Predictive modelling of Namibian fairy circles and their co-occurrence with *Euphorbia* species using Geographical Information Systems (GIS)

by

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DECLARATION

I, Christiaan E. Schutte, declare that the dissertation/thesis, which **I**, hereby submit for the degree M.Sc. in Geography at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution

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Predictive modelling of Namibian fairy circles and their co-occurrence with *Euphorbia* species

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Abstract

Fairy circles are an example of patterned vegetation and have only been documented to occur along the coastline of southern Africa, although a very similar vegetation pattern has recently been documented in north Western Australia. After several decades of investigation, the cause of fairy circles is still open to debate. The current Namibian-based project studied the "*Euphorbia* spp. allelopathy" theory which states that fairy circles are the product of a localized allelopathic affect in the soil caused by the previous presence and subsequent death of *E. damarana* and *E. gummifera*.

In the first part of this study, a GIS-based site suitability analysis for the occurrence of fairy circles was done using rainfall, altitude and land cover as site selection criteria. Thereafter 100 random sample points, each within a 10 km radius, were generated within the predicted site and investigated using Google Earth. It was found that 65 of the 100 locations contained fairy circles including a large distribution of fairy circles located in the south east of Namibia and also in the Kalahari Desert, that had not previously been documented. It was observed from the satellite images that several of the random sites did not have grass cover, and therefore would not have 'shown' fairy circles if they were present. From the site suitability analysis several additional sites where fairy circles co-occur with *Euphorbia spp.* were documented.

The second part of the study focused on the landscape scale characteristics of fairy circles, *E. damarana* and *E. gummifera*. Aerial and satellite imagery were used to make observations of Euphorbia plants over time, while a number of analytical techniques were used to compare the size and spatial patterning of fairy circles to Euphorbia plants. In terms of results, first, the aerial image comparison showed that *E. gummifera* is eventually replaced by fairy circles. Second, using a T-test it was found that there is no statistical difference in size between fairy circles and *E. damarana*. Third, the spatial patterning of fairy circles was examined and compared to the distribution of *E. gummifera* and *E. damarana* using a range of geospatial point pattern techniques. Sites where fairy circles co-occur with either *E. damarana* or *E. gummifera* were included in the point pattern analysis as mixed sites. The analysis using point pattern analysis showed that fairy circles have the most uniform distribution, compared to the Euphorbia and mixed plots. Interestingly, the regularity of the pattern associated with the mixed plots are in-between that of fairy circles and the Euphorbia plots. *E. damarana* have also been shown to have a regular spatial pattern, while the regularity of the pattern associated *E. gummifera* only slightly departs from complete spatial randomness.

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List of Acronyms

USGS	United States Geological Website
MAP	Mean Annual Precipitation
GIS	Geographical Information System
MAMSL	Meters Above Mean Sea Level
ASTER	Advanced Spaceborne Thermal Emission and Reflection Radiometer
TAP	Tree Atlas Project

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Chapter 1: Introduction

1.1 Background

A natural phenomenon occurring in the arid grasslands of the pro-Namib Desert has puzzled the scientific community for decades. Within these ephemeral grasslands are thousands of regularly spaced circular patches not containing any vegetation cover and commonly referred to as ‘fairy circles’.

Despite a plethora of research investigating the soil chemistry, microbiology, associated grass and other inherent fairy circle properties there are still a number of competing theories attempting to explain their origin. One of the main theories attempts to link fairy circles to the activities of social insects (Moll, 1984; Tinely, 1971). This ‘social insects’ theory postulates that ants and/or termites found in areas where fairy circles occur create these barren patches by harvesting the grass and/or seeds in a circular fashion around the immediate vicinity of a nest. Research examining the termite hypothesis has generally consisted of termite present/absent observations of trenches dug through fairy circles during field work. Several ant and termite species have been observed in and around fairy circles at various locations, however direct evidence of these insects creating fairy circles is lacking (Getzin et al. 2015, Van Rooyen et al. 2004). Another theory examining ‘fairy circles’ is the gas theory which suggests that abiotic gas rising up from cracks in the bedrock underneath the surface disturbs the soil chemistry and results in oxygen depletion that inhibits vegetation growth (Naudé et al. 2011).

The “*Euphorbia spp.* allelopathy theory” suggests that fairy circles are caused by various *Euphorbia* species (nearly perfectly round, highly poisonous shrubs, some of them endemic to the Namib Desert) and that upon dying, the *Euphorbia* spp. leave chemical compounds behind in the soil that inhibits the growth of new vegetation leading to barren circles (Meyer et al. 2015, Theron 1979). Fairy circles have however also been observed to co-occur with various *Euphorbia* species including *E. damarana* and *E. gummifera*. The first documented co-occurrence of fairy circles and *E. damarana* was found in the north-western parts of Namibia by (Theron 1979). The site of co-occurrence is characterized by the presence of fairy circles, *E. damarana* and large numbers of dead Euphorbia plants. The plants are in different stages of decay which vary between large dead bushes to only a few branches that are left lying in what resembles a fairy circle (see Figure 1.1). In this figure the remains of a dead *E. damarana* and a new barren patch can be seen and many more like this occur at this site. The sizes of fairy circles are also very similar to that of the *E. damarana* and bioassays proved that the plant exhibits allelopathic properties (Theron 1979). However, the allelopathy theory was criticized on the basis that *E. damarana* is mostly found in a stony habitat and not the characteristic sandy soils associated with fairy circles (Van Rooyen et al. 2004). More recently, the co-occurrence of fairy circles with *E. gummifera* has been documented in the south-western parts of Namibia where large numbers of the plants are also dead (Meyer et al. 2015). Here, the fairy circles are much smaller than those in the north-western parts and very similar to the sizes of *E. gummifera*. A characteristic compound from the *Euphorbia* genus was also found in the soil from inside fairy circles and not in the soil from between fairy circles. Using the historic imagery tool in Google Earth as well as ground-truthing, Meyer et al. (2015) showed that some of the more decayed bushes were replaced by fairy circles between 2003 and 2012. This supports the *Euphorbia spp.* allelopathy theory developed by (Theron 1979).

Figure 1.1: Fairy circles co-occurring with *E. damarana* at the Giribes Plain in north-western Namibia. The remains of a dead *E. damarana* can be seen and many more like this occur at this site.

Although proponents of the vegetation self-arrangement theory don't agree that Euphorbias are the cause of fairy circles, they agree with Meyer et al. (2015) that agents such as the poisonous plants can result in disturbances to the vegetation (Getzin et al. 2015). It was also noted that these areas where fairy circles co-occur with *Euphorbia* species are an exception to the rule (Getzin et al. 2014). It has also been argued that *Euphorbia* species are irregularly distributed (compared to the highly regular distribution of fairy circles) and can, therefore, not be responsible for the formation of fairy circles by (Getzin et al. 2015).

A number of researchers have sought to determine the characteristics required for fairy circles to occur within the physical landscape. These include Cramer et al. (2013)

who studied the edaphic characteristics of fairy circles as well as variation in fairy circle size, density and landscape occupancy with edaphic characteristics and water availability at a local scale (50 km) and with climate and vegetation properties at a regional scale. The scientists found that fairy circle landscape occupancy is negatively correlated with precipitation and soil nitrogen concentration, supporting the idea that fairy circles are the product of resource-competition. Using an empirical model, the scientists also found that regional fairy circle presence/absence is extremely predictable and is found along narrow ranges of vegetation biomass, precipitation and temperature. This suggests that fairy circles are likely a climate-dependent emergent phenomenon.

Later Getzin et al. (2015) developed a mathematical model based on parameters including soil-water diffusion, precipitation and an above ground biomass variable to reproduce the same regular pattern. He suggested that pattern formation is the cause of fairy circles which led to the development of the theory of “vegetation self-arrangement” which states that competition between the root systems of neighbouring grass tufts are so intense that it causes the grass to die back in the observed fairy circle pattern.

A more recent attempt to solve the fairy circle mystery includes Tarnita et al. (2017) who used a combination of mathematical modelling and field work to unite the two most prominent theories (social insect theory and the vegetation self-arrangement theory). First, she provided examples that termites are capable of producing the same regular pattern as fairy circles and then combined the mathematical model of fairy circles (developed by Getzin et al. 2014), with an existing mathematical model of social insects and reproduced the same regular pattern.

A range of different techniques and methods have been used to study different aspects associated with the characteristics of fairy circles. For example, chemical analysis has been performed on the soil both inside and outside fairy circles to determine differences (Naudé et al. 2011, Albrecht et al. 2001). Pot-based experiments have also examined the germination and growth of plants that were grown in soil from both inside and outside of fairy circles (Van Rooyen et al. 2004) while aerial photography, satellite imagery and Geographical Information Systems (GIS) have been extensively used to study the spatial distribution of fairy circles (Tarnita et al. 2017, Cramer et al. 2016 and Albrecht et al. 2001). Most of the geographically orientated studies have focussed on characterising the spatial distributions associated with fairy circles. For example, a study performed by researchers from the University of Cape Town in South Africa created an empirical model to predict the occurrence of fairy circles (see Cramer et al. 2013). The results of this model suggested that fairy circles are a climate dependend emergent phenomenon, as discussed above. In another geographically orientated study, satellite imagery was used to observe if differences in fairy circle populations could be observed over time, i.e. could disappearances and/or appearances be witnessed (Tschinkel 2012). From this study, it was proposed that fairy circles go through a natural cycle of birth (a barren path is formed in the grassland), maturation (barren patch persists for years) and death (barren spot is overgrown with grass).

The current study will attempt to test the Euphorbia allelopathy theory by using a range of geospatial techniques. This study will examine the extent to which fairy circles co-occur with various *Euphorbia* species throughout the Namib Desert. This will be done by identifying and documenting sites of co-occurrence but first modelling the distribution of fairy circles through a site suitability analysis. Historical aerial imagery will be obtained to examine what happens to the locations where Euphorbia plants grew over time. Lastly, the spatial patterning of *E. damarana* and *E. gummifera* will be determined and compared to that of fairy circles. Sites where fairy circles co-occur with either *E. damarana* or *E. gummifera* will also be included as “mixed” sites and be compared to the spatial distributions of fairy circles and the *Euphorbia* plants.

1.2 Aims and Objectives

This section provides an overview of the aims and objectives developed for the study.

1.2.1 Aims

The main aims of this study are to examine the spatial occurrence of fairy circles and *E. damarana* and *E. gummifera* in Namibia and to predict under which environmental conditions fairy circles will be formed.

1.2.2 Objectives

In order to achieve the main aim of this study, the following objectives have been established:

Objective 1: To predict the distribution of fairy circles at the sub-continental scale

This involves the creation of a GIS site suitability model which is able to predict the occurrence of fairy circles. The model will be validated and inspected in relation to the Euphorbia allelopathy theory.

Objective 2: To study the age, size and pattern of fairy circles at the landscape scale

This involves examining historical aerial imagery of fairy circles and *Euphorbia* species, to observe changes over time in their populations. Next the size of fairy circles will be compared to the size of *E. damarana* in north-western Namibia, and to *E. gummifera* in south-western Namibia. Lastly, spatial point pattern analysis will be used to compare the spatial patterning of fairy circles to that of both *E. damarana* and *E. gummifera*.

1.2.3 Brief description and layout of dissertation

The study is divided into two sections: The first part of the study will attempt to answer the question: where do fairy circles occur? This will entail creating a site suitability model to predict where fairy circles are likely to occur. This will be done through the construction of a site suitability model using Geographical Information Systems (GIS). Answering this question will help to explain the cause of the fairy circles as they occur in a well-defined belt mainly along Namibia's coastline.

The second part of the study involves the characterization of the size, spatial patterning and the longevity of fairy circles, populations of *E. damarana* and *E. gummifera* as well as areas where fairy circles and these species co-occur ('mix sites').

Chapter 1 provides a short background to the study. A brief overview concerning the different theories regarding the origin of fairy circles is outlined. In the second part of chapter one, the aim of the current study is defined and the objectives needed to achieve the aim introduced.

Chapter 2 provides an outline of fairy circles: their history, development, characteristics and the various theories that have been proposed for their formation.

Chapter 3 attempts to predict the occurrence of fairy circles using a site suitability model. Three variables; rainfall, altitude and land cover, is used to create the site suitability model.

In **Chapter 4** historic aerial imagery is compared to modern high resolution satellite imagery to understand what happens to a population of *E. gummifera* over 40 years. The sizes of fairy circles were compared to the sizes of *E. damarana* and *E. gummifera* at the sites where they co-occur. Finally point pattern analysis is used to characterise the spatial pattern of fairy circles, *E. damarana*, *E. gummifera*, and mixed plots (containing fairy circles and *E. damarana* or fairy circles and *E. gummifera*).

Chapter 5 provides an overview of the study aims and objectives. The results from the two main objectives are analysed and a conclusion summary is provided regarding the results of each objective and attempts to unite the findings of the two objectives in relation to the fairy circle phenomenon.

Chapter 2: Literature review

2.1 Introduction

Research has largely indicated that the fairy circle phenomenon is confined to a narrow strip, roughly 50 km – 100 km inland from the Atlantic Ocean, which stretches down from south-western Angola, through Namibia to north-western South Africa (Cramer et al. 2016, Juergens 2013). Figure 2.1 shows the distribution of fairy circles along Namibia's coast and provides a visual illustration of fairy circles. The two most striking characteristics of fairy circles are that they exhibit an almost completely circular shape and the surface inside the circles is devoid of vegetation. Although fairy circles have been around for at least a number of decades there is still some uncertainty regarding the actual age of this phenomenon.

2.2 Physical characteristics of fairy circles

The physical characteristics of fairy circles are very important in understanding how they form and include the associated grass species, the sandy substrate on which they occur, their peculiar size, shape and pattern, as well as their life span. All these characteristics will be briefly discussed in the following section.

In terms of the grass species, the vegetation on which fairy circles occur are comprised of grass species commonly referred to as the matrix grasses. Grass is a very important characteristic of fairy circles, for without the grassy cover fairy circles will not be visible.

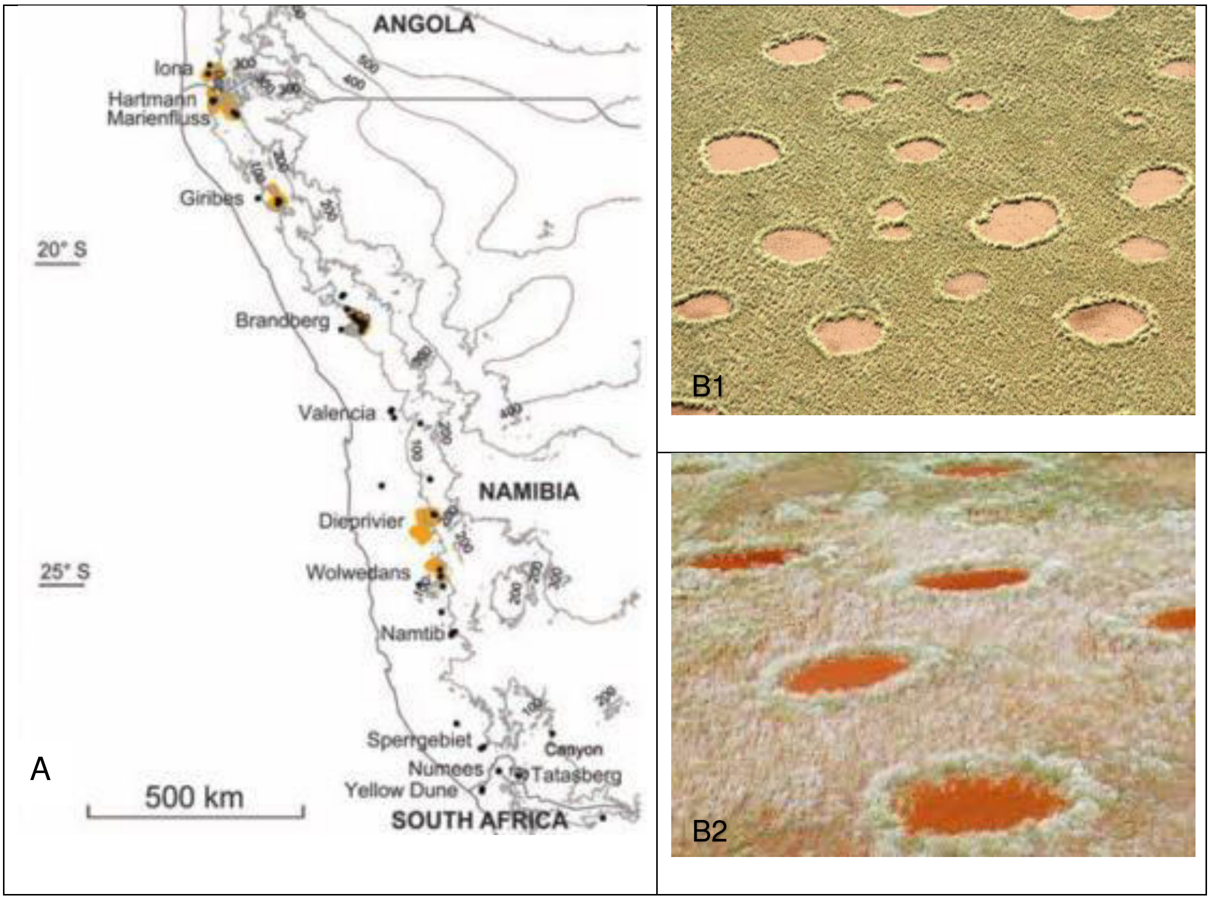

Figure 2.1: A: Fairy circle locations (black dots) and fairy circle hotspots (yellow polygons) are shown on the left, adapted from (Juergens 2013). Fairy circles are illustrated on the right. B1: Fairy circles at the Namib Rand Nature Reserve (CNN 2017), B2: Fairy circles at the Namib Rand Nature Reserve (BBC Earth 2014).

The grasslands in which fairy circles are found are ephemeral and thus biomass is highly dependent on rainfall and can be completely absent during drought years (Van Rooyen et al. 2004). The distribution of the grasses on which fairy circles commonly occur extends beyond the rainfall isohyets containing fairy circles (Cramer et al. 2016). Several grass species have been associated with fairy circles including; *Stipagrostis uniplumis, S. giessii*, *S. ciliata*, *S. obtusa* and *S. hochstetteriana* (Cramer et al. 2013, Tschinkel 2012, Van Rooyen et al. 2004). In the far southern part of Namibia and in the Richtersveld area of the country fairy circles are also found in a succulent shrub land, where grasses are mostly absent and where small shrubs replace the role of the matrix grasses (Van Rooyen et al. 2004). In north-western Namibia, the most well known fairy circle sites occur in the Hartmann's and Marienfluss valleys, as well as in Giribes Plains. At these sites, the matrix grass between fairy circles mostly consist of the short-lived grass species *S. uniplumis*, while the perennial belt comprises of either *S. giessii* or *S. hochstetteriana*, which are both perennial species. South of the Kuiseb River *S. obtusa* replaces *S. uniplumis* in the matrix grass, and *S. ciliata* forms the perennial belt. In certain instances, *S. obtusa* forms both the matrix grass and the perennial belt.

Associated with much of the grass cover is the well-known perineal belt (PB) which is a thick ring of grass that is much taller than the matrix grass (Figure 2.2A). In some instances, the difference in size between the PB and the grass matrix is related to the different species present, in others the same species occurs on both the periphery and in the matrix grasses (Cramer et al. 2016). The PB is essential for this ecosystem functioning as it provides valuable resources to many organisms (Juergens 2013). A lesser known but similar grass related feature often documented with fairy circles is the grass in the immediate vicinity around the circle forming a "halo-like" effect instead of a PB (Figure 2.2B). Both these attributes have been linked to the higher soil moisture content inside the fairy circles (Tschinkel 2012).

In terms of soil composition, fairy circles generally occur on soils with extremely high infiltration rates and low nutrient holding capacities (Cramer et al. 2016). It has been suggested that the disjunctive distribution of fairy circles along the Namibian coast is a result of their pronounced restriction to sandy soils (Juergens 2013). While fairy circles usually occur on sandy soils, characterized by low fertility, soil from inside fairy circles is significantly less suitable for plant growth than soil from the outside (Cramer et al. 2016).

Albrecht (2001) found that the soil moisture content of soil from inside fairy circles is five times higher than that of soil from outside while Picker et al. (2012) studied the soil properties of fairy circles eight months after the last seasonal rainfall ended and documented a fivefold decrease in soil moisture from the centre of fairy circles towards the surrounding grasses. He noted that the wetness gradient could not have been due to evapotranspiration by the matrix grasses as it was during the dry season and the grasses were dormant. The researchers further noted that the PB consisted of *S. uniplumis* that was flowering during the dry season while the matrix grasses were dormant. The researchers attributed this to the higher soil moisture content of fairy circles.

Juergens (2013) analysed long-term data containing information on the environmental properties and changing aspects of fairy circles. The researcher recorded the volumetric soil water content of fairy circles for the period 2006 to 2012 and found that in excess of 53 mm of water was stored in the upper 100 cm of the soil of fairy circles (even throughout the dry season), in an area that receives on average only 100 mm of rainfall per year. Due to the large pore sizes, the substrate associated with fairy circles drains rapidly which allows fairy circles to collect water during rainfall events and to not lose water to evapotranspiration.

The rapid percolation of rain water to deeper soil layers assists in reducing evaporation loss and the development of the PB is dependent on the longevity of the water resource beneath fairy circles.

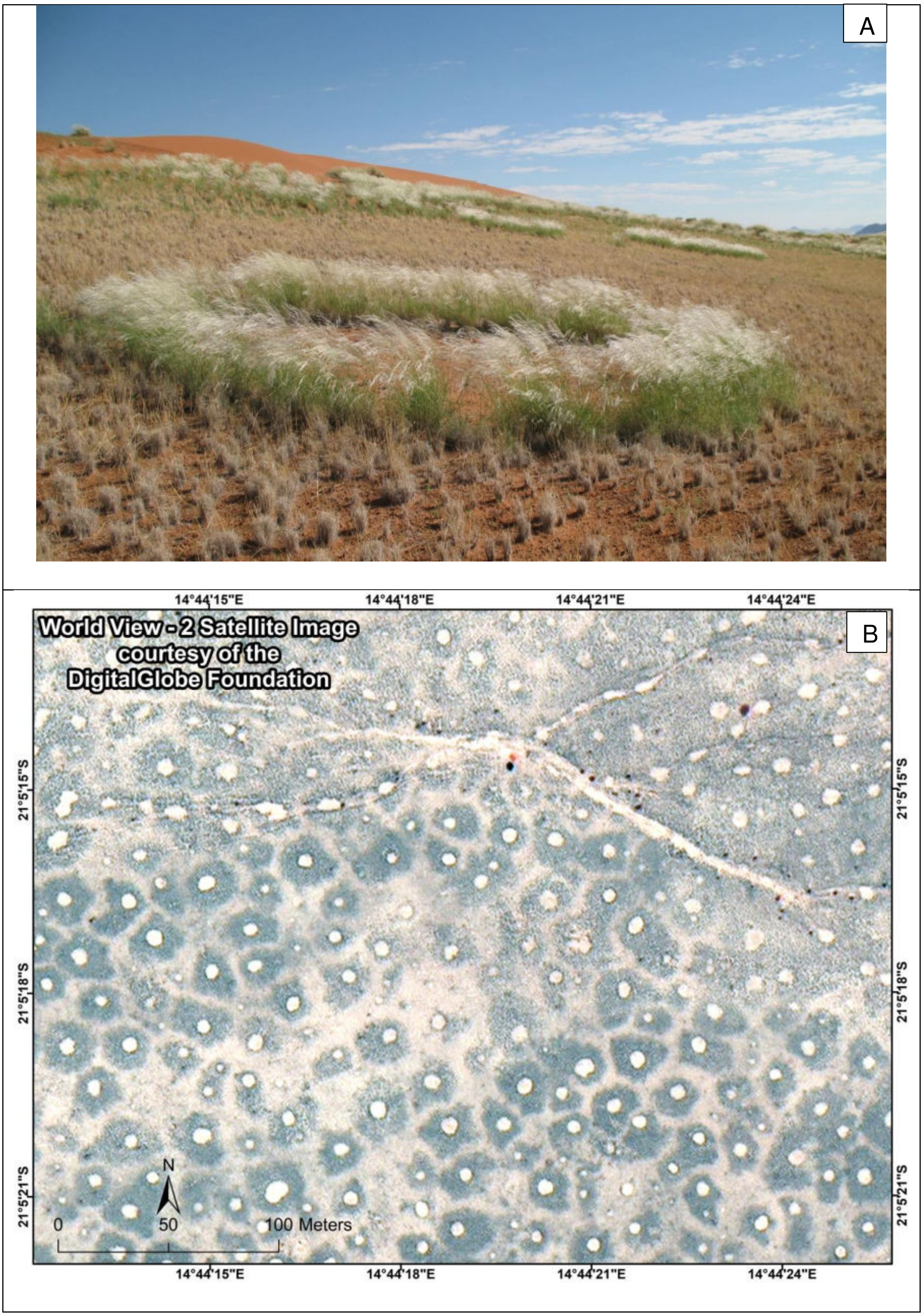

Figure 2.2: A: The perennial belt (PB) around fairy circles appearing healthier than the matrix grass, (National Geographic 2013). B: Satellite image taken near Brandberg shows fairy circles with the grass forming a "halo-effect" instead of a PB surrounding the fairy circles. Note the elliptical shape of fairy circles situated along drainage lines.

Cramer et al. (2016) suggested that soil on which fairy circles emerge has a high capacity for water flux, which could enable landscape hydraulic connectivity. This means that water can move vertically/horizontally through soil-water diffusion. To test this Cramer et al. (2016) conducted water pulse and nitrogen-15 (^{15}N) pulse experiments and found that water and ^{15}N can indeed migrate horizontally through the soil. This illustrates that edaphic resources in the sandy soil at the Namib Rand Nature Reserve are highly mobile and can move up to 7.5 m over a period of three weeks (Cramer et al 2016).

Another interesting attribute of fairy circles is their shape. The name “fairy circle” eludes to the fact that fairy circles are mostly completely circular, however, on close inspection the edges are slightly distorted. It has also been observed in various places that the shape of fairy circles can sometimes change from circular to more of an ellipsoid (Figure 2.2B). This most often occurs where fairy circles are situated along drainage lines with the longer axis parallel to the drainage line (Meyer et al. 2015).

Closely related to the shape of fairy circles is their size which generally decreases from approximately 12 m in diameter in the north of Namibia to 2 m in diameter in the south (Van Rooyen et al. 2004).

Regarding their patterning, fairy circles are typically over-dispersed and highly regular. The regularity/uniformity associated with the spatial pattern of fairy circles are consistent with plant – plant interactions in general as the main vegetation-patterning mechanism (Juergens 2015). According to the vegetation self-arrangement theory, fairy circles, or rather the grasses that constitute fairy circles, compete for resources and this process then results in the observed uniform pattern.

Fairy circles undergo a natural cycle consisting of formation, development and maturation, and eventually the fairy circle becomes overgrown with grass and disappears into the matrix grasses (Tschinkel 2012, Albrecht et al. 2001). Tschinkel (2012) examined two satellite images taken four years apart in an attempt to determine the age of fairy circles and concluded that they have a lifespan between 40 and 60 years with additional investigations indicating that the age of fairy circles could range between five (5) and 165 years.

2.3 Fairy circle origin

This section examines the theories used to explain the cause of fairy circles. Four main theories have been used to explain fairy circle formation, these include the Social Insects Theory (SI), The Vegetation Self-Arrangement Theory (SA), The Gas Theory (Gas) and the Euphorbia allelopathy Theory (EU). The publication dates of the seminal studies used to explain fairy circles based on these theories are shown in Figure 2.3 together with the theory they espouse.

2.3.1 Social insect theory

The earliest publication relating to fairy circles is Tinely (1971) who suggested that fairy circles are the weathered remains of fossilized termite nests. His proposal was generally not well received, however, the role of insects themselves in the formation of fairy circles is still being investigated by researchers.

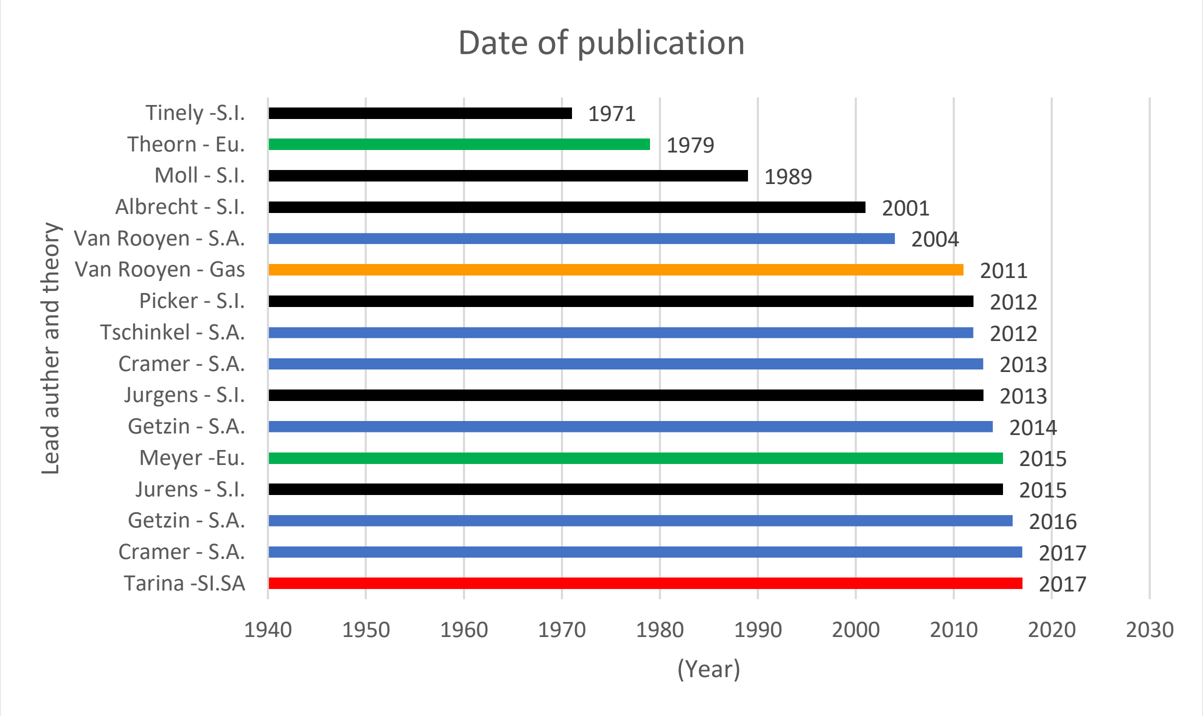

Figure 2.1: Main fairy circle publication dates. **S.I.:** Social Insect theory. **S.A.:** Self-Arrangement theory, **S.I.S.A.**: Social Insect and Self-Arrangement theory, **Eu**: Euphorbia theory. The earliest attempts to provide an explanation to the cause behind fairy circles refers to fossilised termite mounds and *E. damarana*. Subsequent studies focused on the active role social insects as causal agents, vegetation self-arrangement and recently the combination of the two. Only one additional study concerning the Euphorbia theory was conducted decades after the first and have not been seriously considered.

Empirically Moll (1984) was the first to explore the role of social insects in fairy circle creation by digging trenches through fairy circles and observing termite activity. He then suggested that these insects could be responsible for creating these patterns. This resulted in a number of studies that investigated both termites and ants as causal agents in fairy circle formation (see for example Juergens 2013, Picker et al. 2012, Albrecht et al 2001). The mechanisms through which these social insects create fairy circles can be divided into direct and indirect processes. In a direct process, insects harvesting seeds and/ or seedlings from inside fairy circles are thought to directly contribute to fairy circle formation (Juergens 2013, Moll 1984). In an indirect process active termite nests could produce inhibitory substances that could in turn have detrimental effects for vegetation and contribute to the fairy circle phenomenon (Albrecht et al. 2001).

Moll (1984) proposed that the absence of grass cover inside fairy circles was a consequence of termites, specifically the species *Hodotermes mossambicus*, having consumed the grass seeds in the direct vicinity of their nests. However, Van Rooyen et al. (2004) documented many small seedlings in fairy circles after good rainfall, indicating that the deficiency of seeds could not be the primary cause for fairy circle formation. The researchers also suggested that fairy circles remain bare since seedlings do not survive when the rains have ended. Termites do not consume a plant entirely, i.e. the leaves, the tuft and the roots, and no remains of grass or any other plant species are located inside fairy circles. In most instances where dead plants were found inside fairy circles, it comprised of the entire dried remains, mostly of juvenile grass seedlings (Van Rooyen et al. 2004).

Moreover, fairy circles are restricted to a minor part of the distribution range of *H. mossambicus* with no comparable phenomenon found in the remaining extent of the termite's range (Van Rooyen et al. 2004). This poses the question why do termites only create fairy circles in a small portion of their habitat? Additionally, Coaton and Sheasby (1975) noted that the habitat of *H. mossambicus* does not enter into sand dunes. However, fairy circles do occur on dune slopes and interdune spaces (Van Rooyen et al. 2004).

The termite hypothesis involving *H. mossambicus* has been criticised for its lack of supportive data (Grube, 2002). For example, Van Rooyen et al. (2004) dug trenches through well-developed fairy circles during 2000 and 2001 and found no evidence of termite tunnels. The researcher did find termites above-ground, however, their presence was not directly associated with fairy circles.

Albrecht et al. (2001) hypothesised that a semi-volatile chemical substance is produced inside termite nests which inhibits the growth of vegetation in fairy circles by decreasing resistance to dehydration. These researchers were the first to use aerial photography to analyse the spatial pattern produced by fairy circles located in the Wolwedans area of the Namib Rand Nature Reserve. They found a similar spatial distribution pattern for fairy circles and termites and suggested that this points towards an association between fairy circles and termites. They were not able however to demonstrate the presence of the semi-volatile substance in fairy circle soil. Subsequently the mechanism proposed by Moll (1984) and others that termites cause fairy circles by producing chemical substances that lead to the death of the grass were not confirmed.

Juergens (2013) examined species distribution maps and found only the sand termite, *Psammotermes allocerus*, at all fairy circle hotspots. It should be noted that similar to the distribution of *H. mossambicus*, fairy circles are restricted to a fraction of the range of *P. allocerus*, with no comparable phenomenon found in the remaining extent of the termite’s distribution. Other species such as *H. mossambicus* is mostly limited to the summer rainfall climate and *Microhodotermes viator* to the winter rainfall climate. Another species, *Baucaliotermes hainsii*, is restricted to areas south of the southern central Namib. Juergens found three ant species; *Messordenticornis viator*, *Anoplolepis steingroeveri*, and *Tetramorium* species, at several fairy circle locations in his study area, but none of them in all.

Later Juergens and colleagues (2013) found high frequencies (80 to 100%) of the termite *P. allocerus* at his study sites in western Namibia. The characteristic "sheetings" (thin coatings of cemented sand assembled over the foraged plant remains) of *P. allocerus* were found at 80 to 100% of the fairy circle locations. Moreover, *P. allocerus* nests and subterranean tunnels, with the distinguishing black organic wall covering (tapetum), were observed a few centimetres to decimetres beneath the fairy circle, the perennial belt (PB), and the matrix grasses. During the wet season, the amount of these observations was reduced to only half of that observed during the dry season. While these associations imply a contributing role for *P. allocerus* in fairy circle formation, it is probable that they may instead simply point towards the colonisation of fairy circles by the termites.

Picker et al. (2012) did not find any evidence to support the hypothesis of a termite origin for fairy circles. He found a near absence of termites at the Namib Rand Nature Reserve. The lack of association between fairy circles and *H. mossambicus* activity, as well as the extremely low densities of the termite in areas where fairy circles did occur, they noted, was empirical proof that termite foraging was not involved in the creation of fairy circles. Additionally, the establishment of annual grasses would soon cover the bare surface of fairy circles in the absence of an enduring association of termites with each circle. However, the majority of fairy circles remain mostly free of grass cover over time.

Picker et al. (2012) rather highlighted ants as causal agents. He observed 10 times more *A. steingroeveri* ants in fairy circles than in the matrix grasses at his study site in the Namib Rand Nature Reserve. According to Picker and colleagues, fairy circles and North American *Pogonomyrmex* ant nests both have a bare disc surrounding the nest, are over-dispersed and are associated with higher soil moisture.

Getzin et al. (2014) used point pattern analysis to characterise the spatial distribution of fairy circles and developed a mathematical model that could generate the same pattern. A key question of their study was to examine in what way the behaviour of social insects, for example foraging, nest building, nest movement, and intra-specific competition, can result in the interesting regular spatial patterns characteristic of fairy circles. These researchers identified several characteristics of fairy circle patterns including the fact that they are nearly always situated at least a distance of 13 m apart, and that there is no larger scale aggregation in the pattern. Although Picker et al. (2012) and Juergens (2013) have shown strong associations between fairy circles and the presence of ants and/or termites, they fail to offer an explanation for the identified lack of any larger-scale clustering at distances less than 60 m (Getzin et al. 2014). Tschinkel (2012) argued that if termites are really the cause behind fairy circle formation, the termite hypothesis must be able to account for all the vital characteristics of fairy circles, i.e., their circularity, their over-dispersion, the proportion of bare surface and their changing diameter in different soils and latitudes.

In response, Juergens (2015) used point pattern analysis to highlight the fact that termite colonies can produce regular spatial patterns similar to fairy circles. Later Getzin et al. (2015) stated that the regularity of fairy circles is not congruent with the only two insect examples provided by (Juergens 2015). He noted that neither the pair correlation function g(r) of *Macrotermes* nor that of *Pogonomyrmex* displays a first clear peak with high amplitude which is distinct and considerably outside the simulation envelopes of the null model. This means that the pattern associated with the two species of ants, although also regular, are less ordered than the fairy circle pattern. Similar to Juergens (2015), Tarnita et al. (2017) showed that competition between rival termite colonies can produce the large-scale hexagonal patterns found in fairy circles. She also proposed that a combination of the fairy circle model (Getzin et al. 2014) and the social insects model explains the phenomenon the best (Tarnita et al. 2017).

2.3.2 Vegetation self-arrangement theory

Several researchers have suggested that fairy circles are an example of an emergent vegetation spatial pattern, that forms as a result of soil hydraulic and nutritional properties which could enable relatively long-range (several metres) resource transport within the soil (Cramer at al 2016, Getzin et al. 2014). This pattern of vegetation self-arrangement is based on the principals of pattern formation and suggest that in an area as arid as the Namib Desert, competition between the root systems of neighbouring grass tuffs are so intense that it causes the grass to die back in the observed regular pattern. Getzin et al. (2014) proposed that fairy circles and their characteristic regular pattern are produced by an interaction among plants, while Cramer et al. (2016) showed that the arrangement of fairy circles is connected to properties of the soils that allow individual grass tufts to competitively interact with each other for water and nutrients over distances beyond the radius of the root zone (which is normally 1 m).

Albrecht et al. (2001) used the distance to nearest neighbour function to show that competition between fairy circles determines the emergent spatial pattern, while Getzin et al. (2014) provided evidence that the competition is limited to distances of 13 m and shows a ‘strongly hexagonal grid-like pattern’, close to the ideal pattern of hexagonal honeycombs.

Cramer et al. (2016) theorized that the coarse textured sand, where fairy circles occur, produces a hydraulically and nutritionally connected landscape, in which adjacent fairy circles competitively influence each other over several metres. To test if resources could be transported in the soil, Cramer et al. (2016) conducted water-and nitrogen^{15}-pulse experiments and illustrated that edaphic resources were indeed mobile, moving up to 7.5 m over a period of 1 – 3 weeks. It has been shown that fairy circle size is positively correlated with soil infiltration rates and negatively with precipitation (Cramer et al. 2016) which suggests that higher soil infiltration rates and lower rainfall will result in larger fairy circles. However, as precipitation increases from the west to the east and fairy circles in the north and south receive a very similar amount of rainfall, why would fairy circles have been documented to decrease in size from the north to the south?

Getzin et al. (2014) stated that fairy circles are produced by resource depletion, i.e. dehydration. The vegetation self-arrangement theory predicts that new fairy circles develop as a consequence of competition for water during periods of water deficiencies. However, if the notion then is that the spatial patterns of vegetation are caused by competition amongst plants, then the wet fairy circles should immediately support abundant growth of grasses on their surfaces? Juergens (2015) also found no evidence of an increased appearance of fairy circles after below average rainfall.

Another critique of the vegetation self-arrangement theory relates to the nearest neighbour distances which many authors suggest results from competition for resources. Juergens (2015) noted that interaction among neighbouring plants can control their size and distance away from each other. However, Getzin et al. (2014) postulates interaction at a much larger scale; the average distance between two neighbouring grass individuals in the matrix grassland is in the range of 10 cm. When compared to the diameters of fairy circles and interspaces of up to 30 m, this would be equivalent to 300 individual distance units. Is interaction among grass individuals able to create a bare patch 300 times larger than the distance between neighbouring individuals? This seems to be a very unlikely interpretation for explaining the size of fairy circles.

Finally, Juergens (2015) stated that the matrix is homogenously dry while the maximum quantity of water is located in the centre of the fairy circle. It must be clarified why competition could result in the creation of a fairy circle in precisely that location that contains more water than found anywhere else in the fairy circle environment.

A recent attempt has been made by Tarnita et al. (2017) to unite the vegetation self-arrangement theory with the social insect theory using mathematical modelling. The idea is that the two theories and the processes behind them are in fact operating together to produce the regular pattern characteristic of fairy circles. They applied a mathematical model to fairy circles by parameterizing the united model and found that it is able to characterize the vegetation patterns of fairy circles more accurately than the social insects or self-arrangement theories can explain on their own.

