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Nurse plants have the potential to accelerate vegetation recovery in Lapalala Wilderness old fields, South Africa

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Abstract

Nurse plants offer microclimates that are favourable to plant growth of understory native vegetation, thus facilitating ecological restoration in degraded old fields. This study examined the impact of three nurse plants on vegetation diversity and soil physical properties in old fields located at Lapalala Wilderness, South Africa. Vegetation surveys in plots measuring 5 m x 5 m under and outside the canopy of nurse plants in both old field and natural sites were conducted. Top soils under and outside the nurse plants canopy were collected in all plots and quantified for soil moisture, soil penetration resistance and soil water repellency. Results indicate that species diversity was high under plant canopy compared to outside plant canopy for all nurse plants. Soils under nurse plants canopy showed improved soil moisture and soil penetration resistance compared to soils outside plant canopy, but no differences were reported for soil water repellency. The study concludes that the presence of native plants under nurse plants canopy points to a positive vegetation recovery trajectory. For vegetation and soil restoration to be effective in Lapalala Wilderness old fields, nurse plants should be protected and active restoration, e.g. seeding or seedling sowing under nurse plants canopy should be considered.

Les plantes nourricières, ou nurses, offrent des microclimats favorables à la croissance des plantes de la végétation native de sous-bois et facilitent ainsi la restauration écologique d'anciens champs dégradés. Cette étude a étudié l'impact de trois plantes nurses sur la diversité de la végétation et sur les propriétés physiques du sol d'anciens champs situés dans la Réserve de faune de Lapalala, en Afrique du Sud. Nous avons mené des études de la végétation dans des parcelles mesurant 5x5 m, en dehors et sous la canopée des plantes nurses, dans d'anciens champs et dans des sites naturels. Dans toutes les parcelles, nous avons récolté du sol de surface en dessous et en dehors de la canopée des plantes nurses et nous avons mesuré l'humidité du sol, sa résistance à la pénétration et son imperméabilité. Les résultats montrent que la diversité en espèces était plus haute sous la canopée des plantes qu'en dehors de la canopée pour toutes les plantes nurses. Les sols situés sous la canopée de plantes nurses montraient une meilleure humidité et une meilleure résistance à la pénétration que ceux situés en dehors, mais nous n'avons relevé aucune différence pour l'imperméabilité du sol. Notre étude conclut que la présence de plantes natives sous une canopée de plantes nurses augure d'une trajectoire positive de la restauration végétale. Pour que la restauration du sol et de la végétation soit efficace dans les anciens champs de cette réserve de faune, il faut protéger les plantes nurses, et envisager une restauration active, c'est à dire semer et replanter sous la canopée des plantes nurses.

KEYWORDS
abandoned fields, ecological restoration, facilitation, nucleation, pioneer plants

1 | INTRODUCTION

Abandoned agricultural fields, commonly known as "old fields" cover millions of hectares of land in the world (Taylor, Pokorny, Mangold, & Rudd, 2013). Previous studies have shown that the transformation of soil surfaces, the removal of soil seed bank and past fertilization cause most old fields to remain in a degraded state, with little or no native species recolonization (Priest & Epstein, 2011; Taylor et al., 2013). Recently, there has been increasing interest in restoring old fields to their native state (Priest & Epstein, 2011); the aim is to create a diverse and productive environment that has potential to provide ecosystem services (Cramer, Hobbs, & Standish, 2008). Several techniques have been tried to restore native vegetation in old fields, e.g. augmentative restoration (Sheley, James, & Bard, 2009), soil nutrient manipulation (Ruwanza, Musil, & Esler, 2012), topsoil removal (Hölzel & Otte, 2003; van der Wubs, Putten, Bosch, & Bezemer, 2016), perching (Heelemann, Krug, Esler, Reisch, & Poschlod, 2012), nucleation (Reis, Bechara, & Tres, 2010) and seeding (Simons & Allsopp, 2007; Sovu, Tigabu, & Odén, 2010; Van der Vyver, Cowling, Campbell, & Difford, 2012). Results from these above-mentioned techniques have been mixed, with both restoration success and failure. Few studies have examined how nurse plants, as a restoration initiative, can facilitate soil and vegetation recovery in old fields (Rens, Yang, & Liu, 2008; Simons & Allsopp, 2007). Simons and Allsopp (2007) reported that seedlings transplanted under adult *Galenia africana* shrubs showed higher survival rates; this a result of the creation of favourable microhabitats that facilitate plant growth.

Ecological restoration studies have focused mostly on competition, ignoring positive interactions that facilitate plant recovery (Rens et al., 2008). The facilitative interaction between woody nurse plants has been shown to trigger ecological restoration through the creation of favourable microclimates for seed germination and seedling recruitment (Rens et al., 2008; Siles, Rey, Alcántara, & Ramírez, 2008). Nurse plants are known to improve soil temperature, humidity and soil nutrients as well as shelter plants from animal grazing (Bruno, Stachowicz, & Bertness, 2003; Padilla & Pugnaire, 2006; Rens et al., 2008). Castro, Zamora, Hódar, Gómez, and Gómez-Aparicio (2004) conclude that the use of nurse plants is a viable restoration technique that facilitates plant succession. Also, Gómez-Aparicio et al. (2004) showed that legumes that act as nurse plants can improve the survival and growth of target species in deserts and Mediterranean semiarid areas. Other studies have shown that nurse plants can change soil physico-chemical properties, although such changes in soils are not obvious (Norisada et al., 2005; Rens et al., 2008).

