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Original article

Relative importance of perch and facilitative effects on nucleation in tropical woodland in Malawi☆

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ABSTRACT

Individual trees in open vegetation such as woodlands can act as "nuclei" for the colonization of forest tree species, which consequently lead to the formation of forest patches. This phenomenon is known as nucleation. The mechanism of nucleation is generally attributed to two factors: trees provide perches for frugivores that increase seed deposition (perch effect), and tree crowns ameliorate environmental conditions, which improves seedling establishment (facilitative effect). Few studies have attempted to distinguish the relative importance of these two factors. In this study, I separated these two effects in a woodland in northern Malawi. I chose *Ficus natalensis* as a potential nuclei tree because large individuals of this species are commonly located at the center of forest patches within open woodland at the study site. I monitored several environmental variables, seedling survival, seedling composition, and seed rain at three microsites: under *F. natalensis*, under *Brachystegia floribunda* (a dominant woodland species), and in open sites. Both tree species provided similar favorable conditions for the establishment of forest species compared to open sites. Thus, the survival of forest tree seedlings under *F. natalensis* and *B. floribunda* was similar, and substantially higher than seedling survival in open sites. However, communities of naturally occurring seedlings differed significantly between *F. natalensis* and *B. floribunda*. These results indicate that the facilitative effect alone cannot explain the nucleation pattern. I attribute this result to the perch effect of *F. natalensis* because the forest seedling species recorded under *F. natalensis* reportedly have small, brightly colored diaspores, which are indicative of dispersal by birds. Seed deposition of forest species under *F. natalensis* was significantly higher than that under *B. floribunda* or in open sites. My findings reinforce the idea that trees will lead to nucleation when they enhance seed deposition and have a positive effect on the post-dispersal stage.

1. Introduction

Open vegetation such as grasslands and woodland areas intermingled with closed-canopy forests are common in many tropical regions. Because these tropical forest/open vegetation mosaics cover such large areas, changes to their vegetative structure and composition, and the resulting feedbacks, could have significant implications for biodiversity and the carbon cycle (Mitchard et al., 2009). Although there has been a major loss of forest area caused by logging and other factors, recent studies have also documented the expansion of tropical forests into open vegetation areas in many parts of the world (Puyravaud et al., 2003; Favier et al., 2004; Bowman et al., 2010). Understanding the processes and mechanisms of forest expansion has broad implications for biodiversity conservation and the management of forest/open vegetation mosaics.

The occurrence of individual trees in open vegetation can act as nuclei for the colonization of forest tree species. This process, known as nucleation (Yarranton and Morrison, 1974), can aid colonization of forest tree species, leading to the formation of forest patches. The mechanism of nucleation is generally explained by two different ecological processes (Corbin and Holl, 2012; Zahawi et al., 2013): the perch effect and the facilitative effect. By providing perch sites and fruit, trees in open areas can attract frugivores from nearby forests, and this increases the seed rain of animal-dispersed forest species under their crowns. Additionally,

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trees in open areas can facilitate forest tree establishment by mitigating stressful environmental conditions, such as high irradiance, high temperatures, and soil water deficits.

Many studies have attempted to verify the mechanisms of nucleation by comparing seedling composition under putative nucleus trees to that in open matrix (e.g., Duarte et al., 2006; Carlucci et al., 2011; Arantes et al., 2014; Fujita and Mizuno, 2015). For instance, Duarte et al. (2006) found more seedlings of forest species established under crowns of *Araucaria angustifolia* than in open matrix in southern Brazilian grasslands. They attributed this result to the perch effect, given that most seedlings under the crowns had vertebrate-dispersed diaspores. They also suggested that *A. angustifolia* facilitated the establishment of forest species by ameliorating microclimatic conditions such as air humidity and soil water content under the crowns. Other studies have drawn similar conclusions (e.g., Carlucci et al., 2011; Arantes et al., 2014). However, few studies have attempted to separate the relative importance of perch and facilitative effects in the nucleation process (but see Pausas et al., 2006; Albornoz et al., 2013). Nucleation might be generated by either perch or facilitative effect. For instance, nucleation may commence if seeds of forest species are disproportionally deposited under crowns that have neutral effects on post dispersal fate. Alternatively, if the seeds are randomly distributed in space but trees in open areas provide suitable conditions for forest tree species beneath the crowns, nucleation may also occur. Indeed, Vieira et al. (2013) found more seedlings from non-animal dispersed species under *Combretum leprosum*, suggesting that the facilitative effect is the main process driving nucleation in southern Brazilian grasslands. Separating the role of perch and facilitative effects is necessary to fully understand the mechanism of the nucleation.

