A Technical Report for

PROJECT PALMS

An Assessment of Threatened Palm Microhabitat Characteristics

July 2023

Contents

Summary

The Sainte Luce Littoral Forest (SLLF), southeast Madagascar, supports a large variety of endemic and threatened species, including populations of threatened palm species. Project Palms aims to expand existing knowledge of population size, distribution, demographic structure, health, threats, and natural history of six threatened species in five fragments of the SLLF. Through targeted supplementation and protection, utilising nursery generated seedlings, the project also aims to improve the long-term viability of each palm species within three protected fragments of the SLLF.

SEED's Conservation Research Programme (SCRP) conducted microhabitat assessments of at least 20 individuals from each of the six species of threatened palms: *Beccariophoenix madagascariensis* (VU), *Chrysalidocarpus prestonianus* (VU), *Chrysalidocarpus psammophilus* (EN), *Chrysalidocarpus saintelucei* (EN), *Dypsis brevicaulis* (CR), and *Dypsis scottiana* (VU).

Habitat density, slope angle, and elevation were the most important variables for explaining the differences in microhabitat preferences between individual palms. *B. madagascariensis* were more likely to be found in a lower density habitat than the other species. *C. psammophilus* and *D. scottiana* were observed on less steep slopes than the other species. *D. brevicaulis* preferred slopes that were not north-facing, and *D. scottiana* preferred slopes that were not west-facing.

The palms of all species were observed in low or very low light environments, with canopy cover between 50% and 70%. The most common tree species surrounding each palm species was also analysed and varied by species. *ambora*, *falinandro*, and *saridobaka* were the most common species observed surrounding the palms.

All species preferred dry or very dry soil composed of sand with medium or high proportions of organic matter, showing that the palms preferred soils with high infiltration rates. *D. brevicaulis* most strongly preferred soil composed of sand with medium proportions of organic matter, and *C. saintelucei* most strongly preferred sand with high proportions of organic matter. The pH of the soil surrounding the palms was highly acidic for all species, although *C. prestonianus* preferred soils that were less acidic than the rest of the species observed. The soil surrounding the palms was typically dull (low chroma) and dark (low value) or between dark and light (intermediate value). The most common soil hues were reds and yellow-reds, and the most common soil colour names were reds, browns, and greys. Soil hues and colour names can be indicative of the drainage of the soil.

The preferred microhabitat conditions for each species could help researchers identify suitable locations for transplanting palms in the SLLF. The data from the microhabitat assessments will contribute to increasing the understanding of these palms and enable the formation of a context-specific, community-grounded, and evidence-based Conservation Action Plan.

1 Introduction

1.1 Background

Madagascar is one of the world's highest conservation priorities (Myers et al., 2000). With 98% of palm species endemic to the island, it has one of the most unique and diverse palm collections in the world (Méndez et al., 2022). However, ecosystems across Madagascar are in decline, with 4.36 million hectares (25%) of Madagascar's forest cover lost to deforestation between 2001 and 2021 (Global Forest Watch, 2022). Littoral forests are one of the rarest and most threatened ecosystems in Madagascar, and considered a national conservation priority (Ganzhorn et al., 2001), with an estimated 90% loss of original forest cover (Krishnan et al., 2012).

The southeast Anosy region contains some of the few remaining viable littoral forests in Madagascar (Bollen & Donati, 2006). The Sainte Luce Littoral Forest (SLLF), comprising 17 fragments, is one of three larger fragmented littoral forests remaining in the region. Sainte Luce, with approximately 2,600 inhabitants, is just one of the local communities supported by the forest through the provision of natural resources for firewood, construction materials, and local livelihood generation (Bollen & Donati, 2006; Hyde Roberts et al., 2020; SEED Madagascar, 2021).

Although a critically important natural resource for the Sainte Luce community, most of the 13 species of palm supported by the SLLF are threatened[1] with extinction (Bennet, 2011; Couvreur & Baker, 2013). The six target palm species for this study are all threatened and in decline locally, *Beccariophoenix madagascariensis* (VU), *Chrysalidocarpus prestonianus* (VU), *Chrysalidocarpus psammophilus* (EN), *Chrysalidocarpus saintelucei* (EN), *Dypsis brevicaulis* (CR), and *Dypsis scottiana* (VU) (Hyde Roberts et al., 2020; Rakotoarinivo & Dransfield, 2012a; 2012b; 2012c; 2012d; 2012e; 2012f).

Extant populations in the SLLF are threatened by habitat fragmentation and degradation, drought, increased vulnerability to fire, and proposed mining activities by QIT Madagascar Minerals (QMM) (Bollen & Donati, 2006; Vincelette et al., 2007; Krishnan et al., 2012; Ashraf et al., 2021). With 83% of endemic palm species threatened with extinction in Madagascar (Rakotoarinivo et al., 2014), it is crucial to understand the local pressures on palms, and map viable pathways for their conservation and continued availability. A previous study by SEED Madagascar (SEED) identified rapidly declining populations of *B. madagascariensis* and *C. saintelucei* in Sainte Luce (Hyde Roberts et al., 2020). While limited information exists on the current demography and distribution of the other four target species, it is believed that the local populations of these threatened species are in decline.

1.2 An Overview of Project Palms

Project Palms seeks to improve the conservation status of these six threatened palm species through increasing understanding of the distribution, population, phenology, and natural history of each species, which will inform *in situ* planting efforts. The project aims to improve understanding of the preferred microhabitat conditions of each species, through the completion of focussed assessments on their environment (e.g., environmental, topographic, and soil characteristics), the learnings from which will help inform local restoration efforts and contribute to the sustainable growth and survival of each species.

To grow, plant species must successfully adapt to a combination of biotic and abiotic characteristics (Bazzaz, 1991; Klanderud et al., 2015), with microhabitat specialisation found to be important for several plant groups (Svenning, 2004). Svenning (2004) observed that Amazonian palm and palmoid species are distributed according to microhabitat variables, with the primary factors determining distribution being hydrology, pedology, topography, and vegetation structure (Eiserhardt et al., 2011). Significant habitat heterogeneity and geographic isolation in Madagascar, amongst other evolutionary processes, has produced high national palm species richness and endemism (Rakotoarinivo et al., 2014). However, understanding of environmental conditions controlling the

[1] Threatened is an umbrella term consisting of Vulnerable (VU), Endangered (EN) and Critically Endangered (CR) species (IUCN Standards and Petitions Committee, 2022).

distribution, phenology, survival, and growth of palm species in Madagascar is limited. This assessment aims to contribute to understanding of the specific microhabitat conditions preferred by Project Palms' six target species.

2 Methodology

2.1 Study Site

Research was conducted in five littoral forest fragments (S6, S7, S8, S9, and S17) within the SLLF in the Anosy region of Madagascar (24° 46' S, 47° 10' E) (Figure 1). S6 and S7 are designated as Community Resource Zones (CRZ), from which natural resource use is permitted. S8 and S9 are part of Madagascar's National Protected Areas network, classified as conservation zones under IUCN Category V Protected Areas regime. S8 is comprised of two fragments, S8 North (S8N) and S8 South (S8S), and five remnants (S8R1-5). Much of S17 is privately owned land, with an area designated as a CRZ.

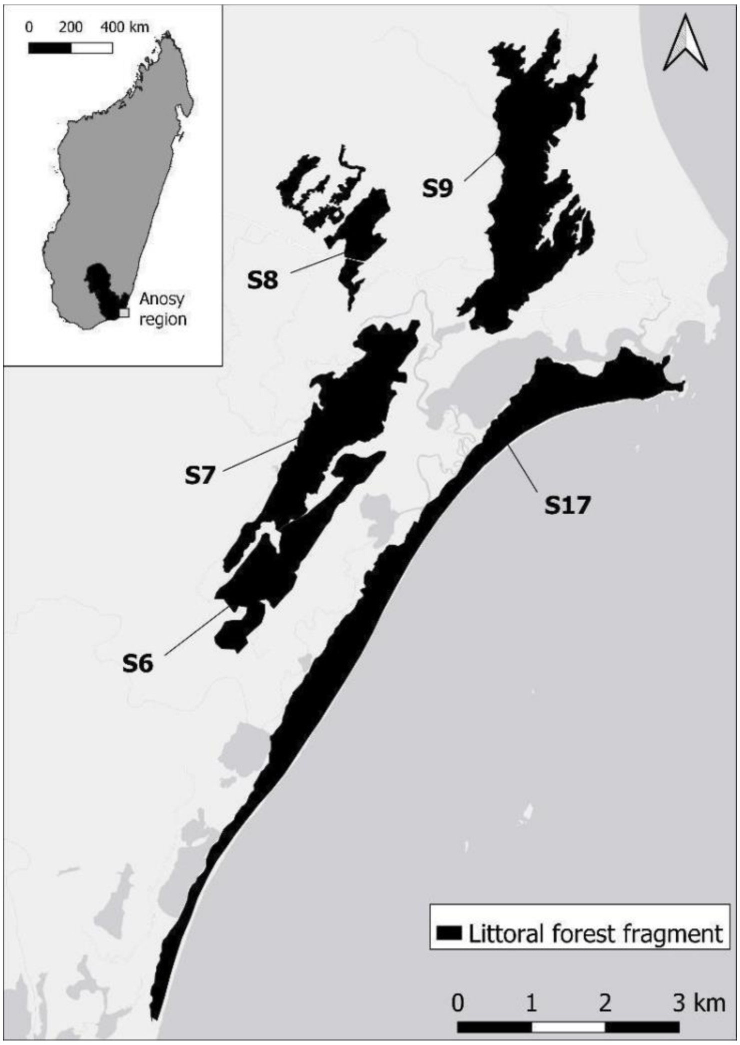

Figure 1: Study site.

2.2 Data Collection

Between June 2022 and July 2023, 123 assessments of individuals from all palm species were completed (Table 1). Microhabitat assessments were conducted on adult palms that were identified during the Palms Population Census or that had been previously encountered by SEED's Conservation Research Programme (SCRP). Sub-adults were also included in microhabitat assessments for *C. saintelucei* due to the limited number of adult individuals observed. Environmental, topographic, and soil characteristics from at least 20 individuals of each species throughout SLLF fragments S6, S7, S8, S9, and S17 were assessed.

