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Original article

Dispersal traits determine passive restoration trajectory of a Nigerian montane forest

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ABSTRACT

Passive restoration methods offer great promise for tropical regions where resources are limited but the success of such efforts can be variable. Using trait-based theory, we investigated the likely trajectories of passive restoration efforts in a degraded Nigerian montane forest system recently protected from burning and cattle grazing. We quantified the density, species richness, and functional trait dispersion of dispersed seeds and seedling communities at increasing distances from the forest edge. We then determined which plant traits are responsible for colonisation by quantifying changes in functional-trait dispersion and relative frequencies of dispersal-linked traits with increasing distance from the forest. We found a rapid decrease in density and species richness, and significant species turnover in both seeds and seedlings just beyond the forest edge. This was mirrored by a significant decline in functional-trait dispersion and a shift in the relative frequencies of dispersal-linked traits. These findings suggest that the reassembly of plant communities adjacent to remnant forest is dependent on functional traits present in these remnant source populations, providing support for the incorporation of trait-based theory in restoration management.

1. Introduction

Throughout the tropics, anthropogenic pressures have led to such severe forest loss and degradation (Asner et al., 2009; Geist and Lambin, 2002) that there is now a global effort towards their restoration (Chazdon, 2008; Holl, 2012) and the return of ecosystem goods and services to local communities (Benayas et al., 2009; Lamb et al., 2005). 'Active' restoration strategies, where intervention techniques are used to re-establish forest, can be costly and impractical in areas where community involvement is essential but resources are very limited (Holl and Aide, 2011; Parrotta et al., 1997). Alternatively, 'passive' restoration strategies, which involve only the restriction or total prevention of land-use practises from degraded land, are more easily employed and require minimal resources (Holl and Aide, 2011; Morrison and Lindell, 2011).

Although potentially useful, passive restoration can be very slow and often ineffective depending on landscape and ecological conditions (Duncan and Chapman, 1999; Laing et al., 2011; Myster, 2004). Factors such as insufficient seed rain (Cubiña and Aide, 2001; Duncan and Chapman, 1999; Martínez-Garza and Howe, 2003; Muñiz-Castro et al., 2006), seed bank composition (Kalesnik et al., 2013), seed and seedling predation (Myster, 2004; Nepstad et al., 1990), lack of suitable microsites for germination (Eriksson and Ehrlén, 1992), and competition from grasses (Chapman and Chapman, 1999; Duncan and Chapman, 1999) can collectively hinder forest regeneration. Moreover, passive strategies can lead to undesirable trajectories of ecosystem restoration because they are highly dependent on the potential for natural seed dispersal from nearby remnant habitat (Cole et al., 2011; del Castillo and Ríos, 2008; Martínez-Garza and Howe, 2003). For example (Kalesnik et al., 2013) showed that after 30 years of abandonment, commercial forests of exotic willow and poplar in Argentina remained mixed secondary forest with a high frequency of invasive species.

The likelihood of forest tree species dispersing into and establishing within adjacent degraded habitat is highly variable and depends on a wide array of measurable factors including fruit and

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seed traits (Cole, 2009; Dosch et al., 2007; Ingle, 2003; Muller-Landau et al., 2008; Muñiz-Castro et al., 2006; Teegalapalli et al., 2010). Seed traits have also been shown to be important for determining the success of propagules from seed banks, which may explain further variation in the reassembly of regenerating plant communities (Pywell et al., 2003). However, despite the wealth of evidence illustrating the importance of plant traits in mediating community assembly (Cornwell and Ackerly, 2009; Shipley et al., 2006), the role that fruit and seed traits play in determining dispersal of propagules into adjacent regenerating habitats and their germination potential at the early colonisation stage still requires further investigation (Lebrija-Trejos et al., 2010). This is especially necessary in African forests where, to our knowledge, there have been no studies that have identified the trait determinants of both seed dispersal distances *and* resulting seedling establishment with increasing distance from remnant forest systems into adjacent grassland.

Here we go beyond differentiating between seed size, wind and animal dispersal (Cubiña and Aide, 2001; Duncan and Chapman, 1999; Muñiz-Castro et al., 2006; Teegalapalli et al., 2010), and in addition include dispersal traits such as fruit colour and fruit type, which may affect frugivore choice (Gautier-Hion et al., 1985b) and even secondary dispersal (Babaasa et al., 2004). To detect the role of dispersal-linked traits in shaping assembly trajectories of forest regeneration, we first measured the potential for seed dispersal and seedling establishment from nearby remnant-forest habitat into grassland recently protected from cattle grazing and burning. Secondly, we quantified the dependence of seed rain and seedling species functional-trait composition on the distance from these remnant forests. As such, this study aims to provide an indication of the potential for using dispersal-linked traits in the prediction of restoration trajectories for future passive-restoration attempts in Afromontane forests.

