Tree growth, recruitment, and survival in a tropical dry woodland: The importance of soil and functional identity of the neighbourhood

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ABSTRACT

Understanding the processes that foster species coexistence is a longstanding goal in community ecology. Trade-offs in species performances for different ecological functions have been proposed as a general mechanism of species assemblage. The nature of these trade-offs can be revealed by analysing the demographic characteristics of species combined with their functional traits (FT) and the surrounding environment.

The respective roles of soil, stand structure, and the functional dissimilarity of the neighbourhood, to the variations of growth, recruitment, and survival were determined for 19 most frequent tree species examined at the individual level in a tropical dry woodland (miombo; Democratic Republic of the Congo).

Four functional groups can be recognised by contrasting life-history strategies and mainly related to tree stature, leaf phenology, leaf area (LA), leaf nutrient content, ectomycorrhizal status, and dispersal mode. Growth is regulated by the functional dissimilarity of the neighbourhood, local stand structure, and soil conditions. Recruitment is comparatively less impacted by functional neighbourhood but is mainly influenced by stand basal area and mean DBH as well as available calcium. At the community level, survival is mainly explained by physical and chemical soil variables and by both negative and positive effects of traits dissimilarity with the neighbourhood.

Functional dissimilarity of the neighbourhood has the greatest positive effect on growth and survival, whereas competitive hierarchy is detrimental for growth of Caesalpinioideae species in particular, and for survival to a lesser extent.

The general involvement of foliar traits and stand basal area on demographic performances indicates that competition for light is a key axis of species niche differentiation along the fast-slow continuum, even in this tropical dry woodland. Our results also pointed out a trade-off between water resources and phosphorus availability or aluminium avoidance, which separates growth strategies and leads to habitat specialisation.

Multiple trade-offs allow species coexistence, with distinct drivers for tree growth, recruitment, and survival. Combining demographic and trait-based approaches provides unique key insights to understand species coexistence mechanisms.

1. Introduction

One of the main challenges of tree community ecology is to identify the drivers of species assemblage and elucidate the mechanisms of species coexistence (HilleRisLambers et al., 2012). Deterministic assembly processes predict habitat specialisation and the presence of trade-offs promoting species coexistence (Rees et al., 2001; Kneitel and Chase, 2004). Variation of the abiotic environment is one factor allowing species coexistence at the local scale, each in its specialised habitat. But even in a near homogenous edaphic environment, species can coexist by partioning time or access to light (Barot and Gigoux, 2004), if they present differences in life history involving contrasting morphological, physiological or phenological trait values. Opposing strategies among species leading to niche complementarity can also be

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observed in their demographic characteristics: growth, recruitment, and mortality rates. As one species cannot simultaneously maximally allocate its resources to the different physiological functions and anatomical characteristics related to the different components of its fitness (i.e. growth, survival, reproduction), life history differences and demographic trade-offs can emerge (Lusk and Smith, 1998; Easdale et al., 2007; Russo et al., 2008). The growth-survival trade-off is often mentioned as a mechanism of coexistence in forest ecosystems (Sterck et al., 2006; Wright et al., 2010; Adler et al., 2014). However, examining the variation of demographic rates using a global tropical forest dataset, Condit et al. (2006) showed that the most diverse forests had the least demographic variation and that this trade-off was clearly not sufficient to explain coexistence in those ecosystems. More accurate knowledge is therefore needed to understand the interplay between species coexistence, demographic rates, and functional characteristics.

Assembly mechanisms and species coexistence are generally analysed through the lens of species abundance data (e.g., Vleminckx et al., 2015, 2017; Muledi et al., 2017). However, this approach can be inaccurate when the system is not at equilibrium or when local exclusion is not reached (Schurr et al., 2012). Moreover, the static view of species abundance in a community is unable to assess past environmental conditions or recent disturbance unequivocally (Blonder et al., 2017). Other processes like limited dispersal can also confine recruits to suboptimal habitats (Ozinga et al., 2005; Pinto and MacDougall, 2010) whereas source-sink dynamics through the mass effect induced by high rates of regional dispersal can upset local community abundances (Lasky et al., 2013). These different influences can be better detected via measures of tree growth rates and/or from recruitment and survival data which involve measurements at several time steps. Demographic rates, unlike species abundances, are direct measurements of the species fitness (Laughlin et al., 2018; Salguero-Gómez et al., 2018), and can therefore offer a more relevant insight into the drivers of the community assembly (HilleRisLambers et al., 2012; Bin et al., 2016; Salguero-Gómez et al., 2018, for a review).

Tree demographic rates (equally referred to as 'vital rates') first depend on the species' own life history strategy (Swaine et al., 1990; Lusk and Smith, 1998; Gourlet-Fleury and Houllier, 2000; Adler et al., 2014; Pausas and Keeley, 2014). Many authors have attempted to classify groups of species based on their life history characteristics (Franco and Silvertown, 1996; Adler et al., 2014; Salguero-Gómez, 2017). In forests, life history strategies can be described by the forest layer type (e.g. understorey, canopy or emergent, Rüger et al., 2018), by the successional status (e.g. pioneer, secondary, late; Swaine and Whitmore, 1988), but also by light-demanding guilds separated by different light requirements (e.g., shade tolerant, mid-tolerant, long- or short-lived light-demanding; Vleminckx et al., 2014). Other authors have chosen to separate the tree community directly based on the vital rates (Gourlet-Fleury et al., 2005; Mugasha et al., 2016), but a classification encompassing both traits and demographic performances remains a delicate task (Salguero-Gómez et al., 2018).

A fair view of the effects of life history strategies on the demographic rates of a community is provided by the analysis of functional traits (FT) (Adler et al., 2014; Salguero-Gómez, 2017). Different authors have indeed highlighted the value of functional traits related to the different components of fitness to explain and predict varying vital rates in different types of ecosystems (e.g., Poorter and Bongers, 2006; Hérault et al., 2011; Wigley et al., 2016; Laughlin et al., 2018). Indeed, the functional nature of a trait in a given environment and community assemblage can only be confirmed through the effect it has on species' fitness or its components (i.e., vital rates) (Violle et al., 2007; Laughlin et al., 2018). Moreover, the sole use of trait-environments relationships can be ambiguous and has recently been shown to sometimes poorly correlate with the functional nature of traits highlighted by their effects on vital rates (Laughlin et al., 2018). Demographic approaches of community ecology also benefit from using traits, as their combination can provide deeper insights into the mechanisms through which vital

rates are affected (Salguero-Gómez et al., 2018). In addition, combinations of certain traits have been shown to reflect different demographic trade-offs, such as the fast-slow continuum (Reich, 2014; Prado-Junior et al., 2016), the growth-survival trade-off related to reproduction strategies (Salguero-Gómez, 2017), or the 'stature-recruitment' trade-off which highlights the relationships between regeneration functional traits (e.g. seed mass, dispersal mode) and recruitment (Rüger et al., 2018).

The resulting trade-offs among demographic rates constrain the range of viable life history strategies in a given environment. Since the multi-dimensional niche of species consists of several independent axes of resources (Kneitel and Chase, 2004; Hérault et al., 2011), and because the relative importance of these axes is context-specific and often non-generalisable (HilleRisLambers et al., 2012; Wigley et al., 2016), the study of specific communities is necessary to detect and understand original combinations of functional trade-offs related to the local environmental constraints.

Soil potentially also has a large effect on demographic performances. Nutrient supply and soil water availability may influence spatial and temporal patterns of growth (Baker et al., 2002, 2003a). This has been shown at regional (Baker et al., 2003b; Quesada et al., 2009) and local scales (Baker et al., 2003b; Russo et al., 2005). In addition, the dynamics of functional groups have been shown to respond differently to soil resources, which are important factors of niche differentiation (e.g. Russo et al., 2005; Kariuki et al., 2006; Brenes-Arguedas et al., 2008).

