

# Tree populations show low regeneration of valued species in West Africa

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## ABSTRACT

Tree populations have declined substantially in West Africa in recent decades, raising concerns since trees provide numerous ecosystem goods and services. Regional information on the population status of tree species could guide more effective conservation and regeneration of natural vegetation. Here, we report results of the first regional analysis of tree population structure across the Sahel and Sudan zones, a meta-study of vegetation

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inventories, including 23,586 individual trees sampled across nine countries. We evaluated current status and forecast future trends of 16 species and one genus of trees of ecological and socio-economic importance. Size class distribution (SCD) reflects the population structure of an individual species and can provide early warning of composition change and population decline. SCD is analysed widely at a local scale, but analysis at a regional scale is needed to detect widespread population changes. Many native species lacked trees in the smaller size classes, implying unsustainable populations and future decline. Some species show sound regeneration at the regional scale, but high variation among sites. Eight species, including *Adansonia digitata* and *Azizelia africana*, show regional declines in regeneration and risks of future extirpations. Four of these severely lack regeneration. Protected areas show higher tree regeneration, but protected status did not assure good regeneration. Our results identify priority tree species across West Africa, indicate a more urgent need for conservation and regeneration of native tree species, and highlight the benefit of effective conservation. More widespread protection could increase tree populations, conserving biodiversity, and ecosystem services essential for people's livelihoods.

## 1. Introduction

The Sahel and Sudan zones of West Africa have in recent decades experienced major environmental and socio-economic changes that have influenced landscape and people (UNCCD, 2019). The human population residing in the zone is among the fastest growing in the world, increasing more than six-fold from 1950 to 2022 and projected to double from 2022 to 2050 (UN, 2022). In addition, climate change has caused vegetation change (IPCC, 2022). As most people depend on land for agriculture, wood, and non-timber forest products, these trends put severe pressure on ecosystems and the associated ecosystem goods and services (Heubach et al., 2011; CILSS, 2016). Trees play a crucial role in providing goods as well as regulating climate, providing habitats for biodiversity, and contributing to carbon sequestration (IPBES, 2019).

Climate change, overexploitation, intensifying agriculture, browsing, and bushfire decrease the growth, survival, and regeneration of trees (Sambou, 2004; Staver et al., 2009; Amahowe et al., 2018; Dago et al., 2021). Tree densities have declined across the Sahel and Sudan zones from a combination of human impact, environmental stress and drought-induced tree mortality due to climate change (Gonzalez, 2001; Ouédraogo et al., 2006; Wezel and Lykke, 2006; Gonzalez et al., 2012; Balima et al., 2018). These declines raise major concerns since trees offer vital ecosystem goods and services, including habitat for animal and plant biodiversity, carbon sequestration, improved soil quality, shade, atmospheric water for precipitation, preservation of surface water, and control of floods and soil erosion (Amani et al., 2021; Nabaloum et al., 2022; Osman et al., 2023).

Size class distribution (SCD) of a tree species consists of the frequency of trees in different tree diameter size classes, indicating regeneration potential and offering insights on compositional and structural vegetation changes at the landscape level (Lai et al., 2006). The frequency of life stages in a tree population (referred to as tree population structure) investigated through SCD has proven useful for tracking the conservation status of individual species and monitoring composition changes (Hall and Bawa, 1993; Condit et al., 1998; Westphal et al., 2006; O'Connor and Goodall, 2017). An exponentially declining SCD with a high proportion of young individuals compared to older ones, also called a reverse J-shaped distribution, indicates a population with a good regenerative potential, whereas a SCD that is flat or completely lacks young individuals reveals a population in decline or at risk of extirpation (Merganić and Sterba, 2006; Glèlè Kakai et al., 2016).

