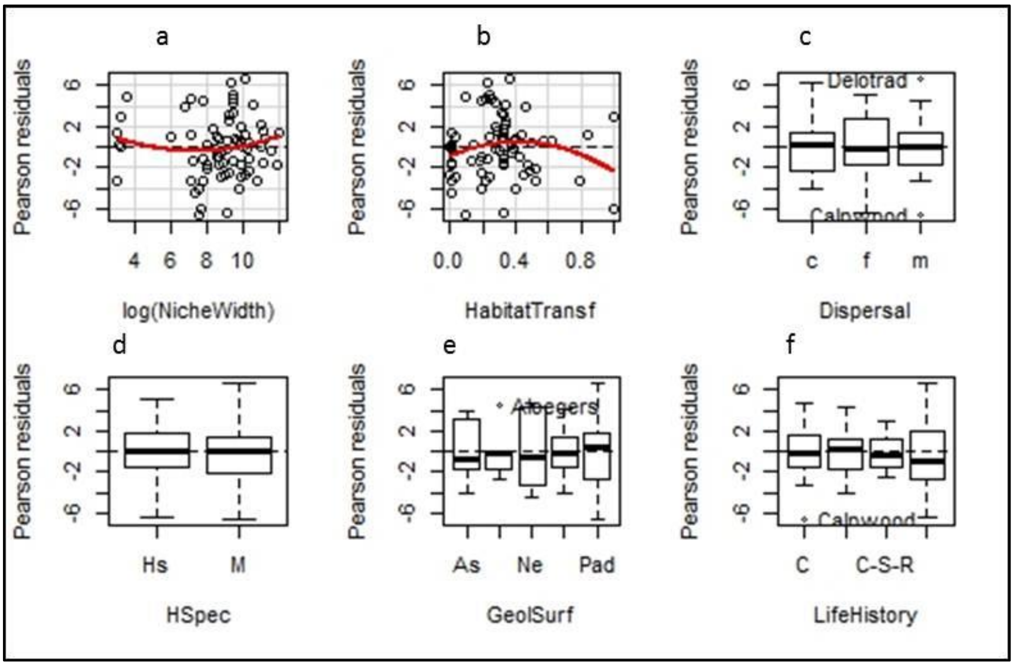

Figure 38: Model validation graphs for the linear regression model of $\log_{10}$ Rarity Index and the response variables $\log_{10}$ Niche Width, Habitat Transformation, seed Dispersal Distance, Life History Strategy, Land Surface and Habitat Specificity. Pearsons residuals versus a) Niche width; b) Habitat Transformation, c) Dispersal Distance d) Habitat Specificity e) Land Surface and f) Life History Strategy. Outliers are shown with species code names.

Appendix 11: Generalized linear model selection using a backward selection approach in which non-significant explanatory variables were removed sequentially starting with the least significant variable.

Step 1: Generalized linear model of log$_{10}$ Rarity Index and explanatory variables log$_{10}$ Niche Width, Habitat Transformation, seed Dispersal Distance, Life History Strategy, Land Surface and Habitat Specificity

glm1 <-
glm(log$_{10}$(Rarity)~log$_{10}$(NicheWidth)+HabitatTransf+Dispersal+HSpec+GeolSurf+LifeHistory,data=rdata)

```
Deviance Residuals:
     Min        1Q    Median        3Q       Max
-2.88375  -0.76117  -0.01094   0.66980   2.88685

Coefficients:
                  Estimate Std. Error t value Pr(>|t|)
(Intercept)        1.29025    1.10406   1.169   0.2474
log10(NicheWidth)  1.58348    0.21599   7.331 8.92e-10 ***
HabitatTransf     -1.16789    0.88101  -1.326   0.1902
Dispersalf         1.03948    0.45558   2.282   0.0263 *
Dispersalm        -0.06618    0.46513  -0.142   0.8874
HSpecM             0.56165    0.37579   1.495   0.1405
GeolSurfEsc       -0.40909    0.91534  -0.447   0.6566
GeolSurfNe        -0.14709    0.84005  -0.175   0.8616
GeolSurfNo         1.69651    0.69886   2.428   0.0184 *
GeolSurfPad        0.77120    0.65741   1.173   0.2456
LifeHistoryC-S    -0.40596    0.49767  -0.816   0.4181
LifeHistoryC-S-R  -0.35003    0.92841  -0.377   0.7076
LifeHistoryS      -0.55722    0.40868  -1.363   0.1781
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 1.999214)

    Null deviance: 391.44  on 69  degrees of freedom
Residual deviance: 113.96  on 57  degrees of freedom
  (27 observations deleted due to missingness)
AIC: 260.76
```