Finally, an increasing number of studies has emphasised the effect of the neighbourhood on the demographic rates of trees, be it for growth (Sánchez-Gómez et al., 2008; Uriarte et al., 2010), recruitment (Brown and Karubian, 2016), or survival (Olano et al., 2009; Wang et al., 2012). We focused on negative effects of neighbouring trees on individual performances, as a result of competition for shared resources or through common natural enemies, that is, two crucial mechanisms for tropical forest dynamics (e.g. Comita et al., 2009; Fortunel et al., 2016). Such negative effect is commonly observed in the context of competition for light, which increases with stand density (Sánchez-Gómez et al., 2008). A negative effect of the neighbourhood on a focal tree can however be related either to high or to a low functional similarity. First, negative interactions with neighbourhood may reflect the relative position of species on a hierarchy of competitive ability (Kunstler et al., 2012; Fortunel et al., 2016). In this case, it is the absolute value of traits which matters and places the different species higher or lower on the competitive ability scale, given the local environmental conditions (Kunstler et al., 2012; Fortunel et al., 2016). In parallel, neighbourhood negative effects on individual performances can also be related to limiting similarity, with functionally similar neighbourhood decreasing individual performances. Indeed, the effect of competition or natural enemies within a species or among species with similar trait values is generally larger – providing that traits are good predictors of resource use and defences against enemies – and has been shown to affect individual performances (Adler et al., 2014; Ledo, 2015; Fortunel et al., 2016; Chen et al., 2016; Zambrano et al., 2017; Grossman et al., 2017). Trees often grow faster, recruit more, and survive better when surrounded by more dissimilar neighbours (Brown and Karubian, 2016). This can be interpreted as a result of a release of the intraspecific competition through the mechanisms of limiting similarity or negative density dependence (natural enemies, Janzen-Connell effect) (Agrawal and Fishbein, 2006; Chen et al., 2018). It can also be the consequence of real neighbourhood complementarity (Sapijanskas et al., 2014; Chen et al., 2016).

In this study, we investigate the drivers of the vital rates of a tropical dry woodland in southern Africa to uncover the mechanisms of tree species coexistence. Tropical dry woodlands of the Zambezian region (generally referred to as miombo woodlands) have been poorly studied compared to other tropical forests. The miombo woodland is characterised by a marked seasonal drought and frequent disturbances

(wildfire) (Frost, 1996). In miombo woodlands, constraints on growth, recruitment, and mortality are poorly understood, and plant life history strategies remain little known.

Here, we investigate the influence of fine-scale soil physico-chemical heterogeneity, stand structure features, and functional composition of neighbourhood on individual tree demographic performances in a wet miombo woodland. To do so, we report a 4-year interval census of tree growth, stem recruitment, and survival from a 10-ha forest dynamics plot located in a miombo woodland near Lubumbashi, DRC (Muledi et al., 2017, 2018). This dataset encompasses an unprecedentedly large number of species of the wet miombo and was used to determine the main factors controlling demographic rates in this environment. The following specific questions are addressed on the basis of generalised linear (mixed) models at the individual level:

(1) Are the drivers of tree demographic performance identical for growth, recruitment, and survival? (2) What is the relative importance among the influence of soil variables, stand structure, and neighbourhood effects (i.e. local functional dissimilarity) on demographic rates? (3) Can we observe classical demographic trade-offs (growth-survival, recruitment-adult growth, recruitment-survival, adult stature-recruitment) in this community?

Tree species of the miombo present a high diversity in wood density and leaf phenology (presence of evergreen, semi-evergreen and deciduous species). This suggests a separation between fast-growing acquisitive pioneer and slow-growing conservative species (Reich, 2014; Méndez-Alonzo et al., 2012). Based upon the results of two previous studies on the same site describing species-habitat associations (Muledi et al., 2017) and ectomycorrhizal-host relations to the environment (Bauman et al., 2016), we hypothesized that the fast-slow continuum will manifest following three axes of resources limitations: the classical light gradient, but also the water and nutrient availability. We expected that (1) soil heterogeneity explains a large part of growth differences among species, in particular water retention capacity (low gravel loads, high clay content), P availability and Al toxicity; (2) traits linked to resource conservation syndrome, (high values for LDMC, WD, seed mass, low values for LA, SLA), or to the access to supplementary resource pools via ectomycorrhizae, will be fostered by higher demographic performance in this environment experiencing long drought period, element deficiencies or toxicity.

2. Materials and methods

2.1. Study site

This research was carried out in the Mikembo Natural Reserve, a 530-ha miombo woodland located ca. 35 km NE of Lubumbashi, Upper Katanga, DR Congo. In 2009, a permanent plot of 10 ha (200 × 500 m; 160 quadrats of 25 × 25 m each) was installed (11°28′57″ to 11°29′05″S, 27°40′12″ to 27°40′28″E; 1220 m a.s.l.) (Muledi et al., 2017, 2018). The climate is Sudanian with mean annual temperature of 20.5 °C, mean annual rainfall of 1239 mm, and six months of dry season from May to October (Schmitz, 1971). Geological substrate consists of dolomitic shales and siltstones from Neoproterozoic Nguba and Roan Groups (Batumike et al., 2006). The flat topography of the site is regularly punctuated by termite mounds up to 8 m high. Soils are characterised by low pH and nutrient content and a textural gradient associated to higher P and lower Al contents (coarse sandy loam, west side) or higher water availability and nutrient content (clay and sandy clay, east side) (Muledi et al., 2017). The vegetation is typical miombo woodland of the wet type, with *Julbernardia paniculata, Diplorhynchus condylocarpon*, and *Marquesia macroura* as most frequent species. Tree species exhibit large differences in leaf structure and phenology, wood density, and ectomycorrhization status (Bauman et al., 2016). The site has been protected from fire and fuel-wood cutting since 2003. Before this date, this woodland has been subjected to fire and, at least in part, to slash and burn cultivation. Traces of human disturbance such as

cultivation ridges and charcoal were observed in the eastern portion of the plot with higher clay content and lower gravel load, probably because of easier soil tillage conditions (Muledi et al., 2017). From the age-diameter relationships presented in Schmitz (1971) for several species in the same region, we estimated the oldest tree of the plot being over 100 years old.

The 10-ha plot was systematically inventoried for all living and dead trees ≥ 10 cm DBH (diameter at breast height at 130 cm). Trees were tagged, mapped, identified to the species level, and measured for DBH in 2010 and 2014, at the beginning of the dry season. The plot comprises thirty-three termite mounds (*Macrotermes* sp.) covering 5% of the plot area. Termite mound soil has particular chemical and physical properties, and, termite mounds host tree communities that are completely distinct from the surrounding matrix (Cuma Mushagalusa et al., 2018); therefore, termite mounds were not included in this study.

2.2. Demographic performances

Basal area increment (BAI, $cm^2\,y^{-1}$) was chosen as representative of tree growth. It was correlated ($r = 0.72$) with the mean diameter increment (MDI, $cm\,y^{-1}$). BAI was calculated as $BAI = \pi\,(DBH_1^2 - DBH_0^2)/4$, where DBH_1 and DBH_0 are diameter at breast height in the 2014 and 2010 censuses, respectively. Negative diameters increments were observed for a few individuals. None of these values exceeded or even approached the threshold of -0.4 cm/y proposed by Baker et al. (2002) separating natural variation and measurement errors. Therefore, these negative values were interpreted as stem shrinkage during the dry season and were retained in the dataset. They were no cases of individuals with growth rates more than 4 standard deviations from the mean, considered as measurement errors (Rüger et al., 2011). BAI was used as the response variable in linear models built to model individual growth (see Section 2.6, below). The response variables used for stem recruitment and mortality were simple vectors of 1 and 0, as we modelled these variables using logistic regressions (see Section 2.6, below).

