Forest and woodland expansion into forestry plantations informs screening for native agroforestry species, Maputaland South Africa

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Abstract

Expansion of natural forest or woodland in forestry plantations can potentially provide insight about the behaviour of plant communities in human-modified ecosystems. Here, we investigate the expansion of native woody vegetation into abandoned areas within timber plantations, whereby management decisions (and consequently different conditions of land abandonment) had led to variation in vegetation composition and structure. These differences were assessed to identify native species suitable for agroforestry systems within forestry plantations. Elements of sub-tropical dry forest (the reference forest) had expanded into (i) clear-felled and then abandoned plantations, and (ii) unharvested abandoned plantations. Two-way indicator species analysis, Non-metric multidimensional scaling, and Indicator species analysis were used to describe compositional intergradation between natural forest and secondary vegetation, and to assess correlation with environmental variables of fire and stand structure. Areas of vegetation expansion contained 53 native woody species from 26 families, about half the number sampled in the reference forest. The understory composition of unharvested plantation sites closely resembled regrowth forest, whereas clear-felled plantations had developed a species composition resembling woodland, comprising savanna species. Substantial intergradation among compositions of woodland, plantations and regrowth forest implied that regrowth forest was a likely propagule source for native species, but that past plantation management practices acted as an environmental filter resulting in slightly different vegetation types. Useful woody species S*clerocarya birrea*, *Vangueria infausta*, *Trichilia emetica*, *Strychnos spinosa*, *Annona senegalensis*, and *Hyphaene coriaceae* were considered ecologically suitable for testing in silvo-pasture agroforestry systems owing to their occurrence in disturbed, open-canopy, fire-exposed environments (see also the graphical abstract in the supplemental files).

1. Introduction

Many native South-African trees are well suited to agroforestry systems on account of their use value (Van Wyk 2011; Vermaak et al. 2011) and because of their capacity to tolerate environmental disturbances (Geldenhuys 1994; Mucina et al. 2006). Their ecological attributes of adaptation to fire (Charles-Dominique et al. 2017), herbivory (Nzunda et al. 2007), and low light conditions (Rolo et al. 2016), render forest species useful where there is a need to diversify ecosystem services in land-use, such as forestry plantations (Silva et al. 2019). Different agroforestry practices can be used in forestry plantations to enrich ecosystem goods and services (Nair 2007; Baral et al. 2016). These include preserving natural or modified natural forests (Wiersum 2004), developing semi-natural mixed-species systems (Geldenhuys et al. 2017), or planted systems (Leakey and van Damme 2014) which may supply browsing resources for silvo-pastures (Cubbage et al. 2012), managing trees for timber products (Syampungani et al. 2015) or non-timber forest products (Shackleton et al. 2018). Ideal species include those which underpin forest recovery or expansion owing to their ease of establishment, or those species which function as ecological or biocultural keystone species thereby contributing towards multiple uses and services (Leakey and van Damme 2014; Shackleton et al. 2018).

The spatial distribution of native trees in the South African landscape is widespread; however, most natural forests are embedded within fire-exposed grasslands or savannas and therefore occupy a relatively small proportion of total land area. Fires confine forests to refugia to prevailing wind

patterns (Geldenhuys 1994). In dissected or mountainous landscapes, forests persist in fire shadow areas (often cool moist slopes or riparian areas) that afford almost complete protection (Geldenhuys 1994). In areas with less topographic variation, such as coastal plains, forests persist in similar but less conspicuous locations. Along the coastal plain, forests occur as a narrow belt or as patches within a matrix of fire-exposed grassland, wetlands or agriculture (Mucina et al. 2006), indicating that many species typical to forest-grassland ecotones are likely fire-tolerant to some extent (van Wyk et al. 1996).

Forest ecotone communities are the interface between least-disturbed forest interiors and typically disturbed fire-exposed communities. They contain fast-growing, rapidly regenerating species that, in response to fire-suppression, naturally encroach into nearby grassland (Geldenhuys 1994; O'Connor et al. 2014). Following fire exclusion, a forest can rapidly increase surface area at the expense of adjacent grassland, by up to 6 % per annum when receiving about 1000 mm of precipitation per annum (O'Connor et al. 2014). Forest expansion can also occur in human-modified environments which are fire-suppressed such as in timber plantations or alien plant stands (Geldenhuys 1997, 2017).

The distribution of a native species in natural or semi-natural environments can provide insight into its ecological preferences that can be used to screen its suitability for use within agroforestry systems. Species associated with grassland or savanna are expected to suit silvo-pasture agroforestry systems because they tolerate both fire (Charles-Dominique et al. 2017) and herbivory (Nzunda et al. 2007). However, species-specific ecological information is sparse, especially for less common but potentially useful species (Shackleton et al. 2018). Such information can be gathered through classification and gradient studies (Von Maltitz et al. 1996) restoration experiments (Rolo et al.

2017), study of functional traits (Charles-Dominique et al. 2017), or by investigating growth of native species in human-modified environments (O'Connor and Kuyler 2009).

In human-modified environments, the pool of native species is expected to be filtered because many - species would not tolerate the altered disturbance regimes of these environments (Martínez-Ramos et al. 2016). Species that initially colonise a modified environment are influenced by the composition of, and distance to, a source natural forest and the availability of seed dispersal agents (Geldenhuys et al. 2017). Following colonisation of a new site, individual survival may be affected by factors such as herbivore abundance, competition for light (Rolo et al. 2016), fire exposure (Charles-Dominique et al. 2017) and human activities. In abandoned timber plantations, different management regimes are expected to affect the composition and structure of colonising native species. We expect to find trees tolerant of fire (i.e., savanna species) in grassy fire-exposed abandoned clear-felled sites, whereas within the understory of abandoned unharvested plantation stands we expect to find shade-tolerant forest species. In this way, management decisions manifest as anthropogenic environmental filters, which would affect the composition of expanding woody vegetation.

This study aimed to determine whether the secondary vegetation that had established on abandoned clear-felled plantation areas or within non-felled abandoned plantation stands represented forest or woodland expansion and whether the establishing species were ecologically suitable for inclusion into systems of agroforestry that could enhance the ecosystem goods and services of forestry plantations.