Table 1: Number of microhabitat assessments completed per species, organised by SLLF fragment.

Species	S6	S7	S8	S9	S17	Total
B. madagascariensis	6	2	10	2	0	20
C. prestonianus	0	1	1	10	8	20
C. psammophilus	0	4	12	4	0	20
C. saintelucei	2	9	9	1	0	21
D. brevicaulis	0	0	20	0	0	20
D. scottiana	4	4	5	8	1	22

2.2.1 Environmental Characteristics

The environment surrounding each adult palm was observed and characterised to provide additional information on the habitat that different palm species are found in.

2.2.1.1 Habitat Density

Habitat density was measured using a point-centred-quarter (PCQ) methodology. Density was inferred by measuring the distance from the palm to the nearest small (6.5cm-12cm circumference, 'density 2') and large (> 12.5cm circumference, 'density 1') tree in each cardinal direction. The species of each of these trees was identified by a local expert guide and recorded to examine the local floral community.

2.2.1.2 Canopy Cover and Height

Canopy coverage measurements were taken five meters from the base of the palm in each cardinal direction using a transparent plastic case with 16 equally spaced black dots drawn on the cover. At each point, the plastic case was held vertically three meters from the ground towards the sky, recording the number of points that were not obscured by the canopy. The canopy cover was then calculated as a percentage.[2] Canopy height (distance from tree base to canopy apex) (m) was recorded for each of the large trees identified during the PCQ method at the cardinal points. Due to the dense nature of the SLLF, it was necessary for experienced staff to visually estimate height of individual trees.

2.2.1.3 Sunlight Level

The level of sunlight was recorded in each cardinal direction using a Soil Survey Instrument (4 in 1 Soil Survey Instrument) which categorised it as LOW-, LOW, LOW+, NOR-, NOR, NOR+, HIGH-, HIGH, HIGH+, determining light availability.

2.2.2 Topographic Characteristics

Topographic characteristics, including slope angle, aspect, and elevation were collected. Slope angle was measured using a digital level application installed onto a smartphone. Aspect was measured by assessing the direction of slope in the habitat and measuring the degrees from north using a compass when facing down the slope. Elevation measurements were made using a Garmin 62S Global Positioning System (GPS).

2.2.3 Soil Characteristics

To gain a more detailed understanding of the soil conditions that support successful growth of each palm species, information on the soil characteristics for each individual palm was collected.

2.2.3.1 Soil Composition

A detailed description of the physical properties of the soil at each palm site were recorded, including soil texture and leaf litter coverage. Soil texture information was visually estimated and defined into distinct categories that could be applied to each palm site. Categories included pure sand (100% sand), sand with low organic matter

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[2] Percentage canopy cover was calculated by counting the number of points that were not obscured by the canopy in the four cardinal directions. This value was divided by 16 to find the average proportion of points that were not obscured by the canopy across the cardinal directions. The proportion was multiplied by 100 to obtain the average percentage of points not obscured. This percentage was subtracted from 100 to calculate the average percentage of points that were obscured by the canopy across the four cardinal directions.

(~75% sand), sand with medium organic matter (~50% sand), sand with high organic matter (~25% sand), organic matter with little sand (<25% sand), and organic matter with no sand (0% sand). When deemed unusual, leaf litter coverage was visually observed, and a description recorded.

2.2.3.2 Soil Colour

A sample of soil was taken from a depth of 10cm and placed onto a white piece of paper next to a standardised Munsell soil colour chart, so that hue, value and chroma could be described and recorded (Munsell Colour, 2017; Figure 2).[3] Together, hue, value, and chroma characteristics each refer to an overarching colour, which was recorded as soil colour.

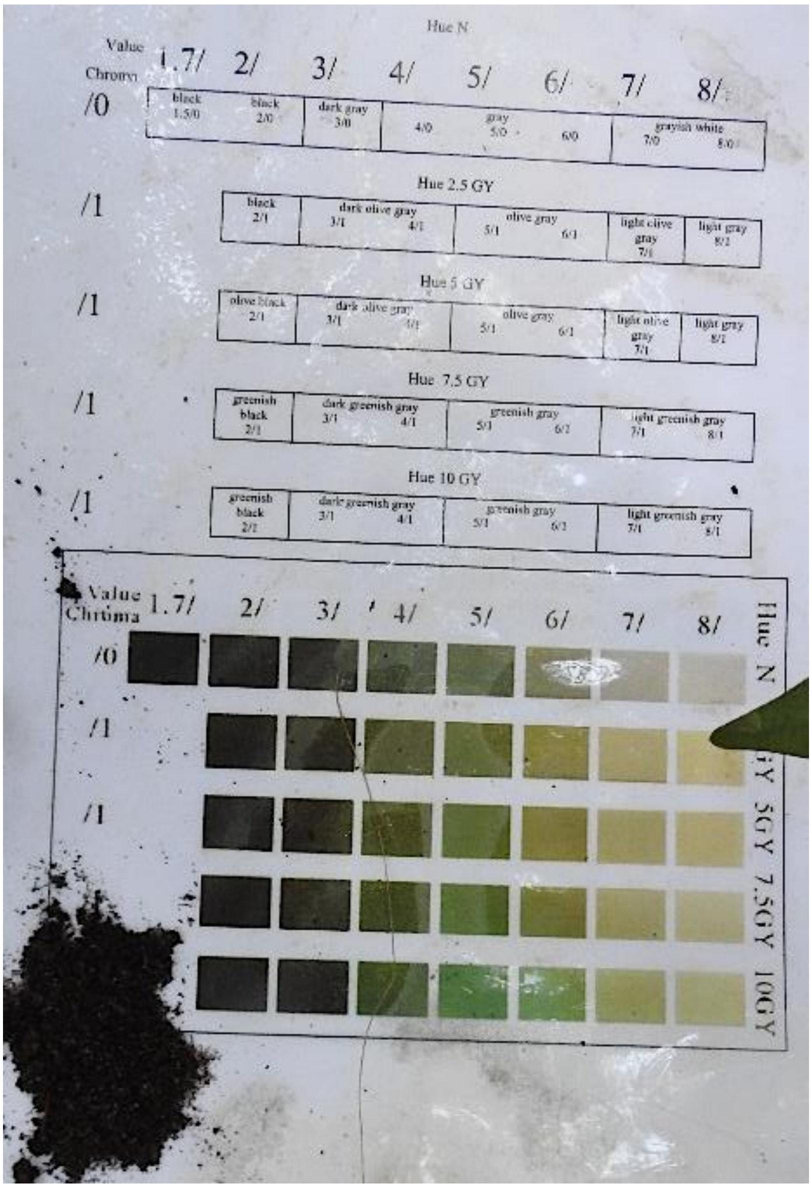

Figure 2: Determining soil colour against a standardised Munsell Soil Colour Chart.

[3] Hue refers to the primary colour of the soil, a letter notation was used to denote this. A number is also recorded for hue measurements, as there are multiple hues for each base colour. For example, 7.5YR denotes a hue of 7.5 with a Yellow-Red base colour. Value determines how light the colour is. Value was indicated by a scale between 1.7 to 8, running from darkest colours to palest. For example, a value of 6 would be a lighter shade than a value of 1.7. Chroma is a measure of how strong the colour is, which was indicated with a number between 0 and 8, running from weakest to deepest.

2.2.3.3 Soil Moisture

Soil moisture content was measured using a 4 in 1 Soil Survey Instrument one meter away from the palm's base in each cardinal direction, with assigned categories of DRY+, DRY, DRY-, NOR, WET-, WET, and WET+ depending on moisture content.

2.2.3.4 Soil Infiltration Rate

Soil infiltration was measured by clearing surface vegetation one metre to the north of the palm's base, recording the time it took for 500ml of water to completely drain through a cylinder inserted 15cm into the soil. This process was repeated twice to ensure survey conditions were standardised between sites. Soil infiltration rate was recorded as millilitres filtered per second. If water did not drain through the cylinder and there was water remaining on the surface after 30 minutes, the area was recorded as saturated. The infiltration rate recorded for the second soil infiltration rate test was used for the infiltration rate in the analysis. If the area was recorded as saturated for the first infiltration rate test, and a second infiltration rate test was not performed, the infiltration rate that was used in the analysis was 500ml/30 minutes, or 0.28ml/sec.

2.2.3.5 Soil pH

Soil samples were collected from one meter away from the palm's base in each cardinal direction, with pH measured to determine the physicochemical properties of the soil. PH measurements were analysed ex-situ, using a Hanna Halo 2 Soil pH probe. Measurements were taken by inserting the probe into the soil sample and recording the pH reading once stabilised. The probe was rinsed with de-mineralised water between samples and was fully calibrated and cleaned with electrode cleaning solution for soil deposits between samples of different species.

2.3 Statistical Analysis

Statistical analyses were performed using R Statistical Software (v4.1.2; R Core Team, 2021). Mean, standard deviation, median, maximum, and minimum values for each variable were calculated using the '*arsenal*' R package (v3.6.3; Heinzen et al., 2021).

2.3.1 Principal Component Analysis

Principal component analysis (PCA) was performed using the '*vegan*' R package (v2.6.4; Oksanen et al., 2022) and '*stats'* R package (v4.1.2; R Core Team, 2021). The full PCA methodology can be found in Annex 1.

The purpose of the PCA was to determine which quantitative environmental variables have the greatest contribution to the variation in microhabitat characteristics of the six species, and to examine the differences in quantitative microhabitat characteristics between the species. PCA will only be used for quantitative variables (Zelený, 2021a), which included density 1, density 2, canopy cover, canopy height, soil chroma, soil value, infiltration rate, pH, slope angle, and elevation.[4]

The PCA finds the linear combinations of the original variables that explain the greatest amount of variation in the microhabitat data of the individual palms. The data for each individual palm was plotted along axes for each variable.

The PCA reports the proportion of the total variance explained by each axis or principal component. The PCA also reports the loading scores of the most important variables for each principal component. A higher loading score of a variable for a given axis indicates that the data are more spread out for that variable along the axis than with a lower loading score. The variables with higher loading scores for an axis are more important in explaining the variation in the data along the axis than variables with lower loading scores.