According to Tarnita et al. (2017) colonies of insects construct central nests and forage outwards to obtain resources to fuel colony-population growth and survival. While foraging, the termites harvest the grass surrounding the nest and in doing so they create fairy circles. Mature (established) colonies produce reproductive future queens/kings that disperse randomly throughout their simulated landscapes and attempt to initiate new colonies. Once a new colony is established, the termites create a new fairy circle by harvesting the grass surrounding the nest. Resource availability is constant and uniformly distributed. When the growing foraging areas (fairy circles) of adjacent colonies overlap, conflicts follow via territorial aggression, as is common in numerous social-insect species. Conflict outcomes depend on relative colony size with larger colonies more likely to eradicate smaller ones, but similar-sized colonies co-exist, whereupon a shared boundary develops. It is generally known that two fairy circles can in some instances occur right next to one another, with their boundaries connected. Although this system is intrinsically dynamic owing to frequent births and deaths of colonies, the quantities of interest finally reach a stationarity point (fluctuating around a well-defined constant average).

2.3.3 The gas theory

Naudé et al. (2011) found that gas micro-seepage (particularly hydrocarbon microseepage) is present inside fairy circles. This is thought to disturb the soil micro-environment and result in oxygen depletion that impedes plant growth. Critics of this hypothesis argue that although hydrocarbon micro-seepage is known to result in plant death, this process occurs heterogeneously at the landscape scale and not with the regular and homogeneous pattern observed for fairy circles (Getzin et al. 2014). Although this theory has already been published in 2011, no results on bioassays has been published yet to confirm it.

2.3.4 The Euphorbia allelopathy theory

The “*Euphorbia* spp. allelopathy” theory is one of the earliest attempts made at explaining the cause of fairy circles. The theory was initially proposed by Theron (1979) who witnessed fairy circles during an expedition to north-western Namibia. Alongside these circles, he found a small population of *E. damarana* in southern parts of the Giribes Plain. *E. damarana* is a nearly circular shrub that showed a strong correlation in size with the fairy circles (Theron 1979). He also noted that many of the *E. damarana* plants were dying off. *E. damarana* is commonly known to be highly poisonous, the tubular leaves of the plant contain a white latex substance. Indeed, Theron (1979) showed in experiments that the latex contains growth-inhibiting compounds. He hypothesised that when the plant dies, and the latex is released into the soil, it has an allelopathic effect that inhibits the growth of grass inside the circle.

Three *Euphorbia* species have been found to co-occur with fairy circles: they are *E. damarana* and *E. gummifera*, and to a lesser extent, *E. gregaria* (Figure 2.4). *E. damarana* is closely related to both *E. gummifera* and *E. gregaria*, however the former is separated from the latter two by vast geographical distances; *E. damarana* occurs only to the north of the tropic of Capricorn; the most southern recording of these plants is 300 km from the most northern location where *E. gummifera* has been noted (Leach 1975). Despite being highly poisonous, *E. damarana* is grazed by black rhino, kudu, springbok and Oryx. *E. damarana* occurs in various habitats, but mainly on rocky or gravel plains. Although being the least distributed of these, *E. gummifera* is widespread throughout south-western Namibia, occurring mainly from Lüderitz south towards the Orange River, forming the border between Namibia and South Africa, usually not further than 80 km from the coast (Leach, 1975). *E. gummifera* also contains latex that is an irritant and is mainly found on plains and hill slopes, growing on sandy or rocky substrates (Curtis et al. 2005). *E. gregaria* is widespread through much of southern Namibia (Curtis et al. 2005) and extends from Lüderitz eastwards into the Kalahari, although they are also found in the Richtersveld. *E. gregaria* is mostly found on hillsides, plains and rocky outcrops and grows on rocky substrates, as well as sand and sandy loam (Curtis et al. 2005). According to Leach (1975), *E. damarana*, reaches a maximum size of approximately 6 m in diameter and a height of up to 3 m, *E. gummifera* reaches 1.8 m in height and a diameter approximately 2 m, while *E. gregaria* also has a size of 2 m.

There are three criticisms of the Euphorbia theory. First, *E. damarana* grows mainly in areas comprising of either very coarse material (e.g. Etendeka basalt) or having a very thin layer of top soil (Becker et al. 2010; Van Rooyen et al. 2004). This however is not the type of substrate commonly associated with fairy circles. Second, a number of researchers have found fairy circles without the presence of *E. damarana,* Becker et al. (2000) for example could not locate any *E. damarana* plants within the Giribes Plain, Marienfluss Valley or in the Hartmann's Valley despite the presence of fairy circles in these locations. They concluded that the co-occurrence of *E. damarana* and fairy circles is perhaps coincidental. However, Theron (1979) did indeed observe *E. damarana* in Giribes. Third, Getzin et al. (2015) concluded from observations (not calculations) that *E. damarana* is irregularly distributed which is in contrast to the uniform pattern of fairy circles.

Meyer et al. (2015) observed that fairy circles and *Euphorbia* species do not only co-occur about 1 km from the Giribes Plain where they were documented by Theron (1979), but also in several other locations near Kolmanskop, south and west of Aus, Garub, Wolwedans and at several places near Uis. The researchers noted that *E. gummifera* co-occurs with fairy circles on sandy soils in the south west of Namibia. Their study site was located approximately 100 km inland from Lüderitz and large numbers of these plants are also in a process of dying, similarly to those near the Giribes Plain. Meyer et al. (2015) found evidence that euphol, a characteristic compound from the *Euphorbia* genus, is present in soil from inside fairy circles and not in the matrix soil. They also showed that there is a correlation in the sizes of fairy circles and *E. gummifera*. The fairy circles and *E. gummifera* in south-western Namibia had average diameters of 3.53 m and 3.44 m, respectively. Interestingly, the fairy circles and *E. damarana* documented by Theron (1979) in north-western Namibia were larger with average sizes of 6.2 m and 6.4 m. A third site, where thousands of fairy circles co-occur *with E. damarana* on immense sandy plains, and major die-back of *E. damarana* is observed, has been documented in the current study.

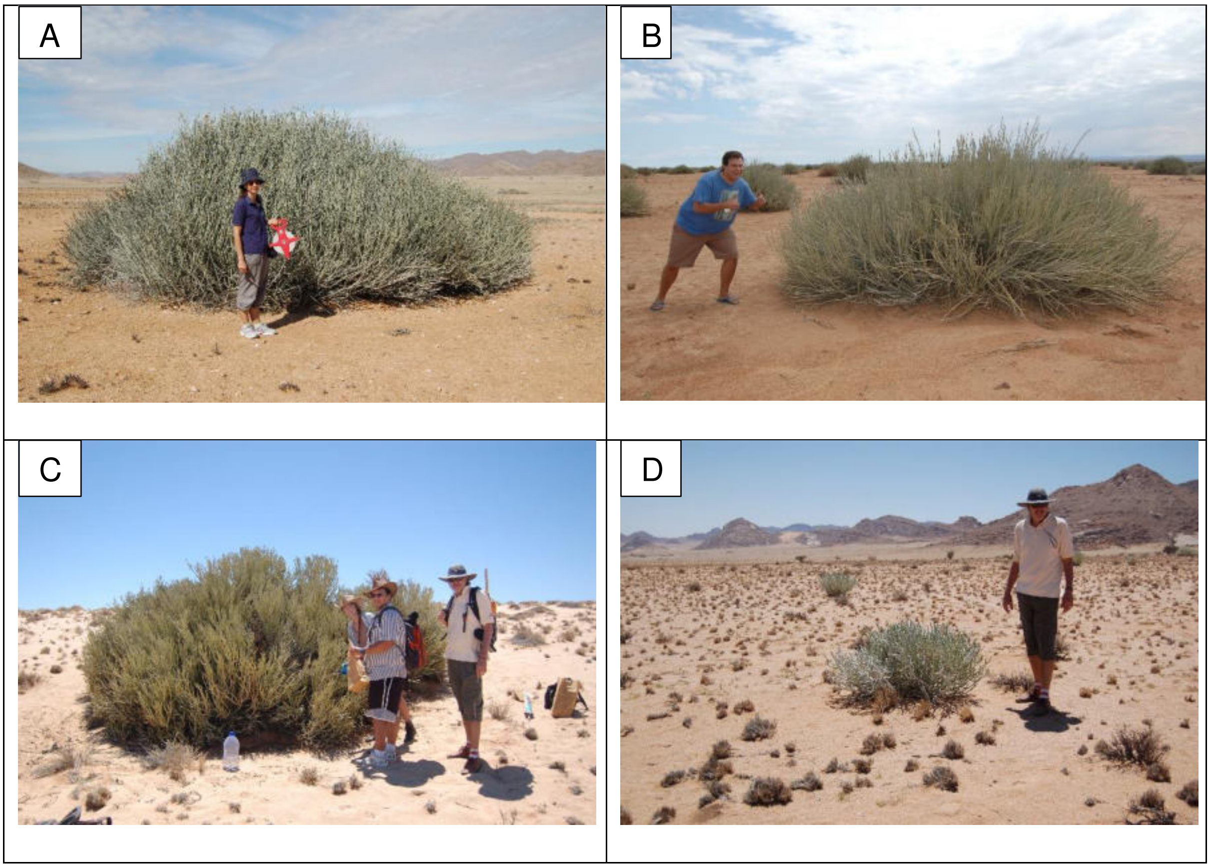

Figure 2.2: *Euphorbia* species with people included for scale. A: *E. damarana*. B: *E. gregaria*. C: *E. gummifera*. D: *E. mauritanica*.

Chapter 3: Site suitability analysis

3.1 Introduction

In this chapter a GIS site suitability analysis was conducted to identify possible locations for fairy circles in Namibia and compare it with the distribution of succulent *Euphorbia* species. Previous examples where site suitability analysis has been employed include landfill site selection (Nas et al. 2009), environmental impact assessments processes (Warner et al. 2012) and in the selection of areas for conservation importance (Boldstad et al. 2008).

Many studies have shown that fairy circles occur in south-western Africa, along a very narrow band approximately 50 km inland at its closest to the Atlantic Ocean, and up to 100 km inland at its furthest (Picker et al. 2012). A number of maps have been produced showing the distribution of fairy circles along this narrow belt. Indeed, several point-based maps have been compiled by plotting known locations where fairy circles occur, while polygons have been used to highlight where fairy circles extend over large areas (often referred to as 'fairy circle' hotspots) (Juergens 2013, Picket et al. 2012, Van Rooyen et al. 2004). Cramer et al. (2013) was the first to create a prediction map of where fairy circles are likely to occur. Their analysis was based on a simplified Boosted Regression Tree (BRT) model. The researchers evaluated several bioclimatic variables in the BRT model against fairy circle presence/absence data acquired from Google Earth. The study determined that three explanatory variables could explain where fairy circles occur including temperature, Mean Annual Precipitation (MAP) and the first principal component of an enhanced vegetation index created by the authors (1st PC of EVI). The researchers found that fairy circles occur in narrow ranges of both MAP and vegetation biomass relative to the range in the vicinity of the circles, additionally this narrow band of fairy circles occurs within a much wider distribution of the component grasses.

The current study builds upon this previous research by adding a number of additional variables to produce a site suitability map predicting the location of fairy circles in this region. Like the previous research, MAP was a key variable in the current study as well as altitude and land cover. The latter two variables have not been previously used to study fairy circle occurrence.

An important aspect of the fairy circle phenomenon is that the substrate on which fairy circles occur are always sandy (Juergens 2013). Therefore, soil samples were analysed to determine the physical properties of the soil from areas where fairy circles co-occur with *E. damarana* and *E. gummifera* and the results of this assessment was grouped under the land cover part of this study.

3.2 Study area

The study site for this part of the study is the entire Namibia which borders Botswana, Angola, South Africa and Zambia. The western border of Namibia is formed by the Atlantic Ocean and the coastline is approximately 1 570 km in length. To the east of Namibia lies Botswana, with a small portion of the country in the far north east bordering on Zambia (Figure 3.1). Namibia covers an area of approximately 823 680 km^2. Fairy circles are known to occur within the ephemeral grasslands of the Namib Desert, considered by many to be the oldest desert in the world (Lancaster 2010).

3.2.1 Altitude

Much of Namibia consists of a wide, flat plateau that extends north, south and east into the neighbouring countries (Mendelson et al. 2002). The height of the plateau ranges between 900 – 1 300 mamsl. There is however great variation in altitude to the west and south where the escarpment rises from the coast. The coastal plain rises to an elevation of approximately 800 – 900 mamsl and is approximately 50 – 100 km in width. The incisions into the landscape made by the major river systems are often spectacular and exposes ancient underlying rocks.

The Hartman- and Marienfluss Valleys, as well as Giribes Plain are situated in the north west of Namibia at an elevation between 500 and 700 mamsl (Van Rooyen et al. 2004). The valleys are surrounded by hills and fairy circles are known to occur within these flat sandy valleys. Located in central western Namibia, Brandberg is the highest point in Namibia and rises sharply above the flat, surrounding plains to a height of 2 579 mamsl (Figure 3.1). Fairy circles are known to cover extensive areas from the north, east and to the south of Brandberg while *E. damarana* also covers extensive areas at this site. The area where the fairy circles and *E. damarana* co-occur lies between an altitude range of between 500 – 800 mamsl. The Namib Rand Nature Reserve is situated in south-western Namibia and forms part of the Namib Sand Sea. The extensive area associated with fairy circles at the Namib Rand Nature Reserve ranges between an altitude of 900 – 1 200 mamsl. Garub is situated further south and fairy circles co-occur at this site with *E. gummifera*. The site is located between an altitude of 800 – 900 mamsl.

These areas are commonly referred to as 'fairy circle hotspots', several of which were visited during fieldwork and are shown in the study area maps. The fairy circle hotspots are well documented and were adapted from the maps created previously (Juergens

2013, Picker 2012, and Van Rooyen et al. 2004). The fairy circle hotspots are shown in relation to the environmental variables that were used to describe the study area. The fairy circle hotspots were also used, in combination with additional literature reviews, to define the criteria needed for the suitability analysis (refer to section 3.3.1).

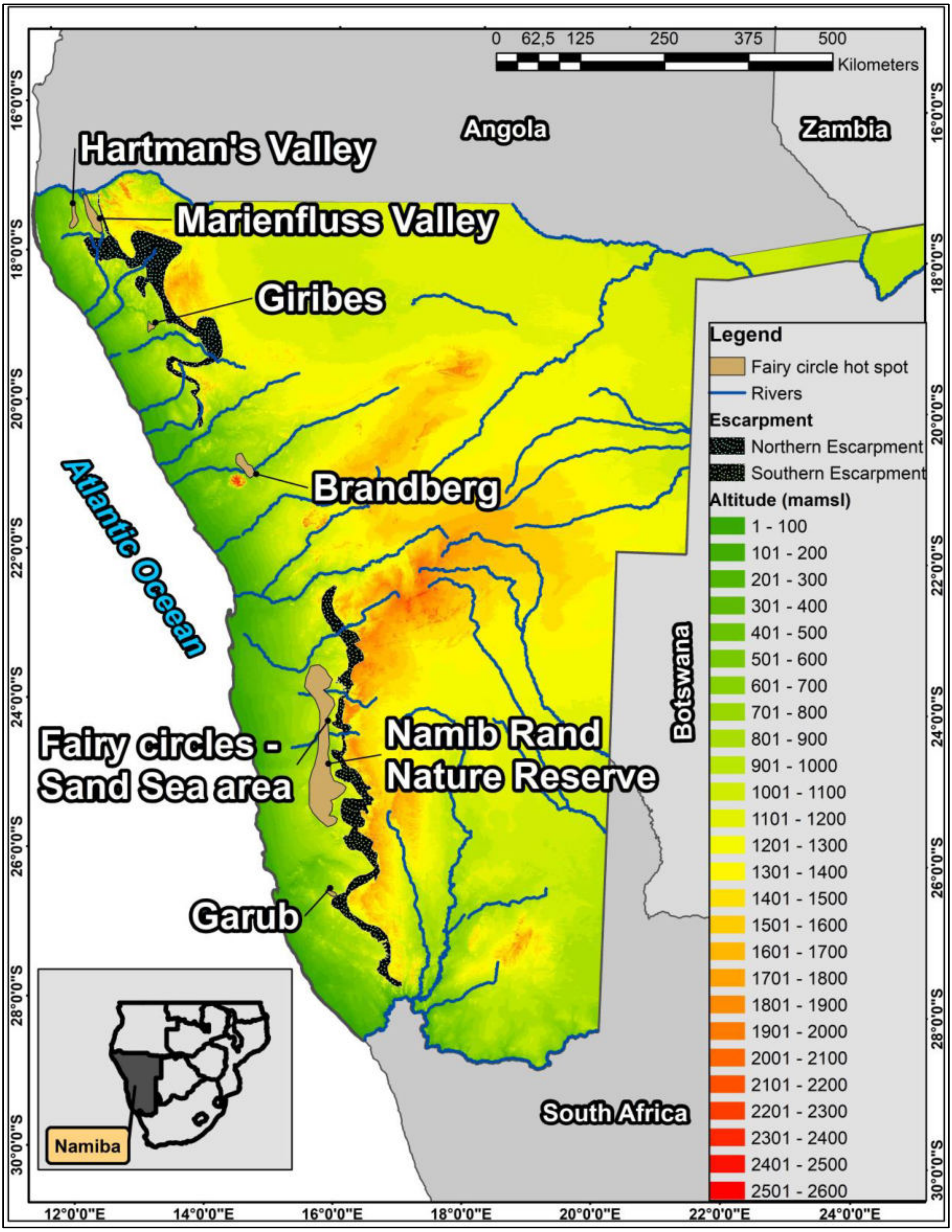

Figure 3.1: Locality map of Namibia, the relief is shown in mamsl (Mendelson et al. 2002). Fairy circle hot spots are indicated. The names of the hot spots refer to known geographical features near the hot spots.

3.2.2 Geology and soils

Geological processes over the last 2 600 million years have shaped the Namibian landscape. The geology of Namibia can be broadly classified into two geological zones (Mendelson et al. 2002). One is found in western Namibia where great rock formations are visible in a rocky landscape of valleys, escarpments, mountains and large open plains. In the east, sands and other sediments cover most of the surface and the landscapes are much more uniform. The rock formations of Namibia are clearly visible in many places. Much of this is due to the arid environment which has produced little top soil and vegetation to cover the underlying rocks (Mendelson et al. 2002). The underlying geology of Namibia is shown in Figure 3.2. Fairy circle hot spots were overlaid onto the geology data set, obtained from Mendelson et al. (2002). The geology of the Hartman's valley and the Giribes Plain is the rock formation Huabib Basin (SS Sh). The underlying geology of the Marienfluss valley, the Namib Rand Nature Reserve and Garub is Kalahari and Namib Sand (S) whereas the underlying geology of Brandberg is Damara Granites (G).

A map of the soils of Namibia is shown in Figure 3.3. Fairy circle hot spots were overlaid onto the soils data set Mendelson et al. (2002). Overall there is a lot of variation in the soils of Namibia, from the deep Kalahari sand to the clay sands of the Cuvelai system (Mendelson et al. 2002). Only the dominant soils of Namibia are however shown in Figure 3.3.

The soils of the Hartman's valley, the Namib Rand Nature Reserve and the Brandberg are Eutric regusols. Eutric refers to soils that are fertile with high base saturation, while regusols are medium or fine texted soils of actively eroding landscapes, the thin layers lying directly above the rocks from which they formed and cannot provide adequate water and nutrients to plants, therefore the vegetation cover is generally sparse

(Mandelson et al. 2002). The Marienfluss valley and Giribes Plain soils are Petric calcisols. Pertic refers to soils that have a solid layer at a shallow depth that remains hard even when wet, while calcisols are found in depressions are other low lying areas, typically contain accumulations of calcium carbonate. The soils of Garub are that of Alluvium sand, gravel plains and calcrete plains.

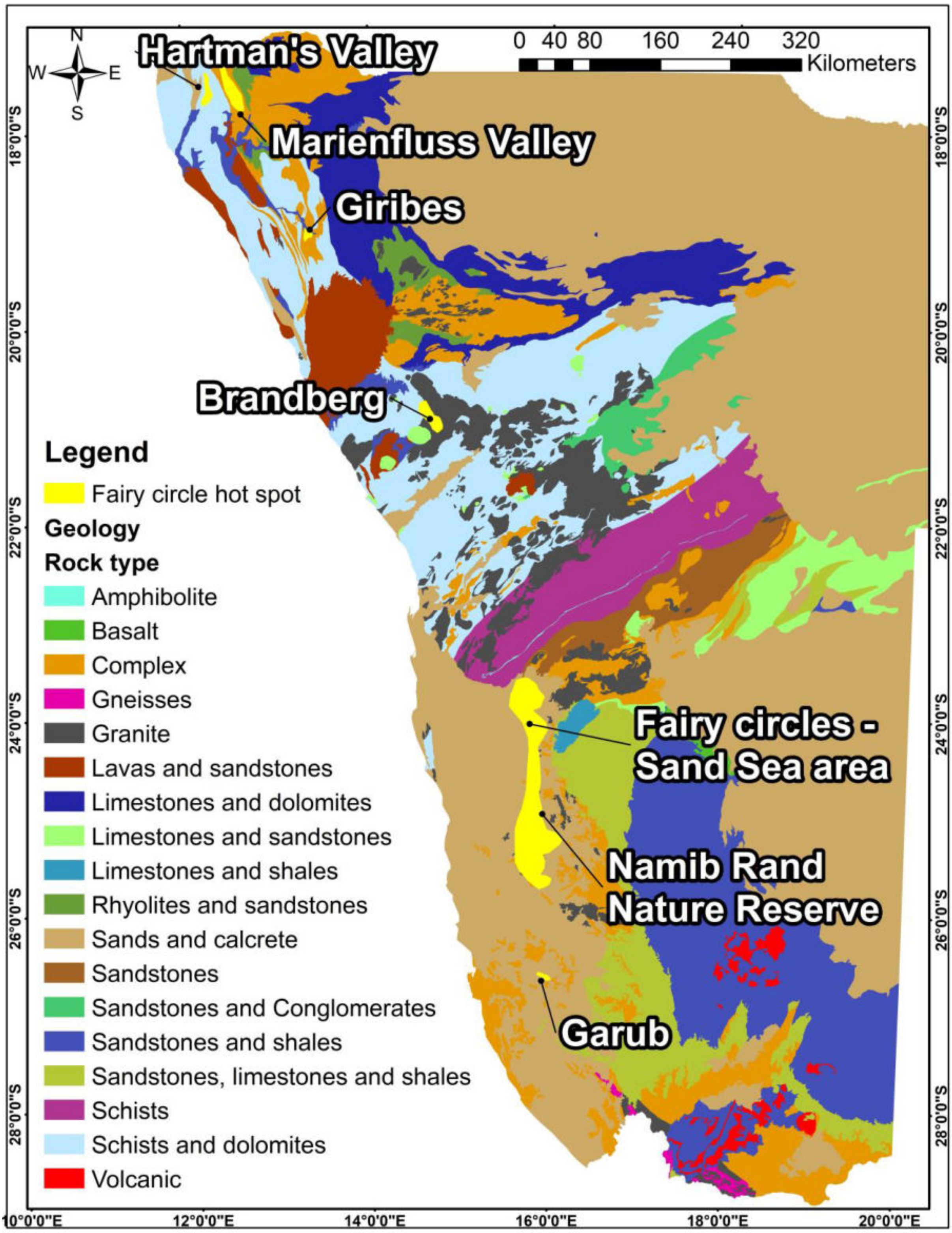

Figure 3.2: Geology of Namibia (Mendelson et al. 2002). Fairy circle hot spots are indicated.

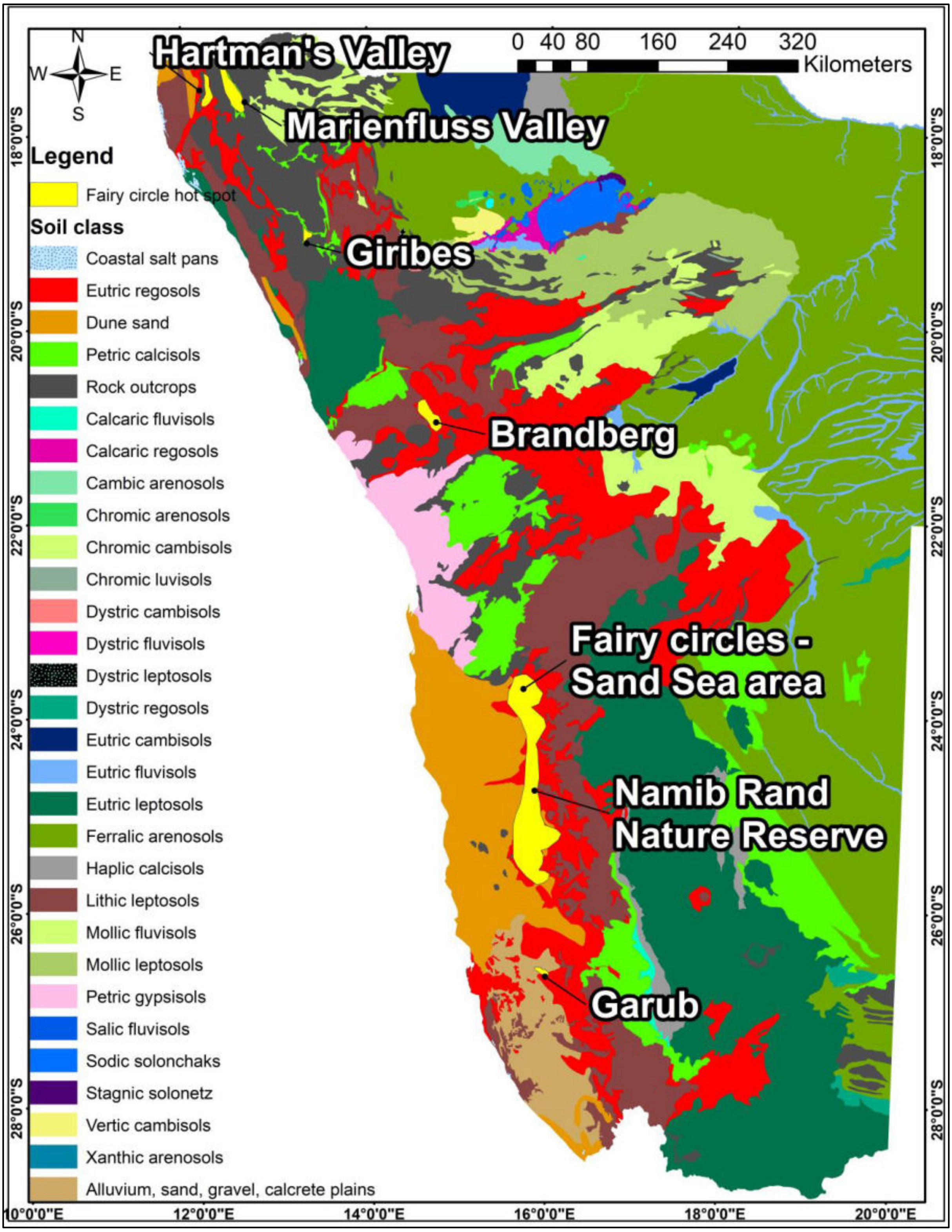

Figure 3.3: Soils of Namibia (Mendelson et al. 2002). Fairy circle hot spots are indicated.

3.2.3 Climate

Climate is a primary determinant of the nature and functioning of ecosystems (Turpie et al. 2010) and greatly influences all aspects of life in Namibia. Although there have been both wetter and drier periods in the past, Namibia's climate has been similar to what it is today for millions of years (Mendelson et al. 2002). The oldest sand dune deposits in the Namib Desert date back to between 13 and 18 million years ago, thus the kind of dry conditions required for their formation must have been present for a significant amount of time. The present-day climate in Namibia is dry, variable and harsh and has shaped the evolution of most animal and plant life (Mendelson et al. 2002). The climate is arid and the lack of moisture is attributed to the country's south-western position on the continent. Namibia is located between two climatic systems; the Intertropical Convergence Zone, which feeds in moist air from the north, and the Subtropical High-Pressure Zone, which pushes the moist air back with dry air. The latter system usually dominates and results in clear skies with dry weather. It is the lack of water in the atmosphere, rather than the absence of rain, that makes Namibia so dry. The dry air means that there are few clouds, radiation from the sun is intense, daytime temperatures are high and water evaporates rapidly. Namibia's climate has generally been arid for millions of years, resulting in an absence of deep soils over much of the country and low levels of nutrients in most soils (Mendelson et al. 2002). All rivers that drain within Namibia are non-perennial, only flowing after heavy falls of rain.

The average annual temperature range in Namibia is shown in Figure 3.4. Fairy circle hot spots were overlaid onto the average annual temperature data set obtained from (Mendelson et al. 2002). Although Namibia is considered a hot country, temperatures vary greatly during the day, day to day and seasonally. Plants and animals have subsequently developed tolerance to a wide range of temperatures. Frequent fog and cloud cover combined with cold south-westerly winds results in lower temperatures near the coast and is the lowest for areas situated at these latitudes. For example, the Average Annual Temperature (AAT) of Hartman's Valley, the Marienfluss Valley and the Namib Rand Nature Reserve is 19 – 21°C, while that of the Giribes Plain is 19 - 20°C. At Brandberg the AAT is 21 - 22°C, while at Garub is it is 16 - 17°C (see Figure 3.4).

The mean annual precipitation (MAP) in Namibia is shown in Figure 3.5. Fairy circle hot spots were overlaid onto the MAP data set, obtained from (Mendelson et al. 2002). The total annual rainfall varies greatly from year to year with most rain falling during sporadic storms in the summer months from September to February. The flow of moisture from the north also makes northern Namibia considerably wetter than the rest of the country, and there is a clear gradient from the wettest areas in the north to the arid, desert areas along the coast and in the south. The Mean Annual Precipitation (MAP) in the Hartman's valley, the Marienfluss valley, Giribes Plain, Brandberg and the Namib Rand Nature Reserve is between 100 – 150 mm/year, while at Garub it is 50 – 100 mm/year, (Figure 3.5). Fog is an important source of moisture along the coastal area. The average number of days with fog per year for the Hartman's valley, the Marienfluss valley and Garub is 20 – 25 days. Giribes Plain receives 5 – 10 days, while Brandberg receives from 5 – 25 days. The Namib Rand Nature reserve receives the fewest days of fog at 1 – 5 days per year.

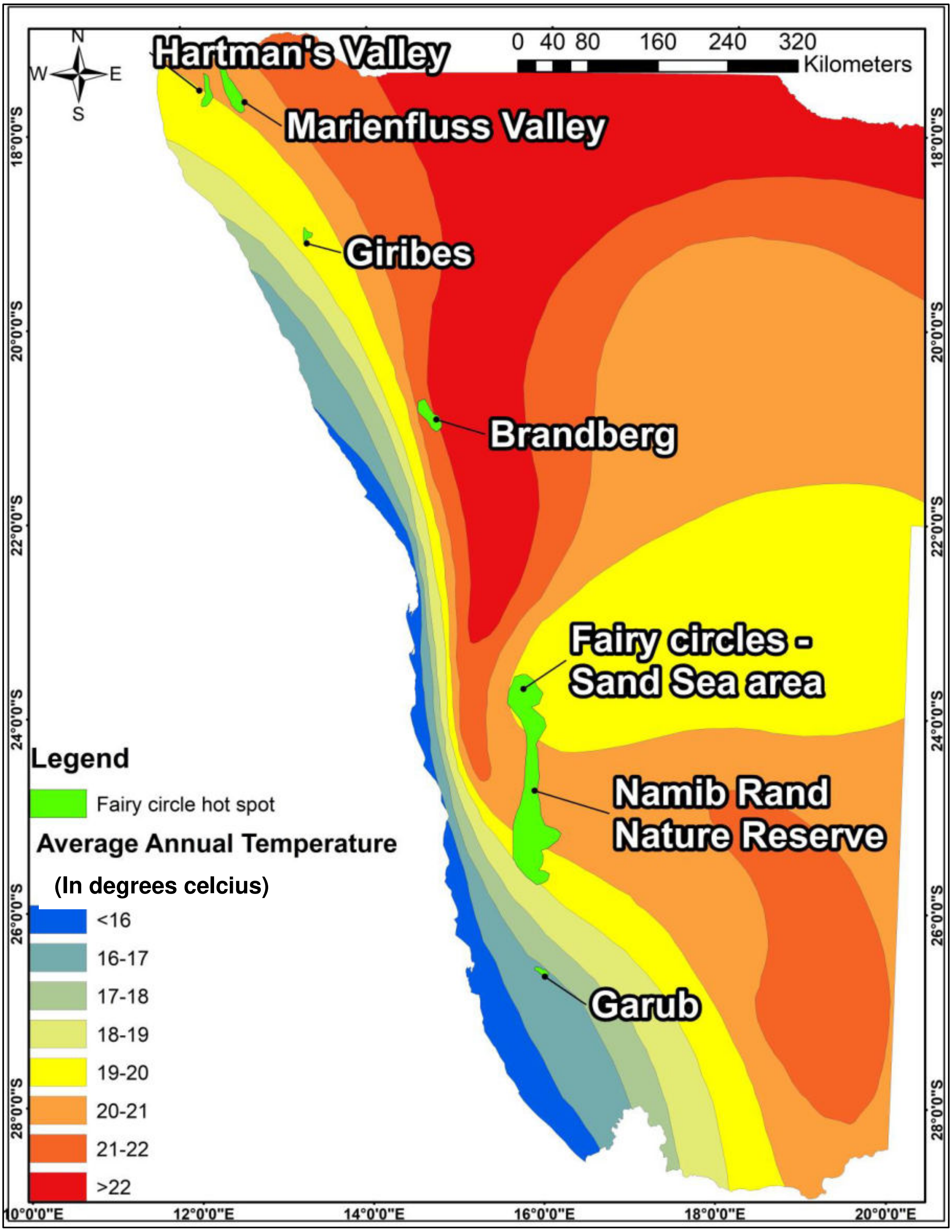

Figure 3.4: Average Annual Temperature (AAT) for Namibia (Mendelson et al. 2002). Fairy circle hot spots are indicated.

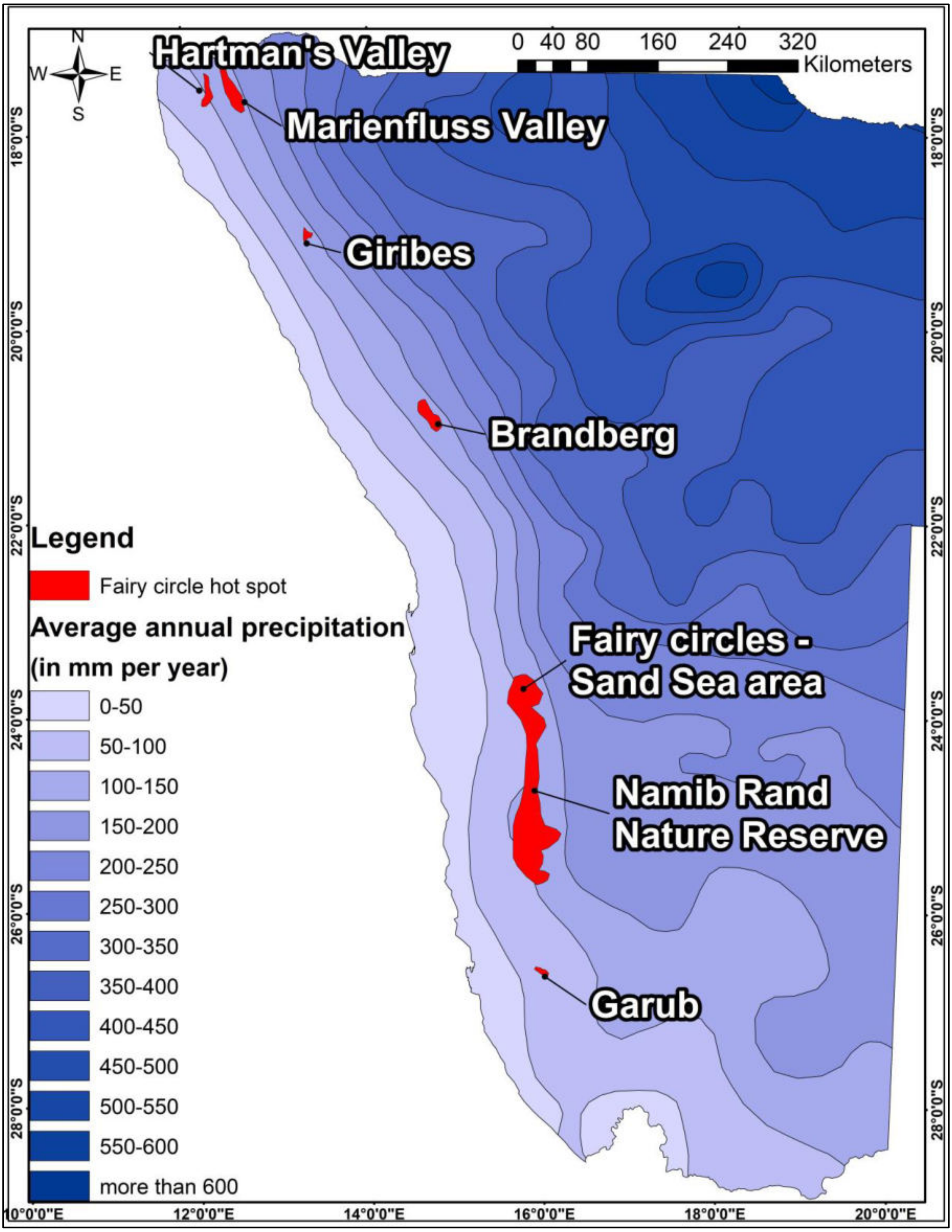

Figure 3.5: Mean annual precipitation in Namibia (Medelson 2002). Fairy circle hot spots are indicated.

3.2.4 Biomes and vegetation

The biomes and major rivers of Namibia are shown in Figure 3.6. Fairy circle hot spots were overlaid onto the biomes data set, obtained from (Mendelson et al. 2002). In contrast to the rich biodiversity found in the north east, an unusual assemblage of mostly endemic plants and animals have evolved to occupy the extremely arid Namib Desert. The classification of broad geographical areas into biomes provides a tool to summarise vegetation types according to the main climatic parameters and associated dominant growth forms (Rutherford et al. 1994). Due to the rainfall pattern of Namibia, vegetation is mostly lush and dense in the north east, and progressively more sparse and short in the west and south. However, this gradient is not clearly delineated and additional factors like soil types and landscapes also affect vegetation types (Mendelson et al. 2002). Twenty-nine known vegetation types have been ascribed to Namibia, each belonging to a biome. The tree- and shrub savanna biome is the most extensive in Namibia. The Namib Desert biome extends northwards from Lüderitz into Angola. The plant cover in this biome varies according to substrate; for example, sand dunes support only few grasses, while a variety of herbs, shrubs and grasses grow on the gravel plains, while shrubs and trees are found along ephemeral rivers. The Nama-Karoo biome has a varied assemblage of plant and animal life, ranging from deciduous shrubland to perennial grasslands and succulent shrubs. Due to the great variation in geology, soils and land forms, a wealth of plant species is found in this biome, although dwarf shrubland dominates. The Nama-Karoo biome includes the escarpment, separating the Namib Desert from the Acacia Tree-and-shrub Savana biomes. The succulent Karoo biome is dominated by both shrubs and dwarf shrub succulents.

The Hartman's Valley, the Marienfluss Valley and Giribes Plain are situated within the Nama-Karoo biome which is located in north-western Namibia, however the Giribes

Plain is located very close to the boundary between the Nama-Karoo biome and the Tree and Shrub Savannah biome. The area where fairy circles occur at the Brandberg area extend into both the Nama-Karoo and Tree and Shrub Savannah biomes. The area where fairy circles occur at the Namib Rand Nature Reserve and the greater Sand Sea area extend into both the Namib Desert and Nama-Karoo biomes. The area where fairy circles occur near Garub extends into both the Namib Desert and Succulent-Karoo biomes. The major vegetation types of Namibia are shown in Figure 3.7. Fairy circle hot spots were overlaid onto the major vegetation types data set, obtained from (Mendelson et al. 2002). The Hartman's valley, the Marienfluss valley and Giribes Plain are situated within the north-western escarpment and iselberg vegetation type. The area where fairy circles occur at Brandberg extend into both the central desert and central-western escarpment and iselberg vegetation types. The area where fairy circles occur at the Namib Rand Nature Reserve and the greater Sand Sea area extend into; the central-western escarpment and iselberg, the Southern desert and the Desert/dwarf Shrubland transition vegetation types. The area where fairy circles occur near Garub extends into Southern desert vegetation type.

