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Pervasive, long-lasting impact of historical logging on composition, diversity and above ground carbon stocks in Afrotemperate forest

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ABSTRACT

Understanding the rate and extent of forest recovery from major disturbance events enable forest managers to establish conservation priorities and allocate limited resources for their management. We examined the extent to which Afrotemperate forest has recovered from widespread, stand-levelling logging that followed the European settlement of south eastern South Africa approximately 150 years ago. We used plot-based tree census data to compare ecological characteristics (diversity, composition, structure) of primary, secondary and degraded Afrotemperate forests. Forests impacted by colonial logging events show no evidence of converging on the composition and above ground standing stock of old-growth forests. Primary forest canopies were dominated by two conifer species (Podocarpaceae) and a suite of long-lived pioneer angiosperms dominated the canopies of secondary forests. Old-growth canopy trees ($\geqslant$20 cm dbh) were taller ($\sim$26 m vs $\sim$16 m) and had broader girths ($\sim$94 cm vs $\sim$54 cm) compared with those in secondary forest. Canopy tree size differences translated to considerable (2 to 3-fold) differences in above ground carbon: we estimated that primary forest stores >240 Mg C ha^{-1} compared with the range of 80.7–114.3 Mg C ha^{-1} estimated for the two secondary forests and 84.3 Mg C ha^{-1} for the degraded forest. Measures of rarefied species richness and diversity (Shannon exponential) were markedly lower for primary forest canopy trees, consistent with the proposition that the composition of Afrotemperate forests converges on podocarp dominance at the old-growth stage. In contrast, diversity measures for small (2.5–10.0 cm dbh) and medium (10.1–19.9 cm dbh) trees were noticeably higher in secondary and degraded forests indicating the considerable conservation value of these formerly disturbed forests.

1. Introduction

The rate and extent to which forest ecosystems recover from anthropogenic disturbance depends on their level of transformation (Boucher et al., 2001; Chazdon, 2003), the duration and type of subsequent land use (Pascarella et al., 2000; Silver et al., 2000) and the proximity and diversity of forests surrounding the disturbed area (Purata, 1986; Thomlinson et al., 1996). Chronosequence studies, which have the implicit assumption that succession follows a predictable continuum, have featured prominently in the theoretical development of tropical forest successional processes (Chazdon et al., 2007; Feldpausch et al., 2007). These studies focus exclusively on the first decades following disturbance with few extending beyond 100 years (Finegan, 1996). Indeed, the difficulty in identifying forests that have remained undisturbed for more than a century (Clark, 1996; Chazdon, 2008) is an important obstacle to examining late stage succession, particularly with the recognition that many tropical forests formerly considered to be old-growth are late secondary forest (e.g., Bush and Colinvaux, 1994). Understanding the nature of recovery from human impact is further complicated by the interaction with natural processes operating at multiple spatial and temporal scales (Chazdon, 2003). Here we evaluate the extent to which Afrotemperate forest has recovered from widespread, stand-levelling logging that followed the European settlement of south eastern South Africa approximately 150 years ago.

Evaluating the recovery of forest from major disturbance is influenced by the measure used to describe plant community structure (Letcher and Chazdon, 2009). For example, the recovery of species composition is likely to take centuries (Finegan, 1996; Guariguata and Ostertag, 2001; Marín-Spiotta et al., 2007) because of the importance of specific life history traits (e.g. shade tolerance) in species replacement patterns in secondary forest. Indeed, functional composition, but not species composition, appears to follow a more predictable trajectory aligned with old-growth forest after

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100 years of secondary succession (Dent et al., 2013). In contrast, the recovery of species richness (Pascarella et al., 2000) or structural measures such as above ground biomass (Saldarriaga et al., 1988; Silver et al., 2000; Letcher and Chazdon, 2009) to pre-disturbance levels may occur within decades. The latter are positive findings because they imply restoration of critical ecosystem services such as carbon sequestration and nutrient cycling to an ecosystem undergoing global transformation. However, the rapid recovery to a diverse ecosystem but one that is dominated by early-successional, shade-intolerant species masks the impact on biodiversity and belies the true extent of the recovery process. A more revealing assessment of recovery is to compare the advanced regeneration composition of late secondary forest with that of old-growth sites (e.g., Guariguata et al., 1997; Dent et al., 2013) or to assess the performance of extinction prone species. For example, tolerance of the matrix is a key predictor of species persistence in disturbed forest ecosystems (Laurance, 2008a). A suite of life-history traits (e.g. slow growth rate, dependence on specialist biotic pollination and dispersal vectors, shade tolerance) place late-successional species at risk of local extinction in fragmented landscapes (Tabarelli et al., 1999; Metzger, 2000; Lawes et al., 2005; Cramer et al., 2007; Lawes et al., 2007a; Sodhi et al., 2008).