[4] The qualitative variables, including soil texture, soil hue, soil colour name, aspect, level of sunlight, and level of moisture could not be used in the analysis. Individuals that were missing data for any of the variables included in the PCA were omitted from the analysis.

A PCA biplot with Type 1 scaling was created using the '*ggplot2'* R package (v3.3.5; Wickham, 2016) and the *'ggfortify'* R package (v0.4.15; Horikoshi & Tang, 2016). The PCA biplot displays information about both the palm individuals, microhabitat characteristics, and the relationships between samples (Zelený, 2021a). Arrows on the biplot are vectors that represent the microhabitat characteristics and points represent the individual palms.Individuals that are closer together on the plot have more similar values for the microhabitat characteristics than individuals that are further apart.

2.3.2 Principal Coordinate Analysis

Principal coordinate analysis (PCoA) was performed using the '*stats'* R package (v4.1.2; R Core Team, 2021). The full PCoA methodology can be found in Annex 2.

The purpose of the PCoA was to analyse the differences in both the qualitative and quantitative microhabitat characteristics between the species. The qualitative variables included in the PCoA were soil texture, soil hue, soil colour name, and aspect direction. The quantitative variables included in the PCoA were the variables used in the PCA.

Individuals that were missing data for any of the variables included in the PCoA were omitted from the analysis. Categorical variables can be used in PCoA, because PCoA plots and quantifies individuals based on the distances between them rather than their values for the original variables.

The distance matrix that was the input for the PCoA was created based on Gower's distance using the '*cluster*' R package (v2.1.2; Maechler et al., 2021) (Annex 3). The relationships between the variables and the PCoA axes were analysed using the '*vegan'* R package (v2.6.4; Oksanen et al., 2022).

A PCoA plot displaying the individual palms and quantitative variables that had statistically significant correlations with the PCoA axes was created using the '*ggordiplots*' R package (v0.4.1; Quensen, 2021). A second PCoA plot displaying the individual palms and the soil texture and aspect direction variables was created using the '*vegan'* R package (v2.6.4; Oksanen et al., 2022) and the '*graphics*' R package (v4.1.2; R Core Team, 2021).

Individuals that are positioned closer together on the PCoA plot are more similar than individuals that are positioned further from one another (Buttigieg & Ramette, 2014). The arrows on the PCoA plot represent the relationships between quantitative variables and the PCoA axes.

3 Results

3.1 Environmental Characteristics

3.1.1 Habitat Density

Mean ($\bar{x}$) habitat density, measured by the distance to the nearest large tree (D_1) and distance to the nearest small tree (D_2), varied between species. *C. psammophilus, C. saintelucei*, *D. brevicaulis*, and *D. scottiana* were all observed in similarly dense areas of forest.

B. madagascariensis ($\bar{x}$ D_1 = 3.61m, $\bar{x}$ D_2 = 2.62m) was observed in less dense areas of the forest than *C. psammophilus, C. saintelucei, D. brevicaulis,* and *D. scottiana.* The mean densities for *C. prestonianus* ($\bar{x}$ D_1 = 3.40m, $\bar{x}$ D_2 = 3.87m) suggest that this species was also observed in less dense areas of the forest than *C. psammophilus, C. saintelucei, D. brevicaulis*, and *D. scottiana.* However, the densities observed for *C. prestonianus* have a high standard deviation (s) (s D_1 = 5.17, s D_2 = 7.08) (Table 2) and may be influenced by a few large distances. *C. prestonianus* had the highest maximum distance from both the larger and smaller circumference trees (max. D_1 = 25.18m, max. D_2 = 33.63m).

Table 2: Summary of environmental characteristics for each species of palm.

Species	*n*	Mean (SD) Density 1 (m)	Mean (SD) Density 2 (m)	Mean (SD) Canopy Cover (%)	Mean (SD) Canopy Height (m)	Mode Sunlight Level
B. madagascariensis	20	3.61 (1.11)	2.62 (0.90)	55.4 (16.1)	8.97 (2.22)	LOW-
C. prestonianus	20	3.40 (5.17)	3.87 (7.08)	56.8 (19.0)	9.13 (3.06)	LOW-
C. psammophilus	20	1.87 (0.72)	1.12 (0.41)	66.3 (13.5)	7.13 (1.95)	LOW-
C. saintelucei	21	2.88 (1.62)	1.67 (0.88)	55.8 (14.6)	7.65 (1.42)	LOW-
D. brevicaulis	20	2.38 (1.09)	1.34 (0.52)	68.9 (12.0)	7.93 (1.73)	LOW-
D. scottiana	22	2.31 (1.01)	1.19 (0.83)	55.7 (12.7)	6.69 (1.61)	LOW-

B. madagascariensis had higher D_1 values than the other five species (Figure 3), including *C. prestonianus*. *B. madagascariensis* had a higher median ($\tilde{x}$) D_1 value ($\tilde{x}$ D_1 = 3.25m) than *C. prestonianus* ($\tilde{x}$ D_1 = 2.27m), *C. psammophilus* ($\tilde{x}$ D_1 = 1.73m), *C. saintelucei* ($\tilde{x}$ D_1 = 2.29m), *D. brevicaulis* ($\tilde{x}$ D_1 = 2.34m), and *D. scottiana* ($\tilde{x}$ D_1 = 2.16m).

Both *B. madagascariensis* and *C. prestonianus* had higher D_2 values than the other species (Figure 4). *B. madagascariensis* ($\tilde{x}$ D_2 = 2.55m) and *C. prestonianus* ($\tilde{x}$ D_2 = 2.28m) had higher median D_2 values than *C. psammophilus* ($\tilde{x}$ D_2 = 1.06m), *C. saintelucei* ($\tilde{x}$ D_2 = 1.69m), *D. brevicaulis* ($\tilde{x}$ D_2 = 1.30m), and *D. scottiana* ($\tilde{x}$ D_2 = 1.04m).

The most frequently observed tree species in the immediate surroundings of the palms were *ambora* (*n* = 31, 6.3%), *falinandro* (*n* = 31, 6.3%), and *saridobaka* (*n* = 28, 5.6%). *Ambora* was the most frequently observed tree species surrounding *C. prestonianus* (*n* = 12) and *D. brevicaulis* (*n* = 9). *Ambora*, *fantsikahitsy*, *kalavelo*, and *sagnira* were the most frequently observed tree species surrounding *C. psammophilus* (*n* = 8 for each). *Saridobaka* was the most frequently observed tree species surrounding *D. scottiana* (*n* = 9). *Bamby* was the most frequently observed tree species surrounding *C. saintelucei* (*n* = 7). *Falinandro* was the most frequently observed tree species surrounding *B. madagascariensis* (*n* = 5).

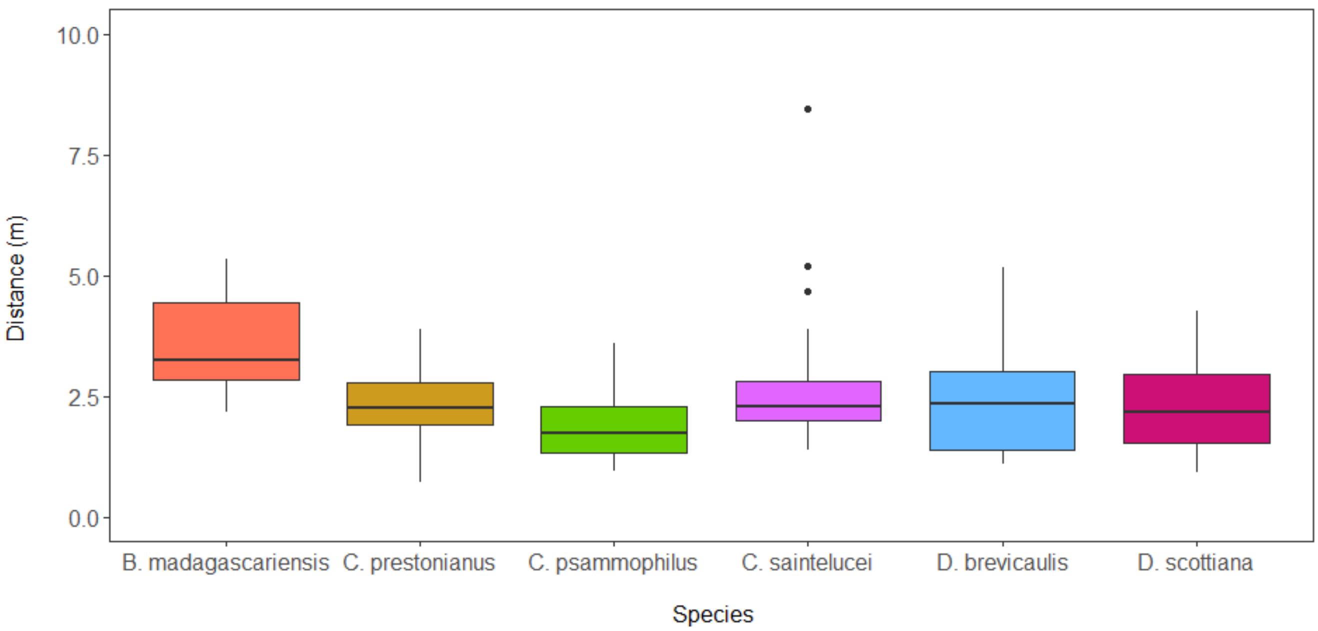

Figure 3: Distances to the nearest trees with circumferences > 12.5cm (density 1) for each palm species. Each distance measurement is an average of distances to trees in each of the four cardinal directions around the palm.[5]

[5] One data point is not visible on the plot because the y-axis was limited to 10m in order to illustrate differences between species. The point that is not shown on the plot is a density 1 value of 25.18m for *C. prestonianus*.