Trees in the genus *Ficus* (Moraceae) make effective nuclei because their syconia attract many frugivores, and the microhabitat under their dense crowns is suitable for the establishment of forest trees (Slocum and Horvitz, 2000; Slocum, 2001; Schlawin and Zahawi, 2008). In northern Malawi (southeast Africa), circular patches of forest occur within tropical woodland, with large fleshy-fruited trees, especially *Ficus natalensis*, located at their centers (Fujita, 2014). These circular patches are a common feature of nucleated forest patches, rather than fragmented forests (Favier et al., 2004; Duarte et al., 2007). Thus, this region is a suitable field site for testing the nucleation process.

The aim of this study was to elucidate the mechanisms of nucleation by separating the importance of perch and facilitative effects. To address this topic, I compared seedling compositions among three microsites within tropical woodland: under *F. natalensis*, under *Brachystegia floribunda* Benth., and in open microsites. *F. natalensis* and *B. floribunda* have dense crowns that can provide suitable habitat for the establishment of forest tree species. However, *B. floribunda* bears dry pods that are explosively dispersed (Chidumayo and Frost, 1996) and do not attract frugivores, making it unlikely to have a perch effect on seed deposition. If seedling abundance of forest species is higher under *F. natalensis* than under *B. floribunda* or in open microsites, and if the established seedlings are primarily animal-dispersed species, it suggests the importance of perch effect during nucleation. In contrast, if the abundance and composition of seedlings do not differ under *F. natalensis* and *B. floribunda*, it would suggest that facilitation is the driving force. To address these predictions, I (1) analyzed the environmental conditions in the three microsites, (2) monitored seedling survival of *Syzygium guineense* ssp. *afromontanum* F. White (a forest tree species) in the three microsites for 2.5 years, (3) analyzed the seedling composition in the three microsites, (4) quantified the seed rain of *S. guineense* ssp. *afromontanum* in the three microsites and (5) observed animal visitors at fruiting *F. natalensis* trees.

2. Materials and methods

2.1. Study area

The study was conducted in northern Malawi (southeastern Africa). In southeastern Africa, approximately 2.7 million km^2 of land are covered with tropical woodland called miombo woodland, which consist of leguminous species in three closely related genera: *Brachystegia*, *Julbernardia* and *Isoberlinia* (Fabaceae subfamily Caesalpinioideae; Campbell et al., 1996). This region also contains patchy montane rainforest, which differs from miombo woodland in floristic composition and structure (White et al., 2001). The distributions of miombo woodlands and forest have shifted over wide areas of landscape (Vincens et al., 2003). Ekblom (2008) suggested that climatic conditions after 1850 AD have been favorable for forest expansion.

For these experiments, I selected an area typical to this region in a rural zone managed by the village of Ntchuka (10°58′ S, 34°04′ E) on the north Vipya Plateau in northern Malawi (a map of the study area is available, see Fujita, 2014). Mean annual rainfall on the north Vipya Plateau exceeds 1270 mm, with most rainfall occurring during the wet season between December and April (Chapman, 1970). The bedrock of the Vipya Plateau is composed of undifferentiated basement complex rocks, primarily gneisses (Chapman, 1970). Soil of the study area is a well-drained red and sandy clay loam. The study site is predominantly covered by miombo woodland, although some montane rainforest occurs on mountain crests (>1800 m asl), in valleys, and in several circular forest patches (~10–1800 m^2) on mountainous slopes (1700–1800 m asl). With the exception of montane rainforests, most of the land is burned by humans approximately every 2–3 years during the dry season (September–December). Fires are set to clear footpaths, because overgrown paths are difficult to traverse and pose a risk of hiding snakes. Montane rainforests are typically less flammable due to their dense canopy that excludes grasses and maintains a more humid understory (Hoffmann et al., 2012a). Therefore, fire is unlikely to penetrate far into the forest. Antelopes such as the common duiker (*Sylvicapra grimmia*) were seen at the study site. Few trees are harvested from this area because it is located far from local villages.

2.2. Study species

F. natalensis is a medium to tall tree species (up to 30 m) distributed in eastern and southern Africa. In the study area, it grows primarily in miombo woodland and is also located at the center of montane rainforest patches. Its syconia (1.1 ± 0.1 × 1.0 ± 0.1 cm, n = 10) change from green to yellowish during ripening. *F. natalensis* has two periods of fruit ripening each year: August–October and January–April. Fruit bats and birds are potential seed dispersers (McCarthy et al., 1998).

Brachystegia floribunda (Fabaceae, Caesalpinioideae) is a medium to tall tree (≤20 m) that is the dominant species in the miombo woodland of northern Malawi, where this study was conducted. The tree produces woody pods (up to 12.5 × 4.0 cm) from October–January; the pods explosively disperse their seeds (Chidumayo and Frost, 1996).

2.3. Data collection

2.3.1. Environmental conditions

To examine whether *F. natalensis* and *B. floribunda* have similar facilitative effects on the establishment of forest tree species, I monitored environmental variables in three microsites: under *F. natalensis*, under *B. floribunda*, and in open microsites. I selected