

Factors limiting plant recruitment in a tropical Afromontane Forest

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Abstract

Predicting how forest species composition may change in response to global change is essential for meaningful management. Which species are most likely to successfully recruit depends on a multitude of factors, but processes operating at the seed-to-seedling transition being especially important. Here, we explore how insufficient seed dispersal (dispersal limitation) and ecological filtering of seedlings (establishment limitation) influence species recruitment in an Afromontane Forest. We combined census data from seeds in seed traps and seed-seedling transition plots in a Nigerian montane forest to measure dispersal and establishment limitation across species, life history strategies, and seed sizes. From 106 seed traps and 318 seedling plots, we recorded 11,278 seeds from 38 species and 2688 seedlings of 61 species. All species except for one liana showed strong dispersal limitation while 23 out of the 30 species showed establishment limitation. The two lianas sampled had significantly lower dispersal limitation compared to the trees investigated in the study. Our results suggest that both dispersal and establishment limitation are markedly high in this Afromontane forest than would be expected in a lowland counterpart.

KEYWORDS

lianas, montane forest, Nigeria, recruitment limitation, seed rain, seed-to-seedling transition

1 | INTRODUCTION

Understanding how anthropogenic drivers such as climate change, forest fragmentation, and hunting are altering forest composition has become a key question in tropical ecology (Feeley & Silman, 2011; Laurance, 2004; Soh et al., 2019). As anthropogenic effects increase in their extent and severity, taxonomic and functional composition are changing and species interaction networks are breaking down (Lewis, 2009; Lewis et al., 2009). Different species respond in different ways to change (Feeley et al., 2007); while some species increase in abundance, others decline or may even be driven to local extinction (Brook et al., 2008). For example, a study of seedling recruitment in hunted versus non-hunted forests

in Nigeria demonstrated a disproportionate increase in seedlings of wind-dispersed species in hunted sites (Effiom et al., 2013). In Ghanaian lowland dry forests, the relative frequency of deciduous species is increasing as droughts become more common and last longer (Aguirre-Gutiérrez et al., 2019). Thus, being able to predict species trajectories is essential for effective management of forests (Ganivet & Bloomberg, 2019; Grimshaw, 2001), biodiversity conservation (Feeley et al., 2007; Fort & Grigera, 2021) and for predicting future carbon stocks (Muller-Landau, 2004).

Processes happening at the seed-to-seedling transition play a crucial role in determining an individual's fate and therefore community structure and diversity (Clark et al., 2013; Dalling & John, 2008). During these early stages of development, potential recruits must

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pass through a series of biotic and abiotic filters; mortality rates are high and have a major impact on the relative abundance of species in the next generation. For the best chance of recruitment within a population, seeds must first disperse into all potential regeneration niches; failure to do so is referred to as *dispersal limitation* (sensu Clark et al., 1998). In tropical forests where the majority of species have fleshy, animals dispersed fruits (Howe & Smallwood, 1982), dispersal limitation is strongly influenced by frugivore numbers (Peres et al., 2016) and frugivore behavior (Morales et al., 2013).

Establishment limitation (Clark et al., 1998) occurs when there are insufficient niches available for the amount of seeds dispersed. Establishment limitation results from biotic and/or abiotic factors including seed predation, competition among seedlings for resources, seedling herbivory, or hostile environmental conditions. Which individuals survive these ecological filters and which are culled is influenced by species traits; trade-offs among traits during this seed-to-seedling transition are hypothesized to reduce single species advantages and thus promote the maintenance of species diversity (De La Peña-Domene et al., 2018; Tilman, 1994). For example, traits adaptive for efficient dispersal such as small seed size may be maladaptive for interspecific seedling competitive ability (Muscarella et al., 2013). Such trade-offs will also influence how species respond to different anthropogenic disturbances (De La Peña-Domene et al., 2018).

Anthropogenic activities impact the seed-to-seedling transition in many different ways; for example, by modifying the microclimate and habitat which may increase the mortality of seeds and seedlings of species that are susceptible to a deteriorated environment (Wang et al., 2019). It may also introduce significant fluctuations in the population of plants natural enemies which will in turn impact regeneration—for example, in small and fragmented habitats where top predators are absent, seed predation and herbivory rates will be significantly higher leading to weakened seed-to-seedling transitioning (Aliyu et al., 2014; Dirzo et al., 2014). Seed dispersal is also impacted as many dispersers especially specialist dispersers are lost or their populations decimated (Forget & Jansen, 2007; Mcconkey et al., 2012; Newbold et al., 2013). These factors all influence recruitment probabilities with major implications for tree species composition.

Species life history traits which lead to somewhat predictable outcomes across ecological filters include successional status (Zhu et al., 2018), growth form (Lu et al., 2015) and dispersal mode (Muscarella et al., 2013). For example, light-demanding, fast-growing pioneer species are generally more fecund but their seedlings tend to be less competitive than shade tolerant, late successional species (Kobe, 1999; Mccarthy-Neumann & Ibáñez, 2013). Canopy trees tend to produce more seeds than understory trees, but their seedlings face stronger conspecific negative density dependence (Terborgh et al., 2014).

