Resource use in indigenous forests of the Eastern Cape, South Africa and its effects on bird communities
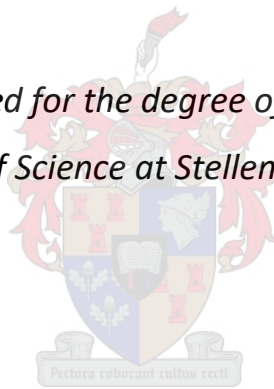
by

Jessica Leaver

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Promoter: Prof. M.I. Cherry

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Declaration

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Abstract

Indigenous forest represents South Africa's most limited and fragmented biome, but supports disproportionality high levels of biodiversity. Furthermore, forests provide a range of resources for people, particularly the rural poor, and are thus of high socio-economic value. This is particularly true in the Eastern Cape, which harbours 46% of South Africa's remaining indigenous forest cover, and some of the country's most economically impoverished populace. Forest management in this region is thus required to balance the needs of resource users with the conservation of forest biodiversity through sustainable use. However, *de facto* open-access systems of resource use prevail*,* and there is concern that unregulated harvesting of forest products is driving forest degradation. Supporting this, a recent study found forest bird ranges to have declined in the region over the past 20 years, despite no loss of forest cover over the same time period. However, little research has investigated the link between resource use, habitat modification and forest avifauna in the Eastern Cape. Consequently, this study aimed to investigate patterns of resource use in state forests across the Eastern Cape; and the impact of different harvest regimes on forest habitat structure, and avifaunal communities. Specifically, three key resource use types were investigated: understory trees harvested for poles; canopy trees harvested for crafts and timber; and bark harvested for medicinal use.

Regionally, harvest rates were low to moderate, however, the nature and extent of harvesting was site- and species-specific. Of particular concern was the high rate of ring-barking of focal canopy tree species of medicinal value, resulting in the mortality of 29% of harvested trees. Harvest activities modified habitat structure at the ground, understory and canopy layers, with the severity of impact dependent on the nature and extent of harvesting. Overall, harvest activities increased the frequency of canopy disturbances, with concomitant thickening of ground- and understory-layer foliage. At the regional-scale, avifaunal communities were shaped by variation in forest structure and harvest regimes, mediated by species' feeding traits. Furthermore, harvest activities negatively affected functional organization of bird communities, dependent on the nature and extent of harvesting, but did not reduce species richness or the diversity of functional traits. At the forest-scale, the bird community in a montane forest was structured by harvest-mediated habitat modification, as well as elevation. Specifically, forest-specialist species richness was negatively affected by habitat modification, while forest-generalist species richness was positively affected. Similarly, avifaunal community composition was affected by habitat modification caused by timber harvesting in a scarp forest.

Based on avifaunal reponses to harvesting, findings of this study indicate that resource use may be sustainable, but that better management is required to mitigate negative ecological impacts

associated with high levels of extraction. By providing insight into the ecological implications of harvesting, this study contributes to the development of ecologically-informed resource use management strategies. While this represents an important contribution, the sustainable use of forests cannot be achieved without increased capacity of the state to implement management actions which integrate the ecological and social issues of forest management.

Opsomming

Inheemse woude verteenwoordig Suid-Afrika se mees beperkte en gefragmenteerde bioom, maar ondersteun buitegewone hoë vlakke van biodiversiteit. Verder, verskaf woude 'n verskeie natuurlike bronne aan mense, veral arm mense, woonagtig in landelike woudgebiede, en bied dus 'n hoë sosio-ekonomiese waarde. Dit is veral so in die Oos-Kaap, waar 46% van Suid Afrika se oorblywende inheemse woude, maar ook van ons armste mense voorkom. Woudbestuur om die balans tussen bron-verbruikers en bewaring van woudsbiodiversitiet op 'n volhoubare wyse te balanseer, word dus in hierdie streek dringend benodig. Maar, feit is, onbeperkte toegang tot die verbruik van natuurlike bronne is aan die orde van die dag, en daarom heers daar kommer dat diesulke onbeheerde oes van produkte die degradering van woude dryf. Ondersteuning vir hierdie toedrag van sake word deur 'n onlangse studie, wat bevind het dat voëlgemeenskappe in hierdie woude die afgelope 20 jaar gedaal het, gemaak. Dit, alhoewel woudbedekking oor die selfde tydperk uitgebrei het. Maar min wetenskaplike navorsing het tot op hede die verwantskap tussen bron-verbruik, habitat- versteuring en woud-voëlgemeenskappe in die Oos-Kaap deeglik ondersoek. Gevolglik was die doel van hierdie studie gemik om die patrone van bron-verbruik in staatsbestuurde woude van die Oos-Kaap te ondersoek; asook die impak wat verskillende oespatrone op habitatstruktuur en voël-gemeenskappe mag hê. In hierdie studie word drie bronverbruikers-tipes spesifiek ondersoek: die oes van onderbome vir pale; oes van oorhoofse bome vir handgemaakte en konstruksie houtprodukte; asook die insameling van bas vir medisinale gebruike.

In streeksverband was gevind dat alhoewel die koers van oesting laag tot matig plaasvind, die aard en intensiteit van oesting, terrein- en spesies-spesifiek was. 'n Spesifieke bekommernis was die hoë insidensie van ringbas-verwydering van belangrike oorhoofse bome met medisinale waarde. So is 'n mortaliteit van tot 29% gevind by bome waarvan daar geoes was. Oestingsbedrywighede het die habitatstruktuur op grondvlak-, en plantegroei onderdak - asook en kapkroon-boom gebiede beduidend versteur, met die graad van impak wat gekoppel was aan die mate en uitgebreide aard van oesting. Oorsigtlik gesien, het die oestingsbedrywighede die frekwensie van kroon-versteuring, met gevolglike verdigting van grond en onderboom plantegroei veroorsaak. Op 'n streeksvlak, is voëlgemeenskappe, deur veranderde spesies-voedingswyses, deur die gepaardgaande variasie in woudstruktuur en deur oes-benaderings stelsels, bepaal. Verder het oestingsbedrywighede, afhangend van die aard en intensiteit van oesting, die funksionele organisasie van voëlgemeenskappe negatief beinvloed, maar tog is spesiesrykdom of die funksionele diversiteit nie verlaag nie. Deur vergelykend na variasie tussen woude te kyk, is gevind dat die voëlgemeenskappe van bergagtige woude deur oestingsbemiddelde habitatsversteuring, asook hoogte bo seespieel, bepaal word. Resultate dui daarop dat spesifiek, spesialis-woudspesies-rykdomnegatief deur habitat

habitatversteuring beinvloed is, terwyl algemene-woudspesies-rykdom positief beinvloed verhoog is. Op die selfde manier is die samesteling van voëlgemeenskappe deur habitatversteuring van hout-oesting in 'n skarpwoud beinvloed.