An SCD shows a snapshot in time, and thus should be interpreted with caution. In the absence of long-term monitoring, however, SCDs constitute a good proxy for population regenerative potential and future population changes (Schumann et al., 2010; Ouédraogo et al., 2013). The shape parameter (*sh*) of a fitted Weibull function summarizes the form of the SCD and thereby the population structure, but it has limitations. It cannot reveal the underlying complexity, e.g. the absence of trees in particular size classes could be the result of natural vegetation dynamics or human impact. Despite this limitation, Weibull analysis of SCDs, combined with field experience, provides important information about the development of tree populations through space and time

(Schumann et al., 2011; Jurisch et al., 2012). Several studies have suggested management planning based on local SCDs, as these provide insight on declining tree species and forecast population changes (Sinsin et al., 2004; Djossa et al., 2007; Houéto et al., 2012; Idrissa et al., 2018; Birhane et al., 2020). Early warning of future threats to species that are apparently common, but lack proper regeneration, allow action to halt the decline at an early state when conservation or assisted regeneration is still a possibility. To inform conservation efforts, it is crucial to recognize declining tree species at different spatial scales.

The present study is the first regional-scale investigation of SCD patterns of West African tree species. The objective is to present an overview of tree population structure using a meta-approach and thereby determine regeneration potential of key tree species, investigate to what extent land protection affects tree population structure, and inform conservation and management decisions by forecasting population changes and trends at a regional scale.

## 2. Methods

### 2.1. Study design

Datasets from 37 scientists were compiled into one meta-dataset comprising 23,586 individual trees sampled across nine countries: Benin, Burkina Faso, Ghana, Côte d'Ivoire, Mali, Mauritania, Niger, Senegal, and Togo (Suppl. Mat. 1). All sites were situated in the Sahel and Sudan zones of West Africa, which extends ~2500 km from east to west and ~1000 km from north to south (Fig. 1). Based on scientific literature, we chose to focus on tree species that are socio-economically important to local communities and serve important ecological functions (Arbonnier, 2004; Lykke et al., 2021). We selected 16 species and 1 genus (hereafter referred to as 17 species): *Acacia senegal*, *Acacia nilotica*, *Adansonia digitata*, *Azizelia africana*, *Balanites aegyptiaca*, *Bombax costatum*, *Dalbergia melanoxylon*, *Daniellia oliveri*, *Detarium microcarpum*, *Diospyros mespiliformis*, *Ficus* spp., *Khaya senegalensis*, *Parkia biglobosa*, *Prosopis africana*, *Sclerocarya birrea*, *Tamarindus indica* and *Vitellaria paradoxa*. The genus *Ficus* included 23 species (see Suppl. Mat. 1). The number of individual trees per species varied from 132 to 6367.

### 2.2. Data preparation

The meta-dataset was compiled from field investigations with measures of tree diameter taken 1.3 m above the ground (referred to as diameter at breast height (DBH)) and with measures of trees down to 5 cm DBH. Only the largest stem was included in multi-stemmed individuals and only trees with DBH >5 cm were included to assure consistency among datasets. Most of the studies used stratified random sampling plots, which is the standard method for vegetation studies. A few were based on plotless sampling established in an overall stratified random design. Two studies used systematic sampling on grids. All data were merged into one Excel sheet, verified for misspellings, and, for data points with any questions, verified with the data provider. Geographic coordinates, name of collection site, and protection status were included

(see details on data preparation in Suppl. Mat. 1). Each data provider assigned protection status as either protected (national park or other government protected area) or unprotected (agricultural fields, pastures, unprotected savanna) (Suppl. Mat. 2).

### 2.3. Data analysis

A fitted Weibull distribution is often used to distinguish among different types of SCD due to its smoothing abilities. The mathematical definition of a Weibull distribution is:  $f(x) = \frac{sh}{sc} \left( \frac{x-\alpha}{sc} \right)^{sh-1} \cdot e^{-\left( \frac{x-\alpha}{sc} \right)^{sh}}$  where  $f(x)$  is the density function of trees,  $\alpha$  is the location parameter,  $sc$  is the scale parameter, and  $sh$  is the shape parameter. The location parameter  $\alpha$  determines the position on the x-axis and is equal to the minimum tree diameter. We set  $\alpha$  to 5 cm as default since this was the lowest DBH value included in the meta-dataset. The scale parameter  $sc$  determines the position of the peak of the curve. Finally, the shape parameter  $sh$  describes the shape of the curve. The latter is particularly useful as an indicator of the population structure. Values of  $sh < 1$  generally indicate populations with high regeneration (reverse J-shaped distribution), whereas values of  $sh$  near or  $> 1$  (flatter, unimodal, or left-skewed distributions) indicate populations with lower regeneration. Many factors affect the  $sh$  value and it must be interpreted with caution, but generally the higher the  $sh$ , the higher the tendency for population decline and vulnerability to extirpation (Merganić and Sterba, 2006; Glèlè Kakai et al., 2016). For all 17 species, SCDs were based on 5 cm wide DBH classes and Weibull distributions were fitted to the SCD using Maximum Likelihood estimation. For the six most common species (referred to as focus species) – *Azizelia africana*, *Balanites aegyptiaca*, *Daniellia oliveri*, *Detarium microcarpum*, *Diospyros mespiliformis*, and *Vitellaria paradoxa* – SCD plots were prepared for sites with sufficient sampling size and Weibull analyses were compared across groups defined by protection status and site. All statistical analyses were rendered in R (R Core Team, 2022) and the geo-spatial analyses in QGIS (QGIS.org, 2020).