The relative importance of dispersal and establishment limitation vary both across sites (Muscarella et al., 2013; Norden et al., 2009; Werden et al., 2020) and temporally (Clark et al., 2013). They are far from independent (Schupp et al., 2002) and are high for most species in tropical forests (Muscarella et al., 2013).

Despite the pan-tropical implications of the seed-to-seedling transition, syntheses of processes operating at this level have been strongly biased toward the neotropics (Howe & Miriti, 2004; Howe & Smallwood, 1982; Hubbell, 1979; Wills et al., 1997). Afrotropical studies are relatively rare (Clark et al., 2013; Cordeiro & Howe, 2003; Effiom et al., 2013; Olsson et al., 2019), and especially so in Afromontane locations. This needs to be redressed because while tropical montane forests represent only a small subset of all tropical forests, they harbor significant biodiversity and endemism (Abiem et al., 2020; Brujinzeel & Scatena, 2010; Bussmann, 2004). They offer important ecosystem services (Soh et al., 2019), are significant carbon stores (Spracklen & Righelato, 2014; Yepes et al., 2015) and likely play an important role in local hydroclimatic and biogeochemical cycles (Schröter et al., 2005).

Tropical Afromontane forests differ from lowland tropical forests in several ways which may impact their seed-seedling dynamics: They are typically small and have likely been fragmented for hundreds, if not thousands of years (Linder, 2014). Relatively harsh abiotic conditions such as cooler temperatures, seasonally dry conditions, and stronger winds, (Adie et al., 2017; White, 1983) result in fewer resources, lower crop sizes (Marshall et al., 2005), and less nutritious fruits (Chapman et al., 2016) than lowland tropical forests. They have fewer species (Chapman et al., 2016; Grimshaw, 2001), with conspecific negative density dependence less prevalent than in lowland forests (Abiem et al., 2021). Edge effects introduce abiotic and biotic challenges (Magnago et al., 2015; Murcia, 1995) and possibly associated with this, lianas are noticeably common (Chapman & Chapman, 2001; Magnago et al., 2015; Reis et al., 2020). Anthropogenic drivers such as hunting, grazing, and logging may accentuate these differences by altering historical seed-to-seedling transition processes. Understanding the components and processes of recruitment limitation in these small but globally significant forests (Chapman et al., 2016) will inform current ecological theory and allow us to predict future trends in their functional composition.

One approach to investigating the relative contribution of dispersal and establishment limitation to recruitment limitation is to observe seed rain, seedling emergence, and seedling survival (Clark et al., 1998; De La Peña-Domene & Martínez-Garza, 2018; Muller-Landau et al., 2002). In this study in montane Nigeria, we combine seed rain and seedling census data to calculate dispersal and establishment limitation for 30 common forest species. We test for the effects of successional status, growth form, dispersal mode, and seed size on recruitment limitation. Based on the findings of previous studies from elsewhere, we test the following hypotheses:

- (i) We will find high levels of dispersal limitation among large seeded, animal dispersed species, but especially chimpanzee-dispersed species because, in contrast to other primates, chimpanzees are now rare at Ngel Nyaki (Dutton et al., 2016).
- (ii) We will find high levels of establishment limitation in small seeded, as opposed to large seeded species because large seeds have a survival advantage in the face of environmental stresses such as drought, herbivory, and/or shade (Werden et al., 2020).

(iii) There will be trade-offs between life history traits such that species with high dispersal limitation will relatively have lower establishment limitation and vice versa. However, lianas will show low dispersal and establishment limitations because they are more adapted to disturbance (Schnitzer & Bongers, 2011).

2 | METHODS

2.1 | Study site

Our study was conducted in the 20.28 hectares Ngel Nyaki Forest Dynamics plot (07°04'05" N; 11°03'24" E) located at an elevation of 1600m in the Ngel Nyaki Forest Reserve, a sub-montane seasonally dry forest on the Mambilla Plateau in Nigeria, close to the Cameroon border (Chapman & Chapman, 2001). A detailed description of the plot is presented in Abiem et al. (2020) and the forest more generally in Chapman and Chapman (2001). Relevant to this study is that nowhere in the plot is further than 300m away from grassland and at one point the plot includes both forest edge and *Sporobolus* grassland. Outside of the plot, this grassland is heavily grazed by cattle and annually burnt by the Fulani pastoralists. Edge effects are consequently severe (Barnes & Chapman, 2014) and lianas such as *Clerodendrum bucholzii*, *Thunbergia* sp, *Psydrax acutifolia*, and *Landolphia* spp are common throughout the canopy (Chapman & Chapman, 2001). Populations of large-bodied frugivores including hornbills (*Tockus* sp), turacos (*Tauraco* spp.), primates, including the Nigeria-Cameroon chimpanzee (*Pan troglodytes* ssp. *elliotti*), and putty-nosed monkey (*Cercopithecus nictitans*) have markedly declined since the 1970s (Chapman et al., 2004). Seed predation is high both in grassland and forest (Aliyu et al., 2014; Dutton & Chapman, 2015), and we never observe piles of undispersed seeds beneath trees.