We predicted forest species would be dominant colonists of abandoned, unharvested plantations owing to shading and fire-exclusion, whereas clear-felled plantations would have been colonised by fire-tolerant, forest ecotone, and savanna species. In all, a compositional gradient was expected from

natural forest, through to regrowth forest, abandoned plantations and abandoned clear-felled plantations. Furthermore, on account of environmental differences, it was predicted that each of these four environments would support a distinct composition of species. Vegetation structure was expected to change along a gradient from forest to woodland. The main questions were therefore whether (i) the composition of secondary vegetation correspond with the composition of naturally occurring forest and if so, was this consistent with a forest successional process? (ii) Had the type of plantation abandonment influenced the composition of natural forest expansion? (iii) Did the correspondence of species occurrence and environmental conditions provide a means for selecting tree species for different systems of agroforestry?

2. Materials and methods

2.1 Site description

Manzengwenya plantation (27°12'S, 32°43'E; Fig 1a) was established in the 1950s replacing mostly grassland and seasonal wetlands which are a dominant component of Indian Ocean Coastal Belt vegetation of South Africa (Mucina et al. 2006). The plantation, located on a sub-tropical coastal plain (45 – 90 m above mean sea level), experiences a mean annual precipitation of 964 mm and a mean annual temperature of 21°C (Mucina et al. 2006). Soils are leached, acidic aeolian sands with little clay and carbon, but this varies from dystric regosols on dune crests to humic gleysols in dune slacks and depressions (Everson et al. 2019). The plantation, approximately 15,000 ha, has supported at least two rotations of *Pinus elliottii* and two rotations of *Eucalyptus* sp. for the purpose of industrial timber and pulp products. However, a series of natural disturbances including fire, drought, and floods, from the late 1990s onward damaged many plantation compartments. Some compartments were clear-felled and then abandoned, after which an open canopy tree community developed through succession (hereafter termed 'Woodland'). Other compartments were abandoned leaving plantation trees standing (hereafter termed 'Plantation'). Native vegetation in these areas signified a natural expansion of species into former grassland areas, not regeneration of woody

species in prior forested areas (Chazdon et al. 2016). Also present were mature natural forest (hereafter termed 'Natural forest') and patches of natural forest regrowth (hereafter termed 'Regrowth Forest') on former areas of traditional swidden agriculture (Everson et al. 2019) pre-dating establishment of the plantation.

2.2 Sampling approach

The study area was initially stratified into (i) Natural forest, containing potentially mature and regrowth forest, (ii) Plantations, and (iii) Woodland. Natural forest was defined as having a closed canopy (>80% tree cover) (Staver et al. 2011), no historical evidence of plantation activity (e.g., stumps), and located within the boundary of natural forest or woodland that existed prior to plantations as determined from geo-referenced aerial photographs captured in 1947 (Everson et al. 2019). Composition of natural forest patches was sampled along transects aligned perpendicularly to the forest edge using a sequence of plots (Fig 1b) that was considered to represent a forest chronosequence from the oldest, least disturbed parts of the forest through to the youngest stands at the forest edge (van Wyk et al. 1996). Plantation or woodland plots, collectively termed 'secondary vegetation', were aligned parallel to the reference forest with the centre of the plot being 15 m – 30 m from the forest edge in order to minimise any effect of spatially related gradients (Geldenhuys 1997) (Fig 1c). Botanical nomenclature follows Boon (2010).

Forest (60 plots in 15 transects), plantation (30 plots in two transects) and woodland (26 plots in two transects) were sampled at an average of 150 m intervals covering a distance of 11 000 m. Nested circular plots sampled tree regeneration. The radius of the main plot was 11.3 m (400 m^2), and the inner sub-plot 5.65 m (100 m^2). All trees ≥5 cm stem diameter at breast height (DBH at 1.3 m above ground level) were recorded by species and stem DBH in the main plot. Tree regeneration, termed 'saplings', was defined as woody plants with stems 1-4.9 cm DBH, and recorded by stem counts per

species within the sub-plot. In the main plot, multiple stems were recorded for trees ≥5cm DBH; and recorded by stem count in the sub-plot. Height of tree regeneration was ignored because it was affected by fire. The average height of the vegetation canopy within each plot was estimated using a hypsometer for trees >5 m high, or otherwise a measuring pole was used. Percentage canopy cover was estimated using an ordinal scale: 1 = 0-5; 2 = 5-25; 3 = 25-50; 4 = 50-75; 5 = 75-95; 6 = 95-100 % (Daubenmire and Daubenmire 1968). Variation in slope, aspect, and soils was judged to be minimal within the sampling areas (van Wyk et al. 1996; Everson et al. 2019) and was therefore not considered.

2.3 Environmental co-variates

The recent historical evidence for fire was estimated for each woodland and plantation transect by inspecting Landsat ™ imagery for burn scars between 1995 and 2015. Plots in each transect were assumed to have the same burning history. Burn scars were identified in true-colour by identifying changes in non-vegetated areas (dark hue pixels) to vegetation recovery (green pixels) after fire events in Landsat™ Quickview and geo-referenced images to show plot positions (Verlinden and Laamanen 2006). Validation of this process was conducted using maximum likelihood classification in ESRI (2011). Fire-return intervals in woodland or plantation were calculated as: $RI = (Y/T_1) + (Y/T_2)/2$, where RI was the estimated fire-return interval, T = number of burn scars per transect, Y = observed number of years.