 Gebaseer op die reaksies van voëlgemeenskappe op oesting in woude, dui die bevindinge van hierdie studie aan dat bron-verbruik volhoubaar mag wees, maar dat beter bestuur nodig is om die negatiewe ekologiese impakke verwant aan hoë verbruik teen te werk. Deur insig te kry rakende die ekologiese implikasies van oesting, maak hierdie studie 'n belangrike bydrae tot die ontwikkeling van ekologies-gebaseerde bronverbruik-bestuurstrategië.   Alhoewel hierdie bevinding 'n beduidend is, kan die volhoubare verbruik in woude nie geskied sonder 'n toenemende inisiatief van die Staat om toepaslike bestuursaksies, wat ekologiese en sosiale aangeleenthede rakende woud-bestuur integreer, in te stel en te handhaaf nie.   Dit verteenwoordig 'n belangrike bydrae, maar die houbare gebruik van woude sal net behaal word as die staat sy hoedanigheid om bestuursaksies uit te voer wat ekologiese asook sosiale sake van woudbestuur integreer.

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CHAPTER I: INTRODUCTION

1.1. Introduction

Globally, the need to conserve natural forests is receiving increasing attention, and it is now widely accepted that forests enable natural ecological processes that are beneficial to, if not vital for human society (Miura et al., 2015; Watson et al., 2018). Ecologically, these benefits include oxygen provisioning and carbon sequestration, regulation of water regimes, maintenance of soil quality and stabilization, nutrient cycling and modulating climate (FAO, 2010; Lewis, et al. 2019). Furthermore, forests are a key component of biodiversity, both in themselves and in the habitat they provide for other species, supporting an estimated two-thirds of the world's terrestrial species richness (Gardner et al., 2009). Economically, forests form the basis of a number of industries in many countries, and are thus a major component of formal income sectors including timber, processed wood, paper and fruit (FAO, 2010). In developing nations, the geographic overlap of areas characterised by remaining natural forest and rural poverty (Sunderlin et al., 2005; 2008) means that a substantial portion of the economic value of forests in these regions is derived informally through the use of forest products by the rural poor. This includes use of a range of forest resource that help economically impoverished households meet daily basic needs of energy, shelter, healthcare, food, fodder for livestock, and income derived through the trade of certain products (Shackleton et al., 2011). Consequently, forests and the resources they provide comprise a critical contribution to the livelihood strategies of millions of households in developing nations (Iqbal, 1993; Hegde et al., 1996; Sabra and Walter, 2001; Shackleton and Shackleton, 2004; Shackleton et al., 2011).

1.2. Forest products for rural development and forest conservation

Recognition of the socio-economic value of forest products has resulted in forest management policies in developing nations being increasingly reformed. Specifically, there has been a shift from preservationist policies of the past, wherein forest where managed largely for timber production to the benefit of a few large companies or the state, to more inclusive policies that aim to develop natural forests for the sustainable use of a range products, thereby promoting more equitable distribution of forest benefits (Robertson and Lawes, 2005). This growing interest in managing forests for the use of

forest products emerged in the 1990s, motivated by the rationale that this would contribute not only to rural development but also to conservation objectives (Arnold and Pérez, 2001). Consequently, impetus for these changes in forest policies was not only due to increased recognition of the socio-economic importance of forest products, but also by increasing concern that conventional forest uses, such as logging, were driving a 'deforestation crisis' such that forests required urgent conservation attention (Sills et al., 2011). Thus, the notion of managing forests for a range of forest products was underpinned by three main propositions; i) forest products contribute to rural livelihoods and welfare, ii) exploitation of forest products is less ecologically destructive than large-scale timber harvesting and other forest uses, and therefore provides a sound foundation for sustainable forest management, and iii) increased commercialisation of forest products should add to the perceived value of forests and therefore increase incentive to conserve forest resources (Arnold and Pérez, 2001). The latter point reflects the 'conservation through commercialisation' hypothesis, which proposes that the commercialisation of forest products would act as a market-based instrument to enhance environmental protection (Evans, 1993).

While the value of forest products to rural livelihoods and welfare has been widely accepted (Hegde and Enters, 2000; Cocks and Møller, 2002; Angelsen and Wunder, 2003; Shackleton and Shackleton, 2004; Cocks and Dold, 2006; Paumgarten and Shackleton, 2011), the potential win-win situation wherein managing forests for a range of products would promote rural development and conservation objectives, has been brought into question (Crook and Clapp, 1998; Arnold and Pérez, 2001; Shackleton, 2001). Specifically, as the number of studies investigating the ecological implications of forest product harvesting increased, over-exploitation and concomitant negative ecological effects began to emerge as a common characteristic, particularly for products traded on a commercial basis, with this largely attributed to poor resource management (Peters, 1994; Tewari, 1998; Peres et al., 2003; Ticktin, 2004). Consequently, the notions that forest product harvesting provides a foundation for sustainable forest management; and that commercialisation of products would encourage this, have been challenged, and the critical issue of failing resource use management raised. Specifically,

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the *de facto* open-access systems that prevail in forests in many developing nations (Thapa and Weber, 1995; Castley and Kerley, 1996; Sunderlin et al., 2005). Consequently, essential preconditions needed for market-oriented forest conservation to be effective, namely, resource management regualtions; strong enforcement; and stable and secure property rights (Crook and Clapp 1998), are lacking in many developing nations. This has been observed to facilitate over-exploitation and economic exhaustion of a range of forest resources in developing nations (Cunningham, 2001; TIcktin, 2004; Marshall et al., 2006).

