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Research article

Revisiting biotic and abiotic drivers of seedling establishment, natural enemies and survival in a tropical tree species in a West Africa semi-arid biosphere reserve

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ABSTRACT

Biotic and abiotic drivers of seedling establishment and survival are fundamental not only for elucidating processes occurring at plant early life stages, but also for assisting species natural regeneration. Keystone, multipurpose and economically important tree species such as *Afzelia africana* Sm. are reportedly facing recruitment constraints, yet little is known about how abiotic and biotic factors shape the species seedling dynamics. Here, we monitored the species seedlings over one year across three seasons in West Africa savannahs to determine how conspecific and heterospecific biotic neighborhood and habitat heterogeneity correlate with initial seedling density, leaves' fungal infection and herbivory and how all these factors combined, influence the species seedling survival.

Seedling densities increased with increasing conspecific adult densities, and were highest in tree savannahs and on sandy-silt soils. Leaves' fungal infection and herbivory were also positively associated with conspecific adult density, but were more abundantly observed in tree savannahs than in shrub savannahs. Seedling survival was constrained on higher slope, and negatively affected by conspecific adult density, especially in shrub savannahs.

There was a strong evidence for negative density-dependence effects of conspecific adults on seedling survival, which operated through negative effects of herbivory and fungal infection. Habitat heterogeneity was also an important driver, which modulated biotic factors' effects on seedling survival: tree savannahs promote positive conspecific density-dependence of seedling fungal infection and herbivory more than shrub savannahs. Nonetheless, seedlings were more sensitive to natural enemies in shrub savannahs, suggesting increased negative conspecific density-dependence effects on seedling survival in less dense vegetation, possibly as a result of enhanced specialization of predators and pathogens on a limited set of species. The study brings important insights into the mechanisms that drive the establishment and survival of the species seedling, which should be considered in the design of management activities aiming at the conservation of this endangered species.

1. Introduction

The International Union for Conservation of Nature (IUCN) classified *Afzelia africana* Sm. (Fabaceae-Caesalpinioideae), as vulnerable across its native range of distribution: West, Central and East Africa. However, recent studies and reports consistently pointed to a critical conservation status of the species in West Africa (Assogbadjo et al., 2017; Nacoulma et al., 2017) and East Africa (Biara et al., 2020), due to increased interest in its wood and services. There are also studies that further reported a number of constraints hindering *A. africana* natural regeneration:

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logging activities, uncontrolled exploitation of bark and leaves for valuable medicinal and fodder purposes, mammal browsing, fires, and recruitment bottleneck at the juvenile stage (Amahowe et al., 2019; Ouédraogo and Thiombiano, 2012; Sinsin et al., 2004; Zida et al., 2007). In West Africa (e.g., Burkina Faso and Benin), studies on *A. africana* argued for the poor regeneration potential, as a result of high sensitivity of seedlings to fire, browsing and drought (Bationo et al., 2001, 2000) and increased logging pressure on adult individuals (Mensah et al., 2014; Sinsin et al., 2004). Because early plant survival is a biological process structuring and shaping plant species composition and dynamic (Harcombe, 1987), it is important that we understand the relative importance of the biotic factors affecting plant survival at the early stages for better insights, prediction, conservation and management. It is equally important to assess how the species seedlings respond to abiotic variables, and which of the biotic and abiotic variables are likely to promote the species seedling survival.

Habitat type and abiotic factors are known to define resources availability and utilization, species coexistence and structuring patterns (Comita et al., 2009; Yan et al., 2015). For instance, habitats with more individual trees create microsites with favorable environmental conditions that facilitate establishment and survival and early recruitment, as shown for example for conifer seedlings (Legras et al., 2010; Maher et al., 2005). These habitats also promote litter fall, which in turn generates favorable microsites for species regeneration (Facelli and Pickett, 1991) and promotes seedling growth or resistance to mortality through litter decomposition and nutrient availability (Brearley et al., 2003). Abiotic factors such as climate, light, soil and topography co-determine resources availability, which influence the distribution, abundance and composition of seedlings, saplings and adult trees (Comita et al., 2009; García-Guzmán and Benítez-Malvido, 2003). Further, topography can induce heterogeneity in other abiotic components such as soil moisture and belowground nutrients, which are important for plants (Daws et al., 2002). For instance, slope influences gravity-driven processes and displacement of eroded soil material, water, and plant debris, which are important for stem growth; steeper slope could constrain stem mechanical stability and growth, while increasing nutrients and water runoff (Mensah et al., 2016).

Low recruitment potential can also be attributed to difficult seedling emergence and high mortality due to biotic processes such as plant–-plant interactions (competition or allelopathy) and plant-animal interactions (predation, herbivory). On the one hand (plant–plant interactions), heterospecific individuals and conspecific adults may have negative effects on initial seedling survival by competing for resources (Comita et al., 2009; Lin et al., 2014), either individually (via specific traits and growth mechanisms; Lu et al., 2015; Umaña et al., 2018) or relatedly (via phylogenetic relatedness structure of neighbors; Webb et al., 2006). On the other hand (plant–animal interactions), abundance and proximity of conspecific adults may attract host-specific predators or pathogens and mammal herbivores, leading to considerable negative impact on survival and recruitment of natural regeneration, in line with the Janzen-Connell hypothesis (Connell, 1971; Janzen, 1970). Specialized natural enemies such as fungi, herbivores and soil pathogens often maintain biotic interactions with their hosts (Bagchi et al., 2014; Wright, 2002), which possibly increase mortality or reduce growth for seedlings located close to reproductive adults or in areas of high conspecific density, in line with the natural enemies-mediated conspecific negative density dependence (CNDD) mechanism. CNDD would eventually be strong as predators and pathogens would tend to specialize on a given species. Accordingly, some previous studies that investigated the effects of local biotic neighborhoods on seedling survival have lent support to CNDD (Bai et al., 2012; Comita et al., 2009; Johnson et al., 2017; Queenborough et al., 2007). Nevertheless, conspecific positive density dependence (CPDD) can also occur if (i) conspecific seedlings and adult trees facilitate seedling survival of the focal species; (ii) habitat preferences lead to clustering of conspecifics (Inman-narahari et al., 2016); or (iii) as predicted by the stress gradient hypothesis, facilitation increases and competition decreases with higher abiotic stress (Bertness and Callaway, 1994; Jia et al., 2011).

Because simply categorizing biotic neighborhood effects into conspecifics and heterospecifics may obscure the variation in the effects of different species on any focal species, recent studies have also suggested to incorporate phylogenetic relatedness structure of neighbors in biotic neighborhood analyses (Paine et al., 2012; Webb et al., 2006; Wu et al., 2016). This is primarily because (i) phylogenetically close species are closely related, thus are more likely to share the same or similar pests and pathogens (Liu et al., 2012; Webb et al., 2006) and (ii) the effect of neighbors on a focal plant could be higher if they are phylogenetically similar, and lower if they are phylogenetically distant and less related (Cao et al., 2018; Zhu et al., 2017). Further, in a recent study, Wu et al. (2016) reported that a failure to account for habitat variables and phylogenetic relationships may obscure the importance of conspecific and heterospecific neighbor densities for seedling survival, also supporting the importance of phylogenetic relatedness structure.

While biotic and abiotic factors are expected to play a vital role in maintaining species diversity in tropical forests, their mutual interaction and relative importance for promoting the conservation of endangered species is still highly debated. For instance, individual and interactive effect of abiotic and biotic factors may vary on temporal and taxonomic scales (Comita et al., 2009; Inman-narahari et al., 2016; Queenborough et al., 2009). On the other hand, the effect of biotic factors may strongly depend on that of the abiotic ones. For example, abiotic factors such as vegetation and soil types may differently attract natural enemies such as pathogens and insect herbivores that may have negative incidence on seedlings. Similarly, differential topographical patterns, including slope, elevation and aspect, modulate light and wind exposure, solar irradiance and soil moisture, which can change the spatial pattern of fungal outbreaks, as shown in temperate forests (Solla and Camarero, 2006).

Here, we analysed both abiotic and biotic factors governing *A. africana* seedling establishment, natural enemies and survival. The study was conducted in the Pendjari Biosphere Reserve (PBR), a semi-arid environment located in the Sudanian zone in the north-west part of the Republic of Benin in West Africa. First, we explored the variation in seedling density, fungal infection and herbivory patterns between the censuses. We did this mainly to determine whether seasonality would influence the seedling density, fungal infection and herbivory patterns. Second, we evaluated the relative importance of abiotic and biotic drivers of *A. africana* seedling establishment, leaves' fungal infection and herbivory. Specifically, we analysed the response of *A. africana* seedling density, leaves' fungal infection and herbivory to conspecific and heterospecific biotic neighborhood and habitat heterogeneity. We expect (i) more seedlings with increasing conspecific adult densities and (ii) increased fungal infection and herbivory with increased conspecific seedling and adult densities. While we expected these CPDD effects (Fig. 1), we also expected that habitat (e.g., vegetation and soil types) heterogeneity would modulate *A. africana* seedling establishment and response to leaves' fungal infection and herbivory, but we do not know the magnitude and direction of these effects. Third, we assessed how *A. africana* leaves' fungal infection and herbivory, in addition to the habitat heterogeneity (vegetation and soil types, slope, elevation, number of mounds), biotic neighborhood (heterospecific density, conspecific adult density and species phylogenetic relatedness structure) determined the species seedling survival. We hypothesized that seedling survival would be more responsive to biotic factors than abiotic ones (Fig. 1), due to the microscale coverage of the study. Finally, taking into account habitat heterogeneity, we analysed the direct and indirect (via natural enemies – fungal infection, and herbivory) effects of adult biotic neighborhood on the species seedling survival. We hypothesized that habitat heterogeneity would mediate how adult biotic neighborhood would attract natural enemies and their influence on seedling survival.