## 3. Results

### 3.1. Population structure at the regional scale

The  $sh$  values describing the shape of the curve of the 17 species

ranged from 0.66 to 1.52 at the regional scale (Fig. 2). *Acacia senegal*, *Ficus* spp., *Acacia nilotica*, *Daniellia oliveri*, *Diospyros mespiliformis*, *Khaya senegalensis*, *Tamarindus indica*, *Detarium microcarpum*, and *Balanites aegyptiaca* all showed reverse J-shaped distributions with  $sh < 0.9$  indicating potentially stable populations with some regeneration at the regional scale. The  $sh$  value, however, masked local variations and irregularities in population structure of the species. *Acacia senegal* displayed an abrupt decline from the first to the second size class and several size classes had similar numbers of individuals. *Ficus* spp. showed a very steep decline from the 5–10 cm class to the 10–15 cm class. *Acacia nilotica* and *Khaya senegalensis* had similar numbers of individuals in the two smallest size classes.

For *Dalbergia melanoxylon*, *Vitellaria paradoxa*, *Parkia biglobosa*, and *Bombax costatum*,  $sh$  was near 1, indicating a moderate regeneration likely to be insufficient to maintain the population size. *Dalbergia melanoxylon* displayed an abrupt decline in numbers in size classes larger than 10–15 cm. *Parkia biglobosa* lacked individuals in the smallest size class. For four species,  $sh$  was between 1.1 and 1.6, indicating poor regeneration, discontinuous regrowth, or decline. *Prosopis africana*, *Sclerocarya birrea*, and *Azizelia africana* lacked individuals in the smallest size classes. *Adansonia digitata* showed a pronounced lack of regeneration with only 12 of 400 individuals with DBH  $< 20$  cm and half of the individuals with DBH  $> 150$  cm.

### 3.2. Protected versus unprotected areas

Protected areas displayed better regeneration potential as reflected in a lower average  $sh$  compared to unprotected areas, with the sole exception of *Daniellia oliveri* (Fig. 3).

### 3.3. Variation among sites

Several species showed high variation among sites. *Azizelia africana* had poor regeneration ( $sh > 1$ ) in 17 of the 18 sites where it occurred (Suppl. Mat. 3a). Good regeneration was limited to one site, Boukoussera. The species is presumably in decline or even at risk of extirpation throughout the region. *Balanites aegyptiaca* had stable populations in Welor Classified Forest and Gountouré, whereas other sites had poor regeneration, e.g. Gorom-Gorom, Tougan, and Kirtachi (Suppl. Mat. 3b). *Daniellia oliveri* had good regeneration in half of the sites and flatter or uneven distributions in the other half, indicating constraints in regeneration (Suppl. Mat. 3c). Three sites, Comoé-Léraba