1.3.   Factors affecting resource use patterns

In response to increasing concern around the sustainability of forest product harvesting, and the need for a better understanding of the ecological effects of resource use in the context of failing management systems, several studies have emerged over the past 30 years (Vàsquez and Gentry, 1989; Cunningham, 1993; Godoy and Bawa 1993; Rawat, 1997; Tiwari, 2000). Specifically, studies examining the factors that influence resources use patterns (Uma Shaanker et al., 2004a; Steele et al., 2015), and the ecological impacts of forest product harvesting (Uma Shaanker et al., 2004b; Ticktin, 2004; Brites and Morsello, 2012) have shed much light on this complex socio-ecological issue. In the case of the former, studies have revealed that the nature (i.e. plant part harvested and harvesting method) and extent of resource use depends on a range of ecological, social and economic factors (Ambrose-Oji, 2003; Uma Shaanker et al., 2004a; Boudreau et al., 2005; Karanth et al., 2006; Varghese and Ticktin, 2008; Steele et al., 2015). Examples of ecological factors are the abundance and distribution of the resource (i.e. availability), its regeneration potential, recruitment and maturation rates, and the availability of substitutes (e.g. accessible woodlots or plantations). Social factors include issues around land tenure and accessibility; governance arrangements and adherence; labour constraints; population density; ecological knowledge; and cultural norms and preferences. Economic variables influencing this complex issue include the existence of alternative livelihood options (e.g. ownership of arable land, employment opportunities, state grants etc.), the level of poverty, and the relative cost of alternatives, (which culminate to determine a household's level of dependency on

natural products), the commercial demand and value of the product, and access to markets (which determine the level to which a resource is commercialised). Consequently, various factors operating at multiple spatial and temporal scales affect resource use patterns at the local-scale, which has subsequently been shown to be site-specific (Shackleton et al., 2007b; Sassen and Shiel, 2013; Steele et al., 2015) given that each forest and resource-user community represent different capacities to respond to economic, social, cultural, political and environmental conditions that operate at broader scales. A unique set of livelihood strategies, trade dynamics, and harvest opportunities and practices thus exist at the local-scale (Ham and Theron, 2001; Shackleton et al., 2007b; Thapa and Chapman, 2010; Paumgarten and Shackleton, 2009; 2011; Steele et al., 2015).

1.4.   Factors affecting ecological impacts of resource use

Under most extractive practices, gains in rural livelihoods through forest product harvesting come at some ecological cost (Uma Shaanker et al., 2004b). However, the magnitude of this is dependent on the floristic composition of the forest, the nature and intensity of harvesting, and the particular species or type of resource harvested (Peters, 1994; Ticktin, 2004; Uma Shaanker et al., 2004b; Brites and Morsello, 2012). These factors ultimately affect the two parameters which determine whether a resource is harvested sustainably or not, namely: i) the extent to which harvesting affects the future availability of a resource in the forest, and ii) the extent to which harvesting interferes with the biological diversity of a forest, i.e. its structure and functioning (Ros-Tonen et al., 1998). Information regarding the impact of resource use at multiple levels is thus required to assess its ecological sustainability. In this regard, studies investigating ecological impacts have shown that at the individual level, growth rates, survival and reproduction may be negatively affected by harvesting (Hall and Bawa, 1993; Peters, 1994; Cunningham, 2001). At the population-level, genetic, spatial and age structure, sex ratio and population size of target species may be affected (Murali, et al., 1996; Uma Shaanker et al., 2004b; Gaoue and Ticktin, 2007; Ndangalasi et al., 2007). At the community-level, changes in species richness and composition may arise in areas exposed to harvesting (Obiri et al., 2002; Sagar and Singh, 2004; Thapa and Chapman, 2010; Sassen and Sheil, 2013).

While these studies have contributed largely to our understanding of the ecological implications of forest product harvesting, much of the existing research has focussed on the issue of over-exploitation at the individual- and population-level, resulting in a dearth in knowledge regarding broader ecosystem-level implications (Ticktin, 2004; Brites and Morsello, 2012). For example, few studies have examined changes in plant-plant and plant-animal interactions in response to harvest disturbances (Moegenburg and Levey, 2003; Forget and Jansen, 2007). Consequently, while the body of knowledge regarding the ecological impacts of forest product harvesting, and the factors that affect this, has grown substantially over the past 30 years, ecological studies are biased towards those examining impacts on availability while relatively fewer studies have examined broader-scale impacts on biological diversity, and the mechanisms driving this (Ticktin, 2004; Brites and Morsello, 2012). This gap in our knowledge represents a limitation in our understanding of the ecological implications of resource use, and therefore our ability to develop effective sustainable use practices. This is of concern given that the demand for subsistence and commercial use of forest resources is not predicted to decline (Shackleton et al., 2011).

1.5.   Birds as indicators to measure ecological impacts of resource use

A possible reason for the lack of studies at broader ecological levels is that measuring ecosystem-level responses to human disturbances is highly complex, given the multi-faceted nature of environmental change. This is made even more complex in the case of forest product harvesting, which encompasses a range of disturbance types. In this regard, indicators which act as surrogate measures of environmental change may provide a vital diagnostic tool to assess ecological impacts of resource use disturbances beyond direct impacts on harvested species (Noss, 1999; Rempel et al., 2016). In this regard, birds have been shown to be valuable and effective biodiversity indicators for several reasons (Noss, 1999; Canterbury et al., 2000; O'Connell et al., 2000; Gregory and Strien, 2010; Rempel et al., 2016). First, bird communities are sensitive to human-mediated habitat modification, and they occupy various trophic levels such that variation in bird responses to disturbance provides insight into the mechanisms through which disturbances operate (Cleary et al., 2007; Shahabuddin and Kumar, 2007;

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Jayapal et al., 2009; Ehlers Smith et al., 2015; Ibarra and Martin, 2015; Asefa et al., 2017). From a practical perspective, birds are widespread, relatively easy to identify and survey, and their phylogenetic status is well-defined, making them an ideal study taxon in the context of applied ecology (Gregory and Strien, 2010). Furthermore, there is a long-standing connection between people and birds, such that ecological responses demonstrated through changes in bird communities may resonate more strongly with people, compared to responses by other, less relatable taxa. From a socio-economic perspective, the resonance between birds and people has resulted in a global multi-billion dollar sub-sector of eco-tourism based on birdwatching, representing an important potential avenue for rural development and alternative income sources for communities close to forests that harbour high bird diversity (Sekercioglu, 2006; Biggs et al., 2011; Steven et al., 2015).