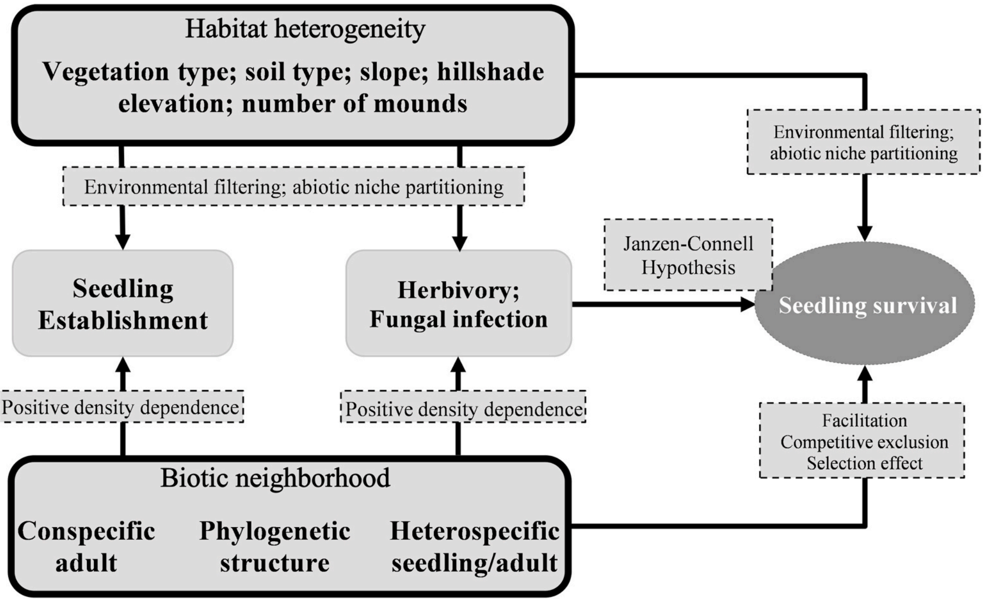

Fig. 1. A conceptual framework explaining (i) how seedling establishment (densities) and natural enemies (fungi and herbivores activities) are determined by habitat heterogeneity (via environmental filtering, and abiotic niche partitioning) and biotic neighborhood (density dependence); and (ii) how conspecific and heterospecific biotic neighborhood and habitat heterogeneity, in addition to natural enemies are expected to influence seedling survival.

2. Material and methods

2.1. Study area

The present study was conducted in the Sudanian zone of the Republic of Benin. Out of the three climatic zones (Guinean, Sudano-Guinean, and Sudanian) covered by the country, the Sudanian zone is the driest. The Sudanian zone also falls under the West African semi-arid zone, which covers the southern parts of Senegal, Gambia, Mali, Niger, Chad and upper parts of Guinea-Bissau, Guinea, Togo, Benin, Nigeria, and Cameroon. The data used in this study were collected in the Pendjari Biosphere Reserve (10°40′–11°28′N and 0°57′–2°10′E) in the Sudanian zone. The reserve covers a total area of 4661 km^2, which comprises the Pendjari National Park (2660 km^2), the Pendjari hunting zone (1750 km^2) and the Konkombri hunting zone (251 km^2). The Pendjari Biosphere Reserve belongs to the W-Arly-Pendjari (WAP) national parks, a trans-frontier network of reserves between the republics of Niger, Burkina Faso and Benin.

The climate is that of West Africa semi-arid zone (750–1250 mm of annual rainfall), and characterized by a unimodal rainy season (May to October), and a dry season (October–April). The annual rainfall is 1100 mm and annual mean temperature 26.6 °C (Atanasso et al., 2019). The vegetation is a mosaic of shrub and tree savannahs, woodlands, grasslands, gallery forests or riparian forests and dry forests, with savannahs being the most dominant. These formations provide habitat to many species of fauna, including a great variety of bird species. The most dominant species include Sudanian or Sudano-Guinean species such as *Vitellaria paradoxa* C.F. Gaertn., *Lannea acida* L., *Pterocarpus erinaceus* Poir. *Detarium microcarpum* Guill. and Perr. and *A. africana* Sm.

2.2. Sampling and data collection

Data were collected following four transect-lines of 1.5 Km each, randomly established across four *A. africana* stands identified in a recent study (Atanasso et al., 2019). These stands cut across two main vegetation types namely trees and shrubs savannahs. There was a minimum distance of 1 km between two consecutive transects. A total of 146 permanent regeneration plots of 10 m × 10 m were established along the four transect lines, with a fixed distance of 40 m between two consecutive plots. Information on abiotic variables such as soil type, number of mounds, slope and elevation were recorded at plot level during the first census only. Three types of soils were identified: silty-sandy, silty-clayey and rocky. Slope was measured using a clinometer and varied from 0.5 to 40% while elevation, taken at the corner of each plot using a Global Positioning System, ranged from 216 to 387 m.

Within each plot, the following primary biotic data were collected: *A. africana* seedling abundance, basal diameter and stem height. Seedlings were considered as any plant with a height < 1m. This is because at that stage, individual seedlings are generally highly sensitive to biotic and abiotic factors and mortality. Other biotic variables recorded included conspecific adult density, heterospecific density and natural enemies in each seedling biotic neighborhood (Chanthorn et al., 2013; Comita et al., 2009). For natural enemies, we collected information on fungal infection and insect and mammal herbivory on *A. africana* seedlings. Fungal infection on *A. africana* was measured as presence/absence of gall cluster on all *A. africana* seedlings within each plot (Chanthorn et al., 2013). Similarly, herbivory (by insects and mammals) was measured as presence/absence of opened, cut and removed leaves. Data were first collected in June 2016 in the rainy season, following a North-South direction; each *A. africana* seedling identified in the first census, was tagged with a unique number, to facilitate further data collection during the two additional censuses at the beginning (October 2016) and towards the end of dry season (March 2017), where survival was measured at individual level (as 1 if the seedling was identified in the subsequent census, and 0 if not).

2.3. Statistical analyses

2.3.1. Assessing the variation in seedling density, fungal infection and herbivory patterns between the censuses

We expected that seedling characteristics would vary across the three censuses. Therefore, we used boxplots to explore the variation in seedling density, fungal infection and herbivory patterns between the censuses (Supplementary Information SI1). We performed this analysis mainly to determine whether seasonality would influence the seedling density, fungal infection and herbivory patterns.

2.3.2. Assessing the relative importance of abiotic and biotic drivers of seedling establishment, leaves' fungal infection and herbivory

We analysed the response of *A. africana* seedling density, leaves' fungal infection and herbivory to conspecific and heterospecific biotic neighborhood and habitat heterogeneity, by testing for significant fixed effects of vegetation and soil types, slope, elevation, number of mounds, conspecific adult density and heterospecific density, using Generalized Linear Mixed Models (GLMM), with transect as a random factor. Seedling density (count data) was modelled using the negative binomial distribution after testing for over-dispersion with the package "qcc" in the R statistical software version 4.0.0 (R Core Team, 2020), and comparing the fits of Poisson regression, quasi-Poisson regression and negative binomial regression (Zuur et al., 2009). Fungal infection was quantified using plot level number of seedlings with fungus-infected leaves. Herbivory (both insect and mammal) was quantified using plot level number of seedlings with leaves showing both insect and mammal herbivory. Using the same independent variables and incorporating conspecific seedling diameter (hereafter stem size) as potential driver of natural enemies in the modelling procedure described above, we performed negative binomial GLMMs for fungal infection and herbivory separately. The GLMMs were fitted by maximum likelihood (ML) method (Bates et al., 2015), and for each census (Supplementary Information SI2). Due to the high number of independent variables and the likelihood of autocorrelation, a multimodel inference followed by a full averaging procedure using the package "MuMIn'' (Barton, 2018), was performed on the negative binomial GLMMs, in order to determine which model best fits the data (Mensah et al., 2018b). The optimal models were selected based on the Akaike Information Criterion (AICc). Small difference (<2) in AICc between two subset models indicates that these models are equally supported. The model-averaged coefficients were obtained using the subset of models with ΔAICc <2. In addition to the significance of the predictors retained in the finally selected models, we computed for all predictors their relative importance (Supplementary Information SI3). For easier interpretation of the results, bivariate relationships and boxplots were also constructed. Vegetation and soil types were treated as categorical abiotic variables. When fitted models showed significant vegetation and soil effects, further models were fitted for each vegetation and soil type to examine whether the effect of biotic and abiotic interactions varied with habitat heterogeneity (Supplementary Information SI4).