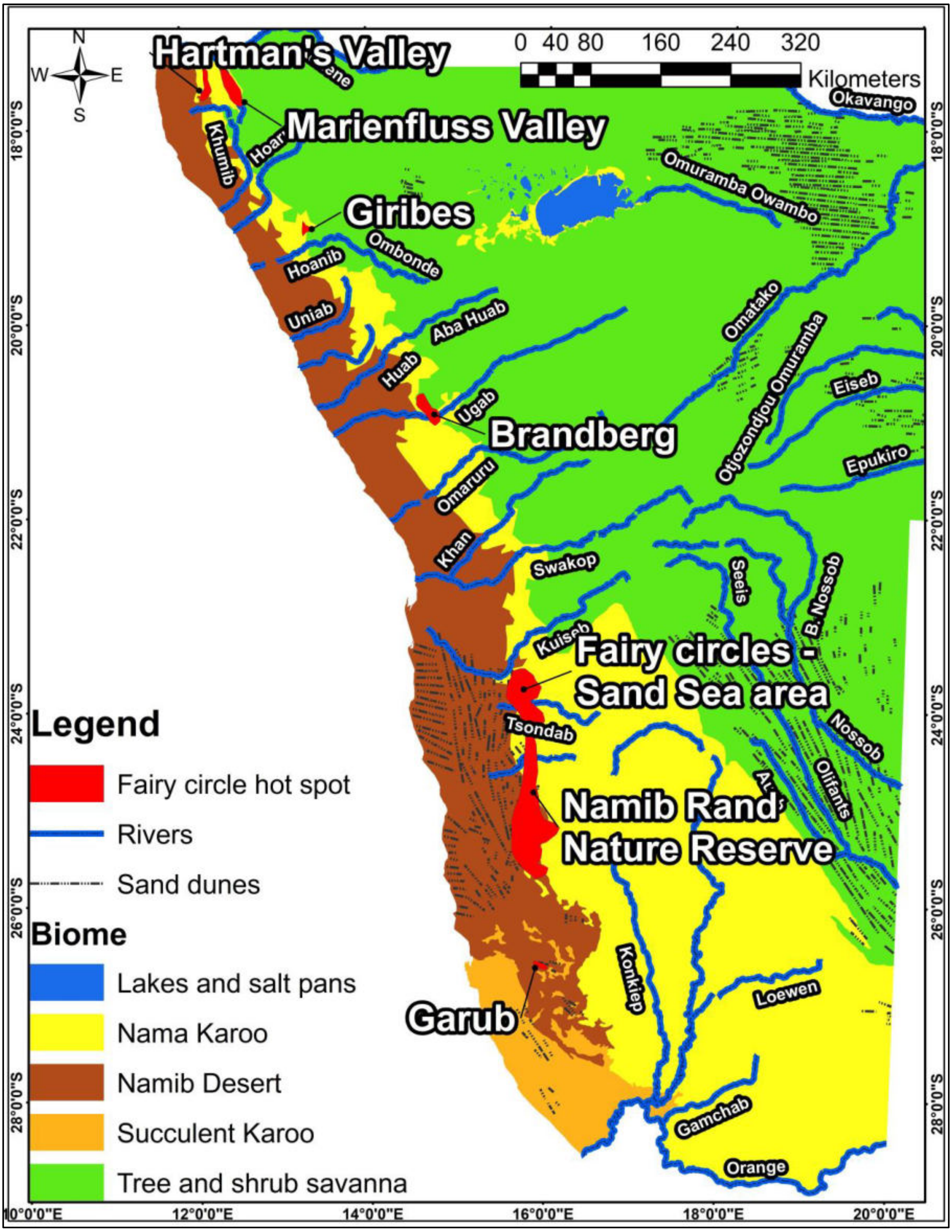

Figure 3.6: The biomes and major rivers of Namibia (Medelson 2002). Fairy circle hot spots are indicated.

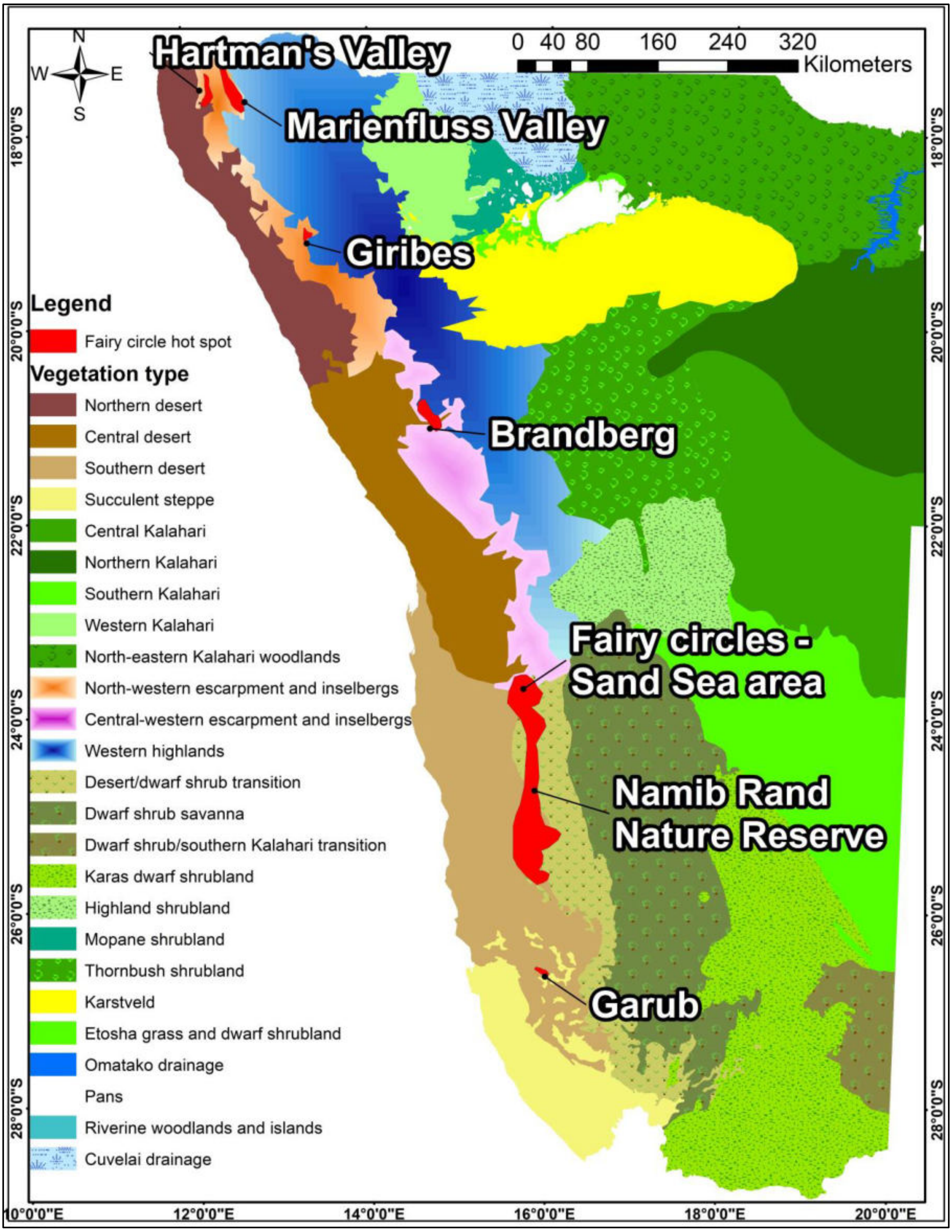

Figure 3.7: The major vegetation types in Namibia (Mendelson et al. 2002). Fairy circle hot spots are indicated.

3.2.5 Landscapes

The major landscapes of Namibia are shown in Figure 3.8. Fairy circle hot spots were overlaid onto the major landscapes data set, obtained from (Mendelson et al. 2002). Hartman's Valley, the Marienfluss Valley and the Giribes Plain are all located in the Kunene Hills landscape, north-western Namibia. Ancient rivers and their tributaries have left a highly dissected terrain behind with the substrate consisting of deep sandy aeolian deposits. While the sandy substrate of the Hartmann's Valley, Marienfluss Valley and the Giribes Plain, are of aeolian origin, there are several other areas in this landscape, where the substrate is of alluvial origin, formed by the Otjihaa, Gomatum and the Hoanib rivers (Cramer et al. 2016).

Both the Namib Rand Nature Reserve as well as Garub are located within the Namib gravel plain landscape. Gravel and thin layers of sand cover most of the Namib Plains, out of which many rocky outcrops and hills protrude. Some of these are large hills or mountains that are included under the iselberg category of landscapes, but there are also many smaller outcrops of granite, as well as dykes and sills. The very arid coastal plain coastal climate means that water erosion is limited, and the overall landscape is predominantly flat. However, several large rivers flow along valleys that cut through to the sea, occasionally carrying water from heavy rains in the interior. The Namib Plains and the Namib Sand Sea together make up much of the coastal plain, which although generally flat, rises up to 800 mamsl in places in the east (within the fairy circle range).

The area associated with fairy circles at the Namib Rand Nature Reserve extend into the Namib Sand Sea. This landscape consists of several large areas of sand dunes along the coast including one dune stretching between Luderitz and Walvis Bay which is perhaps Namibia's most prominent hallmark. This great sand sea is 100 -150 km wide in breadth and 400 km in length. Transverse and barchan dunes cover coastal areas where the winds are strongest, while linear dunes running roughly south to north dominate the inland areas. A few grasses grow on the inland dunes, but the most mobile dunes near the coast are devoid of plants. On the other hand, the dunes are home to a diverse fauna of insects and other mammals. The Hoanib, Kuiseb and Kunene Rivers stop the northward march of the three main dune fields.

The area near Brandberg is located within the central western plains landscape, which stretches back from the coast and reaches up to 450 km inland in some places. Largely formed by erosional processes that cut back into higher ground and carved out the catchment areas of several major rivers (i.e. Ugab). Much of the area lies between 500 and 1000 mamsl and consist of metamorphic rocks that were forced up out of the sea during the formation of Gondwana Land approximately 500 million years ago.

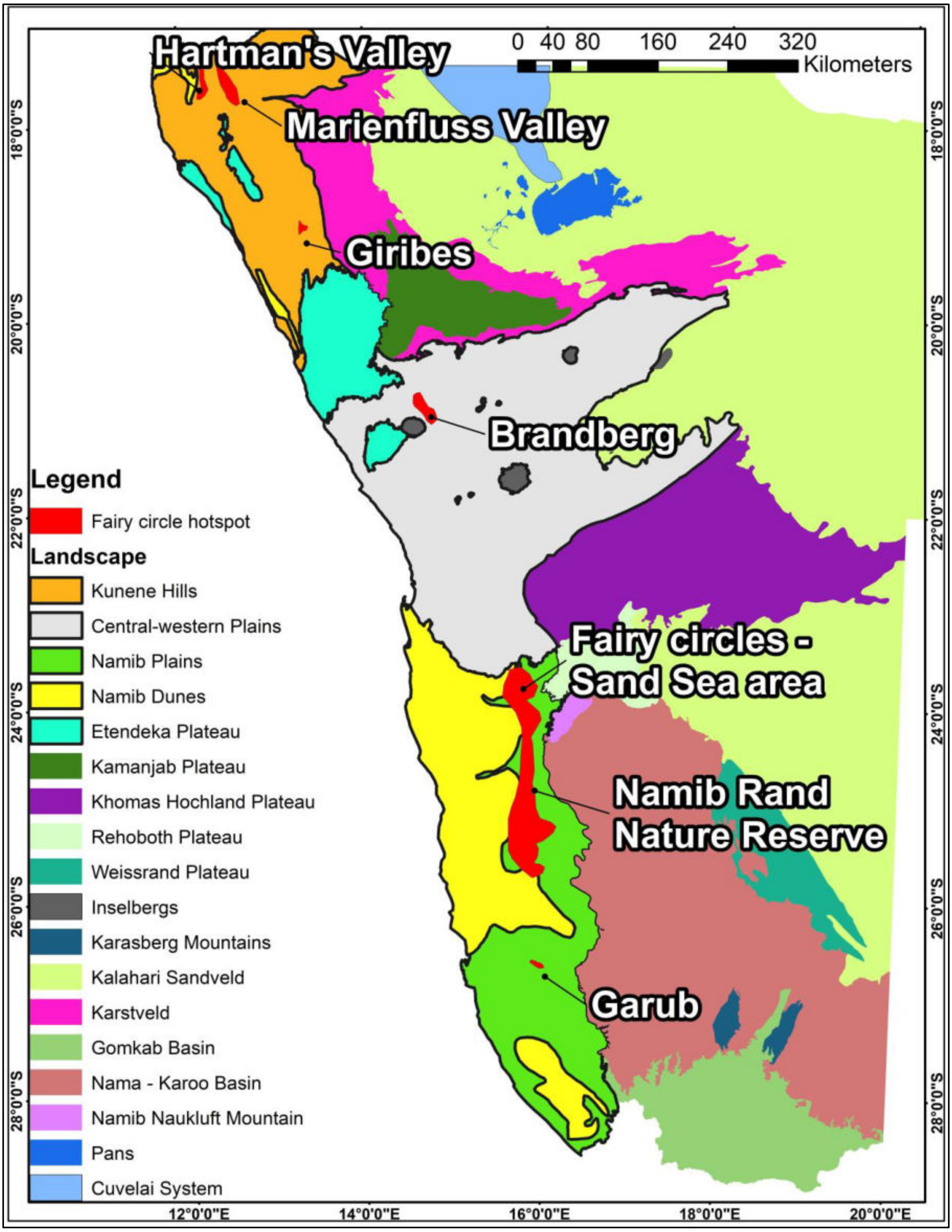

Figure 3.8: The Landscapes of Namibia (Mendelson et al. 2002). Fairy circle hot spots are indicated. Fairy circles are known to occur in the Kunene Hills, Central Western Plain, the Namib Sand Sea and the Namib Plain.

3.3 Methods

In this section the site suitability analysis predicting the location of fairy circles was undertaken. The criteria that was used to construct the suitability model is firstly outlined and the steps undertaken to obtain data that could accurately represent the defined criteria is described. All the data was available in electronic format and entered into ArcMap (ESRI) where it was prepared for the analysis. Various GIS operations were performed on the data to create the suitability map. The resultant map was then validated by creating 100 random sample points and inspecting them in Google Earth for the presence/absence of fairy circles. The presence of the three *Euphorbia* species, *E. damarana, E.* gummifera and *E.* gregaria were then investigated in the areas where the suitability map predicted the occurrence of fairy circles.

3.3.1 Defining the criteria for the formation of fairy circles

Several environmental factors have been found to be associated with the presence of fairy circles (see Cramer et al. 2016, Cramer et al. 2013, Juergens 2013). This section describes how the criteria was selected from relevant literature and applied to create a suitability model (Table 3.1).

Table 3.1: Criteria that was used to model fairy circle distribution.

Variable	Criteria
Mean annual precipitation (MAP)	50 – 150 mm
Altitude	500 – 1200 mamsl
Grassland and land substrate as Land cover	Ephemeral grasslands underlain by sand

Rainfall:

Although fairy circles are closely associated with the 100 mm rainfall isohyet, they have also been found to be in areas that are just outside this range. According to Juergens (2013) fairy circles are generally confined to areas with a MAP of 80 mm to 120 mm. However, the conservative approach was followed, and the precipitation range outlined by Becker and Getzin (2000) and Cramer et al. (2016) of 50 mm to 150 mm MAP was used.

Altitude:

Altitude is another important predictor variable of where fairy circles are likely to occur. Previous literature studies restrict fairy circles to the specific altitudinal range from 500 m to 1 200 m above mean sea level (Viljoen 1980, Van Rooyen et al. 2004). This was then used as delineating criteria in the suitability model.

Landcover:

Fairy circles most often occur in grasslands on sandy soil. In this study it was attempted to combine these two variables into one predictor variable, in contrast to Cramer et al. (2016) who separated the Enhanced Vegetation Index (EVI) and the particle sizes of the sandy soil where fairy circles occur. In this study soil samples were taken from locations where fairy circles co-occur with Euphorbia *species*. This was done to determine the physical properties of the soil from areas where fairy circles co-occur with *E. damarana* and *E. gummifera*. It should be noted that this did not form part of the data used in suitability analysis but formed part of the process to correctly classify the land cover types according to the true surface type (refer to Section 3.3.3).

Previous studies have used Landsat TM 5 imagery to study the fairy circle phenomenon. For example, Getzin et al. (2008) visually inspected Landsat TM imagery and successfully identified areas in north-western Namibia that contained sandy deposits and fairy circles. These researchers were also able to identify sandy accumulations from Landsat imagery because they appear different than surrounding land cover classes due to their spectral properties. In the current analysis Landsat imagery was subjected to an unsupervised image classification technique (see methods for more detail) to group the pixels into different land cover types based on similar spectral properties. The land cover classes corresponding to grassland on sandy deposits was determined. The false colour composite of band 7 (mid InfraRed), 4 (InfraRed) and 2 (Green) is ideal for geological studies in deserts (USGS - website 2018). Similarly, Juergens et al. (2012) used Landsat 7 ETM composite images with the band combination of band 7, band 4 and band 2 to conduct vegetation studies in central western Namibia. This band combination was similarly used in this study and vegetation and substrate was combined into a single variable namely land cover. The dates of the imagery were an important consideration and it was decided to choose a year where the grass biomass would be high. Namibia received higher than average rainfall during 2008 and 2009 and it was considered that the grass biomass would be most suitable during these years.

Landcover: Soil characteristics

By combining the occurrence of grasslands and sandy deposits into a single variable using satellite data, it allows the assessment of vast areas that are often inaccessible to most researchers. However, it still remains important to gather field data to inform the land cover classification process. As mentioned above soil samples were analysed to determine the physical properties of the soil from areas where fairy circles co-occur with *E. damarana* and *E. gummifera.* During field work soil samples were taken from Giribes Plain (9 samples), Brandberg (9 samples) and Garub (3 samples). The sand fraction was determined for the soil samples. The sand fraction characterises soil particles according to size. For the sand fraction test, the samples were put through sieves of the following sizes classes; >1000ɥm, >500 ɥm, >250 ɥm, >100 ɥm, >53 ɥm and <53 ɥm to collect different sized particles. Particle size analysis was performed to identify the sand, silt and clay fractions present in each sample. The method comprises two parts, dispersion of the soil and separation of particles into size groups (Bowman and Hutka 2002). To allow the soil to disperse completely, the soils were pre-treated to remove organic material and salts. The next step involved removing each particle size group (sand, silt and clay) from the pre-treated soil water mixture, settled in a cylinder. This is accomplished by allowing the soil particles of different size to settle out of the solution at different times. A floating device, with measure units, was placed in the pre-treated soil water mixture. A first reading was taken at the start of the experiment. Then 6.5 hours later a second reading was taken and together with the first was used to calculate the concentration of sand, clay and silt. Some calculations are needed for this method, including using a scaling factor (Bowman and Hutka 2002). The fractions were subsequently dried and weighed, the sand, silt and clay fractions must add up to 100%. This was done to characterise the soils at sites where fairy circles co-occur with *E. damarana* and *E. gummifera.*

3.3.2 Data acquisition and entry

All data used in the study was freely available in electronic format and more information about it is provided in Table 3.2.

Table 3.2: Data source specifications.

Data set	Format	Coordinate system	Source
Average annual precipitation	Vector – (shapefile - polygon)	WGS 1984	Environmental Information Services-Website of Namibia (EIS, 2018)
Altitude	Raster – (41 x DEMs) Resolution: 30 m x 30 m	UTM Zone 33 S	United States Geological Service Website
Land cover[1]	Raster – (20 x Satellite images) Resolution: 30 m x 30 m	UTM Zone 33 S	United States Geological Service Website

The Atlas of Namibia:

The rainfall data used in the analysis was obtained from the Atlas of Namibia (Mendelson et al. 2002). The rainfall data set was available in vector shapefile and contained categorical data. The scale of the data set was at the sub-continental scale. The rainfall data only had the WGS1984 geographic coordinate system associated with it and was projected to the same projection as the altitude and land cover data sets (see below). The data set was developed from actual rainfall monitoring data obtained from a variety of sources including private and governmental organisations (Mendelson et al. 2002). For more details regarding the development of the rainfall data set see the Namibia Resource Consultants (1999).

ASTER satellite:

Elevation data was obtained from the United States Geological Society's (USGS) website in the form of several ASTER DEMs developed from the ASTER satellite. The

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[1] Refer to Appendix I for details regarding the imagery dates.

Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) is an advanced multispectral imager that was launched on board NASA's Terra spacecraft in December 1999 (USGS, 2018). A product from the ASTER Satellite data are digital elevation models (DEMs). Both absolute and relative DEM's can be ordered. An absolute ASTER DEM is generated by using ground control points (GCP) supplied by the requestor. The software uses the GCPs to tie the DEM to known points on the ground and yields a product with real ground elevations. The absolute DEM is geo-coded using customer-supplied ground control points (GCPs). A relative ASTER DEM is generated by using only the satellite ephemeris data and will yield a product with ground elevations that are quite near those of an absolute DEM (USGS, 2018) The DEMs were obtained in raster format. A total of 41 DEMs were downloaded from the USGS website through the Earth Explorer interface. The spatial reference of the DEMs was UTM Zone 33S, which is based on the WGS84 datum. The spatial resolution of DEMs was 30 m x 30 m.

Landsat satellite:

It was decided to use Landsat TM 5 imagery, which is geometrically-, radiometrically- and atmospherically corrected. This decision was based on the fact that in 2003 the scan line corrector (SLC) of the Landsat 7 satellite failed. This resulted in data gaps, leaving individual scenes with only 78 percent of their pixels (USGS - website 2018). The spatial reference associated with the Landsat scenes were identical to the ASTER satellite scenes, i.e. UTM Zone 33S. A total of 20 Landsat 5 TM satellite scenes were obtained taken between the months of March and May of 2009, although where a particular scene was not available for 2009, a scene from 2008 was selected. Refer to Appendix I for the identification and date of image. The search criteria used to search for the imagery was set to only include imagery with 0 % cloud cover. The scene dimensions are 170 km north-south by 183 km east-west, with a resolution of 30 m by 30 m. Considerable processing of satellite imagery was required to extract the land cover data and is discussed in the model building step below.

3.3.3 Building the model

The ArcGIS model for the analysis is shown in Figure 3.9. Three predictor variables were used to construct the site suitability model: they were mean annual precipitation (shown in blue), altitude (shown in orange) and land cover (shown in green).

As previously indicated, fairy circles are known to occur in areas with MAP of between 50 mm to 150 mm per year. In order to extract this data a shapefile containing the MAP data for the study area was obtained. To ensure that all the data layers contained the same spatial reference, the shapefile containing the MAP was projected to the UTM Zone 33S projection. Next a Boolean operation was performed to isolate the 50 – 150 mm MAP for the study area, the attribute selection was as follows:

"MAP = (50 – 100 mm.y^{-1} AND 100 – 150 mm.y^{-1})"

This is represented by the blue portions of the model below.

As previously indicated, fairy circles are known to occur in areas with an elevation range of between 500 m to 1 200 m above mean sea level. In order to extract this data 42 ASTER DEM's were imported into ArcMap and mosaicked into a single layer. This data set was then reclassified to contain areas with an elevation between 500 and 1 200 mamsl by assigning a "1" to elevations within this range and a "0" to elevations outside of this range (both less and greater than the ideal altitudinal range). This layer was then converted to a vector data set. This is represented by the orange portions of the model.

The next step in building the model was to identify the areas where both the ‘suitable’ rainfall and the ‘suitable’ altitude overlap and this area will be referred to as the “ideal rainfall and altitude” area. This was done using the intersection tool in ArcMap.

The next step in the building of the model, was to extract areas within the ideal rainfall and altitudinal range where the underlying land cover is sandy plains covered by grasslands. This involved using the Landsat TM 5 imagery to extract the pertinent criteria (i.e., sandy plains covered by grasslands). In order to do that a false colour image (B=7,4,2), was created for each Landsat scene (refer to section 3.3.2 above for the motivation behind using this specific combination of spectral bands).

Landsat scenes are compiled by the USGS in such a way that the sides of adjacent images overlap. This can result in processing errors and had to be prevented by clipping the images. Clipping is a raster processing tool that is used to reduce the spatial extent of the image. This was done by creating a new polygon feature class that defined the reduced spatial extent of the image. This effectively means that the side of the image that overlapped with an adjacent image was “cut-off”. The newly created features classes were in the shape of a square and the position of each square was determined by the previous square’s position.

In order to extract the desired land cover, i.e. sandy plains covered by grasslands, the images had to be classified into different land cover types according to their spectral properties. The *ISO-Cluster Unsupervised Image Classification* technique was applied to each image. This image classification technique entails grouping pixels with similar spectral values together into a group. Each image was grouped into 15 land cover classes representing features on the surface of the earth. It must be noted that surface features were represented by more than one land cover type; i.e. bare rock surfaces could be represented by more than two classes. Rock surfaces typically included iselbergs, rocky out crops, and desert pavement (coarse gravel plains).

The raw land cover classification data was manually inspected and classes representing the same surface features grouped into a single land cover class so that the different land cover types corresponded to either rock, vegetation or sandy grass plains. Several measures were taken to correctly classify the land cover types according to the true surface type. This included using Google Earth, the Landsat imagery, ArcMap World Imagery base, the National Land Cover data set for Namibia (FAO 2010) and shapefiles containing the location of various sandy accumulations (Mendelson et al. 2002) as reference to identify different features. The area in Google Earth corresponding to the different images were visually assessed while assigning the land cover classes. The Landsat imagery, ArcMap base map and the National Land cover data set layers were placed underneath the raw image classification data and the “slider” tool was used to view the underlying data.

These processed land cover types were then reclassified so that the grasslands were contained in one land cover type and all other classes in one. This was done by assigning a value of “1” to the identified grassland land cover type and assigning a value of “0” to all the non-grassland land cover classes. The “extract by attribute” tool was used to isolate the grasslands only and exclude all the other land cover classes. These 22 grassland raster data sets were then combined into a single layer with the “mosaic to new data set” tool and represented the grasslands identified for the study area.

The final step in building the model was to do an intersection of the ‘ideal rainfall and altitude’ and the grassy covered sandy plains. This was done by clipping the land cover data sets to the ideal rainfall and altitude layer. This resulted in a final site suitability map indicating areas that are predicted to have the presence of fairy circles in mainly Namibia.

3.3.4 Model validation

The final site suitability model was validated in four ways. Firstly, six field excursions were undertaken during March 2015, March 2016, July 2016, November 2016, March 2018 and August 2018 in order to inspect the study area (as the study was conducted for the entire Namib Desert, it was impossible to inspect the entire study site). Most of the routes travelled during the various field trips fell within the band where fairy circles were predicted to occur, and extended from the south-western corner northwards, along the eastern side of the Namib Sand Sea, past Brandberg and up to the Giribes Plain. Sites where fairy circles and / or *E. damarana* and / or *E. gummifera* occur, was documented by recording the GPS locations. This helped in identifying the land cover types.

Figure 3.9: GIS model. Blue corresponds to determining the ideal rainfall range, the orange part corresponds to determining the ideal altitude range and the green part determining the ideal land cover. The grey area represents the validation part of the modelled fairy circle distribution, while the purple area represents the control.

Secondly, random sample points (100) were generated within the area predicted to contain fairy circles. Next a buffer of 10 km was generated around each point, exported to Google Earth and inspected to determine whether in fact fairy circles were located where they were predicted to occur. This is represented by the grey in Figure 3.9. The third way involved creating a control for the study by identifying areas where none of the criteria were present and where the area is considered to be unsuitable for the formation of fairy circles. Random sample points were then generated in this area to determine whether in fact fairy circles were located where they were not predicted to occur. The historical imagery tool had to be used, as the coverage of the imagery varies both in terms of spatial and temporal resolution; i.e. certain sites had several years of imagery, others only one or two years of coverage (sometimes during the dry season when grass was absent), while other sites were not covered with imagery of adequate spatial resolution. Both sets of polygons were then exported into Google Earth, where they were inspected for the presence/absence of fairy circles.

Random sample points:

In order to validate the site suitability model results one hundred points were randomly generated in the area predicted by the site suitability model to contain fairy circles (positive control). A buffer of 10 km was constructed around each sample point and the resultant polygons exported as a *.kml file. This file was then manually inspected in Google Earth for the presence or absence of fairy circles. When there were more than 10 bare circular patches in the same area with a minimum size of 2 m, they were considered to constitute the presence of fairy circles.

The second part of the validation process was to confirm that areas where fairy circles were predicted to be absent, did not contain fairy circles, using the identified criteria (negative control). The resultant area, 29 380 km^2, was smaller than the modelled fairy circle distribution of 55 955.14km^2. The total area covered by the 100 random points, used to inspect the modelled fairy circle distribution (positive control), was 31 500 km^2. To inspect an area within the negative control of the *relative* same size as that of the modelled fairy circle distribution, 83 random points was generated with an 8 km buffer drawn around each point resulting in a total area of 16 600 km^2. 83 points were needed to account for the difference in size between the two areas This resulted in an area of 200 km^2 per point, compared to 315 km^2 of the 100 positive control random sample points. This area was then manually checked for the presence or absence of fairy circles.

3.3.4 Comparison with Euphorbias

To compare the site suitability map with the distribution of three species of *Euphorbia*; *E. damarana*, *E. gummifera* and *E. gregaria*, the distribution maps for all three *Euphorbia* species were obtained from Tree Atlas Project (TAP) of Namibia (Curtis et al. 2005). The information provided by the TAP were gathered mostly from voluntary participation of the public (Curtis et al. 2005). The information provided by the TAP is a summary of the data and gives an indication of broad trends and characteristics of the woody species of Namibia (Curtis et al. 2005). The data were collected by grid cell, with a grid based on 15' x15' or quarter-degree square. This is approximately 27km by 27km. Atlassers (voluntary participants collecting data for the TAP project) recorded their observations for each quarter-degree square on a printed atlas sheet, with a new sheet for each month. Atlassers were required to fill in according to the *Guidelines for Atlassers* (TAP 1997). Three data sets were obtained, one for each species of

Euphorbia. Each layer was overlaid onto the modelled fairy circle distribution and each layer was also intersected with the modelled fairy circle distribution.

3.4. Results and Discussion

3.4.1 Site suitability prediction model

Figure 3.10 shows the output from the first step of building the model, illustrating the areas that receive between 50 – 150 mm of MAP. As can be seen from the figure, the ideal rainfall range is found mainly in a narrow band from the north to the south and covers an area of 220,734 km². Towards the south it widens and expands more inland up to a distance of 400 km at it furthest point. This indicates that the precipitation range containing fairy circles near the coastline, extends into the south east of Namibia.

Figure 3.11 depicts the ideal altitude for fairy circle distribution (i.e., between 500 – 1 200 mamsl). The Digital Elevation Model (DEM) used to construct the ideal altitude range for the model is included in Appendix II and was created by combining the 41 individual DEMs into a single raster data set. Similar to the ideal rainfall range, the ideal altitudinal range stretches from north to south. Unlike the ideal rainfall range however the ideal altitudinal range does not extend to the coast in some places but is much broader than the ideal rainfall range, covering an area of 252 897 km² and stretching further inland. There are several areas where the ideal altitudinal range extends more inland; close to the Hartman's Valley and Marienfluss Valley, a big area between Giribes Plain and Brandberg, as well as a large area in the south that roughly corresponds to the ideal rainfall range in this area. Slightly to the north of Brandberg, the ideal altitudinal range extends inland up to a maximum distance of 315 km. The

Ugab River and associated tributaries have cut back the escarpment here to a great extent, hence the ideal altitudinal range extends far inland here.

Figure 3.12 shows the intersection between the ideal rainfall range and ideal altitudinal range. The resultant area is considerably smaller and covers an area of 148 203 km². The map extends into the south east of Namibia, indicating that these areas have the potential for fairy circles to occur there, although this has not been documented previously. However, the region shown in the ideal rainfall and altitudinal range covers extensive areas where the underlying land cover is not only sandy grass plains, but also include various other classes, for example large rock outcrops and more dense vegetation where fairy circles are not predicted to occur.

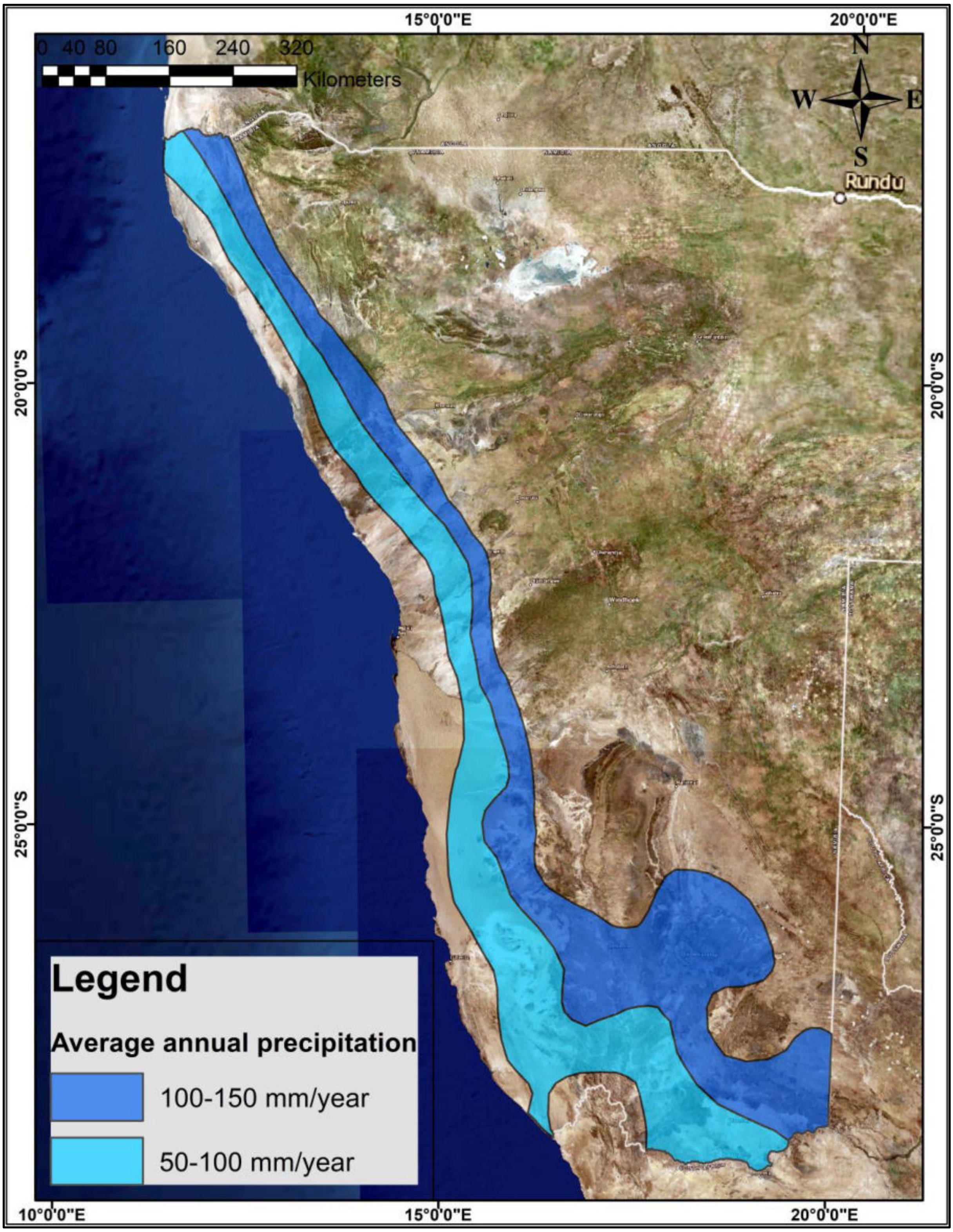


Figure 3.10: The ideal rainfall range for fairy circles, defined as 50 - 150 mm/year.

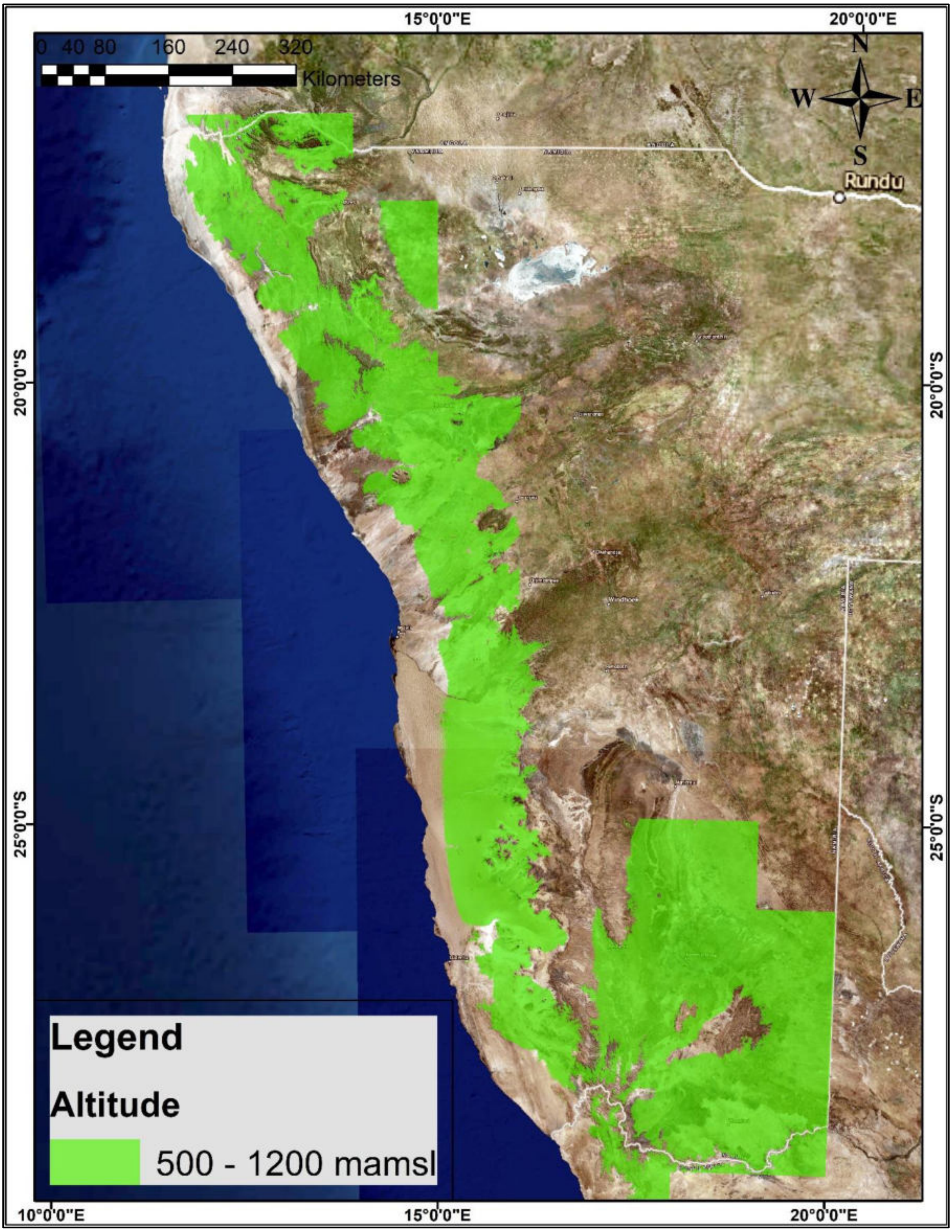


Figure 3.11: Ideal altitudinal range (500 – 1200 mamsl) for fairy circles.

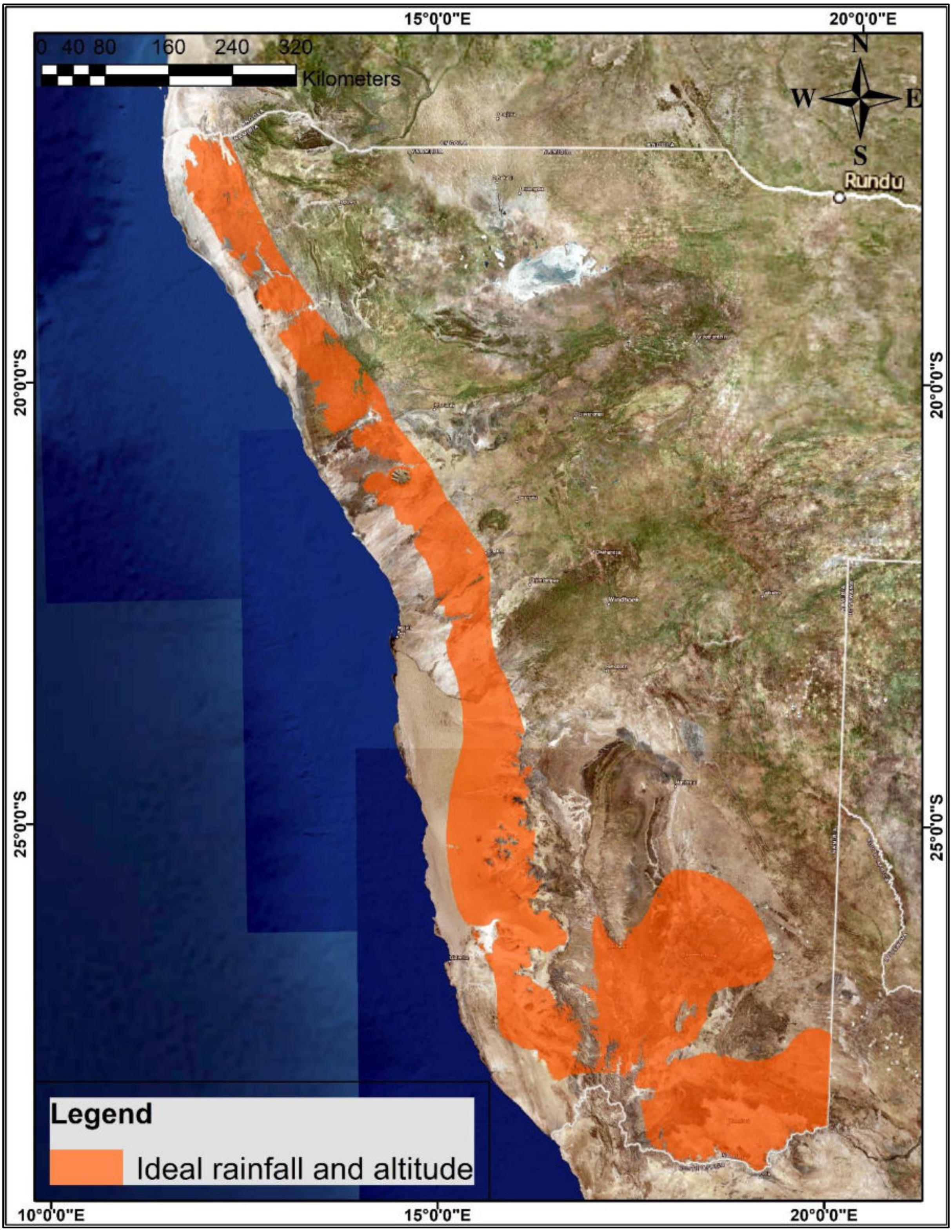


Figure 3.12: The ideal rainfall and altitude range. Note how the area extends into south eastern Namibia.

To illustrate the image classification process, Figure 3.13 A and B and Figure 3.14 A and B, shows the various outputs from the image classification for the greater Giribes area. The Giribes Plain, situated between mountains and rocky outcrops, is easily identified from the satellite image shown in Figure 3.13 A. Figure 3.13 B shows that the ISO-clustered unsupervised classification grouped the land cover into discrete, unsigned classes, the Giribes Plain consists of three land cover types, different from the surrounding mountains and rocky outcrops. In Figure 3.14 A the unsigned classes have been inspected and assigned into one of the three predefined land cover classes. The sandy grass plains were extracted into a single layer, as shown in Figure 3.14 B.