2.2 | Seed and seedling censuses

We collected seed rain data weekly over 3 years (2016–2019) from 106 1×1 m gauze seed traps. Our traps comprised a simple wooden square frame on which we stapled a gauze of 1 mm mesh width, and which was fixed 1 m above the ground on 1 m high wooden stakes. We prevented seed predation by surrounding the traps with approximately 5×0.5 m chicken wire mesh. We recorded and identified to species level all seeds, fruits, flowers and other reproductive parts of plants collected in the traps. Fruits collected were categorized as either mature, or as aborted, immature and/or damaged. We estimated the number of seeds in undamaged, mature fruits by multiplying the number of fruits for each species by the species-specific average number of seeds found in the fruit. These estimates were added to the number of undamaged seeds to determine the total number of viable seeds falling into each trap (Wright et al., 2005).

Since seed traps are located above the ground, they capture only fruits and seeds falling directly from trees, as well as those spat and/or defecated by birds, bats, and arboreal mammals, but not seeds from

dispersers such as rodents and other terrestrial animals. We placed the seed traps along existing trails within the plot, but at least 20m from the outer edge of the plot to avoid collecting seeds falling from the canopies of non-censused trees outside the plot (Muller-Landau et al., 2008). Traps were located at 10 m intervals on alternating sides of the trail and at least 10 m away from the trail (Wright et al., 2005).

To determine the short-term survival of very young seedlings and thus better understand ecological filters, we undertook a series of 10, three-monthly seedlings censuses. For this, we first established 318, 1×1 m seedling plots associated with the 106 seed traps (Harms et al., 2000; Wright et al., 2005). We placed three plots 2 m away from each of three sides of each seed trap (Figure 1). We assigned each plot to its appropriate 5×5 m grid (subquadrat) within the 20.28ha plot (Abiem et al., 2020) for which we had detailed enumeration data for every reproductively mature tree >1 cm DBH. We regarded every seed trap with its accompanying seedling plots as a census station. Within each plot, starting in October/November 2017, we recorded every woody plant (trees, shrubs, and lianas) seedling ≤50cm tall and measured their height from the ground to apical bud (Harms et al., 2000, Wright et al., 2005). From the first census on, to distinguish new from previously recorded recruits we tagged each seedling with an aluminum tag bearing a unique identification number. Species were identified using the reference collection of the Nigerian Montane Forest Project. Some of the seeds that could not be identified from references were sown, and germinated seedlings were then identified. A small number of seedlings (seven species) could not be positively identified.

2.3 | Species life history traits

We classified species in our seed traps and seedling plots based on successional status of tree species (pioneer and non-pioneer), dispersal mode (animal, ballistic, gravity and wind), and growth form (emergent tree, canopy tree, understory tree/shrub, and liana). We recorded average dry seed weight for each species from twenty seeds collected from fruits of at least five individual trees per species across the forest (Abiem et al., 2020).

2.4 | Data analyses

All analyses were performed using R.3.5.0. Statistical software package (R Core Team, 2018). In order to quantify seedling abundance at each station relative to seed abundance in the seed traps, we modeled the relationship between seed and seedling abundance using a generalized linear model with a negative binomial error distribution and a log link.

2.4.1 | Dispersal and establishment limitation

Following the methods of De La Peña-Domene and Martínez-Garza (2018), we calculated dispersal and establishment limitation