2.3.3. Assessing seedling survival response to biotic neighborhood, leaves' fungal infection and herbivory and habitat heterogeneity

We also assessed how *A. africana* seedling survival was influenced by biotic neighborhood, leaves' fungal infection and herbivory, and habitat heterogeneity. Survival was quantified at plot level as the number of seedlings that survived during the last census over the total number of seedling initially identified during the first census. In addition to conspecific adult density and heterospecific density which can influence seedling survival, previous studies have suggested to incorporate phylogenetic relatedness structure of neighbors in biotic neighborhood analyses (Paine et al., 2012; Wu et al., 2016). Accordingly, we first constructed a phylogenetic super-tree of all species in our plots (Supplementary Information SI5), using Phylomatic (http://www.phylodiversity.net), which utilizes the Angiosperm Phylogeny Group III phylogeny as a backbone. These trees were constructed using the updated time-calibrated phylogeny of seed plants using multigene molecular and fossil data (Zanne et al., 2014). From these phylogenies, we then computed the plot level net relatedness index (NRI; see Webb et al., 2006 and Zhu et al., 2017), which is the standardized effect size of the mean pairwise distance between species in each plot, calculated by comparing the observed phylogenetic relatedness to the pattern expected from a null model of phylogeny randomization.

In addition to the abovementioned habitat heterogeneity variables, we included hillshade, which is based on an overall consideration of aspect, slope, mean annual solar azimuth and altitude (or zenith) (Burrough and McDonell, 1998). Hillshade has been shown to have significant or marginally significant positive effect on survival of evergreen, shade-tolerant, and hygrophilous trees in an old-growth temperate forest (Zhu et al., 2017). Data on hillshade were extracted from a digital elevation model with a resolution of 30 m × 30 m using the plot coordinates and packages 'raster', 'sp' and 'rgdal' in R software. We used a generalized linear model (binomial GLM) to test for initial leaves' fungal infection and herbivory, habitat heterogeneity (vegetation and soil types, number of mounds, slope, elevation and hillshade), conspecific adult density, heterospecific density and net relatedness index effects on the species seedling survival. Because of the high number of variables and possibility of confounding effects (see Supplementary Information SI6), we also fitted three binomial GLMs, separately for (i) habitat heterogeneity (vegetation and soil types, number of mounds, slope, elevation and hillshade; i.e. 'habitat' model), (ii) conspecific adult density, heterospecific density and net relatedness index (i.e. 'community' model), and (iii) fungal infection and herbivory (i.e. 'natural enemies' model). Note that because of the high number of predictors for the 'habitat' model, we additionally performed a step-wise elimination of non-significant effects (p-value > 0.05) to select the best fitting model.

Finally, we used Structural Equation Modelling (SEM) to test for possible mediation by natural enemies (fungal infection and herbivory) of the adult biotic neighborhood effect on seedling survival, in addition to habitat heterogeneity. To simplify the analytical framework of the SEM, we only considered the independent variables that were significant in the previous models, and combined fungal infection and herbivory into a defined latent variable termed as "natural enemies" (Mensah et al., 2020a). We fitted two separate SEMs respectively for the two vegetation types (tree savannahs and shrub savannahs), testing for seedling survival response to conspecific adult density via natural enemies (fungal infection and herbivory), in addition to the effects of terrain slope and elevation (which were retained in the GLMs). Prior to the SEMs, data were transformed for linearity. The SEMs were fitted using "lavaan" package (Rosseel, 2012) in the R statistical software. The goodness of fit of the SEM was assessed using the Chi square statistic, comparative fit index (cfi), and root mean square error of approximation (rmsea) (Grace and Bollen, 2005; Mensah et al., 2020b, 2018a).

3. Results

Seedling density generally decreased over time from the first census to the final (SI1). A significant decline was observed between the second census (beginning of dry season) and the third census (end of the dry season). In contrast, leaves' fungal infection and herbivory did not differ significantly between the first and second censuses (SI1).

3.1. Effects of biotic neighborhood and habitat heterogeneity on A. africana seedling density, leaves' fungal infection and herbivory

Results of the initial and finally selected negative binomial GLMMs are presented in SI2 and Table 1, respectively. There were significant effects of conspecific adult density, vegetation and soil types on *A. africana* seedling density (Table 1; SI2). Initial seedling densities increased significantly ($\beta = 0.61$; $p < 0.001$; Table 1) with increasing conspecific adult densities (Fig. 2). Shrub savannahs showed a regression coefficient which was 1.28 significantly lower than that of the baseline (i.e. tree savannahs), indicating that seedling densities were higher in tree savannahs than in shrub savannahs (Fig. 2). Sandy silt soils also exhibited higher seedling densities than silty clay and rocky soils ($\beta = 1.06$; $p < 0.001$; Table 1; see also Fig. 2). In general, the most important factors for *A. africana* seedling density are conspecific adult density, vegetation and soil types (Fig. 3). Unlike these factors, heterospecific density and elevation showed non-significant effects, although being retained in the final model (Table 1).

Increasing conspecific adult density also increased significantly

Table 1

Final selected model resulting from the multi-model inference on the GLMM with biotic and abiotic factors influencing initial (first census) seedling densities, leaves' fungal infection and herbivory. Graphical representation of significant effects are presented in Fig. 2. The original fitted full models for the three censuses are presented in supplementary information SI2. P-values lower than 0.05 are indicated in bold. Legend: Est coefficient estimate; adj.SE adjusted standard error.

Explanatory variables	Initial seedling density		Fungal infection		Herbivory	
	Est±adj.SE	Pr(>|z|)	Est±adj.SE	Pr(>|z|)	Est±adj.SE	Pr(>|z|)
Conspecific adult density	0.611 ± 0.172	**<0.001**	0.035 ± 0.012	**0.004**	0.035 ± 0.010	**0.001**
Heterospecific density	0.080 ± 0.137	0.558	0.008 ± 0.012	0.497	0.002 ± 0.006	0.757
Vegetation: Shrub savannah	−1.283 ± 0.406	**0.002**	−0.051 ± 0.019	**0.007**	−0.041 ± 0.014	**0.002**
Soil type: Sandy silt	1.063 ± 0.412	**0.010**	0.016 ± 0.018	0.386	0.030 ± 0.014	**0.026**
Soil type: Rocky	−0.119 ± 0.522	0.820	−0.008 ± 0.016	0.632	−0.011 ± 0.016	0.471
Elevation	−0.005 ± 0.006	0.392	−0.010 ± 0.017	0.546	−0.004 ± 0.010	0.679
Slope	–	–	−0.010 ± 0.017	0.571	−0.006 ± 0.014	0.644

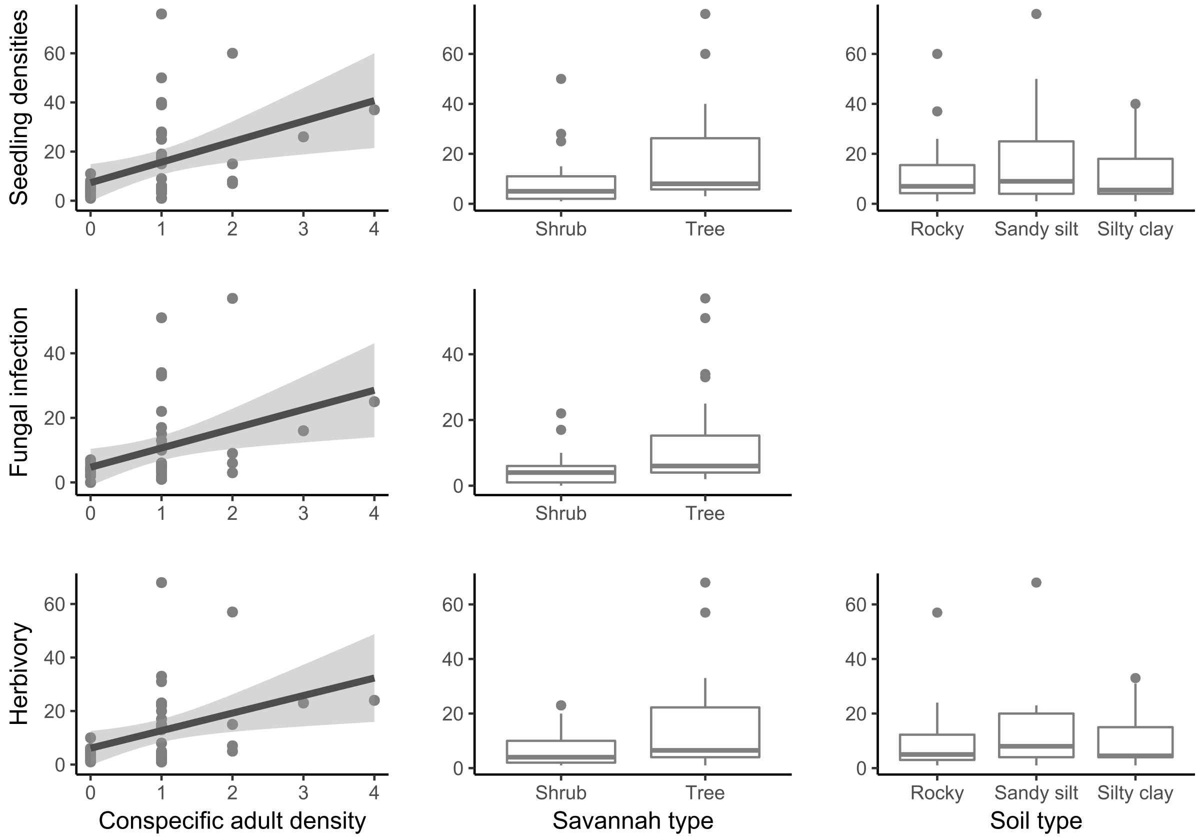

Fig. 2. Relationship of plot-level conspecific adult density, vegetation and soil types with initial seedling density, fungal infection and herbivory (first census).