We also computed the relative population stem recruitment and mortality rates of each tree species in order to include them as explanatory variables in the linear models of the growth, recruitment, and mortality response variables already described (for the analyses of the whole community only; see Section 2.6). The relative population stem recruitment was calculated for a given species as $Recr.\ rate = (\ln N_1 - \ln S)/t$, where N_1 is the number of living stems at the second census in 2014, S is the number of survivors for the target species in 2014 and t is the time interval between census years, (ln) is the natural logarithm. Stem mortality rate was measured for each species as $Mort.\ rate = (\ln N_0 - \ln S)/t$, where N_0 is the number of living trees in 2010, S is the number of survivors (number of stems present in 2010 that are still alive in 2014) and t is the time interval between these two measurements (Condit et al., 1999). The plot-specific species mean growth rate (BAI) was also used as explanatory variable for the community-level models of recruitment and mortality, to assess demographic trade-offs based on a local measurement of growth.

2.3. Soil analyses

Soil variables were measured on five bulked 0–20 cm depth soil cores collected in each quadrat of 25 × 25 m. Sixteen edaphic variables were selected to reflect the soil physical and chemical variability of the site, i.e. soil clay content (%Clay), soil depth (Depth), bulk density (BD), gravel load (GL), pH in water (pH-H_2O), organic matter content (OM), carbon on nitrogen mass ratio (C/N ratio), the Al saturation rate (Al_{Sat}), concentrations in plant-available forms of elements (Ca, Mg, K, Al, Fe, $Mn)_{Av}$. Protocols of soil analyses are given in Bauman et al. (2016) and Muledi et al. (2017). Two forms of soil phosphorus were determined with Olsen method (P_{Olsen}) and NH_4-Acetate-EDTA extraction (P_{EDTA}).

2.4. Functional traits

All traits were measured following the protocols of Pérez-Harguindeguy et al. (2016). Eleven functional traits were considered in this analysis by averaging 10 individuals for each species and each trait: maximum tree height (H_{max}, m), leaf area (LA, cm^2), specific leaf area (SLA, cm^2 g^{-1}), leaf dry matter content (LDMC, mg g^{-1}), the degree of deciduousness (Deci), leaf nitrogen concentration (LN, µg g^{-1}), leaf phosphorus concentration (LP, µg g^{-1}), wood density (WD, g cm^{-3}), seed dry mass (SM, mg), root ectomycorrhization status (Ecto, binary) and fire tolerance (FTol). H_{max} could not be calculated in a regular way because only the 10% highest trees were measured for height in each 50 × 50 quadrat. However these truncated values were correlated (Pearson $r = 0.69$) with D_{max} corresponding to the 95% distribution of all tree diameters of each 25 × 25 quadrat. Ectomycorrhization status was obtained from Bâ et al. (2011) and checked in another study on the site (Bauman et al., 2016). For leaf phenology, three categories were recognized, and used to define a deciduousness variable with the following values: 0 (evergreen), 0.5 (semi-evergreen: leaves shed < 30 days before budbreak), and 1 (deciduous: leafless for more than 30 days in the dry season). Fire tolerance index (FTol) was derived from Trapnell (1959), Lawton (1978) and Cauldwell and Zieger (2000) and comprised three categories: 0 (not tolerant), 0.5 (semi-tolerant), 1 (tolerant). Four missing values for fire tolerance were obtained using a Bayesian Hierarchical Matrix Factorization gap-filling method (Schrodt et al., 2015), taking other traits and taxonomy into account. For each functional trait, we quantified the functional dissimilarity of each individual tree relative to its neighbourhood (i.e. 25 × 25 m quadrat) through a functional distance index (FD). The FD for trait T was calculated as: $T_{FD} = \sum_{i=1}^{n} (F_{ind} - F_i)/n$, where F_{ind} and F_i are the trait value of the focal individual and neighbour i, respectively, and n is the total number of neighbours in the quadrat. The resulting predictor variables (H_{max}, LA, SLA, LDMC, Deci, LN, LP, WD, SM, Ecto, and FTol)$_{FD}$ represent the functional dissimilarity of the neighbouring individuals. A positive relationship between individual performances and FD was interpreted as the sign of a limiting similarity mechanism, whereas a negative relationship between individual performances and FD was considered as the sign of a competitive hierarchy mechanism. Six other functional traits were included in Table S2 to describe species and functional groups: life form (micro- or mesophanerophyte) and dispersal mode (auto, autochorous; anemo, anemochorous; zoo, zoochorous) (Meerts, 2016; White, 1962), leaf C/N ratio (LCN), leaf N/P ratio (LNP), and leaf lignin content (Lign, %) (Bauman et al., 2016), as well as maximum tree diameter (DBH_{max}) (this study).

2.5. Stand structure and characteristics

Three structural attributes and characteristics of the stand were calculated for each quadrat: basal area (m^2 ha^{-1}), mean DBH (cm), and mean relative DBH (without units). Quadrat basal area (m^2 ha^{-1}) is a classical index to reflect the general intensity of competition (Biging and Dobbertin, 1995). Mean DBH was interpreted as a proxy for the natural or anthropogenic disturbance regime, reflecting the successional stage of the community in the quadrat.

2.6. Statistical treatments

The analyses were performed at the species-level, at the community-level, and with respect to the functional groups highlighted in a separate analysis.

2.6.1. Species-level analyses

The analyses of growth, recruitment, and survival were performed on the individual data. All predictor variables were Box-Cox transformed to linearise relationships and stabilise variances, with the exception of binary variables and mortality rates which present many null values. Nineteen species present in a minimum of 50 quadrats were selected for

separated analyses at the species level. The same species were also analysed altogether, in what we will refer to as a community-level analysis. Inside each quadrat, the percentage of the total stem number from the target species was 91.5 ± 7.4%, which is more than the minimum of 80% of species representation prescribed by Pakeman and Quested (2007) for trait analyses. Initial tree size expressed as DBH, soil variables, stand structural attributes as well as neighbouring functional environment (FD) in the corresponding quadrat of the focal individual were chosen as predictors of tree growth, stem recruitment, and survival.

A preselection of predictor variables was conducted to avoid multicollinearity (Dormann et al., 2013) (see Appendix S1 – Section 1 for details). This preselection consisted in computing all the pairwise Pearson's correlations between explanatory variables and to remove one of the variables of all the pairs displaying an absolute correlation value higher than 0.7 (see Table S1). Some variables were therefore excluded for the benefit of their correlated counterpart and might not be ignored during the interpretation of the results for a complete view on the explanatory variables.

All variables were standardised to have zero mean and unit standard deviation, which facilitated the interpretation and allowed the ranking of the effects through the importance value (Comita et al., 2009). For each species, we determined the limiting sample size on the basis of a minimum of 10 observations per predictor variable, and in all cases limited the maximum number of predictors to 10, for the sake of parsimony. Generalised linear models were used to infer the determinants of tree demographic rates at the specific and at the community level. Multiple linear regressions were applied to describe tree growth for each species separately, with the following model: BAI = $\beta_0 + \beta_1 x_1 + \cdots + \beta_n x_n$, where $\beta_0 \cdots \beta_n$ are regression coefficients and $x_1, x_2 \cdots x_n$, are explanatory variables. Multiple logistic regressions were used in combination with the logit link function to model the probability of tree recruitment (Pr) and survival (Ps). The binary variable (recruit/adult) or (dead/alive) were constructed using the logistic model: Logit (Pr) or (Ps) = $\beta_0 + \beta_1 x_1 + \cdots + \beta_n x_n$, where Pr and Ps are probability of recruitment and survival, respectively.