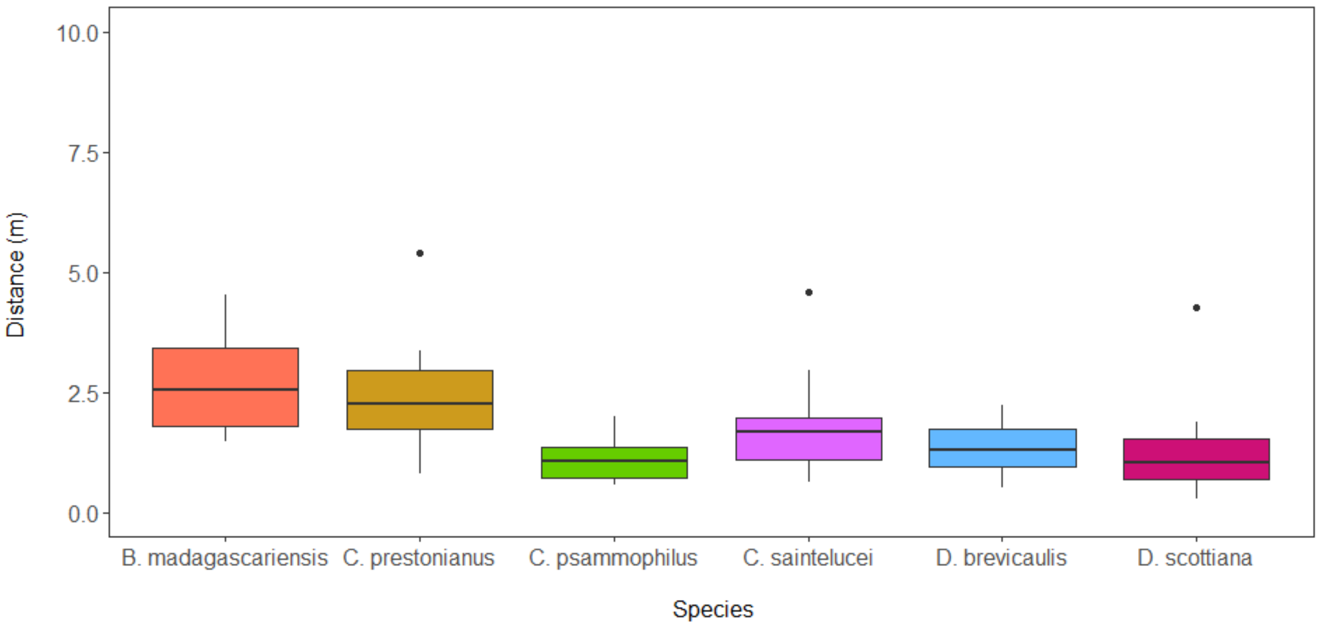

Figure 4: Distances to the nearest tree with circumference of 6.5cm-12cm (density 2) for each palm species. Each distance measurement is an average of distances to trees in each of the four cardinal directions around the palm.[6]

3.1.2 Canopy Cover and Height

Percent canopy cover varied between the six species, though all species were generally found in areas with medium canopy cover (50-75%). *D. brevicaulis* ($\bar{x}$ 68.9%) and *C. psammophilus* ($\bar{x}$ 66.3%) were found in areas with highest percent canopy cover, whereas *B. madagascariensis* were found in areas with the lowest percent canopy cover ($\bar{x}$ 55.4%). *C. prestonianus*, *C. saintelucei*, and *D. scottiana* were all found in forests with a medium level of canopy cover (Table 2). The percent canopy cover ranged from 0% to 87.5% overall.

Mean canopy height (H) did not vary greatly between the six species. *C. prestonianus* ($\bar{x}\ H = 9.13$m) and *B. madagascariensis* ($\bar{x}\ H = 8.97$m) were found in slightly taller areas of forest than *D. brevicaulis* ($\bar{x}\ H = 7.93$m), *C. saintelucei* ($\bar{x}\ H = 7.65$m), *C. psammophilus* ($\bar{x}\ H = 7.13$m), and *D. scottiana* ($\bar{x}\ H = 6.69$m) (Table 2).

3.1.3 Sunlight Level

All species were observed most frequently in low or very low levels of sunlight. In 85% of the assessments, the sunlight levels were lower-than-normal (LOW-, LOW, LOW+, NOR-) in all four directions around the palm. The percentage of individuals observed in lower-than-normal light in all four directions varied slightly between species. For example, 90% of *B. madagascariensis* and *D. brevicaulis* and 91% of *D. scottiana* were observed in lower-than-normal light in all four directions, while 75% of *C. prestonianus* were observed in lower-than-normal light in all four directions.

3.2 Topographic Characteristics

All species were observed on slopes facing in all four cardinal directions and at least six of the eight intermediate directions. In general, the species were observed with similar frequencies on slopes facing in each cardinal direction and did not demonstrate a strong preference for slopes facing in a particular direction.

D. brevicaulis was observed with lower frequency on north-facing slopes (10%) than on slopes facing south (60%), east (50%), or west (40%).[7] *D. scottiana* was observed with lower frequency on west-facing slopes (18%) than on

[6] One data point is not visible on the plot because the y-axis was limited to 10m in order to illustrate differences between species. The point that is not shown on the plot is a density 2 value of 33.63m for *C. prestonianus.*

[7] These percentages add up to more than 100%. If an individual was recorded on a slope facing in an intermediate direction that included two cardinal directions (f. e. NW), both cardinal directions were counted (f.e. N and W).

slopes facing east (50%), north (45%), or south (32%). Mode intermediate aspect directions for each species are listed in Table 3.

Table 3: Summary of topographic characteristics for each species of palm.

Species	n	Mode Aspect Direction	Median Slope Angle (°)	Mean (SD) Elevation (m)
B. madagascariensis	20	S, W	16.0	17.7 (7.3)
C. prestonianus	20	NW, SE	16.0	24.6 (13.2)
C. psammophilus	20	S	9.7	19.2 (9.2)
C. saintelucei	21	N	18.0	14.6 (7.0)
D. brevicaulis	20	SE	15.5	25.9 (7.3)
D. scottiana	22	N	8.0	18.3 (8.1)

Median slope angle (*S*) varied between 8.0° and 18.0°. *C. saintelucei* ($\tilde{x}$ *S* = 18.0°), *B. madagascariensis* ($\tilde{x}$ *S* = 16.0°), *C. prestonianus* ($\tilde{x}$ *S* = 16.0°), and *D. brevicaulis* ($\tilde{x}$ *S* = 15.5°) had higher median slope angles, whereas *D. scottiana* ($\tilde{x}$ *S* = 8.0°) and *C. psammophilus* ($\tilde{x}$ *S* = 9.7°) had lower median slope angles. Elevation (*E*) of each species ranged from a mean elevation of 14.6m to 25.9m. *C. saintelucei* were found at the lowest elevations ($\bar{x}$ *E* = 14.6m), whereas *D. brevicaulis* were found at relatively higher elevations ($\bar{x}$ *E* = 25.9m) (Table 3).

3.3 Soil Characteristics

3.3.1 Soil Composition

Overall, the palms were most frequently observed in soils composed of sand with high proportions of organic matter (38.2%) or sand with medium proportions of organic matter (38.2%) and less frequently in sand with low proportions of organic matter (20.3%). The palms were not frequently observed in soils composed of organic matter with no sand (2.4%) or organic matter with low sand (0.8%). Soil composition of where palms were observed varied between species (Table 4).

Table 4: Percentage of palm observations in each soil type by species.

	Sand with low organic matter (%)	Sand with medium organic matter (%)	Sand with high organic matter (%)	Organic matter with low sand (%)	Organic matter, no sand (%)
B. madagascariensis	20.0	35.0	45.0	0.0	0.0
C. prestonianus	15.0	50.0	35.0	0.0	0.0
C. psammophilus	20.0	35.0	40.0	0.0	5.0
C. saintelucei	4.8	19.0	61.9	4.8	9.5
D. brevicaulis	30.0	60.0	10.0	0.0	0.0
D. scottiana	31.8	31.8	36.4	0.0	0.0
All	20.3	38.2	38.2	0.8	2.4

3.3.2 Soil Colour

All species were observed in dull soils with low chroma (*C*) ($\bar{x}$ *C* = 1.9-3.2). C. psammophilus ($\bar{x}$ *C* = 3.2) were observed in soils with the highest mean chroma, while D. brevicaulis ($\bar{x}$ *C* = 1.9) were observed in soils with the lowest mean chroma (Table 5). The value (*V*) of the soil in which the palms were observed was low to intermediate for all species ($\bar{x}$ *V* = 3.4-4.0), so all species were typically observed in dark or intermediate coloured soil. The most frequently observed soil hues overall were 7.5R (28.5%), 5YR (13.0%), and 10R (12.2%) (Annex 4 & 5).

Table 5: Summary of soil colour characteristics for each species.

Species	*n*	Mean (SD) Chroma	Mean (SD) Value	Mode Hue	Mode soil colour
B. madagascariensis	20	2.1 (1.1)	3.6 (1.4)	7.5R	Dark reddish brown
C. prestonianus	20	2.2 (1.6)	3.6 (1.4)	7.5R	Dark reddish brown
C. psammophilus	20	3.2 (1.6)	3.4 (0.9)	7.5R	Dark reddish brown
C. saintelucei	21	2.8 (1.6)	3.4 (1.3)	7.5R, 5YR	Dark reddish brown, Dark reddish grey
D. brevicaulis	20	1.9 (1.3)	4.0 (1.4)	5RP, 10YR	Dark reddish grey, Dark brown, Dark purplish grey, Grey
D. scottiana	22	2.2 (1.3)	3.6 (1.4)	7.5R	Dark reddish brown

3.3.3 Soil Moisture

Nearly all palms were found in soils with moisture levels classified as either *dry* or *very dry* (DRY-, DRY, or DRY+). The only palms that were observed in soil that was not dry were three *C. saintelucei* individuals that were observed in soil classified as *very wet* (WET+), one *C. saintelucei* observed in soil classified as *wet* (WET), and one *C. saintelucei* in soil classified as *very dry* (DRY+) but observed as "visibly wet", potentially identifying a fault occurring with the soil probe.