fungal infection (β = 0.035; p = 0.004; Table 1) and herbivory (β = 0.035; p = 0.001; Table 1). On the other hand, fungal infection and herbivory decreased in shrub savannahs compared to tree savannahs (β = - 0.051 and – 0.041, respectively; p < 0.05; Table 1; Fig. 2). In addition, seedling herbivory was higher on sandy silt soils compared to other soil types (Table 1; Fig. 2). Overall, for the first two censuses, conspecific adult density and vegetation type were the most important variables of seedling density, fungal infection and herbivory. For the third census, the relative importance of conspecific density for seedling density decreased while slope became more important (SI2; SI3).

3.2. *Habitat heterogeneity dependent effect of conspecific adult density on A. africana seedling density, fungal infection and herbivory*

Vegetation and soil types were the most important habitat heterogeneity factors for seedling densities, fungal infection and herbivory (Table 1). Further analyses revealed significant increase in initial *A. africana* seedling densities with increasing conspecific adult density only in tree savannahs, and on sandy silt and rocky soils (Table 2; SI4). On the other hand, slope showed negative and significant influence on *A. africana* seedling densities in tree savannahs only (Table 2; SI4).

The positive effect of conspecific adult density on fungal infection and herbivory varied with vegetation types. Increasing conspecific adult density significantly increased both fungal infection and herbivory in tree savannahs (β = 0.40; p = 0.029 for fungal infection and β = 0.42; p = 0.025 for herbivory; Table 2; SI4), unlike shrub savannahs where a positive but non-significant positive association was noted (p < 0.2; Table 2; SI4).

3.3. *Biotic and abiotic drivers of A. africana seedling survival*

Factors such as soil type, hillshade and number of mounds did not show any significant effects, and were left out of the final selected model (Table 3; SI6) after performing stepwise selection procedure on the

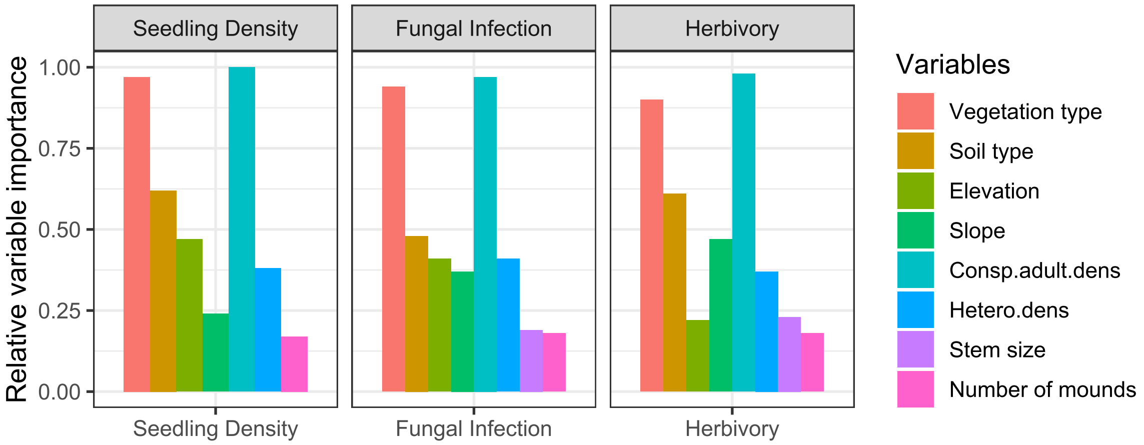

Fig. 3. Relative importance of biotic and abiotic factors used as predictors of initial seedling density, fungal infection and herbivory. The patterns for the additional two censuses are presented in SI3 and SI4.

Table 2
Coefficient estimates of the models testing for *A. africana* initial seedling densities, leaves fungal infection and herbivory response to biotic and abiotic factors for (i) each vegetation separately and (ii) each soil type separately. Only coefficient estimates are given here; detailed statistics are presented in SI4. Estimates with p values lower than 0.05 are in bold and the level of significance is indicated by "*" for <0.05 and "**" for <0.01.

	Vegetation type		Soil type		
	Shrub savannah	Tree savannah	Silty clay	Sandy silt	Rocky
Initial seedling densities					
Elevation	−0.021	0.003	−0.063	−0.005	0.000
Slope	0.046	**−0.053***	0.106	0.127	−0.029
Conspecific adult density	0.981	**0.404***	−0.640	**1.772****	**0.566****
Heterospecific density	0.337	0.096	0.584	0.227	0.015
Fungal infection					
Conspecific adult density	1.181	**0.403***			
Heterospecific density	0.341	0.141			
Elevation	−0.017	0.001			
Slope	0.103	−0.045			
Herbivory					
Conspecific adult density	0.881	**0.422***			
Heterospecific density	0.172	0.171			
Elevation	−0.019	0.007			
Slope	0.059	**0.074***			

Table 3
Results of the 'habitat', 'community' and 'natural enemies' models testing the influence of biotic and abiotic factors on *A. africana* seedling survival. The integrative full model is presented in SI6.

	Estimate	Std. Error	*z/t value*	*p value*
'habitat' model				
(Intercept)	4.371	1.014	4.309	<0.001
Elevation	−0.013	0.004	−3.012	0.003
Slope	−0.051	0.017	−2.937	0.003
Vegetation: Tree savannah	0.968	0.277	3.496	<0.001
'community' model				
(Intercept)	1.507	0.247	6.112	<0.001
Heterospecific density	0.239	0.123	1.953	0.051
Conspecific adult density	−0.450	0.102	−4.411	<0.001
Net relatedness index	−0.177	0.174	−1.018	0.309
'natural enemies' model				
(Intercept)	0.763	0.248	3.085	0.002
Herbivory	0.309	0.235	1.314	0.189
Fungal infection	0.332	0.202	1.646	0.100

initial fitted model. However, we found significant negative effect of elevation ($\beta = -0.013$; $p = 0.003$; Table 3; SI7) and slope ($\beta = -0.051$; $p = 0.003$; Table 3; SI7). Vegetation type also affected seedling survival, with tree savannahs showing regression coefficient which was 0.96 significantly higher than that of shrub savannahs (Table 3; SI7). On the other hand, conspecific adult density negatively influenced seedling survival ($\beta = -0.45$; $p < 0.001$; Table 3; SI7), but the net relatedness index and heterospecific density showed no significant effects ($p > 0.05$). Similarly, fungal infection and herbivory did not show any significant effects on seedling survival.

3.4. *Mediation role of fungal infection and herbivory in linking A. africana seedling survival response to conspecific adult density*

Because seedling survival showed significant response to conspecific adult density (Table 3), the mediation effects of fungal infection and herbivory were analysed using SEMs. The outputs of the SEMs testing for seedling survival response to conspecific adult density via fungal infection and herbivory, revealed chi-square values of 13.27 ($p = 0.039$) and 3.49 ($p = 0.745$), respectively for tree savannahs and shrub savannahs SEMs. Of the two SEMs, only that of shrub savannahs showed satisfactory statistics ($p > 0.05$; cfi = 1.0, and rsmea = 0; Fig. 4), indicating good fit and absence of significant deviations between the data and the model. Accordingly, conspecific adult density had significant positive direct effect on both fungal infection and herbivory ($\beta = 0.46$; $p = 0.011$; Table 4), which in turn showed negative and significant effect ($\beta = -0.42$; $p = 0.048$; Table 4; Fig. 4) on seedling survival in shrub savannahs.