We applied a corrected AIC-based model selection approach (Burnham and Anderson, 2002) provided by the *glmulti* package (Calcagno and de Mazancourt, 2010) which allows us to assess model-selection uncertainty and to perform multi-model inference. In order to bypass an exhaustive analysis of all variable combinations, we used a genetic algorithm method which only explored an optimised subset of all possible models (Calcagno and de Mazancourt, 2010). We made a consensus of 10 simulations of the genetic algorithm to improve convergence and to avoid local optimum issues. A model averaging was performed to estimate coefficients and variability by taking the first 50 best-ranking models into account, weighted by the Akaike Information Criterion value corrected for small samples (AIC$_c$).

The presence of a significant spatial autocorrelation in the residuals of all 50 best-ranking models was assessed and explicitly taken into account when present, using Moran's eigenvector maps (MEM; Dray et al., 2006). This was done following the recommendations of Bauman et al. (2018a,b), in the *adespatial* package (Dray et al., 2019), to select both the spatial weighting matrix and a subset of spatial predictors, hence optimising the detection of any spatial structure in the model residuals using a minimum number of spatial predictors in an accurate and unbiased way (details in Appendix S1). Whenever a significant spatial autocorrelation was detected in model residuals, the predictor coefficients of the corresponding model were re-estimated after inclusion of the optimised selected subset of MEM variables in order to yield unbiased estimates. We then retained predictor variables with importance value ≥ 0.7 for inference. We used the unconditional coefficient estimates of the averaged model to evaluate the intensity and the sign of the effect of each retained predictor.

For logistic regressions, the retained explanatory variables and averaged coefficients were included in a reduced model and we assessed the predictive ability of the global and the reduced models. The predictive ability of the logistic models was assessed by plotting the

Table 1

Functional traits values and relative demographic rates of the 19 species studied. Funct. Group = functional groups; Recr. rate = relative recruitment rate; Mort. rate = relative mortality rate. Asterisks indicate missing values obtained using a Bayesian Hierarchical Matrix Factorization gap-filling method (see Section 2). Variable code H_{max} maximum tree height, LA leaf area, SLA specific leaf area, LDMC leaf dry matter content, Deci degree of deciduousness, LN leaf nitrogen, LP leaf phosphorus, WD wood density, SM seed mass, Ecto ectomycorrhization status, FTol fire tolerance index.

Species	Code	Funct. Group	Mean BAI (cm² y⁻¹)	Recr. rate	Mort. rate	H_{max} (m)	LA (cm²)	SLA (cm² g⁻¹)
Brachystegia spiciformis Benth.	BraSpi	1	27.4	0.02	0.004	22	91.1	88.3
Brachystegia wangermeeana De Wild.	BraWan	1	7.5	0.05	0.001	19	52.7	119.2
Combretum collinum Fresen.	ComCol	1	13.5	0.03	0.000	17	43.2	98.0
Julbernardia globiflora (Benth.) Troupin	JulGlo	1	12.6	0.12	0.000	20	119.3	120.8
Julbernardia paniculata (Benth.) Troupin	JulPan	1	12.1	0.10	0.005	19	155.1	91.6
Marquesia macroura Gilg	MarMac	2	52.8	0.02	0.002	23	24.9	130.6
Monotes katangensis (De Wild.) De Wild.	MonKat	2	8.6	0.04	0.000	16	60.1	89.4
Parinari curatellifolia Planch. Ex Benth.	ParCur	2	16.5	0.04	0.000	18	47.6	84.0
Albizia antunesiana Harms	AlbAnt	3	17.5	0.08	0.018	17	199.1	86.6
Dalbergia boehmii Taub.	DalBoe	3	4.9	0.12	0.057	15	66.5	113.5
Pericopsis angolensis (Harms) Van Meeuw.	PerAng	3	20.1	0.02	0.010	18	107.2	113.8
Philenoptera katangensis (De Wild.)	PhiKat	3	11.6	0.04	0.010	13	135.3	82.5
Pterocarpus angolensis DC.	PteAng	3	10.0	0.05	0.042	18	149.5	118.0
Pterocarpus tinctorius Welw.	PteTin	3	15.9	0.05	0.008	20	130.9	103.8
Diplorhynchus condylocarpon (Müll. Arg.) Pichon	DipCon	4	15.0	0.05	0.001	19	21.8	129.6
Hexalobus monopetalus (A. Rich.) Engl. & Diels	HexMon	4	5.0	0.06	0.000	10	26.3	96.6
Pseudolachnostylis maprouneifolia Pax	PseMap	4	8.6	0.05	0.003	15	19.7	120.4
Strychnos innocua Delile	StrInn	4	7.2	0.02	0.005	14	14.8	90.2
Uapaca nitida Müll. Arg.	UapNit	4	6.2	0.05	0.005	15	60.0	95.1
Mean ± SD								
Group 1			15 ± 8	0.06 ± 0.04	0.0021 ± 0.0024	19.4 ± 1.8	92 ± 47	104 ± 15
Group 2			26 ± 24	0.03 ± 0.01	0.0006 ± 0.0010	19.0 ± 3.6	44 ± 18	101 ± 25
Group 3			13 ± 6	0.06 ± 0.03	0.0243 ± 0.0203	16.8 ± 2.5	131 ± 44	103 ± 15
Group 4			8 ± 4	0.04 ± 0.02	0.0028 ± 0.0022	14.6 ± 3.2	29 ± 18	106 ± 17

Species	LDMC (mg g⁻¹)	Deci	Funct. Group	LN (µg g⁻¹)	LP (µg g⁻¹)	WD (g cm⁻³)	SM (mg)	Ecto	FTol
Brachystegia spiciformis Benth.	38.8	0.5	1	2.2	1129	0.652	418	1	0
Brachystegia wangermeeana De Wild.	49.0	0.5	1	2.3	1678	0.607	524	1	0
Combretum collinum Fresen.	43.4	0.5	1	2.3	1897	0.754	406	0	0
Julbernardia globiflora (Benth.) Troupin	39.5	0.5	1	2.2	1467	0.727	328	1	0
Julbernardia paniculata (Benth.) Troupin	40.2	0.5	1	1.9	1666	0.677	362	1	0
Marquesia macroura Gilg	35.7	0	2	1.8	1440	0.701	21	1	1*
Monotes katangensis (De Wild.) De Wild.	36.2	0	2	1.6	1891	0.756	42	1	1
Parinari curatellifolia Planch. Ex Benth.	34.3	0	2	1.1	776	0.571	4357	0	1
Albizia antunesiana Harms	35.8	1	3	2.4	1144	0.521	68	0	0
Dalbergia boehmii Taub.	36.4	1	3	3.6	1897	0.595	34	0	1
Pericopsis angolensis (Harms) Van Meeuw.	40.4	1	3	3.4	1850	0.830	271	1	0.5*
Philenoptera katangensis (De Wild.)	38.6	1	3	2.9	2052	0.720	237	0	1
Pterocarpus angolensis DC.	36.1	1	3	3.0	1923	0.508	215	0	1
Pterocarpus tinctorius Welw.	37.0	0	3	2.6	1181	0.782	277	0	1*
Diplorhynchus condylocarpon (Müll. Arg.) Pichon	39.8	1	4	2.1	1920	0.632	203	0	1
Hexalobus monopetalus (A. Rich.) Engl. & Diels	31.8	1	4	3.3	2782	0.552	813	0	0
Pseudolachnostylis maprouneifolia Pax	41.3	1	4	1.4	1217	0.635	60	0	0.5
Strychnos innocua Delile	33.6	1	4	1.9	1330	0.657	725	0	1
Uapaca nitida Müll. Arg.	31.5	1	4	1.6	1352	0.576	477	1	1*
Mean ± SD									