The restoration technique centred on nurse plants aims at the formation of suitable microclimates underneath tree canopies that are favourable to the opening of a series of stochastic events linked to ecological restoration (Reis, Bechara, Espindola, Vieira, & Lopes, 2003). The stochastic events that facilitate ecological restoration include among other things the arrival of native species seeds (mainly dispersed by birds and animals attracted to these nurse plants) and the formation of soil conditions that positively facilitate plant germination and growth (Reis et al., 2010). In most cases, nurse plant theories on restoration have suggested that herbs and grass species colonize under canopy vegetation first, before trees and shrubs take over, as decomposition of herbs and grasses improves soils (Reis et al., 2010). Therefore, an understanding of the role of nurse plants in old field restoration can be integrated into the ecological restoration management plans. The objective of this study was to measure the influences of nurse plants canopy on understory species diversity and soil physical properties. Based on the nurse plant theory, the study asks the question whether nurse plants canopy affects species diversity and soil physical properties underneath them. Results of this study are discussed in the context of recent attempts to restore degraded old fields at Lapalala Wilderness, which is located in the Limpopo province of South Africa.

2 | METHODS

2.1 | Study area

The study area was the Lapalala Wilderness, a privately owned game reserve located in the Waterberg district of Limpopo Province, South Africa (Figure 1). Three old field sites (site 1 - 23°51′53.83′′S and 28°18′09.55′′E, site 2 - 23°51′52.15′′S and 28°17′51.58′′E, site 3 - 23°51′48.12′′S and 28°17′35.04′′E) that are adjacent to natural sites (site 1 - 23°51′48.91′′S and 28°18′12.36′′E, site 2 - 23°51′42.56′′S and 28°17′53.53′′E, site 3 - 23°51′37.83′′S and 28°17′41.09′′E) were selected for this study (Table 1). The vegetation type at the study area falls within the savannah biome. In the Lapalala Wilderness, vegetation was first classified as mixed bushveld by Acocks (1988) and Waterberg Mountain Bushveld by Mucina and Rutherford (2006). The reserve is mostly underlain by acid, ancient sandstones of the Kransberg subgroup of the Waterberg groups, which produce nutrient-poor sandy soils. However, the central parts are dominated by basic norite/epidiorite substrates which produce nutrient-rich clay soils. Two perennial rivers, namely the Palala River and the Blocklands River converge in the reserve (Kearney, Seamark, Bogdanowicz, Roberts, & Roberts, 2008). The area experiences mild

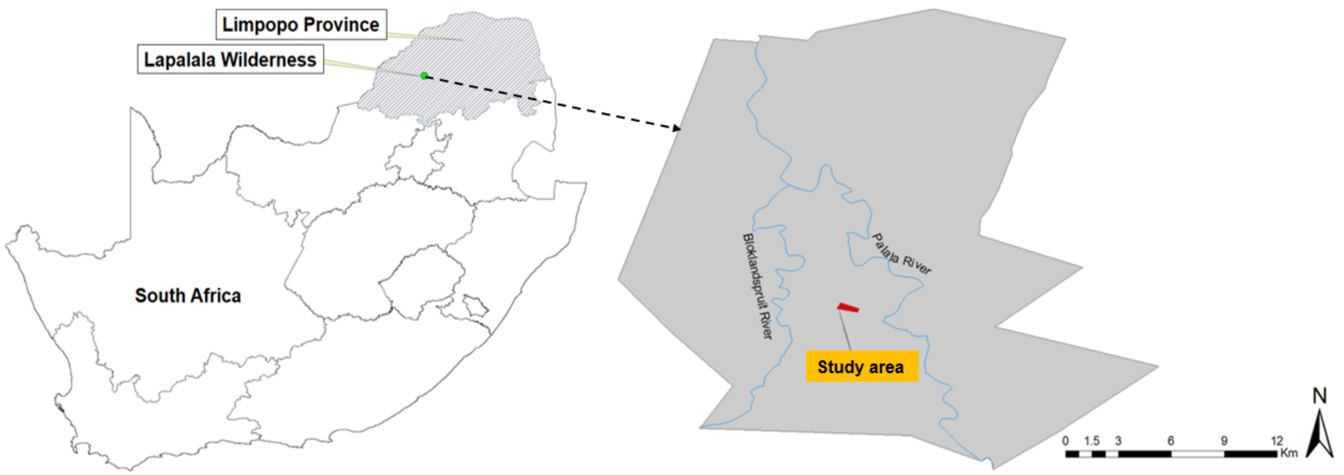

FIGURE 1 The location of the study area in Lapalala Wilderness located in the Limpopo province of South Africa

TABLE 1 Characteristics of the three paired study sites located in Lapalala Wilderness in the Limpopo Province of South Africa. Old filed sites and natural sites were adjacent to each other

Site number	Site identification	Site status	Coordinates
Site 1	Site 1a	Old field site	23°51′53.83″S, 28°18′09.55″E
	Site 1b	Adjacent natural site	23°51′48.91″S, 28°18′12.36″E
Site 2	Site 2a	Old field site	23°51′52.15″S, 28°17′51.58″E
	Site 2b	Adjacent natural site	23°51′42.56″S, 28°17′53.53″E
Site 3	Site 3a	Old field site	23°51′48.12″S, 28°17′35.04″E
	Site 3b	Adjacent natural site	23°51′37.83″S, 28°17′41.09″E

climate with mean minimum and maximum temperatures of 4°C and 20°C in July and 14°C and 30°C in January (Hulsman et al., 2010). Rainfall falls in summer with an average annual rainfall ranging from 400 to 600 mm (Hulsman et al., 2010). The reserve hosts a variety of animals that include eland, impala, zebra, wildebeest, baboon, antelope, buffalo and giraffe.