4. Discussion

While several studies have shed light into the general drivers of the low recruitment potential in *A. africana*, most of these studies primarily pointed to negative effects of human disturbance, especially tree harvesting, branch and bark pruning on adult trees (Nacoulma et al., 2017; Sinsin et al., 2004), climatic and seasonal patterns (Assogbadjo et al., 2017; Mensah et al., 2014), and to some extent, fire and browsing (Bationo et al., 2001), which have appeared to be more anecdotal than analytic. In strictly protected areas, human disturbance effects can be

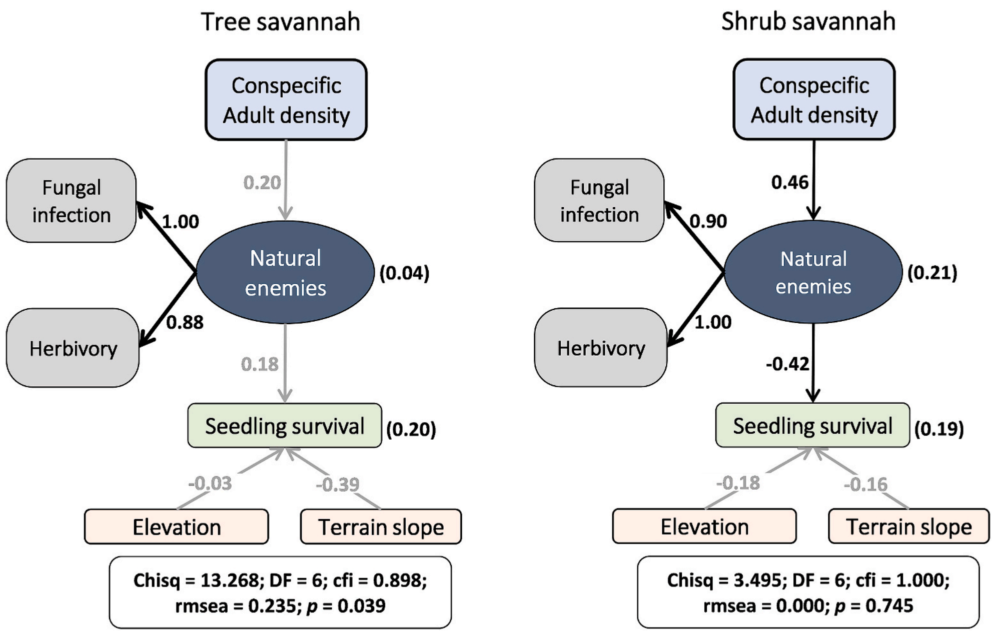

Fig. 4. Structural Equation Model-fit statistics and path summary relating seedling survival to conspecific adult density, fungal infection and herbivory, in addition to the effects of terrain slope and elevation. The single-pointed arrows represent causal paths. The values without parentheses are the standardized path coefficients. Significant paths ($p < 0.05$) are represented with black arrows and non-significant paths ($p > 0.05$) by grey arrows. The values with parentheses are the coefficients of determination, indicating the total variation in a dependent variable that is explained by the combined independent variables. Detailed statistics and significance of paths are shown in Table 4.

Table 4
Summary of the SEMs testing the indirect (via natural enemies – fungal infection, and herbivory) effects of conspecific adult neighborhood on the species seedling survival. Est: path standardized coefficients; SE: standard error.

Path	Est.	SE	*z value*	*p value*
Tree savannah				
From Slope to Seedling survival	−0.39	0.27	−1.50	0.134
From Elevation to Seedling survival	−0.03	0.28	−0.09	0.926
From Conspecific adult density to Natural enemies	0.20	0.18	1.12	0.263
From Natural enemies to Seedling survival	0.18	0.17	1.08	0.280
Model Fit statistics				
Comparative fit index	0.898			
root mean square error of approximation	0.235			
Chi square statistic	13.268			
P-value	0.039			
Remark	Rejected			
Shrub savannah				
From Slope to Seedling survival	−0.16	0.27	−0.61	0.542
From Elevation to Seedling survival	−0.18	0.26	−0.70	0.482
From Conspecific adult density to Natural enemies	0.46	0.18	2.54	0.011
From Natural enemies to Seedling survival	−0.42	0.21	−1.97	0.048
Model Fit statistics				
Comparative fit index	1.000			
root mean square error of approximation	0.000			
Chi square statistic	3.495			
p value	0.745			
Remark	Accepted			

ruled out, and both abiotic and biotic processes are expected to modulate tree seedling establishment and survival. The present study adds insights into the biotic and abiotic drivers of the species recruitment in a protected biosphere reserve. After monitoring the dynamics of *A. africana* seedlings across both dry and rainy seasons, we found that microscale habitat heterogeneity (slope, elevation and vegetation type) and biotic neighborhood (conspecific adult density, fungal infection and herbivory) are the main drivers of *A. africana* seedling establishment and survival. Specifically, we found that (i) seedling density increased with increasing conspecific adult density, and were higher in tree savannahs than shrub savannahs; (ii) seedling leaves' fungal infection and herbivory were positively associated with conspecific adult density, and were more frequent in tree savannahs; (iii) seedling survival was constrained on higher slope; (iv) there was a lower potential for seedling survival in shrub savannahs, and with increasing conspecific adult density and (v) conspecific adult density promoted seedling leaves' fungal infection and herbivory, which in turn reduced seedling survival especially in shrub savannahs.

4.1. Conspecific positive density-dependence effects on A. africana seedling establishment, leaves' fungal infection and herbivory

Conspecific neighborhood had the strongest influence on *A. africana* seedling density, leaves' fungal infection and herbivory. Seedling density, leaves' fungal infection and herbivory increased with increasing density of conspecific adult trees, indicating a CPDD. Our finding corroborates with previous studies that reported the occurrence of CPDD in tropical (Chanthorn et al., 2013; Comita et al., 2009; Inman-narahari et al., 2016) and temperate forests (Kuang et al., 2017) and extends the generality of CPDD to tropical savannah ecosystems. Seedling density was higher where the density of conspecific adult neighbors was higher probably due to dispersal limitation. This finding suggests that dispersal limitation is an important factor modulating tree seedling dynamics in tropical savannahs as reported earlier by Kuang et al. (2017) for temperate forests. Moreover, the CPDD effects on seedling density may be explained by similar habitat preferences of both seedlings and conspecific adults and facilitation whereby conspecific adults create favorable environments that increase the likelihood of seedling establishment, resulting in high seedling density (Comita et al., 2009). The positive effect of conspecific adult density on leaves' fungal infection and herbivory may be attributed to the specialization of *A. africana* foliar pathogens and herbivores responsible for the leaves' infection and damage (Connell, 1971; Janzen, 1970), implying an increase in the prevalence of the natural enemies with increasing density of conspecific hosts. However, we found that the relative importance of CPDD decreased over time in favor of the abiotic factors, as evidenced by the absence of CPDD effect and the significant effects of vegetation and slope on seedling density for the last census (SI2; SI3). Thus, the findings suggest that the strength of CPDD may decrease with time in tropical savannah ecosystems, possibly due to a shift in the relative importance of different biotic and abiotic interactions over time (SI3; SI4).

4.2. Density-dependent seedling establishment, leaves' fungal infection and herbivory vary with vegetation and soil type

Our results suggest that habitat heterogeneity (vegetation and soil types) modulates how conspecifc adult density affects *A. africana* seedling establishment, leaves' fungal infection and herbivory (Table 2). As hypothesized, we found evidence of positive conspecific density-dependent seedling establishment, fungal infection and herbivory, which was more significant in tree savannahs than shrub savannahs, and on sandy silt and rocky soils than silty clay soil. These results indicate that the magnitude of the conspecific density-dependent effects varied with the habitat, which may reflect habitat preferences resulting from environmental filtering (Cao et al., 2018; Zhu et al., 2015). The significant CPDD effects on *A. africana* seedling density, fungal infection and herbivory in tree savannahs unlike shrub savannahs can be explained by the facilitation of seedling establishment and occurrence of host-specific pathogens and herbivores by conspecific adult trees through shading, which lowers heat and water stress (Sack, 2004; Semchenko et al., 2012) and favors seedling growth and proliferation of pathogens and herbivores. In fact, we found that tree savannahs in the study area had a denser vegetation (i.e., greater canopy closure; pers. obs.) and higher density of conspecific adult trees (123 trees ha^{-1}) than shrub savannahs (60 trees ha^{-1}), which would probably result in lower available understorey light in the former habitat. Moreover, shading may increase the activity of pathogens and herbivores due to low irradiance (Augspurger, 1984; Inman-narahari et al., 2016). Hence, tree savannahs have habitat characteristics that promoted the positive effects of conspecific density-dependence on seedling density, fungal infection and herbivory more than shrub savannahs through habitat filtering.

Similarly, the effects of CPDD depended on soil types, with high conspecific adult density resulting in higher seedling density, fungal infection and herbivory on sandy silt and rocky soils. This interactive effect of CPDD and soil types indicates that soil structure and conditions (e.g., nutrient and water availability) may be an important factor that mediates *A. africana* seedling establishment, leaves' fungal infection and herbivory response to conspecific density-dependence. Indeed, soil type mediates the density of plant, and the direct relationships are built on adult density and seedling density, leaves' fungal infection and herbivory (SI8). However, the mechanism behind this interaction remains unknown, particularly considering the qualitative assessment of soil conditions in this study. The significant CPDD on sandy silt and rocky soils could be consistent with the stress gradient hypothesis (Bertness and Callaway, 1994; Jia et al., 2011), which posits that facilitation increases under stressful conditions, if we assume that sandy silt and rocky soils have lower nutrient content and soil water retention capacity than silty clay soil. However, further study will be necessary to unravel the main (e.g., soil physical and chemical properties, management practices) and underlying (e.g., slope, elevation) covariates responsible for the observed interaction between CPDD and soil types and confirm the stress gradient hypothesis. Overall, the abiotic characteristics of the habitat a seedling finds itself in influence how the biotic neighborhood impacts on its growth dynamics and natural enemies' activity.