The analysis shows log$_{10}$ Niche Width as highly significant ($p < 0.001$) and Far Dispersal Distance and no affinity to a land surface to be significant ($p < 0.05$)

Step 2: Remove the least significant variable, Life History from the model.

glm2 <- glm(log$_{10}$(Rarity)~log$_{10}$(NicheWidth)+HabitatTransf+Dispersal+HSpec+GeolSurf,data=rdata)

```
Deviance Residuals:
    Min       1Q   Median       3Q      Max
-3.7344  -1.0337  -0.0509   0.7580   2.8707

Coefficients:
                  Estimate Std. Error t value Pr(>|t|)
(Intercept)        1.01974    1.02173   0.998  0.32164
log10(NicheWidth)  1.63604    0.21375   7.654 7.32e-11 ***
HabitatTransf     -1.21383    0.84627  -1.434  0.15587
Dispersalf         0.60268    0.40872   1.475  0.14475
Dispersalm        -0.10493    0.44308  -0.237  0.81348
HSpecM             0.21582    0.35481   0.608  0.54495
GeolSurfEsc       -0.48541    0.86440  -0.562  0.57619
GeolSurfNe         0.04671    0.79139   0.059  0.95310
GeolSurfNo         1.73802    0.61266   2.837  0.00593 **
GeolSurfPad        0.67102    0.58327   1.150  0.25382
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 2.104749)

    Null deviance: 422.01  on 80  degrees of freedom
Residual deviance: 149.44  on 71  degrees of freedom
  (16 observations deleted due to missingness)
AIC: 301.47
```

The analysis shows log$_{10}$ Niche Width as highly significant ($p < 0.001$)and Dispersal Distance (Far) and no affinity to a Land Surface to be significant ($p < 0.05$)

Step 3: Remove the least significant variable, habitat specificity from the model.

glm3 <- glm(log$_{10}$(Rarity)~log$_{10}$(NicheWidth)+HabitatTransf+Dispersal+GeolSurf,data=rdata)

```
Deviance Residuals:
    Min       1Q   Median       3Q      Max
-3.8145  -1.0351   0.0145   0.8616   2.9061

Coefficients:
                  Estimate Std. Error t value Pr(>|t|)
(Intercept)        0.96947    1.01391   0.956  0.34219
log10(NicheWidth)  1.66530    0.20735   8.031 1.34e-11 ***
HabitatTransf     -1.15111    0.83628  -1.376  0.17295
Dispersalf         0.57877    0.40504   1.429  0.15735
Dispersalm        -0.07210    0.43785  -0.165  0.86967
GeolSurfEsc       -0.52143    0.85859  -0.607  0.54555
GeolSurfNe         0.05513    0.78780   0.070  0.94440
GeolSurfNo         1.76473    0.60840   2.901  0.00494 **
GeolSurfPad        0.71750    0.57571   1.246  0.21670
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 2.086332)

    Null deviance: 422.01  on 80  degrees of freedom
Residual deviance: 150.22  on 72  degrees of freedom
  (16 observations deleted due to missingness)
AIC: 299.9
```

The results of this analysis show Log_{10} Niche Width is highly significant ($p < 0.001$) and no affinity to a land surface is significant ($p < 0.01$).

Step 4: Remove the least significant variable Dispersal Distance, from the model.

glm4 <- glm($\log_{10}$(Rarity)~$\log_{10}$(NicheWidth)+HabitatTransf+GeolSurf,data=rdata)

```
Deviance Residuals: 
   Min      1Q  Median      3Q     Max  
-3.433  -1.009  -0.063   1.095   2.698  

Coefficients:
                  Estimate Std. Error t value Pr(>|t|)    
(Intercept)         1.0882     0.8697   1.251  0.21428    
log10(NicheWidth)   1.6659     0.1954   8.525 4.94e-13 ***
HabitatTransf      -0.8132     0.7895  -1.030  0.30594    
GeolSurfEsc        -0.3549     0.7391  -0.480  0.63229    
GeolSurfNe          0.1889     0.7270   0.260  0.79562    
GeolSurfNo          1.7320     0.5218   3.319  0.00133 ** 
GeolSurfPad         0.7009     0.4987   1.406  0.16350    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1 

(Dispersion parameter for gaussian family taken to be 2.051721)

    Null deviance: 466.64  on 91  degrees of freedom
Residual deviance: 174.40  on 85  degrees of freedom
  (5 observations deleted due to missingness)
AIC: 335.92
```

The results of this analysis shows Log$_{10}$ Niche Width is highly significant ($p < 0.001$ and no affinity to a land surface is significant ($p < 0.01$).