3.3.4 Soil Infiltration Rate

The median soil infiltration rates are reported because the mean soil infiltration rates are strongly influenced by outliers, with median soil infiltration rates providing a better representation of the soil infiltration rates for each species. Soil infiltration rates (*I*) were similar for *B. madagascariensis, C. psammophilus*, and *D. scottiana* ($\tilde{x}\ I_2$ = 3.75-4.25ml/sec). *C. prestonianus* ($\tilde{x}\ I_2$ = 5.16ml/sec) were found in soils with slightly faster infiltration rates, whereas *D. brevicaulis* ($\tilde{x}\ I_2$ = 3.02ml/sec) and *C. saintelucei* ($\tilde{x}\ I_2$ = 3.11ml/sec) were found in soils with slightly slower infiltration rates (Table 6).

Table 6: Summary of soil characteristics for each species. OM denotes organic matter.

Species	*n*	Mean (SD) pH	Median Infiltration rate (ml/sec)	Mode Soil Moisture	Mode Soil Texture
B. madagascariensis	20	3.89 (0.47)	4.06	DRY+	Sand with high proportion of O.M.
C. prestonianus	20	4.63 (0.59)	5.16	DRY+	Sand with medium proportion of O.M
C. psammophilus	20	3.95 (0.51)	4.25	DRY+	Sand with high proportion of O.M.
C. saintelucei	21	3.84 (0.52)	3.11	DRY+	Sand with high proportion of O.M.
D. brevicaulis	20	4.09 (0.44)	3.02	DRY+	Sand with medium proportion of O.M.
D. scottiana	22	4.18 (0.70)	3.75	DRY+	Sand with high proportion of O.M.

3.3.5 Soil PH

The palms were observed in highly acidic substrates ($\bar{x}$ pH 3.84-4.63) with a pH range between 3.11-6.01. *C. prestonianus* ($\bar{x}$ pH 4.63) were observed in soils that had higher pH values (less acidic) than the soils in which the other five species were observed (Figure 5) (Annex 6). *B. madagascariensis*, *C. psammophilus*, *C. saintelucei*, *D. brevicaulis*, and *D. scottiana* were observed in soils with similar acidity.

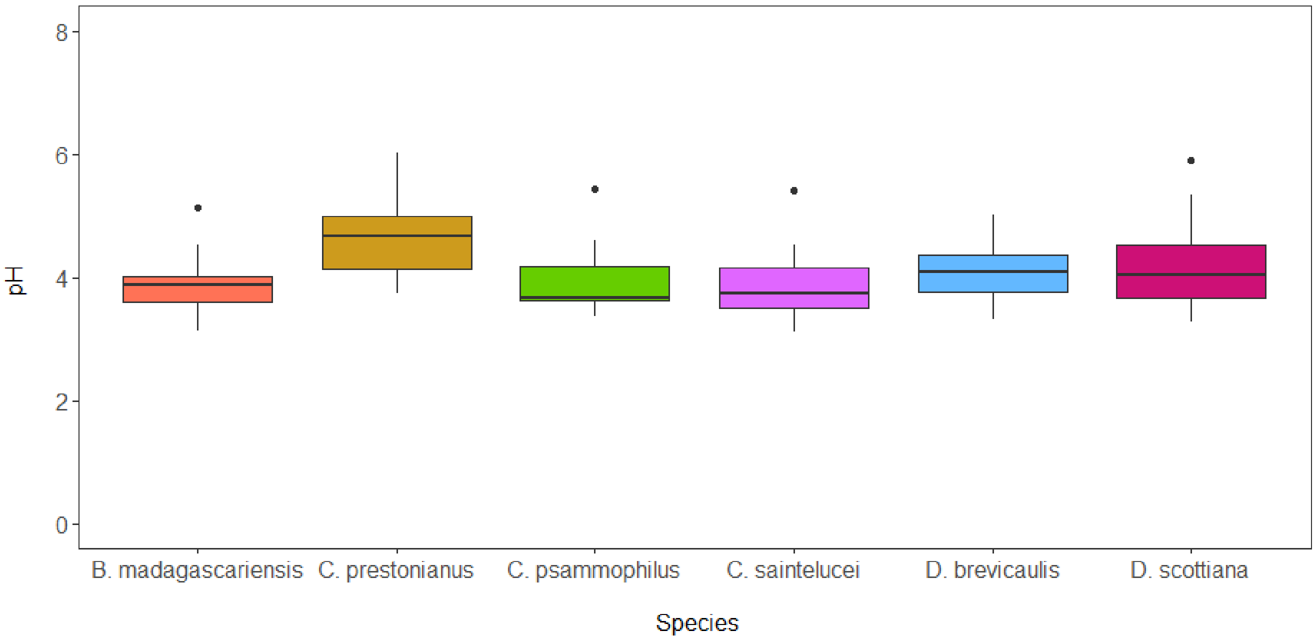

Figure 5: The distribution of pH for each palm species. Each pH measurement is an average of the pH measured in each of the four cardinal directions around the palm.

3.4 Principal Component Analysis

The first principal component (PC1) explained 22.71% of the total variance in the microhabitat data for the individual palms. The second principal component (PC2) explained 14.32% of the total variance. Combined, the first two principal components explained 37.03% of the total variance.

The variables with the greatest contribution to the PC1 were density 1 (loading score = 0.616), density 2 (loading score = 0.604), and canopy cover (loading score = -0.436). The variables with the greatest contribution to PC2 were slope angle (loading score = 0.600), elevation (loading score = 0.509), pH (loading score = 0.397), and canopy height (loading score = 0.377).

B. madagascariensis may be associated with less dense habitats. The points for *B. madagascariensis* are positioned at higher values along PC1 and the arrows for density 1 and density 2 compared to the other species (Figure 6). This suggests that the *B. madagascariensis* individuals have higher density 1 and density 2 values than individuals of the other species.

The points for *C. psammophilus* are located at lower values along PC1 compared to other species (Figure 6). *C. psammophilus* individuals had higher canopy cover values and lower density 1 and density 2 values than individuals of other species.

Compared to the points for other species, the points for individuals of *D. scottiana*, C. *psammophilus*, and *C. saintelucei* are located at lower values on PC2 (Figure 6). *D. scottiana* and *C. psammophilus* were observed at lower slope angles than the other palm species but were not observed at lower elevations than the other species (Table 3). Consequently, the positions of the points for *D. scottiana* and *C. psammophilus* at lower values along PC2 indicate that *D. scottiana* and *C. psammophilus* were found at lower slope angles than the other species. *D. scottiana* and *C. psammophilus* individuals also had lower canopy height values than other species (Table 2). *C. saintelucei* individuals were observed at lower elevations than other species but were not observed at lower slope angles than other species (Table 3).

The points for *D. brevicaulis* and *C. prestonianus* are located at higher values on PC2 (Figure 6). *D. brevicaulis* and *C. prestonianus* were observed at higher elevations than other species (Table 3). *C. prestonianus* individuals were also observed in soil with higher pH values than other species (Table 6).

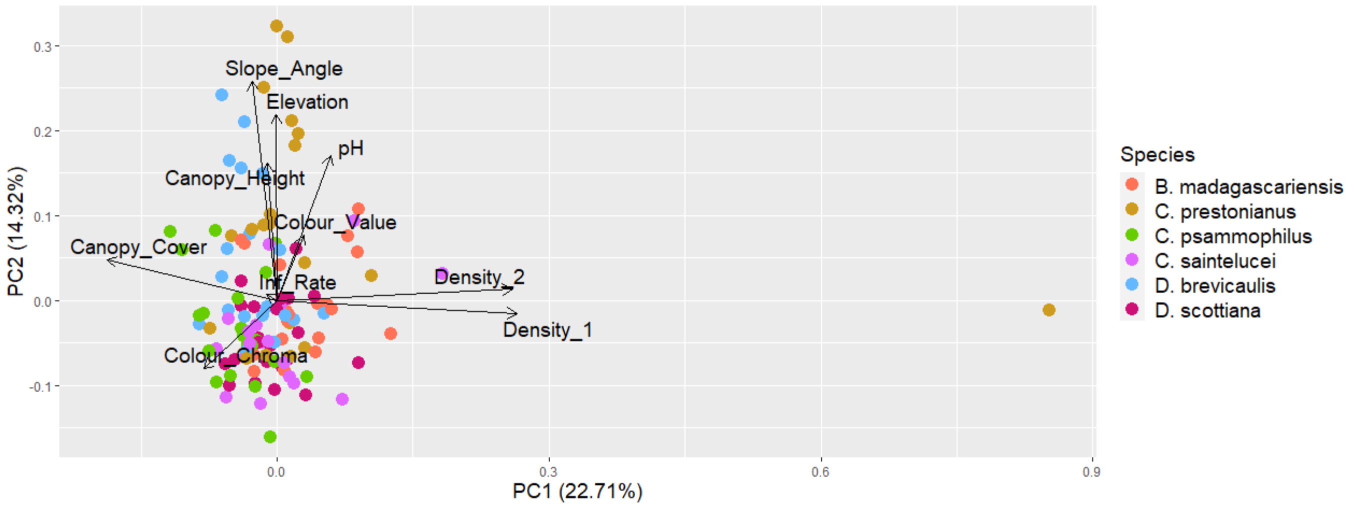

Figure 6: Principal components analysis based on palms microhabitat data for 121 individuals of the six target palm species. The ordination diagram displays biplot arrows for the environmental variables and points for individual palms. The points for individual palms are coloured by species.

3.5 Principal Coordinate Analysis

The first axis of the PCoA explains 8.1% of the variation in the microhabitat data for the individual palms, and the second PCoA axis explains 6.2% of the variation in the microhabitat data. The first two PCoA axes explain about 14.3% of the variation in the microhabitat data.

The relationships between the PCoA ordination and density 1, chroma, value, and infiltration rate were statistically significant (p <.05). The species do not appear to be separated by differences in these variables (Figure 7). Individuals that were observed in soil with higher chroma and lower value are located at lower positions on the y-axis, and individuals observed in soil with lower chroma and higher value are located at higher positions on the y-axis.