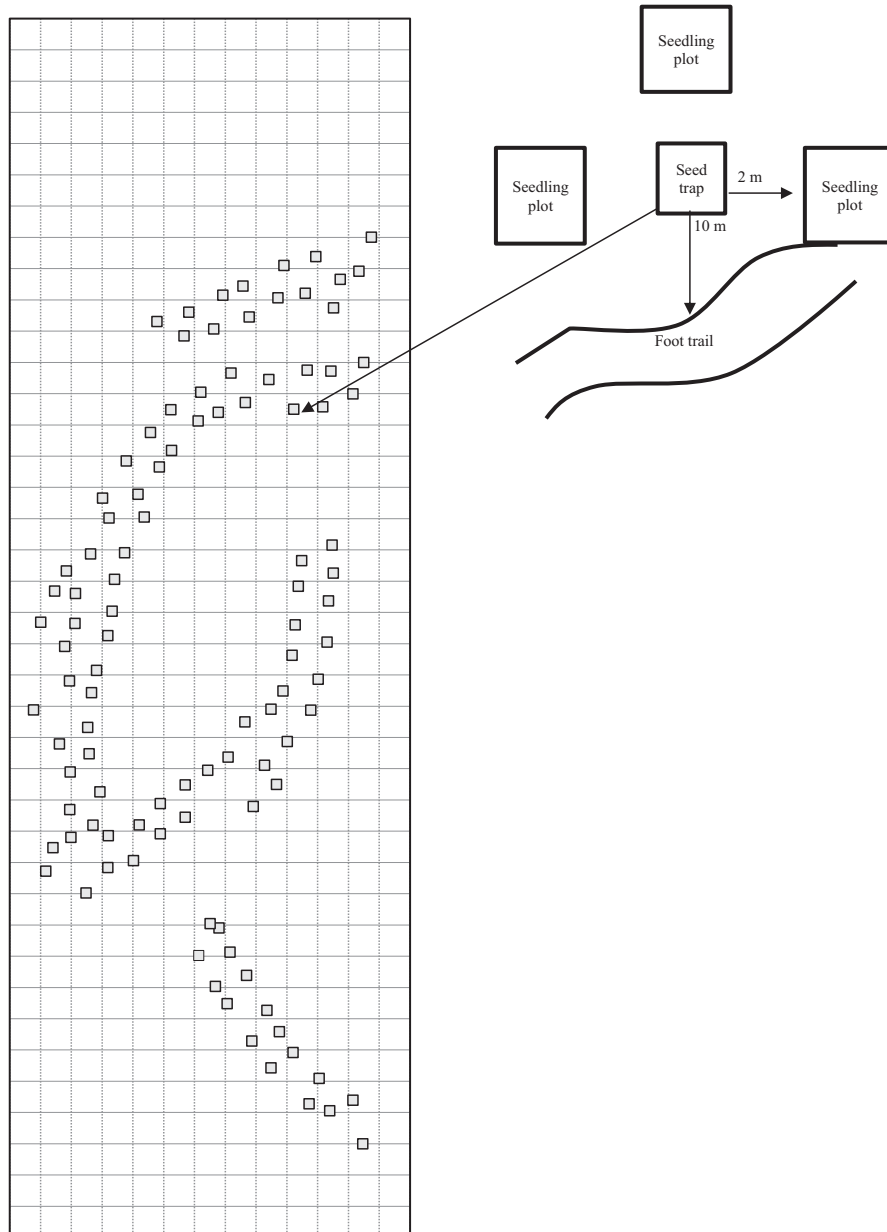


FIGURE 1 Position of seed traps placed in the 20.28 ha plot (gray grid lines = 20 × 20 m quadrats) and an illustration of seedling sampling plots around a seed trap. Every seedling plot is 2 m away from the seed trap

using density-weighted indices for the 30 species for which we had both seeds and seedling data (Table 1). Using density-weighted indices take into consideration the relative abundance of seeds and seedlings of each species, a factor ignored in previous calculations (Muller-Landau et al., 2002) yet which might significantly affect the probability of a species being successfully recruited (De La Peña-Domene & Martínez-Garza, 2018).

The density-weighted dispersal limitation index is:

$$\text{Dispersal limitation} = 1 - \frac{\left(\frac{a}{n}\right) + \left(\frac{si}{S}\right)}{2}$$

where a = number of seed traps which received seed(s) of the given species; n = the total number of seed traps; s_i = the number of seeds of species i ; and S = the total number of seeds sampled across all traps.

A dispersal limitation index of ≤ 0.33 indicated low dispersal limitation, an index of >0.33 and ≤ 0.67 as moderate dispersal limitation and values >0.67 indicate severe dispersal limitation (De La Peña-Domene & Martínez-Garza, 2018).

For establishment limitation, the density-weighted establishment limitation index is

$$\text{Establishment limitation} = 1 - \frac{\left(\frac{r}{am}\right) + \left(\frac{pi}{P}\right)}{2}$$

where r = the number of stations that recorded both seeds and seedlings of a given species; am = number of traps receiving the seeds of species i at a given time multiplied by the area in square meters; pi = the number of recruits of species i recorded at the

TABLE 1 Characteristics of focal species and their dispersal and establishment limitation values