2.2 | Selected nurse plants

Three native tree species were selected to represent nurse plants in this study. These tree species, namely *Vachellia nilotica*, *Peltophorum africanum* and *Senegalia nigrescens* were selected because they form the bulk of the tree species that are scattered in the old fields. *V. nilotica* (Fabaceae) is a native tree species that grows to an average height of 6 m and has a somewhat flattered or round crown. Paired thorns grow from the branches of the tree, whereas the leaves consist of feather-like pairs of pinnae. Besides being used for medicinal purposes, e.g. cough remedy, the tree is also used for firewood and is browsed by animals (Van Wyk & Van Wyk, 2013).

Peltophorum africanum (Fabaceae) is a semideciduous to deciduous tree species that grows to about 15 m and has a spreading canopy. The leaves are acacia-like and are covered with fine hair. The tree has many uses, e.g. bee-keeping, used to make furniture, firewood and the leaves and pods are eaten by livestock. *Senegalia nigrescens* (Fabaceae) is a deciduous small to medium-sized tree that grows to a height of between 5 and 18 m and has a long cylindrical shape and round crown. It has paired knob thorns on the trunks and branches. The leaves consist of pairs of pinnae and the plant can be used to make fence posts and for firewood.

2.3 | Experimental design

To compare vegetation and soil physical properties underneath the canopies of nurse plants and on adjacent open areas, above-mentioned three paired sites were used (old field sites that share boundaries with adjacent natural sites). The paired sites were separated by a road, whereas the sites were approximately 200 m apart to provide a measure of independence (Galatowitsch & Richardson, 2005). The pairing of sites helped minimize variability is soil types. The old fields were previously used for tobacco and cattle farming some 35 years ago, but are currently used for animal grazing. They are dominated by a few woody pioneer species and low grass cover.

In each of the above-mentioned three paired sites, five plants per nurse plant species were selected for measurements. This resulted in a total of 90 nurse plants being surveyed (3 nurse plant species x 5 plants x 6 sites). Plant height, diameter at breast height (DBH) and tree crown (canopy area of influence on the ground) for each nurse plant were measured using a tape measure. Underneath the canopy of each nurse plant, a 25 m^2 plot (5 m x 5 m) was set up, with the identified nurse plant being the centre of the plot (these were referred to as under canopy plots). To ascertain that changes in both vegetation and soils underneath the nurse plant canopy are a result of the measured plant, adjacent plots of similar above-mentioned dimensions were set up 5 m away from the tree canopy (these are referred to as outside canopy plots).

2.4 | Vegetation measurements

A detailed vegetation survey was conducted in all the plots under and outside nurse plants in April 2017. The richness and density of all trees and shrubs were determined through counting the total numbers of individual plant species present in the plot, whereas that for herbs and grasses was determined through counting the total numbers of individual plant species present in a 1 m^2 quadrat positioned at the right-hand corner. Species were assigned to four broad growth forms based on morphology, namely trees, shrubs, herbs, and grasses. In addition, plant samples were collected and subsequently identified at Lapalala Wilderness and in the herbarium of the Department of Botany at the University of Venda.

2.5 | Soil physical properties measurements

Within each plot under and outside nurse plants for all sites, a soil core measuring 8 cm in diameter and 8 cm depth was collected after the careful removal of overlying debris. After soil collection, gravimetric soil moisture and soil water repellency were measured under laboratory conditions at the University of Venda. Soil penetration resistance levels, measured in kg/cm^2, were measured under field conditions in all above-mentioned soil collection points using a pocket penetrometer (SOILTEST, Inc), which when pushed into the soil, a metal ring marks the penetration level (Leung & Meyer, 2003).

Prior conducting laboratory measurements, collected soils were sieved using a 2 mm sieve. Gravimetric soil moisture was assessed by weighing wet soils, drying them in a drying oven at 105°C for 72 hr, and then re-weighing them to obtain the water content (Black, 1965) which was then converted to a percentage. Soil water repellency, a measure of reduction in the rate of wetting and retention of water in soils mainly caused by hydrophobicity on soil particles (Hallett, 2008) was measured using the Water Droplet Penetration Time (WDPT) method. Sieved soils were air-dried, set into Petri dishes and kept in laboratory conditions for 7 days at approximately 18°C which is similar to average autumn Thohoyandou temperatures. The WDPT test was conducted by placing five drops of distilled water to the surface of the soil samples (Doerr & Thomas, 2000) and recording the time taken for the drop to penetrate the soil. The drops were placed using a syringe and the average penetration time for the five drops was taken to represent the WDPT for each sample. WDPT classes used in this study were, wettable (below 5 s), slightly water repellent (5-60 s), strongly water repellent (60-600 s), severely water repellent (600-3,600 s) and extremely water repellent (above 3,600 s) (Bisdom, Dekker, & Schoute, 1993).