Most importantly, and beyond their value as ecological indicators, birds are a vital component of forest ecosystems, exhibiting the broadest range of ecological functions among vertebrates, including seed dispersal, pollination and pest control (Sekercioglu, 2006). Consequently, declines in forest bird abundance and diversity are likely to reflect declines in ecosystem function (Sekercioglu, 2012). Consequently, understanding bird responses to human disturbances affecting forest ecosystems is of ecological and socio-economic importance (Sekercioglu et al., 2004). Despite this, relatively few studies have assessed bird responses to forest product harvesting, representing a critical gap in our knowledge given that resource use represents on of the the most widespread human pressures in natural forests in developing nations (Luoga et al., 2000a; Kumar and Shahabuddin, 2005; Shahabuddin and Kumar, 2007; Thapa and Chapman, 2010; Sassen and Sheil, 2013).

1.6.   Bird responses to resource use

While limited in number, studies that have assessed bird responses to informal forest product harvesting have revealed several important findings, and paved the way for future studies. Specifically, findings indicate that disturbance derived from resource use has significant impacts on bird communities, but that this varies depending on the measure of biodiversity used, and forest type. For example, overall species richness was not shown to differ across disturbed and undisturbed sites in an

Afrotemperate forest in KwaZulu-Natal, South Africa (Krüger and Lawes, 1997), and tropical scrub forests in northwestern India (Shahabuddin and Kumar, 2007). On the other hand, overall species richness was higher in disturbed compared to protected Afrotemperate forests of the Ethiopian highlands (Asefa et al., 2017); higher in moderately disturbed areas compared to undisturbed and highly-disturbed sites in spiny forests of southern Madagascar (Gardner et al., 2016) and in the tropical forests of the western Himalayas in India (Bhattacharyya et al., 2019); and lowest in heavily utilised forests in the Himalayan subalpine zone in Nepal (Laiolo, 2003). Thus, while responses based on species richness have been shown to vary, studies are consistent in their findings that bird responses to disturbance depend on the ecological and life-history traits of species. Specifically, level of habitat specialisation, primary diet, size and foraging strategy affect species' responses to disturbance (Laiolo, 2003; Shahabuddin and Kumar, 2007; Gardner et al., 2016; Asefa et al., 2017). For example, Asefa et al. (2017) showed that species richness of forest-specialists and canopy-foragers was lower in harvested forests compared to protected forests, while Gardner et al. (2016) found species richness of locally endemic species to be highest in undisturbed sites. Similarly, Shahabuddin and Kumar (2007) showed that species composition differed across disturbed and undisturbed sites, with insectivorous species less abundant in disturbed areas, while Laiolo (2003) found that insectivorous gleaners and granivores avoided heavily harvested forests. Also consistent across studies was the finding that bird responses to resource use were largely mediated by modifications to habitat structure caused by harvesting activities, such as changes in dead wood availability, soil compaction, canopy cover, tree abundance, size and height (Du Plessis, 1995; Krüger and Lawes, 1997; Laiolo, 2003; Watson et al. 2004; Jayapal et al., 2009; Shahabuddin and Kumar, 2007; Asefa et al. 2017).

While these studies provide important insights into bird responses to resource use, they are few and far between, and represent case studies from disparate locations. Furthermore, there is an evident lack of studies from temoerate African forests. Nonetheless, findings from these studies emphasise the importance of measuring bird responses based on a number of diversity metrics, and not just on species richness alone, as this has been shown to mask trait-based responses to disturbance.

Specifically, these studies show that bird responses to disturbances are largely based on their ecological and life-history traits, suggesting that trait-based measured of diversity may be more appropriate in measuring biodiversity responses to disturbances, compared to taxonomic-based measures (Díaz and Cabido, 2001; Petchey and Gaston, 2002; Mason et al., 2005; Mouillot et al., 2013). Secondly, these studies highlight the importance of habitat modification in driving bird responses to resource use, and thus the need to understand how different harvest activities affect forest habitat structure. However, knowledge derived from existing studies is limited in that they examine bird responses to categorical measures of disturbance, i.e. by comparing diversity measures across sites broadly categorised based on level of disturbance. This may limit insight into changes in functional organisation which are likely to occur along a more continuous disturbance gradient (McGill et al., 2006; Cadotte et al., 2011). Moreover, in broadly classifying areas based on their overall level of disturbance, these studies are limited in their ability to assess potential variability in bird responses to different resource use types. This is particularly important in the case of forest product harvesting, which includes a range of activities, from stripping of medicinal bark, to canopy tree felling, which are likely to have variable impacts on habitat structure, and thus bird communities.

1.7. Forests and their management in South Africa

Forests in South Africa occur as a fragmented and discontinuous belt along the eastern and southern escarpment mountain ranges and coastal lowlands, forming part of two global biomes: the warm temperate evergreen forest biome (Afrotemperate forests), and subtropical coastal forest biome (Mucina and Geldenhuys, 2006). Once more widespread and continuous in their distribution, palaeoclimatic changes over the past 180 000 years, augmented more recently by anthropogenic disturbances, have resulted in the current fragmented and limited distribution of forest cover in the country (Partridge et al., 1990; Vogel, 1990; Eeley, et al., 1999), such that today forests comprise less than 1% of South Africa's land cover (Geldenhuys and McDevette, 1989). Despite their small surface area, forests make a disproportionably high contribution to South Africa's biodiversity: they house the second highest plant species richness per unit area after the fynbos biome (Gibbs Russell 1985; 1987;

Berliner, 2009), and the highest number of endemic and threatened vertebrate species (Castely and Kerley, 1996; Berliner, 2009), with 13% of the county's IUCN red listed vertebrate species depend on forest habitats (EWT, 2002). Moreover, 14% of South Africa's bird species occur in forests (Geldenhuys and McDevette, 1989), with eight species IUCN red listed, of which half are endemic to South Africa (Berliner, 2009).