5

Table 1 (*continued*)

Species	LDMC (mg g^{-1})	Deci	LN (µg g^{-1})	LP (µg g^{-1})	WD (g cm^{-3})	SM (mg)	Ecto	FTol
Group 1	42 ± 4	0.5 ± 0.0	2.2 ± 0.2	1570 ± 290	0.68 ± 0.06	410 ± 70	0.8 ± 0.4	0.0 ± 0.0
Group 2	35 ± 1	0.0 ± 0.0	1.5 ± 0.4	1370 ± 560	0.68 ± 0.10	1470 ± 2500	0.7 ± 0.6	1.0 ± 0.0
Group 3	37 ± 2	0.8 ± 0.4	3.0 ± 0.5	1680 ± 400	0.66 ± 0.14	180 ± 110	0.2 ± 0.4	0.8 ± 0.4
Group 4	36 ± 5	1.0 ± 0.0	2.1 ± 0.7	1720 ± 650	0.61 ± 0.44	460 ± 320	0.2 ± 0.4	0.7 ± 0.4

ROC curve (Receiver Operating System) of a graph of true positive rate against false positive rate constructed with an independent subset of 10% of the whole dataset (10-fold cross validation). Then the area under this curve (AUC) was determined, and yielded mean scores of 0.68 and 0.61 for recruitment and survival, respectively. Sensitivity and specificity at the optimal cut point of this curve (where the sum of sensitivity and specificity is maximal) was assessed with the 'ROC' function of the *Epi* package (Carstensen et al., 2018). Internal and cross-validation (10-fold) estimates of accuracy were determined using the 'CV.binary' function from the *DAAG* package (Maindonald and Braun, 2010). The McFadden's pseudo-r^2 of the mortality and recruitment reduced models were on average 0.04 and 0.02, respectively (a value of 0.2 is considered high for such analyses) (McFadden, 1974). Indicators of the predictive capacity of all logistic models (pseudo-r^2, sensitivity and specificity of the optimal cut point, AUC and others) can be found in Table S5.

2.6.2. Community-level analyses

At the community level, a corresponding (i.e. either Gaussian or binomial) mixed model was used, by adding a random intercept for species identity to the models described in the previous section, and by allowing it to have random slopes with respect to the initial DBH, as ontogenetic influences on growth, survival, and recruitment can strongly differ among tree species. These generalised linear mixed models (GLMM) have the advantage of estimating all species' coefficients simultaneously while learning from these to estimate the coefficients for the unknown population of species (from which our species were theoretically sampled). We refer to these latter coefficients as community-level coefficients. Unlike the species-level analyses, focusing on the coefficients of the community-level approach will allow us to explore community-level trends with respect to soil, stand structure, and the functional composition of tree neighbourhood.

2.6.3. Functional group-level analyses

We used a Principal Coordinate Analysis (PCoA) with 17 quantitative and qualitative trait data (see Table 1) and Gower dissimilarity index (Laliberté and Legendre, 2010) to identify the potential axes of niche differentiation, followed by a Ward clustering (Legendre and Legendre, 2012) to separate tree species in functional groups.

The community-level approach described above was then used separately for the species of each functional group. The GLMM performed at the functional group level aim to highlight particular relationships with and trade-offs with respect to the functional neighbourhood of trees, their soil conditions and local stand structure. These analyses will also test whether the functional groups suggested by descriptive ordination and clustering methods are ecologically sound and confirm the demographic and functional trade-offs (see Introduction).

All statistical treatments were carried out using the statistical computing program R, version 3.6.0 (R Development Core Team, 2018).

3. Results

3.1. Functional groups and demography

In 2010, the 10-ha plot comprised a total of 3118 stems (DBH > 10 cm), corresponding to 85 species, 58 genera and 33 families. The total number of stems increased to 3902 in the second census in 2014. The five most frequent species in the site were *Julbernardia paniculata* (26.9%), *Diplorhynchus condylocarpon* (9.3%), *Marquesia macroura* (6.5%), *Brachystegia wangermeeana* (6.6%), and *Julbernardia globiflora* (5.5%) (Table S6). The PCoA allowed separating the community into four groups on the basis of their FT (Fig. 1 and Table S4). This highlighted three main axes of niche differentiation: 1) H$_{max}$, Ecto, Deci, LDMC, dispersal mode (zoo, auto) and life form (micro, meso), correlated to the first component 2) FTol, evergreeness,
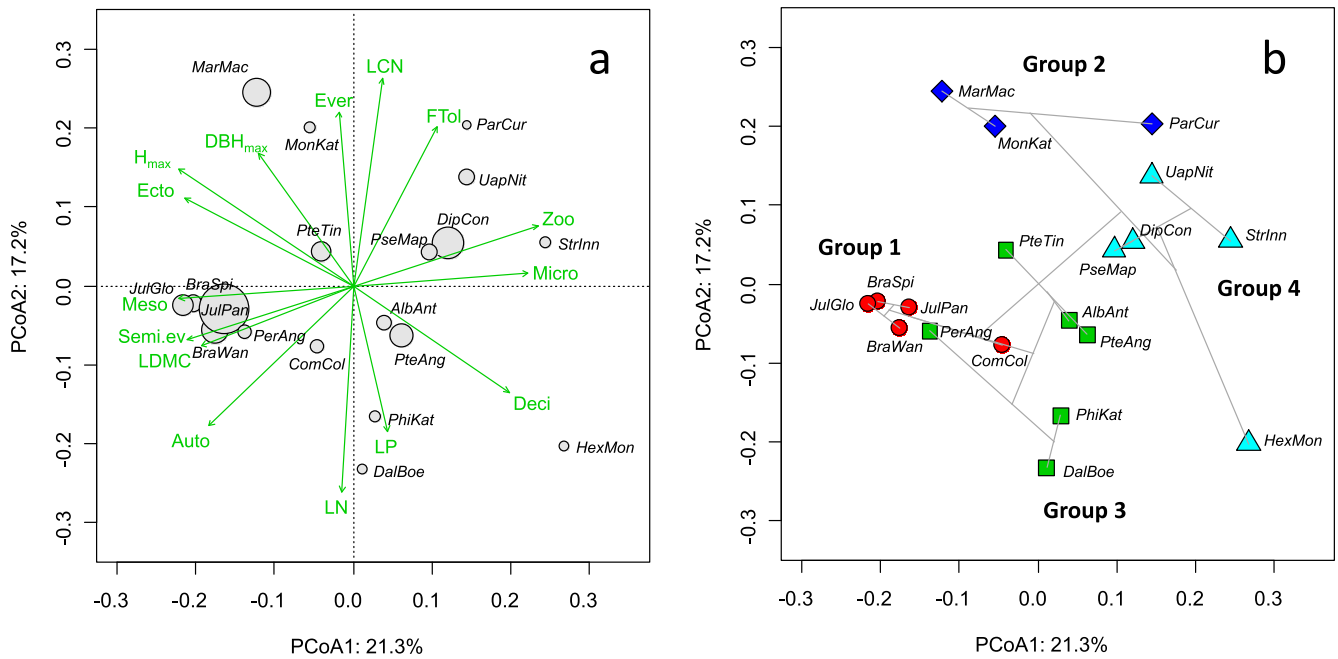
Fig. 1. Projection of Principal coordinate analysis (PCoA) based on Gower distances of functional traits, demographic rates and growth rates (BAI) of the 19 most abundant tree species of the site. The first two components represent a total of 70.34% of the variability a) Projection of the significant original variables and of the species (full names can be found in Table 1). Categorical variables (dispersal mode and leaf phenology) were treated as dummy variables and weighted by the corresponding number of category. The size of the circles are proportional to species abundances. Only significant axes ($P < 0.05$) are represented after free permutation test ($n = 999$). b) Separation in four functional groups by a Ward clustering (Borcard et al., 2018). Different shapes represent the four functional groups: circle = group 1, diamonds = group 2, squares = group 3, triangles = group 4. Functional trait H_{max} is maximum tree height, DBH_{max} maximum tree diameter, LDMC leaf dry matter content, LN leaf nitrogen, LP leaf phosphorus, LCN leaf C/N ratio, Ecto ectomycorrhization status, FTol fire tolerance index, Deci degree of deciduousness, Ever evergreen, Semi.ev semi-evergreen, Meso mesophanerophyte, Micro microphanerophyte, Zoo zoochorous, Auto autochorous. Values in the axis labels are percentages of variance explained.