2.6 | Data analysis

To compare differences in plant morphology for the three nurse plants (plant height, diameter at breast height, and tree crown), a *t*-test was used to compare old field sites and natural sites. Species richness, Shannon–Wiener diversity index, Simpson's index of diversity and Evenness index were calculated for each plot and were used to examine differences between old field sites and natural sites. Proof of normality and homogeneity of variance were assessed on both vegetation and soil data using Kolmogorov–Smirnov tests and Levene's test respectively and data were normally distributed. The effect of sites and canopy positions on both vegetation and soil data were compared using the split-plot ANOVA in R (R Development Core Team, 2015) using the library *MASS*. For each of the above-mentioned vegetation diversity indices and measured soil physical properties of gravimetric soil moisture and soil penetration resistance levels, split-plot ANOVA was compared on sites and canopy positions being nested in sites. Multivariate analysis was done using Canoco for Windows 5 (Šmilauer & Lepš, 2014). Data were log-transformed before Principal Component Analysis (PCA) was done to eliminate the influence of extreme values on ordination scores. Principal component analysis was performed to investigate how tree canopy position in old field sites and natural sites changed species composition using species count data.

3 | RESULTS

3.1 | Effect of nurse plants canopy on vegetation diversity

Height, diameter at breast height and tree crown for all the nurse plants showed no significant ($p > 0.05$) differences in old field sites compared to natural sites (Table 2). Overall, results of this study show that both site and canopy position had significant ($p < 0.05$) effect on species richness and diversity (Table 3). Species richness, Shannon–Wiener diversity index, Simpson's index of diversity and Evenness index were all significantly ($p < 0.05$) higher in natural sites compared to old field sites for all the three nurse plants, except for evenness index for *V. nilotica* which showed no significant ($p > 0.05$) differences (Table 3). When canopy position was nested in sites, species richness and Shannon–Wiener diversity index for all the three nurse plants, Simpson's index of diversity for *P. africanum* and Evenness index for *S. nigrescens* were significantly ($p < 0.05$) higher under the tree canopy compared to outside the tree canopy (Table 3). Species richness for trees and shrubs were significantly ($p > 0.001$) higher in natural sites compared to old field sites for all the nurse plants. When canopy position was nested in sites, the richness of trees and shrubs were significantly ($p < 0.01$) higher under the tree canopy of *V. nilotica* and *P. africanum* only compared to outside these tree canopies (Table 3). Similarly, species richness for herbs was significantly ($p > 0.001$) higher in natural sites compared to old field sites for all the nurse plants. When canopy position was nested in sites, the richness of herbs were significantly ($p < 0.01$) higher under the tree canopy compared to outside tree canopy for all the nurse plants (Table 3). Species richness for grasses was significantly ($p > 0.05$) higher in natural sites compared to old field sites for *V. nilotica* only (Table 3). When canopy position was nested in sites, the richness of grasses was significantly ($p < 0.01$) higher under the tree canopy of *V. nilotica* only compared to outside this tree canopy.

TABLE 2 Plant height, plant diameter at breast height (DBH) and tree crown (canopy area of influence on the ground) of three examined nurse plants from old field sites and natural sites

Nurse plants	Measurements	Old field sites	Natural sites	Statistics *t*	*p*
Vachellia nilotica	Height (m)	2.76 ± 0.13	2.68 ± 0.13	0.43	0.67
	Diameter (cm)	22.89 ± 1.73	22.74 ± 1.27	0.07	0.95
	Tree crown (m)	8.48 ± 0.41	8.63 ± 0.48	0.23	0.82
Peltophorum africanum	Height (m)	4.83 ± 0.39	4.07 ± 0.33	1.49	0.15
	Diameter (cm)	26.16 ± 1.68	25.73 ± 1.54	0.19	0.85
	Tree crown (m)	8.63 ± 0.48	8.98 ± 0.59	0.46	0.65
Senegalia nigrescens	Height (m)	6.55 ± 0.62	6.31 ± 0.60	0.28	0.78
	Diameter (cm)	30.02 ± 2.57	28.00 ± 1.68	0.66	0.52
	Tree crown (m)	7.26 ± 0.44	7.53 ± 0.43	0.44	0.66

Note. Data are means ± *SE* and *t*-test results are shown.

TABLE 3 Comparison of indices of diversity between old field sites and natural sites for the three measured nurse plants