D. brevicaulis individuals appear to be separated from *C. saintelucei* individuals along the x-axis of the PCoA ordination diagram (Figure 8). Nearly all individuals of *D. brevicaulis* are located at lower positions on the x-axis, while nearly all individuals of *C. saintelucei* are located at higher positions on the x-axis. The soil texture "*Soil with medium organic matter*" is located at a lower position than "*Soil with high organic matter*" on the x-axis. This could be because "*Soil with medium organic matter*" is associated with *D. brevicaulis*, and "*Soil with high organic matter*" is associated with *C. saintelucei*. The highest frequency of "*Soil with medium organic matter*" was observed for assessments of *D. brevicaulis* (60%). The highest frequency of "*Soil with high organic matter*" was observed for assessments of *C. saintelucei* (61.9%).

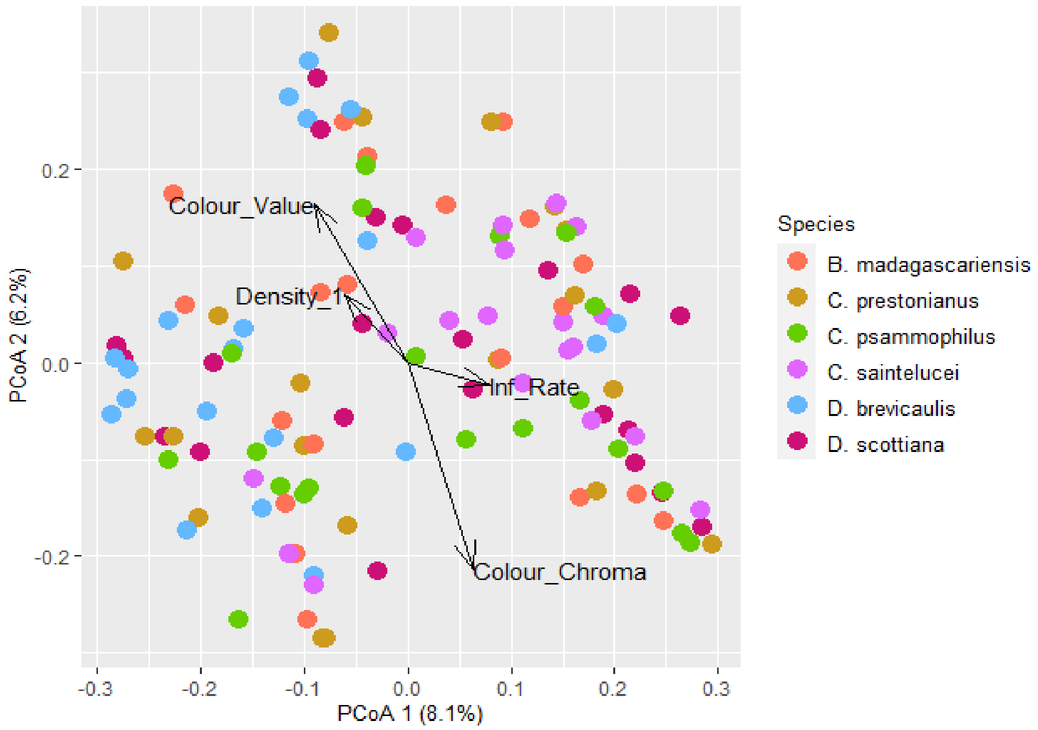

Figure 7: Principal coordinates analysis based on palms microhabitat data for 121 individuals of the six target palm species. The ordination diagram displays points for individual palms. The points for individual palms are coloured by species.

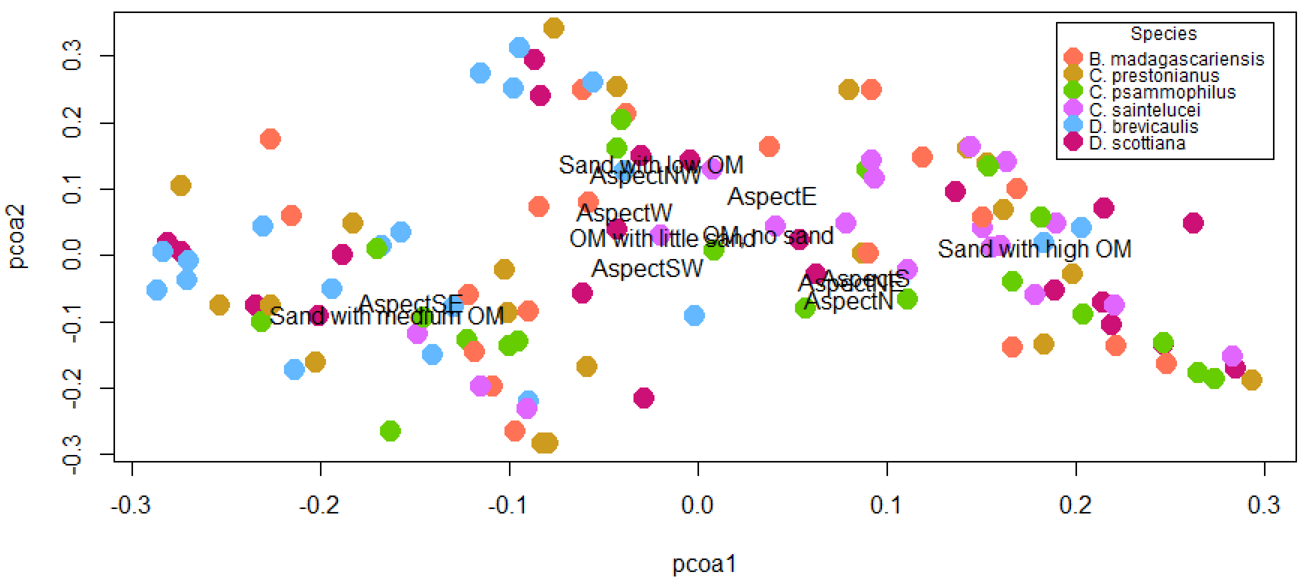

Figure 8: Principal coordinates analysis based on palms microhabitat data for 121 individuals of the target palm species. The points represent individual palms and are coloured by species. The text labels display the categorical variables: soil texture and aspect direction.[8] OM denotes organic matter.

4 Discussion

4.1 Discussion of Findings

Microhabitat assessments of at least 20 individuals from each of the six threatened species of palms in the SLLF have been completed. The findings from the assessments contribute to an understanding of the microhabitat requirements and natural history of these palm species, which will help to inform local conservation and

[8] The position of a level of a categorical variable on each axis represents the average of the scores along each axis (x and y-coordinates) of the individual palms for which the given level of the categorical variable occurred.

restoration efforts. Namely, differences in microhabitat characteristics observed between species will provide important context when deciding optimal locations to plant palm seedlings in the future.

4.1.1 Environmental Characteristics

Svenning (2004) examined the relationships between the distributions and abundances of palm species and microhabitat characteristics in the lowland rainforests of Amazonian Ecuador. The variables analysed in this study were altitude, inclination, topographic position, drainage, and canopy height. These variables were found to have significant relationships with the distributions of 14 of the 23 palm taxa analysed, highlighting the importance of microhabitat characteristics for palm species.

Descriptions for Hogg et al. (2013a) note that *B. madagascariensis*, *C. prestonianus*, and *C. saintelucei* prefer "generous canopy cover". In the current study, the mean canopy cover for *B. madagascariensis*, *C. prestonianus*, and *C. saintelucei* was between 55.4% and 56.8% which would equate to a medium level of canopy cover. Analysis shows that *B. madagascariensis*, and possibly *C. prestonianus*, prefer lower density forest than the other species. Although all species were observed in low light, certain species such as *B. madagascariensis*, *D. brevicaulis,* and *D. scottiana*, were observed less frequently in higher light environments so may have a stronger preference for low light environments than the other species. *C. psammophilus* and *D. brevicaulis* were observed in areas with the highest percent canopy cover.

Looking specifically at *C. saintelucei*, a study by Hogg et al. (2013b) found that the mean canopy cover for the sampled *C. saintelucei* palms was 63.5%, which is higher than the canopy cover percentage found for *C. saintelucei* in the present study (55.8%). It is important to note that direct comparisons cannot be drawn between the results of Hogg et al. (2013a; 2013b) and the current study because different methodologies were used, and differences in microhabitat characteristics observed in the studies may be the result of the different methodologies. For example, one reason for the difference found in the canopy cover preferred by *C. saintelucei* could be that Hogg et al. (2013b) used a densiometer to measure canopy cover.

4.1.2 Topographic Characteristics

D. brevicaulis was observed with low frequency on north-facing slopes, and *D. scottiana* was observed with low frequency on west-facing slopes. North-facing slopes and west-facing slopes in the southern hemisphere generally have higher sun exposure, higher temperatures, and lower moisture levels than south-facing slopes and east-facing slopes (Måron et al., 2015; Elnaker & Zaleski, 2021).

C. prestonianus and *D. brevicaulis* were observed at higher elevations than other species and *C. saintelucei* was observed at lower elevations. The mean elevations of *C. prestonianus* and *D. brevicaulis* are about 10m greater than the mean elevation of *C. saintelucei*. A 10m difference in elevation would only be meaningful if it were the difference in elevation between the top and bottom of a hill, because different parts of a hill would have different environmental characteristics despite small elevation differences. A study by Svenning (2004) observed that the distribution of palm species and palm community composition had the strongest relationship to topographic position. Svenning's (2004) study recorded topographic position, indicating whether the palm was observed on the upper two-thirds of hill, the lower two-thirds of a hill, or on bottomland. Svenning's results suggested that topography might be important for the structure of palm communities because it is correlated with soil conditions and forest structure. In future studies, recording the topographic position of observed palms could provide insight into soil conditions and forest structure.

Dransfield & Rakotoarinivo (2012) surveyed the palms on the mountain of Ivohibe in Tsitongambarika, a forested area north of Taolagnaro. Dransfield & Rakotoarinivo (2012) observed one *D. brevicaulis* individual growing in an open forest on sandy soil, and juvenile *C. prestonianus* individuals growing in anthropogenic grasslands. Areas of high relief occur within Tsitongambarika, with narrow ridgetops and a total elevation of about 400m. Although the specific topography at which each species was observed wasn't recorded, juvenile *B. madagascariensis, C. psammophilus,* and *C. saintelucei* individuals were observed growing on ridge tops and small crown forest on thin soil, overlooking rock outcrops. This description could suggest that these species were observed in steep habitat. All species in the current study were observed on sloping terrain; *B. madagascariensis* were observed growing on steep sloping terrain whereas *C. psammophilus* and *D. scottiana* were observed on less steep sloping terrain. Dransfield & Rakotoarinivo (2012) note that the size of *C. saintelucei* varied with the aspect. For example, on exposed ridge-tops *C. saintelucei* individuals were small, growing up to 5m tall with close internodes, whereas in sheltered areas, they grew up to 8m tall. These observations align with observations of *C. saintelucei* from this study, where adults have been recorded at a height of 5m in areas of open forest with no surrounding canopy cover.