An index of light interception was provided by an estimate of Leaf Area Index (LAI) taken using a LICOR LAI-2200 plant canopy analyser during mid-summer. The estimate of LAI was intended to represent the closest average value of each transect rather than provide a measure for each plot. For each of the two woodland and two plantation transects, 60 points were collected. Points were an average of five readings (1.3 m in height) taken at 20 m intervals in a horizontal line along each
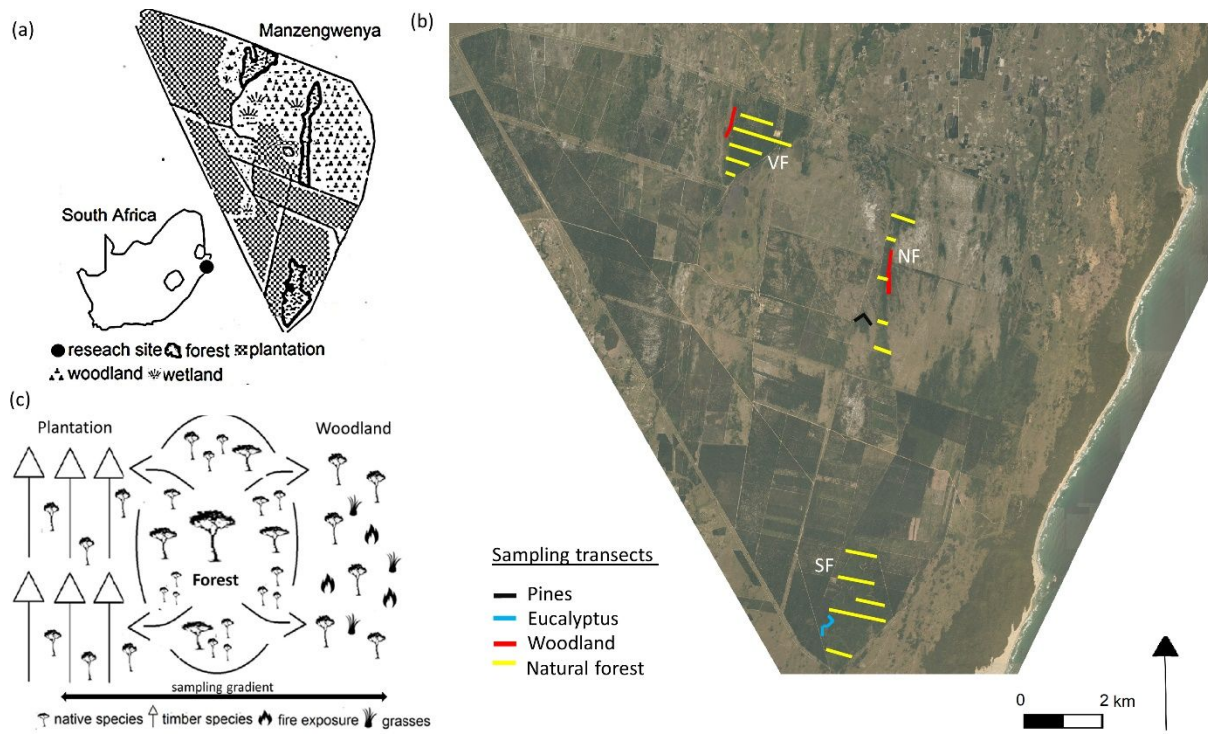
Fig 1. (a) Location of the study site and general layout of Manzengwenya plantation (b) Plot locations, illustrating how transects were orientated in relation to forest patches (VF =Vasi forest, NF = Northern forest, SF = Southern forest) and expansion sites. (c) A diagram showing the sampling layout in relation to the perceived pattern of forest expansion into fire-exposed secondary woodlands and shaded plantations.

transect. LAI of woodland or plantation was calculated as: $LAI = (\bar{x}T_1) + (\bar{x}T_2)/2$,where $\bar{x}$ was the mean LAI of five records, and T was the mean of LAI readings in each transect.

2.3 Statistical analysis

Gradients of understory vegetation composition and canopy structure were examined using classification and ordination techniques. These multivariate exercises were conducted using sapling data because this size class excluded most plantation trees, thereby allowing a direct comparison among vegetation types (Geldenhuys, 1997).

Two Way Indicator Species Analysis (TWINSPAN), a polythetic divisive technique, was expected to separate mature forest and regrowth forest from plantation and woodland plots by the first division. In other words, forest plots which grouped with woodland or plantation plots were logically related to disturbance and classified as regrowth forest. Forest plots not associated with secondary vegetation were classified as mature forest. TWINSPAN has been criticised because groupings are strongly influenced by the first axis being derived by correspondence analysis (McCune and Mefford 2018) but a preliminary ordination revealed plots were strongly ordered along a single axis. Composition of a plot for the input matrix was described by the number of stems per hectare. Default cut levels of 0, 0.02, 0.05, 0.1, and 0.2, as provided by Community Analysis Package, were used in the analysis (Seaby and Henderson 2007).

Vegetation structure was assessed using both canopy and understory data. Variables compared were stem density (ha^{-1}), basal area ($m^2\,ha^{-1}$), mean DBH (cm), canopy height (h) and canopy-cover (%). Comparisons across the four vegetation groupings were undertaken using Welch's ANOVA, with

means compared using Tukey's test. Stem class distributions (at increments of 5cm DBH;

Geldenhuys and Murray 1993) were compared among vegetation types using a Kruskal-Wallis test

and individually assessed using Dunn's post-hoc test. Comparisons were undertaken using the Real

Statistics package (Zaiontz 2016).

Indicator Species Analysis (ISA) provides a combined measure of species abundance and fidelity,

termed 'indicator value' (IV) to a vegetation type (Dufrene and Legendre 1997). ISA assessed the

ecological suitability of species to environmental conditions. Comparisons of canopy (basal area m^2

ha^{-1}) and understory (stems ha^{-1}) indicator species provided insight into recruitment and successional

patterns across the four vegetation types. Only species with indicator values larger than expected by

chance ($p<0.05$) were analysed.

Non-metric Multidimensional Scaling (NMS), an indirect gradient analysis technique, was applied to

describe the dominant compositional gradients in the sapling data across the four vegetation types

and to assess the strength of covariation with environmental (RI) and canopy structural variables

(mean DBH, stems ha^{-1}, basal area m^2 ha^{-1}) of plots. A strength of NMS is that by maximizing rank

order correlation, it makes few assumptions about the distribution of data (McCune and Mefford

2018). Predictions were that a gradient of forest succession would be best explained by the axis

which correlated positively with canopy structural variables and negatively with the fire-return

interval (RI). The RI for woodland or plantations plots was the mean value for each transect. The

ordination was conducted using stem density, the Bray-Curtis distance, at 250 iterations. Both ISA

and NMS were conducted using PCord ver7 (McCune and Mefford 2018).

3.Results

3.1 Environmental covariates

Woodlands experienced a shorter fire return interval, estimated at 2.8 – 6.6 years, than plantations, estimated at 6.8 – 8.4 years. LAI was on average less in woodlands, ranging between 0.42 – 1.44, than in plantations, which was estimated to range between 1.32 – 3.12.

3.2 Classification

The first division of TWINSPAN was successful in separating mature forest from other vegetation types that included woodland, abandoned plantations, and approximately half the natural forest (Fig 2). These forest plots were classed as 'regrowth forest' as they were associated with plots of recently known disturbance history. The mature forest represented a composition of species distinct from recent disturbance and contained known mature forest understory species (for example, *Isoglossa woodii* – Acanthaceae).