		Old field sites		Natural sites		Sites		Sites (Canopy position)	
Nurse plants	Diversity indices measure	Under canopy	Outside canopy	Under canopy	Outside canopy	*F*	*p*	*F*	*p*
Vachellia nilotica	Species richness	14.67 ± 1.05	8.07 ± 0.44	20.07 ± 0.95	16.33 ± 0.52	75.35	**<0.001**	23.20	**<0.001**
	Shannon–Wiener	2.06 ± 0.08	1.70 ± 0.08	2.46 ± 0.04	2.31 ± 0.04	63.72	**<0.001**	9.27	**<0.001**
	Simpsons index of diversity	0.82 ± 0.02	0.77 ± 0.03	0.87 ± 0.01	0.87 ± 0.01	26.07	**<0.001**	1.92	0.16
	Evenness index	0.77 ± 0.02	0.82 ± 0.03	0.82 ± 0.01	0.83 ± 0.01	3.28	0.08	1.84	0.17
	Species richness per growth form								
	Richness of trees and shrubs	5.80 ± 0.59	2.67 ± 0.43	7.53 ± 0.62	6.73 ± 0.46	29.63	**<0.001**	9.21	**<0.001**
	Richness of herbs	5.33 ± 0.69	2.53 ± 0.31	6.80 ± 0.73	6.40 ± 0.58	19.71	**<0.001**	5.54	**0.01**
	Richness of graminoids	3.87 ± 0.27	4.87 ± 0.26	6.40 ± 0.55	4.33 ± 0.52	5.59	**0.02**	7.36	**0.01**
Peltophorum africanum	Species richness	14.47 ± 0.76	8.93 ± 0.66	18.88 ± 0.87	18.15 ± 0.90	73.33	**<0.001**	12.11	**<0.001**
	Shannon–Wiener	2.18 ± 0.08	1.70 ± 0.08	2.47 ± 0.04	2.41 ± 0.07	57.27	**<0.001**	13.40	**<0.001**
	Simpsons index of diversity	0.84 ± 0.02	0.77 ± 0.02	0.89 ± 0.01	0.88 ± 0.01	30.77	**<0.001**	6.05	**0.01**
	Evenness index	0.82 ± 0.01	0.79 ± 0.02	0.85 ± 0.01	0.83 ± 0.01	4.99	**0.03**	1.29	0.29
	Species richness per growth form								
	Richness of trees and shrubs	4.73 ± 0.38	2.67 ± 0.35	7.29 ± 0.55	7.00 ± 0.47	58.09	**<0.001**	5.26	**0.01**
	Richness of herbs	4.87 ± 0.35	2.93 ± 0.32	5.76 ± 0.36	5.92 ± 0.50	26.02	**<0.001**	6.55	**0.01**
	Richness of graminoids	5.40 ± 0.29	5.87 ± 0.40	6.35 ± 0.38	5.54 ± 0.61	1.04	0.31	1.40	0.26
Senegalia nigrescens	Species richness	15.00 ± 0.71	9.67 ± 0.71	18.88 ± 0.76	17.40 ± 0.76	62.42	**<0.001**	14.19	**<0.001**
	Shannon–Wiener	2.22 ± 0.06	1.71 ± 0.07	2.52 ± 0.04	2.39 ± 0.06	67.64	**<0.001**	20.36	**<0.001**
	Simpsons index of diversity	0.85 ± 0.01	0.77 ± 0.02	0.90 ± 0.01	0.88 ± 0.01	40.54	**<0.001**	10.70	**<0.001**
	Evenness index	0.83 ± 0.02	0.77 ± 0.02	0.86 ± 0.01	0.84 ± 0.01	12.95	**<0.001**	5.02	**0.01**
	Species richness per growth form								
	Richness of trees and shrubs	4.67 ± 0.43	3.00 ± 0.45	6.73 ± 0.64	6.33 ± 0.54	26.91	**<0.001**	2.71	0.08
	Richness of herbs	5.47 ± 0.41	3.33 ± 0.44	6.67 ± 0.44	5.93 ± 0.51	17.50	**<0.001**	6.17	**0.01**
	Richness of graminoids	5.20 ± 0.35	5.93 ± 0.38	6.27 ± 0.34	5.47 ± 0.41	0.42	0.52	2.66	0.08

Note. Data are means ± *SE* and significant nested ANOVA results highlighted in bold.

P. africanum and *S. nigrescens* showed no significant ($p > 0.05$) difference in evenness index when sites were nested in canopy position (Table 3).

A total of 48 plant species were recorded in all sites, of which 29 were trees and shrubs, 9 were herbs and 10 were grasses (Appendix). Principal component analysis for all the nurse plants showed that sites influenced the distribution of individual species more than canopy position. The above is more visible in the two selected nurse plants of *P. africanum* and *S. nigrescens* were species separation between sites is clear as compared to *V. nilotica* (Figure 2). Generally, the tree and shrub species of *Terminalia sericea*, *Senegalia Senegal* and *Euclea undulata* as well as the herb species *Gomphrena celosioides* and *Hibiscus sp* dominated under *V. nilotica* canopy in old field sites (Figure 2a). The herb species *Solanum incanum* and *Pseudognaphalium sp* as well as the grass species *Cynodon dactylon* and *Brachiaria deflexa*, assembled more underneath *P. africanum* in old fields (Figure 2b). The tree species *Mimusops zeyheri*, the herb species *Xerochrysum bracteatum* and *Felicia sp* and the grass species *Panicum maximum*, *Digitaria eriantha* and *Heteropogon contortus* dominated under *S. nigrescens* in old field sites (Figure 2c).

3.2 | Effect of nurse plants canopy on soil physical properties

Comparisons between sites showed significant ($p < 0.05$) differences in gravimetric soil moisture content for all the nurse plants (Figure 3). Higher soil moisture content was reported in natural sites compared to old field sites. When canopy position was nested in sites, gravimetric soil moisture content were significantly ($p < 0.01$) higher under the tree canopy compared to outside the tree canopy for all the nurse plants. However, the above-mentioned differences were only recorded in old field sites, not in natural sites which showed no significant ($p > 0.05$) differences (Figure 3). Similarly, comparisons between sites showed significant ($p < 0.001$) differences in soil penetration resistance levels for all the nurse plants (Figure 3). Higher soil penetration resistance levels were reported in old field sites compared to natural sites. When canopy position was nested in sites, soil penetration resistance levels were significantly ($p < 0.01$) higher outside the tree canopy compared to under the tree canopy for all the nurse plants (Figure 3). Soils in all sites and canopy positions were wettable thus recording WDPT values of less than 5 s (Figure 4).