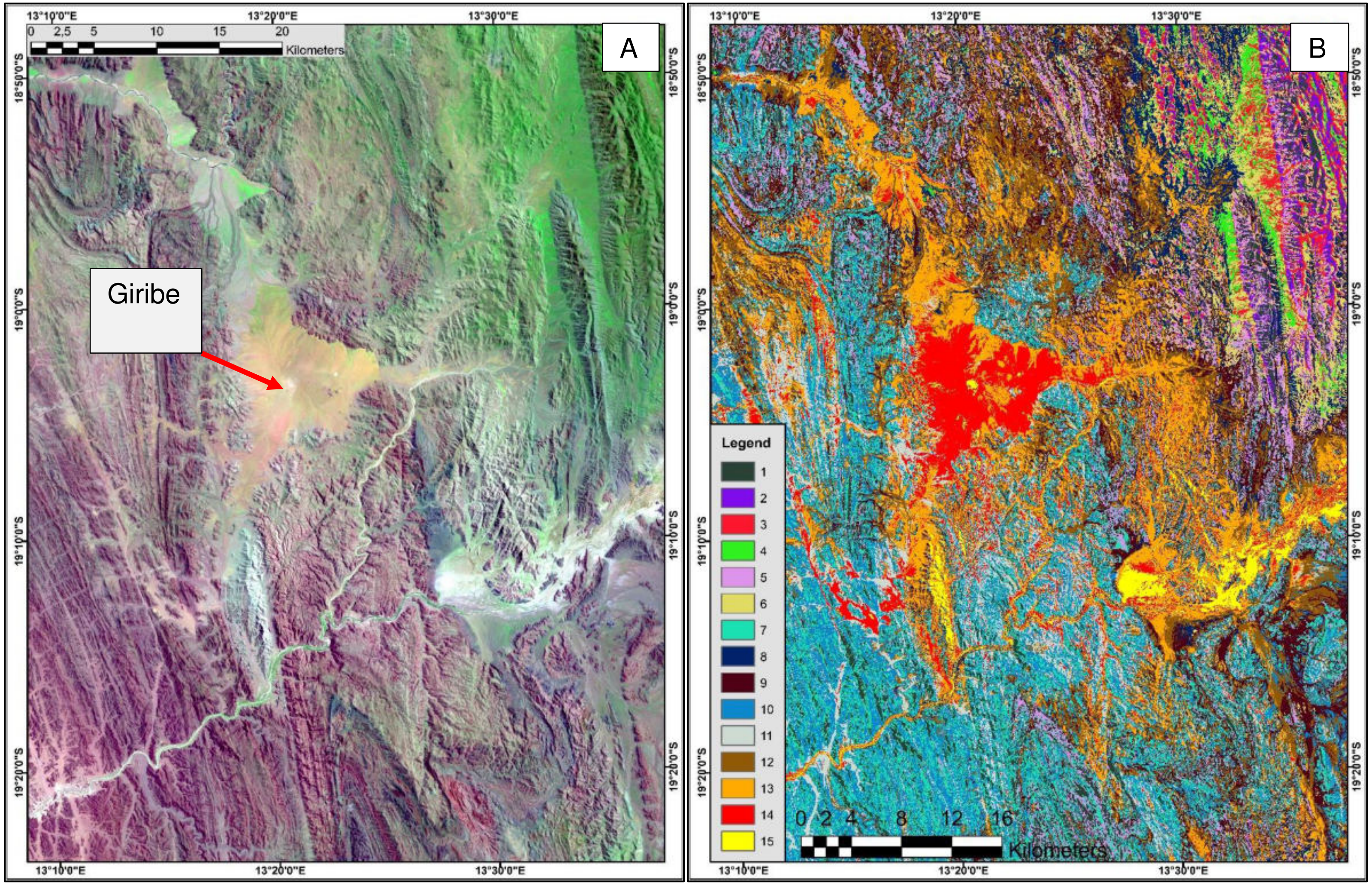


Figure 3.13: The land cover classification process is illustrated by using the greater Giribes area as an example. A: A portion of an individual Landsat 5 TM false colour composite image, the bands 7,4,2 was used to construct the image B: The resultant 15 class ISO-Cluster Image classification before manual inspection of the raw classified data.

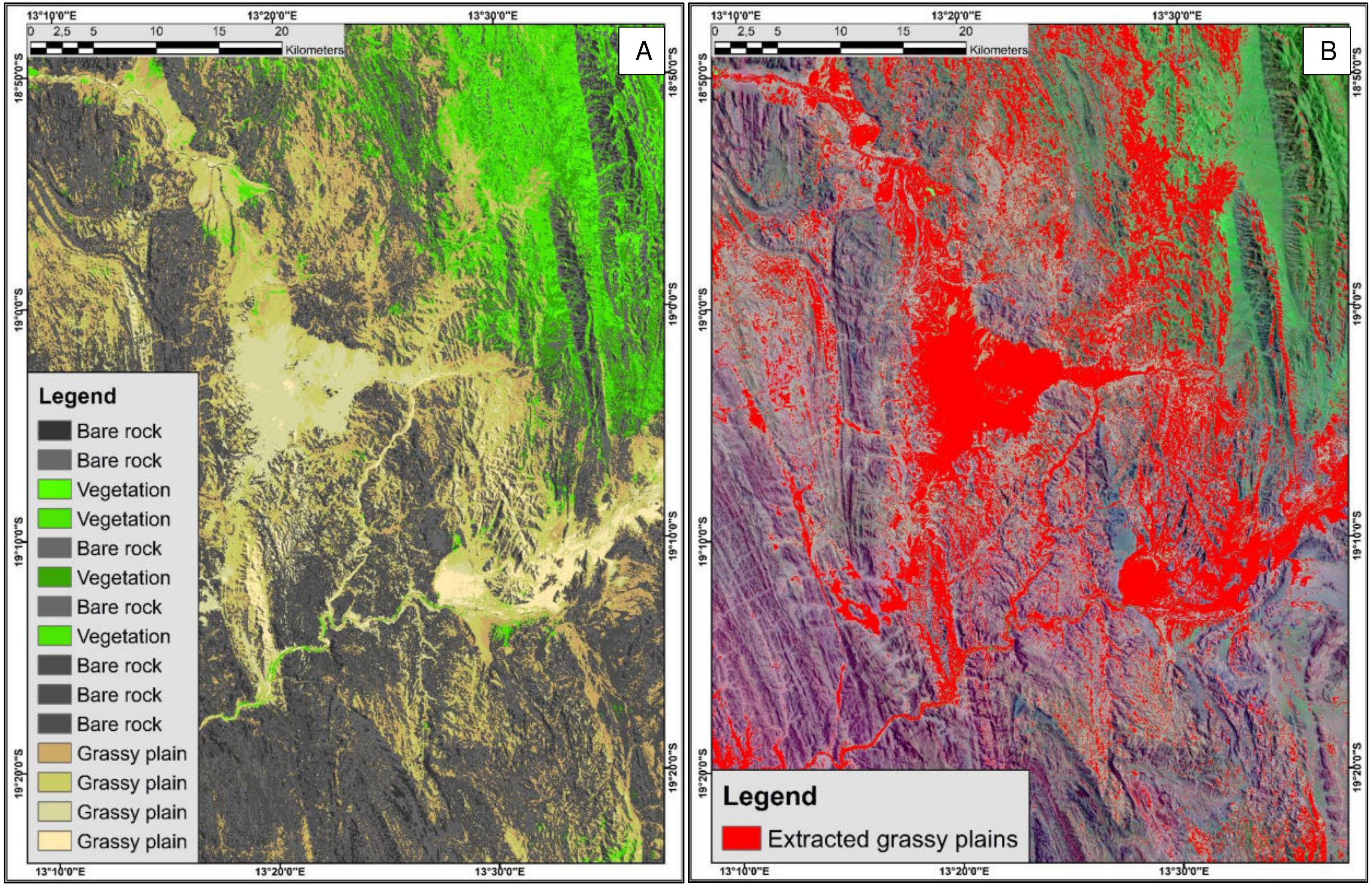


Figure 3.14: A: The reclassified ISO Cluster classified image. B: The grasslands on sandy soil extracted from the image classification process are shown in red.

Figure 3.15 shows the combined sandy grass plains for the entire study area, covering 104 443 km². During the land cover classification process, it was observed that the land cover type ‘bare rock’ was the most easily distinguishable from the other classes. The ‘vegetation class’ was also easily identified, and consisted of more lush vegetation, for example thick vegetation found along rivers and dense bush. However, separating gravel plains from sandy plains proved the most difficult. Desert pavements, a type of gravel plain, for example those characteristic of the Etandeka Plateau, was included under bare rock. During field work, the location of several desert pavements was recorded along the route travelled. This aided in correctly identifying this land cover type. Less coarse gravel plains were also observed; these gravel plains are often covered by thin layers of sand. Fairy circles and *E. gummifera* co-occur on these gravel plains near Garub. Additionally, Cowen et al. (2015) studied fairy circles found on gravel plains north of the Kunene River. As the satellite images were obtained after years of good rainfall, the abounded grass cover made it more difficult to distinguish between the less coarse gravel plains and the sandy plains. Therefore, these ‘less coarse gravel plains’ were included under the sandy grass plains class. As a result, large areas south of Brandberg and north of the Kunene River, were included under the sandy grasslands layer.

Finally, a combined layer was formed by intersecting the ideal rainfall and altitudinal range with the grasslands on sandy soil layer. This output represents the areas where all three predictor variables are present and thus the most likely areas where fairy circles could occur (Figure 3.16). The modelled fairy circle distribution covers an area of 55 955.14 km². The modelled fairy circle distribution indicates that there is a potentially vast area in the south east of Namibia where fairy circles could occur that has not been previously identified.

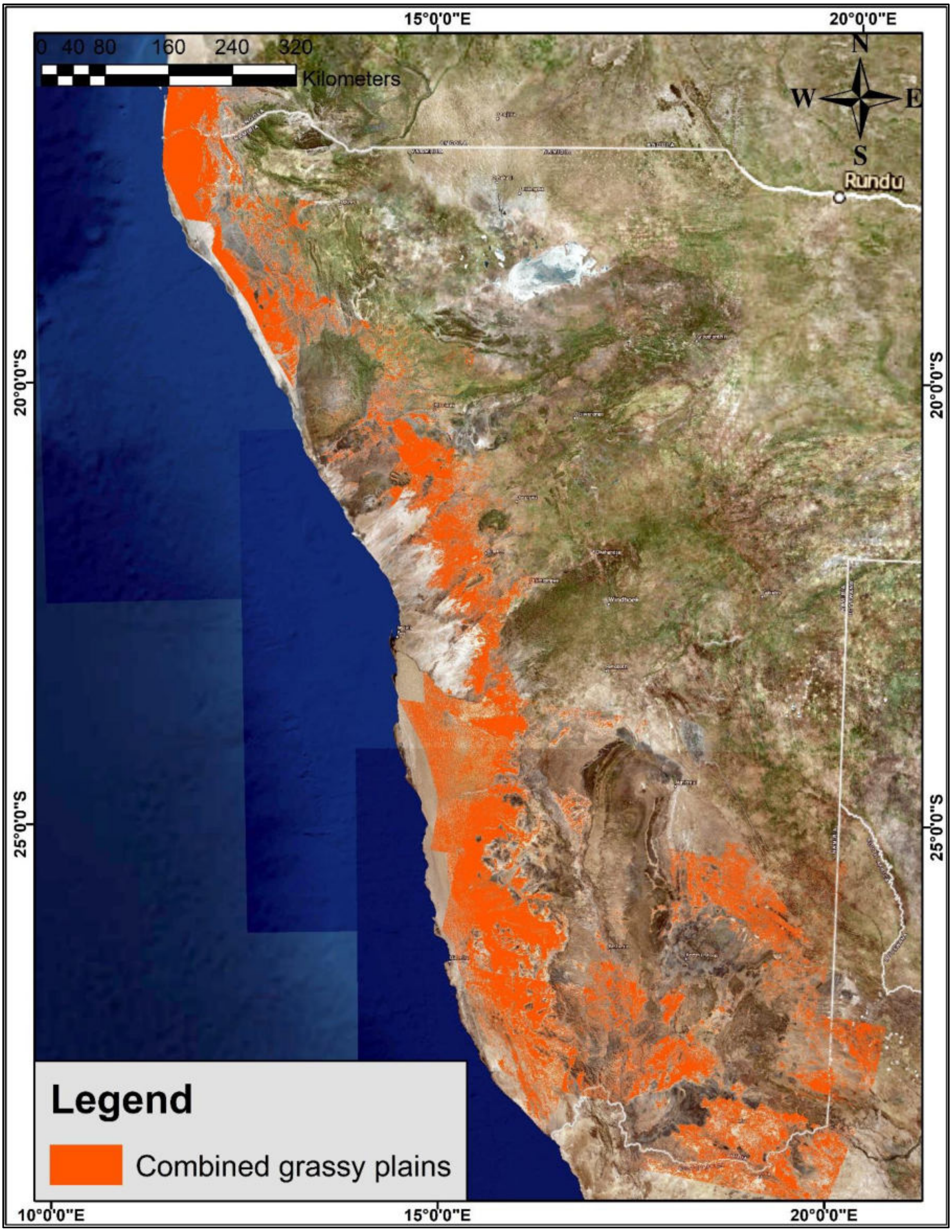


Figure 3.15: The combined land cover classification map for the study area.

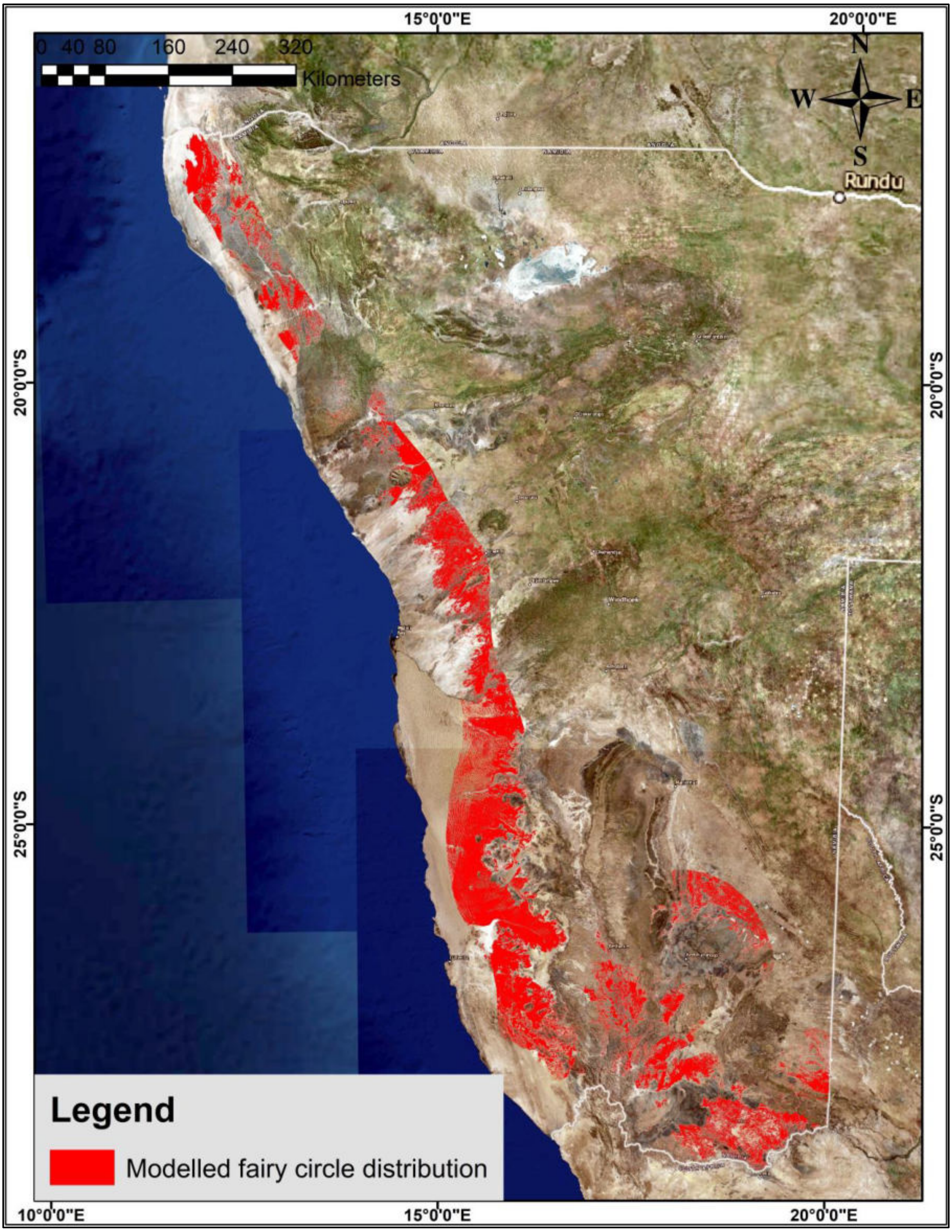


Figure 3.16: Site suitability prediction map for fairy circle distribution.

Soil samples:

Figures 3.17 - 19 shows the particle size classes for Giribes Plain, Brandberg and Garub, respectively. The soil samples taken from these sites mostly contained coarse particles in the following size classes; > 500 ɥm, > 250 ɥm, and > 100 ɥm. Particle sizes of > 1000 ɥm were also noted for Brandberg and Garub. while particles of > 53 ɥm were also found for Garub. All the samples had low proportions of fine particles of < 53 ɥm. Figures 3.20 - 22 shows the sand, silt and clay content determined for the soil samples taken at Giribes Plain, Brandberg and Garub. Based on the results it is clear that the soil of these locations contains mostly sand and very little silt and clay.

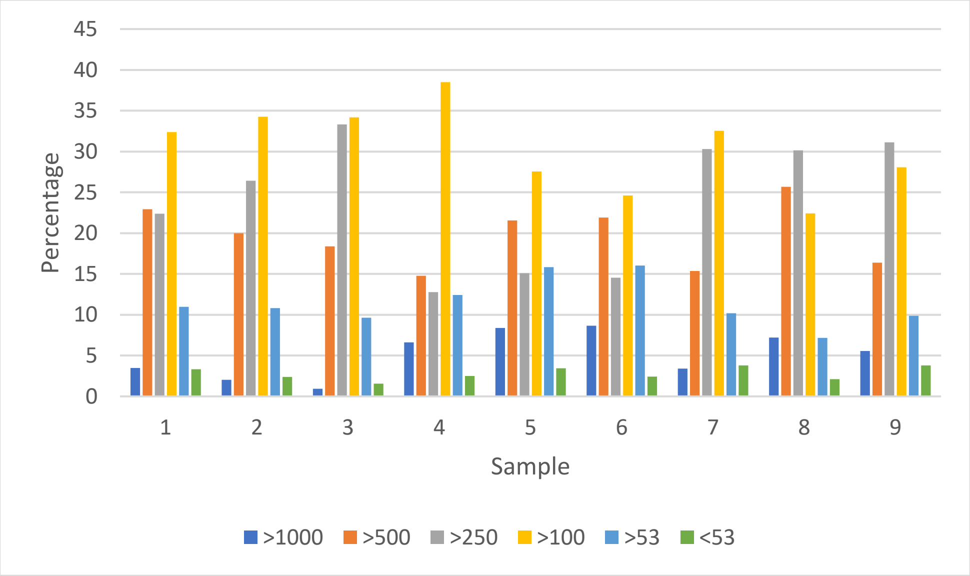


Figure 3.17: Particle sizes for soil samples of Giribes Plain.

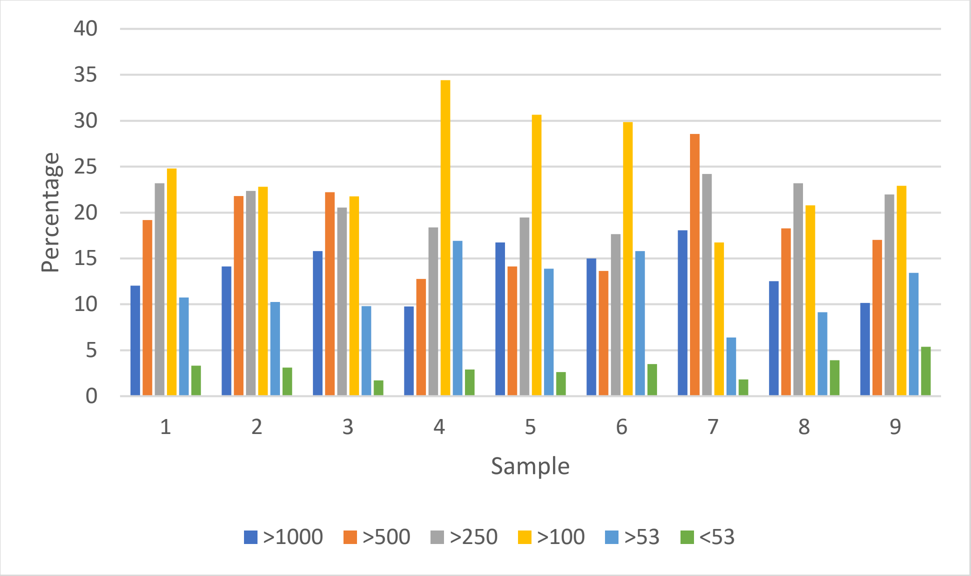


Figure 3.18: Particle sizes for soil samples of Brandberg

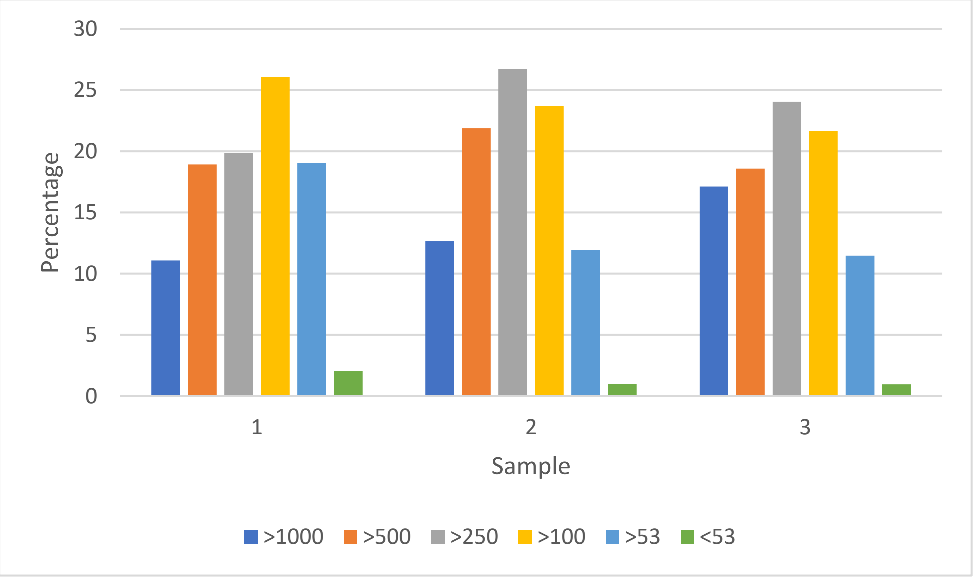


Figure 3.19: Particle sizes for soil samples of Garub.

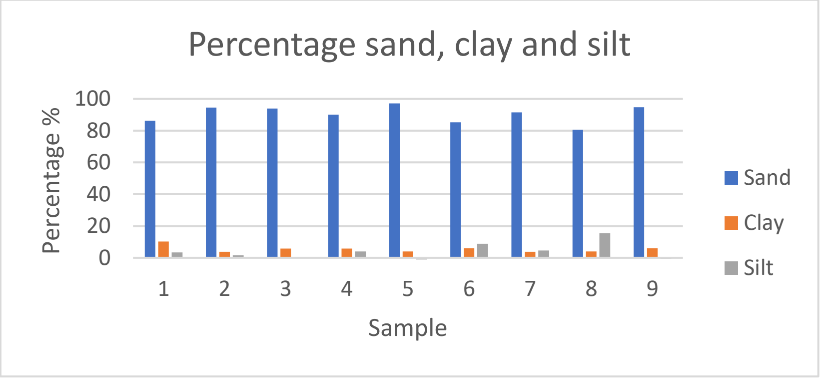


Figure 3.20: Sand, silt and clay content for soil samples from Giribes Plain.

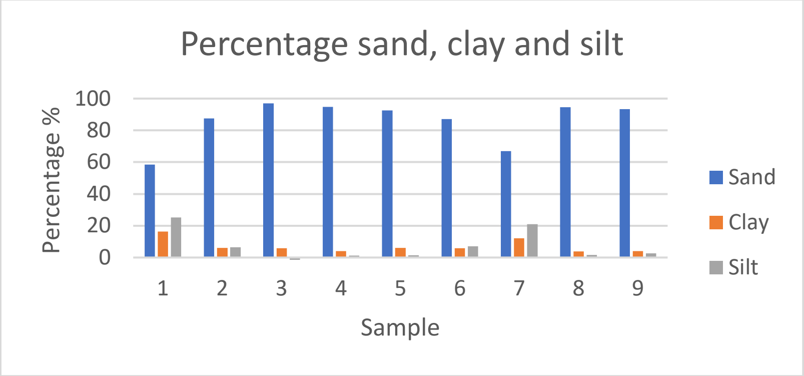


Figure 3.21: Sand, silt and clay content for soil samples from Brandberg.

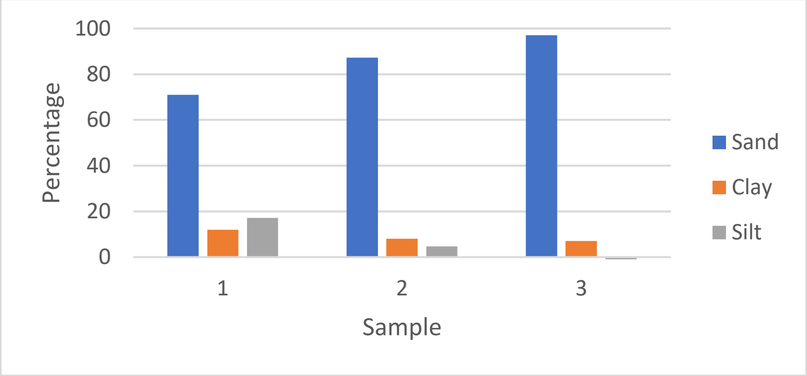


Figure 3.22: Sand. silt and clay content for soil samples from Garub.

3.4.2 Validation

Random points:

The first step of the validation process involved generating one hundred random points on the areas predicted to have fairy circles. These 100 points were then checked to see whether there were in fact fairy circles as predicted by the model. Eighty-three random points were also generated in the areas which were not predicted to contain fairy circles. Each of these areas were also checked for the presence or absence of fairy circles. The results of the validation process are illustrated on the validation map in Figure 3.23 below.

Fairy circles were found in the buffer areas in 65 out of the 100 points generated for the modelled fairy circle distribution providing a fairly accurate representation of fairy circle occurrence. A significant finding was that, contrary to other literature studies and maps, fairy circles can be found inland as far as 400 km in the south east of Namibia as well as in the South African part of the Kalahari Desert (some of these areas were ground-truthed in 2018). Indeed, from observations made on Google Earth fairy circles occur over large areas in the south east (Figure 3.23). Fairy circles here were mostly noted in inter-dune spaces, similar to fairy circles occurring in inter-dune spaces along the eastern margins of the Namib Sand Sea. The red area indicates the modelled fairy circle distribution, while the yellow and grey areas represent the 100 random points generated within the modelled fairy circle distribution; fairy circles were found in the yellow areas, while fairy circles were not found in the grey areas. The purple areas represent the 83 random points generated within the control; no fairy circles were found in the control. For the area predicted to not contain fairy circles, none of the 83 random points contained fairy circles within the 8 km radius.

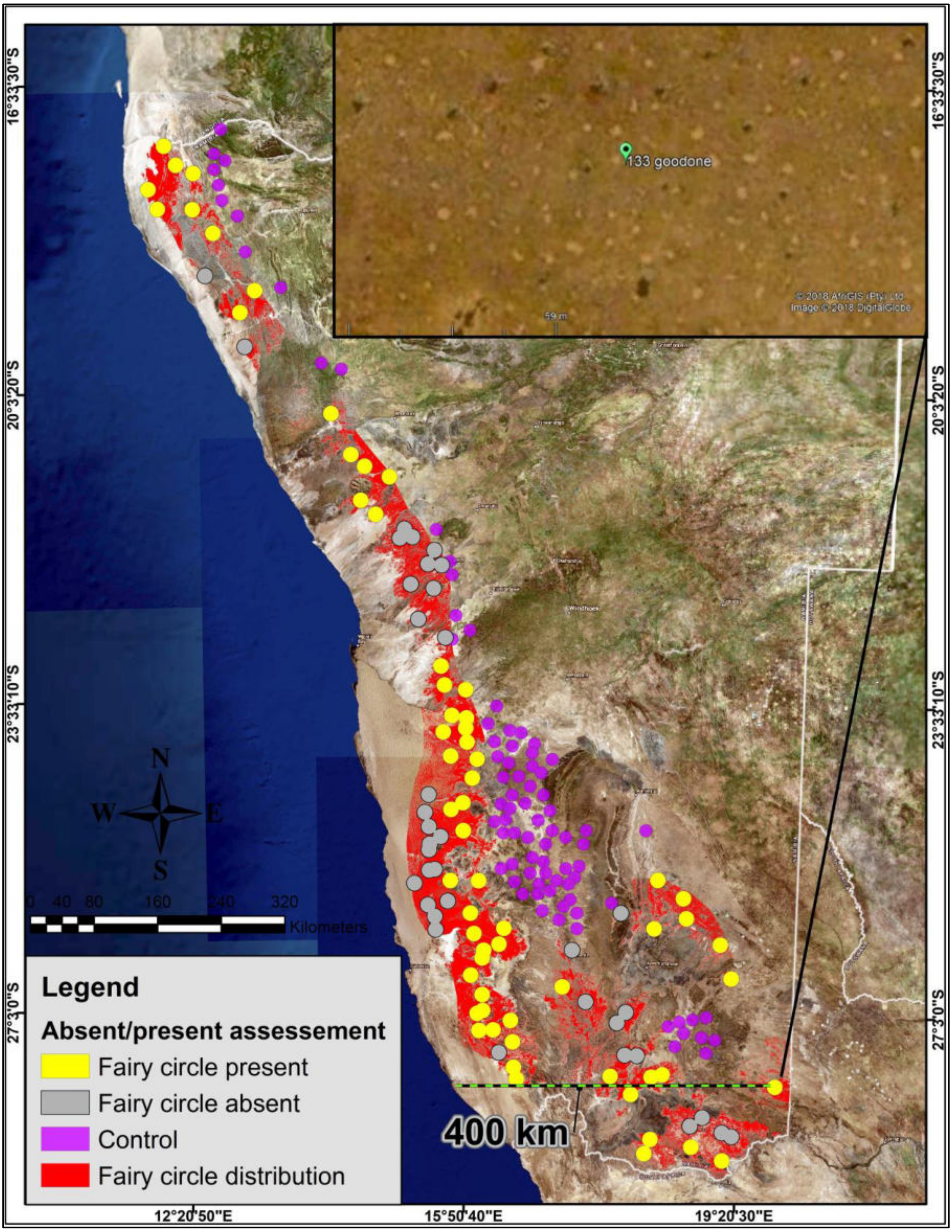


Figure 3.23: Fairy circles validation map of random points. Yellow indicates areas where fairy circles have been observed, while fairy circle were not observed in grey areas. Purple areas indicate the negative control, where no fairy circles were predicted and also not found.

3.4.3 Comparison with Euphorbias

The site suitability map was then compared with the distribution of three species of *Euphorbia*; *E. damarana*, *E. gummifera* and *E. gregaria.* Figures 3.24 - 26 show the distribution maps of each *Euphorbia* species and the suitability prediction map.

Two factors should be taken into consideration regarding the Euphorbia distribution data sets. First, it is common knowledge that plant species are under-collected in remote areas and are mostly restricted to areas where there are roads (Russel et al. 1984). Whereas the suitability model is unrelated to human access and covers areas not reachable by the average botanist. The second factor to consider is that the Euphorbia distribution includes all areas where MAP is not restricted to 50 – 150 mm MAP, where the altitude is not restricted to between 500 – 1 200 mamsl and where the land cover is not restricted to sandy plains covered in grass. The area where the modelled fairy circle distribution overlaps with the Euphorbia distribution illustrates the area where all three predictor variables are present and within the Euphorbia distribution. There are also numerous fairy circle locations, acquired through the Google Earth inspections that fall within the area where the fairy circle distribution overlaps with the distributions of the various *Euphorbia* species.

***E. damarana*:**

The distribution of *E. damarana* is confined to the north-western and central western parts of Namibia (Figure 3.24) and covers the largest area between the three species of Euphorbia. The distribution of *E. damarana* is associated to an extent with the fairy circle distribution from approximately 70 km south of the Angolan border, through to Brandberg and up to approximately 100 km north of the Namib Sand Sea. The yellow areas in Figure 3.24 indicate areas where the distribution of *E. damarana* overlaps with the modelled fairy circle distribution. This area excludes all areas falling within the distribution of *E. damarana* where the three predictor variables are not all present. Indeed, it has been suggested that *E. damarana* prefers a rocky substrate and also occurs outside the modelled fairy circle distribution, on rocky outcrops for example, where fairy circles are not predicted to occur. Several areas were observed where fairy circles co-occur with *E. damarana* that have not been documented before. Figure 3.24 A shows fairy circles and *E. damarana* co-occurring at Brandberg. This suggests that the co-occurrence is more general than previously thought (Getzin et al. 2015, Becker et al. 2010).

***E. gummifera*:**

The distribution of *E. gummifera* is confined to the south-western parts of Namibia (Figure 3.25) and covers the smallest area between the three species of *Euphorbia*. The distribution of *E. gummifera* is only associated to a limited extent with the fairy circle distribution, from slightly south of the Sand Sea to the Orange River that forms the border between Namibia and South Africa. The yellow areas in Figure 3.25 indicate areas where the distribution of *E. gummifera* overlaps with the modelled fairy circle distribution. This area excludes all areas falling within the distribution of *E. gummifera* where the three predictor variables are not all present. Figure 3.25 A shows fairy circles co-occurring at Garub.

***E. gregaria*:**

The distribution of *E. gregaria* is widespread throughout the southern parts of Namibia (Figure 3.26). The distribution of *E. gregaria* is associated to a fair extent with the fairy circle distribution in the southern parts of Namibia. Ground observations of a possible location considered to be *E. gregaria* and fairy circles confirmed that the plants observed on Google Earth are *E. gregaria*. Figure 3.26 A shows this location where fairy circles co-occur with *E. gregaria*. This is the first documented co-occurrence of fairy circles with *E. gregaria*. A large area where *E. gregaria* occur has been observed and large numbers of these plants are dying. Fairy circles have also been observed in some places at this location, although Google Earth coverage is poor and the grass cover is also very low. This location is seen as being possibly in the beginning stages of developing into an area with high densities of fairy circles. Figure 3.26 B shows fairy circles occurring with what is suspected *Euphorbia* species just south of the Orange River in South Africa, but must still be confirmed in the field.

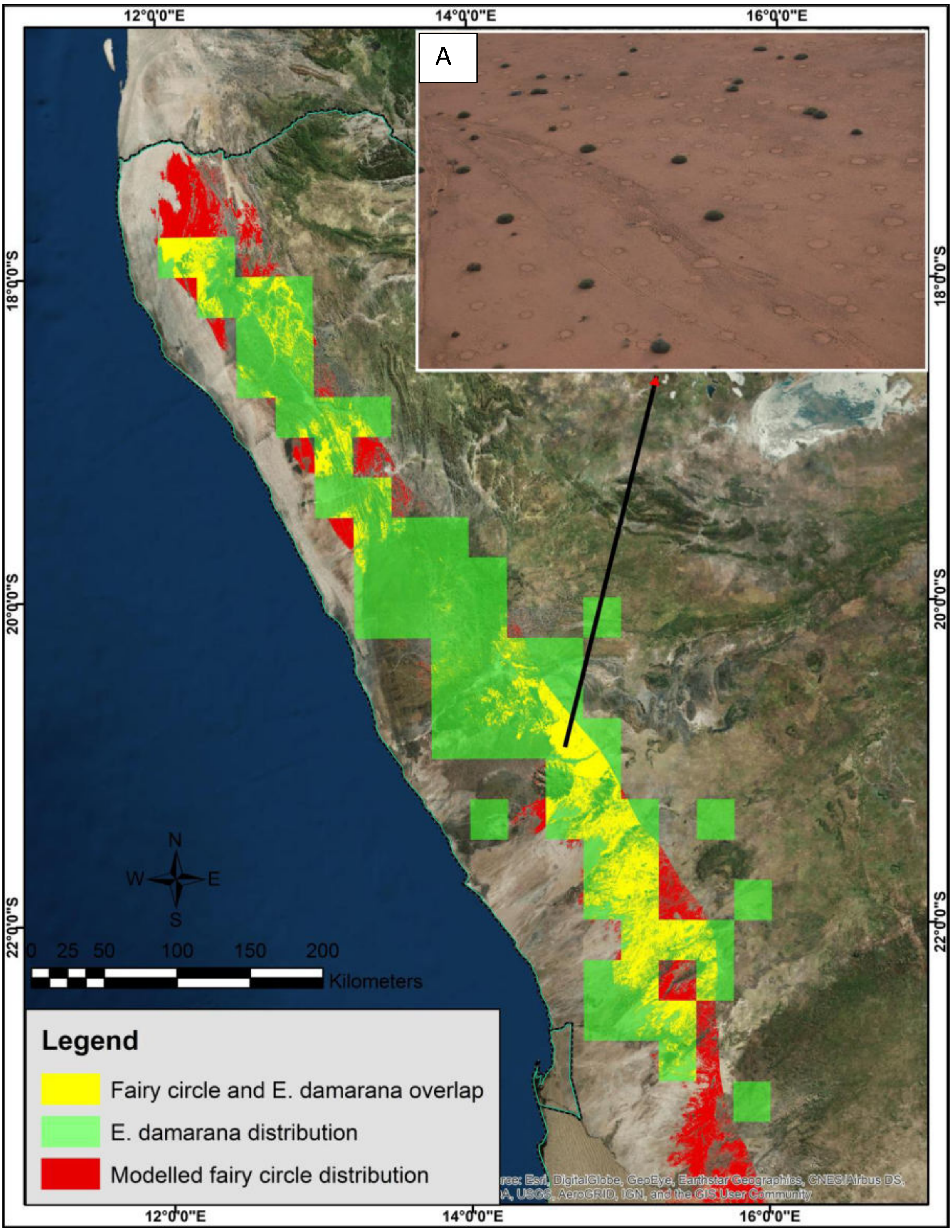
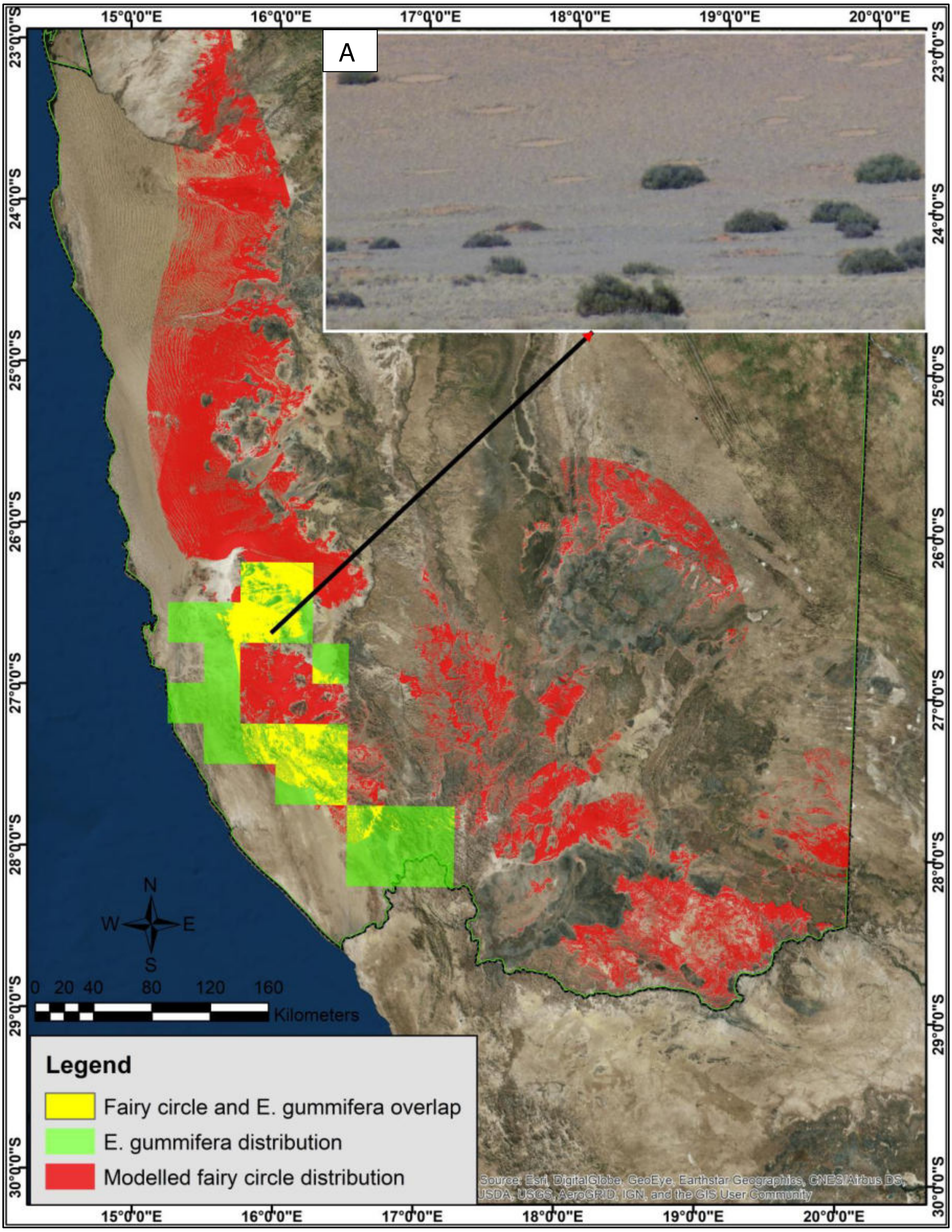


Figure 3.24: *E. damarana* distribution in relation to the modelled fairy circle distribution. The yellow areas indicate areas where the distribution of *E. damarana* overlaps with the modelled fairy circle distribution. A: Fairy circles co-occurring with *E. damarana* at Brandberg.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 3.25: *E. gummifera* distribution in relation to the modelled fairy circle distribution. The yellow areas indicate areas where the distribution of *E. gummifera* overlaps with the modelled fairy circle distribution. A: Fairy circles co-occurring with *E. gummifera* at Garub.