4.3. Habitat heterogeneity and conspecific negative density dependence drive A. africana seedling survival

Our results also suggest a lower potential for seedling survival with increasing conspecific adult density, in shrub savannahs, and on higher terrain slope and elevation (Table 3). Previous studies showed that topography profoundly affects abiotic conditions which, in turn, influence the structure, function, and dynamics of ecological communities (Fortunel et al., 2018; Jucker et al., 2018). In plant communities, local topographic heterogeneity is linked with a broad set of abiotic conditions (e.g., soil water availability, nutrient content and soil texture, microclimate, exposure, flood regimes) that can influence stand structure, dynamics, and composition (Chadwick and Asner, 2016; Uriarte et al., 2018). *Afzelia africana* seedling survival was influenced by topographical factors, particularly slope and elevation. Seedling survival was potentially lower on higher terrain slope and elevation. These results therefore suggest that even small variations in topographical parameters mainly slope (range of slope values) and elevation (range of elevation) modulate early survival, possibly through displacement of eroded soil material, water, and plant debris (Yang et al., 2018). For instance, water run-off is expected to increase at higher slope, leading to greater loss of topsoil, which in turn may constrain plant establishment and survival, due to loss of nutrients and mechanical instability. On lower slope sites, plants will benefit more from the accumulation of nutrients and reduced run-off. Our results therefore confirm the general patterns that the structure and composition of plant communities are shaped by topographical filtering; specifically, *A. africana* seedlings were revealed to be very sensitive to high topographical patterns.

Afzelia africana seedling survival was also influenced by the vegetation types. In addition to the significant slope and elevation effects on survival, the study showed that shrub savannahs did not facilitate survival. Two possible reasons could explain the lower potential for seedling survival in shrub savannahs compared to tree savannahs. First, this may be inherently related to the lower conspecific adult density in shrub savannahs, through limited production and availability of seeds, as compared to tree savannahs. The second, and most plausible argument is that specialization of natural enemies (pathogens and herbivory, which negatively affect survival) is likely higher in less dense vegetation, and substantially lethal for the species seedling.

Conspecific adult density also negatively influenced seedling survival, indicating that *A. africana* seedlings surrounded by higher density of conspecific adult showed lower survival, despite being abundant (section 5.1). As seedlings are often aggregated around the nurse trees, it is likely that they suffer strong intra- and interspecific competition for resources and are also easy prey for natural enemies. In contrast, we did not detect any significant heterospecific density effect on seedling survival, which corroborates with previous studies that reported no clear trend between heterospecific neighbor density and plant survival (Zhu et al., 2015). Therefore, the interspecific interaction effects may be ruled out, and the significant negative effects of conspecific adult density suggest that CNDD effects control early seedling survival in *A. africana*. This is also consistent with recent conclusions that conspecific density negatively affects seedling survival (Comita et al., 2009; Johnson et al., 2017; Zhu et al., 2015). For instance, Zhu et al. (2015) in the tropical forest of Barro Colorado Island showed that seedlings were negatively impacted by their conspecific adult neighbors at the early life stages. Further, there are insights that the importance of CNDD effects vary with seedling size and conspecific life stage (Yan et al., 2015; Zhu et al., 2015), possibly due to ontogenetic shifts in plant defense and tolerance (Boege and Marquis, 2005). Interestingly, few studies conducted in West Africa suggest that tree seedling survival and establishment are highly susceptible to beyond water stress, nutrient shortage and shade, herbivory and fires (Bationo et al., 2001; Zida et al., 2007). The CNDD effects on *A. africana* seedlings as revealed in this study, are possibly mediated through biotic interactions, especially competition and natural enemies such as fungi and herbivores (Fig. 4; Table 4), as also shown in the Barro Colorado Island forest and other forests (Liu et al., 2012; Mangan et al., 2010).

4.4. Fungal infection and herbivory as drivers of conspecific negative density dependence effects on A. africana seedling survival

Our initial result (Table 1) suggests that *A. africana* seedlings that occur close to the conspecific adults are subject to specialized natural enemies such as pathogens and insect herbivores, in line with the Janzen–Connell hypothesis (Connell, 1971; Janzen, 1970). We further predicted that the strong CNDD at the seedling stage found in this study (Table 3) was driven predominantly by specialist natural enemies such as pathogenic fungi and herbivores. However, unlike conspecific adult density, fungal infection and herbivory were not retained as significant factors in the final GLMs testing the effects of abiotic and biotic factors on individual seedling survival, suggesting confounding or correlated effects between natural enemies and conspecific adult density (Table 3; SI6). Interestingly, the results of the SEMs fitted for plot level data revealed that conspecific adult density promoted seedling leaves' fungal infection and herbivory, which in turn reduced seedling survival especially in shrub savannahs (see Table 4; Fig. 4). Therefore, the negative effects of conspecific adult density are partly the result of activities of attracted host-specific natural enemies (fungi, insect and mammal herbivores) on seedlings. In other words, fungal infection and herbivory mediate the negative effects of conspecific adult density on seedling survival. Studies by Bationo et al. (2001) and Ouédraogo-Koné et al. (2008) reported that herbivore pressures through seedlings consumption and trampling hinder seedling survival and regeneration process of the species. However, our findings further suggest habitat-dependent mediation by fungal infection and herbivory of conspecific adult density on seedling survival.

4.5. Negative conspecific density-dependence effects on seedling survival in shrub savannahs: do less dense habitats enhance specialization of predators and pathogens?

We found evidence of negative conspecific density-dependent seedling survival, which was more significant in shrub savannahs than tree savannahs. This result suggests that the magnitude of these effects varied with the habitat. Our results further support previous studies that showed that CNDD effects may vary with time, life stage, habitat and species (Comita et al., 2009; Johnson et al., 2017; Zhu et al., 2015). Interestingly, we found that despite the significant CPDD effects on seedling fungal infection and herbivory in tree savannahs (Table 1), seedlings were more sensitive to natural enemies in shrub savannahs than in tree savannahs (Table 4; Fig. 4). Our results therefore imply that habitat also modulates biotic interactions and effects on *A. africana* seedling survival; the increased survival in tree savannahs despite CPDD effects on seedling fungal infection and herbivory can result from less specialization of pathogens and predators where resources are abundant; hence seedlings may escape mortality probably because of less specialization of pathogens and predators in denser vegetation. Unlike tree savannahs, the CNDD effects on seedling survival in shrub savannahs suggests that less dense vegetation seems to facilitate specialization of predators and pathogens on limited set of species, which may lead to greater pathogen-induced mortality of seedlings in shrub savannahs. More research is needed to determine whether these differential conspecific density-dependence effects result from increased predators and pathogens but less specialization in tree versus shrub savannahs.

5. Conclusion and management perspectives

This study examined the relative importance of abiotic and biotic drivers for a tropical tree species seedling survival in a dryland ecosystem. The context of the study being a dryland ecosystem brings in an interesting perspective, since most studies of CNDD have been conducted in wetter forests or grasslands. However, it should be noted that the study only examined leaf fungal infection and herbivory as natural enemies, and mortality could have also been caused by damping off diseases or root infections (plant-soil feedback) as well, which could not be assessed here. Further, while the limitation of the study to only one species may undermine the generalization of the results to community-wide implications of CNDD and CPDD in dry ecosystems, the inclusion of the heterospecific aspects and phylogeny structures takes into account the possible plant-plant interaction at community level. Overall, we found that while seedling densities and rates of herbivory and fungal infection correlated positively with adult densities, seedling survival declined overtime with greater density of conspecific adults, and on higher slope. There was further evidence that herbivory and fungal infection mediated negative relationship between conspecific adults and seedling survival, and more particularly in shrub savannahs. Therefore, the study brings important insights into the mechanisms that drive the regeneration/survival of the species, which could be used as a basis for the design of management activities aiming at the conservation of this endangered species.

From a management perspective, our results suggest that plantations of *A. africana* should favor mixed-species plantation to limit fungal infection and herbivory on seedlings consistent with the biotic resistance hypothesis. The finding that seedlings were more sensitive to natural enemies in shrub savannahs suggests that similar management actions should not be envisaged in degraded shrub and tree savannahs. In particular, there should be more efforts in shrub savannahs to ensure that seedlings planted survive and recruit to further stages (e.g. saplings). Because seedling survival was constrained on higher slope, enrichment campaigns to plant or restore *A. africana* on terrains with higher slope might require more efforts (e.g., a relatively higher density of seedlings at initial planting stage might maximize the number of individuals at later stages). In addition, areas with appropriate/suitable topographical conditions such as low slope and elevation may be targeted for enrichment. For the purpose of assisting the natural regeneration of the species, we recommend that management activities are directed towards areas with high abundance of conspecific adult trees, which are also areas prone to high seedling densities and high fungal infections and herbivory (both insects and mammals). The application of fungicides and insecticides could be proposed to reduce the fungal infection and insect herbivory near the conspecific adults in human-made plantations.

Declaration of competing interests

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.jenvman.2020.111268.