Species	Total observed seeds	Total observed recruits	Seed mass (g)	Primary dispersal mode	Life history	Growth form	Dispersal limitation	Establishment limitation
<i>Anthonotha noldeae</i>	53	59	6.57	Ballistic	Pioneer	Canopy tree	0.903	0.714
<i>Bridelia speciosa</i>	258	4	–	Animal	Pioneer	Understory tree	0.965	0.899
<i>Carapa oreophila</i>	1	3	8.51	Gravity	Non-pioneer	Understory tree	0.995	0.999
<i>Chrysophyllum albidum</i>	374	46	1.03	Animal	Non-pioneer	Canopy tree	0.922	0.607
<i>Clausena anisata</i>	134	42	0.08	Animal	Pioneer	Understory tree	0.980	0.659
<i>Dicranolepis grandiflora</i>	24	13	0.4	Animal	Non-pioneer	Understory tree	0.980	0.748
<i>Drypetes gossweileri</i>	18	9	0.01	Animal	Non-pioneer	Canopy tree	0.976	0.898
<i>Ekebergia</i> sp	1	51	0.34	Animal	Non-pioneer	Canopy tree	0.995	0.491
<i>Erythrocarpa hispida</i>	3	17	–	Wind	Pioneer	Understory tree	0.995	0.497
<i>Entandophragma angolense</i>	311	12	1.73	Wind	Non-pioneer	Emergent tree	0.892	0.923
<i>Garcinia smeathmannii</i>	11	41	3.34	Animal	Non-pioneer	Understory tree	0.981	0.867
<i>Isolona</i> sp	497	59	1.82	Animal	Non-pioneer	Understory tree	0.766	0.789
<i>Landolphia landolphioides</i>	1614	838	1.23	Animal		Liana	0.576	0.351
<i>Leptaulus zenkeri</i>	379	6	0.12	Animal	Non-pioneer	Canopy tree	0.790	0.962
<i>Macaranga occidentalis</i>	1650	1	0.001	Ballistic	Pioneer	Understory tree	0.909	1.000
<i>Newtonia buchananii</i>	309	25	0.14	Wind	Non-pioneer	Emergent tree	0.883	0.836
<i>Noronhia africana</i>	146	145	1.31	Animal	Non-pioneer	Canopy tree	0.975	0.723
<i>Pavetta corymbosa</i>	119	1	0.03	Animal	Non-pioneer	Understory tree	0.971	1.000
<i>Parkia filicoideae</i>	3	1	0.77	Animal	Non-pioneer	Canopy tree	0.990	0.750
<i>Paullinia pinnata</i>	495	700	0.42	Animal		Liana	0.747	0.411
<i>Pleiocarpa pycnantha</i>	63	5	0.25	Animal	Non-pioneer	Understory tree	0.969	0.916
<i>Pouteria altissima</i>	182	77	3.19	Animal	Non-pioneer	Emergent tree	0.879	0.590
<i>Psorospermum aurantiacum</i>	426	8	0.05	Animal	Pioneer	Understory tree	0.967	0.665
<i>Psychotria peduncularis</i>	4	160	0.03	Animal	Pioneer	Understory tree	0.995	0.470
<i>Rytiginia</i> sp	14	3	–	Animal	Pioneer	Understory tree	0.990	0.749
<i>Santiria trimera</i>	177	8	1.32	Animal	Non-pioneer	Canopy tree	0.870	0.941
<i>Shirakiopsis elliptica</i>	352	7	–	Ballistic	Non-pioneer	Canopy tree	0.980	0.999
<i>Strombosia scheffleri</i>	20	5	–	Animal	Non-pioneer	Canopy tree	0.961	0.937
<i>Trichilia monadelphpha</i>	276	2	0.5	Animal	Non-pioneer	Canopy tree	0.917	0.966
<i>Zanthoxylum lepreurii</i>	20	4	0.03	Animal	Pioneer	Understory tree	0.994	0.999

Note: Dashes (–) signify insufficient data.

station, and p is the total number of recruits across all species. An establishment limitation index of ≤ 0.33 indicated low establishment limitation, an index of >0.33 and ≤ 0.67 as moderate establishment limitation and values >0.67 indicate severe establishment limitation (De La Peña-Domene & Martínez-Garza, 2018). We performed a Pearson's correlation test to examine the relationship between dispersal and establishment limitation and used generalized linear models with a negative binomial error distribution to examine the relationship between these limitations and seed size (seed weight and seed length). We used a Kruskal-Wallis analysis of variance to compare dispersal and establishment limitation among species of different successional association (pioneer vs non-pioneer), dispersal modes (wind, ballistic, and animal), growth

form (canopy tree, emergent tree, liana, and understory tree), and habitat associations (edge, core, and generalist).

3 | RESULTS

3.1 | Seed and seedling density and diversity

Over our 3-year study, we recorded 11,278 undamaged seeds from 38 species in 106 seed traps and 2688-recruited seedlings from 61 species within 318, 1×1 m seedling plots associated with the seed traps distributed throughout the 20.28 ha plot. From the seeds sampled, seven species were absent as seedlings. Number of seedlings

per species varied from 0 to 838 (Table S1). Nine forest species were represented by more than 50 seedlings each; the emergent tree *Pouteria altissima*, the canopy trees *Isolona* sp., *Ekerbergia* sp and *Anthonotha noldeae*, the understory trees/shrubs *Noronhia africanus*, *Dracaena* sp, and *Psychotria peduncularis*, and two lianas *Paullinia pinnata* and *Landolphia* sp. The lianas had markedly more seedlings than any other life forms (Table S1).

There was only a weak, albeit significant relationship between seed abundance and seedling abundance ($df = 105, p = .02$; Figure 2). Only a small variation in seedling abundance was explained by seed

abundance. For every unit increase in seed abundance, there was a 0.001 increase in seedling abundance.