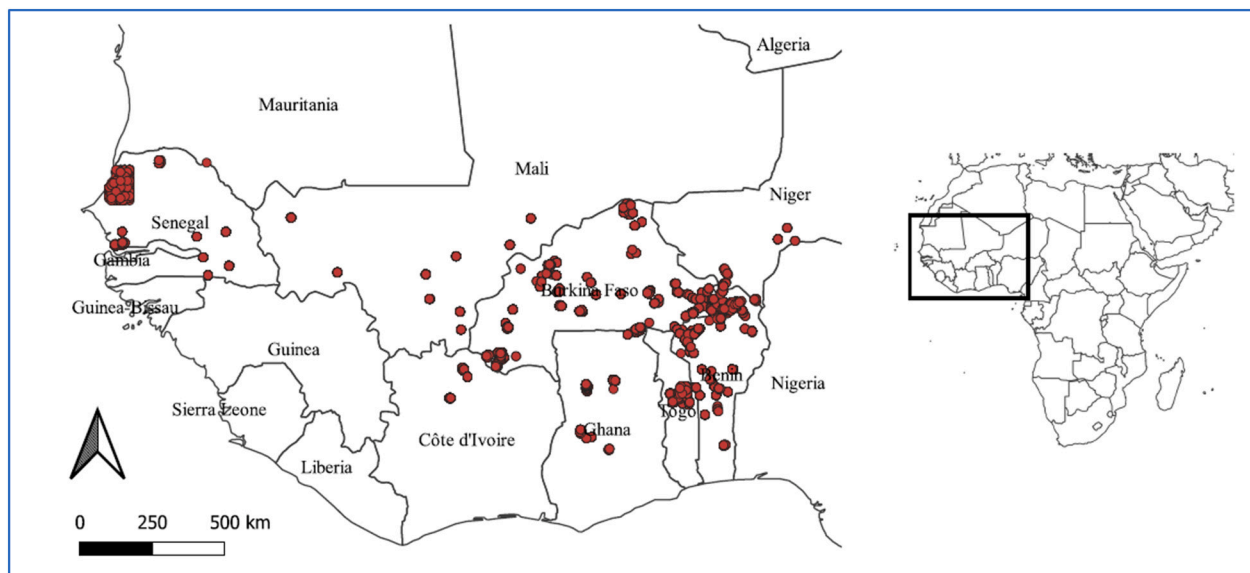
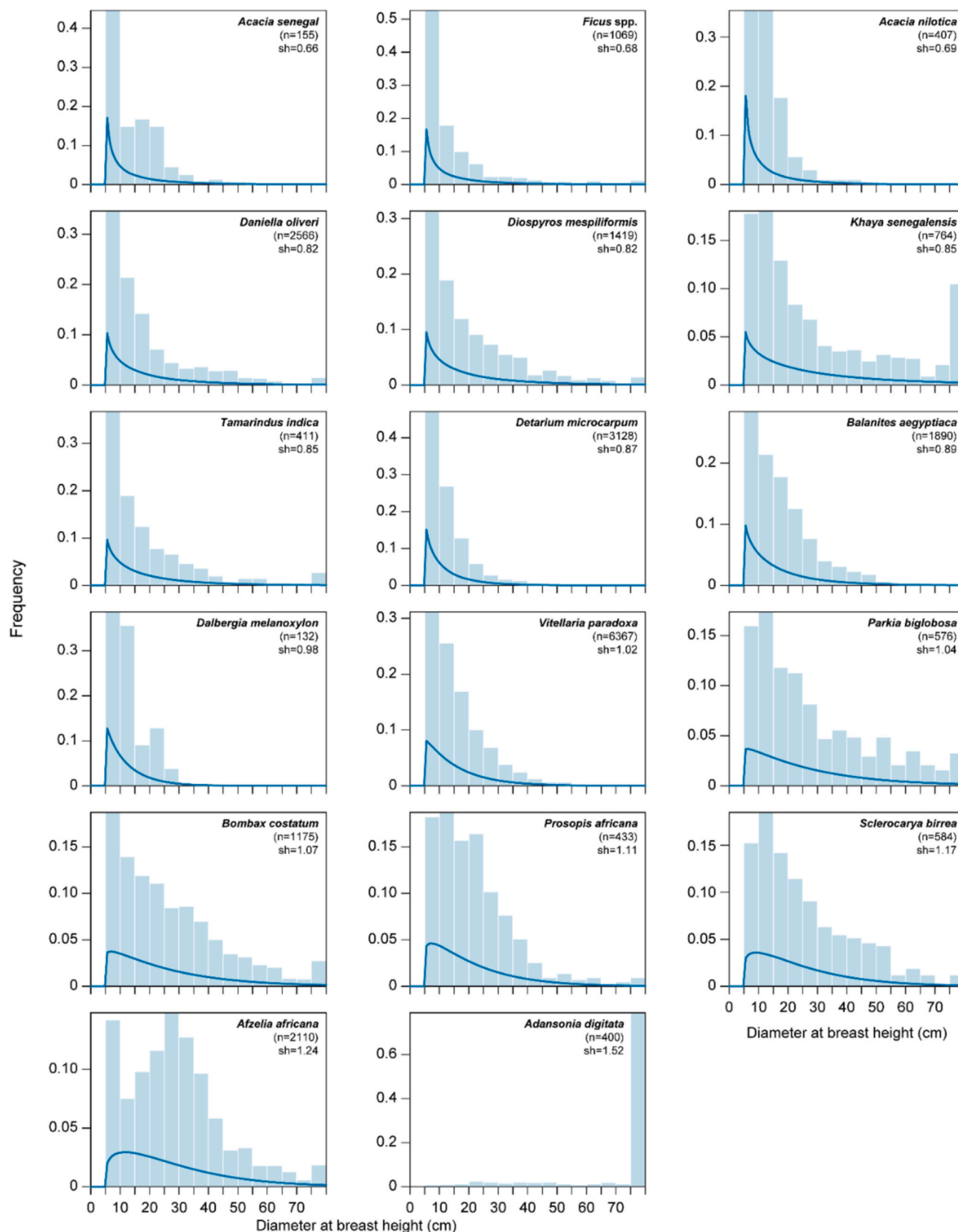