The majority (46%) of South Africa's remaining forest cover occurs in the Eastern Cape Province (von Maltitz et al., 2003), which falls within the Maputaland-Pondoland-Albany Biodiversity Hotspot (Berliner, 2009). Beyond this ecological distinction, this province is characterised as one of South Africa's poorest and least developed regions, incorporating two of the former 'homelands' of the Apartheid era (Cocks and Møller, 2002). Although these areas were amalgamated into the Eastern Cape Province following the advent of democracy in 1994, they are still characterised by a weak economy, poor infrastructure, and high levels of unemployment and rural poverty. The geographical convergence of remaining natural forests with regions characterised by severe rural poverty seen across developing nations (Sunderlin et al., 2005) is thus evident in the Eastern Cape. Consequently, forest resources contribute significantly to the diversification of rural livelihoods in the region, allowing households to optimise livelihoods, respond to change, spread risk and overcome difficulties (Shackleton and Shackleton, 2004). Specifically, forest resources contribute to livelihood strategies through three possible mechanisms: i) direct or substance use, ii) as a safety net function, i.e. acting to ease household poverty in times of adversity, and, iii) through income derived through trade of forest products.

As in many other developing nations, the important socio-economic and ecological value of forests has been recognised in South Africa, and forest policies reformed accordingly. Specifically, the National Forest Act (NFA) of 1998 aims to balance the needs of resource users with the conservation of forest conservation through developing forests for sustainable use. Furthermore, the NFA recognises that "the economic, social and environmental benefits of forests have been distributed

unfairly in the past", and that the role of the state in forest management needs to change. Specifically, the NFA aims to reform the historical legacy of the nationalisation of forests, which occurred under the Cape Colony's Forestry Act of 1888, and resulted in the majority of South Africa's forests being declared property of the state (Cooper and Swart, 1992; Brown, 2003). Consequently, economic gains from forest were largely seized by the white elite through extensive colonial era logging, while local communities were evicted from, or subject to restricted access to state forests and their resources (Brown, 2003). The NFA thus aims to move South Africa into a new era of inclusive forest management through Participatory Forest Management (PFM) as a means to develop shared responsibility of forest management between key stakeholder groups and the state, with this largely motivated by recognition of the state's inability to manage the country's forests effectively without the support and involvement of local communities (Obiri and Lawes, 2002; Robertson and Lawes, 2005). However, few examples of successful PFM implementation have emerged, with this largely associated with failing institutional and traditional structures to regulate forest resource use since democracy. Consequently, forest resource management in South Africa is currently in limbo, with neither the state, nor local communities, nor a combination of the two, taking responsibility for the management of natural forests (Obiri and Lawes, 2002; Robertson and Lawes, 2005; Shackleton, 2010). As a result, forest resource use management in South Africa is currently governed by a *de facto* open-access system.

1.8. Ecological implications in the face of changing resource use demands

While extensive colonial era logging has had significant and long-lasting impacts on forest composition and structure in South Africa (Lawes et al., 2007a), this activity was outlawed in 1939, such that commercial-scale logging has not occurred in forests of the Eastern Cape for the past 80 years in all except one forest complex (i.e. the Amathole region), where limited commercial harvesting was re-introduced in 1975 (von Maltitz, et al., 2003). Consequently, the unregulated use of a range of forest products is currently considered one of the major disturbances faced by forests in this region, and there is increasing concern that, in the context of lacking resource use management, and the high dependency of rural livelihoods on forest resources, harvesting of forest products may compromise

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forest biodiversity (Geldenhuys, 1989; Cooper and Swart, 1992; Du Plessis, 1995; Castley and Kerley, 1996; Dold and Cocks, 2002; von Maltitz et al., 2003; Berry et al., 2005; Berliner, 2009; Hoppe-Speer et al., 2015; Cooper et al., 2017). In support of this, a number of studies have shown that resource use has resulted in over-exploitation of certain species and products, such as fuelwood, medicinal bark, poles and timber (Du Plessis, 1995; Dold and Cocks, 2002; Obiri, 2002; Obiri et al. 2002; Geldenhuys, 2004; Berry et al., 2005), with concomitant changes in plant species composition and forest structure (Obiri et al., 2002; Berry et al., 2005; Boudreau and Lawes, 2005; ; Lawes et al., 2007a; Hoppe-Speer et al., 2015).

While these studies indicate that resource use may result in negative ecological impacts in certain areas, it is essential to consider the effect of the ever-changing socio-economic, -cultural and -political conditions on resource use demand when considering the link between environmental degradation and rural poverty in the Eastern Cape (Hajdu, 2005; Shackleton et al., 2013; Shackleton and Luckert, 2015; Falayi et al., 2019). For example, rapid modernisation and urbanisation at the macro-scale have been shown to have profound impacts on resource use patterns at the local-scale (Shackleton et al., 2013). Specifically, since the 1990s, electrification in many rural areas, changes in homesteads from traditional (round, thatched huts built largely from forest products) to more modern designs (square houses built with bricks and corrugated iron), and increased access to cash incomes from government grants and jobs, have resulted in several authors reporting declines in the direct use of certain forest products, such as poles used for construction (Hajdu, 2005; Cawe and Geldenhuys, 2007; Chalmers and Fabricius, 2007; Geldenhuys et al. 2013; 2016; Shackleton et al., 2013). Furthermore, the increasing trend of deagrarianisation in rural areas due to multiple socio-economic and political shifts has resulted in reduced rates of forest clearing for cultivation, and subsequent increases in forest cover due to revegetation of abandoned cultivated fields (Chalmers and Fabricius, 2007; De Klerk, 2007; Shackleton et al., 2013). Consequently, unlike many other parts of Africa, there has been an overall increase in forest cover in the Eastern Cape over the past 30 years (Chalmers and Fabricius, 2007; de Klerk, 2007; Shackleton et al., 2013; Cooper et al., 2017).

