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Functional diversity mediates contrasting direct and indirect effects of fragmentation on below- and above-ground carbon stocks of coastal dune forests

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ABSTRACT

Changes in structure and functioning of tree communities in response to forest fragmentation may alter tropical forest's capacity to store carbon and regulate climate. However, evidence for indirect effects of forest fragmentation on above – and belowground carbon pools through changes in forest biodiversity is scarce. Here we focus on understanding the relative importance of taxonomic and functional diversity and tree cover to explain above- and below-ground carbon stocks in coastal dune forest fragments. We surveyed tree species composition and structure in six coastal forest patches varying in size from 215 to 13350 ha, in Kwa-Zulu Natal, South Africa. For each fragment, we estimated carbon stocks of two pools, aboveground biomass (AGC) and soil organic carbon (SOC). We used structural equation models to test if and to what extent the effects of forest fragmentation on AGC and SOC were mediated by tree cover and taxonomic and functional diversity. Our results showed that forest fragmentation directly reduced AGC, but increased SOC. In contrast, forest fragmentation indirectly, through decreasing functional diversity, increased AGC, but decreased SOC. Small patches therefore had few tree species that were functional similar and had high AGC, but low SOC, which led to a negative relationship between species richness and AGC. Tree cover was not affected by fragmentation, and had a direct positive effect on AGC but not on SOC. Our results suggest that forest fragmentation simultaneously affect multiple processes which directly and indirectly affects carbon stocks of different pools. Fragmentation may trigger a process of biotic homogenization, in which a few species are positively related with carbon storage above-, but not below-ground.

1. Introduction

Deforestation, forest fragmentation and degradation threaten biodiversity and affect ecological functions (Barlow et al., 2016; Haddad et al., 2015; Lewis et al., 2015). Following habitat loss and fragmentation, species richness generally decreases, while assemblages become less even and more structurally homogenous (Collins et al., 2017). Such changes in biological diversity often reduce ecological functions (Isbell et al., 2011; Liang et al., 2016). For example, the loss of biodiversity has a strong negative effect on above ground carbon storage, not only in simple temperate systems, but also in structurally diverse and complex tropical forests (Poorter et al., 2015). However, other components of the carbon cycle, such as soil carbon stocks, may increase following fragmentation (Barros and Fearnside, 2016). Higher rates of tree mortality, as well as changes in vegetation structure, composition, and function could boost decomposition of organic matter, thereby transferring carbon to the soil compartment and increasing soil carbon stocks (Laurance et al., 2011). Such increases in soil carbon following fragmentation could offset above-ground carbon losses - however if, and how this happens remains unclear.

The majority of studies investigating fragmentation impacts on forest carbon stocks have focussed on carbon stored aboveground in living trees. The soil organic carbon stock, which has been estimated to contribute between 36–60% of total carbon stocks in the tropics (Dixon et al., 1994; FAO, 2010; Malhi et al., 1999), has remained understudied in comparison. In particular, linkages between soil carbon stocks and tree functional diversity remain an important knowledge gap, even though plant species diversity has been directly linked to soil carbon (Lange et al., 2015). Plant traits, such as whole plant structure or the partitioning of biomass among plant organs, control carbon inputs into soil through primary productivity and belowground carbon allocation, while other traits, such as growth rate, control carbon loss from soil