3.3 Vegetation structure

Overall, mature forest had the most developed structure, having the largest basal area and mean DBH (Table 1). Regrowth forest had the greatest stem density but was slightly less developed than mature forest, though more developed than plantations or woodland: regrowth forest showed a lower average DBH than mature forest which was consistent with forest undergoing recovery from historical cultivation; native species contributed towards 97 % of basal area in woodland but only 14 % in plantations which comprised either Pine or Eucalyptus species in the canopy; canopy cover of about a fifth of woodland plots was equal to regrowth forest indicating potential for structural

Manzengwenya Plantation (116 plots)

Eigenvalue = 0.39

Secondary vegetation and Regrowth Forest
No of plots = 87
Plot composition: Woodland 30 %
Plantation 26 %
Forest 31 %

Indicator species: *Sclerocroton integerrimus*
Dichrostachys cinerea

Mature Forest
No of plots = 29
Composition: Forest 97 %
Plantation 3%

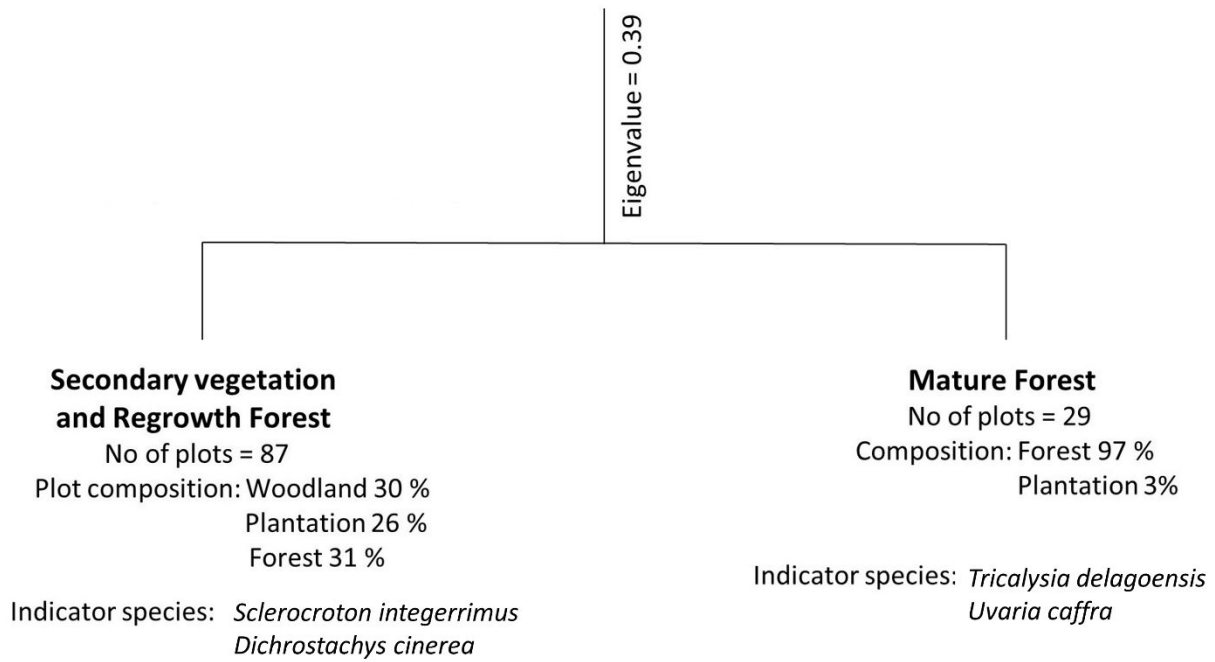Indicator species: *Tricalysia delagoensis*
Uvaria caffra

Fig 2. TWINSPAN dendrogram showing secondary vegetation and regrowth forest plots on the left-side of the first division, with mature forest plots and a single plantation plot on the right-side of the division. TWINSPAN indicator species are presented below group names.

Table 1. Means and standard deviations by vegetation unit of canopy structural variables

Variable	Mature Forest ($n = 28$)		Regrowth Forest ($n = 32$		Plantation[1] ($n= 30$)		Woodland ($n=26$)		Welch's ANOVA[2]
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	F
Diameter at breast height (cm)	11.9$_a$	3.6	8.1$_b$	1.8	7.6$_b$	2.1	6.4$_c$	1.2	21.3
Canopy density (stems ha^{-1})	1108$_a$	572	1525$_b$	551	732$_c$	709	401$_d$	183	46.3
Canopy basal area (m^2 ha^{-1})	29.1$_a$	18.1	24.9$_a$	16.3	8.1$_b$	9.1	3.2$_b$	2.1	35.8
Canopy height (m)	8.2$_a$	1.7	6.2$_b$	1.9	10.9$_c$	2.1	3.7$_d$	0.5	144.6
Canopy cover (%)	88$_{ab}$	11	81$_a$	11	95$_b$	6	60$_c$	10	47.8
Sapling density (stems ha^{-1})	5221	3409	3961	3585	3457	2323	3493	1583	3.5

[1]Plantation structural variables of DBH, density and basal areas refers to native species and excludes pine and eucalyptus timber species
[2]All *F tests* were significant ($P \leq .05$). Significant differences among means within a row are indicated by different subscripts (Tukey's post hoc comparisons with $P \leq .05$).

transition from woodland to regrowth forest. Mature forest had the greatest mean understory stem density followed by regrowth forest, woodland, and then plantation. The coefficient of variation was high, implying considerable structural variation among understory stems across the four vegetation types.

Distribution of DBH classes tended to follow a negatively skewed distribution, with the major contributing stem sizes below 15 cm DBH (Fig 3). Mature forest had the greatest range of stem sizes, with approximately five percent of stems being larger than 60 cm DBH. Regrowth forest had a slightly larger range than plantations. No stems greater than 30cm DBH were recorded in woodland. A Kruskal-Wallis test showed a significant difference in the distribution of stem classes across all vegetation types (h = 9.8, *df* = 3, p = 0.02). Post hoc tests revealed mature forest, and woodland differed individually (p = 0.005). Of the common species in the dataset, only *Sclerocarya birrea* (Anacardiaceae) growing in woodland did not follow the predominately negatively skewed stem class distribution (see Appendix 1 in the supplemental files).