and leaf nutrient content (LN, LP, LCN), correlated to the second component. Functional group 1 (*B. spiciformis*, *B. wangermeeana*, *C. collinum*, *J. globiflora*, and *J. paniculata*, mostly Fabaceae subfam. Caesalpinioideae) comprises ectomycorrhizal trees with large H_{max} (17–22 m), mainly semi-evergreen with high LDMC, high WD and low fire tolerance (Table 1). This group displayed intermediate to high BAI (15 ± 8 cm^2 y^{-1}), high recruitment rates (0.06 ± 0.04), and represented the late-successional canopy layer. Group 2 comprised three evergreen species (*M. macroura*, *M. katangensis*, *Pa. curatellifolia*), with large H_{max} (16–23 m), WD (0.68 ± 0.06 g cm^{-3}), and BAI (26 ± 24 cm^2 y^{-1}), but differed from the first group by the low LA, generally low SM (mainly wind-dispersed), and the lowest recruitment and mortality rates (0.06 ± 0.04 and 0.0006 ± 0.001, respectively; Table 1). These trait values typically correspond to a profile of conservative, stress-tolerant life strategy. Group 3 comprised six species (*A. antunesiana*, *D. boehmii*, *Pe. angolensis*, *P. katangensis*, *Pt. angolensis*, *P. tinctorius*, all Fabaceae, mainly Faboideae) non-ectomycorrhizal, deciduous with high LA, LN and LP, low LCN and SM (mainly autochorous), and medium H_{max} (13–20 m). This group was characterized by high recruitment rates (0.06 ± 0.03) and the highest mortality rate (0.0243 ± 0.0203). Functional traits and demography point to a fast-growing, acquisitive strategy. Finally, group 4 included five species (*D. condylocarpon*, *H. monopetalus*, *P. maprouneifolia*, *S. innocua*, *U. nitida*) mostly microphanerophytes with $H_{max} < 15$ m, deciduous with high LP, low LA and WD, animal-dispersed propagules, mostly non-ectomycorrhizal and fire-resistant. This group has low BAI and presents intermediate values of recruitment and mortality rates. This corresponded to the understorey species strategy.

3.2. Modelling tree vital rates

As expected, individual growth (BAI) was positively influenced by initial DBH of individuals for 18 species out of 19. Other significant

predictors of growth were, in decreasing order of importance: the functional dissimilarity of the neighbourhood, soil variables, and stand structure variables (Fig. 2a, Table S7). The main influencing variables were DBH (18 species out of 19; not represented in Fig. 2) followed by WD$_{FD}$ (6 species), BD (associated to Al$_{Sat}$) (5 species), Ca$_{Av}$ (5 species), FTol$_{FD}$ (4), OM (3 species), and quadrat mean DBH (3 species). The individual DBH and OM always had a positive effect on growth, while the sign of the effect was species-dependent for the remaining above-mentioned variables. The effect of the other variables appeared for < 3 species out of 19.

The growth of the whole community was mainly driven by the individual's DBH (47.96), relative mortality rate (8.48), BD (−5.96), quadrat mean DBH (−3.38) and BA (−3.21) (in brackets: values of the coefficient estimates). For all the groups, growth was negatively impacted by stand structure variables (i.e. quadrat mean DBH and quadrat total BA; Fig. 2). BD had a negative effect on growth of the functional groups 1 and 4. Remarkably, Group 1 and 3 were both influenced by Deci$_{FD}$ and LP$_{FD}$ but in opposite directions (negative and positive, respectively). Proportionally, Group 2 appeared to only be slightly influenced by soil or the surrounding species compared to the other groups.

946 stems were recruited from 2010 to 2014, for a total of 3370 stems of the whole non-termitophilous community, of which 871 stems belonged to the 19 species studied. *J. paniculata* had the largest number of recruits (393, i.e. 45% of total recruits) (Table S6). The recruitment rates were the lowest for *Pe. angolensis* (8.2%), *M. macroura* (7.9%), and *S. innocua* (7.1%). At the species level, recruitment was only marginally influenced by soil variables (4 species out of 19 were influenced by soil and only two for more than one soil variable, Fig. 2b, Table S8). The quadrat mean basal area negatively influenced recruitment for three species. Ca$_{Av}$ had a positive effect for recruitment of three species, at the community level, and for groups 1 and 3. Recruitment of all groups was systematically influenced by the stand structure variables. However, in the same way as for the community and species levels, BA had a negative effect and Mean DBH a positive effect on recruitment. Recruitment of
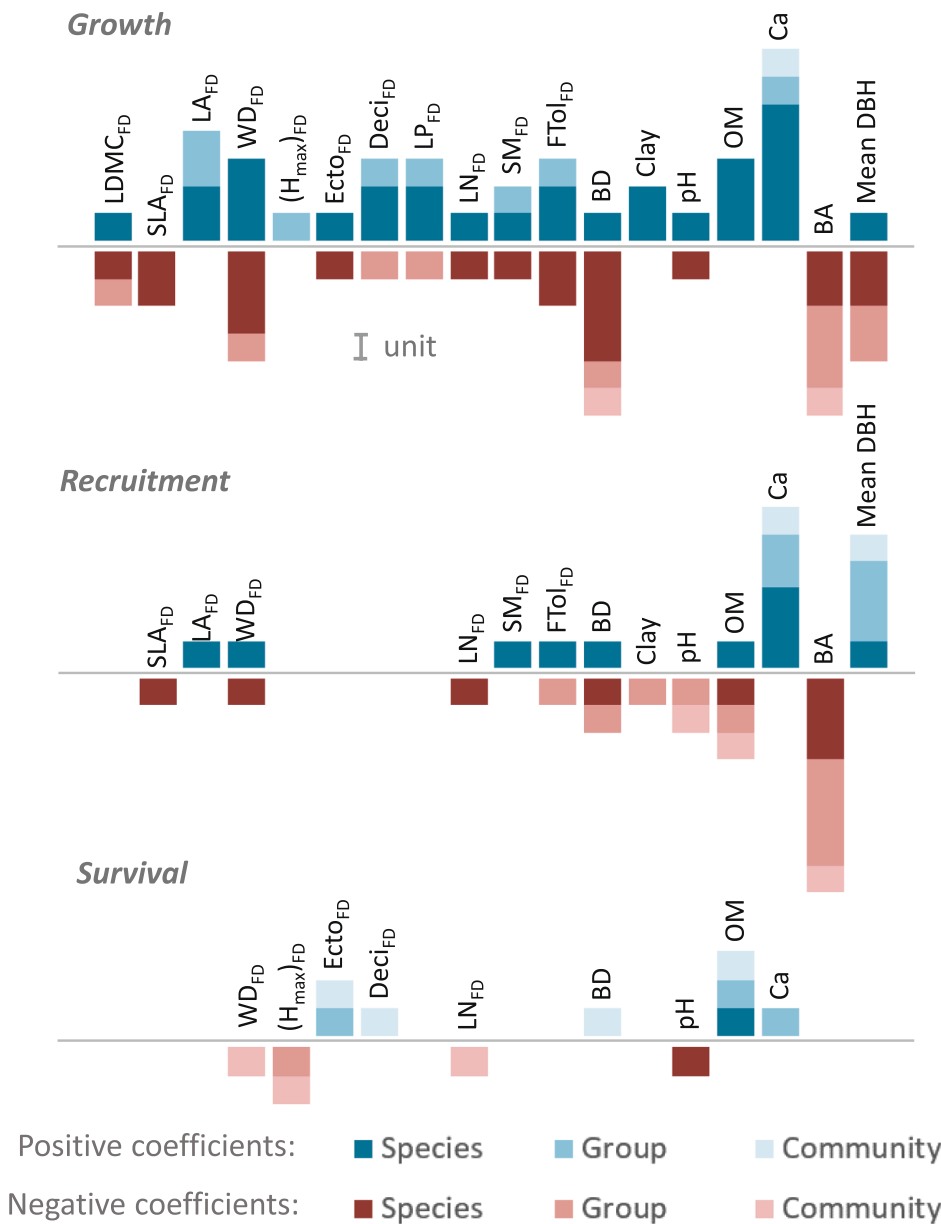
Fig. 2. Number of times each predictor was statistically significant in the multiple linear models of growth, recruitment and survival at the species, group, and community-level. Significance associated to positive and negative coefficients are in cyan and red, respectively. Each unit corresponds to the occurrence of the predictor in one of the 19 models (species level), one of the 4 model (group level) or in the single model (community level). Initial DBH influenced growth of 18 species out of 19 and was not represented in this graph. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