2. Methods

2.1. Study site

The study was conducted at Ngel Nyaki Forest Reserve on the Mambilla plateau in Taraba State, Nigeria. The plateau is part of the Cameroonian Highlands Ecoregion (Olson et al., 2001). Ngel Nyaki reserve covers a total area of 4600 ha and includes 750 ha of continuous forest embedded within a savannah-grassland landscape (Beck and Chapman, 2008; Chapman and Chapman, 2001). The forest is mid-altitude to sub-montane at 1400–1600 m asl (Chapman and Chapman, 2001), the mean annual rainfall is approximately 1800 mm (Nigerian Montane Forest Project [NMFP] rainfall data) and the mean monthly maximum and minimum temperatures for the wet and dry seasons are 26–13 °C, and 23–16 °C, respectively (Matthesius et al., 2011).

Since the 1950's, when cattle grazing pressure became severe on the Mambilla Plateau (Bawden and Tuley, 1966), areas of overgrazed grassland dominated by *Sporobolus pyramidalis* and *Hyperrhenia rufa* have been created within Ngel Nyaki forest by the annual fires lit by Fulani pastoralists to clear forest and stimulate grass growth in the grasslands around the forest perimeter. Fires run down grassy spurs leading into the forest and penetrate the forest edge so that, over time, forest gaps comprising overgrazed grassland have been created. These grassland areas are predominantly grassland with a scattering of tall herbs including *Dissotis* species (Melastomaceae), *Ocimum gratisimum* and *O. basilicum* (Lamaceae) and *Guizotia* species (Asteraceae). Small shrubs of *Maesa lanceolata* and *Psorospermun febrifugum* were occasionally present in all sites. As part of an initiative to promote forest regeneration, in 2006 we established fences and fire breaks across the opening of these grassland areas where the pasture penetrates into the forest to prevent further livestock and fire encroachment. The grassland sites described in this study had therefore all been free of grazing and burning for four years. The sites were at least 1000 m apart, located around the perimeter of Ngel Nyaki forest.

2.2. Quantification of seed rain and seedling establishment

Sampling was carried out within four grassland areas that ranged in size from *ca* 4400 m^2 to *ca* 8800 m^2, dispersed throughout Ngel Nyaki forest. Within each of the four areas, five sampling transects were established, spaced 10 m apart, at least 10 m from the fence-line and at least 30 m from the forest edge at the end of the grassland area undergoing restoration (Fig. 1). Each transect consisted of eight seed traps, spaced equidistantly at 5 m intervals, from 5 m within the forest edge to 30 m out from the edge in the adjacent grassland (Fig. 1). The edge (0 m) was defined as the drip line of the outermost canopy trees at the forest perimeter. Seed traps consisted of a 0.5 × 0.5 m piece of mesh netting held 0.3 m above the ground with a wooden frame in order to prevent the surrounding vegetation from interfering with seeds falling into the traps and were protected by chicken wire to prevent the removal of seeds by seed predators.

All seed traps were visited weekly over a five year period from January 2006 to December 2010, upon which all seeds found within the traps were counted and identified to the species level. In the most recent year of sampling (2010), we sampled seedling establishment across all trap locations whereby all trees and shrubs $\leq$ 1 m tall and present within 2 m in any direction from a seed trap (an area of approximately 12.5 m^2) were counted and

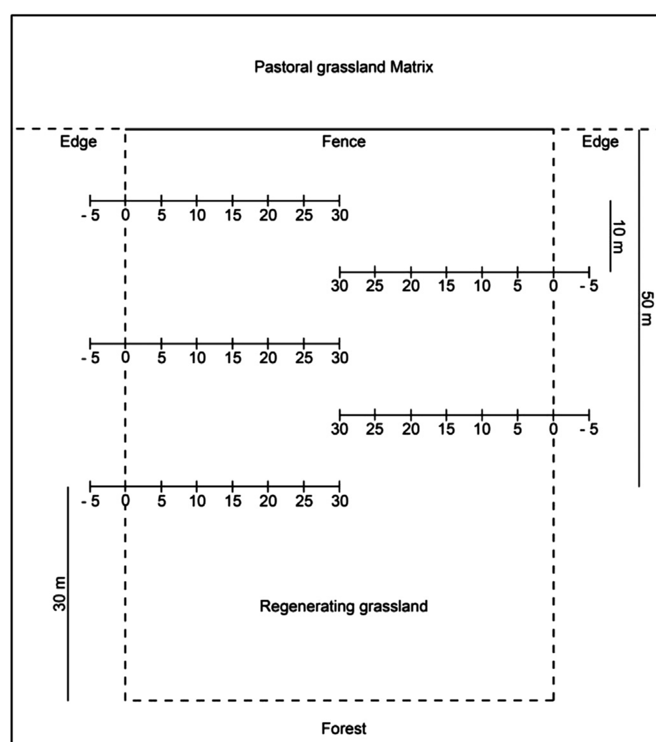

Fig. 1. Layout of the four sampling-point transects in the regenerating grassland sites. Values marked on the transects indicate the distance from the forest edge with negative values used to denote sampling points within the forest and "0" to denote the forest edge.