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Seeded pioneer die-offs reduce the functional trait space of new-growth coastal dune forests

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ABSTRACT

The planting or seeding of pioneer species to promote restoration apparently contributes little to the establishment of late-successional species, despite the common assumption that they facilitate forest regeneration. We evaluate the consequences of planting pioneers for coastal dune restoration by measuring plant traits (specific leaf area, wood density, $\delta^{13}C$ and maximum plant height), species composition and canopy openness in three rehabilitating forests of different ages, where a pioneer species (*Acacia karroo*) was seeded, and one undisturbed old-growth forest. We surveyed woody species composition in 2010 and in 2015 to assess how changes in *A. karroo* influences community structure of rehabilitating forest. Our results showed that the number of adult individuals of *A. karroo* decreased progressively with forest age, indicating that the demise of individuals of *A. karroo* opens canopy gaps in rehabilitating sites. This accorded with a significantly higher variation of canopy openness levels in the oldest rehabilitating site. Rehabilitating sites tended to progress towards a reduced trait space as they aged, contrasting with the old-growth forest that showed an expanded trait space. Communities located at high levels of canopy openness were dominated by species with lower values of specific leaf area and wood density, indicative of acclimation to high light conditions and fast-growing strategies. Our results suggest that changes in light availability due to canopy gap formation, can act as an environmental filter which may deflect forest regeneration trajectories. We show that coupling a trait-based approach with environmental measurements can give insight in regeneration trajectories of rehabilitating sites and, therefore, better inform restoration practices. Preventing the formation of large canopy gaps in restoration programs using pioneers as a regeneration pathway may facilitate the natural recovery of degraded forest.

1. Introduction

The planting or seeding of fast-growing species (i.e. pioneers) is commonly used to initiate and promote ecological restoration (Chazdon, 2008; Cusack and Montagnini, 2004; Lamb et al., 2005). Support for this practice comes from natural forests where shade-tolerant guilds (i.e. late-successional) replace pioneers following a disturbance event (Chazdon, 2011; Dent et al., 2013; Lebrija-Trejos et al., 2010a). However, the reliance on the establishment of pioneers to restore vegetation through succession needs further investigation (Boyes et al., 2011; McNamara et al., 2006; Podadera et al., 2015; Vleut et al., 2013). Contrary to popular belief pioneers may not facilitate forest regeneration, but simply tolerate or even inhibit the colonization of late-successional species (Connell and Slatyer, 1977).

Pioneer species have high growth and mortality rates (Russo et al., 2008; Wright et al., 2010). Their high growth rates accords with a facilitating role, because it can promote a quick increase of tree cover during early successional stages, promote the establishment of shade-tolerant species, and inhibit self-replacement (Dent et al., 2013; Lebrija-Trejos et al., 2010a). On the other hand, the high mortality rates of pioneers may inhibit the establishment of late-successional species (Vleut et al., 2013). For instance, simultaneous die-offs of pioneers could open large canopy gaps, which can facilitate their self-replacement and hinder the establishment of late-successional species (Bazzaz, 1979; Whitmore, 1989). Thus, seeding pioneers may jeopardize restoration by inhibiting secondary species from colonizing regenerating forests. However, how the demise of planted pioneers influences regenerating pathways in rehabilitating forest has rarely been assessed.

The functional traits of plants have been used to evaluate and plan restoration programs (Asanok et al., 2013; Laughlin, 2014; Nguyen et al., 2014). Conceptually, the regeneration of forests should progress from a functionally narrow subset of species with similar trait values during the early stages of succession (i.e. trait convergence), towards an increasingly wide functional trait space at late successional stages (i.e. trait divergence) (Buzzard et al.,

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2015; Lasky et al., 2014b; Lohbeck et al., 2014). More generally, this interpretation can be accommodated into a filter model framework to explain successional processes (Meiners et al., 2015). Of all the potential colonizers from the regional species pool, environmental conditions will only select for those species with traits that promote establishment and persistence (i.e. environmental filters). Afterwards, competition and/or other determinants of performance will reorganize species (Meiners et al., 2015). In this way, if the demise of pioneers promotes an abrupt change in environmental conditions, it may remove species with traits that cannot cope with the altered conditions (i.e. shade-tolerant) and deflects the regeneration trajectory away from the targeted vegetation 'endpoint' (Mouillot et al., 2013). Assessing how the functional trait space varies in a regenerating, new-growth forest that uses pioneers may therefore provide information about the processes structuring the community (e.g. environmental filters).

However, addressing only how the functional trait space change over time may not fully unravel the drivers that control vegetation dynamics. For instance, studies that failed to find deterministic changes in functional structure during succession may have overlooked the strong relationship between plant traits and their environment (Lebrija-Trejos et al., 2010b). Indeed, in systems where human-induced disturbances have strongly altered community composition, trait-environment relationships have responded deterministically (Amatangelo et al., 2014). If the environment plays an important role in shaping community structure, the inclusion of environmental factors relevant to the studied systems, together with functional structure, may provide more insight into the mechanisms that drive forest development (Lebrija-Trejos et al., 2010b). By assessing linkages between functional traits and environmental variables, restoration efforts can be better informed. In addition, by understanding how biotic and abiotic factors are linked in studies of forest development, responses to disturbance and subsequent community assembly can be compared among different sites (Meiners et al., 2015).