Authors' contributions

SM conceived the ideas and designed methodology; SM acquired the funding; JA and SM gathered the data; SM analysed the data, and wrote the manuscript, with contribution, advice and editorial support from FN, KD and KVS; AA and RGK supervised the work. All authors reviewed the drafts and gave final approval for publication.

References

Amahowe, I.O., Azihou, A.F., Natta, A.K., Biaou, S.H., Biaou, S., Agoi, D., Salomon, B., 2019. Constraints of seedling survival and recruitment under adult tree of a multi-use species Afzelia africana Sm and Pers in Sudanian region of Benin (West Africa). Agrofor. Syst. 93, 1147–1156. https://doi.org/10.1007/s10457-018-0218-6.

Assogbadjo, A.E., Mensah, S., Glèlè Kakaï, R.L., 2017. The relative importance of climatic gradient versus human disturbance in determining population structure of Afzelia africana in the Republic of Benin. South. For. 79, 125–132. https://doi.org/10.2989/20702620.2016.1255406.

Atanasso, J.A., Mensah, S., Azihou, A.F., Djossa, B.A., Glèlè Kakaï, R., Assogbadjo, A.E., 2019. Heterospecific tree density and environmental factors affect Afzelia africana Sm . Population structure in the Pendjari biosphere reserve , West Africa : implications for management and restoration. Trop. Conserv. Sci. 12, 1–12. https://doi.org/10.1177/1940082918822604.

Augspurger, C.K., 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. Ecology 65, 1705–1712. https://doi.org/10.2307/1937766.

Bagchi, R., Gallery, R.E., Gripenberg, S., Gurr, S.J., Narayan, L., Addis, C.E., Freckleton, R.P., Lewis, O.T., 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. Nature 506, 85–88. https://doi.org/10.1038/nature12911.

Bai, X., Queenborough, S.A., Wang, X., Zhang, J., Li, B., Yuan, Z., Xing, D., Lin, F., Ye, J., Hao, Z., 2012. Effects of local biotic neighbors and habitat heterogeneity on tree and shrub seedling survival in an old-growth temperate forest. Oecologia 170, 755–765. https://doi.org/10.1007/s00442-012-2348-2.

Barton, K., 2018. MuMIn: Multi-Model Inference. R Package version 1.42.1.

Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using **lme4**. J. Stat. Software 67, 1–48. https://doi.org/10.18637/jss.v067.i01.

Bationo, A.B., Ouedraogo, J.S., Boussim, I.J., 2000. Afzelia Africana Sm . (Caesalpiniaceae) : Étude de la prédation des graines dans une savane boisee du Burkina Faso. Bois et Forêts des Tropiques 264, 55–56.

Bationo, A.B., Ouedraogo, J.S., Guinko, S., 2001. Longévité des graines et contraintes à la survie des plantules d' Afzelia africana Sm. dans une savane boisée du Burkina Faso. Ann. For. Sci. 58, 69–75.

Bertness, M.D., Callaway, R., 1994. Positive interactions in communities. Trends Ecol. Evol. 9, 191–193. https://doi.org/10.1016/0169-5347(94)90088-4.

Biara, E., Egeru, A., Mensah, S., Biira, J., Kadigo, M.M., 2020. Socio-economic factors influencing Afzelia africana Sm. use value and traditional knowledge in Uganda: implications for sustainable management. Environ. Dev. Sustain. https://doi.org/10.1007/s10668-020-00673-6.

Boege, K., Marquis, R.J., 2005. Facing herbivory as you grow up: the ontogeny of resistance in plants. Trends Ecol. Evol. 20, 441–448. https://doi.org/10.1016/J.TREE.2005.05.001.

Brearley, F.Q., Press, M.C., Scholes, J.D., 2003. Nutrients obtained from leaf li tter can improve the growth of dipterocarp seedlings. New Phytol. 160, 101–110. https://doi.org/10.1046/j.0028-646x.2003.00851.x.

Burrough, P., McDonell, R., 1998. Principles of Geographical Information Systems. Oxford University Press (OUP).

Cao, J., Zhang, C., Zhao, B., Li, X., Hou, M., Zhao, X., 2018. Seedling density dependence regulated by population density and habitat filtering: evidence from a mixed primary broad-leaved Korean pine forest in Northeastern China. Ann. For. Sci. 75, 25. https://doi.org/10.1007/s13595-018-0706-x.

Chadwick, K.D., Asner, G.P., 2016. Tropical soil nutrient distributions determined by biotic and hillslope processes. Biogeochemistry 127, 273–289. https://doi.org/10.1007/s10533-015-0179-z.

Chanthorn, W., Caughlin, T., Dechkla, S., Brockelman, W.Y., 2013. The relative importance of fungal infection , conspecific density and environmental heterogeneity for seedling survival in a dominant tropical tree. Biotropica 45, 587–593. https://doi.org/10.1111/btp.12044.

Comita, L.S., Uriarte, M., Thompson, J., Jonckheere, I., Canham, C.D., Zimmerman, J.K., 2009. Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. J. Ecol. 97, 1346–1359. https://doi.org/10.1111/j.1365-2745.2009.01551.x.

Connell, J., 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Dynamics of Numbers in Populations. Proceedings of the Advanced Study Institute, Pudoc, Wageningen, pp. 298–312.

Daws, M.I., Mullins, C.E., Burslem, D.F.R.P., Paton, S.R., Dalling, J.W., 2002. Topographic position affects the water regime in a semideciduous tropical forest in Panama. Plant Soil 238, 79–90.

Facelli, J., Pickett, S., 1991. Plant litter: its dynamics and effects on plant community structure. Bot. Rev. 57, 1–32. https://doi.org/10.1007/bf02858763.

Fortunel, C., Lasky, J.R., Uriarte, M., Valencia, R., Wright, S.J., Garwood, N.C., Kraft, N.J.B., 2018. Topography and neighborhood crowding can interact to shape species growth and distribution in a diverse Amazonian forest. Ecology 99, 2272–2283. https://doi.org/10.1002/ecy.2441.

García-Guzmán, G., Benítez-Malvido, J., 2003. Effect of litter on the incidence of leaf-fungal pathogens and herbivory in seedlings of the tropical tree nectandra ambigens. J. Trop. Ecol. 19, 171–177. https://doi.org/10.1017/S0266467403003195.

Grace, J.B., Bollen, K.A., 2005. Interpreting the results from multiple regression and structural equation models. Bull. Ecol. Soc. Am. 86, 283–295. https://doi.org/10.1890/0012-9623(2007)88[50:UFCAFW]2.0.CO;2.

Harcombe, P.A., 1987. Tree life tables: simple birth, growth, and death data encapsulate life histories and ecological roles. Bioscience 37, 557–568.

Inman-narahari, F., Ostertag, R., Hubbell, S.P., Giardina, C.P., Cordell, S., Sack, L., 2016. Density-dependent seedling mortality varies with light availability and species abundance in wet and dry Hawaiian forests. J. Ecol. 104, 773–780. https://doi.org/10.1111/1365-2745.12553.

Janzen, D., 1970. Herbivores and the number of tree species in tropical forests. Am. Nat. 104, 501–528. https://doi.org/10.1117/12.602879.

Jia, X., Dai, X.-F., Shen, Z.-X., Zhang, J.-Y., Wang, G.-X., 2011. Facilitation can maintain clustered spatial pattern of plant populations during density-dependent mortality: insights from a zone-of-influence model. Oikos 120, 472–480. https://doi.org/10.1111/j.1600-0706.2010.18674.x.

Johnson, D.J., Condit, R., Hubbell, S.P., Comita, L.S., 2017. Abiotic niche partitioning and negative density dependence drive tree seedling survival in a tropical forest. Proc. R. Soc. B 284. https://doi.org/10.1098/rspb.2017.2210.

Jucker, T., Bongalov, B., Burslem, D.F.R.P., Nilus, R., Dalponte, M., Lewis, S.L., Phillips, O.L., Qie, L., Coomes, D.A., 2018. Topography shapes the structure, composition and function of tropical forest landscapes. Ecol. Lett. 21, 989–1000. https://doi.org/10.1111/ele.12964.

Kuang, X., Zhu, K., Yuan, Z., Lin, F., Ye, J., Wang, X., Wang, Y., Hao, Z., 2017. Conspecific density dependence and community structure: insights from 11 years of monitoring in an old-growth temperate forest in Northeast China. Ecol. Evol. 7, 5191–5200. https://doi.org/10.1002/ece3.3050.

Legras, E.C., Vander Wall, S.B., Board, D.I., 2010. The role of germination microsite in the establishment of sugar pine and Jeffrey pine seedlings. For. Ecol. Manage. 260, 806–813. https://doi.org/10.1016/j.foreco.2010.05.039.

Lin, F., Comita, L.S., Wang, X., Bai, X., Yuan, Z., Xing, D., Hao, Z., 2014. The contribution of understory light availability and biotic neighborhood to seedling survival in secondary versus old-growth temperate forest. Plant Ecol. 215, 795–807. https://doi.org/10.1007/s11258-014-0332-0.