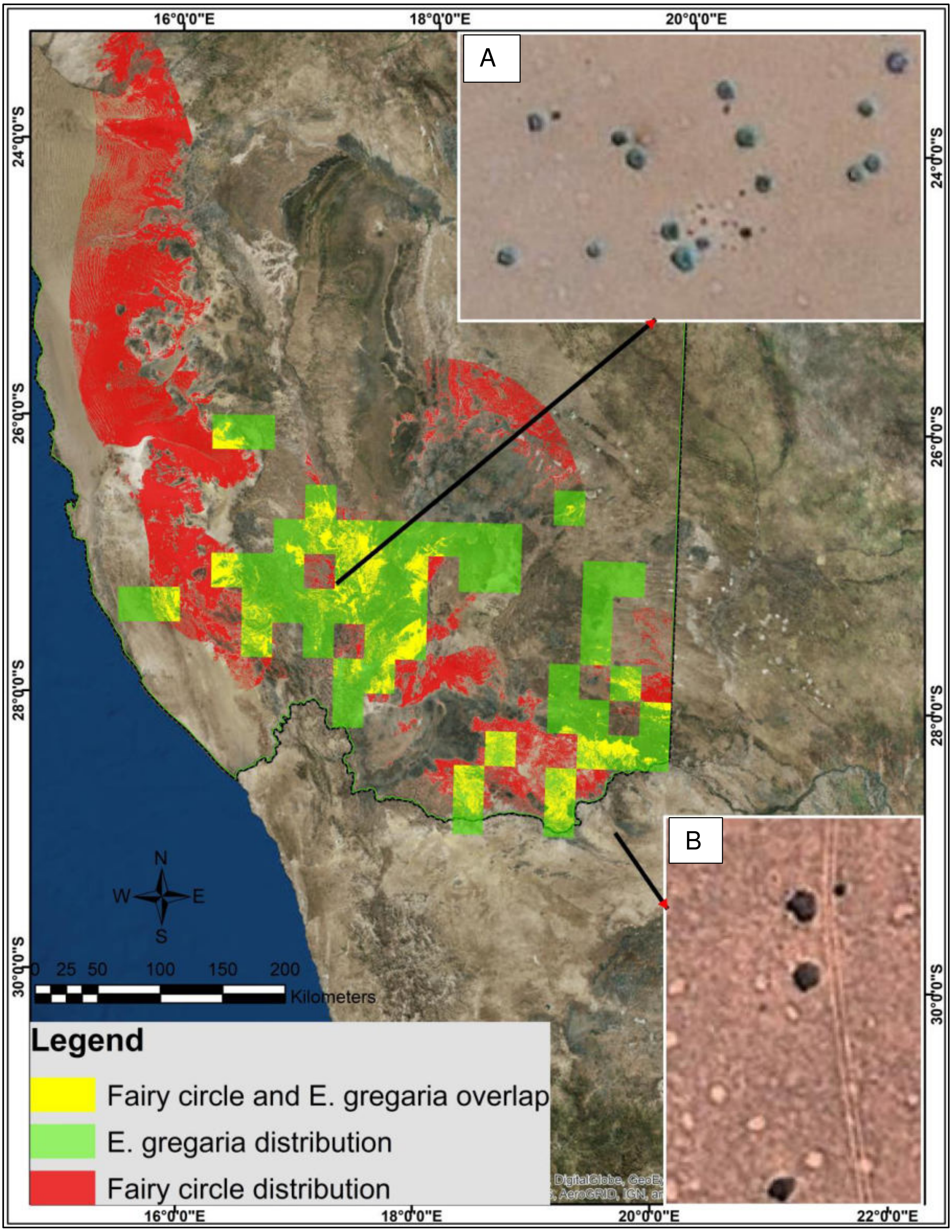


Figure 3.26: *E. gregaria* distribution in relation to the modelled fairy circle. The yellow areas indicate areas where the distribution of *E. gregaria* overlaps with the modelled fairy circle distribution. A: Confirmed fairy circle co-occurrence with *E. gregaria.* B: Suspected Euphorbia plants co-occurring with fairy circles in South Africa.

Figure 3.27 shows the overlap between a combined Euphorbia distribution (*E. damarana, E. gummifera* and *E. gregaria)* with the suitability model. Rainfall is probably a determinant in the plant's distribution, and also the fairy circle's. The ideal rainfall range is therefore also shown in Figure 3.27; from this it is shown that the Euphorbia distribution is also closely associated with areas between 50 – 150 mm MAP, although deviating slightly. In contrast, the termite distribution maps that have been investigated showed that the range of all species of termites extends far beyond the 50 – 150 mm MAP.

There are also numerous fairy circle locations, acquired through the Google Earth inspections that fall within the area where the fairy circle distribution overlaps with the distributions of the various *Euphorbia* species. There are three prominent areas where there is no overlap between the site suitability map and the Euphorbia distribution. The most extensive of these areas lies in close proximity to the Namib Sand Sea, where fairy circles covers vast areas of land, extending east into the valleys of the escarpment, and west into the sand sea itself. Figure 3.27 A shows the extent of the fairy circle distribution along the Namib Sand Sea. Van Rooyen et al. (2004) however noted the presence of Euphorbias in the Namib Rand Nature Reserve, where these plants co-occur alongside fairy circles. This raises the question whether Euphorbia plants could once have been abundant in this region? And if so, could they have created the vast plains of fairy circles observed here? Approximately 150 km south east of this area, is another area where the Euphorbia distribution does not overlap with the modelled fairy circle distribution.

There is a large area between the Giribes Plain and Brandberg where the Euphorbia distribution is present, but the modelled fairy circle distribution is absent. This area is located in the Etandeka Platea, where the substrate is rocky, sand is mostly absent in the landscape and these land cover types were excluded during the land cover classification process. During field excursions, the presence of *E. damarana* was noted in abundance here, and contrary to the sites of co-occurrence, there are not large numbers of *E. damarana* dying here.

Between Brandberg and the Sand Sea is a large stretch where the modelled fairy circle- and Euphorbia distribution overlap. This stretch of land is known as the Central Western Plains, the surface consists of vast gravel plains and sand is mostly absent. The pronounced extent of the suitability map in this landscape is owed to the high biomass during the years when the satellite images were taken. During the validation process, fairy circles were observed to occur in the central western plains, but only on sandy deposits.

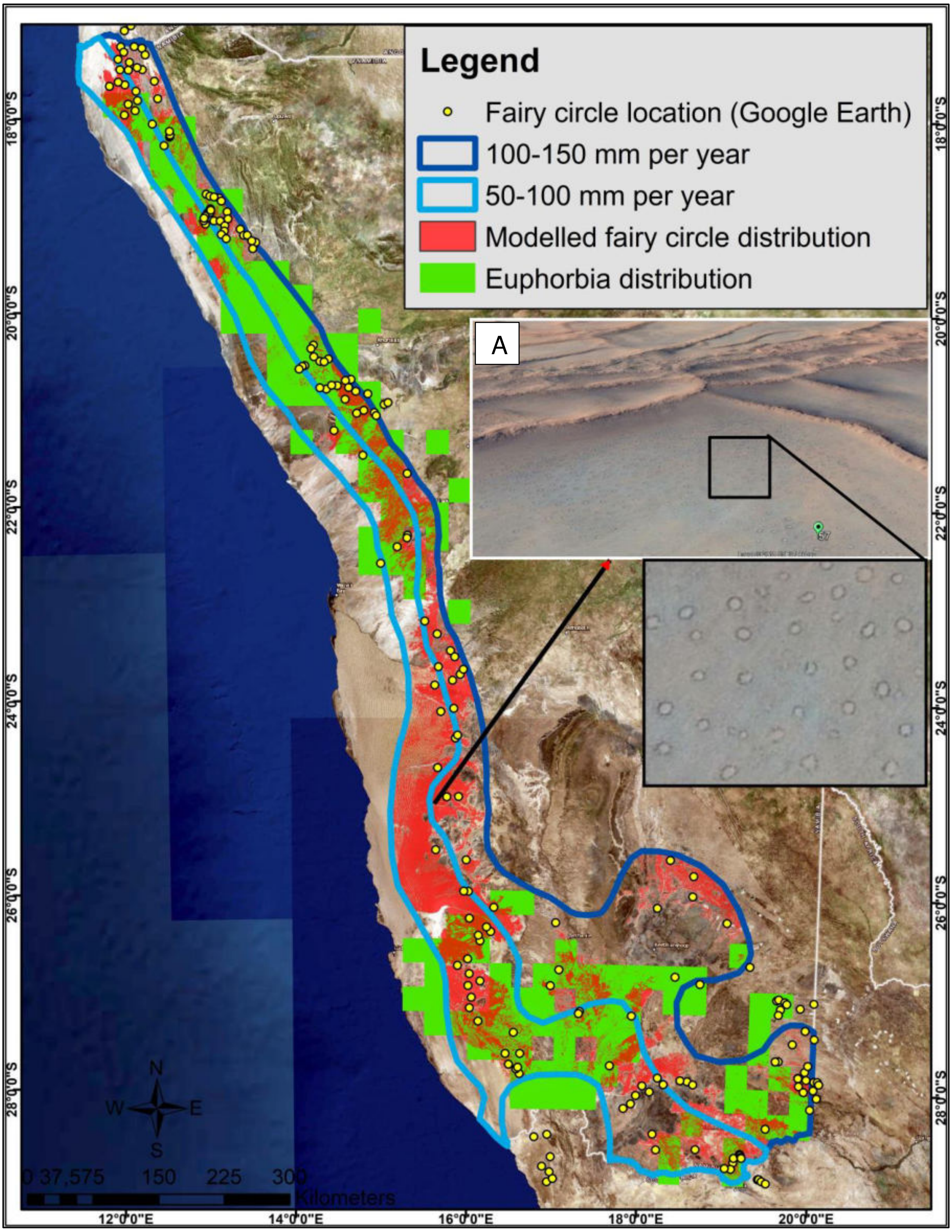


Figure 3.27: The site suitability prediction map is shown in relation to *E. damarana*, *E. gummifera* and *E. gregaria* that have been combined into one layer (green). Note the close association of the Euphorbia distribution to areas of 50 -150 mm MAP. The yellow points indicate fairy circle locations identified from Google Earth inspections. A: Fairy circles occur over vast areas along the Namib Sand Sea.

3.5 Conclusion

In this chapter a GIS site suitability model was constructed to predict where fairy circles may be located based on three predictor variables. The validation of the model involved the generation of 100 random circles (10 km diameter) within the modelled fairy circle distribution. These areas were inspected for the presence or absence of fairy circles and generated a 65 % hit-rate. Next, 83 random circles (8 km in diameter) were generated within the ‘negative control’ (where the three predictor variables were absent) and also inspected for fairy circles. None of the negative control random points contained any fairy circles. This showed that the modelled fairy circle distribution is a fairly accurate representation of where fairy circles could occur. The resulting finding from the model that fairy circles occur in the far south east of Namibia, including the Kalahari Desert, is a significant new finding in the fairy circle phenomenon. It is believed that the 65% hit rate was lower than reality as a result of a lack of grass cover during dry seasons on several of the available Google Earth images which significantly lowered the accuracy percentage of the model in the validation.

In an attempt to determine whether there is an association between fairy circles and *Euphorbia* species, the site suitability map was compared to the distribution of three species of Euphorbia; *E. damarana*, *E. gummifera* and *E. gregaria*. It is hypothesised that only where these plants occur on sandy soils will fairy circles be created. Indeed, soil samples taken from areas where fairy circles co-occur with *E. damarana* and *E. gummifera* showed that the soils from these areas contain very high proportions of sand and very little silt or clay. However, further testing on this is required to determine if the soil properties are different in areas where they do not co-occur. Three species of *Euphorbia* have been documented to co-occur with fairy circles, including the first documented co-occurrence of fairy circles with *E. gregaria*. A very large area has been identified where large numbers of *E. gregaria* are dying and several fairy circles were observed between the dead plants. This area is considered to be in the beginning stages of transitioning into an area with low numbers of *E. gregaria* and large numbers of fairy circles. This indicates that there is a potential association between fairy circles and the *Euphorbia* species, but more research is required to validate this.

Chapter 4: Landscape scale characteristics of fairy circles

4.1 Introduction

In this chapter historical aerial imagery of locations where fairy circles co-occur with *E. damarana* and *E. gummifera*, was exmained and the same locations compared to modern satellite imagery to determine what happened to these populations over time. Next, the size of fairy circles were compared to both *E. damarana* and *E. gummifera*, to determine if there is a statistical difference in size between fairy circles and these plants. Lastly, spatial point pattern analysis was used to to characterise and compare the spatial patterning of fairy circles with both *E. damarana* and *E. gummifera*.

4.1.1 The age of fairy circles

According to Albrecht et al. (2001) and Tschinkel (2012) fairy circles undergo a natural cycle consisting of initial formation followed by development and maturation, before they are eventually overgrown with grass and disappears into the matrix grasses. In 1978 Theron (1979) marked the location of several fairy circles and dead *E. damarana* in the Giribes Plain. Later Van Rooyen et al. (2004) revisited the same locations in 2001, Meyer et al. (2015) in 2013 and myself in 2017 and we can report that the fairy circles were still intact, suggesting that fairy circles do not disappear after several consecutive years of low and/or high rainfall. Indeed, the researchers noted that between 1978 and 2015 there were several dry as well as wet periods and the marked fairy circles should therefore have disappeared according to most theories. This supports the notion that fairy circles do not merely appear in random locations after rainfall when the ephemeral grassland develops but rather the same fairy circles continuously appear and disappear.

Tschinkel (2012) examined two satellite images taken four years apart to determine the age of fairy circles and concluded that they have a lifespan of between 40 and 60 years. The underlying assumption used by the researchers differs from that of Theron (1979) in that Tschinkel (2012) assumed that fairy circles are in a constant flux of birth and death, where fairy circles form and are overgrown. On the other hand, Theron (1979) believe that fairy circles can only be formed where *E. damarana*, and *E. gummifera* has died. Therefore, in a given space where fairy circles are present, the same fairy circles will persist until they eventually disappear. As the appearance and/or disappearance of the ephemeral grassland is highly dependent on local rainfall, precipitation data must be assessed in conjunction with satellite data. Furthermore, grass seedlings do commonly establish within the barren area of fairy circles following rains and rarely survive the following dry period (Cramer et al. 2016).

Juergens (2015) suggested that new fairy circles are generated during wet years. During a time-series analysis of fairy circles (Figure 4.1) in the Giribes Plain (for the period 2007 to 2015) the researchers showed a change in fairy circle population, triggered by a series of good rainfall years (from 2008 to 2011) followed by three dry years (2012 to 2014). They suggested that the series of photographs shows the formation of eight new fairy circles that increased in size from 2009 to 2013, while in 2014 all these new fairy circles disappeared after three consecutive years of drought. Juergens (2015) claims that the same trend was observed in annual monitoring of 160 fairy circles within Giribes Plain. Juergens explained this by suggesting that wet years result in higher standing biomass and greater termite reproductivity that could expand colonies. In the series of photographs the bio-mass of the matrix grasses are also observed to fluctuate during the same period. In the most recent photograph taken in 2015, the matrix grasses are entirely absent surrounding the fairy circles.

The question then is would those same fairy circles reappear when there is sufficient rainfall for the matrix grasses to grow? And if so, it would raise more questions such as: why did the fairy circles not persist like the remaining fairy circles? Why do these “short lived” fairy circles have no perennial belt? And were they present prior to the above average rainfall years, i.e. 2007? If the Euphorbia hypothesis is accepted, those might be very old fairy circles, in which case the allelopathic effect left in the soil could have been reduced by decades of exposure to a harsh desert climate. Tarnita et al. (2017) modelled fairy circle population dynamics by including the matrix grasses, as individual grass tuffs and suggested that there could be great variation in the age of fairy circles and could range between 5 and 165 years.

If fairy circles do indeed form as a result of the death of *E. damarana, E. gummifera* and *E. gregaria*, it could change the current assumptions on the age calculations of fairy circles. Therefore, one of the objectives of this study was to conduct long term photographic observations of fairy circles, *E. damarana* and *E. gummifera*.

4.1.2 The size of fairy circles

Theron (1979) observed that the sizes of fairy circles varied throughout his study site in the Giribes Plain. He compared the average diameter of fairy circles with *E. damarana* in different locations inside the Giribes Plain. The first site was located in the plain itself where the researchers found that the average diameter for fairy circles and *E. damarana* were 6.2 m and 6.4 m, respectively. At the second site, located more south and against a ridge, the average diameter for fairy circles and *E. damarana* were 9.3 m and 6.8 m, respectively.

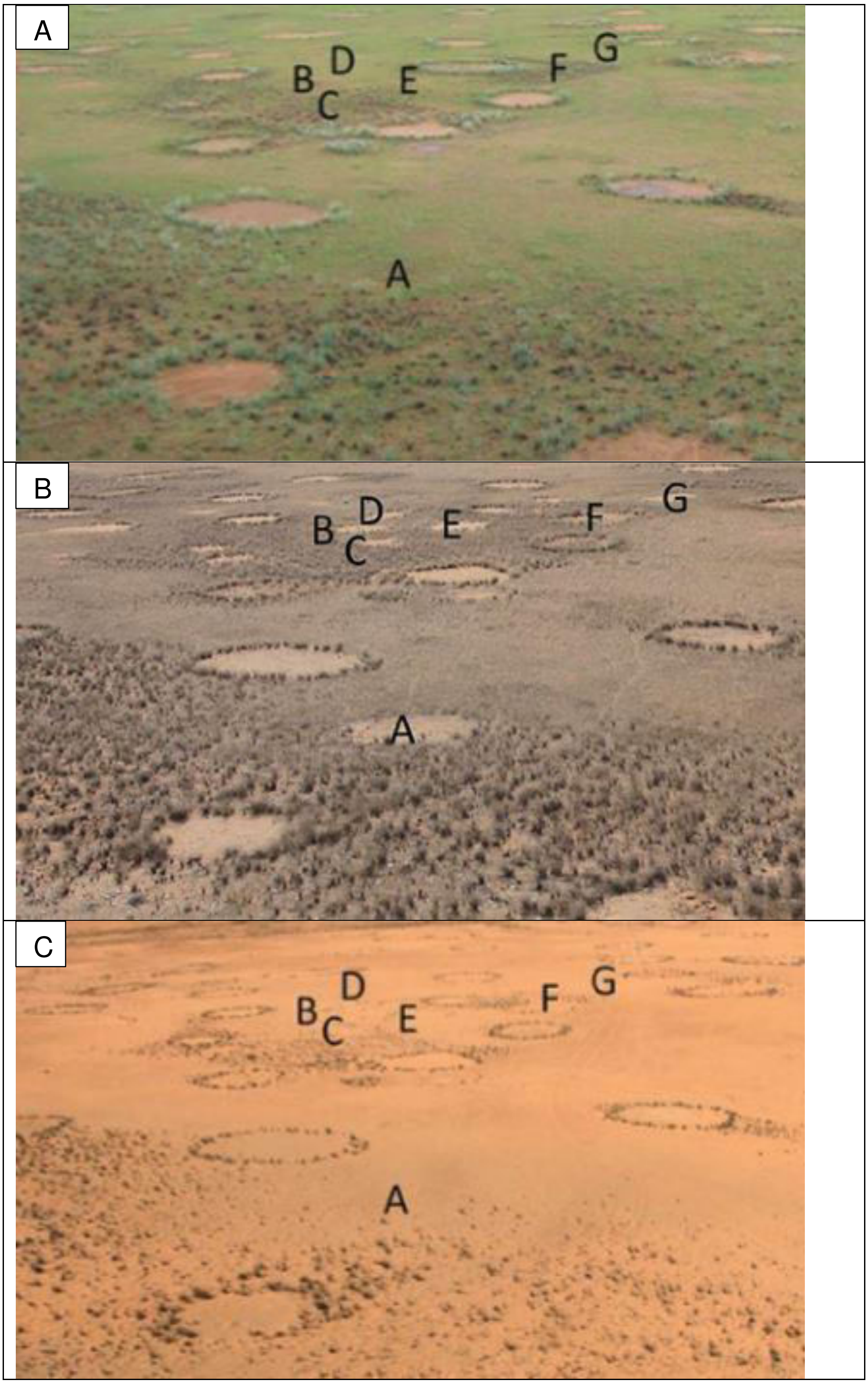


Figure 4.1: Fairy circles in the Giribes Plain after; A: above average rainfall during 2008, B: normal rainfall during 2012, and C: after low rainfall during 2015, (adapted from Juergens (2015). Juergens suggest that the letters correspond to the location of newly formed fairy circles visible in 2102 (B).

Van Rooyen et al. (2004) found the largest fairy circles occurring in the Hartmann's Valley with an average diameter of 10 m, whereas those in the Marienfluss valley were found to be 7.5 m in diameter, in Giribes Plain they are 6.2 m, near Tsondab Vlei (Namib Sand Sea) they are 5 m, while in the Spergebiet and in the Richtersveld, they are 2 m. Picker et al. (2012) found that fairy circles in Giribes Plain were larger than those in the Marienfluss valley, with average diameters of 7.3 m and 5.4 m respectively. Cramer et al. (2016) found fairy circles in the Namib Rand Nature Reserve with a mean diameter of 6.9 m. Meyer et al. (2015) documented the average fairy circle size in the Spergebiet, near Garub to be 3.5 m.

Great variation in the size of fairy circles has been documented. Researchers have mentioned previously that fairy circle size is negatively correlated with precipitation (Cramer et al. 2016). However, according to the Euphorbia allelopathy theory (section 2.3.4) (Meyer et al. 2015), the size of fairy circles will be determined by the "parent" plant that gave rise to the circle. If this hypothesis is correct one would expect fairy circles and *E. damarana*, and fairy circles and *E. gummifera* to have similar sizes where they occur. As mentioned above, Meyer et al (2015) found that the size of fairy circles in south-western Namibia is very similar to the size of *E. gummifera*, while Theron (1979) found that the size of fairy circles in north-western Namibia is very similar to the size of *E. damarana*.

4.1.3 The spatial patterning of fairy circles

Point patterns are frequently encountered in applied geography including examining the spatial patterning of plants. As the spatial patterns of plants carry information about the processes which produced them and because they form the template on which processes will take place in the future, spatial patterns of plants hold an enduring interest for plant ecologists (Law et al. 2009). Most often, these patterns are investigated to determine if the events are regularly spaced over the study area, or if the events exhibit clustering in a specific location (O'Sullivan et al. 2010).

Generally speaking there are two interrelated approaches that are used to describe a point pattern quantitatively; the first approach involves point density, while the second involves point separation. These two approaches are related to the two distinct aspects of spatial patterns: first- and second order effects. First order effects are variation in the intensity of a process across space and is estimated as the observed spatial density of events and absolute location is important (O'Sullivan et al. 2010). In a point pattern, clear variations across space in the number of events per unit area are observed that arise because of variation in some factor that makes locations more or less attractive for events to occur in them. For example, soil with favourable properties could result in more plants growing in a certain location than compared to an area where the soil in less favourable. Second order effects suggest interaction between events, depending on the distance between them and relative location is important (O'Sullivan et al. 2010). In point patterns, such effects are manifest as reduced or increased distances between neighbouring or nearby events. For example, increased distances could be indicative of competition between plants (Wang et al. 2017).

Although the distinction between the two are important in practice it is very difficult to distinguish between these effects simply by observing spatial variations in the density of events (O'Sullivan et al. 2010).

In this study, sample plots representing fairy circles, *E. damarana* and *E. gummifera* were used in the analysis and are discussed in below. The centre of fairy circles, *E.*

damarana and *E. gummifera* plants were considered the events in the point pattern. It is important to note that this representation of the objects is necessary in order to generate spatial point pattern statistics. Moreover, previous studies have also used the same methodology (see Ternita et al. 2017, Getzin et al. 2016). One limitation of this methodology is that the resultant representation does not account for the whole area covered by each object and thus does not consider the distance from each event's periphery to the next periphery.

The spatial patterning of fairy circles, *E. damarana*, and *E. gummifera* were examined using a number of spatial statistics including Voronoi tessellations (Voronoi 1989), the 'distance to nearest neighbour ratio' (Clark and Evans, 1954), the pair correlation function (Ripely et al. 1998) and the L-function (Ripely et al. 1999).

Voronoi Tessellations:

Voronoi tessellations have often been used to characterise the spatial patterning of fairy circles. This technique involves determining for all points in a particular pattern (i.e. in this study either a fairy circle or plant centre) the surrounding area, referred to as a tile, which is the closest to that particular point than to any other points in the pattern (Jang et al. 2016). Two properties of the resultant tiles are important. First, the number of corners of each tile describes the regularity of the pattern, i.e. the larger the number of tiles with 6 corners, the more regular the pattern. Second, the distribution of each tile area is important. In this study only the number of corners of each tile was determined. Indeed, Getzin et al. (2014) was the first to create Voronoi tessellations for fairy circles and showed that the tiles mostly consist of six corners. Figure 4.2 below shows an illustration of the Voronoi tessellations created for the fairy circles in this study. This is noteworthy because the more tiles with six corners, the more regular the distribution. In a completely regular pattern all the points have six surrounding neighbours and the distance between all points are exactly the same. Both Juergens (2015) and Tarnita et al. (2017) showed that Voronoi tessellations determined for termite nests also have mostly six surrounding neighbours. However, the underlying idea of a regular pattern is that some kind of repulsive action between events in a pattern causes them to disperse uniformly over an area. Jang et al. (2016) showed that the distribution of Voronoi tiles for fairy circles are virtually indistinguishable from metazoan epithelial cells. This shows that various process, operating over vastly different scales, can lead to the same type of Voronoi tile distribution. Voronoi tessellations were created in this study for fairy circles, *E. damarana* and *E. gummifera* to determine how many neighbours surround a given circle/plant.

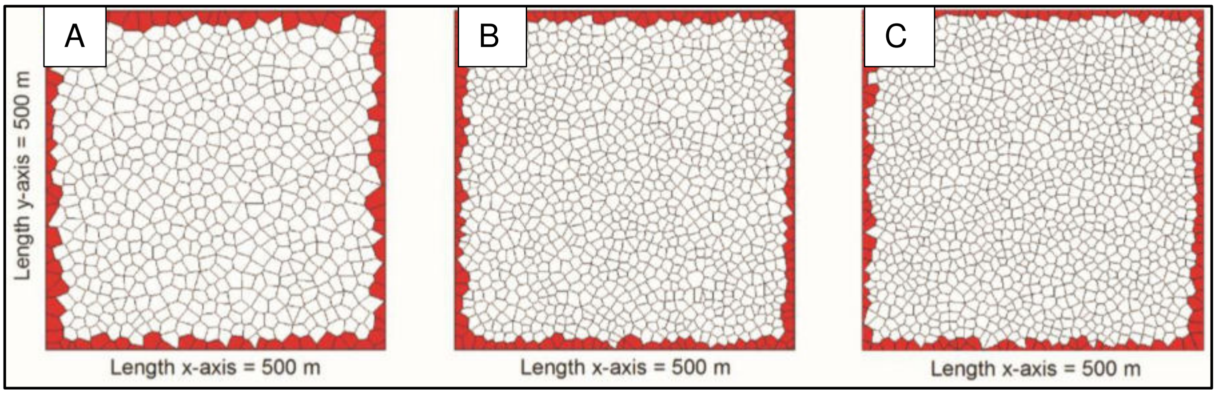


Figure 4.2: Voronoi tessellations created for fairy circles (A – C), (adapted from Getzin et al 2015).

Distance to nearest neighbour:

The distance to nearest neighbour approach provides a more direct description of the second-order properties of the pattern than density-based techniques. The nearest-neighbour distance for an event is the distance from that event to the nearest event also in the point pattern.

The nearest event in the pattern to each event can be calculated with the following formula (Clark and Evans, 1954):

$$R = \frac{\bar{r}_A}{\bar{r}_E}$$

where R = the nearest neighbour indiex;

$\bar{r}_A$ = average distance from randomly selected plants to their nearest neighbours;

$\bar{r}_E$ = expected mean distance between nearest neighbours. Under the Poisson distribution with intensity λ, we have

$$\bar{r}_E = \frac{1}{2\sqrt{\lambda}}$$

This method produces an R-value; a value of zero is calculated when objects exhibit clustering in certain parts of the study area and 1.0 if the objects are randomly distributed throughout the study area. An R-value of more than 1.0 is indicative of a 'regular pattern', also referred to as 'over dispersion'. Objects distributed in a perfect hexagonal pattern give a value of 2.149.

Albrecht et al. (2001) determined the 'distance to nearest neighbour ratio' of fairy circles at the Namib Rand Nature Reserve and found it to be 1.68 which indicates that fairy circles display an over-dispersed spatial pattern. These researchers also calculated the average nearest neighbour distances of these fairy circles to be 14.4 m. Cramer et al. (2016) determined the average nearest neighbour distance for fairy circles located at the Namib Rand Nature Reserve to be 12.9 m. Juergens (2015) interprets this as the distance at which fairy circles are controlled by competition for water/nutrients amongst themselves. However, there are locations where fairy circles have been observed to exhibit clustered spatial distribution patterns, but that is not the norm. Cramer et al. (2013) found that the ‘distance to nearest neighbour ratio’ of fairy circles ranged from 0.58 (clumped) to 1.67 (regular), while a statistically significant 58 % of these sites showed a regular distribution. Therefore, in this part of the study the nearest neighbour distance was calculated for fairy circles, *E. damarana* and *E. gummifera* to determine the distance up to which competition is limited.

Pair Correlation Function:

Several second-order statistics, such as the commonly used Ripley’s K-function or the pair-correlation function, use the information on all inter-point distances (see Wiegand et al. 2007). The K-function is the expected number of points in a circle of radius r, centred at an arbitrary point, divided by the intensity of the pattern. The pair correlation function g(r) results if the circles of Ripley’s K-function are replaced by rings (Law et al. 2009). The pair correlation function is based on the distribution of distances of pairs of points and is a powerful tool that can be used to describe the second order structure of a spatial point pattern, i.e., the small-scale spatial correlation structure of the point pattern (Wiegand et al. 2007). To reveal the degree of smaller-scale order effects in the pattern of fairy circles, *E. damarana* and *E. gummifera*, the pair-correlation function g(r) was used. This function measures the expected density of points at a given distance r of an arbitrary point, divided by the intensity, ƛ, of the pattern. The pair correlation function enables an analyst to get a clearer picture of any separation distances at which there are few or many pairs of events.

The pair correlation function of a point pattern can be calculated with the following formula (Law et al. 2009):

$$g(r) = \frac{1}{\lambda^2} p(r)$$

Under complete spatial randomness (CSR), g(r) = 1. Values of g(r) < 1 indicate regularity (or also called overdispersion), while values of g(r)> 1 indicate aggregation (or clustering).

L-function:

Finally, the L-Function is the cumulative counterpart of the pair correlation function (Wiegand et al. 2007). The L-function makes visual interpretation of the K-function easier and results from a square root transformation of the K-function (Wiegand et al. 2007). The L-function was used to assess departures from complete spatial randomness (CSR) at larger distances.

The L-function is given by the following formula (Wiegand et al. 2007):

$$(L) = r(\frac{\sqrt{K(r)}}{\pi} - 1)$$

L(r)=0 indicates CSR, L(r)<0 indicates regularity (or overdispersion), L(r)>0 indicate aggregation (or clustering).

The methods discussed above will provide an indication of whether or not, and over what distances, a pattern is clustered or not. However, they are not a statistical assessment of the data because it remains unclear how far the functions need to depart from ‘1’ (for the pair correlation function) and ‘0’ (for the L-function) to be unusually high or low values. Computer simulations are generally used to estimate approximate values (O’Sullivan et al. 2010). For instance, a Monte Carlo procedure is used randomly to locate *n* events in the study area. Each randomly generated point pattern is then analysed with the same methods applied to the pattern under investigation, i.e., either the pair correlation function or the L-function. The results of the randomly generated point pattern are then used to construct an envelope of the results, inside which a pattern generated by CSR would be expected to reside (O'Sullivan et al. 2010). Model testing is a central step of spatial point pattern analysis and simulation envelopes are commonly used to assess the goodness-of-fit of a point process model to point pattern data (Wiegand et al. 2016, Diggle, 2003). All the summary statistics will be assessed in this study against complete spatial randomness (CSR) using the 5th highest and lowest values of 199 Monte Carlo simulations in order to produce 95% simulation envelopes.

Getzin et al. (2014) used a number of spatial statistics to characterise the spatial distribution of fairy circles in the Marienfluss Valley and in the Giribes Plain. The pair correlation function used in their analysis revealed several important characteristics associated with the spatial pattern of fairy circles Firstly, the pair correlation function showed that there are no fairy circles situated directly next to each other and are separated by several meters (Figure 4.3 A). The graph of the pair correlation function displays a pronounced peak at 12 m, which is the most frequent distance to the nearest neighbour and points towards a 'hexagonal' spatial arrangement where each fairy circle has six neighbours located at approximately the same distance from the respective circle (Getzin et al. 2015). The graph then shows an oscillation around the null model, indicating an extremely high degree of ordering of the pattern that persists well beyond the nearest neighbours. This oscillation is also reflected in the L-function. Finally, the pattern is characterised by large scale homogeneity that is reflected in both the pair correlation function and the L-function

Therefore, the final part of the spatial point pattern analysis was to determine the pair-correlation function and L-function for fairy circles, *E. damarana* and *E. gummifera*.

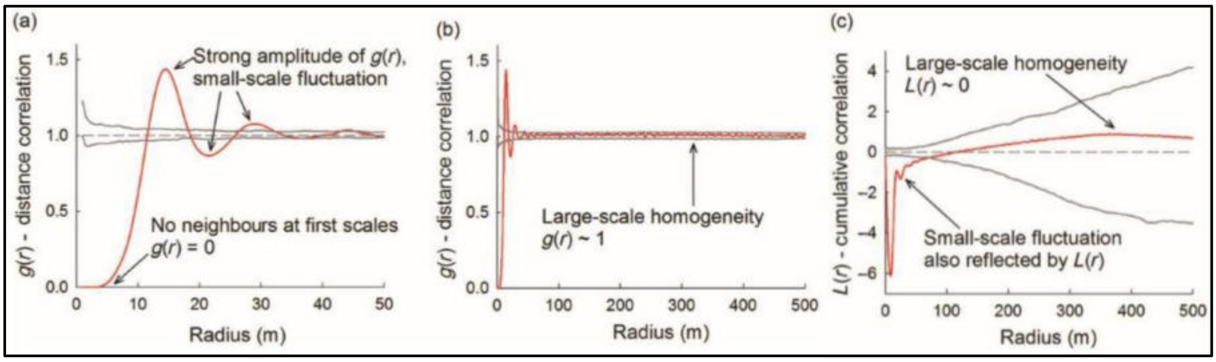


Figure 4.3: The pair correlation function (graphs a and b) and the L-function (graph c) (adapted from Getzin et al. 2015). a and b are both illustrations of the pair correlation, but at smaller and larger scales, respectively.

4.2 Methods

4.2.1 Study area selection and experimental design

In order to compare the spatial distribution of fairy circles with the two *Euphorbia* species, analyses were conducted at 1) fairy circle sites, at 2) *E. damarana* populations at 3) *E. gummifera* populations, and at 4) areas where fairy circles co-occur with one of the two plant species. Several localities of co-occurrence have been identified and are described below. These areas are all on sandy soil and are named 'mixed sites' in this study. The mixed areas where fairy circles and *E. damarana* (northern Namibia) or *E. gummifera* (southern Namibia) co-occur, is hypothesised as to be transitioning from high numbers of Euphorbias and low numbers of fairy circles, to areas where the plants will become less and the fairy circles more, up to a point in the future when only fairy circles will be present.

Study plots were chosen carefully by placing them in areas where the terrain was homogeneous, free of obstructions like dry river beds that could introduce bias into the analysis. The sampling design ensured that independence was met by placing sample plots a minimum distance of 1 km apart, although larger distances were frequently the case. The plots were considered to accurately represent 1) fairy circles, 2) *E. damarana* populations 3) *E. gummifera* populations and 4) mixed populations (co-occurrence of one of the *Euphorbia* species and fairy circles), at four locations; 1) Giribes Plain and 2) Palmwag (both north-western Namibia), 3) Brandberg (central-western Namibia) and 4) Garub (south-western Namibia). Representative samples of each of these four areas were taken by constructing a total of 19 sample squares (Table 4.1).

Site one: Giribes Plain

Giribes Plain is located in north-western Namibia at 19°03'47.05"S and 13°20'21.31"E, close to the town of Sesfontein (see Figure 4.4). This is the most northern site that was visited and represents two types of sites, one with only fairy circles and one with a small population of *E. damarana* mixed with fairy circles. Giribes is surrounded by hills but the topography inside the plain itself is flat and the underlying substrate is sand. The plain is covered by grass from the *Stipagrostis* genus with thousands of fairy circles spread out over the plain. In the southern parts of the Plain, there is a small population of *E. damarana* mixed with fairy circles. Three sample plots were identified at the Giribes Plain; two 500 m x 500 m plots containing only fairy circles and one of 250 m x 250 m containing a mix of fairy circles and *E. damarana* (the small size of this plot is due to its location). The fairy circle only plots are named Giribes C1 and Giribes C2 and the mixed plot named Giribes M1 (Table 4.1).

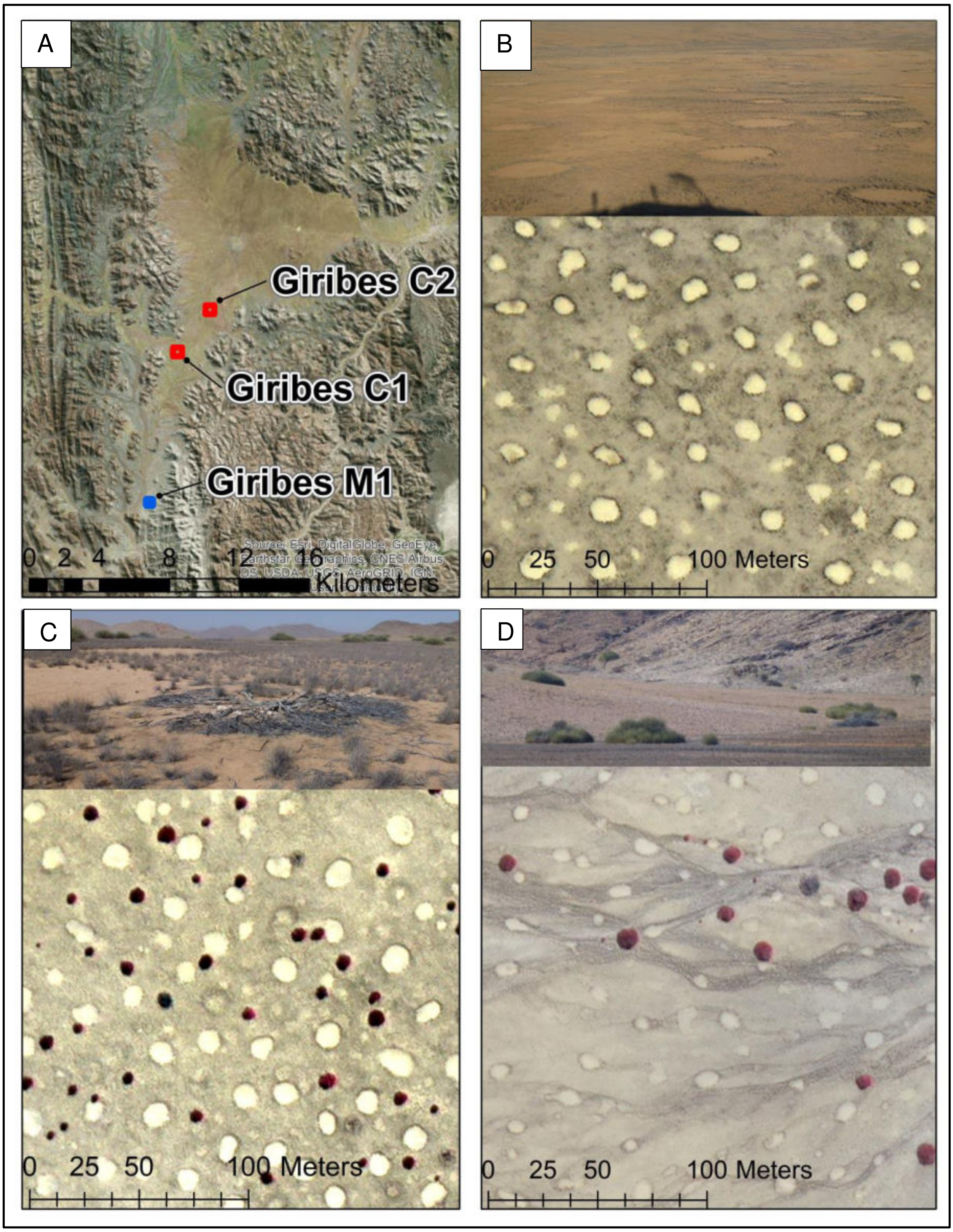
Table 4.1: Naming convention for the 19 sample plots in the four areas of Namibia.