4.1.3 Soil Characteristics

Hogg et al. (2013a) describes habitat preferences for the six palm species, in which there are some similarities and differences with the microhabitat characteristics observed in the present study.

The soil moisture each species was most frequently observed in was dry or very dry soil, composed of sand with medium or high proportions of organic matter. Analysis showed that *D. brevicaulis* and C. *saintelucei* had the strongest preference for particular soil textures, with *D. brevicaulis* preferring soils that are composed of sand with medium proportions or organic matter, and *C. saintelucei* preferring soils that are composed of sand with high proportions of organic matter.

Hogg et al. (2013a) indicates that *D. scottiana* inhabits dry forest edges as well as moist interior patches, which agrees with the results from the current study in which *D. scottiana* was observed in dry soil. Hogg et al. (2013b) studied the soil moisture preferences of *C. saintelucei* and found that *C. saintelucei* preferred soils with a moisture of around 2.7 on a scale of 10 (where 10 is the wettest) and that *C. saintelucei* sample sites had a higher moisture than random control plots. The descriptions for *B. madagascariensis*, *D. brevicaulis*, *C. prestonianus*, and *C. psammophilus* in the study by Hogg et al. (2013a) note that the species prefer well-drained soils. In the current study the soil surrounding the palms had high infiltration rates, likely a result of the sandy composition of most soils*. C. prestonianus* was observed in soil with the highest median infiltration rate, while *D. brevicaulis* and *C. saintelucei* were observed in soil with the lowest median infiltration rates. This aligns with findings from Hogg et al. (2013a). Soil with a high moisture content is able to absorb less water, due to the soil already being saturated a slower rate of infiltration is expected. Therefore Hogg et al. 2013b observing *C. saintelucei* in soils with a higher moisture aligns with this study observing *C. saintelucei* in soils with the lowest median infiltration rate.

According to Victorian Resources Online (2020), soils exhibiting reddish colours contain oxidised iron, relatively high oxygen levels, and are typically dry or well-drained. The yellow colour in soils is also produced by iron oxides, but yellow soils are not as well-drained as red soils. Grey colours are produced by unoxidized iron and are indicative of soil that is not well-drained, and the brown colour in soil is produced by organic matter, which aids water retention of the soil (Lal, 2020). The most common soil colour hues in the current study were reds and yellow-reds, and the most common soil colour names included different variations of reds, browns, and greys. Additionally, the soil surrounding the palms had a low or intermediate chroma and value. Although soils with low chroma values are usually indicative of wet soils, the soil surrounding the palms was largely dry. Lower observed values are likely a result of higher organic matter content, making the soil darker in colour. Soil observed within this study ranged from well-draining to saturated.

The palms were observed in highly acidic soils. *C. prestonianus* preferred less acidic soils compared to the other five species. Hogg et al. (2013b) observed a higher mean pH for *C. saintelucei* (6.75) than the mean pH for *C. saintelucei* observed in this study (3.84). The range of pH values for control sites and C. *saintelucei* sites in the Hogg et al. (2013b) study (4.9 to 8.0) was also higher than the range of pH values found in this study (3.11 to 6.01). Therefore, the pH values encountered in this study are lower than expected. Some sources agree palms generally prefer neutral or slightly acidic pH (Moore & Marika, 2008). Jenkinson (2008) observed that the soil in the Taolagnaro region is acidic. In the study by Jenkinson, which used the same data as Hogg et al. (2013a), pH was measured at the site using a soil probe that could only measure values between pH 3.5 and 9, as this was the expected range. Therefore, a higher acidity (lower pH) would not have been observed due to the limitations of the pH probe. There is limited knowledge on soil pH within the area, therefore further studies assessing soil pH would be useful to distinguish why the measured pH was lower than expected.

4.1.4 Principal Component Analysis

The first principal component of the PCA shows that differences in habitat density and canopy cover account for part of the variance in microhabitat characteristics of individual palms. The second principal component of the PCA shows that differences in topography, specifically slope angle and elevation, also account for part of the variance in the microhabitat characteristics of individual palms. However, about 60% of the variance in the microhabitat characteristics of the individual palms was not explained by the first two principal components.

The PCA was not able to represent a large percentage of the variation in the microhabitat characteristics of the individual palms in a few dimensions. This could be because variables were not strongly correlated with one another, and variation between individuals occurred in several different directions, so could not be reduced to a few directions for analysis. However, the PCA was useful for detecting differences in microhabitat characteristics between species, and providing a summary and visualisation of these differences.

4.1.5 Principal Coordinate Analysis

The first two axes produced by the PCoA explained very low percentages of the variance in the microhabitat characteristics of individual palms. The categorical variables, including soil colour hue, soil texture, soil colour name, and aspect direction, may have produced a large amount of variance between individuals. The PCoA did demonstrate that a high frequency of palms observed on slopes facing in a southeast direction were observed in soil with medium proportions of organic matter. The PCoA axes do not contain information about the original variables, so it was difficult to extract meaning from the gradients formed by the axes. However, similar to the PCA, the PCoA was useful for highlighting differences in microhabitat characteristics between species that could have been otherwise overlooked.

4.2 Limitations of the Study

A limitation of the study was the small sample size. The sample size was 20 individuals for four species, 21 individuals for *C. saintelucei*, and 22 individuals for *D. scottiana*. Small sample sizes decrease the probability that the samples are representative of the populations and that differences between species would be detected by the analyses. Additionally, this leads to the outliers in the data having a greater effect on the results of an analysis. In this study, several of the variables in the analyses had outliers, including density 1, density 2, canopy cover, canopy height, infiltration rate, and slope angle. For the descriptive statistical analysis of slope angle and infiltration rate, the median was reported rather than the mean, because the mean was strongly influenced by outliers. This would also influence the results of the PCA and PCoA, as outlying results would increase the variance of data. For example, the PCA axes are formed in the direction of the greatest variance, so the outliers would affect the direction in which the axes are formed. In the PCoA, observations with outliers could have large distances from other observations. Resampling methods, such as bootstrapping or jackknifing, could be used to improve the analysis.

The analysis of the categorical variables, such as identifying the differences between the values, was challenging for a few reasons. For example, the sunlight and moisture levels were measured in the four cardinal directions and were assigned a value along the scale of LOW- to HIGH+ for sunlight and from DRY- to WET+ for soil moisture. The difference between an observation with LOW- sunlight in two directions and HIGH+ sunlight in two directions and an observation with NOR sunlight in all directions, for example, would be difficult to assess. Sunlight and moisture levels were not included in the PCA and PCoA because they were not represented by single variables. In a future analysis, a strategy could be developed to combine the variables for sunlight and moisture levels into single variables that can be used in analysis. If possible, some of the variables that were categorical in this study, such as sunlight levels, moisture levels, and soil texture could be measured quantitatively in a future study.

The PCoA might not fully reflect the similarities and differences in soil hue and soil colour names between individuals. In the calculation of the distance between individuals, if the soil hues or soil colours of the individuals were different, a value of '1' was assigned, and if the soil hues or soil colours were the same, a value of '0' was assigned. The distance calculation did not assess the similarity between the hues or colour names. For example, the difference between 7.5R and 10R would be considered the same as the difference between 7.5R and 5BG. In future studies, a variable could be created that groups the hues and colour names by their main colour, such as reds, yellow-reds, and browns, or multiple variables could be created for the presence and absence of each colour. The analyses for this report did not thoroughly investigate the soil characteristics of each species. A more detailed analysis and interpretation of the soil hue, chroma, value, name, and texture are necessary.

5 Conclusion

The SLLF is inhabited by many palm species, of which six are threatened: *B. madagascariensis, C. prestonianus, C. psammophilus, C. saintelucei, D. brevicaulis,* and *D. scottiana.* Through Project Palms, SEED works to improve the conservation status of these palm species. Previous research in other parts of the world has demonstrated the importance of microhabitat characteristics in determining where different palm species grow. In this study, microhabitat assessments have provided data on the environmental, topographic, and soil characteristics preferred by each of the six species. Several similarities and differences were observed in the microhabitat preferences of the species, with these analyses useful in guiding palm conservation and local planting initiatives.

Defining outcomes of these assessments include palms of all species observed in low or very low light environments, with canopy cover between 50% and 70%. The most common tree observed surrounding the palms were *ambora*, *falinandro*, and *saridobaka*. All species preferred dry or very dry soil composed of sand with medium or high proportions of organic matter, showing that the palms preferred soils with high infiltration rates. *D. brevicaulis* most strongly preferred soil composed of sand with medium proportions of organic matter, and *C. saintelucei* most strongly preferred sand with high proportions of organic matter. The pH of the soil surrounding the palms was highly acidic for all species, although *C. prestonianus* preferred soils that were less acidic than the rest of the species observed.

The data from this study begins to contribute to understandings of how environmental conditions influence the distribution of palm species in Madagascar. Further analysis of the microhabitat data from this study could be useful, especially for qualitative data, including soil preferences. To support the current findings and identify species preferences that were not observed in this study, microhabitat data could also be collected from additional individuals of each species. A deeper understanding of the microhabitat characteristics for each of the threatened palm species will ensure that the palms' requirements for growth, survival, and health can be fulfilled by local conservation efforts.

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7 Annexes

Annex 1 – Principal Component Analysis Methodology

Principal component analysis (PCA) was performed using the '*vegan*' R package (v2.6.4; Oksanen et al., 2022) and '*stats'* R package (v4.1.2; R Core Team, 2021).