3.2 | Dispersal and establishment limitation

Of the 30 woody plant species for which we were able to quantify dispersal and establishment limitation, 29 had high to extremely high dispersal limitation indices (>0.67) (Table 1). Only the liana *Landolphia* sp showed moderate dispersal limitation (0.576).

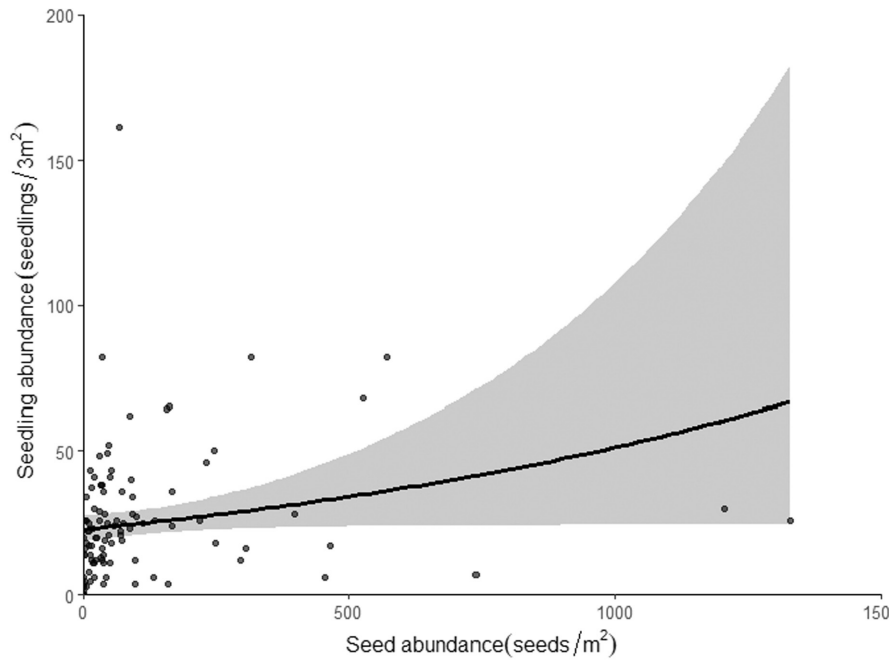


FIGURE 2 Relationship between seedling abundance and seed abundance for 106 seed trap/seedling stations in the 20.28 ha Ngel Nyaki Forest dynamics plot, showing negative binomial generalized linear model with a log link (black line) and 95% confidence interval (gray)

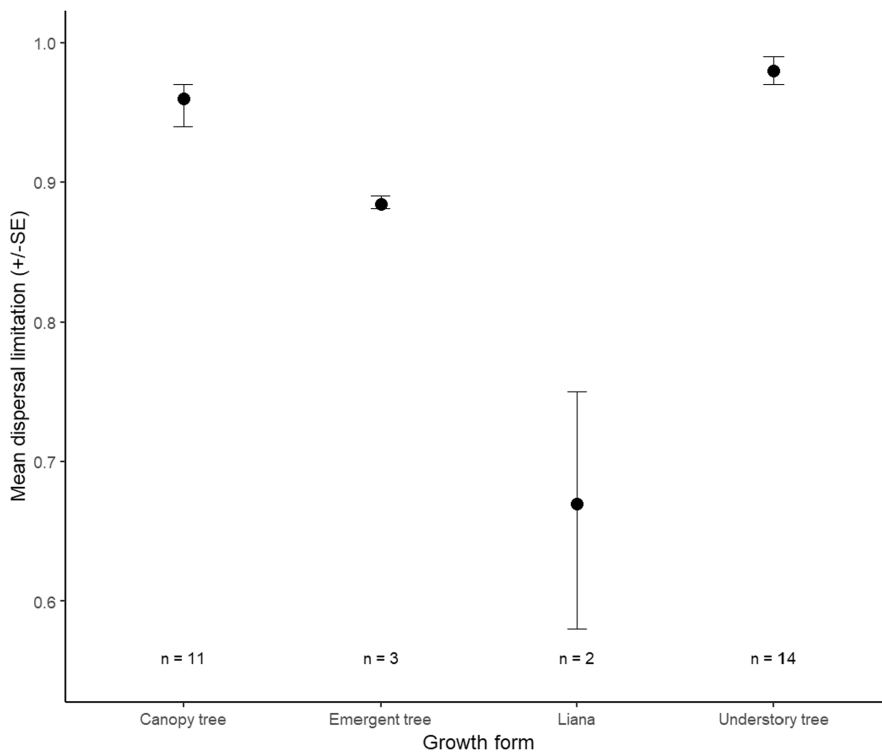


FIGURE 3 Comparison of mean dispersal limitation across the different growth forms (n is the number of species sampled in each category)

Establishment limitation was more variable across species, ranging from 1.0 (*Macaranga occidentalis* and *Pavetta corymbosa*) to 0.3 (*Landolphia* sp) but was mostly high, with 23 of the 30 species having indices of >0.67 (Table 1).