3.4 Indicator Species Analysis (ISA)

Indicator species analysis highlighted key species associated with each vegetation type and provided insight into patterns of recruitment relating to forest succession. Mature and regrowth forest had more than twice the number of indicator species of woodland or plantation (Table 2) which reflected that natural forest had a greater richness of species than secondary vegetation. *Hymenocardia ulmoides* was the most abundant canopy species in mature forest. Though slower growing, canopy
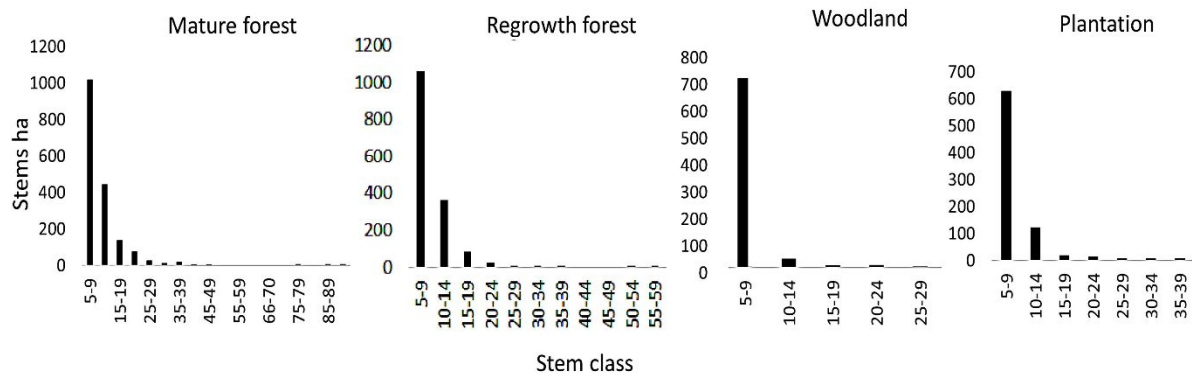
Fig 3. Size class distributions of the four vegetation types with bars indicating the density of stems per five cm diameter (DBH) class.

species such as *Manilkara discolor* (Sapotaceae) and *Strychnos gerardii* (Strychnaceae) were also considered important components in the mature forest canopy. Fast growing, pioneer species in the mature forest, *Brachylaena discolor* (Asteraceae) and *Apodytes dimidiata* (Icacinaceae), reflected vegetation recovery. Three species *Teclea gerardii* (Rutaceae), *Celtis africana* (Celtidaceae) and *Clausena anisata* (Rutaceae) highlighted ongoing canopy recruitment in mature forest. In regrowth forest, *Sclerocroton integerrimus* (Euphorbiaceae) had considerably greater IV in the canopy than most other regrowth indicator species. *Canthium inerme* (Rubiaceae) showed a pattern of recruitment within regrowth forest. Three species, *Albizia adianthifolia* (Fabaceae), *Zanthoxylum capense* (Rutaceae) and *Dalbergia obovata* (Fabaceae) indicated recruitment in regrowth forest with a probable transition to the canopy of mature forest.

Indicators for woodland were all savanna species, thereby demonstrating the ecological distinctness of this vegetation type. *Sclerocarya birrea* was the only canopy indicator. The sapling-sized species tended to consist of small trees or shrubs including *Dichrostachys cinerea* (Fabaceae) and *Vangueria infausta* (Rubiaceae). Recruitment of *Phoenix reclinata* (Arecaceae) in woodland suggests this vegetation type may be undergoing transition to regrowth forest. Plantation areas contained only a single indicator species indicating the pool of species occurring in shaded understory conditions was shared with woodland and regrowth (Table 2).

3.5 Indirect gradient analysis

A three-dimensional NMS solution revealed the least stress in the data (stress = 19.1, p = 0.05). The first axis explained 31 percent of compositional variation, while the second and third axis explained 18 and 13 percent respectively. On the first axis, vegetation centroids aligned linearly, whereby the

Table 2. Indicator species analysis of the canopy and understory components across vegetation types

Species	Canopy IV	Understory IV	Species	Canopy IV	Understory IV
Mature forest			**Regrowth forest**		
Hymenocardia ulmoides	46.9		*Sclerocroton integerrimus*	51.8	
Brachylaena discolor	41.6		***Canthium inerme[2]***	30.6	20.9
Apodytes dimidiata	39.5		*Psydrax locuples*	27.9	
Albizia adianthifolia[3]	37.6		***Phoenix reclinata[5]***	20.6	
Trichilia emetica	34.2		***Tricalysia delagoensis[4]***	14.5	
Clausena anisata[1]	32.8	41.4	***Dalbergia obovata[3]***		36.9
Zanthoxylum capense[3]	30.1		***Albizia adianthifolia[3]***		20.1
Dalbergia obovata[3]	27.4		*Ochna natalitia*		15.3
Celtis africana[1]	21.4	14.3	***Zanthoxylum capense[3]***		18.3
Schrebera alata	16		**Plantation**		
Manilkara discolor	14.3		*Canthium setosum*		10
Strychnos gerardii	14.3		**Woodland**		
Mimusops obovata	13.1		*Sclerocarya birrea*	24.1	
Suregada zanzibarica	11		***Phoenix reclinata[5]***		28.8
Teclea gerardii[1]	10.7	13.4	*Dichrostachys cinerea*		36.3
Tricalysia delagoensis[4]		40.7	*Vangueria infausta*		16.7
Grewia caffra		28.4	*Strychnos spinosa*		16
Monanthotaxis caffra		26.9	*Strychnos madagascarensis*		11.2
Xylotheca caffra		25.3	*Commiphora zanzibarica*		10
Peddiea africana		25			
Psydrax obovata		15.3			
Isoglossa woodii		14.3			
Acacia krauseana		11.9			

* Species in bold indicated correspondence with more than one vegetation type or size class, subscripts refer to the ecological interpretation of co-occurrence.

[1] Mature forest canopy species with recruitment in mature forest
[2] Regrowth forest canopy species with recruitment in regrowth forest
[3] Mature forest canopy species with recruitment in regrowth forest
[4] Mature forest understory species but canopy species in regrowth forest
[5] Regrowth forest canopy species with recruitment in woodland

overlapping ellipses of woodland, plantation, and regrowth forest illustrated the extent of compositional intergradation (Fig 4). The position of mature forest on the right of the first axis showed its composition was comparatively distinct from secondary vegetation but less so from regrowth forest.