In this study, we combine functional trait indices with canopy openness measurements to assess the role of seeded pioneers, and identify a possible mechanism that could drive forest development in rehabilitating coastal dune forest in KwaZulu-Natal, South Africa. Here, the pioneer species, *Acacia karroo* was seeded after sand tailings were reshaped into dunes (van Aarde et al., 1996). Previous studies within these forests have shown how tree species composition changes following the senescence of *A. karroo* (Grainger and van Aarde, 2013). However, it is uncertain if canopy gaps that are formed through the senescence of the pioneer species promote an increased functional trait space as expected in a successional context (Lohbeck et al., 2014), or promotes a set of species with similar trait values (i.e. environmental filters). We specifically aim to answer: What are the implications of the demise of *A. karroo* on regenerating trajectories of rehabilitating coastal dune forest? We hypothesize that the formation of canopy gaps will act as an environmental filter and lead to the establishment of species with a narrow set of traits (i.e. fast growing, acclimated to high light conditions) deflecting the regeneration trajectory away from the reference site. Overall, we expect that coupling functional traits with light availability will help to better inform restoration programs that uses pioneers as a regenerating pathway.

2. Material and methods

2.1. Study area

Our study sites were located within a set of rehabilitating forests on mined coastal sand dunes and within an undisturbed, old-growth coastal dune forest (Sokhulu forest, 28°27′S, 32°25′E; hereafter old-growth) in KwaZulu-Natal, South Africa (Fig. 1). The studied forests were located approximately 60 km north of Richards Bay (28°43′S, 32°12′E) and formed part of the Indian Ocean Coastal Belt (IOCB) forests of southern Africa (Mucina and Rutherford, 2006). The IOCB covers a narrow strip (less than ~35 km wide) along 800 km of the eastern seaboard of South Africa

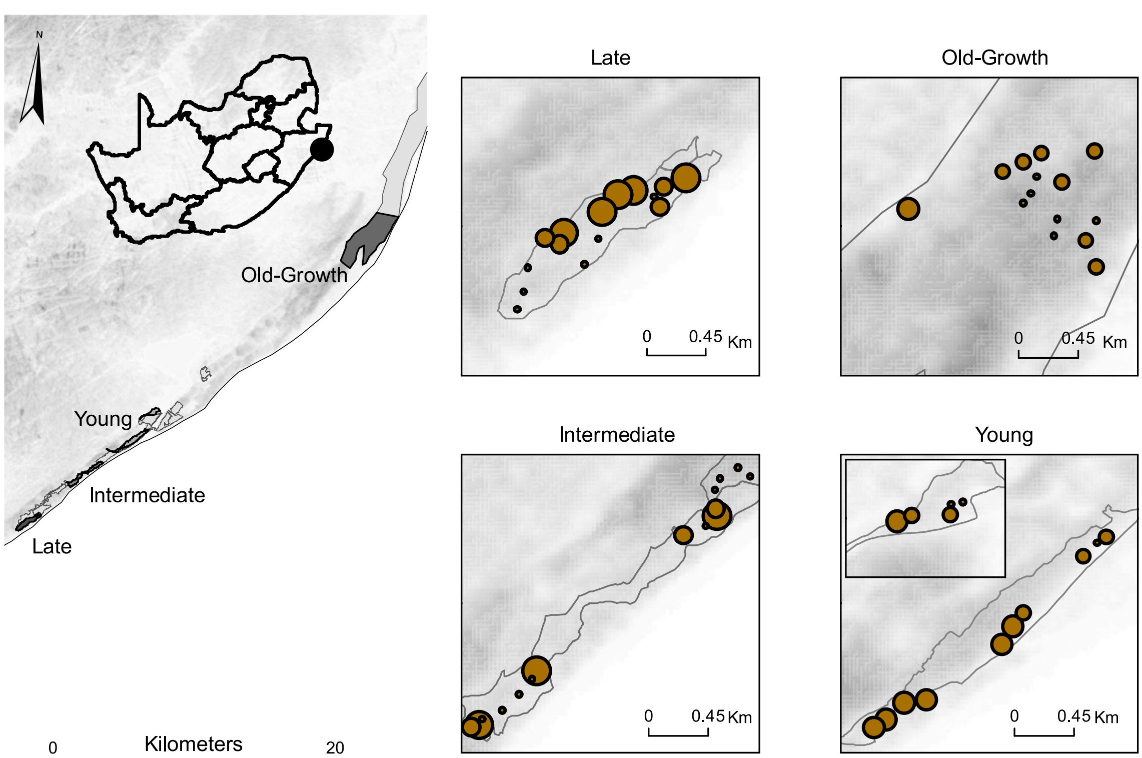

Fig. 1. Overview of the study area and sampling sites. Sampling points are depicted by circles, of which the size is proportional to canopy openness levels.