groups 1 and 3 was positively influenced by Ca_{Av}. Except for one value for group 2, functional dissimilarity of the surrounding individuals did not change recruitment rates at the group level.

A total of 125 individuals died between 2010 and 2014 (90 for the 19 most represented species). *D. boehmii* presented the highest mortality rate (21.4%), followed by *Pt. angolensis* (15.3%) and *J. paniculata* (2.0%), whereas 5 species of the 19 had no mortality (Table S6). Survival could be modelled for very few species, due to the lack of power for such regression method with low sample size (Fig. 2c, Table S9). So, only two models including predictors have been constructed for individual species (for *J. paniculata* and *Pt. angolensis*). At the community level, functional dissimilarity (WD, H_{max}: negative effects; Ecto, Deci: positive effects) and soil variables (BD, OM; positive effects) influenced survival. Only group 3 could be modelled for survival. It was positively influenced by BD, Ca_{Av}, OM, and $Ecto_{FD}$.

The analyses showed significant correlations among demographic rates, partially supporting demographic trade-offs. In this way, a positive relation between individual recruitment and growth rate (mean plot-species-specific BAI) was observed at the community level (Table S8). A positive relation was also identified between individual growth and

population mortality rate (Table S7). A negative relationship between species BAI and population recruitment rate was also confirmed ($r^2 = 0.15$, $P = 0.10$) as well as positive relation between individual recruitment and population mortality rate for group 3 (Table S8), in accordance with a fast-growing strategy. However, contrary to the theoretical expectations related to the stature-recruitment axis strategy (Rüger et al., 2018), we found positive relation between individual growth and the population recruitment rate in the community (Table S7).

4. Discussion

The general objective of this study was to identify the drivers of tree species dynamics in a miombo woodland using demographic and functional data of the 19 most frequent species. Such African dry tropical woodlands are original and poorly studied systems offering the opportunity to evaluate the importance of different coexistence mechanisms and highlight specific trade-offs in tropical tree vital rates. In this context, separating the effects of the environment (soil chemical and physical properties), stand structure, and the neighbourhood (functional dissimilarity and dominance) on demographic rates is of great relevance.

4.1. Relations of vital rates with soil and stand structure variables

The influence of soil fertility on tree growth has been shown experimentally (Allen, 1986; Wright et al., 2011; Grossman et al., 2017; Cuma Mushagalusa et al., 2018), or at regional scales (e.g., Quesada et al., 2009). However, relationships of growth, recruitment, and survival rates with soil fertility have rarely been found at local scale (but see Baker et al., 2003b; Russo et al., 2005; Zemunik et al., 2018). In this study, tree growth was positively influenced by Ca_{Av} and OM and negatively affected by BD and/or Al_{Sat}. Structural variables (quadrat BA and mean DBH) affected growth negatively (*J. paniculata, A. antunesiana*, the whole community and groups 1, 3 and 4), and always had a negative impact on recruitment (3 species, the whole community and all the groups). Whereas the successional stage (mirrored by the mean DBH) almost always reduced growth, it was beneficial for recruitment, pointing out a positive effect of the time lapsed since the last major local disturbance. Basal area was correlated to stand density and displayed negative relations with growth and recruitment, hence reflecting competition for light or other resources (neighbourhood crowding). At the community and functional group levels, the successional stage of the quadrat had a large negative effect on growth, but a positive effect on recruitment.

At the species level, negative effects of BD and Al_{Sat} on growth of groups 1 and 4 could be explained by a trade-off between access to water (high water holding capacity and deeper soils on clay texture, which favours growth of *Pa. curatellifolia* and *U. nitida*) versus higher P availability (P_{Olsen}, P_{EDTA}) offset by potential Al toxicity (high Al_{Sat}) in coarse sandy loam soils with lower water holding capacity (which is detrimental for growth of *C. collinum, J. globiflora, J. paniculata, P. maprouneifolia,* Group 1 and 4, and the whole community). Growth of species from group 2 and 3 was not affected by such habitat characteristics and seemed to tolerate water shortage and Al toxicity. Species negatively impacted for growth on coarse sandy substrate with higher Al_{Sat} and P availability present higher LDMC and lower LNP than the other species (LDMC = 41.1 ± 1.7 vs. 37.0 ± 4.2, respectively; Welch *t*-test: $P < 0.01$ and LNP = 12.4 ± 1.6 vs 15.2 ± 4.0, respectively; $P < 0.05$). Likewise, groups 1 and 4 had lower LNP than species of groups 2 and 3 (LNP = 13.1 ± 2.5 vs 16.2 ± 4.3; $P = 0.09$). In the context of woody savannas, Hodgson et al. (2011) as well as Wigley et al. (2016) showed a negative relation between LDMC and soil N fertility. The reverse situation occurs in our site where growth of species with high LDMC was negatively affected on coarse sandy loam soils with lower N but high P supply. The contrast of LDMC values among species could therefore rather be driven by P availability. Calcium availability influenced growth positively for 5 species and species of group 1. This nutrient is less available on soil with high BD and Al_{Sat}. Among the species influenced by this trade-off, many were ectomycorrhizal (*J. globiflora, J. paniculata*, and the large majority of group 1). This might support that ectomycorrhizal species have a particular status with respect to their nutrient supply, and particularly for P (Högberg, 1990, 1992). By contrast, growth of species from group 2 and 3 were not affected by Al_{Sat} and water shortage on coarse sandy loam, and could benefit from higher P concentration in such habitat.

Soil also influenced stem recruitment for some species. When significant, the effect of Ca_{Av} was always positive for recruitment, including at the group level (groups 1 and 3) and the whole community level. Survival was explained by edaphic constraints (positive influence of BD, Al_{Sat} and OM) at the community level. This is in line with another study (Wang et al., 2012).

4.2. Competitive hierarchy or limiting similarity?

Overall, we identified a negative effect of the neighbourhood on individual growth resulting from the hierarchy of competitive ability. The latter was detected through a negative relation of growth with the local functional dissimilarity (FD), which reflects the competition with species showing a contrasting and dominating value of the functional trait considered in the local environment (competitive hierarchy). The growth rate of the focal individual could be reduced as a consequence of the dominant species or group of the quadrat (competitive hierarchy, Kunstler et al., 2012). This negative effect was observed for species of group 1, impacted by functional dissimilarity of neighbours for LDMC, Deci, and LP. They could be impacted by species of group 3 whose growth is precisely positively influenced by $Deci_{FD}$ and LP_{FD}. Competitive hierarchy also affected the growth of group 4 and other species with lower WD (*B. wangermeeana, A. antunesiana*, and *D. condylocarpon*), negatively influenced by neighbours with higher WD.