The first axis represented a gradient of understory species composition and structure from woodland vegetation through to mature forest, being positively correlated with canopy cover ($R^2 = 0.39$) and canopy basal area ($R^2 = 0.31$) but negatively correlated with RI ($R^2 = 0.39$). Mean DBH was weakly correlated with the first axis ($R^2 < 0.2$) and not shown. The NMS ordination summarised the ecological preferences of individual species (Fig 4). For example, *Dichrostachys cinerea* preferred fire-exposed, open canopy conditions, and may, therefore, serve as a precursor of forest establishment. Centrally located species showed either a slight preference towards fire-exposure (e.g., *Strychnos spinosa*) or tolerance towards canopy cover (e.g., *Albizia adianthifolia*). Species imbedded within mature forest (e.g., *Isoglossa woodii*) preferred well-structured forest and avoided fire.

4. Discussion

4.1 The response of native woody species to forestry plantations

The early successional coastal forests in Maputaland contain a pool of species typical for the region, which provide initial biological and structural conditions for development towards mature forest (van Wyk et al. 1996; Von Maltitz et al. 1996; West et al. 2000). Our findings were consistent with this
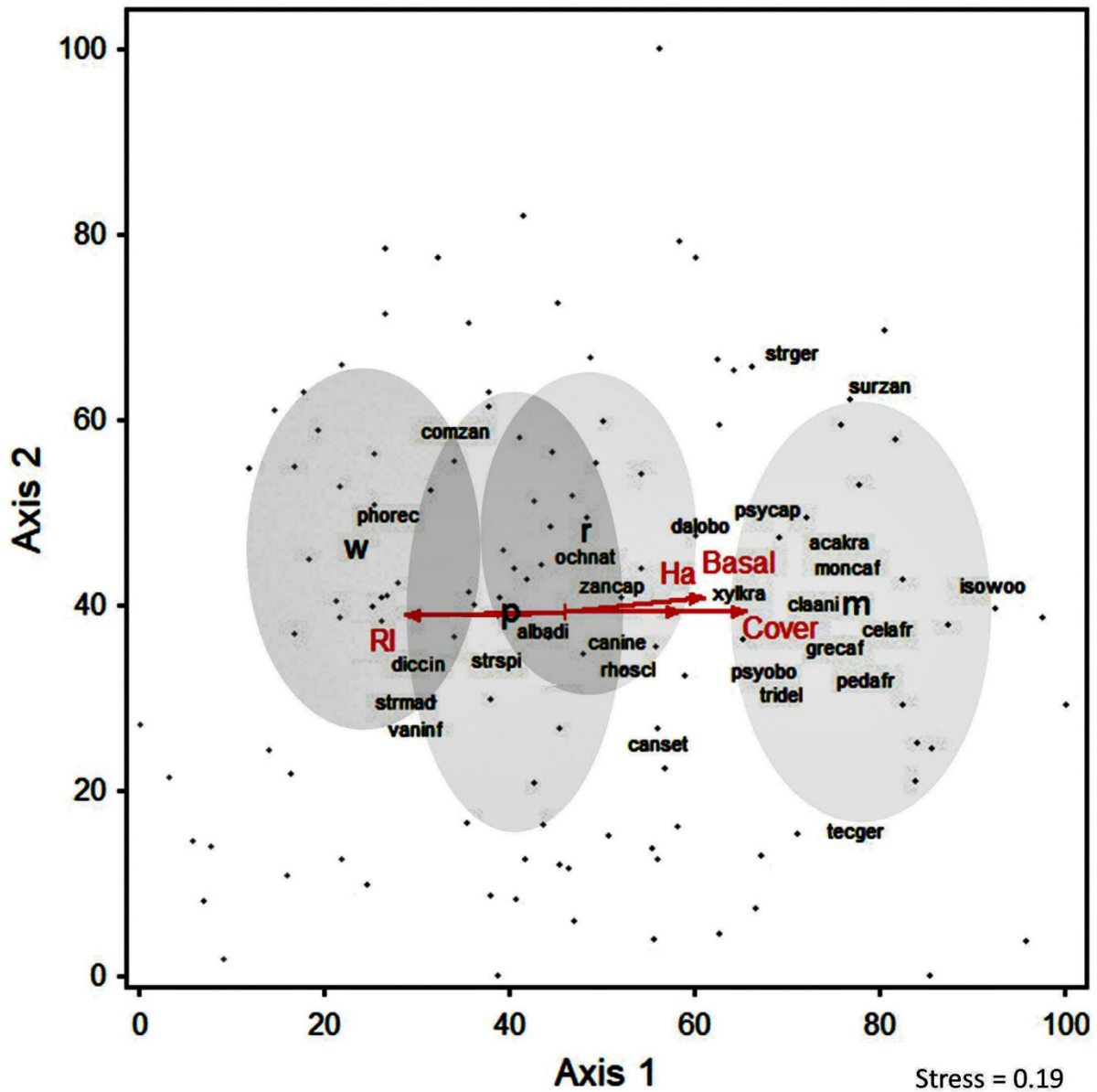
Fig 4. NMS ordination of understory vegetation showing a gradient from woodland through to mature forest along the first axis, corresponding with measured structural (Ha = stems ha^{-1}, Basal = Basal area m^2-ha^{-1}, Cover = % canopy cover) and environmental co-variables (RI = fire return interval). Black dots indicate a plot's position and the centroid of each vegetation type is marked by its first letter (w, woodland; p, plantation; r, regrowth forest; m, mature forest). Ellipsoids surrounding vegetation centroids represent the standard deviation from the mean value of the 1st and 2nd axis scores. Species with a covariance of greater than 0.3 with the first axis are indicated by initials: acakra = *Acacia kraussiana*, albadi = *Albizia adianthifolia*, canine = *Canthium inerme*, canset = *Canthium setosum*, , claani = *Clausena anisata*, comzan = *Commiphora zanzibarica*, dalobo = *Dalbergia*

obovata, diccin = *Dichrostachys cinerea*, celafr = *Celtis africana*, grecaf = *Grewia caffra*, isowoo = *Isoglossa woodii*, moncaf = *Monanthotaxis caffra*, ochnat = *Ochna natalitia*, pedafr = *Peddiea africana*, phorec = *Phoenix reclinata*, psycap = *Psychotria capensis*, psyobo = *Psydrax obovata*, rhosch = *Rhoicissus schlechteri*, strger = *Strychnos gerardii*, strmad = *Strychnos madagascarensis,* strspi = *Strychnos spinosa,* surzan = *Suregada zanzibarica*, tecger = *Teclea gerardii, Tricalysia delagoensis = tridel,* vaninf = *Vangueria infausta*, xylkra = *Xylotheca kraussiana*, zancap = *Zanthoxylum capensis*.