Forests in South Africa are among the most species-rich temperate forests worldwide (Silander, 2001) but cover a small (~0.56%, Low and Rebelo, 1996) land area. Afrotemperate forests follow an archipelago-like distribution in the south eastern part of the country (Lawes et al., 2004a). Situated within a grassland matrix, these forests are generally located in the fire shadows of steep south facing slopes or deeply incised ravines (Geldenhuys, 1994). Indeed, this restricted distribution may serendipitously have contributed towards their long-term conservation. Unlike the large intact blocks that characterise forest in the tropics, forested landscapes of the Afrotemperate zone are difficult to access and their steep, rocky topography generally precludes agricultural activity. Forests in the region have therefore largely escaped the modern global trend of systematic clearing for timber or agriculture. However, many inland forests were extensively exploited for their timber during the colonial period that started in the mid-1800s and continued intermittently until the early-1940s (Fourcade, 1889; King, 1941; McCracken, 2004). Once cleared by colonial woodcutters, the forests were left to recover by natural successional processes. The current structure and composition of inland forests is a legacy of that earlier major logging disturbance (Lawes et al., 2007b; Adie and Lawes, 2009a).

Afrotemperate forests present a complex management challenge to conservation authorities in the province of KwaZulu–Natal. Nearly 75% of all forests are either located in, or within 1 km of communal lands. Forest patches within community land are threatened by subsistence harvesting to service fuel and building requirements (Robertson and Lawes, 2005). Land ownership is divided between the State, with responsibility devolved to national government and provincial conservation authority, private landowners (predominantly commercial timber companies) and tribal authority (Obiri and Lawes, 2002). Legally, forests on communal land are state-owned. However, from a practical perspective the community assumes ownership and resource use is administered locally through the Traditional Authority. The Afrotemperate landscape is composed of hundreds of predominantly small (mean size ~16 ha, Adie and Lawes, unpublished data) patches that have a naturally fragmented distribution in a remote and mountainous terrain (Lawes et al., 2004b). Forests are therefore largely inaccessible to conventional management by conservation authorities, which operate under severe manpower and financial constraints. Understanding the rate at which dominant ecological characteristics (diversity, structure) recover from major disturbance will inform management authorities on forest prioritisation and how management resources should be allocated. Presently, management activities are confined to a handful of larger (>200 ha) 'flagship' forests at the expense of the majority.

We examine the extent of recovery from colonial logging of Afrotemperate forest in southern KwaZulu-Natal by comparing three measures of tree community reassembly (species diversity, species composition, above ground standing carbon) in secondary forest against known stands of primary forest. There are no reliable historical records relating to the timing and distribution of logging activities or to the volumes of timber extracted during the colonial period. Concern for the widespread destruction of forest resources was identified towards the end of the nineteenth century (Fourcade, 1889), at least 30 years after logging was initiated in the region. Reliable chronosequence data are therefore absent. We assume the composition and structure of primary forest represents the upper limit (c.f., Keith et al., 2009) of Afrotemperate forests but make no assumptions regarding the composition of pre-disturbance ecosystems, which is probably not possible anyway (Clark, 1996; Chazdon, 2008).

2. Methods

2.1. Study region

We assessed the level of anthropogenic disturbance to five Afrotemperate forests in an archipelago extending north of Bulwer in the KwaZulu-Natal (KZN) midlands to Weza in the far south of the province adjacent to the Eastern Cape (EC) border (Fig. 1). Forests have a widespread and naturally fragmented distribution throughout this remote region (~5900 km^2 in extent). Approximately 1300 forest patches with a combined estimated area of 20,800 ha occur in this area (Adie and Lawes, unpublished data). Four forest patches exceed 500 ha in extent but most are small (mean size = 16.0 ha, median size = 2.6 ha). Forests are typically distributed between 1000 and 1600 m above sea level. Mean annual precipitation for the region is 965 mm (range: 724–1181 mm). Rainfall is concentrated in the summer months (November to March, >75% of total) with a protracted dry season over winter (May to August, <5% of total). The climate is warm temperate with mean temperatures of 19 and 10 °C in the hottest (January) and coldest (July) months, respectively (Schulze, 2007). The landscape is mountainous with deep river valleys.

Here, secondary forest refers to forests that develop following catastrophic disturbance (Guariguata and Ostertag, 2001; Putz and Redford, 2010). Evidence of severe logging episodes (sawpits, sliptrails, wagon roads), dating to the colonial period (mid-1800s to the early twentieth century), are widespread in Afrotemperate forests (Lawes and Eeley, 2000; Lawes et al., 2007b). Indeed, the prevalence of angiosperm-dominated canopies among forests that were logged extensively is consistent with the proposal that angiosperms assume the colonising role following major disturbance in Afrotemperate forest (Lawes et al., 2007b; Adie and Lawes, 2009a). The defining characteristic of primary (or old-growth) forest is the predominance of large (>70 cm dbh, Clark, 1996), ancient trees due to the extended absence of stand-replacing disturbance (Enright and Ogden, 1995; Luyssaert et al., 2008; Putz and Redford, 2010). In Afrotemperate forest, the Podocarpaceae are longer-lived, attain sizes (height and girth) that far exceed associated angiosperms (Lawes et al., 2006) and, relative to co-occurring angiosperms, their shade tolerance facilitates continuous regeneration beneath an intact canopy (Adie and Lawes, 2009a, 2009b). Old-growth Afrotemperate forest is thus dominated by podocarp species. Forest degradation refers to the anthropogenic-induced long-term reduction in carbon density (IPCC, 2003; Angelsen, 2009).