4 | DISCUSSION

Results of this study have shown that species richness and diversity is high under canopy compared to outside canopy of all the three nurse plant species in the old field sites. This shows a positive effect of *V. nilotica*, *P. africanum* and *S. nigrescens* nurse plants on the measured vegetation and soil parameters. These results concur with several studies that have shown that the presence of nurse plants especially trees and shrubs in areas targeted for ecological restoration facilitate the establishment of understory vegetation (Castro et al., 2004; Reis et al., 2010; Rens et al., 2008; Siles et al., 2008). Several studies have already confirmed that nurse plants (mainly trees and shrubs) affect underneath environment through light penetration, shading, rainfall interception, quality and quantity of litter which is linked to improved soil fertility and structure (Buba, 2015; Rens et al., 2008; Sharma & Sharma, 2013). However, the nature of understory vegetation is also affected by tree type, leaf area and size, canopy architecture and root systems of the nursing tree or shrub species (Buba, 2015; Ludwig, de Kroon, Berendse, & Prins, 2004).

In this study, all the nurse plants were found to positively affect species richness and diversity of all growth forms under the canopy in comparison to outside the canopy, although grasses had higher numbers outside the tree canopy in old fields. This contradicts the notion that mostly herbaceous and grass species tend to dominate underneath tree canopy, this linked to the theory of increased soil nitrogen which promotes dominance of a few fast-growing nitrogen acquiring species (Bengtson, Falkengren-Grerup, & Bengtsson, 2006; Vockenhuber et al., 2011). Therefore, the reported influence of the nurse plants on all growth forms, especially under *V. nilotica*, could be an indication that the recovery process is trajecting towards the intermediate natural succession stage (Reis et al., 2010). Reis et al.

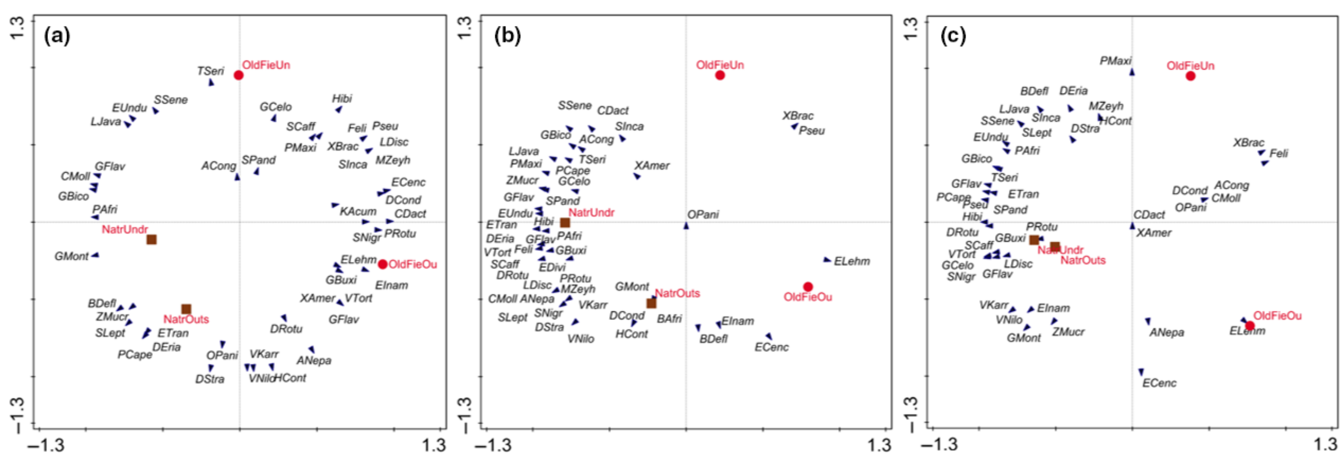

FIGURE 2 Principal component analysis (PCA) bi-plots of measured species (►) from the sites (● = old field sites and ■ = natural sites) for the three selected nurse plants of (a) *Vachellia nilotica*, (b) *Peltophorum africanum* and (c) *Senegalia nigrescens*. The first letter of the genera name and the four letters of the species names are presented with full names in Appendix