Liu, X., Liang, M., Etienne, R.S., Wang, Y., Staehelin, C., Yu, S., 2012. Experimental evidence for a phylogenetic Janzen-Connell effect in a subtropical forest. Ecol. Lett. 15, 111–118. https://doi.org/10.1111/j.1461-0248.2011.01715.x.

Lu, X.H., Zang, R.G., Huang, J.H., 2015. Relationships between community level functional traits of trees and seedlings during secondary succession in a tropical lowland rainforest. PloS One 10, 1–12. https://doi.org/10.1371/journal.pone.0132849.

Maher, E.L., Germino, M.J., Hasselquist, N.J., 2005. Interactive effects of tree and herb cover on survivorship, physiology, and microclimate of conifer seedlings at the alpine tree-line ecotone. Can. J. For. Res. 35, 567–574. https://doi.org/10.1139/x04-201.

Mangan, S.A., Herre, E.A., Bever, J.D., 2010. Specificity between Neotropical tree seedlings and their fungal mutualists leads to plant—soil feedback. Ecology. https://doi.org/10.2307/27860837.

Mensah, S., du Toit, B., Seifert, T., 2018a. Diversity–biomass relationship across forest layers: implications for niche complementarity and selection effects. Oecologia 187, 783–795. https://doi.org/10.1007/s00442-018-4144-0.

Mensah, S., Houehanou, T.D., Sogbohossou, E.A., Assogbadjo, A.E., Glèlè Kakaï, R., 2014. Effect of human disturbance and climatic variability on the population structure of Afzelia africana Sm. ex pers. (Fabaceae-Caesalpinioideae) at country broad-scale (Bénin, West Africa). South Afr. J. Bot. 95, 165–173. https://doi.org/10.1016/j.sajb.2014.09.008.

Mensah, S., Salako, V.K., Assogbadjo, A.E., Glèlè Kakaï, R., 2018b. Differential responses of taxonomic, structural, and functional diversity to local-scale environmental variation in afromontane forests in South Africa. Trop. Conserv. Sci. 11, 1–13. https://doi.org/10.1177/1940082918762372.

Mensah, S., Salako, V.K., Seifert, T., 2020a. Structural complexity and large-sized trees explain shifting species richness and carbon relationship across vegetation types. Funct. Ecol. https://doi.org/10.1111/1365-2435.13585.

Mensah, S., Valère, K., Assogbadjo, A., Glèlè, R., Sinsin, B., Seifert, T., 2020b. Functional trait diversity is a stronger predictor of multifunctionality than dominance : evidence from an Afromontane forest in South Africa. Ecol. Indicat. 115, 106415. https://doi.org/10.1016/j.ecolind.2020.106415.

Mensah, S., Veldtman, R., Assogbadjo, A.E., Glèlè Kakaï, R., Seifert, T., 2016. Tree species diversity promotes aboveground carbon storage through functional diversity and functional dominance. Ecol. Evol. 6, 7546–7557. https://doi.org/10.1002/ece3.2525.

Nacoulma, B.M.I., Lykke, M.A., Traoré, S., Sinsin, B., Thiombiano, A., 2017. Impact of bark and foliage harvesting on fruit production of the multipurpose tree Afzelia africana in Burkina Faso (West Africa). Agrofor. Syst. 91, 565–576. https://doi.org/10.1007/s10457-016-9960-9.

Ouédraogo-Koné, S., Kaboré-Zoungrana, C.Y., Ledin, I., 2008. Important characteristics of some browse species in an agrosilvopastoral system in West Africa. Agrofor. Syst. 74, 213–221. https://doi.org/10.1007/s10457-007-9095-0.

Ouédraogo, A., Thiombiano, A., 2012. Regeneration pattern of four threatened tree species in Sudanian savannas of Burkina Faso. Agrofor. Syst. 86, 35–48. https://doi.org/10.1007/s10457-012-9505-9.

Paine, C.E.T., Norden, N., Chave, J., Forget, P.M., Fortunel, C., Dexter, K.G., Baraloto, C., 2012. Phylogenetic density dependence and environmental filtering predict seedling mortality in a tropical forest. Ecol. Lett. 15, 34–41. https://doi.org/10.1111/j.1461-0248.2011.01705.x.

Queenborough, S.A., Burslem, D., Garwood, N., Valencia, R., 2007. Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. Ecology 88, 2248–2258.

Queenborough, S.A., Burslem, D.F.R.P., Garwood, N.C., Valencia, R., 2009. Taxonomic scale-dependence of habitat niche partitioning and biotic neighbourhood on survival of tropical tree seedlings. Proc. R. Soc. B Biol. Sci. 276, 4197–4205. https://doi.org/10.1098/rspb.2009.0921.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rosseel, Y., 2012. lavaan: an R package for structural equation modeling. J. Stat. Software 48, 1–36.

Sack, L., 2004. Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? Oikos 107, 110–127. https://doi.org/10.1111/j.0030-1299.2004.13184.x.

Semchenko, M., Lepik, M., Götzenberger, L., Zobel, K., 2012. Positive effect of shade on plant growth: amelioration of stress or active regulation of growth rate? J. Ecol. 100, 459–466. https://doi.org/10.1111/j.1365-2745.2011.01936.x.

Sinsin, B., Eyog-Matig, O., Assogbadjo, A., Gaoue, O.G., Sinadouwirou, T., 2004. Dendrometric characteristics as indicators of pressure of Afzelia africana Sm. dynamic changes in trees found in different climatic zones of Benin. Biodivers. Conserv. 13, 1555–1570.

Solla, A., Camarero, J., 2006. Spatial patterns and environmental factors affecting the presence of Melampsorella caryophyllacearum infections in an Abies alba forest in NE Spain. For. Pathol. 36, 165–175. https://doi.org/10.1111/j.1439-0329.2006.00446.x.

Umaña, M.N., Zipkin, E.F., Zhang, C., Cao, M., Lin, L., Swenson, N.G., 2018. Individual-level trait variation and negative density dependence affect growth in tropical tree seedlings. J. Ecol. 106, 2446–2455. https://doi.org/10.1111/1365-2745.13001.

Uriarte, M., Muscarella, R., Zimmerman, J.K., 2018. Environmental heterogeneity and biotic interactions mediate climate impacts on tropical forest regeneration. Global Change Biol. 24, e692–e704. https://doi.org/10.1111/gcb.14000.

Webb, C.O., Gilbert, G.S., Donoghue, M.J., 2006. Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. Ecology 87, 123–131. https://doi.org/10.1890/0012-9658(2006)87[123:PSMSSA]2.0.CO;2.

Wright, S.J., 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. Oecologia 130, 1–14. https://doi.org/10.1007/s004420100809.

Wu, J., Swenson, N.G., Brown, C., Zhang, C., Yang, J., Ci, X., Li, J., Sha, L., Cao, M., Lin, L., 2016. How does habitat filtering affect the detection of conspecific and phylogenetic density dependence? Ecology 97, 1182–1193. https://doi.org/10.1890/14-2465.1.

Yan, Y., Zhang, C., Wang, Y., Zhao, X., Gadow, K. Von, 2015. Drivers of seedling survival in a temperate forest and their relative importance at three stages of succession. Ecol. Evol. 5, 4287–4299. https://doi.org/10.1002/ece3.1688.

Yang, S.-Z., Fan, H., Li, K.-W., Ko, T.-Y., 2018. How the diversity, abundance, size and climbing mechanisms of woody lianas are related to biotic and abiotic factors in a subtropical secondary forest, Taiwan. Folia Geobot. 53, 77–88. https://doi.org/10.1007/s12224-017-9306-z.

Zanne, A.E., Tank, D.C., Cornwell, W.K., Eastman, J.M., Smith, S.A., Fitzjohn, R.G., McGlinn, D.J., O'Meara, B.C., Moles, A.T., Reich, P.B., Royer, D.L., Soltis, D.E., Stevens, P.F., Westoby, M., Wright, I.J., Aarssen, L., Bertin, R.I., Calaminus, A., Govaerts, R., Hemmings, F., Leishman, M.R., Oleksyn, J., Soltis, P.S., Swenson, N.G., Warman, L., Beaulieu, J.M., 2014. Three keys to the radiation of angiosperms into freezing environments. Nature 506, 89–92. https://doi.org/10.1038/nature12872.

Zhu, Y., Cai, H., Jiang, F., 2017. Variation of the biotic neighbourhood and topographic effects on tree survival in an old-growth temperate forest. J. Veg. Sci. 28 (6), 1166–1177. https://doi.org/10.1111/jvs.12580.

Zhu, Y., Comita, L.S., Hubbell, S.P., Ma, K., 2015. Conspecific and phylogenetic density-dependent survival differs across life stages in a tropical forest. J. Ecol. 103, 957–966. https://doi.org/10.1111/1365-2745.12414.

Zida, D., Sawadogo, L., Tigabu, M., Tiveau, D., Odén, P.C., 2007. Dynamics of sapling population in savanna woodlands of Burkina Faso subjected to grazing, early fire and selective tree cutting for a decade. For. Ecol. Manage. 243, 102–115. https://doi.org/10.1016/j.foreco.2007.02.013.

Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R, Statistics for Biology and Health. Springer New York, New York, NY. https://doi.org/10.1007/978-0-387-87458-6.