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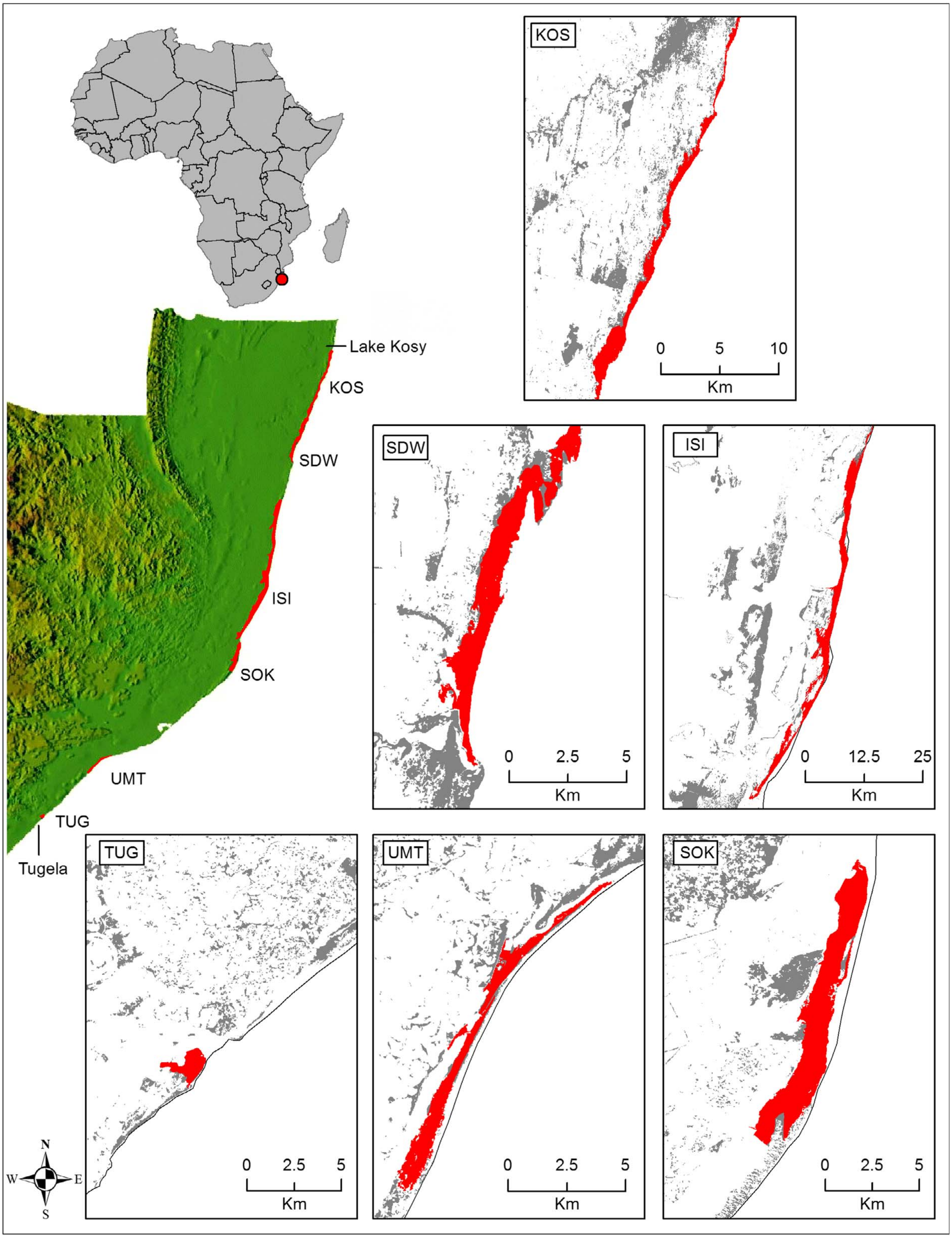

Fig. 1. Coastal dune forest fragments delineations. Red colours depict forest fragments included in this study from Lake Kosi in the north, to the mouth of the Tugela river in the south. Insets depict studied fragments (red) and surrounding forest fragments (grey) in detail. Names of fragments follow the notation of Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

through respiration and volatilization of organic compounds (De Deyn et al., 2008). This dependencies suggests that changes in the functional composition of tree communities after fragmentation can simultaneously mediate above- and below-ground carbon stocks.

Tree communities along forest edges often resemble disturbed communities with low functional diversity (Laurance et al., 2011). In these systems, pioneer tree species and lianas benefit from the creation of more open canopies while mature trees, typical of closed forest canopies, suffer greater mortalities due to unfavourable micro-climatic conditions (Laurance et al., 2011). Such compositional changes in the