Step 5: Remove the least significant variable, Habitat Transformation from the model.

glm5 <- glm(log$_{10}$(Rarity)~log$_{10}$(NicheWidth)+GeolSurf,data=rdata)

```
Deviance Residuals:
    Min       1Q   Median       3Q      Max
-3.5225  -1.0261  -0.0728   0.9253   3.5030

Coefficients:
                  Estimate Std. Error t value Pr(>|t|)
(Intercept)        1.48510    0.77427   1.918 0.058237 .
log10(NicheWidth)  1.46457    0.17808   8.224 1.31e-12 ***
GeolSurfEsc       -0.07571    0.71100  -0.106 0.915429
GeolSurfNe         0.20090    0.74624   0.269 0.788371
GeolSurfNo         1.90321    0.53065   3.587 0.000542 ***
GeolSurfPad        0.91104    0.50077   1.819 0.072160 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

(Dispersion parameter for gaussian family taken to be 2.161814)

    Null deviance: 491.40  on 96  degrees of freedom
Residual deviance: 196.73  on 91  degrees of freedom
AIC: 357.86
```

The result of this model shows $\log_{10}$ Niche Width and no affinity to a land surface to be highly significant ($p < 0.001$) and Post African and other dissected surfaces and the intercept to be significant ($p < 0.1$).

Appendix 12: Generalized additive model selection using a backward selection approach in which non-significant explanatory variables were removed sequentially starting with the least significant variable.

Step 1: Generalized additive model of log$_{10}$ Rarity Index and explanatory variables log$_{10}$ Niche Width, Habitat Transformation, seed Dispersal Distance, Life History Strategy, Land Surface and Habitat Specificity

gam1 <- gam(log10(Rarity)~s(log10(NicheWidth))+s(HabitatTransf)+Dispersal+HSpec+GeolSurf+LifeHistory,data=rdata)

```
                 Estimate Std. Error t value Pr(>|t|)    
(Intercept)        6.6345     0.6567  10.102  3.8e-14 ***
Dispersalf         0.9175     0.4339   2.115   0.0390 *  
Dispersalm        -0.1353     0.4393  -0.308   0.7593    
HSpecM             0.4272     0.3597   1.188   0.2401    
GeolSurfEsc        0.6060     0.9752   0.621   0.5369    
GeolSurfNe         0.4541     0.8584   0.529   0.5989    
GeolSurfNo         1.8402     0.6775   2.716   0.0088 ** 
GeolSurfPad        1.1542     0.6709   1.720   0.0910 .  
LifeHistoryC-S    -0.3484     0.4690  -0.743   0.4607    
LifeHistoryC-S-R  -0.2564     0.8989  -0.285   0.7766    
LifeHistoryS      -0.4587     0.3870  -1.185   0.2409    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                       edf Ref.df      F  p-value    
s(log10(NicheWidth)) 1.353  1.615 25.803 9.69e-08 ***
s(HabitatTransf)     2.554  3.178  2.762   0.0476 *  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =   0.69   Deviance explained = 75.3%
GCV score = 2.2315  Scale est. = 1.7563    n = 70
```

The model resulted in the parametric terms no affinity to a land surface (GeolSurfNo; $p < 0.01$), Dispersal distance far ($p < 0.05$), Post African and other dissected surfaces (GeolSurfPad; $p < 0.1$) and the intercept ($p < 0.001$)to be significantly different from the null hypothesis

For the smoothed terms or non-parametric terms both Log$_{10}$ Niche Width ($p < 0.001$) and Habitat Transformation ($p < 0.05$) were significantly different from the null hypothesis.