Study site	Type of object	Sample plot name	Sample plot size (in m)
Giribes Plain	Fairy circles	Giribes C1	500 x 500
	Fairy circles	Giribes C2	500 x 500
	Fairy circles and *E. damarana* mix	Giribes M1	250 x 250
Palmwag	*E. damarana*	Palmwag P1	500 x 500
	E. damarana	Palmwag P1	500 x 500
	E. damarana and rock circles mix	Palmwag M1	500 x 500
	E. damarana and rock circles mix	Palmwag M2	500 x 500
Brandberg	Fairy circles	Brandberg C1	500 x 500
	Fairy circles	Brandberg C2	500 x 500
	E. damarana	Brandberg P1	500 x 500
	E. damarana	Brandberg P2	500 x 500
	Fairy circles and *E. damarana* mix	Brandberg M1	500 x 500
	Fairy circles and *E. damarana* mix	Brandberg M2	500 x 500
Garub	Fairy circles	Garub C1	500 x 500
	Fairy circles	Garub C2	500 x 500
	E. gummifera	Garub P1	300 x 300
	E. gummifera	Garub P2	300 x 300
	Fairy circles and *E. gummifera* mix	Garub M1	300 x 300
	Fairy circles and *E. gummifera* mix	Garub M2	300 x 300

Figure 4.4 A shows the sampling design at Giribes Plain. The red squares indicate the two fairy circle plots, Giribes C1 and Giribes C2 while the blue square indicates the mixed plot, Giribes M1. Figures 4.4 B-D are false colour composite images (band

7,4,2). Figure 4.4 B shows a satellite image of fairy circles in the northern parts of Giribes Plain, with accompanying photograph. Fairy circles can easily be identified from the grass matrix. Figure 4.4 C shows the location of the mixed site, note the dead *E. damarana* with living ones in the background, this can also be seen in the satellite image where bright red indicates healthy vegetation and dark tone indicate dead vegetation. Figure 4.4 D shows *E. damarana* situated along drainage lines, several are dead, as observed from the false colour composite. Note the elliptical shape of fairy circles situated in drainage lines.

Field work consisted of verification of the objects being studied remotely. This was done by recording the coordinates of 10 fairy circles and 10 *E. damarana* plants on the satellite images, as well as several fairy circles and dead *E. damarana* plants that was originally marked by Theron (1979) and locating them at Giribes Plain. During field work each object was verified.



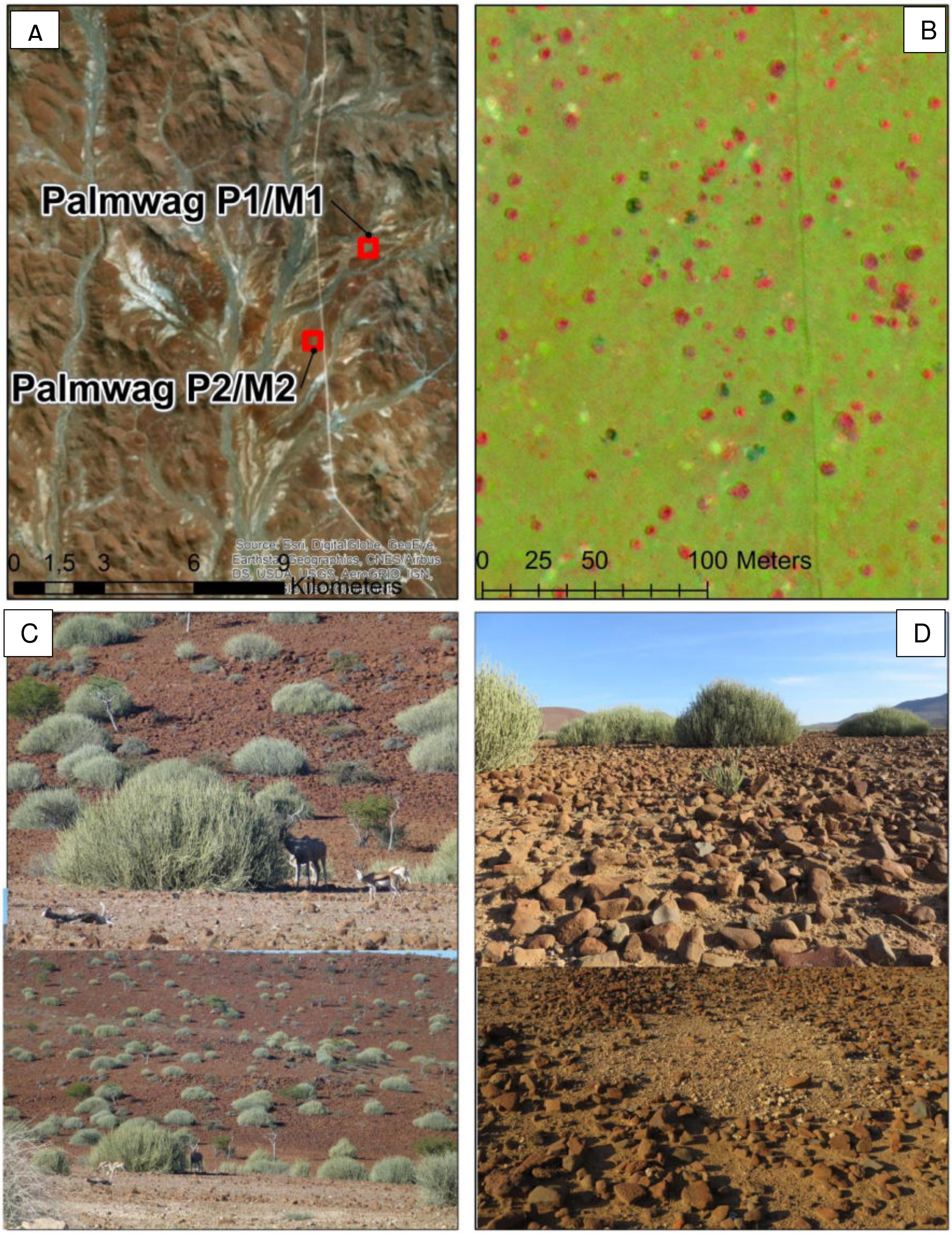
Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN,

Figure 4.4: A: Sampling design at the Giribes Plain, site 1. The red squares indicate the two fairy circle plots, while the blue square indicates the mixed plot. Satellite imagery in B – C courtesy of the **DigitalGlobe Foundation.** B: Fairy circles in the northern parts of Giribes. C and D: Fairy circles co-occurring with *E. damarana.* Bright red indicates healthy vegetation, while dark tones indicate dead vegetation.

Site two: Palmwag

Palmwag is also in north-western Namibia, 115 km south-west of the Giribes Plain, at 19°54'22.29"S and 13°58'55.55"E (Figure 4. 5). This site is in the Etandeka Plateau and the nearest site to the Giribes Plain that could be accessed during field excursions where *E. damarana* populations occur on a rocky substrate without the presence of fairy circles. One of the aims of this study was to compare the spatial characteristics of fairy circles with that of *E. damarana*.

The site is situated between rocky outcrops sloping down into plains and the geology/substrate of this site consists of a desert-pavement, which is a surface covered with tightly packed rocks (Lancaster 2010). Figure 4.5 B shows a false colour composite image (band 7,4,2) of the area, note the green hue, due to the presence of the desert pavement. Between the *E. damarana,* there are many circular disturbances to the desert pavement (Figure 4.5 B and D). These disturbances are similar to fairy circles in that they are also round, but instead of the absence of grass, there is an absence of rocks inside the circle area. The remains of dead *E. damarana* can be seen in some of the “rock circles”, and were confirmed to be in another study. It is therefore hypothesised that the plants somehow cause these disturbances. Because both fairy circles and rock circles are considered here to be a result of dead *E. damarana*, it was decided to include the “rock circles” as mixed sites. Figure 4. 5 A shows the sampling design at Palmwag. The two red squares indicate the two *E. damarana* population plots, Palmwag P1 and Palmwag P2, each 500 m x 500 m. The same squares were used as the mixed plots (the rock circles located between these plants were included) and called Palmwag M1 and Palmwag M2.



Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN,

Figure 4.5: A: Sampling design at Palmwag, site 2. B: *E. damarana* (red spots) and rock circles (white spots), satellite imagery in B courtesy of the **DigitalGlobe Foundation**. C – D: The photographs Illustrates *E. damarana* occurring on the desert pavement along with rock circles. Bright red indicates healthy vegetation, while dark tones indicate dead vegetation and green indicates the desert pavement.

Site three: Brandberg

Brandberg is located approximately 140 km south-south-east of Palmwag in the central-western plains at 21°04'26.85"S and 14°38'48.37"E, near the town of Uis (see Figure 4.6). On the sandy plains near Brandberg, *E. damarana* co-occur with fairy circles and also without fairy circles on higher lying, rocky areas. It was observed that many of the plants in the mixed sandy areas are dead. The environment surrounding Brandberg contains a combination of gravel and sandy plains, several smaller riffs and hills, as well as the Ugab River and several of its major tributaries (Figure 4.6 A). Both fairy circles and *E. damarana* frequently occur along drainage lines where the shape of the fairy circles is elliptical, with the longest axis parallel to the drainage line (Figure 4.6 C) as was seen in Giribes Plain. The two red squares in Figure 4.6 A indicate the two fairy circle plots, Brandberg C1 and Brandberg C2. The two green squares indicate the two *E. damarana* plots, Brandberg P1 and Brandberg P2. The two blue squares indicate the two mix plots, Brandberg M1 and Brandberg M2. All the squares used at this site was 500 m x 500 m. Figure 4.6 B-D shows fairy circles co-occurring with *E. damarana*, both alive and dead *E. damarana* can be seen, also evident from the false colour image composite (band 7,4,2) where a bright red tone indicates healthy vegetation and a dark tone indicate dead vegetation.

Field work consisted of verification of the objects being studied remotely. This was done by recording the coordinates of 10 fairy circles and 10 *E. damarana* plants on the satellite images and locating them at Brandberg. During field work each object was verified (the same method was used as described for Giribes Plain above). The occurrence of fairy circles at this site covers a much larger area than at the Giribes Plain and this was photographed from an air plane.

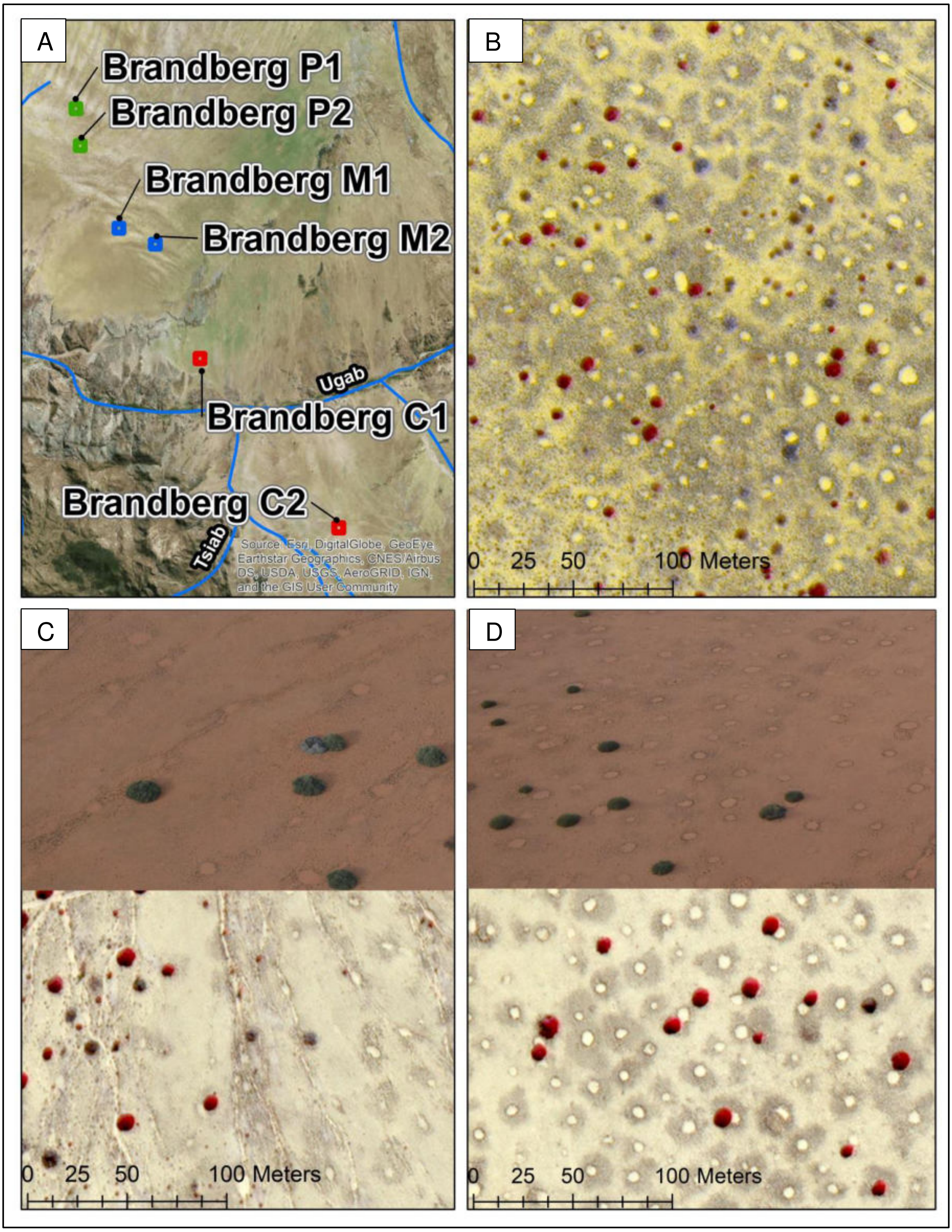


Figure 4.6: A: Sampling design at Brandberg, site 3 central-western Namibia. The red squares indicate the two fairy circle plots, the green squares indicate the two *E. damarana* plots, the blue squares indicate the two mix plots. Satellite imagery in B – D courtesy of the **DigitalGlobe Foundation.** B – D: Fairy circles co-occurring with *E. damarana*, bright red indicates healthy vegetation, while dark tones indicate dead vegetation.

Site four: Garub

Garub is located in south-western Namibia at 26°38'52.17"S and 16°05'5.95"E, approximately 630 km south south-east of Brandberg, between the towns of Aus and Lüderitz (Figure 4.7). At this site, *E. gummifera* occur alongside fairy circles on low sloping sand dunes, where large number of these plants are dead and also on rocky/gravel areas in healthy populations without any fairy circles being present. The environment consists of several rocky out crops that rise above the flat terrain with various gravel plains and sandy deposits/accumulations. Low sloping sand dunes have developed on the lower portions of many the iselbergs (individual mountains), while a non-mobile dune field have developed between the iselbergs. The area is covered by grass from the *Stipagrostis* genus. Fairy circles and *E. gummifera* occur on these sandy deposits and also extend north of the dune fields onto gravel plains. *E. gummifera* occurs to the south of the dune fields on gravel plains, where the plants are not dying in large numbers and no fairy circles were observed. This population was considered to represent a healthy population of *E. gummifera*. The two red squares in Figure 4.7 A indicate the two fairy circle plots, Garub C1 and Garub C2. The two green squares indicate the two *E. gummifera* plots, Garub P1 and Garub P2. The two blue squares indicate the two mix plots, Garub M1 and Garub M2. Only the fairy circle plots were 500 m x 500 m, while the *E. gummifera* and the mixed plots were 300 m x 300 m. In Figure 4. 7 C fairy circles of Garub can be seen co-occurring with *E. gummifera*, also evident from the satellite image where a bright red tone indicates healthy vegetation and a dark tone indicate dead vegetation. In Figure 4.7 D photographs of fairy circles co-occurring with *E. gummifera*, many of which are dead and in different stages of decay.

Similar to the previous two field sites, field work consisted of verification of the objects being studied remotely. This was done by recording the coordinates of 10 fairy circles and 10 *E. damarana* plants on the satellite images and locating them at Garub. During field work each object was verified. The extent of fairy circle occurrence at the mixed site in Garub is more extensive than that of the Giribes Plain but less than that that of the greater Brandberg area.

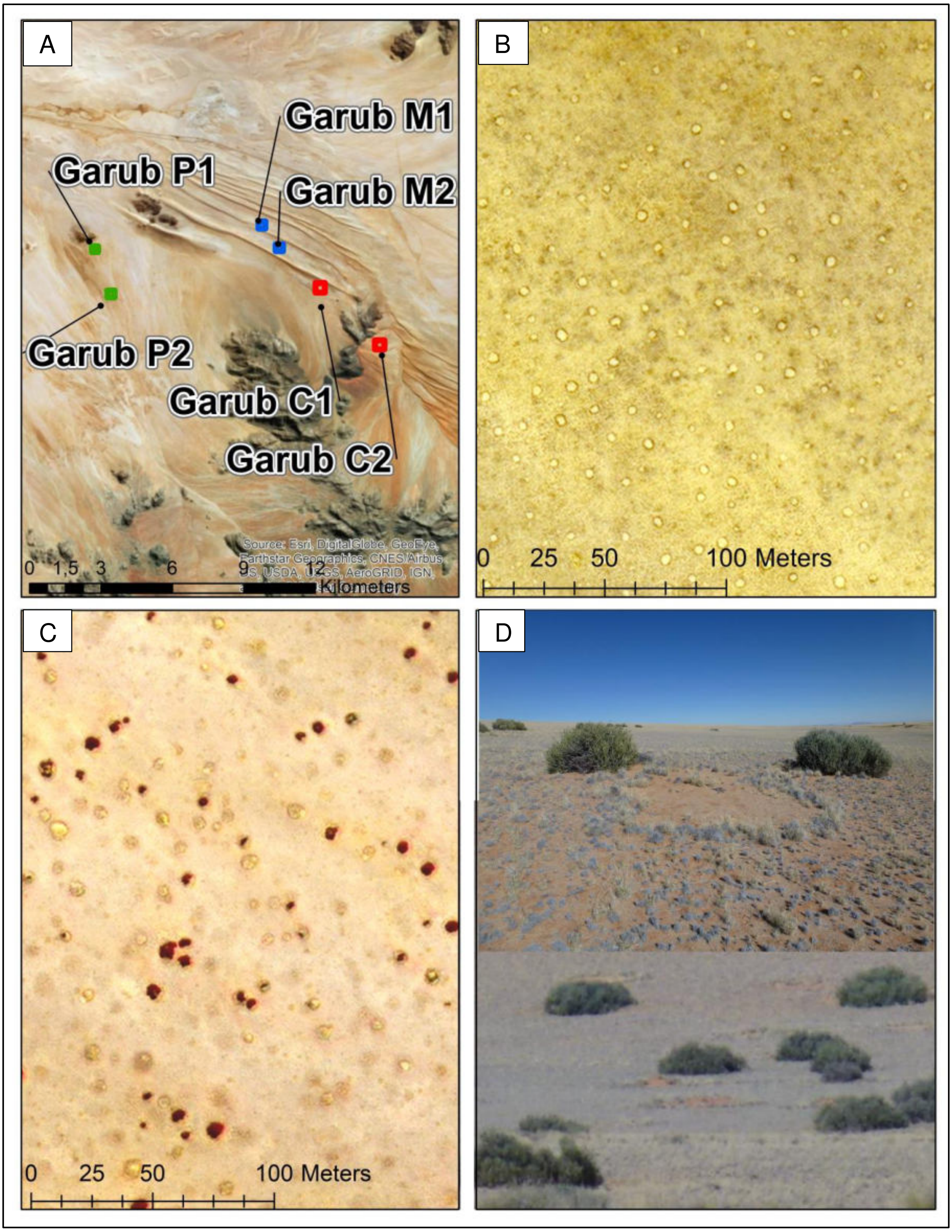


Figure 4.7: A: Sampling design at Garub, site 4 in south-western Namibia. The red squares indicate the two fairy circle plots, the green squares indicate the two *E. gummifera* plots, the blue squares indicate the two mix plots. Satellite imagery in B – C courtesy of the **DigitalGlobe Foundation.** B – D: Fairy circles co-occurring with *E. damarana*, bright red indicates healthy vegetation, while dark tones indicate dead vegetation.

4.2.1 Data acquisition and analysis

According to the Euphorbia allelopathy theory Euphorbia plants create fairy circles, therefore, it is assumed that *E. damarana* and *E. gummifera* will eventually be replaced by fairy circles. If this is indeed the case, it should be possible to observe this change by comparing aerial imagery of the same area during different years. It is, however, unknown how long it will take for a given plant to be replaced by a fairy circle. Obtaining historic aerial imagery of the locations of the four study sites outlined above proved challenging as imagery is only available for certain areas. Nevertheless, historical aerial imagery was obtained from the National Geospatial Institute (NGI) for Giribes Plain, Brandberg and Garub (Table 4.2). However, the resolution was relatively coarse; aerial imagery of Garub had the best resolution, with a scale of 1:36 000 and dates back to 1963 and could be used in the image comparison. The resolution of the aerial images of Giribes Plain and Brandberg were extremely coarse. The aerial image of Giribes Plain had a scale of 1:75 000 and dates back to 1964. The aerial image of Brandberg had a scale of 1:75 000 and dates back to 1981. The ground truth information proved critical to increase confidence in the image comparison. Photoshop was used to enhance the quality of the aerial images and make observations easier.

Table 4.2: Details of the aerial imagery obtained from Giribes Plain, Brandberg and Garub.

Site	Scale	Date
Giribes Plain	1:75 000	1964
Brandberg	1:75 000	1981
Garub	1:36 000	1963

Imagery for the present time for the four study sites were obtained from the Digital Globe Foundation from their World-View I and World-View II satellites. These are next generation earth-observation satellites that have extremely high spatial, spectral and temporal resolution. Both the satellites have a pan-chromatic sensor on-board that records a single band as well as a multispectral sensor that records four wave-lengths; i.e. blue, red, green and near-infrared. The spatial resolution of the pan-chromatic band is 0.5 m (compared to Landsat of 15 m) and the multispectral bands are 1.5 m (compared to Landsat of 30 m). The specifications of the satellite imagery used in this study is shown in Table 4.3 below. The projected coordinate system of the satellite images is “WGS1984 - UTM Zone 33S”.

ArcMap 10.5.1 was used to create the pan-sharpened images of the World-View I and Wold-View II imagery. The locations of the sample plots were carefully determined (as described under the study area and experimental design section above). The objects contained within the sample plots were manually digitised. Polygon feature classes were created for each sample plot assigned the projected coordinate system of the satellite images. To capture the characteristics of interest, the following three additional fields were added to the attribute tables of each sample plot:

- X-coordinate
- Y-coordinate and
- Perimeter.

On-screen digitising was done to capture the spatial extent of the objects and store the spatial information in the newly created features classes. The polygon template was selected and the outline of each object, either a fairy circle, *E. damarana* or *E. gummifera*, was digitised. From the 19 sample plots a total of 12 516 objects were digitised. These consisted of 5 095 fairy circles, 4 763 *E. damarana* (alive and dead plants), 2 167 *E. gummifera* (alive and dead plants) and 491 "rock circles". After all the objects in the sample plot were digitised, the X- and Y coordinates as well as the perimeter of each object was calculated. The attribute tables were exported to excel format and converted to Comma Delineated files (*.CSV).

Table 4.3: Satellite data was obtained from both WorldView-1 and WolrdView-2 satellites, **courtesy of the DigitalGlobe Foundation**

Satellite	Spectral resolution	Spatial resolution	Date	Site
WV-I	Panchromatic	0.5 m	2011	Garub
	Multispectral	1.5 m	2012	
WV-II	Panchromatic	0.5 m	2011	Giribes
	Multispectral	1.5 m	2012	Plain
				Brandberg,
				Palmwag

Age of the fairy circles:

In order to determine the approximate age of the fairy circles it was aimed to locate the specific fairy circles and *E. damarana* previously marked and described by Theron (1979) in Giribes Plain. Determining if these are still intact could show that fairy circles persist for many years and appear/disappear after droughts/rains, respectively. Due to the resolution and quality of the historical aerial photographs of Giribes Plain and Brandberg it could not effectively be used in the image comparison. However, the aerial image for Giribes Plain included the mixed site that was visited in 1978 (50 years ago). The fairy circles and some *E. damarana* are visible in the photograph which dates back to 1964 (more than a decade before Theron (1979) first observed them).

From the low quality aerial image obtained of Brandberg, no fairy circles could be observed (assuming no grass was present the date on which the photograph was taken). *E. damarana* were barely visible and their exact location could not be determined.

The aerial images of Garub had the best resolution but was not good enough for fairy circles to become visible. Fortunately, individual *E. gummifera* plants could be observed and their exact location was determined by comparing the 1963 image to the 2011 image. Where ground control points, for instance rocky outcrops, streams or other similar landmarks could be identified in both images, they were used to georeference screen grabs of the old image. This added greater confidence in terms of identifying the same individual *E. gummifera* plants.

Size comparison:

In order to test for a significant difference in size a number of steps were followed. First, all fairy circles recorded at site 3 (Brandberg) were compared to all the *E. damarana* recorded at site 3, second, all fairy circles recorded at site 4 (Garub) were compared to all the *E. gummifera* recorded at site 4. An independent samples T-test compares the mean of two groups (D'Agostino et al. 2006). A t-test was done in order to test for a significant difference in size between fairy circles and *E. damarana*, as well as between fairy circles and *E. gummifera*. Palmwag is not a good location for size comparison of fairy circles and *E. damarana* plants as it is 115 km inland and 300 mamsl higher than Giribes. It was expected that the average size of these plants will be smaller than at Giribes and no test for a significant difference in size between these two locations was done.

R- workflow:

A schematic representation of the work flow is shown in Figure 4.8. Initially the software packages that were needed for the analysis were downloaded. These included the Spatstat and the Derilcht packages, which was developed specifically for the analysis of spatial point patterns. For the Voronoi tessellations, the tiles were created, edge tiles were removed and the number of corners of each tile was calculated. The distance to nearest neighbour ratio was calculated using the Clark Evans test and the average distance to the nearest neighbour, in meters, was also calculated. Monte Carlo Randomisations are needed to construct simulation envelopes of Complete Spatial Randomness (CSR). Simulation envelopes result from the randomisations and indicate the area where CSR is expected. The pair correlation and L-functions were determined with 199 Monte Carlo Randomisations to construct the simulation envelopes. The L-function was additionally transformed to make the interpretation of the function easier (Getzin et al. 2014). The graphs of the pair correlation and L-functions were plotted and the limits of the x- and y-axis defined for short ($0 \text{ m} < x < 60 \text{ m}$) and long distances ($0 < x < 120 \text{ m}$) in order to assess the deviation of CSR. For the t-test a vector was created containing the perimeter of each object.

At Brandberg, all the fairy circles (i.e. fairy circles from fairy circle only plots and from mixed plots) were grouped together and all the *E. damarana* (i.e. all *E. damarana* from the plant only plots and from the mixed plots) grouped together and the spatial characteristics of the two groups compared.

At Garub, all the fairy circles (i.e. fairy circles from fairy circle only plots and from mixed plots) were grouped together and all the *E. gummifera* (i.e. all *E. gummifera* from the plant only plots and from the mixed plots) grouped together and the spatial characteristics of the two groups compared. The homogeneity of the variance of each pair (i.e. fairy circles and *E. damarana* or fairy circles and *E. gummifera*) was determined using Fisher's F-test and then the T-test was conducted. For the point pattern analysis, the unit of measurement in R-studio was in meters and the X- and Y-coordinates contained in the CSV file was used to construct the point pattern. Next, two vectors, one for the X-coordinates and one for the Y-coordinates, were created. The length of the vector was specified by defining a rectangular window with the following coordinates: x-min and x-max; y-min and y-max, (the corresponding coordinates of each sample plot was subsequently entered). If the sample plots contained duplicate points they were removed, and the point pattern was then plotted.

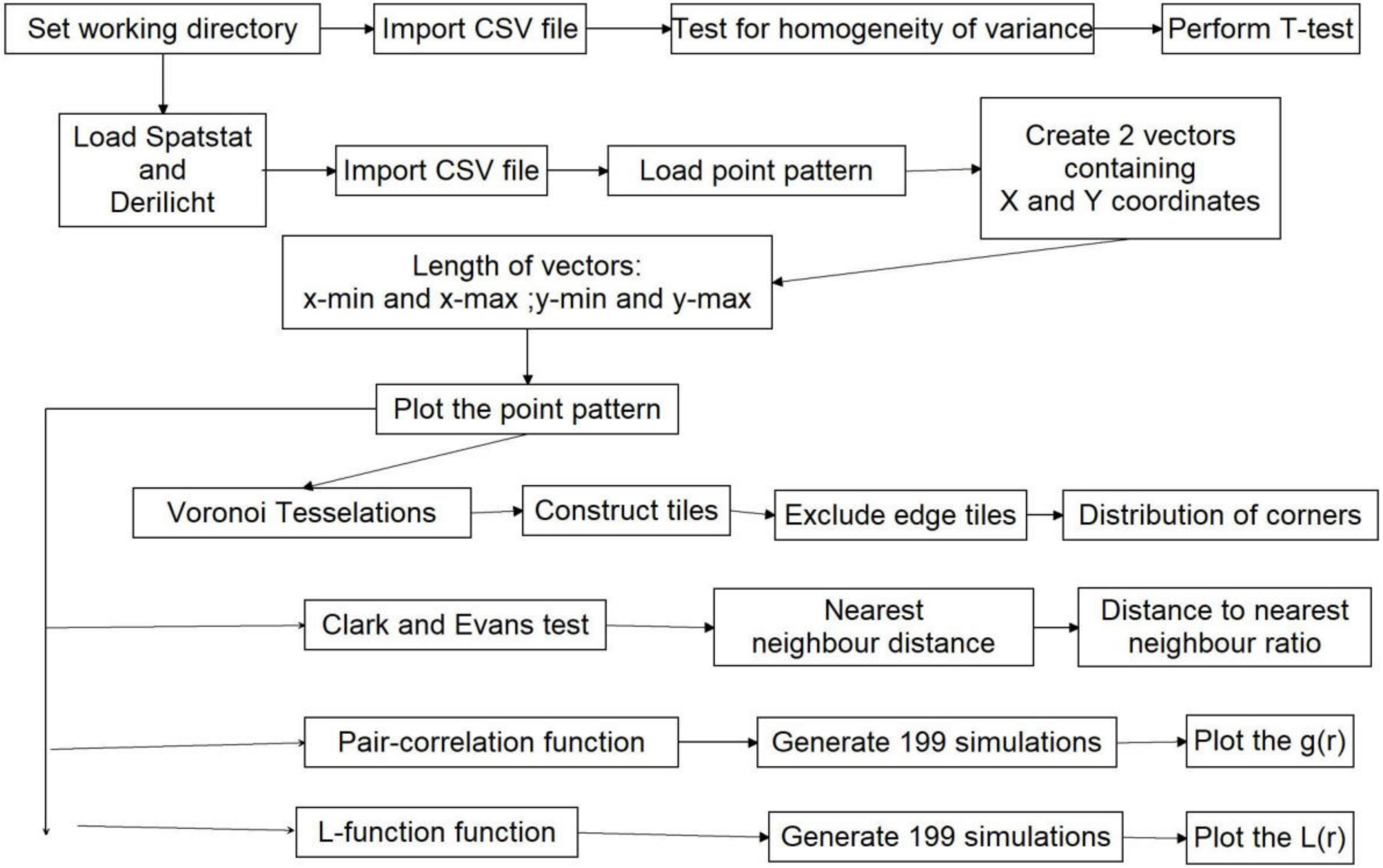


Figure 4.8: Schematic representation of the work flow and statistical analysis as undertaken in R.

4.3 Results and Discussion

4.3.1 Age of fairy circles

Giribes Plain:

A total of 10 fairy circles and 3 dead *E. damarana* that were marked by Theron (1979) were located, ground-truthed, photographed and their GPS coordinates recorded so that they could be located on the satellite image. Although the grass cover was at a minimum, all the fairy circles and the dead *E. damarana* marked in 1978 by the researchers were still intact in 2016 (Figure 4.9 A and B) and the perennial belt (PB) of most fairy circles could be recognised. A low percentage of small grasses were present inside some of fairy circles. As these same marked fairy circles were re-examined by Van Rooyen et al. (2004) and again confirmed in this study, it clearly shows that the minimum age of fairy circles is at least 40 years. These observations support the notion that fairy circles live long and do not disappear after dry spells as the vegetation self-arrangement hypothesis states (Getzin et al. 2014, Cramer et al. 2013, Tschinkel et al. 2012). It also shows that the decay process of *E. damarana* takes an extremely long time.

The mixed site could be observed from the 1964 image and is indicated by the red marking in Figure 4.10, while the yellow marking indicates an area next to the mixed site where ground observations confirmed the black dots to be *E. damarana* situated along drainage lines. These same areas are also shown in the 2012 image (Figure 4.11). Fairy circles and *E. damarana* can be seen in both images, although the resolution of the 1964 image was too low to determine the exact location of fairy circles visible in the old image. Therefore, no deductions can be made from the historical imagery of this site to determine if *E. damarana* plants that died caused the formation of new fairy circles.

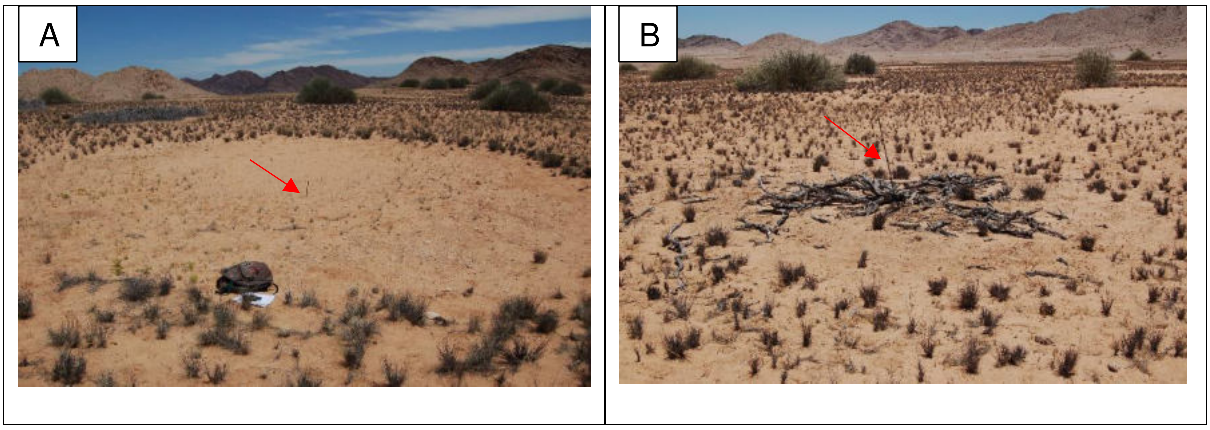


Figure 4.9: Fairy circle (A) and remains of *E. damarana* (B), marked by Theron (1979), the red arrows indicate the position of the metal pens used to mark the fairy circle and dead *E. damarana*.

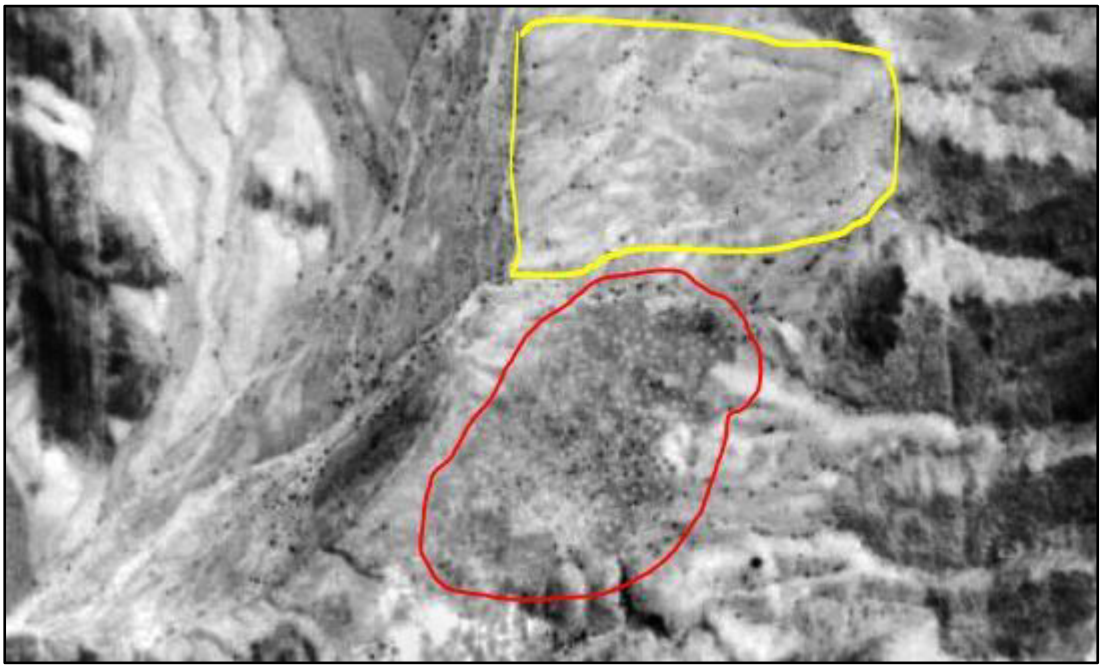


Figure 4.10: Mixed site at Giribes Plain visible in the low resolution 1964 aerial photograph. Red indicates the mixed site, yellow indicates *E. damarana* along drainage lines.

Figure 4.11: Mixed site at Giribes Plain as seen in the 2012 satellite image. Satellite image curtesy of the DigitalGlobe Foundation. Red indicates the mixed site, yellow indicates *E. damarana* along drainage lines.

Garub:

Figure 4.12 A-D shows an area of Garub in 1964, while Figure 4.12 E-H shows the same region taken in 2011. As can be seen from Figure 4.12 several *E. gummifera* have been replaced by fairy circles. The remains of some of the plants were also observed. During field work a subset of these fairy circles, plants and dead plants, were verified. All the objects that were identified from the aerial and satellite imagery were confirmed to be fairy circles or *E. gummifera* plants.

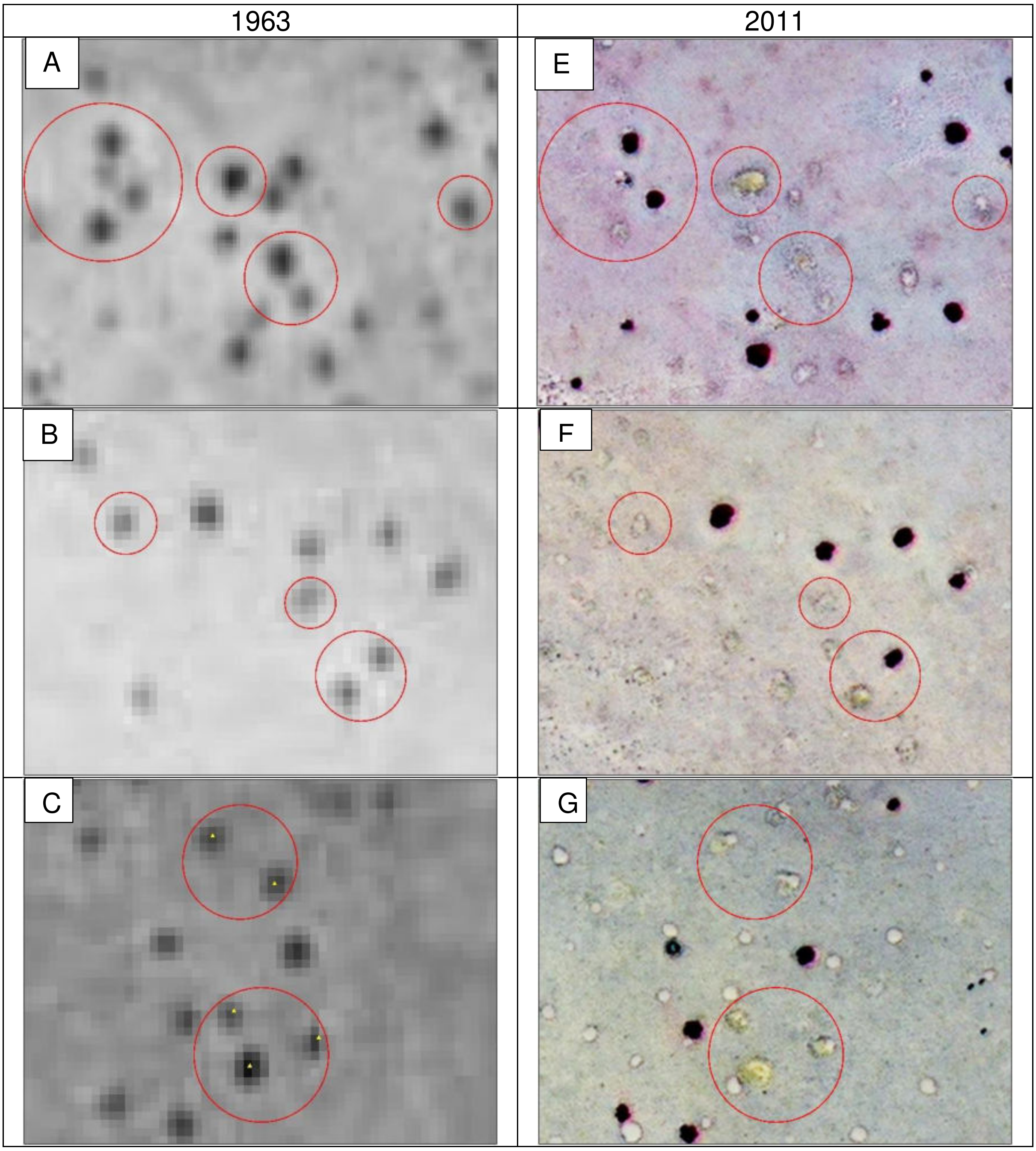
The image comparison revealed that of the test sample of 203 *E. gummifera* plants that were alive in 1963, 69 were dead (remains still present) and 134 of them were replaced by fairy circles in 2011 (Table 4.4). This image comparison clearly illustrates that *E. gummifera* are replaced by fairy circles and indicate that *E. gummifera* are in the process of transitioning into fairy circles at Garub in south-western Namibia.