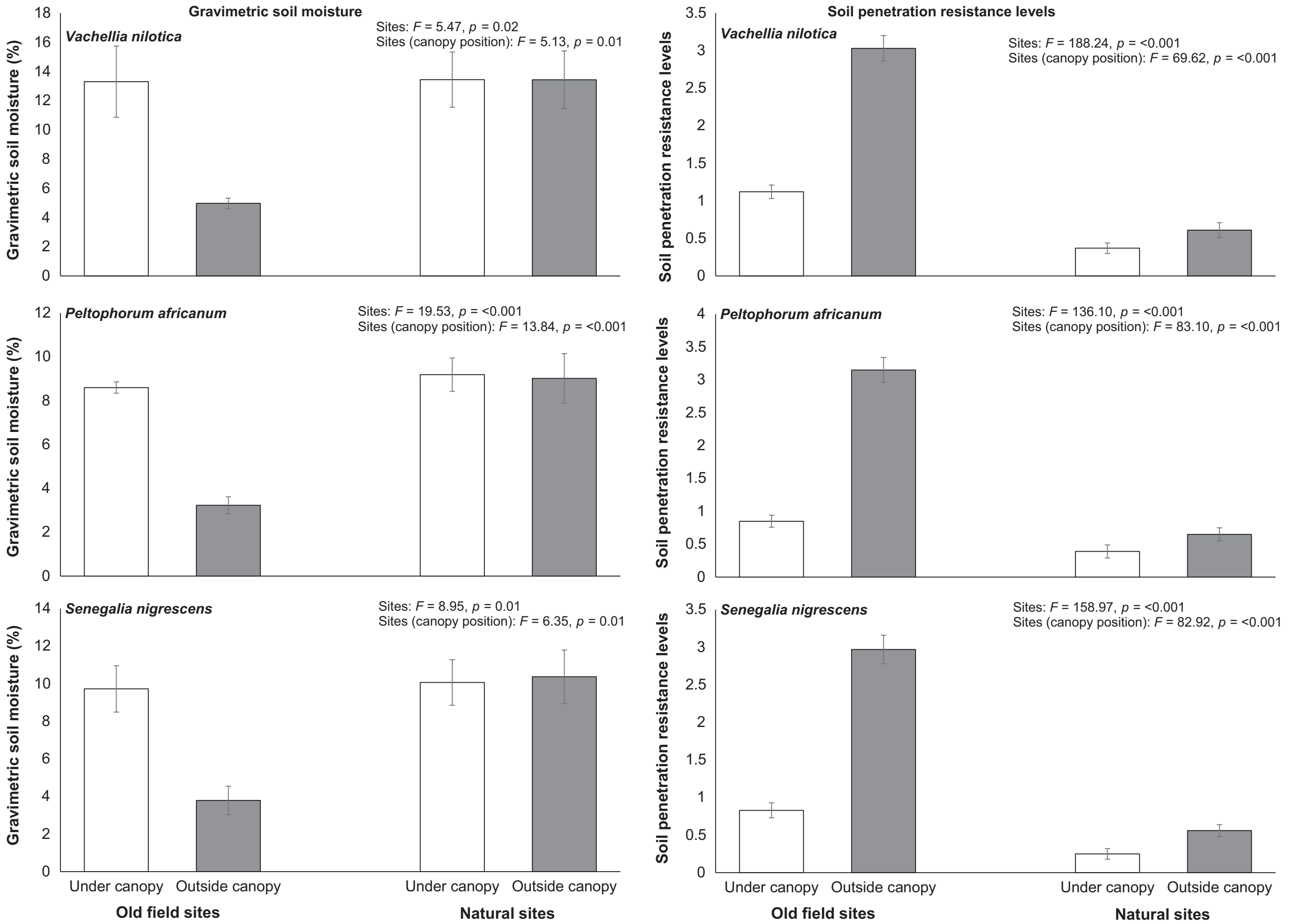

FIGURE 3 Gravimetric soil moisture and soil penetration resistance levels from old field sites and natural sites for the three selected nurse plants. Bars are means ± *SE* and nested ANOVA results are shown

(2010) indicated that the intermediate natural successional stage is characterized by the presence of all growth forms under plant canopy of nurse or pioneer species.

Measured soil physical properties showed varied results between canopy positions for all the nurse plants, thus improved soil moisture content and soil penetration resistance levels, but no differences in soil water repellency. Previous studies have shown that tree canopy cover facilitates a reduction in soil temperature, this mostly due to shading (Emmerich & Verdugo, 2008; Liu et al., 2014). Also, higher soil moisture content underneath tree canopies than in open areas has been reported in the savannah (Treydte, Looringh van Beeck, Ludwig, & Heitkönig, 2008). The higher soil moisture content underneath tree canopy is generally caused by reduced soil evaporation and plant transpiration. The above-mentioned moist soils underneath tree canopy can facilitate organic matter decomposition which is known to be faster under moist soils compared to dry soils (Classen et al., 2015). This will make soils underneath plant canopy more fertile than soils in open areas thus creating under canopy tree microclimates that facilitate plant germination and growth. The fact that soils underneath nurse plants in old field sites are less compact further facilitates the germination of plants under the tree canopy as compared to compact soils in open areas. Indeed, studies have shown that less compact soils facilitate seed germination compared to compact soils that negatively affect germination (Skinner, Lunt, Spooner, & McIntyre, 2009). This is because compaction is associated with increasing soil strength, soil bulk density, soil water tension and decreased porosity and infiltration (Bassett, Simcock, & Mitchell, 2005; Skinner et al., 2009).

4.1 | Implications of nurse plant for ecological restoration at Lapalala Wilderness

The beneficial effect of the nurse trees on species richness and diversity, presumably linked to improved soil physical properties, e.g. measured soil moisture content and compaction, has the potential to facilitate ecological restoration in degraded Lapalala Wilderness old fields. This is supported by the fact that plant species, especially the presences of trees and shrubs underneath the tree canopies in old field sites, were similar to those under and outside plant canopies in natural sites. Several ecological restoration studies have shown that nurse and pioneer plants have the potential to facilitate vegetation recovery in degraded ecosystems (Castro et al., 2004; Padilla &