Fig. 1. Geographic location of sites included in the meta-dataset located across nine countries in the Sahel and Sudan zones of West Africa.



**Fig. 2.** Overview of population structure of 17 species based on size class distribution and Weibull analysis. Graphs are in order of increasing shape value (sh). All trees of DBH  $\geq 75$  cm were grouped into one class.



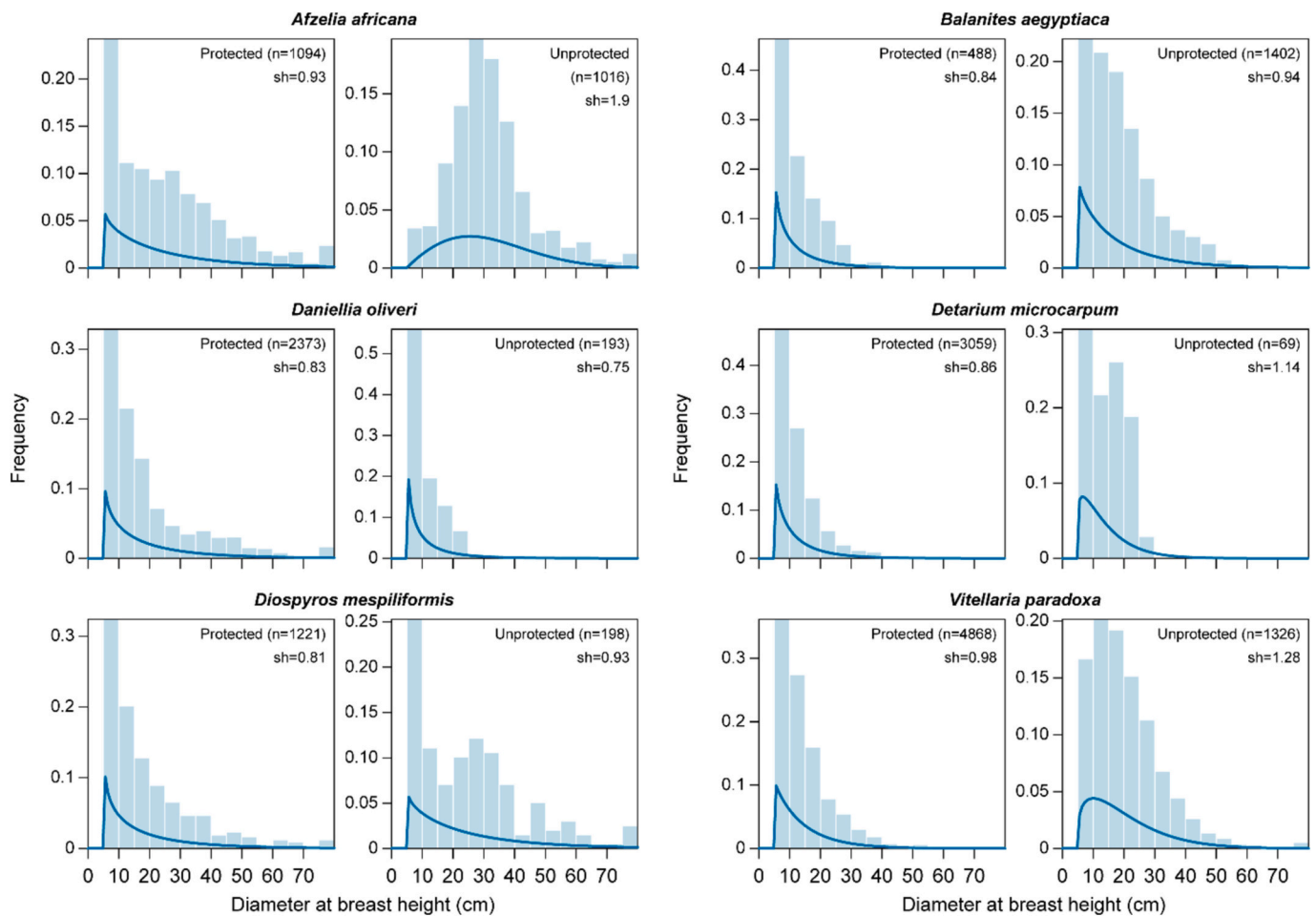


Fig. 3. Overview of population structure of six focus species based on size class distribution and Weibull analysis for protected and unprotected areas.

Reserve, Béléfoungou Classified Forest, and W National Park, had particularly poor regeneration. *Detarium microcarpum* showed good regeneration in three sites, Niangoloko and Boulon-Koflandé Classified Forests and Cassou; however, a distinct drop in the number of trees of DBH >10 cm was frequently observed. Very few trees had a DBH >20 cm and only W National Park had trees of DBH >30 cm (Suppl. Mat. 3d). Regeneration was particularly poor in Niokolo Koba National Park and Béléfoungou Classified Forest. *Diospyros mespiliformis* had good regeneration in several sites, although exhibited some unevenness among size classes. Several sites had poor regeneration, especially Gorom-Gorom, Bétérou, Lataha, and Béléfoungou Classified Forest (Suppl. Mat. 3e). *Vitellaria paradoxa* had some sites with good regeneration, e.g. Boulon-Koflandé Classified Forest and Larabanga, whereas regeneration was particularly poor in Toma, Tamale, and Béléfoungou Classified Forest (Suppl. Mat. 3f).