Dispersal and establishment limitation were not significantly correlated. Dispersal and establishment limitation were not explained by seed size for the 19 species for which seed size estimates were available.

Life history, dispersal mode, and habitat association had no significant effect on dispersal limitation. Growth form was the only variable which influenced dispersal limitation, which was significantly lower for liana species than other growth forms (Figure 3; $H = 11.04$; $df = 3$; $p = .012$). There was no variation in establishment limitation across all functional groups considered.

4 | DISCUSSION

4.1 | Composition and diversity in the regeneration layer

Our analysis of the 3-year data set of seed and seedling dynamics within Ngel Nyaki forest show that 29 out of 30 woody species for which we have data experience severe dispersal limitation (>0.67) and most (20) are severely establishment limited as well. Only about one third of the adult tree species in the plot (Abiem et al., 2020) were represented as seedlings, with even less diversity within the seed traps. Of course, how many seedlings are necessary for a species recruitment is an intractable question (Terborgh et al., 2014), and our results may reflect inconsistent seed years (Sheldon & Nadkarni, 2013), one extreme being no seeds produced and the other extreme high seed years which can lead to strong negative density dependence (Wright, 2005). The position of our traps and seedlings plots may have been such that we missed seeds and seedlings. As observed in some species, for example, *Macaranga occidentalis*, which recorded the highest total number of seeds sampled (1650) from only 4 out of 106 seed traps, the uneven distribution of the seeds is driving the high dispersal limitation rather than the number of seeds available. Nonetheless, the weight of evidence suggests that Ngel Nyaki forest is on a trajectory to becoming less species diverse, with presumably major implications for ecosystem functioning (Diaz et al., 2003; Lewis et al., 2009). Several other tropical studies report a similar trend of decreasing taxonomic diversity in the face of anthropogenic drivers (Alroy, 2017; Malik et al., 2016; Soh et al., 2019).

Our findings support our first hypothesis in as much as we predicted large seeded species would be highly dispersal limited, as has been found in many other forests, which have experienced hunting (Muller-Landau, 2007; Nuñez et al., 2019; Peres et al., 2016). Hunting and reduced fragment size disadvantage frugivores and therefore their large-seeded plant mutualists. Dirzo et al. (2014); Peres et al. (2016); Nuñez et al. (2019) and Ripple et al. (2019) all highlight the negative effect the loss of frugivores have on the dispersal of

large seeded species. Markl et al. (2012) found that while visitation rates to small seeded species were unaffected by disturbance and fragmentation, large-seeded species experienced reduced visitation rates in fragmented sites.

Large seeds can only be swallowed by large-bodied frugivores, as gape width is proportional to body size (Burns, 2013; Chen & Moles, 2015). As large-bodied animals are preferentially hunted, large-seeded plants are disadvantaged (Markl et al., 2012). At Ngel Nyaki, forest elephants have been locally extinct since the 1960s (Chapman et al., 2004) and only 16 adult individuals of the Nigerian/Cameroon chimpanzee have been recorded (Dutton et al., 2016). While this loss of frugivores is negatively impacting *Cordia milenii*, known to depend entirely on chimpanzees for dispersal (Thia et al., 2016), its impact on the dispersal of other large-seeded species needs to be determined. However, *Pouteria altissima* a preferred food of the Ngel Nyaki chimpanzees (Dutton & Chapman, 2015) was relatively well represented in seed traps and was no more dispersal limited than other large-seeded species, including *Chrysophyllum albidum*, which is a preferred food of the much more common Putty-nosed Monkey (Hutchinson, 2015). Generally, it would be expected that light-weighted seeds would be less likely to be dispersal limited because species which have small seeds produce more seed rain per unit area and seeds are often dispersed widely compared to large-seeded species. However, we found no significant difference in dispersal limitation between large and small seeded species.

While surprising for Ngel Nyaki, that *all* species were highly dispersal limited is not unusual for intact tropical forests and corroborates the findings of Muscarella et al. (2013) and De La Peña-Domene et al. (2018) from their studies in Puerto Rico and Mexico, respectively. This suggests that either *all* frugivore species are too few to optimally disperse even small seeds, or that seed limitation, whereby insufficient seeds are produced to fill all available suitable sites (Norden et al., 2009) plays a significant role in recruitment. The answer for Ngel Nyaki forest remains to be determined. Tropical montane forest populations are recognized as being less fecund than lowland populations (Chapman et al., 2016) but given the large fruit crops of many species such as *Anthonotha noldeae* (Barnes & Chapman, 2014) and *Pouteria altissima* (Matthesius et al., 2011), as well as the mid- rather than high elevation location of this site, lack of sufficient seeds seems unlikely. To what extent lianas are depressing fruit production has been shown elsewhere (García León et al., 2018) but needs testing at this site.