expectation in that, with exception of *Hymenocardia ulmoides*, most species encountered in woodland and plantations tended to be common components of secondary or regrowth forest in the region (Von Maltitz et al. 1996; West et al. 2000). Woodland, plantations and regrowth forest exhibited an intergraded linear response towards mature forest. Plantations, more so than woodlands, had facilitated the development of this process which was represented by shade-tolerant forest species with a composition analogous to early or intermediate forest development stages. Species which best described floristic transition from regrowth to mature forest were indicator species that occurred in the understory of regrowth forest but also in the canopy of mature forest. Some of these species had also influenced the composition of plantation areas (see species positions in central areas of the ordination) for example, *Albizia adianthifolia*. However, no further floristic evidence (i.e., moderately ranked mature canopy species) occurred in plantations, showing that 'core' compositional elements of mature forest had not managed yet to infiltrate the understory of plantation stands. Species dispersal can be hazardous process, though a possible reason was regrowth forest or reproductively active clusters of pioneer species in plantations were the primary propagule sources for colonising vegetation, thereby influencing the composition of plantation vegetation (Geldenhuys et al. 2017). Other reasons include plantation stand age, which was relatively young (±20 years), and that occasionally fire would have restricted fire-intolerant species. The finding reiterates the importance of conserving old-growth forest patches as refuges for species which do not regenerate or tolerate common disturbance patterns in human-modified environments (West et al. 2000; Martinez-Ramos et al. 2016).

The composition of secondary vegetation corresponded with the decision to abandon land after clear-felling or abandon plantation stands without harvesting, a decision that would have affected local environmental conditions and then influenced vegetation composition and structure. Woodland sites experienced fire return intervals comparable with savanna vegetation (Wigley et al. 2009) and it was

not surprising to find fire-tolerant savanna species such as *Strychnos spinosa*, *Sclerocarya birrea,* or *Dichrostachys cinerea* (Rutherford et al. 2006) growing in woodland. Fire-tolerance is an essential adaptation for woody species growing in South African forest-grassland mosaic ecosystems, and although precise mechanisms are yet to be fully understood, morphological traits relating to bark thickness (Charles-Dominique et al. 2017), bud development and carbohydrate storage in root organs (Wigley et al. 2009) correlate with expected species distribution patterns in fire-exposed landscapes. This pattern is expected to replicate in highly modified anthropogenic ecosystems provided they offer similar biophysical conditions to natural systems. Fire-adapted trees occurring in savanna or grasslands tend to be most abundant in fire-exposed sites, whereas shade-adapted species of forest ecotones are most abundant in shaded sites less exposed to fire (van Wyk et al. 1996; Rolo et al. 2016). This pattern explained the inverse relationship between RI and structural development on the NMS first axis. Specific plant morphological or biological traits which may have related to species distribution on this axis were not measured; however, the species centre of abundance provides a measure of ecological preference to these human-modified environments (i.e., with or without clear-felling in a forestry plantation). Each species was therefore expected to have responded individually to plantation environments in a manner determined by its adaptations to a particular set of naturally occurring environmental conditions.

4.2 Integrating agroforestry practices into forestry plantations

The main purpose of timber plantations is to supply wood products, however the ecosystem services and other resources plantations provide considerably enhance their value to a community (Brockerhoff et al. 2013; Baral. et al. 2016; Silva et al. 2019). If timber plantations are grown while supporting native plant species known to be of value to a community, then their overall value could be increased.

Different agroforestry approaches can fulfil such objectives whereby modified natural forests (Wiersum 2004), mixed alien-native species systems (Geldenhuys et al. 2017) or planted systems (Leakey and van Damme 2014) are used in conjunction with livestock as silvo-pasture (Cubbage et al. 2012) or to supply non-timber forest products (Shackleton et al. 2018). The ecological processes and composition of species underpinning secondary vegetation have the potential to guide the development of such agroforestry practices. They can do this, firstly, through the composition of different types of secondary vegetation (i.e., woodland or plantations), which are expected to correlate with different management patterns and, secondly, by highlighting the ecological preference of constituent species of each type to these conditions. Practical examples include the application of modified natural forests in the form of multi-purpose shelterbelts (Nair 2007) that supply browse or non-timber forest products, or selecting fire-tolerant multipurpose species for use in fire breaks.

On account of its structural and floristic composition, a strong case can be made for developing woodland vegetation into a silvo-pasture system. Woodland vegetation shows more conservative use of water than plantations (Everson et al. 2019), and in our study it supports at least six species with potential for commercial application (Van Wyk 2011; Vermaak et al. 2011), rendering it potentially suitable for buffer areas surrounding wetlands or other ecologically sensitive areas which are not suited to pure forestry plantations. Disturbance-resilient species are suited to open-canopy silvo-pasture conditions; examples include *Strychnos spinosa, Sclerocarya birrea, Vangueria infausta, Annona senegalensis, Trichilia emetica* and *Hyphaene coriaceae*. These species could be tested in silvo-pasture agroforestry systems that combine a low density of multi-functional trees ($\pm$ 50 – 500 stems ha^{-1}; Cubbage et al. 2012) with pasture for livestock production.

The potential of each species to provide resource or ecosystems services is examined in a companion paper (Starke et al. in prep), which in combination with ecological preference would provide a strong foundation for integration into agroforestry systems. Many species found in secondary vegetation had published plant uses. For the species in this dataset, we found 352 cited plant uses, of which 233 related to the 53 species recorded growing in secondary vegetation. Species offer a wide range of returns such as providing fruit or oil resources (Van Wyk 2011; Vermaak et al. 2011), livestock forage, improving soil conditions through N-fixing legumes (Nair, 2007), medicinal products and food products (Corrigan et al. 2011; Van Wyk 2011). These returns would be affected by vegetation composition and would have been a consequence of management pattern.