It would have been interesting to examine if the fairy circles seen on the 2011 image and still present today, were present in 1963 but the resolution of the aerial photograph did not allow for it. This would have given a clearer picture on the age of fairy circles.

The observations made from the image comparison supports Theron (1979) and Meyer et al. (2015) who hypothesise that *E. damarana* and *E. gummifera* cause the formation of fairy circles.

Table 4.4: Long-term observations of *E. gummifera* at Garub showed that of 203 *E. gummifera* plants identified in 1963, 69 were in the process of dying in 2011 and 134 were replaced by fairy circles.

Object	1963	2011
Alive *E. gummifera*	203	24
Dead *E. gummifera*	Not observed	69
Fairy circle	Not observed	134


1963
2011
A
E
B
F
C
G

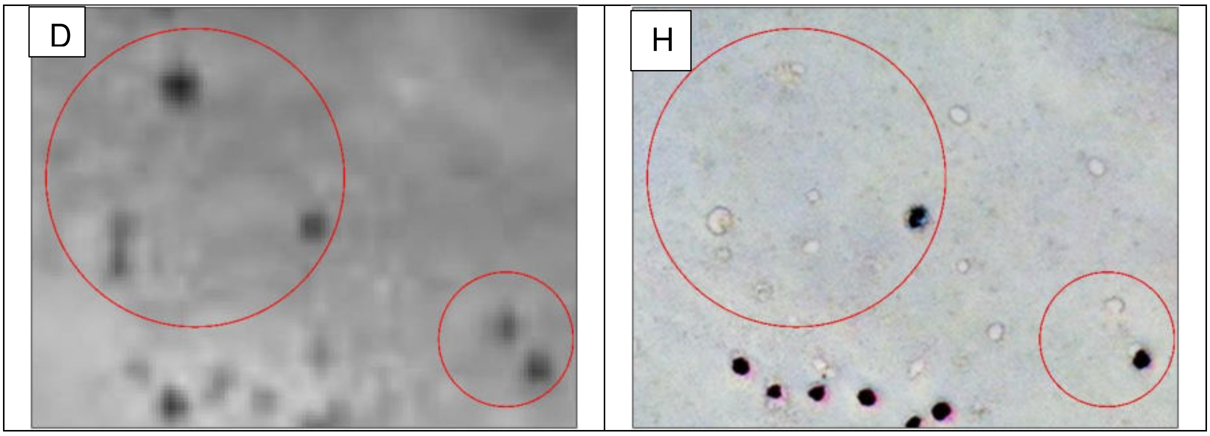


Figure 4.12: Left column: Aerial images of *E. gummifera* in 1963 at Garub in south-western Namibia. Right column: The corresponding area shown in 2011.

4.3.2 Size comparison

The aim of this analysis is to determine if there is a statistically significant difference in size between fairy circles and *E. damarana*; and between fairy circles and *E. gummifera*. The following section describes the results of the T-tests, but also provides additional information about the objects that were digitised, i.e. the size in perimeter, the area and the total area occupied by all the objects in the plot (Table 4.5).

Table 4.5: Mean perimeter and percentage of sample square covered.

Sample plot	Plot type	Mean perimeter (in m)	% Sample square covered
Giribes C1	Fairy circles	30.43	12.75
Giribes C2	Fairy circles	23.22	8.40
Giribes M1	Mixed	26.69	17.73
Palmwag P1	*E. damarana*	13.48	3.81
Palmwag P2	*E. damarana*	13.83	9.35
Palmwag M1	Mixed	13.72	5.03
Palmwag M2	Mixed	12.35	10.39
Brandberg C1	Fairy circles	18.93	6.39
Brandberg C2	Fairy circles	17.41	4.25
Brandberg P1	*E. damarana*	16.47	7.33
Brandberg P2	*E. damarana*	17.46	6.65
Brandberg M1	Mixed	16.01	7.35
Brandberg M2	Mixed	14.95	6.55
Garub C1	Fairy circles	10.59	2.59
Garub C2	Fairy circles	9.30	2.47
Garub P1	*E. gummifera*	8.50	7.25
Garub P2	*E. gummifera*	8.16	4.13
Garub M1	Mixed	14.52	6.63
Garub M2	Mixed	16.61	4.86

4.3.2.1 Northern Namibia

Giribes Plain:

At Giribes two plots consisted of fairy circles only and one plot was a mixed site, consisting of a combination of *E. damarana* and fairy circles (Table 4.5). The first sample plot, (Giribes C1) contained 473 fairy circles which covered 12.7 % of the plot and had an average perimeter of 30.4 m. The second plot, (Giribes C2), contained 516 fairy circles which covered 8.4 % of the plot and had an average perimeter of 23.2 m, indicating the big variation in mean size of fairy circles even in two similar sites less than 1 km apart.

The 166 fairy circles in the mixed plot had an average perimeter of 32.7 m while the 69 *E. damarana* in the mixed plot and had an average perimeter of 20.7 m. Together they covered 2.5 % of the sample plot.

Palmwag:

At Palmwag, the first sample plot (Palmwag P1) contained 676 *E. damarana* plants which covered 3.8 % of the sample plot and had a mean perimeter of 13.5 m (Table 4.5). The second plot, (Palmwag P2) contained 1548 *E. damarana* which covered 9.3 % of the sample plot and had a mean perimeter of 13.8 m. There are 214 rock circles between the *E. damarana* in the first plot (Palmwag M1), they covered 1.2 **%** of the sample plot and have a mean perimeter of 13.1 m. There are 277 rock circles between the *E. damarana* plants in the second plot, (Palmwag M2), they covered 1.0 % of the sample plot and had a mean perimeter of 10.9 m. The *E. damarana* together with the “rock circles” recorded for the two mixed plots covered 5.0 % and 10.3 % of the respective sample plots.

Brandberg:

At Brandberg, the first sample plot (Brandberg C1) contained 573 fairy circles which covered 6.4 % of the sample plot and had a mean perimeter of 18.9 m (Table 4.5). The second fairy circle sample plot (Brandberg C2) contained 452 fairy circles which covered 4.2 % of the sample plot and had a mean perimeter of 17.4 m. The second plot contained less, smaller circles and covered a smaller percentage of the plot.

The first plot contained only plants (Brandberg P1), including 870 *E. damarana* which covered 7.3 % of the sample plot and had a mean perimeter of 16.5 m. The second plants-only plot, (Brandberg P2) contained 716 *E. damarana* which covered 6.6 % of the sample plot and had a mean perimeter of 17.5 m.

There were 537 fairy circles in the first mixed plot (Brandberg M1) which covered 4.0 % of the sample plot and had a mean perimeter of 15.8 m. There were 404 *E. damarana* in the first mixed plot which covered 3.4 % of the sample plot and had a mean perimeter of 16.3 m. Together they constituted 941 objects and covered 7.4 % of the sample plot. There were 466 fairy circles in the second mixed plot (Brandberg M2) which covered 2.6 % of the sample plot and had a mean perimeter of 13.8 m. There were 480 *E. damarana* in the second mixed plot which covered 3.9 % of the sample plot and had a mean perimeter of 16.1 m. Together they constituted 946 objects and covered 6.6 % of the sample plot.

Statistical analysis of size comparison of fairy circles and *E. damarana* (northern Namibia, Brandberg):

To test for a significant difference in size between fairy circles and associated plant species all the recorded fairy circle plots were grouped together and all the *E. damarana* recorded grouped together. The results of the T-test are given in Table 4.6 below. For the T-test, the alternative hypothesis is that there is a statistical difference in the size of fairy circles compared to *E. damarana*. The t-value computed (-0.5647) was less than the tabulated t-value (1.961), while a p-value of greater than 0.05 was obtained (0.57). We can thus accept the null hypothesis Ho of equality of the means. This confirmed that there is statistically no difference in the sizes (in terms of perimeter) between fairy circles and *E. damarana* at Brandberg, with average perimeter of 16.6 m and 16.7 m each, respectively.

Table 4.6: Results of the T-test for Brandberg (fairy circles and *E. damarana*) and Garub (fairy circles and *E. gummifera*).

Object	T-value calculated	T-value tabulated	p-value	Fairy circle (size in m)	Euphorbia (size in m)
Brandberg	-0.5647	1.961	0.57	16.7	16.6
Garub	9.0717	1.961	0.00	10.5	9.5

4.3.2.2 Southern Namibia

Garub:

At Garub, the first sample plot (Garub C1) contained 734 fairy circles which covered 2.6 % of the sample plot and had a mean perimeter of 10.6 m (Table 4.5). The second fairy circle sample plot (Garub C2), contained 930 fairy circles, they covered 2.6 % of the sample plot and had a mean perimeter of 9.3 m.

The first plants-only plot (Garub P1) contained 1 156 *E. gummifera* which covered 7.3 % of the sample plot and had a mean perimeter of 8.5 m. The second plants only plot, (Garub P2) contained 708 *E. gummifera* which covered 4.1 % of the sample plot and had an mean perimeter of 8.2 m.

There were 136 fairy circles in the first mixed plot (Garub M1) which covered 2.0 % of the sample plot and had a mean perimeter of 13.0 m. There were 211 *E. gummifera* in the first mix plot which covered 4.6 % of the sample plot and had a mean perimeter of 16.1 m. Together they constituted 347 objects and covered 6.6 % of the sample plot. There were 112 fairy circles in the second mixed plot (Garub M2) which covered

2.6 % of the sample plot and had a mean perimeter of 16.5 m. There were 92 *E. gummifera* in the second mixed plot which covered 2.2 % of the sample plot and had a mean perimeter of 16.5 m. Together they constituted 204 objects and covered 4.9 % of the sample plot.

Statistical analysis of size comparison of fairy circles and *E. gummifera* (southern Namibia):

The t-test for Garub, combined all the fairy circles and combined all the *E. gummifera*, the results are given in Table 4.6. For the t-test, the alternative hypothesis is that there is a statistical difference in the size between fairy circles and *E. gummifera*. The t-value computed (9.0717) is larger than the tabulated t-value (1.961). A p-value of less than 0.05 was obtained (approximately 0). We can thus reject the null hypothesis Ho of equality of the means. This confirmed that there is a statistical difference in the sizes (in terms of perimeter) between fairy circles and *E. gummifera* at Garub, with mean perimeters of 10.5 m and 9.5 m, respectively.

The results from the size comparison showed that where fairy circles and *E. damarana* co-occur there is no statistical difference between their sizes. While there is a difference in size between fairy circles and *E. gummifera*, although it is quite small (fairy circles were on mean 1 m larger) and much more similar to one another than compared to Brandberg. It should be noted that there was much more variation in both fairy circle and *E. gummifera* size at Garub than compared to Brandberg, where all fairy circles had similar sizes and all *E. damarana* had similar sizes. Another consideration is that all the plots at Brandberg were the same size (500 m x 500 m). At Garub the fairy circle plots were 500 m x 500 m, while the plant and mixed plots were 300 m x 300 m.

4.3.3 Voronoi tessellations

Table 4.7 shows the results of the Voronoi tessellations analysis, i.e. the mean numbers of tiles with six corners as well as the percentage of tiles with six corners. The results indicate that fairy circles, *E. damarana, E. gummifera* and the mixed plots had six neighbours on average with a “hexagonal-like” structure around each individual object. Although all the plots had tiles with six corners on average, the percentage of tiles with six corners differed amongst the sample plots. For example, the fairy circle plots had the highest percentage of tiles with six corners, followed by the mixed plots and then the plants only plots. For the fairy circles, the percentage of tiles with six corners ranged between 33 – 40 % for all plots. For the plants only plots (both *E. damarana* and *E. gummifera*), the percentage of tiles with six corners were approximately 30 % for most plots, except for two *E. damarana* plots, one situated at Palmwag (Palmwag P2) and the other at Brandberg (Brandberg P2), which had 18.66 % and 32.98 % of tiles with six corners, respectively. For the mixed plots, the percentage of tiles with six corners range between 20 – 36 % and is the biggest range between the three types of plots.

At Brandberg, the percentage of tiles with six corners for the two mixed plots were 34.17 % and 35.50 % for Brandberg M1 and Brandberg M2 respectively and fall between that calculated for the fairy circle plots and the *E. damarana* plots at this site. It is also very similar to that calculated for the mixed plot at Giribes (Giribes M1). At Garub, the percentage of tiles with six corners for the first mixed plot (Garub M1) was 33.22 % and is between that of the fairy circles and the plants, while the second mix plot (Garub M2) at this site had 28.98 % of tiles with more than six corners.

Table 4.7: Results of the Voronoi tessellations.

Sample plot	Plot type	Mean number of corners	% with 6 corners of Voronoi tiles
Giribes C 1	Fairy circles	5.91	38.10
Giribes C2	Fairy circles	5.89	33.12
Giribes M1	Mixed	5.87	35.68
Palmwag P1	*E. damarana*	5.91	30.66
Palmwag P2	*E. damarana*	5.92	18.66
Palmwag M1	Mixed	5.91	33.66
Palmwag M2	Mixed	5.93	20.60
Brandberg C1	Fairy circles	5.91	39.07
Brandberg C2	Fairy circles	5.88	37.38
Brandberg P1	*E. damarana*	5.92	30.04
Brandberg P2	*E. damarana*	5.92	32.98
Brandberg M1	Mixed	5.93	34.17
Brandberg M2	Mixed	5.92	35.50
Garub C1	Fairy circles	5.91	36.21
Garub C2	Fairy circles	5.93	36.30
Garub P1	*E. gummifera*	5.93	30.08
Garub P2	*E. gummifera*	5.91	30.32
Garub M1	Mixed	5.88	33.22
Garub M2	Mixed	5.84	28.98

The fact that all the plots examined had on average six surrounding neighbours in the Voronoi results indicated that there are predominantly hexagonal structures around fairy circles, *E. damarana*, *E. gummifera* as well as all the mixed plots. This indicates a regular or uniform spatial distribution. There is however some variation in the degree of hexagonal dominance. This hexagonal dominance is most pronounced in the fairy circle pattern, less pronounced in the pattern associated with the mixed plots and least pronounced in the pattern associated with the two species of *Euphorbia*. This shows that between the three types of sample plots, the spatial pattern associated with fairy circles is the most over-dispersed, followed by the pattern associated with the mixed plots and lastly that of the *E. damarana* and *E. gummifera*.

Why would this be the case? According to pattern formation theory, over-dispersed patterns are caused by repulsive interactions between events in the pattern (O' Sullivan et al. 2010). In ecology, this is often the case between plants that compete for resources, with the end result being over-dispersion. Under this assumption that fairy circles are indeed caused by *E. damarana* and *E. gummifera*, the fairy circle only plots are considered to be the end product of competition amongst *E. damarana* and/or *E. gummifera*, having the most regular pattern. Subsequently, the mixed plots are considered to be in a transition state from Euphorbia only plots to fairy circle only plots and competition is still taking place between the plants. As the Euphorbia plots were taken from areas thought to be ideal for them, competition may be absent in between these plants. Figures 4.13 – 4.15 illustrate the Voronoi tessellation results determined at Brandberg for fairy circles, the mixed plots and *E. damarana*.

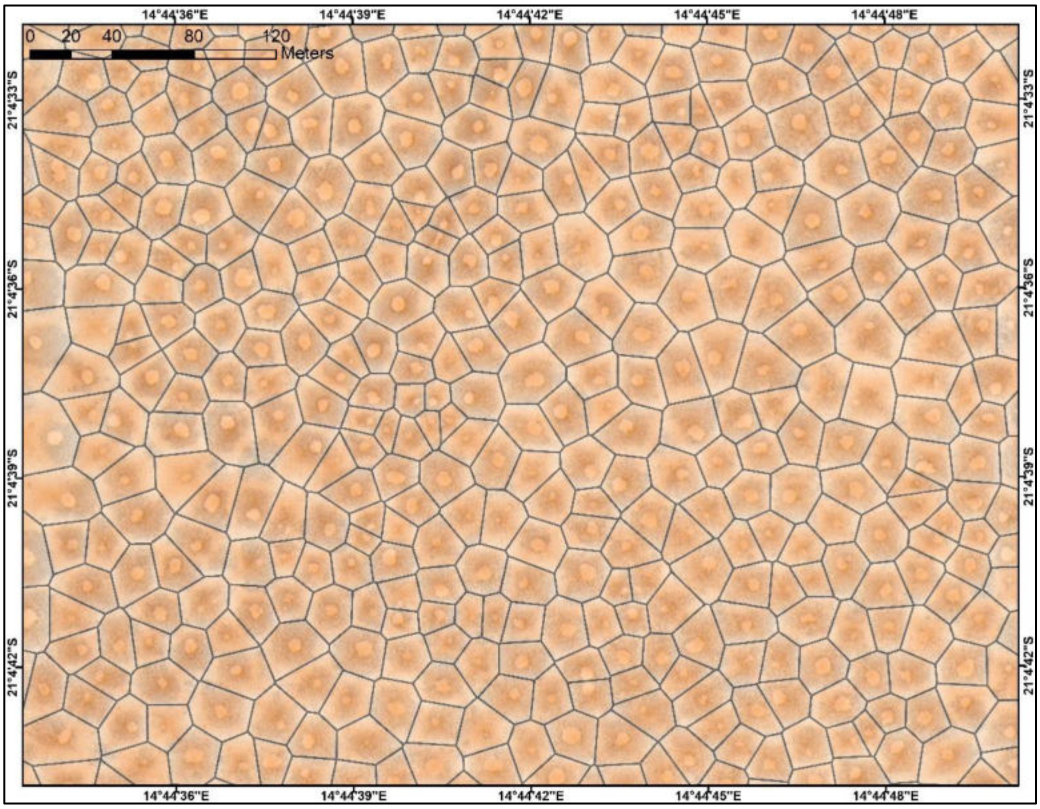


Figure 4.13: Voronoi tessellations created for fairy circles at Brandberg

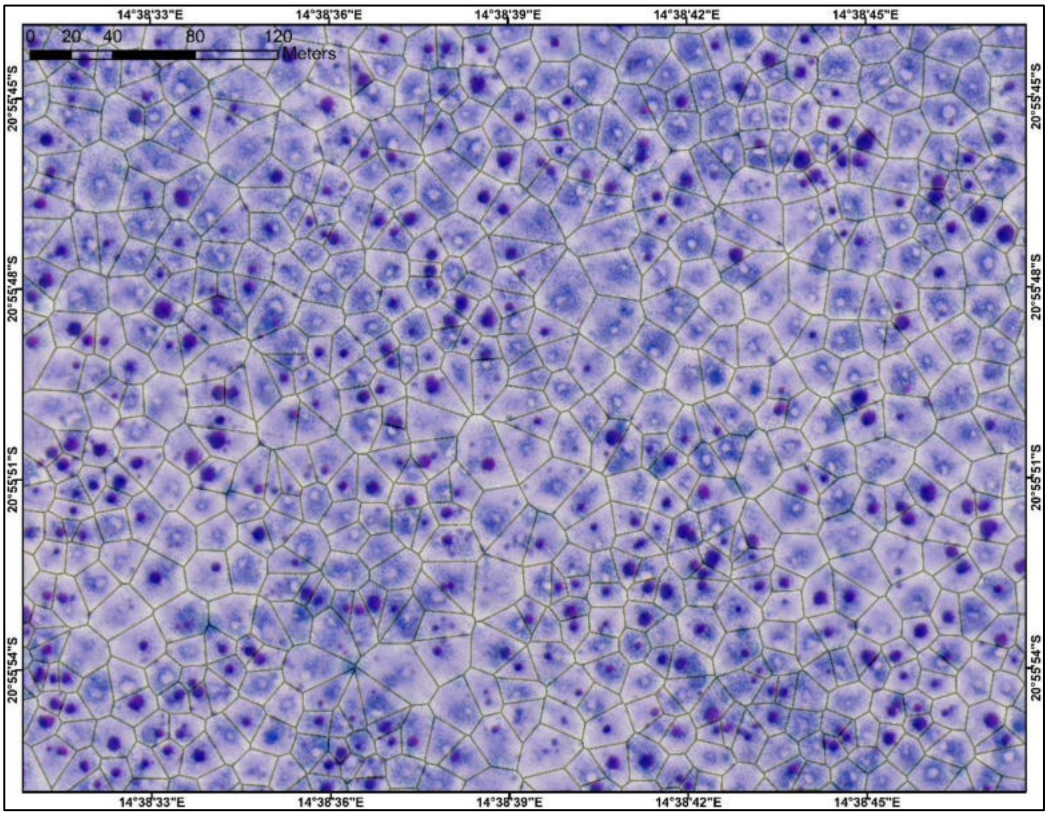


Figure 4.14: Voronoi tessellations created for mixed plots at Brandberg

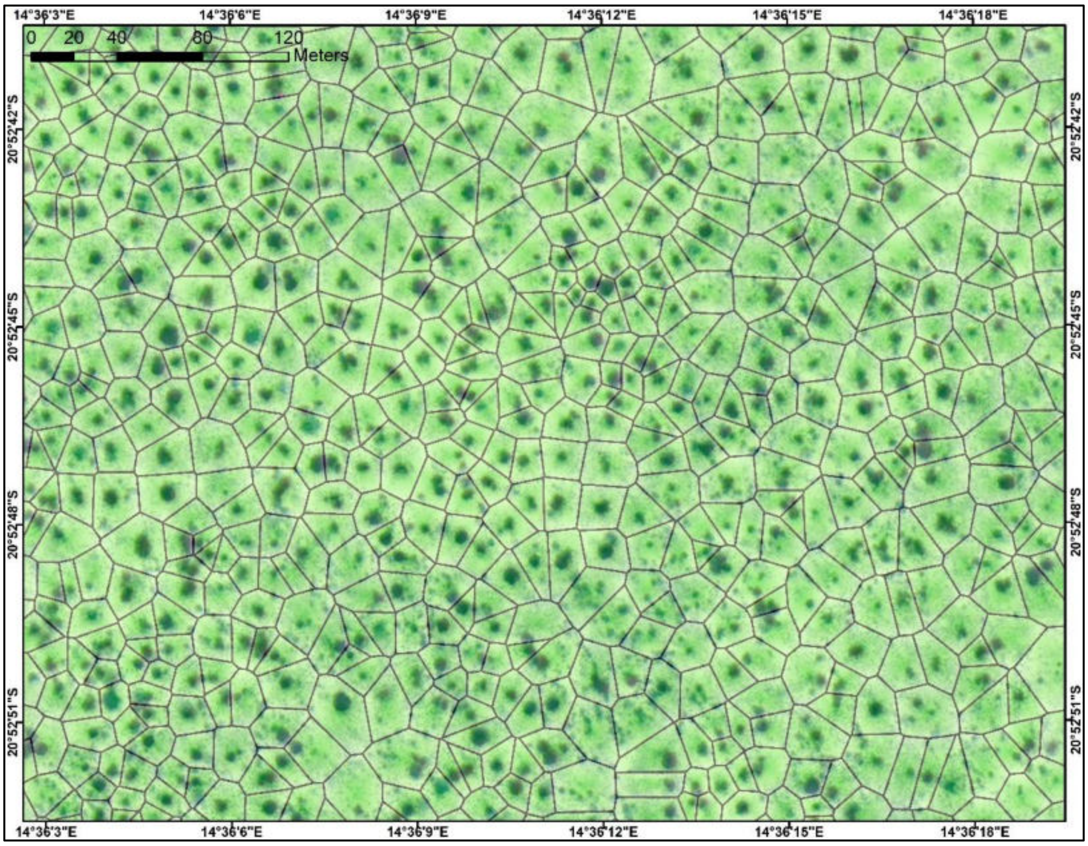


Figure 4.15:Voronoi tessellations created for *E. damarana* at Brandberg.

4.3.4 Distance to nearest neighbour

The mean distance to the nearest neighbour for fairy circles, mixed plots, *E. damarana and E. gummifera* plots are shown in Table 4.8. Fairy circles situated at Giribes Plain and Brandberg where *E. damarana* grows, have very similar nearest neighbour distances of between 15 and 17 m. Whereas fairy circles at Garub (where *E.* gummifera grows) have much shorter nearest neighbour distances of between 9 and 10 m. The average distance to the nearest neighbour for the two *E. damarana* plots at Brandberg was 9 and 11 m. *E. gummifera* had the shortest nearest neighbour distance of approximately 5 m. Note that the plants at each of the two sites of co-occurrence had nearest neighbour distances several meters shorter than “their associated fairy circles”; The mixed plots had nearest neighbour distances of that between fairy circles and *E. damarana*, between 8 and 14m. Could the reason for fairy circles having longer average nearest neighbour distances than the “associated” *Euphorbia* species and mixed sites, be that competition between events have spaced them further apart?

The results of the distance to nearest neighbour ratio (NNR-value) is shown in Table 4.8. It indicates that fairy circles are the most regularly or uniformly distributed, followed by the mixed plots and then the plant plots. The calculated NNR-value for the fairy circles range between 1.36 – 1.49, for the mixed plots between 1.11 – 1.36 and for the plants only plots between 1.05 – 1.21. There was also variation between the fairy circle only plots, with the fairy circles in the north-west being more uniformly distributed than those in the south-west. This was also reflected by the mix plots where the most north-western plot (Giribes M1) was the most uniformly distributed and the south-western sites the least so. This was not reflected by the plant only plots, where *E. damarana* located at site Brandberg was the most uniformly distributed, while the remaining plants only plots were very similar and only very slightly deviates from CSR.

Similar to the Voronoi analysis, fairy circles are the most uniformly distributed, followed by the mixed plots, then *E. damarana* and lastly *E. gummifera*. Why would this be? Again, fairy circles are considered to be the end product of competition between Euphorbias and reflect the most optimised geometric arrangement for resource exploitation, reflected by the high over-dispersion determined for these plots. Competition is evident in the mixed plots as well. Interestingly, *E. damarana* at Brandberg are more over-dispersed than the *E. damarana* at Palmwag. While Palmwag is considered to be representative of a typical location where *E. damarana* occur, Brandberg is considered to be a site where *E. damarana* is transitioning into fairy circles. This could indicate that perhaps conditions are less ideal for *E. damarana* at Brandberg (very sandy soil) and that competition for water and nutrients are causing these plants to be over-dispersed.

Table 4.8: The mean distance to nearest neighbour for the sample plots. Also shown is the distance to nearest neighbour ratio (or NNR-ratio), an NNR-ratio of more than one indicates regularity, an R-value of 1 indicates complete spatial randomness and an R-ratio of smaller than one indicates clustering.

Sample plot	Plot type	Mean distance to nearest neighbour (in m)	NNR-ratio
Giribes C 1	Fairy circles	17.05	1.49
Giribes C2	Fairy circles	15.74	1.42
Giribes M1	Mixed	14.08	1.36
Palmwag P1	*E. damarana*	10.17	1.05
Palmwag P2	*E. damarana*	7.24	1.13
Palmwag M1	Mixed	11.23	1.13
Palmwag M2	Mixed	8.55	1.20
Brandberg C1	Fairy circles	15.31	1.45
Brandberg C2	Fairy circles	16.51	1.41
Brandberg P1	*E. damarana*	10.23	1.21
Brandberg P2	*E. damarana*	11.34	1.21
Brandberg M1	Mixed	10.10	1.29
Brandberg M2	Mixed	10.10	1.24
Garub C1	Fairy circles	10.23	1.38
Garub C2	Fairy circles	9.02	1.36
Garub P1	*E. gummifera*	4.78	1.08
Garub P2	*E. gummifera*	4.92	1.05
Garub M1	Mixed	9.35	1.15
Garub M2	Mixed	11.93	1.11

4.3.5 Pair correlation function

Figures 4.16 - 4. 19 depict the graphs of the pair correlation function for the sample plots located at Giribes Plain, Palmwag, Brandberg and Garub, respectively.

The graph of the pair correlation function is very similar amongst the fairy circle only plots. All the graphs start off outside the simulation envelopes of Complete Spatial Randomness (CSR) and the value of g(r) is approximately 0 up to a distance of 2 m for the fairy circle plots. This is indicative of strong over dispersion for the first few meters and no neighbours are located at these respective distances. The value of g(r) then slowly starts to increase, indicating a decrease in over-dispersion, but still well outside the simulation envelopes. For fairy circle plots situated in Giribes and Brandberg the value of g(r) enters the simulation envelopes at a distance of 17 m, 16 m, 15 m and 17 m, for plots Giribes C1, Giribes C2, Brandberg C1 and Brandberg C2, respectively. While for the two fairy circle plots at Garub (Garub C1 and Garub C2), the value of g(R) enters the simulation envelopes at a distance of 9 m and 8 m respectively. This indicates that at these distances the pattern becomes random, instead of regular, although only for a few meters as the graph passes through the simulation envelops.

The value of g(r) rises to 1.4 for plot Giribes C1 and 1.3 for plots Giribes C2, Brandberg C1 and Brandberg C2, respectively, and forms a significant peak well outside the limits of the simulation envelope. This peak is situated at a distance of 25 m, 23 m, 22 m and 25 m, for plots Giribes C1, Giribes C2, Brandberg C1 and Brandberg C2, respectively. For the plots at Garub the peak was situated at 14 m and 16 m respectively. This peak indicates significant clustering at these distances. This distance corresponds to the most frequent distance to the nearest neighbour. The distance to the first peak for each plot corresponds well with the average nearest neighbour distance calculated for each plot. The rest of the graphs fall within the simulation envelopes for all the fairy circle only plots, indicating large scale homogeneity of the pattern. Note that only one fairy circle plot (Giribes C1) shows an oscillation around the null model, which is indicative of high ordering in the pattern and is also apparent in the L-function for this plot, discussed below. This plot also showed the highest R-value determined with the ‘distance to nearest neighbour ratio’ and is the most uniformly distributed sample plot. It is the only plot that showed all the full set of spatial pattern characteristics as identified by Getzin et al. (2014) and discussed in the method section.

The graph of the pair correlation function begins in a similar way for the Euphorbia plots. As is evident g(r) is equal to approximately 0 and then the value of g(r) slowly starts to increase indicating a decrease in over-dispersion, but still well outside the simulation envelopes (the same as observed for the fairy circles). The rest of the graph differs from the fairy circles. For the plots at Palmwag (Palmwag P1 and Palmwag P2), g(r) enters the simulation envelopes at a distance of 9 m and 7 m, respectively and corresponds to the average nearest neighbour distances calculated for these plots. For the plots at Brandberg (Brandberg P1 and Brandberg P2), the value of g(r) enters the simulation envelopes at a distance of 7 m for both plots and does not correspond to the average nearest neighbour distances for these plots. For the plots at Garub (Garub P1 and Garub P2), g(r) enters the simulation envelopes at a distance of 4 m for both plots and corresponds to the average nearest neighbour distances determined for these plots. This is at markedly shorter distances than compared with the fairy circles. *E. damarana* in Palmwag P2 and *E. gummifera* (located at Garub), have very similar graphs, with a series of significant peaks. While plot Palmwag P1 have two small peaks; at 8 m and again at 12 m. The value of g(r) at the peaks for both *E.*

damarana plots at Palmwag is approximately 1.2, while at Garub this value is much higher, equal to 1.4 and 1.5 for plot Garub P1 and Garub P2, respectively. This indicates over-dispersion for the first several meters but a highly clustered pattern at larger scales, except for plot Palmwag P1, having a more defined peak similar to fairy circles. Interestingly, the plots containing *E. damarana* at Brandberg differed markedly from the other Euphorbia plots by not having a significant peak. Indicating a rather random pattern at distances greater than 7 m, instead of a highly clustered pattern, for these two plots.

As mentioned before, the graph of the pair correlation function for the mixed plots at Palmwag resembled that of the *E. damarana* populations. It should be noted that these mixed plots did not include fairy circles, but “rock circles”, as defined in the study area and experimental design section. The inclusion of the rock circles (214 for Palmwag P1 and 277 for Palmwag P2) had an effect on the pair correlation function by reducing the amount of clustering, rather significantly. These two mixed plots had similar graphs to that of fairy circles.

The pair correlation function for the mixed plots are similar to that of fairy circles. The graph of g(r) is equal to approximately 0 and then slowly starts to increase, indicating a decrease in over-dispersion, but still well outside the simulation envelopes. The graph for all the mixed plots, except at Garub contains a significant peak. For the mixed plot located at Giribes (Giribes M1), g(r) is equal to 1.3 and the peak is located at a distance between 17 m and 25 m. For the two mixed plots at Brandberg, g(r) is equal to 1.2 and the peak is located at a distance of 15 m for both plots. These plots are remarkably similar to the fairy circle plots. The two mixed plots at Garub did not have a significant peak, resembling *E. damarana* at Brandberg.

Only one fairy circle plot showed the high degree ordering as described by Getzin et al. (2014), i.e. an oscillation around the null model. The graph of the pair correlation function for the remaining fairy circle plots were remarkably similar to the mix plots. If *Euphorbia* species are assumed to be causing fairy circles and the mix plots are in a transition stage from many plants and few fairy circles, to few plants and many fairy circles. It can be argued that the mixed plots will become progressively more like the fairy circle plots as more plants die (perhaps due to competition between the plants and/ or environmental stress). *E. damarana* and *E. gummifera* show highly clustered patterns at larger scales, which could indicate that these populations are not experiencing much competition and/ or environmental stress. Interestingly, *E. damarana* at Brandberg does not share this clustering with the Euphorbia plants at Palmwag and Garub. Perhaps indicating that conditions are less favourable where these plants occur at Brandberg.

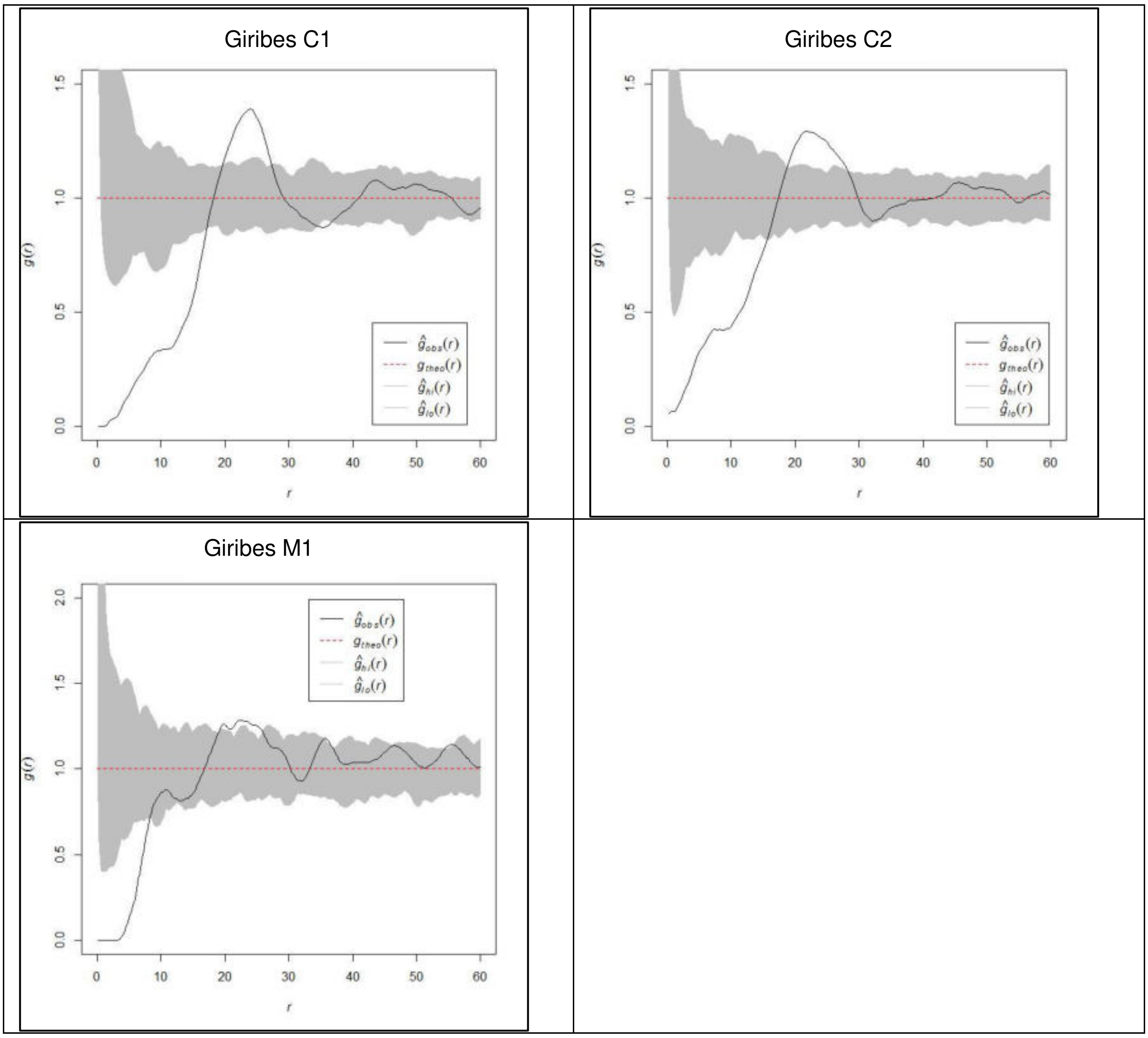
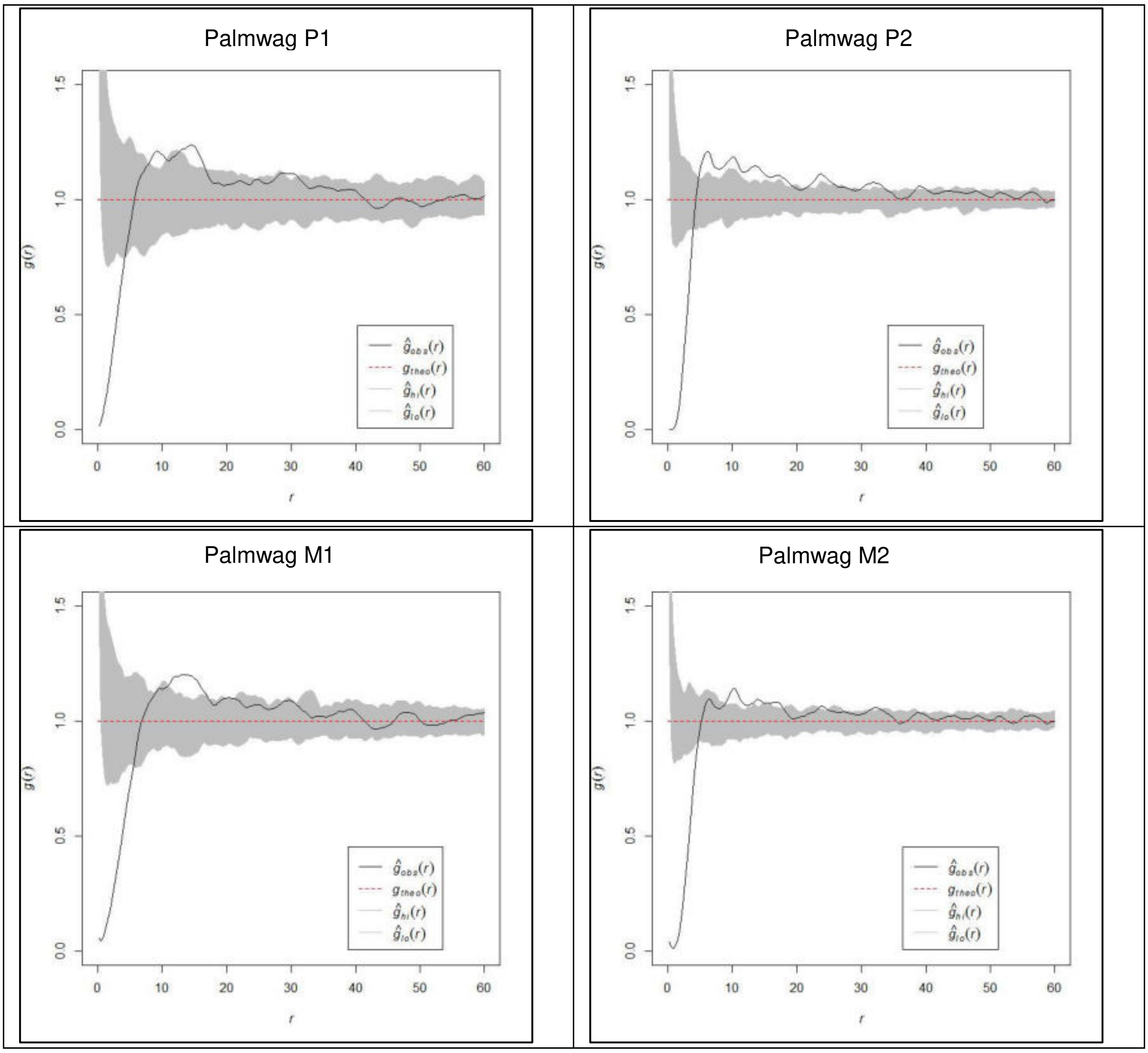


Figure 4.16: Graphs of the pair correlation function for the fairy circle sample plots and the mixed sample plot at Giribes.


Palmwag P1

Palmwag P2

Palmwag M1

Palmwag M2

Figure 4.17: Graphs of the pair correlation function for the fairy circle sample plots and the mixed sample plots at Palmwag.