Contrary to these views of declining forest resource demand, several studies indicate that the harvesting of certain forest products to supply rural and urban populations is unlikely to decline (Mander, 1998; Dold and Cocks, 2002; Cocks and Dold, 2006; Shackleton et al., 2011). This notion is underpinned by evidence of sustained demand for certain forest products in the face of increasing trends of modernisation and urbanisation, suggesting that the factors driving these processes are not mutually exclusive, and that as populations increase, pressure on forest resources is unlikely to decrease. A primary example of this is the fact that the collection of fuelwood still represents the most prominent source of power in rural communities of the Eastern Cape today despite increased electrification in rural areas from 24% in 1996 to 62% in 2011 (Cawe and Geldenhuys, 2007; Madubansi and Shackleton, 2007; Shackleton et al., 2007a; Chirwa et al., 2017; Falayi et al., 2019). Furthermore, the continued reliance on traditional medicines despite the development of western healthcare systems, and in the context of increasing urbanisation, has resulted in an expansive medicinal plant trade network supplying growing urban and peri-urban markets across South Africa (Dold and Cocks, 2002; Tshisikhawe et al., 2012; Williams et al., 2000; 2013). In the context of increasing rates of population growth and urbanisation, the HIV/AIDS epidemic, and a continued dependence on traditional medicines, the species-specific demand for medicinal plants is greater than ever, and concerns over sustainability are widespread. Subsequently, the trade in medicinal plants has been described as "the most complex resource management issue facing conservation agencies, healthcare professionals and resources users in South Africa today" (Dold and Cocks 2002, pg. 589). In a study conducted across six urban centres in the Eastern Cape, 18% of the 166 plant species traded were forest species, despite forests representing a mere 2.2% of the surface area of the province (Dold and Cocks, 2002). At the time of the study, this equated to approximately 7.2 kg/km^2 of plant material being harvested from forests, a figure significantly greater than amounts harvested from other vegetation types in the province. Forest plant species are thus under particular market pressure. Furthermore, several forest species in high demand are poorly adapted to withstand high levels of harvesting, being slow- growing and -reproducing and having specific habitat requirements

(Cunningham, 1993). For such species, market-driven demand soon exceeds supply, resulting in a higher selling price, and increased incentive to harvest increasingly scare plants (Cunningham, 1993; Mander, 1998). Thus, declining availability further encourages unsustainable and destructive harvesting practices, such as ring-barking. With a concurrent break-down of traditional taboos and customs that once acted to regulate harvest levels (Cunningham, 1993), as well as failing institutional regulations (Castely and Kerley, 1996), management of plant resources is essentially an open-access system (Cunningham, 1993). In this context, the commercialisation of medicinal plants has resulted in a 'mine versus manage' approach to harvesting (Cunningham, 1993). The species-specific trade in medicinal plants thus comprises a significant factor driving forest exploitation in the Eastern Cape, with several forest species facing higher risk of extinction, and population declines as a result.

Lastly, declines in agricultural activities have resulted in smaller portions of income earned through the sale of agricultural products, while the sale of forest products has becoming an increasingly important means of income generation for rural households (Shackleton et al. 2007c; Paumgarten and Shackleton, 2011; Clark, 2012; Stander, 2012). Illustrating this, a study conducted across two rural villages in South Africa found that 73% of households selling forest products had started trading in the past five years (Paumgarten and Shackleton, 2009).

1.9.   Knowledges gaps and study aims

Overall, studies on the ecological impacts of resource use have been conducted largely in tropical forests of Southeast Asia and South America (Ticktin, 2004; Shackleton et al., 2011), with comparatively fewer studies done in temperate forests, particularly in Africa. Furthermore, existing studies have focused on plant responses to harvesting at the individual-, population- and community-level, with few studies looking at impacts on forest fauna, especially on ecologically important taxa such as birds, which not only perform a number of vital ecological functions, but may also act as biodiversity indicators. There is thus a need for research aimed at investigating the ecological impacts of resource use in temperate forests beyond the direct impact on harvested plants. Specifically, greater insight on the effect of resource use on ecologically sensitive and important forest taxa such

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as birds is needed. This need is particularly pressing in the Eastern Cape, South Africa, which harbours some of the world's most biodiverse temperate forests (Silander, 2001; Berliner, 2009), upon which many economically impoverished households are reliant for natural resources (Cocks and Dold, 2006; Shackleton et al., 2007a; 2007b; McGarry and Shackleton, 2009; Maroyi, 2017), and where forest bird ranges have been shown to decline over the past 20 years, despite no nett loss of forest cover in the region over the same time period (Cooper et al., 2017).

Studies evaluating household-level resource use over the past 30 years in the Eastern Cape suggest that, while changing socio-economic conditions have resulted in decreased reliance on the direct use of certain forest products, the trade use value of a range of forest products has increased (Paumgarten and Shackleton 2009; 2011; Shackleton et al., 2007c), most evident in the case of medicinal plants (Dold and Cocks, 2002; Williams et al., 2000; 2013). This is of ecological concern, as the harvesting of forest products to supplement incomes has been shown to drive over-exploitation, particularly in the context of *de facto* open-access systems (Cunningham, 1993; Mander, 1998; Dold and Cocks, 2002; Geldenhuys, 2004; Guedje et al., 2007; Lewu et al., 2007; Williams et al., 2013). Despite this, few studies have assessed the current status of resource use in state forests in the Eastern Cape. Specifically, since promulgation of regulations outlined in the NFA pertaining to resource use for subsistence and commercial purposes were issued in 2008 and 2009, to the author's knowledge, only four studies have conducted forest-scale assessments of resource use in disparate locations across the Eastern Cape. These studies, which have assessed resource use in coastal forests of Port St John's Forest Estate (Cawe and Geldenhuys, 2008), and Willowvale Forest Estate (Geldenhuys et al., 2013); mangrove forests along the coast between East London and Port Edward (Hoppe-Speer et al., 2015); and inland mistbelt forests of the Ntabelanga catchments in the Maclear area (Geldenhuys et al., 2016), indicate that resource use patterns are highly variable, with high rates of harvesting, and concomitant negative impacts on forest structure recorded in mangrove forests (Hoppe-Speer et al., 2015), while low levels of resource use were recorded in mistbelt forests in the Maclear area (Geldenhuys et al., 2016).