Apart from competitive interactions, the functional dissimilarity of the neighbourhood (LA_{FD}, $Ecto_{FD}$, and LP_{FD}) also had a positive effect on growth (6 species) (Fig. 2, Table S7). Functional dissimilarity therefore had a large positive effect on growth at the species, group, and community levels. This could be explained by the alleviation of intraspecific competition or shared natural enemies when other strategies were represented in the neighbourhood. By contrast, species recruitment was only weakly influenced by the functional dissimilarity of the surrounding individuals. Chen et al. (2016) showed that the neighbourhood complementarity effects were the strongest for light-demanding species. This was verified here with group 3, characterised by an acquisitive strategy, displaying 10 positive interactions out of 13 with the functional traits of the neighbourhood.

In summary, positive demographic relationships with functional dissimilarity reflected the reduction of competitive interactions between functionally dissimilar species (for species of group 3 in particular). In contrast, functional differences had a negative effect on species with traits associated to weak competitors (e.g. low WD, low or intermediate SLA, FTol).

4.3. Demographic trade-offs and consequences for species coexistence

Demographic trade-offs can emerge from individual strategies of resource allocation in response to multiple axes of environmental constraints. Theoretically, these trade-offs enable predicting community assemblages and ecosystem dynamics (Easdale et al., 2007; Rüger et al., 2018).

The analysis of trait distribution in the miombo tree community allowed identifying four functional groups. Maximum height, ectomycorrhizal status and leaf traits were the major axis of niche differentiation. These groups were also separated by differences in life history traits and demographic rates, as predicted by Adler et al. (2014). The growth-survival trade-off was partially detected in this community. The fast-slow continuum separated group 3 (fast-growing but low survival rate) from group 2 (slow growing conservatives with little observed mortality). Demographic rates corresponded to the classical expectation for these two groups. As seen in the previous paragraph, the predictors for growth, recruitment and survival were different among these species with contrasting strategies. We observed a second axis separating tall species (group 1, high H_{max}, LDMC, and mean WD) and understorey species (group 4, low H_{max}, WD and LDMC), corresponding to a difference in species response to the vertical light gradient. The associated demographic trade-offs were not entirely clear. However, the expected recruitment vs. growth and recruitment vs. survival trade-offs associated to the adult stature (H_{max}) – seedling recruitment axis (King et al., 2006; Rüger et al., 2018) were partially confirmed in this study. We showed a significant negative correlation between species growth and species recruitment rate and a positive relation was found between individual growth and population mortality rate at the community level. Likewise, a positive relationship was detected between individual recruitment and the population mortality rate for group 3, as expected for a fast acquisitive strategy.

Group 4 showed intermediate values of growth as well as relatively low death and recruitment rates, compared to the other groups. Their low recruitment rate did not offset their low capacity for light

interception, a condition for a stable coexistence with tall species (Kohyama, 1993). These species do not correspond to the classical understorey strategy. They presented some trait values associated to the understorey syndrome (low H_{max}, LA, LN, low mortality rate), but they can also be interpreted as drought avoidance strategy. Moreover, these species had low WD and were deciduous, in opposition to the general trend in wet and dry tropical forests understorey (Poorter et al., 2006, 2014). Furthermore, understorey species of group 4 are all fire tolerant and are also found in open landscapes (chipya habitat) as pioneer species in fire-prone environments (Lawton, 1978). On the contrary, species of group 1 are fire sensitive and cannot survive in disturbed environment. They compose the canopy trees of the dry evergreen forest (Lawton, 1978) and may have benefited from the absence of fire on the site since 2003. Thus, the decisive factor regulating the groups 1–4 trade-off could be the successional status of the species and the resistance in the face of disturbance and wildfire in particular.

In line with the Russo et al.'s (2010) study and with the very contrasting values of WD among species, the demographic rates were related to WD for growth and survival (Tables S7, S9). The neighbouring dissimilarity in foliar traits also reliably predicted growth (LDMC, SLA, Deci, LP, LN)$_{FD}$, recruitment (SLA, LA, LN)$_{FD}$, both at the species and community levels, and survival (Deci$_{FD}$ at the community level).

Mortality primarily affected species of the functional group 3, with a fast-growing strategy (Table S9). This higher mortality was partially compensated by higher stem recruitment compared to the other groups. Group 3 also had slow growth at this stage of the forest development, probably explained by the decreased light availability with canopy closure which was detrimental for light-demanding pioneers. This group could however strengthen in the long-term dynamic cycle after fire disturbance (Lawton, 1978; Cauldwell and Zieger, 2000).

Finally, we found a third differentiation axis which was associated to the four functional groups: Individuals with contrasting LDMC and LNP values (groups 1 and 4 vs groups 2 and 3) differed in their growth rates on soils characterised by opposed water holding capacity, Al toxicity and P fertility. This edaphic niche partitioning was not entirely comparable to the species specialisation for habitats highlighted in Muledi et al. (2017) for the same site. Soil drivers of species sorting were partly identical (P, Clay, Al, Ca), but strict species associations were rare and could not be connected to the demographic rates. Yamada et al. (2007) also showed that strong habitat specialisation in a tropical rain forest did not imply strong differences in vital rates across habitats. They suggested that contrasting performances maintaining differences in tree density may arise during exceptional climatic events. In the context of a miombo forest, this could occur after fire events.

5. Conclusion

Demographic data in the miombo woodlands are scarce and the functioning of this forest type ruled by light partitioning but also water and nutrient shortage is comparatively less studied than wet and moist tropical forests. A consistent set of associations has been reported between tree vital rates, soil, stand structure and functional traits. We observed distinct drivers with varying relative importance for individual growth (functional dissimilarity with the neighbourhood, soil variables and stand structure), recruitment (mainly stand structure and soil) and survival (functional dissimilarity and soil).

The interplay of tree vital rates and functional traits highlighted a competitive hierarchy related to leaf traits among the species of some functional groups, but additionally showed more numerous positive effects of the functional neighbourhood on species growth, indicating overall a stronger effect of functional complementarity. These effects were proportionally weaker on recruitment and survival.

The study highlighted different trade-offs, two of them related to functional groups defined by H_{max}, leaf phenology and nutrient content, ectomycorrhizal status and mean demographic rates. One trade-off involved the access to light resource (H_{max}) opposed to higher

recruitment and fire tolerance, the other included a conservative against an acquisitive strategy for resources, probably edaphic (LN, LP, LCN). These trade-offs are two variants of the fast-slow continuum. Another trade-off affecting growth was linked to soil variables and could lead to habitat specialisation following a gradient water vs P availability associated to Al toxicity. This last trade-off was mostly active on the species sorting, according to their LDMC and LNP values.

This study illustrates how the analysis of the forest community through a combination of demographic rates and functional traits allows a functional interpretation of the observed variability of vital rates among tree species and provide unique insights into the mechanisms underlying forest structuration.

CRediT authorship contribution statement

Jonathan Muledi: Investigation, Writing - original draft. **David Bauman:** Investigation, Methodology, Software, Formal analysis, Writing - original draft. **Arnaud Jacobs:** Investigation, Writing - review & editing. **Pierre Meerts:** Conceptualization, Writing - review & editing. **Mylor Shutcha:** Conceptualization, Supervision. **Thomas Drouet:** Conceptualization, Investigation, Methodology, Software, Formal analysis, Writing - original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.117894.

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