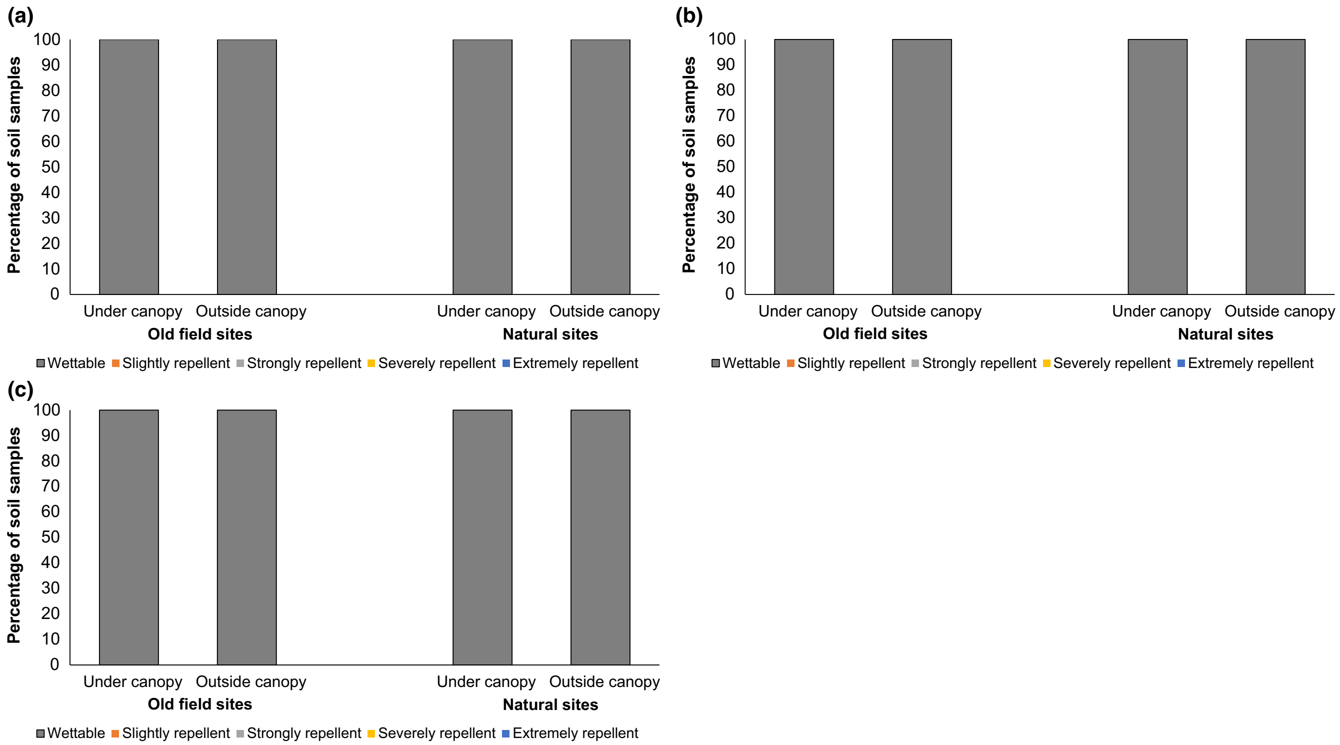

FIGURE 4 Distribution of water repellency classes (based on the Water Droplet Penetration Time (WDPT) method) in soil samples taken from old field sites and adjacent natural sites for the three selected nurse plants of (a) *Vachellia nilotica*, (b) *Peltophorum africanum* and (c) *Senegalia nigrescens*

Pugnaire, 2006; Raf, 2006; Rens et al., 2008). Studies on natural vegetation have shown a positive association between species recovery and the presences of woody nurse plants (Castro et al., 2004; Garci′a, Zamora, Hódar, Gómez, & Castro, 2000). Besides, the protection offered by nurse plants on native plants seedlings by creating suitable microclimates underneath the plant canopy, nurse plants also facilitate diaspora dispersal by frugivorous bird (Heelemann et al., 2012; Pausas et al., 2004).

Given the results of this study, restoration initiatives at Lapalala Wilderness should consider protecting nurse plants by fencing them to avoid animal grazing, given that the old fields are being used for grazing purposes. Previous studies have suggested that if nurse plants are not protected only unpalatable plants will survive underneath the plant canopy (Simons & Allsopp, 2007). Indeed, Brooker and Callaghan (1998) and Castro et al. (2004) confirmed that although nurse plants provide protection against herbivore pressure, they also facilitate ecological restoration to start from unpalatable plants. However, the dominance of unpalatable plants under nurse plants may trigger bush encroachment, where a few species dominate old field restoration (Radloff, Mucina, & Snyman, 2014; Simons & Allsopp, 2007). Therefore, from a restoration point of view, thinning of some dominant and/or encroaching plants underneath the canopy of nurse plants should be considered. Secondly, restoration initiatives at Lapalala Wilderness should consider active restoration through seeding or seedling sowing of native plants underneath the nurse plants. Studies that have actively introduced native plants underneath the canopy of nurse plants have shown that introduced species survive and grow better underneath the canopy of nurse plants than in open areas (Castro et al., 2004).

5 | CONCLUSIONS

All the nurse plants in the old field sites had greatly increased species richness and diversity underneath their canopy compared to outside the canopy. Similarly, the study showed that measured soil physical properties beneath the nurse plants in the old field sites are improving compared to the areas outside the canopy. The presence of native species of all growth forms underneath all nurse plants in the old field sites is an indication that these nurse plants play a key role in vegetation recovery. Therefore, the study concludes that these nurse plants have the potential to drive ecological succession by creating suitable seed germination and seedling establishment microclimates underneath the plants (Rens et al., 2008). The successful utilization of nurse plants in Lapalala Wilderness old fields, though seeding and seedling sowing underneath them as well as protecting them from animal browsing, has the potential to accelerate vegetation recovery.

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