## 4. Discussion

### 4.1. First regional meta-data analysis of tree population structure

A meta-dataset is assembled from separate individual datasets and thus may suffer from inherent sampling skewness. In the present meta-dataset, areas under some type of government protection, such as national parks and classified forests, are overrepresented since they are often favoured by ecologists. Likewise, more studies have been conducted in fields and pastures with high tree density as compared to agricultural areas with no or few trees. Furthermore, data were collected over a 30-year period, with the chance that some of the patterns described could have changed since then. The data set is therefore

skewed towards sites with better conservation status. Even though the results of the present meta-analysis should be interpreted with caution given these limitations, they still represent a unique source of information that will enable us to gain deeper insight into the regenerative potential of key tree species and forecast vegetation dynamics to inform conservation and restoration efforts.

### 4.2. Use and limitations of regional Weibull analysis

The Sahel and Sudan zones cover extensive areas with numerous vegetation types and land use systems. Since the SCD of a given species at the regional scale combines the data obtained across all sites, it may not reflect the high variation that may exist among individual sites. Although SCDs can show some regeneration potential at the regional scale, an examination of local studies provides a deeper understanding of long-term consequences of different types of impact at specific sites, e.g. for *Afzelia africana*, one site accounted for most of the regeneration, raising concern for the long-term fate of the species.