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Consequently, for the vast majority of state forests in the Eastern Cape region, the current state of resource use, and concomitant impacts on forest habitats and biodiversity are largely unknown. Specifically, the impact of resource use on forest avifauna in the Eastern Cape had been largely understudied. Despite several authors highlighting the need for research in this regard over 20 years ago (Geldenhuys, 1989; Castley and Kerley, 1996), only a single study investigating the effects of fuelwood collection on cavity-nesting bird diversity in a single coastal location in the Eastern Cape has emerged (Du Plessis, 1995), while no studies have investigated the implications of other key resource use types, such as tree and bark harvesting, on forest bird communities. Nonetheless, habitat degradation due to resource use has been cited as a threat to a number of forest bird species in South Africa (Hockey et al., 2005; Marnewick et al., 2015), and considered an important factor contributing to the observed increase in the proportion of threatened forest bird species, from 10% in 2009 to 19% in 2014 (Berliner 2009; BirdLife South Africa, 2014). Furthermore, a recent study found that half of the forest-dependent bird species in South Africa, including a number of endemic species, have experienced range declines since 1992, with declines most evident in the Eastern Cape, despite increases in forest cover over the same time period (Chalmers and Fabricius, 2007; de Klerk, 2007; Shackleton et al., 2013; Cooper et al., 2017). Consequently, Cooper et al. (2017) suggest that habitat degradation due to resource use may be a potential driver of forest bird losses in the region. However, in the absence of any studies investigating the link between resource use, habitat modification and forest bird communities in forests of the Eastern Cape, it has been difficult to assess the validity of concerns around the threat of current resource use patterns to forest birds.

To address these knowledge gaps, this study aimed to assess the status of current resource use, and its ecological implications in state forests in the Eastern Cape, using birds as an indicator taxa. Specifically, this study aimed to:

i) determine the current nature and extent of three key resource use types, namely the harvesting of understory trees for poles; canopy trees for timber and crafts; and bark for medicinal use, in state managed forests across the Eastern Cape (Chapter Two)

ii) assess the impact of different harvest regimes on forest habitat structure and heterogeneity (Chapter Three)

iii) investigate the impact of resource use on forest ecosystem functioning and bird community structure at the regional-scale based on trait-based measures of bird diversity (Chapter Four)

iv) examine forest-scale responses of bird species richness and community composition to informal commercial-scale bark and timber harvesting activities, and the mechanisms driving this (Chapter Five; Chapter Six)

These primary aims were proposed with the goal of contributing to the development of ecologically-informed sustainable use practices that consider the implications of resource use on forest components beyond direct impacts on target species. Findings of this study may thus contribute to forest bird conservation efforts needed to mitigate the potential ecological, economic and cultural costs associated with a loss of bird diversity in the Eastern Cape.

CHAPTER II: INFORMAL FOREST PRODUCT HARVESTING IN THE EASTERN CAPE, SOUTH AFRICA: A RECENT ASSESSMENT

Jessica Leaver and Michael I. Cherry

2.1 Abstract

Forest management in many developing nations aims to balance the needs of resource users and the ecological integrity of indigenous forests, in terms of both biodiversity conservation and ecosystem services, particularly carbon sequestration. While South Africa has legislated management policies to achieve this, implementation has been lacking, resulting in concern that unregulated resource use is compromising forest biodiversity. However, there is little information regarding resource use since these regulations were promulgated a decade ago. This study reports on the current nature and extent of forest product harvesting in the Eastern Cape, South Africa, which contains 46% of the country's indigenous forests. Extraction rates and target species of key products, namely poles, timber and bark, were assessed across six forests, representing five forest types. Harvest intensities indicated low to moderate levels of use, but there was considerable variation in levels of resource use at the forest-scale, illustrating the importance of site-specific assessments. Furthermore, resource use was species-specific, indicating that sustainability is dependent on the ecology of preferred species. Of concern was widespread commercial-scale bark harvesting; and relatively high timber extraction from a Pondoland scarp forest, a threatened forest type. We urge implementation of existing regulations, which distinguish between subsistence and commercial use; and commensurate capacity-building of the new Department of Environment, Forestry and Fisheries. In the case of timber and bark, we recommend licensing of the *de facto* commercial harvesting taking place in order to promote regulation.

Keywords: medical bark harvesting; timber harvesting; pole harvesting; resource use; human disturbance; sustainable use

2.2 Introduction

Forest resources can make a critical contribution to rural livelihoods, assisting economically impoverished households meet daily basic needs of energy, shelter, food, medicine and cash incomes (Shackleton and Shackleton, 2004). Consequently, harvesting of forest products by local communities represents a widespread pressure on forests in developing nations (Luoga et al., 2002; Kumar and

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Shahabuddin, 2005; Lawes et al., 2007b; Furukawa et al., 2011a). Increasingly, forest management policies aim to balance the needs of resources users with the conservation of forest biodiversity, but regulation of forest resource use in many developing nations is largely inadequate, as *de facto* open-access systems of management prevail (Robertson and Lawes, 2005). There is thus increasing concern that informal resource use, i.e. harvest activities that are considered illegal or not formally approved by authorities, for subsistence and commercial purposes may compromise the conservation of forest biodiversity (Castley and Kerley, 1996; Gardner et al., 2016). While resource use may not necessarily result in forest habitat loss, long-term harvesting of forest products has driven changes in forest structure and tree species composition in some African forests, even when occurring at relatively low levels (Obiri et al., 2002; Ndangalasi et al., 2007; Furukawa et al., 2011b; Sassen and Sheil, 2013), thereby affecting habitat quality. Furthermore, forest faunal populations of amphibians, birds, bats and reptiles have been shown to be vulnerable to harvest-mediated habitat modification, particularly where species are specialised in their foraging or micro-habitat requirements (Sekercioğlu, 2002; Arcilla et al., 2015; Gardner et al., 2016; Asefa et al., 2017; Leaver et al., 2019a; 2019b).

However, the severity of the ecological impacts of resource use depends on the plant part harvested and intensity of use (Ticktin, 2004). Furthermore, resource use is often highly species- and tree size-specific, resulting in different resource use preferences depending on the type of use (Furukawa et al., 2011a), with preferred species and size-classes being more heavily impacted. The extent to which a resource has been commercialised is of particular importance, as resources used to generate or supplement income are often harvested more intensely, and frequently unsustainability, relative to those used on a subsistence basis, particularly where effective resource use management is lacking (Luoga et al., 2000b; Dold and Cocks, 2002; Geldenhuys, 2004; Shackleton et al., 2005). In South Africa, informal commercial-scale bark harvesting, driven by increasing market-demand for traditional medicines (Dold and Cocks, 2002), has been identified as contributing towards population declines of specific forest tree species under high national-scale demand, namely *Ocotea bullata, Rapanea melanophloeos, Cassipourea gummiflua, Cassipourea flanaganii* and *Curtisia dentata* (Dold and Cocks,