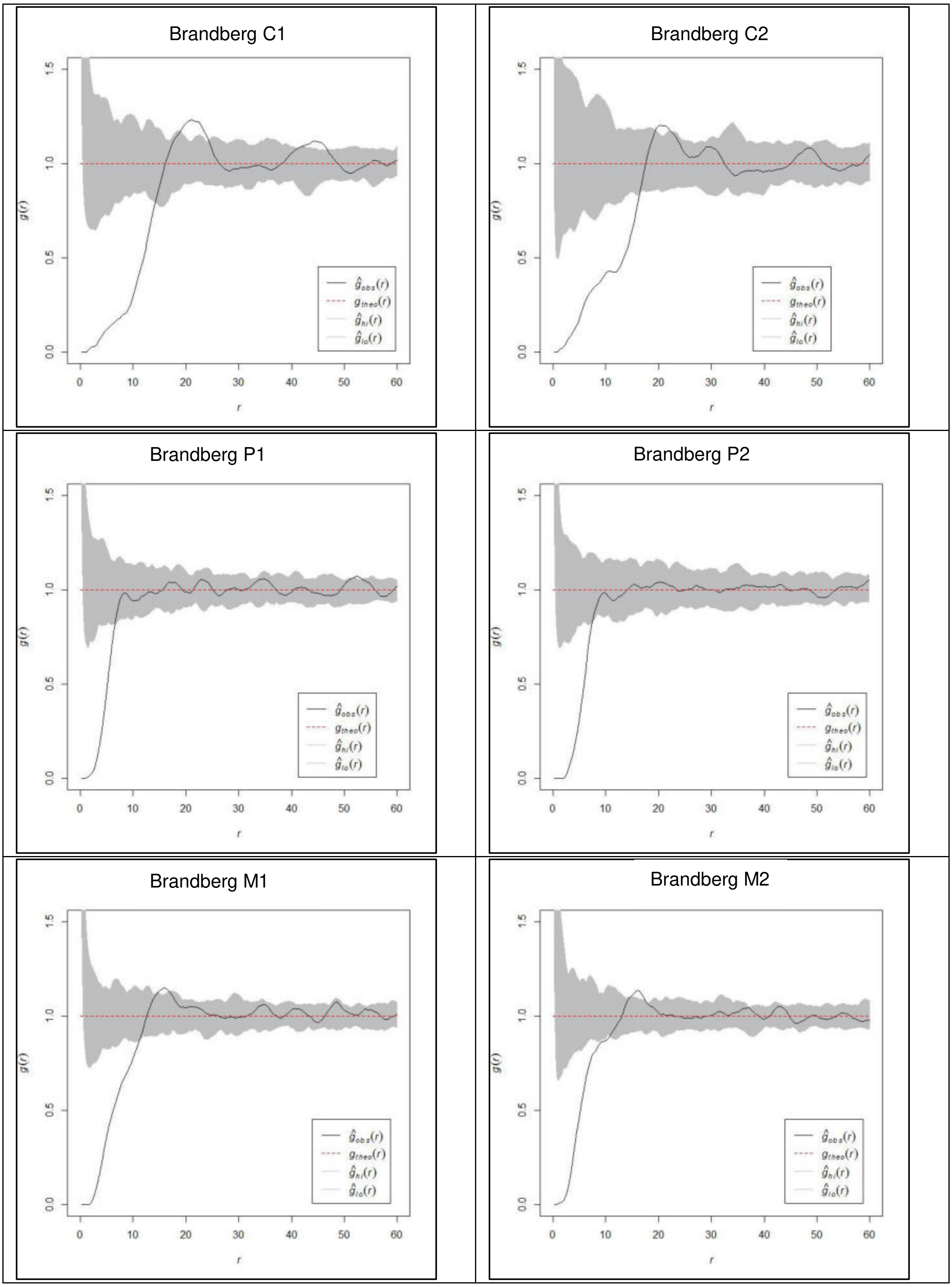


Figure 4.18: Graphs of the pair correlation function for the fairy circle, mixed and *E. damarana* sample plots at Brandberg.

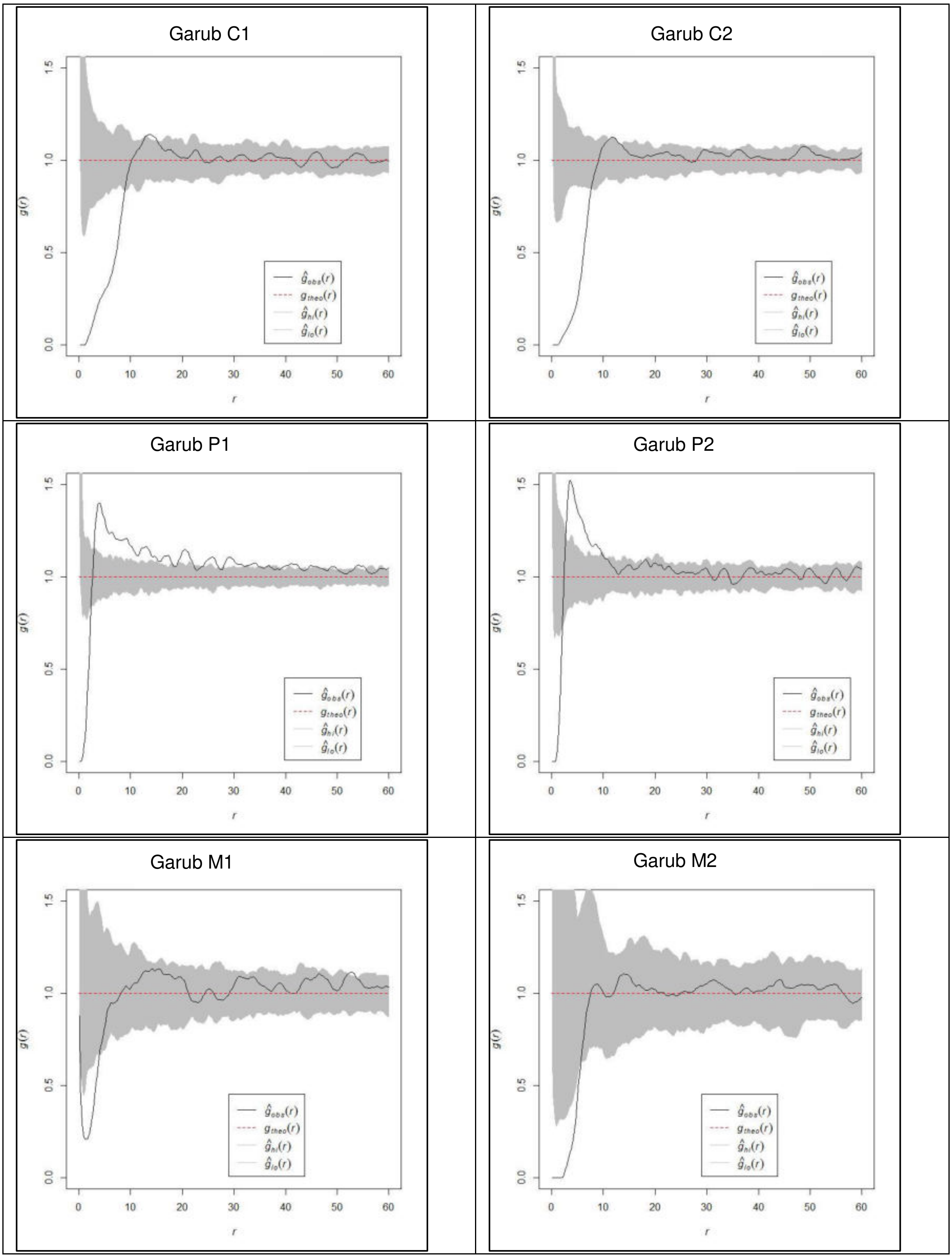


Figure 4.19: Graphs of the pair correlation function for the fairy circle, mixed and *E. gummifera* sample plots at Garub.

4.3.6 L-function

Figures 4.20 - 4. 23 depict the graphs of the L–function for the sample plots located at Giribes Plain, Palmwag, Brandberg and Garub, respectively.

The L-function showed considerable variation between the different types of samples plots, with the graph of the L-function very similar between all the fairy circle plots, characterised by large scale homogeneity. The L-function for the Euphorbia only plots differ markedly from the fairy circle plots and were characterised by large inhomogeneity. One notable exception was the *E. damarana* plots at Brandberg which differed from the other Euphorbia plots and more closely resembled that of the fairy circles. The graph of the L-function for the mixed plots at Giribes, Brandberg and Garub are very similar to that of the fairy circle plots. The mixed plots at Palmwag (consisting of a combination of *E. damarana* and "rock circles"), resembled the *E. damarana* plots at this site. Interestingly when the "rock circles" were included it reduced the large-scale inhomogeneity of these plant only plots.

The graph of the L-function for fairy circle only plots lie outside the simulation envelopes reaching a minimum that range between 15 m and 17 m for the north-western and central-north-western plots (Giribes and Brandberg), and between 8 m and 9 m for the plots at Garub in the south-west. The value of L(r) at these minimums for the fairy circle plots range between -5 and -7, indicating over-dispersion. There is an instance where the graph for plot Giribes C1 briefly touches the simulation envelopes as the graph reflects the small-scale fluctuation also seen in the pair correlation function for this plot. The graph for Brandberg C2 also does this, although to a lesser extent and is not reflected in the pair correlation graph for this plot. For the Giribes and Brandberg fairy circle only plots, L(r) lies within the simulation envelopes from a distance that varies between 45 m, 43 m and 45 m for plots Giribes C1, Brandberg C1 and Brandberg C2, respectively. While the value of L(r) for plot Giribes C2 lies within the simulation envelopes from a distance of 23 m. For plot Garub C1 (in the south-west), L(r) lies within the simulation envelopes from a distance of 25 m for the remainder of the graph. While for plot Garub C2, L(r) lies within the simulation envelopes between 25 m to 85 m and falls slightly outside the simulation envelopes for the remainder of the graph. This indicates that the smaller scale properties of the pattern revealed by the pair correlation function in section 4.3.5., are preserved across a large area (hundreds of meters).

For both *E. damarana* plots at Palmwag, the graph of the L-function, lie outside the simulation envelopes, reaching a minimum at 5 m and 4 m, for the plot Palmwag P1 and Palmwag P2, respectively. The value of L(r) at these minimums for both plots are -3 indicating over-dispersion. From here the graph of the L-function differs between the two plots in that Palmwag P1 forms a pronounced peak between 20 m and 50 m, indicating clustering at these distances, but then lies inside the simulation envelopes for the remainder of the graph. From 12 m for the reminder of the graph, L(r) is greater than 1 and lies outside the simulation envelopes and indicates the presence of large scale clustering in the pattern for Palmwag P2. This could be due to the fact that Palmwag P2 had almost double the amount of *E. damarana*, with a count of 1 548 versus Palmwag P1 with 676.

The graph of the L-function for the two *E. damarana* plots at Brandberg (Brandberg P1 and Brandberg P2) are practically identical to each other. Instead of resembling the graphs of the L-function for the *E. damarana* at Palmwag (characterised by a L(r) values > 1 and outside the simulation envelopes), Brandberg P1 and Brandberg P2 are much more similar to the fairy circles graphs. The L function lies outside the simulation envelopes reaching a minimum at 7 m for both plots, where L(r) is equal to

-4 and -5, respectively, indicating overdispersion. From 22 m for the reminder of the graph, L(r) lies within the simulation envelopes for both graphs, which indicates large scale homogeneity of the pattern; in other words, the smaller scale properties of the pattern revealed by the pair correlation function are preserved across a large area (hundreds of meters).

At Garub, the graph of the L-function for *E. gummifera* was very similar between the two plots (Garub P1 and Garub P2) and resembles that of *E. damarana* in plot Palmwag P1. The L-function, lie outside the simulation envelopes, reaching a minimum at 3 m for both plots. The value of L(r) at these minimums for both plots are -1.5 and -2, respectively, indicating over-dispersion. From 9 m and 8 m, respectively, and for the remainder of the graph, L(r) is greater than 1 and lies outside the simulation envelopes and indicates the presence of large scale clustering in the pattern for both plots.

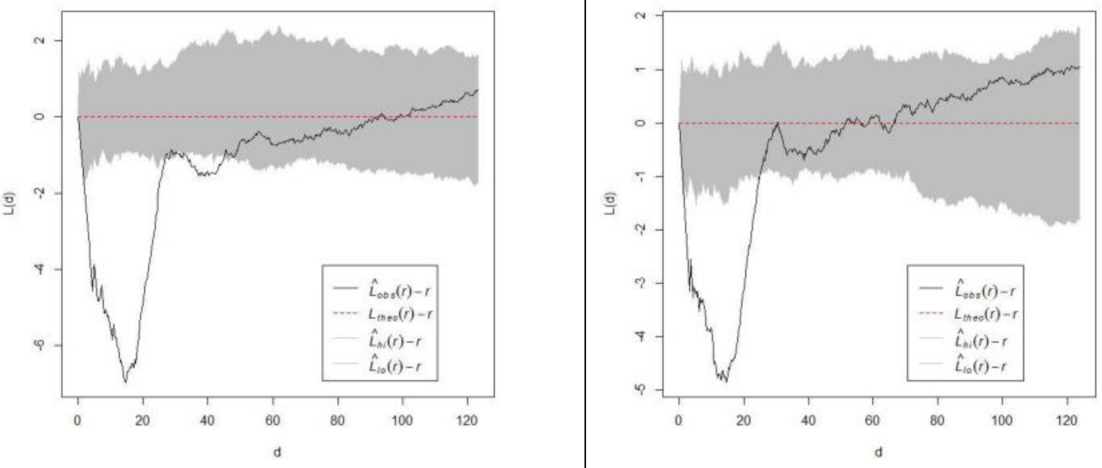
As mentioned before, the graph of the L-function for the mixed plots at Palmwag resembled that of the *E. damarana*. It should be noted that these plots did not include fairy circles, but “rock circles”, as defined in the study area and experimental design section. The inclusion of these rock circles did have an effect on the L-function, reducing the large-scale inhomogeneity of these plant only plots.

The graph of the L-function for all the remaining mixed plots resembled that of the fairy circles indicating regularly for the first few meters. The graph lies outside the simulation envelopes, reaching a minimum at 8 m where L(r) equals -7 for the plot at Giribes (Giribes M1). The L-function for both mixed plots at Brandberg (Brandberg M1 and Brandberg M2) equals -4 at 7m. While at Garub, L(r) equals -3 and -5 for plot Garub M1 and Grub M2, respectively. These minimums are situated at a distance of 5 m for both plots. From 22 m (Giribes M1), 25m (Brandberg M1 and Brandberg M2), and 10 m (for Garub M1 and Garub M2) for the reminder of the graph, L(r) lies within the simulation envelopes which indicates large scale homogeneity of the pattern. In other words, the smaller scale properties of the pattern revealed by the pair correlation function are preserved across a large area (i.e., hundreds of meters). There are however serveral instances where the graph of plot Giribes M1 and Garub M2 slightly deviates from the simulation envelopes near the end of the graph.

Similar to the pair-correlation function, it is argued that the reason for the mixed plots bearing such a remarkable similarity to the fairy circles plots, could be that they are progressively transitioning into fairy circle plots. Also similar to the pair correlation function, *E. damarana* and *E. gummifera* show highly clustered patterns at larger scales, which could indicate that these populations are not experiencing competition and/ or environmental stress. Again, *E. damarana* at Brandberg does not share this clustering with the Euphorbia plants at Palmwag and Garub. In fact, *E. damarana* at Brandberg shares the large scale homogeneity with the fairy circle and mix plots.

Giribes C1

Giribes C2



Giribes M1

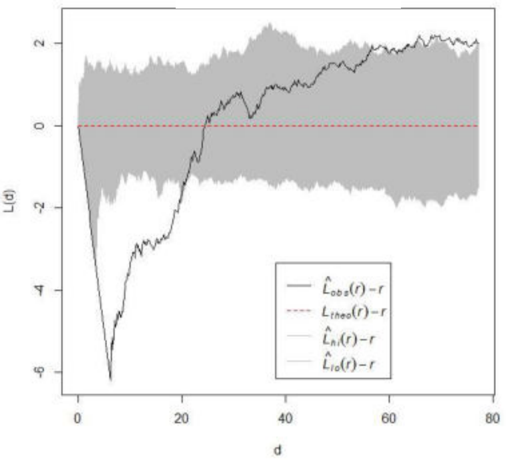


Figure 4.20: L-function for the fairy circle and mixed sample plots at Giribes Plain.

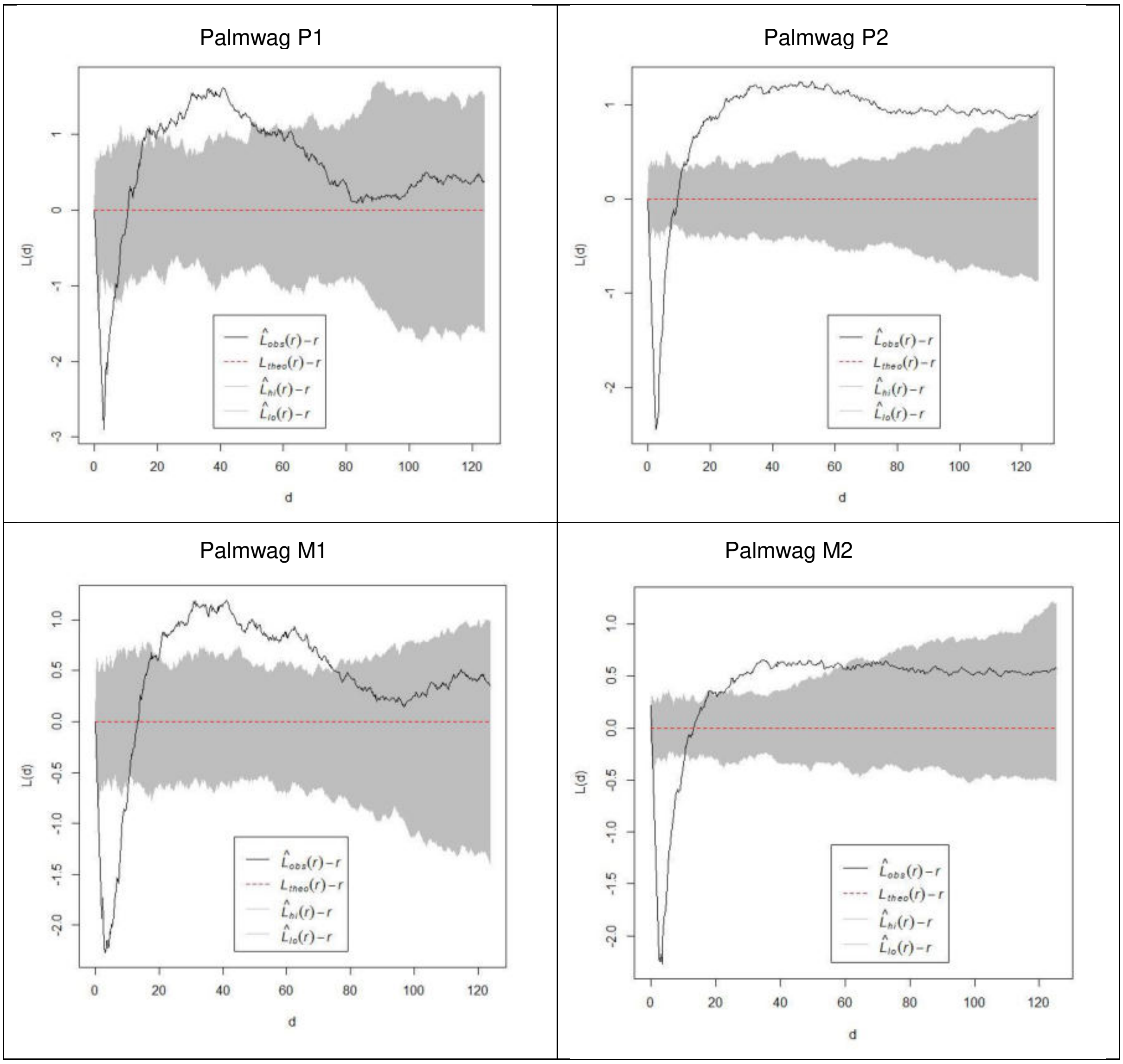
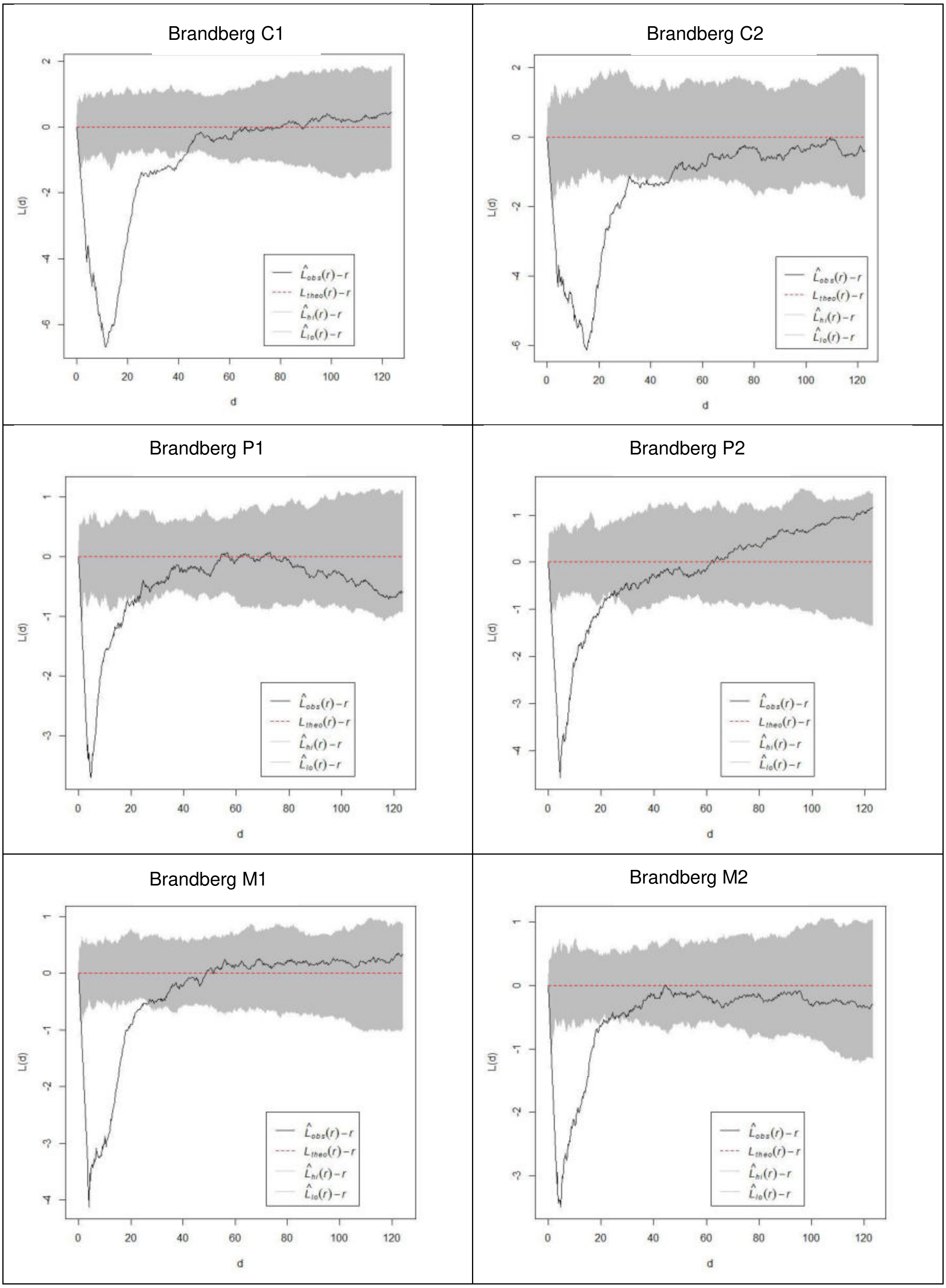


Figure 4.21: L-function for the *E. damarana* and mixed plots at Palmwag.


Brandberg C1

Brandberg C2

Brandberg P1

Brandberg P2

Brandberg M1

Brandberg M2

Figure 4.22: L-function for the fairy circles, *E. damarana* and mixed sample plots at Brandberg.

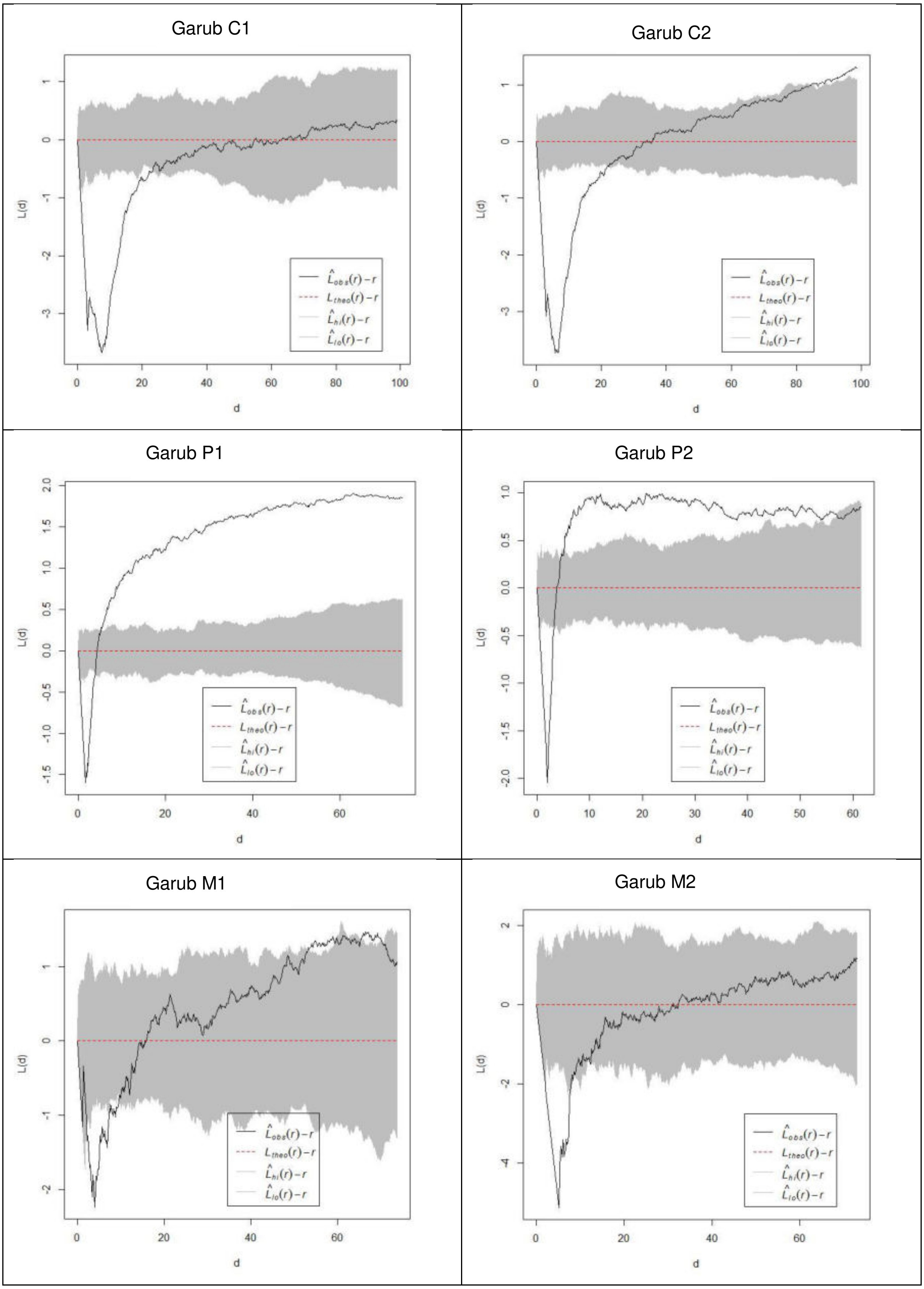


Figure 4.23: L-function for the fairy circles, *E. gummifera* and mixed sample plots at Garub.

4.4 Conclusion

The main aim of this chapter was to investigate several physical characteristics associated with fairy circles and associated plant species in four study sites across Namibia.

The first objective was to conduct long term observations of fairy circles, *E. damarana*, and *E. gummifera* in order to determine an approximate age of the fairy circles and to observe what happens to the Euphorbia populations over time. In the analysis the exact same fairy circles marked by Theron (1979) at Giribes Plain were found, which supports the notion of Van Rooyen et al. (2004) that fairy circles can persist for decades through dry/wet spells. It also puts the age of fairy circles at a minimum age of 40 years. During the aerial image comparison at Garub, the formation of more than 100 fairy circles was documented for the first time as resulting from the death and decay of *E. gummifera*.

In terms of the size comparison it was found that the fairy circles have very similar sizes to that of *E. damarana* where they co-occur at Brandberg, while fairy circles in south-western Namibia have very similar sizes to that of *E. gummifera* where they co-occur. This suggests that instead of rainfall determining fairy circle size (Getzin et al. 2014), it may be determined by the size of the *Euphorbia* species that gave rise to the fairy circle. This could explain why fairy circles are larger in the north west than in the south west; *E. damarana* is much larger then *E. gummifera* that occurs in south-west Namibia.

The spatial point pattern tests revealed that fairy circles and the mixed plots are over-dispersed, but also showed for the first time that *E. damarana* also displays an over-dispersed spatial pattern. Over-dispersed or uniform patterns are associated with repulsive interactions between events in the pattern and in an ecological context often point toward competition for resources. According to the vegetation self-arrangement theory the individual grass tufts are competing between themselves to form fairy circles. The regularity associated with the spatial pattern of fairy circles and the correlation of fairy circle size with distances apart are also consistent with the notion of plant – plant interactions as the major vegetation-patterning mechanism (Tarnita et al. 2017).

According to the Euphorbia theory the *Euphorbia* species compete with each other over distances that are very similar to the distances between fairy circles (i.e. tens of meters), while the distances between grass tufts are much shorter (i.e. tens of centimetres) than the distances between fairy circles. The mixed plots are considered to be in an intermediate state, progression from a high density of plants and low density of fairy circles towards a low density of plants and high density of fairy circles (Meyer et al. 2015). This is supported by the fact that the mixed plots share physical characteristics with both fairy circles and Euphorbias. In terms of the distance to nearest neighbour ratio; the degree of uniformity associated with the mixed plots is between that associated with fairy circles (most regular) and Euphorbias (least regular). The fairy circles and *E. damarana* and *E. gummifera* in the mixed plots at Giribes Plain and Garub have nearest neighbours (either a fairy circle or one of the respective species of Euphorbia) situated at a similar distance to that of the fairy circles, while at Brandberg the mixed plots have nearest neighbours situated at a distance similar to that of *E. damarana*. The pair-correlation function for fairy circles and the mixed sites are similar in that both plots display a significant peak, however the distance at which the peak is formed is greater in fairy circles than for the mixed plots.

Future work should focus on constructing a model, based on that of Tarnita et al. (2017), but instead of variables representative of termite population dynamics, it should be representative of population dynamics of *E. damarana* and *E. gummifera*.

Chapter: 5. General Conclusions

The fairy circle phenomenon has resulted in decades of detailed, independent scientific investigations. The different theoretical schools of thought regarding the origin of fairy circles were discussed in Chapter 2 of this dissertation and include the “Social Insects Theory”, the “Self-arrangement Theory”, a combination of the “Social Insect Theory” and the “Self-arrangement Theory” and finally the “Euphorbia spp. allelopathy” .This study aims to aid to this growing literature by examining the fairy circle phenomenon in relation to the “Euphorbia spp. allelopathy”.

In particular, the Euphorbia theory has not been considered seriously even when convincing evidence that has been produced by Meyer et al. (2015). Reasons for this could be the general lack of observation of the co-occurrence of *Euphorbia* species with fairy circles (Getzin et al. 2015). In Chapter 3 it was illustrated that various *Euphorbia* species co-occur with fairy circles across multiple sites throughout the Namib Desert. In the north-western and central-western parts of Namibia, the distribution of *E. damarana* is closely associated with the fairy circle distribution. While the distribution of both *E. gummifera* and *E. gregaria* are closely associated with the fairy circle distribution in the south-west to the south-eastern parts of Namibia, the occurrence of fairy circles in the south-east of Namibia, including the Kalahari Desert, has been documented for the first time in this study. I also identified a former unknown distribution of fairy circles in the Nama-Karoo biome as a result of the suitability prediction model. Large areas have been identified where *E. gummifera* and *E. gregaria* are dying. There is however a large area to the east of the Namib Sand Sea where the Euphorbia distribution is absent. Termite distribution of *P. allocerus* covers the distribution of the fairy circles but extends beyond the rainfall isohyets associated with fairy circles. This study has showed that *E. damarana*, *E. gummifera* and *E. gregaria* are limited to an almost identical rainfall range as fairy circles.

In Chapter 4 it was shown that the sizes of fairy circles are very similar to that of several *Euphorbia* species, fairy circles more north have similar sizes to *E. damarana*, while in the south-west, fairy circles are smaller than those north, but similar in size to *E. gummifera*. This could potentially explain why fairy circles in the north are larger than fairy circles in the south.

Getzin et al. (2014) found that the distances between fairy circles at Giribes Plain is 13 m. This study showed that the distances between Euphorbias are similar to those observed for fairy circles. In fact, the distances are much more similar to the distances between fairy circles than compared to the distances between grass tufts and fairy circles. Chapter three showed that the soils associated with fairy circles and the sites where *E. damarana* and *E. gummifera* co-occur, is very sandy and consists of the same range of particle sizes as Cramer et al. (2016). These researchers demonstrated that the soil on which the fairy circles occurs has the potential to become a hydraulically connected landscape, which facilitates the transport of water and nutrient up to distances of 5 m. This is similar distances observed for Euphorbias.

Getzin et al. (2014) suggests grasses forms a ring-like structure because a circle has the smallest circumference-to-area ratio. This study has shown that fairy circles exhibits a circular shape because the plants that give rise to them are circular.

Van Rooyen et al. (2004) noted that *E. damarana* plants are better adapted to a rocky habitat and less suited for a sandy one. During the past, climatic conditions could have been more favourable during some periods than others, and the *Euphorbia* species could then have colonised these sandy plains during the wetter periods, where they are still found today. Since sandy soils have low water holding capacity, and because sand might facilitate the formation of a hydraulically connected landscape, these plants would additionally have to compete for water and nutrients. When climatic conditions became less favourable, the lack of water and competition for water and/or nutrients could have resulted in increased competition between these plants and many could have started dying out. The out-competed plants then start to die, while the more favourable ones survive. This then leads to a regular pattern that is indicative of over-dispersion and hence the pattern is formed by competition between plants. As decades pass and climatic conditions become even less favourable, all the plants eventually die out. After many more decades, all the dead plant remains have been removed through decay, the relentless desert wind and perhaps fire. When the occasional rains come, and the ephemeral grassland reappears, thousands of barren patches emerge. However, they are not all the same with some containing thick grass rings around their edges, while in others the rings are absent and small seedlings persist for a short period after the rains retreat. As the harsh desert conditions sets in, the young seedlings die. As the rains come and go the effect left in the soil by the Euphorbias are slowly eroded away, young seedlings survive for longer and longer periods in the older fairy circles until they are eventually overgrown.

In conclusion, there are three points of critique against the Euphorbia theory. Firstly, *E. damarana* prefers a stoney, coarse texted substrate (Becker et al. 2010; Van Rooyen et al. 2004). Secondly, there is a lack of observations where fairy circles co-occur with *E. damarana* (Becker et al. 2010). Thirdly, *E. damarana* is irregularly distributed and could therefore not result in the observed regular pattern of fairy circles (Getzin et al. 2015). This study has documented vast areas where *E. damarana* occurs on sandy plains near Brandberg and other areas, while the occurrence of fairy circles and *E. gummifera* (Meyer et al. 2015) has again been documented in this study. Furthermore, it has also been shown that *E. gregaria* also co-occurs with fairy circles on sandy soils.

It has been suggested that the cause of fairy circles would have to be able to account for all the important properties of fairy circles – their circularity, their over-dispersion, size of fairy circles and their changing diameter in different soils and latitudes. It is argued in this study that the Euphorbia theory can explain these characteristics. Firstly, the circularity of fairy circles can be explained by the fact that *E. damarana*, *E. gummifera* and *E. gregaria* themselves have circular shapes. Secondly, fairy circles are the product of the dying out of the Euphorbia plants, the mixed sites are examples of transition areas and historical imagery in Garub has shown it clearly. The soils are extremely sandy in these areas and could possibly result in a hydraulically connected landscape, enabling the mobilization of edaphic resources for which the Euphorbias compete. This process eventually results in the observed uniform pattern. Thirdly, there is no statistical difference in size between fairy circles and *E. damarana* where they co-occur at Brandberg, this could explain why the fairy circles at Brandberg is that size. In Garub where fairy circles co-occur with *E. gummifera*, the sizes are very similar (although a statistical difference in size was found, fairy circles were on average approximately 1 m larger than the *E. gummifera* plants).

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7. Appendices

Appendix I: Landsat Satellite Imagery Identity and Date

Table 7.1: Landsat imagery identity and date.

Identity of Landsat imagery	Date
LT05_L1TP_181073_20090320_20161027_01_T1	2009/03/20
LT05_L1TP_181074_20090320_20161027_01_T1	2009/03/20
LT05_L1TP_182073_20090327_20161027_01_T1	2009/03/27
LT05_L1TP_177080_20090425_20161026_01_T1	2009/04/25
LT05_L1TP_175080_20090427_20161026_01_T1	2009/04/27
LT05_L1TP_178077_20090518_20161026_01_T1	2009/05/18
LT05_L1TP_176078_20090504_20161026_01_T1	2009/05/04
LT05_L1TP_176079_20090504_20161026_01_T1	2009/05/04
LT05_L1TP_177078_20090511_20161026_01_T1	2009/05/11
LT05_L1TP_177079_20090511_20161026_01_T1	2009/05/11
LT05_L1TP_178079_20090518_20161026_01_T1	2009/05/18
LT05_L1TP_176080_20090504_20161026_01_T1	2009/05/04
LT05_L1TP_175079_20090427_20161026_01_T1	2009/04/27
LT05_L1TP_179075_20090322_20161027_01_T1	2009/03/22
LT05_L1TP_180074_20090430_20161026_01_T1	2009/04/30
LT05_L1TP_180075_20090430_20161026_01_T1	2009/04/30
LT05_L1TP_179076_20090322_20161029_01_T1	2009/03/22
LT05_L1TP_179077_20090322_20161027_01_T1	2009/03/22
LT05_L1TP_179078_20090322_20161027_01_T1	2009/03/22
LT05_L1TP_181072_20090320_20161027_01_T1	2009/03/20

Appendix II: DEM constructed for the study area.

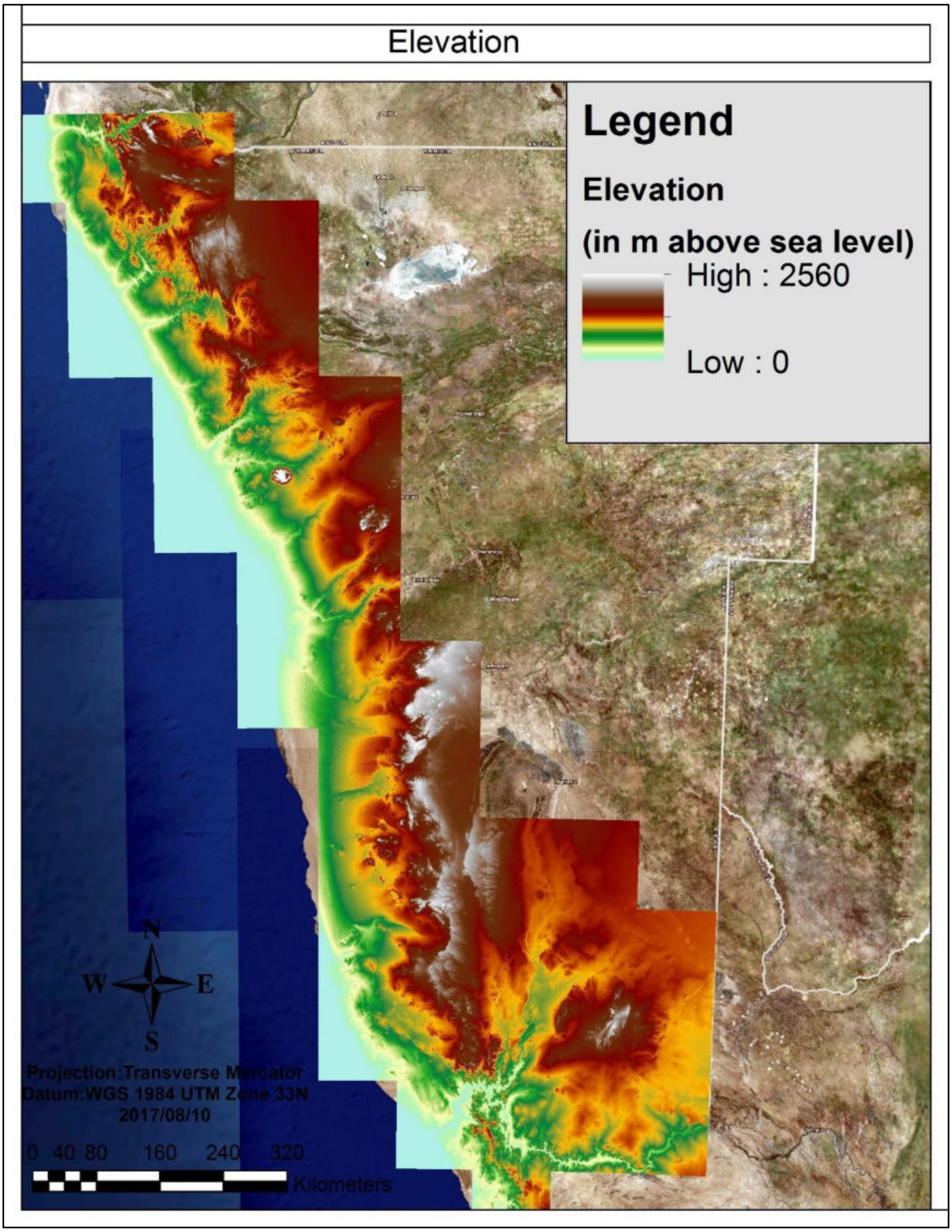

Figure 7.1: DEM constructed for the study area.