Summarizing SCDs with a single parameter derived from the fitted Weibull function is useful for comparative purposes, although it has limitations. The overall shape of the curve, as described by the  $sh$  value, is affected by skewness, kurtosis, position of the curve, range of data, and irregularities in SCDs. Thus, it is necessary to interpret SCDs carefully and draw on experience from field observations. High  $sh$  values and lack of individuals in the smallest size classes most likely reflect declining populations, whereas low  $sh$  values can be caused by several factors. Some species with a low  $sh$  value at the regional scale, e.g. *Acacia senegal* and *Acacia nilotica*, had abrupt deficits of trees in the 10–15 cm DBH class. These species are used for multiple purposes such

as gum, timber, firewood, tannin, and livestock fodder. The irregular SCDs are most likely not driven by natural processes but are the result of extracting trees in certain diameter size classes to obtain wood (Wezel and Lykke, 2006; Ganaba, 2011). *Ficus* spp. showed similar irregular distributions and low representation in certain diameter size classes, which could be caused by fire, drought, bark extraction, or logging for firewood and charcoal (Atakpama et al., 2019; Raji and Downs, 2021). Thus, SCDs with relatively high numbers of individuals in small size classes compared to larger classes could arise from human selection of trees in certain diameter classes, rather than abundant regeneration. Low *sh* values therefore need scrutiny to uncover the underlying causes, whereas high *sh* values generally are signs of low regeneration.

#### 4.3. Effects of protected areas

Protected areas showed more stable population structures than unprotected areas, indicating that human-induced disturbances outside protected areas hinder persistent regeneration. Despite the insufficient management of many protected areas (Houehanou et al., 2013; Mensah et al., 2014), this finding underscores the importance of conservation measures. Five out of six focus species showed better regeneration in protected areas than in unprotected areas. *Daniellia oliveri* was an exception. As it produces large numbers of saplings, it is less vulnerable to overexploitation (Lykke, 1998; Schumann et al., 2011), but a steep decline of trees with DBH >10 cm in protected areas suggested cutting for timber. Despite overall better regeneration in protected areas, several species showed poor regeneration in some protected areas perhaps because of fire, grazing, illegal logging, or overexploitation (Ouédraogo et al., 2006; Ganaba, 2011; Houehanou et al., 2013). In conclusion, protected areas had an overall positive effect on tree regeneration, but protected status did not assure good regeneration.

#### 4.4. Drivers of tree regeneration

To inform conservation and management efforts, it is important to gain a better understanding of the drivers of tree regeneration patterns (McLaren et al., 2005; Schumann et al., 2011; Sabo et al., 2023). *Diospyros mespiliformis*, a multipurpose species, source of hard wood, and an indicator of well-protected gallery forests showed good regeneration in some sites, but poor regeneration in several others, for example, Béléfoungou Classified Forest and Gorom-Gorom, possibly because of degradation of the gallery forests (Lykke et al., 2004). For two valuable timber species, *Diospyros mespiliformis* and *Daniellia oliveri*, trees of DBH >10 cm were underrepresented, possibly an effect of timber exploitation (Gwali et al., 2010; Lykke et al., 2021). Several studies have emphasized that extraction of hard wood and non-timber forest products could lead to a decline of tree populations in the future (Djossa et al., 2007; Fandohan et al., 2010; Idrissa et al., 2018; Gaoue and Ticktin, 2008; Jurisch et al., 2013).

Several of the species endangered by future population decline were exposed to harvest pressure. This applies particularly to *Dalbergia melanoxylon*, which yields some of the most valuable wood in the Sahel. The regional SCD revealed very few trees with a DBH >20 cm. The species is generally considered declining in West and East Africa (Lykke et al., 1999; Ouédraogo et al., 2006; Nyomora et al., 2021). IUCN (2024) classifies it as 'Near Threatened' and CITES (2024) considers it threatened in West Africa unless its trade is regulated. *Parkia biglobosa* is an important component of many agroforestry systems due to its seeds, which are highly appreciated as a fermented food stock. Although IUCN (2024) lists it as being of 'Least Concern', we found poor regeneration and risks of population decline. Several studies have reported seed overharvesting and seedling removal by agricultural practices (Dotchamou et al., 2016; Gaisberger et al., 2017; M'Woueni et al., 2019). The same pattern was observed for *Vitellaria paradoxa*, which IUCN (2024) lists as 'Vulnerable'. The fruits are processed into shea butter, which is traded locally and internationally, providing a major

source of income for many smallholders (Aleza et al., 2015; Dimobe et al., 2020; Nguekeng et al., 2021). Despite its high value, this species lacked regeneration in Tamale and Béléfoungou as a result of agricultural intensification. *Bombax costatum* is less studied, though appreciated for its edible calyces and durable wood. It showed a similar lack of regeneration in the regional SCD, suggesting unsustainable logging and cutting of branches (Zerbo et al., 2022). Even though farmers prefer to maintain these highly appreciated species in the fields, continuous degradation is driven by human activities, such as intensified agricultural practices, overharvesting of fruits, clear cutting, and wildfires (Lykke, 1998; Djossa et al., 2007; Ouédraogo and Thiombiano, 2012). To avoid a future collapse of the tree populations, transformative change is needed for more sustainable agricultural and harvesting practices.