5. Conclusion

Transformation of naturally occurring grassland to forestry plantations had induced an intergraded mosaic of mixed plantation and native species vegetation, whereby management decisions had influenced the compositional response of natural forest expansion. The study highlighted the capacity of native species to respond dynamically to changes in the environment as modified by humans, firstly through the diversity of species available for forest or woodland expansion and, secondly, due to the range of environmental conditions that these species could tolerate. Although integration of native species into agricultural land-use remains a substantial practical challenge (Nair 2007; Silva et al. 2019), our results show that understanding the anthropogenic patterns behind the formation of secondary vegetation may assist with this task. In an ongoing effort to provide landscape resilience, similar land use systems would benefit by exploring how these patterns (i.e., gradients of species response to human-induced environments) align with undisturbed or modified ecosystem configurations. Management of timber plantations would benefit from input based on

vegetation ecology (Geldenhuys 1997, O'Connor and Kuyler 2009), agroforestry (Wiersum 2004; Nair, 2007) and non-timber forest products (Leakey and van Damme 2014; Shackleton et al. 2018) in order to optimise the supply of native plant resources. In light of the threat that woody expansion poses to savanna and grassland in many parts of the world (Staver et al. 2011; O'Connor et al. 2014), such insights would be appropriate for informing approaches to the restoration of disturbed agricultural lands or other restoration initiatives.

6. Acknowledgements

7. References

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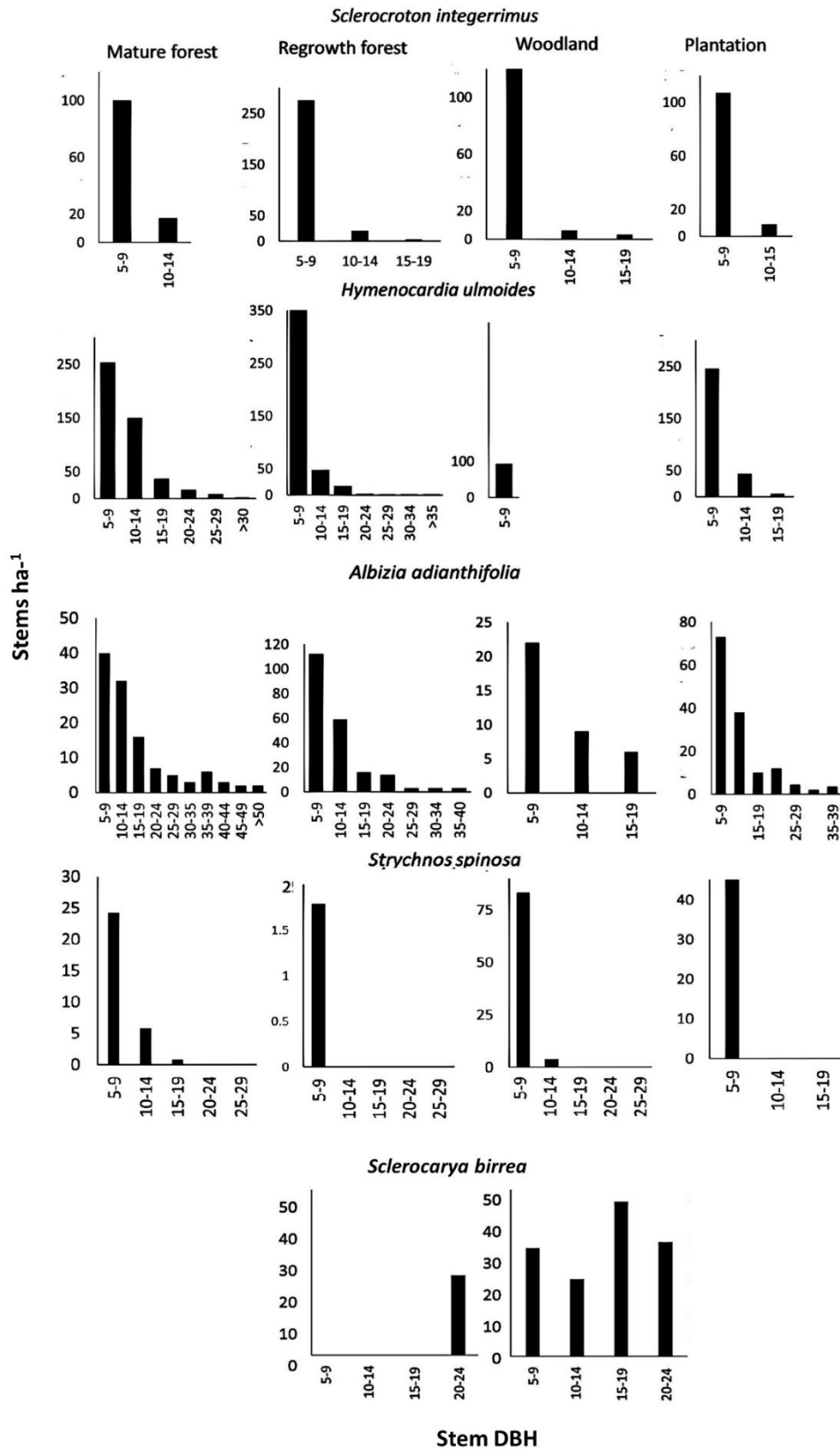
Appendix 1. Stem class distributions (at 5cm increments) of commonly occurring species across the four vegetation types.

Forest and woodland expansion into forestry plantations informs screening for native agroforestry species, Maputaland South Africa

Natural forest

Abandoned plantation

Afforested and then abandoned timber plantations underwent native species colonisation within the plantation understory

Secondary woodland

Secondary woodland developed because of clear-felling and then abandonment of forestry plantation areas

Protected areas of natural forest within a forestry plantation

stems ha ± 1615 (583)
species richness n = 92

Stems ha = ± 732 (709)
species richness n = 38
observed fire return 6.8 – 8.4y
leaf area index ± 1.32 – 3.12.

stems ha ± 401 (183)
species richness n = 37
observed fire-return ± 2.8 – 6.6y
leaf area index ± 0.42 – 1.44

Species composition in the understory of abandoned plantations was similar to natural regrowth forest

Species composition in woodland had a greater range of fire-tolerant savanna species

Forest and woodland expansion

Hymenocardia ulmoides, Albizia adianthifolia

S*clerocarya birrea, Vangueria infausta, Trichilia emetica, Strychnos spinosa, Annona senegalensis,* and *Hyphaene coriaceae*

Plantation species   Native species   Grasses   Fire