We found no evidence in support of our second hypothesis that small seeded species would, because of their inferior competitive ability be more establishment limited than large-seeded species (De La Peña-Domene et al., 2018; Muller-Landau et al., 2008; Muscarella et al., 2013). Theoretically, small seeded species are dispersal-advantaged; however, they have lower probabilities for seed-to-seedling transition than larger seeds; thus, they have higher establishment limitation (Coomes & Grubb, 2003; Harms et al., 2000). We, however, found high levels of establishment limitation across *all* seed sizes and across most species. Based on previous work at our study site, we think this is due to extremely high

seed predation pressure, especially on large-seeded species (Aliyu et al., 2014; Yadok et al., 2019). While hunting has reduced or eliminated populations of large predators such as African civet (*Civettictis civetta*) and the African golden cat (*Caracal aurata*), it may have released larger bodied rodents from some predation pressure. Seed fate experiments at our study site have shown predation, rather than herbivory or drought to be the most common fate among large seeds and their seedlings (Aliyu et al., 2014). The forest dwelling rodents African giant pouched rat (*Cricetomys* spp) and African brush-tailed porcupine (*Atherurus africanus*) are the major predators of large seeds ≥ 15 mm (Yadok et al., 2020). For *Cricetomys* spp., fat content rather than seed size (Yadok et al., 2020) is most important in seed choice. *Cricetomys* spp. also dig up germinating seedlings of large-seeded species to consume what is left of the seed (Pers. Obs.). While pouched rats are scatter hoarders (Aliyu et al., 2014; Nyiramana et al., 2011; Yadok et al., 2019), in contrast to the dispersal abilities of scatter hoarding rodents in the neotropics, evidence from both Rwanda and Nigeria (Nyiramana et al., 2011; Yadok et al., 2019) suggests that in Afromontane forests rodent predatory behavior far outweighs their disperser services. One hypothesis for this is low food availability in Afromontane forests relative to lowland tropical forests (Yadok et al., 2019). This hypothesis needs testing, but it may be that under Afromontane conditions, high predation rates are reducing the establishment of large-seeded species to the level of small seeded species. Vargas and Stevenson (2013) also highlight the importance of predation in establishment limitation in tropical forests. Other factors negatively affecting large-seeded species may be increased light through increased edge effects (Laurance et al., 2001) and increased drought because of climate change reducing fog (Cuni-Sanchez et al., 2019). These same factors may advantage small seeded species, and somewhat equalize establishment limitation among seed sizes. Both need further investigation.

Our investigations into the influence on establishment of other life history traits (growth form, dispersal mode and shade tolerance) and trade-offs among them proved inconclusive. There was a non-significant trend for emergent and canopy species to have lower dispersal limitation than understory species as reported elsewhere by (Caughlin et al., 2014). An explanation for this is that the relative height of emergent and canopy species relative to the understory gives them a higher chance of being successfully dispersed (Chen et al., 2019; Thomson et al., 2011).

The two liana species for which we were able to calculate dispersal and establishment limitation, *Paulinia pinnata* and *Landolphia* sp, were significantly less dispersal or establishment limited than any of the trees. This is not an unexpected finding (Wright et al., 2007). However, rather than being explained by dispersal mechanism (wind rather than animal) as Wright et al. (2007) suggest for neotropical lianas, here it may reflect the fact that fragmentation and disturbance favor lianas over trees and/or that lianas respond faster than trees to increased atmospheric CO₂ (Schnitzer & Bongers, 2011 and references within). Afromontane forests are small forests surrounded by vast grasslands. The edges of this forest are constantly disturbed by fire in addition to the disturbance created by tree fall.

Forest gaps and disturbed edges provide conditions that promote their rapid colonization by lianas. Lianas are intense competitors for trees affecting their recruitment, growth and survival (García León et al., 2018). Our findings show that these two liana species may be on a trajectory to increase in frequency at our study site. Clearly, this is an area where more research should prove fruitful.

In summary, our study is by far the most detailed assessment of the composition of the understory of an Afrotropical montane forest that we are aware of. We have shown that community and functional composition are declining and have come up with hypotheses for the drivers of this decline. Future research needs to test our hypotheses, using seed addition experiments. At the same time, we must continue to research forest restoration techniques (Da Cruz et al., 2020) in order to help maintain this biologically significant Afromontane Forest fragment and others like it.

AUTHOR CONTRIBUTIONS

Iveren Abiem: Conceptualization, Investigation, Formal Analysis, Writing-Original Draft, Writing- Review and Editing, Funding acquisition. **Ian Dickie:** Conceptualization, Formal Analysis, Writing-Review and Editing, Supervision. **David Kenfack:** Conceptualization, Supervision, Funding acquisition. **Hazel Chapman:** Conceptualization, Validation, Resources, Writing-Review and Editing, Supervision, Funding acquisition.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.gf1vhhmt2> (Abiem et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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