#### 4.5. Particularly vulnerable tree species

The results forecast potentially severe declines for some species, including the iconic baobab (*Adansonia digitata*). Unsustainable pruning and leaf harvesting for food and fodder reduce flowering and fruit set, while grazing livestock damages or kills seedlings. Similar negative trends were found in southern Africa (Venter and Witkowski, 2013). The regional SCD of African mahogany (*Azelia africana*), one of the most valuable hardwood timber species in the region, revealed a severe lack of regeneration. IUCN (2024) classifies *Azelia africana* as 'Vulnerable' and without action, some populations are at risk of extirpation and CITES (2024) lists *Azelia africana* as a species for which control of commercial trade is required to avoid extinction. In Boukoussera and Loughba, successful regeneration occurred in plantations protected from wildfires and livestock browsing (Amahowe et al., 2018; Balima et al., 2022; Houehanou et al., 2013; Sinsin et al., 2004). *Sclerocarya birrea* is highly appreciated for its edible fruits. It was underrepresented in the smaller size classes, which indicates a population in decline. Earlier studies that observed a decline of this species cite unsustainable wood harvesting, agriculture, and drought as immediate threats (Gouwakinnou et al., 2009, 2011). *Prosopis africana* had poor regeneration. It is exploited for its termite-resistant wood and valuable fodder. Several other studies have forecasted a decline of this species (Lykke, 1998; Weber et al., 2008; Abdou et al., 2016).

#### 4.6. Conservation and management

This research provides new information on four issues to guide biodiversity conservation efforts and natural resource management practices. First, the regional results identify priority tree species for regeneration of natural vegetation in West Africa. We found a severe lack of regeneration in four species: *Adansonia digitata*, *Azelia africana*, *Sclerocarya birrea*, and *Prosopis africana*. Second, the extirpation risk of eight of the species in this research indicates an urgent need for conservation and regeneration. This is consistent with global analyses indicating a high risk of tree loss in the Sahel and Sudan ecological zones due to climate change, agricultural expansion, logging, and increasing wildfire (Boonman et al., 2024). Third, our results show that regeneration potential is site-specific, meaning that the choice of natural resource management practice – conservation, natural regeneration, assisted regeneration, plantation – requires a site-specific tree inventory. In many parts of the Sahel and the Sudan, small trees (DBH < 5 cm) are abundant enough that the traditional practice of natural regeneration – selecting small trees, pruning, protecting, and raising them to maturity – can successfully restore tree cover (Gonzalez, 2001; Gonzalez et al., 2012; Reij and Garrity, 2016; Hérault et al., 2020). Sites without small trees would require assisted regeneration – reseedling or filling gaps with planted trees. Fourth, the results highlight the benefit of effective conservation of national parks and other protected areas. Even more important than formal declaration of a protected area is effective conservation of the area (Arneth et al., 2023), ideally through community-based natural resource management.

## 5. Conclusion

Regional analysis of SCD is useful to highlight widespread decline and the urgent state of tree populations at risk of collapse, most notably, in this study, populations of iconic species like the baobab and African mahogany. SCDs also provide a means for early warning of conservation needs for species that are apparently common, but without proper regeneration, here exemplified by *Sclerocarya birrea* and *Parkia biglobosa*. Such information is important to halt decline at an early state, when conservation or assisted regeneration is still a possibility. Scrutiny of the variation among local SCDs provides information on successful and unsuccessful land-use planning and management practices for individual tree species, including conservation, natural regeneration, assisted regeneration, and tree planting. Conservation and management practices can be examined for sites with good regeneration and offer models for sites with less successful regeneration patterns.

## CRedit authorship contribution statement

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## Declaration of competing interest

All persons entitled to authorship have been included. All authors have read the submitted version of the manuscript and approve its submission. Any research in the paper not carried out by the authors is fully acknowledged in the manuscript.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2024.110891>.

## Data availability

Data will be made available on request.

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