The purpose of the PCA was to determine which quantitative environmental variables have the greatest contribution to the variation in microhabitat characteristics of the six species, and to examine the differences in quantitative microhabitat characteristics between the species. PCA can only be used for quantitative variables (Zelený, 2021a); variables included in the PCA were density 1, density 2, canopy cover, canopy height, soil chroma, soil value, infiltration rate, pH, slope angle, and elevation. Individuals that were missing data for any of the variables included in the PCA were omitted from the analysis. The qualitative variables, including soil texture, soil hue, soil colour name, aspect, level of sunlight, and level of moisture could not be used in the analysis.

The PCA finds the linear combinations of the original variables that explain the greatest amount of variation in the microhabitat data of the individual palms. The PCA started with a matrix of samples (the assessments of individual palms) and descriptors (the microhabitat characteristics) (Zelený, 2021a). Standardisation of variables was necessary due to different base units of measurement (Buttigieg & Ramette, 2014). Standardisation was achieved by subtracting the mean from each entry in a column and dividing each entry in a column by the standard deviation of the column. The standardisation ensured that all variables had a mean of zero and a standard deviation of one.

The data for each individual palm (sample) was plotted along axes for each variable (descriptor) (Zelený, 2021a). The PCA forms new axes (principal components) through the data points. The first axis is formed through the points in the direction of highest variance between the points; the amount of variance between the points along the first axis is maximised (Buttigieg & Ramette, 2014). The second axis is formed through the points in the direction of the second highest amount of variance. Additional axes are formed in the directions of the next highest amount of variation in the points.

The PCA reports the proportion of the total variance explained by each axis or principal component. PCA redistributes the total variance among new variables, or principal components, so that the first principal components explain the greatest possible amount of the variance, and the last principal components explain the lowest possible amount of the variance (Cheplyka, 2017). If the first few principal components explain most of the variance, the PCA was able to successfully reduce the original variables into a few dimensions. The proportions of variance explained by each axis can be expressed as percentages of the total variance. The PCA is considered very successful if the first few axes explain 70-90% of the total variance, but it can still provide useful information even if the first few axes only explain 30-40% of the total variance (Buttigieg & Ramette, 2014).

The PCA also reports the loading scores of the most important variables for each principal component. The proportion of an axis that is formed by a certain variable is the loading score of the variable for that axis (Starmer, 2018). The loading scores represent a measure of the change in each variable along the axis compared to the change in the other variables along the axis. A higher loading score of a variable for a given axis indicates that the data are more spread out for that variable along the axis than with a lower loading score. The variables with higher loading scores for an axis are more important in explaining the variation in the data along the axis than variables with lower loading scores.

A PCA biplot with Type 1 scaling was created using the '*ggplot2'* R package (v3.3.5; Wickham, 2016) and the *'ggfortify'* R package (v0.4.15; Horikoshi & Tang, 2016).

The PCA biplot displays information about both the individuals (samples), microhabitat characteristics (descriptors), and because Type 1 scaling was used, the relationships between samples (Zelený, 2021a). To create a plot that displays the first and second principal components, the plot is rotated so that the first principal component is horizontal and forms the x-axis, and the second principal component is vertical and forms the y-axis.

Arrows on the biplot are vectors that represent the microhabitat characteristics and points represent the individual palms. Variables with greater lengths along an axis have greater contributions to the axis than variables with shorter lengths along the axis. The. Individuals that are positioned closer to the end of a variable’s vector have higher values for the variable than individuals that are positioned further from the end of the vector.Individuals that are closer together on the plot have more similar values for the microhabitat characteristics than individuals that are further apart.

Annex 2 – Principal Coordinate Analysis Methodology

Principal coordinate analysis (PCoA) was performed using the '*stats*' R package (v4.1.2; R Core Team, 2021).

The purpose of the PCoA was to analyse the differences in both the qualitative and quantitative microhabitat characteristics between the species as the PCA could only be applied to quantitative variables. The qualitative variables included in the PCoA were soil texture, soil hue, soil colour name, and aspect direction. The quantitative variables included in the PCoA were the variables used in the PCA.

Individuals that were missing data for any of the variables included in the PCoA were omitted from the analysis. Categorical variables can be used in PCoA, because PCoA plots and quantifies individuals based on the distances between them rather than their values for the original variables. Even if the individuals cannot be compared quantitatively based on the values of original variables because the original variables are categorical, the individuals can be compared using a distance measure that quantifies the differences in the categorical variables between individuals.

The distance matrix that was the input for the PCoA was created based on Gower's distance using the '*cluster*' R package (v2.1.2; Maechler et al., 2021) (Annex 2). The samples, which are the individual palms, are plotted according to the calculated distances between the pairs of individuals (Bakker, 2022). A PCA is performed on the points to find the axes that explain the greatest possible amount of variation between the points of the individuals. The goal of PCoA is to maximise the linear correlation between the distances between individuals in the distance matrix and the distances between individuals in a low-dimensional space (Palmer, 2023).

The relationships between the variables and the PCoA axes were analysed using the '*vegan*' R package (v2.6.4; Oksanen et al., 2022). Unlike in PCA, the axes produced by PCoA do not contain information about the original variables (Buttigieg & Ramette, 2014). This is because the input of the PCoA is not the original variables, but rather a distance matrix calculated from the original variables, which does not retain information about individual variables. However, there are methods to analyse the contribution of the variables to the PCoA axes (Zelený, 2021b). The contribution of the quantitative variables to the axes was assessed by finding the correlation between the coordinates of the individual palms along each axis and the values of the quantitative variables that correspond to the individuals (Buttigieg & Ramette, 2014). The relationship between categorical variables and the axes was assessed by finding the average value of the coordinates for the individuals that correspond to each level of the categorical variable (v2.6.4; Oksanen et al., 2022). Permutation was used to evaluate whether the relationships between the axes and variables were statistically significant.

A PCoA plot displaying the individual palms and quantitative variables that had statistically significant correlations with the PCoA axes was created using the '*ggordiplots*' R package (v0.4.1; Quensen, 2021). A second PCoA plot displaying the individual palms and the soil texture and aspect direction variables was created using the '*vegan*' R package (v2.6.4; Oksanen et al., 2022) and the '*graphics*' R package (v4.1.2; R Core Team, 2021).

Individuals that are positioned closer together on the PCoA plot are more similar than individuals that are positioned further from one another (Buttigieg & Ramette, 2014). The arrows on the PCoA plot represent the relationships between quantitative variables and the PCoA axes. The length of a variable's arrow along an axis is proportional to correlation of the variable with the axis (v2.6.4; Oksanen et al., 2022). The arrow for a variable points towards the direction in which the variable changes most quickly and has the greatest correlation with the axes. The position of a given level of a categorical variable along each axis represents the average position along each axis of the individuals that correspond to that level.

Annex 3 – Gower's Distance

The distance matrix used in the PCoA was constructed from Gower's distance, which can be used for datasets with quantitative, qualitative, or dichotomous variables. A distance score between two individuals is calculated for each variable in the dataset, depending on the datatype of the variable, and then the Gower's distance for the pair is calculated by averaging the distance scores for all variables (Gower, 1971).

The formula for Gower's distance between individuals *i* and *j* is:

$$\sqrt{1 - S_{ij}}$$

Where S_{ij} is the similarity between *i* and *j*. The similarity between *i* and *j*, S_{ij}, is given by the formula:

$$S_{ij} = \sum_{k=1}^{v} s_{ijk} \Big/ \sum_{k=1}^{v} \delta_{ijk}$$

S_{ij} is the similarity between individuals *i* and *j*. The value s_{ijk} is the distance score assigned to individuals *i* and *j* for the variable *k*. The value δ_{ijk} represents the possibility of making a comparison between individuals *i* and *j* for the variable *k*. If the comparison between *i* and *j* for variable *k* is not possible, because information for the variable is missing for one or both individuals, δ_{ijk} = 0, and if the comparison is possible, δ_{ijk}= 1. Based on the formula, the similarity between *i* and *j* is the average score of the possible comparisons between *i* and *j*.
The distance scores for each variable are calculated differently for quantitative and qualitative variables.
For quantitative variables the distance score s_{ijk} is given by the equation:

$$s_{ijk} = 1 - \frac{|x_i - x_j|}{R_k}$$

s_{ijk} is the distance score between individuals *i* and *j* for variable *k*. x_i is the value of variable *k* for individual *i*, and x_j is the value of variable *k* for individual *j*. R_k is the range of the variable *k* in the dataset. s_{ijk} is 1 if *i* and *j* have the same value for variable *k*, and s_{ijk} is 0 if *i* and *j* are on opposite ends of the range of variable *k*,
For qualitative variables, the distance score s_{ijk} between individuals *i* and *j* for variable *k* equals 1 if the individuals have the same value for variable *k* and equals 0 if the individuals have different values for variable *k*.

Annex 4 – Most Common Soil Colour Names by Species and Overall

Species	Most common soil colour names
B. madagascariensis	Dark reddish brown (25%)
C. prestonianus	Dark reddish brown (25%)
C. psammophilus	Dark reddish brown (25%)
C. saintelucei	Dark reddish brown, Dark reddish gray (14.3% each)
D. brevicaulis	Dark brown, Dark purplish gray, Dark reddish gray, Gray (10%)
D. scottiana	Dark reddish brown (27.3%)
All	Dark reddish brown (20.3%), Dark reddish gray (8.1%)

Annex 5 – Most Common Soil Hue(s) by Species and Overall

Species	Most common soil hue(s)
B. madagascariensis	7.5R (25%)
C. prestonianus	7.5R (35%)
C. psammophilus	7.5R (35%)
C. saintelucei	7.5R, 5YR (28.6% each)
D. brevicaulis	10YR, 5RP (15% each)
D. scottiana	7.5R (36.4%)
All	7.5R (28.5%)

Annex 6 – Soil pH by Species

Species	Mean	SD	Median	Max	Min
B. madagascariensis	3.89	0.47	3.88	5.12	3.13
C. prestonianus	4.63	0.59	4.68	6.01	3.73
C. psammophilus	3.95	0.51	3.68	5.45	3.36
C. saintelucei	3.84	0.52	3.74	5.40	3.11
D. brevicaulis	4.09	0.44	4.08	5.01	3.32
D. scottiana	4.18	0.70	4.04	5.90	3.27