Step 2: Refine the model by removing the least significant variable, Life History

Gam2<-gam(log10(Rarity)~s(log10(NicheWidth))+s(HabitatTransf)+Dispersal+HSpec+GeolSurf,data=rdata)

```
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   6.8040     0.5800  11.730  < 2e-16 ***
Dispersalf    0.4528     0.3900   1.161  0.24962
Dispersalm   -0.2455     0.4218  -0.582  0.56242
HSpecM        0.1077     0.3421   0.315  0.75390
GeolSurfEsc   0.3122     0.9187   0.340  0.73504
GeolSurfNe    0.5227     0.8096   0.646  0.52067
GeolSurfNo    1.6313     0.5960   2.737  0.00789 **
GeolSurfPad   0.8713     0.5960   1.462  0.14834
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                       edf Ref.df      F p-value
s(log10(NicheWidth)) 1.964  2.398 20.682 1.3e-08 ***
s(HabitatTransf)     2.626  3.285  2.403  0.0695 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.653   Deviance explained = 70.3%
GCV score = 2.1679  Scale est. = 1.8309    n = 81
```

This model resulted in the parametric terms no affinity to a land surface (GeolSurfNo; $p < 0.01$), and the intercept ($p < 0.001$) to be significantly different from the null hypothesis

For the smoothed terms or non-parametric terms both Log_{10} Niche Width ($p < 0.001$) and Habitat Transformation ($p < 0.1$) were significantly different from the null hypothesis.

Step 3: Remove the least significant variable, habitat specificity from the model

gam3<-gam(log10(Rarity)~s(log10(NicheWidth))+s(HabitatTransf)+Dispersal+GeolSurf,data=rdata)

```
Parametric coefficients:
            Estimate Std. Error t value Pr(>|t|)
(Intercept)   6.8391     0.5672  12.057  < 2e-16 ***
Dispersalf    0.4432     0.3862   1.148  0.25503
Dispersalm   -0.2327     0.4169  -0.558  0.57855
GeolSurfEsc   0.3075     0.9120   0.337  0.73697
GeolSurfNe    0.5377     0.8014   0.671  0.50445
GeolSurfNo    1.6442     0.5903   2.786  0.00688 **
GeolSurfPad   0.9018     0.5823   1.549  0.12604
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                       edf Ref.df      F  p-value
s(log10(NicheWidth)) 1.985  2.427 21.739 5.93e-09 ***
s(HabitatTransf)     2.616  3.272  2.471   0.0639 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.657   Deviance explained = 70.3%
GCV score = 2.1104  Scale est. = 1.8081    n = 81
```

This model resulted in the parametric terms no affinity to a land surface (GeolSurfNo; $p < 0.01$), and the intercept ($p < 0.001$) to be significantly different from the null hypothesis

For the smoothed terms or non-parametric terms both Log_{10} Niche Width ($p < 0.001$) and Habitat Transformation ($p < 0.1$) were significantly different from the null hypothesis.

Step 4: Remove the least significant variable Dispersal Distance, from the model.

gam4 <- gam(log10(Rarity)~s(log10(NicheWidth))+s(HabitatTransf)+GeolSurf,data=rdata)

```
            Estimate Std. Error t value Pr(>|t|)
(Intercept)  7.22552    0.43638  16.558  < 2e-16 ***
GeolSurfEsc  0.07917    0.75837   0.104  0.91711
GeolSurfNe   0.50153    0.73246   0.685  0.49545
GeolSurfNo   1.43557    0.51012   2.814  0.00612 **
GeolSurfPad  0.68203    0.50011   1.364  0.17637
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Approximate significance of smooth terms:
                       edf Ref.df      F  p-value
s(log10(NicheWidth)) 2.087  2.556 22.188 1.06e-09 ***
s(HabitatTransf)     2.781  3.458  2.527   0.0549 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

R-sq.(adj) =  0.655   Deviance explained = 68.8%
GCV score = 1.9837  Scale est. = 1.7709    n = 92
```

In the final model in which all variables make a significant contribution to the model the parametric terms no affinity to a land surface (GeolSurfNo; $p < 0.01$), and the intercept ($p < 0.001$) are significantly different from the null hypothesis

For the smoothed terms or non-parametric terms both Log_{10} Niche Width ($p < 0.001$) and Habitat Transformation ($p < 0.1$) were significantly different from the null hypothesis. This model explained 68.8% of the deviance.