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2002; Grace et al., 2002; Williams et al., 2013; SANBI, 2017). In the case of *C. dentata* and *O. bullata,* the combination of past timber extraction and current bark harvesting pressure has seen these species decline in abundance across much of their range (Scott-Shaw, 1999), and even become locally extinct in some forests (Lawes et al., 2007b), and are now listed as Near Threatened and Endangered respectively, despite these species being protected under the National Forest Act (1998). Similarly, recent demand for *C. gummiflua* and *C. flanaganii* bark has resulted in their listing as Vulnerable and Endangered respectively (SANBI, 2017). Despite high levels of national exploitation, and resultant declining populations, none of these high-demand species are CITES listed. Millions of South Africans treat ailments with bark (Dold and Cocks, 2002; Cocks and Møller, 2002; Geldenhuys, 2004; Cocks and Dold, 2006); and trade in medicinal plants plays an important role in rural and urban livelihoods, generating an estimated 134 000 income-earning opportunities each year (Mander et al., 2007), particularly for rural women with limited economic opportunities (Mander, 1998; Dold and Cocks, 2002). Despite these important socio-economic implications, trade in medicinal plants is largely conducted in the informal sector (Mander, 2007), and is consequently considered a 'hidden economy' in South Africa (Dold and Cocks, 2002). Declining populations of important medicinal species as a result of poor resource use management is not only of ecological concern, but also has important social and economic implications.

Indigenous forest in South Africa makes up less than 1% of land cover, occurring along a naturally highly fragmented belt along the eastern escarpment, making it one of the most limited and vulnerable vegetation types in the country (von Maltitz et al., 2003). The majority (46%) of forest cover is found in the Eastern Cape Province, falling within the Maputaland-Pondoland-Albany biodiversity hotspot. Beyond this ecological distinction, the Eastern Cape is one of the least developed provinces in the country, characterised by a weak infrastructure, poor economic development and high rates of unemployment and rural poverty (Statistics South Africa, 2017; Table 2). This is largely attributed to economic neglect during the Apartheid-era, when much of the Eastern Cape comprised of the former 'homelands' of the Ciskei and Transkei, followed by post-democracy political failure to address this

legacy (Bank and Minkley, 2005). Consequently, the Eastern Cape is ranked last of the country's nine provinces on the Human Development Index, with a score of 0.649 relative to the national score of 0.699. The unemployment rate is estimated to be 48%, relative to the national rate of 38% (Statistics South Africa, 2019). Furthermore, the province has the highest rate of poverty, as measured by the Food Poverty Line – the value below which individuals are unable to purchase or consume enough food; the lowest number of households living in formal dwellings (70%); and the second lowest annual income per capita (South African Institute of Race Relations 2018). Thus, although forests comprise a mere 2.2% of provincial land cover (Dold and Cocks, 2002), they support disproportionally high levels of biodiversity (Berliner, 2009; Castley and Kerley, 1996) and thousands of rural households which are dependent on their resources for subsistence use and to derive cash incomes (Shackleton and Shackleton, 2004; Shackleton et al., 2007b; 2007c; Paumgarten and Shackleton, 2011).

The majority (70%) of indigenous forest cover in the Eastern Cape is managed by the state (Berliner, 2009) under the newly-formed (2019) Department of Environment, Forestry and Fisheries (DEFF), with the National Forest Act (NFA) of 1998 providing the legislative framework for their management. Specifically, in recognition of their high biodiversity and socio-economic value, the NFA aims to develop and manage indigenous forests for sustainable use so as to conserve forest biodiversity, ecosystems and habitats, while promoting fair distribution of their socio-economic benefits. Consequently, the use of indigenous trees from state-managed indigenous forests is prohibited unless a licence, or exemption has been issued. In 2008 and 2009, respectively, regulations pertaining to forest product harvesting for subsistence; and commercial purposes outlined in the NFA, were promulgated. Specifically, for subsistence harvesting, forest officers (in charge of each forest block) are empowered to make exemptions for members of local communities (defined as living within 10 km of a forest) to harvest dead wood for fuelwood; and medicinal plants and bark (the latter only under the supervision of the forester) for household consumption only, i.e. re-sale is prohibited. For any commercial harvesting, by contrast, a licence is required to be issued by the regional forest office, at the discretion of the regional director.

Unlike many other parts of Africa, forest cover in the Eastern Cape has increased over the past 30 years (Chalmers and Fabricius, 2007; de Klerk, 2007; Shackleton et al., 2013; Cooper et al., 2017). This is attributed to the revegetation of previously cultivated fields in response to increasing trends of de-agrarianisation in rural areas (Chalmers and Fabricius, 2007; Blair et al., 2018; Shackleton et al., 2019), together with carbon fertilization (Bond and Midgley, 2000; Higgins and Sheiter, 2012). However, this secondary forest often includes pioneer shrub and alien invasive species (Shackleton et al., 2013; Jevon and Shackleton, 2015) and may thus not provide suitable habitat for forest-adapted fauna or forest species preferably used by people (Chalmers and Fabricius, 2007). Njwaxu and Shackleton (2019) show that while plant species richness in abandoned fields is comparable to that of indigenous forest within five decades of abandonment, species composition differs. Thus, despite increases in forest cover, several studies have reported unsustainable harvesting from indigenous forests in the Eastern Cape (Dold and Cocks, 2002; Obiri et al., 2002; Geldenhuys, 2004; Hoppe-Speer et al., 2015). This has been attributed to a decline in the capacity of DEFF and its antecedents to control forest resources after democracy in 1994 (Obiri and Lawes, 2002); and the increasing importance of the commercialisation of forest products to supplement household incomes in rural areas (Shackleton et al., 2007; Paumgarten and Shackleton, 2009; Clarke, 2012; Stadler, 2012). Harvesting of natural products has been reported as comprising 10% and 14% of household income in rural villages in the former homelands of the Ciskei and Transkei, respectively (Stadler, 2012). Other studies have reported declining subsistence use of forest products in rural Eastern Cape since the 1990s, attributed to changing socio-economic conditions, namely: increasing urbanization, leading to emigration of people out of rural areas (Chalmers and Fabricius, 2007); modernisation, e.g. increased electrification, leading to declining demand for fuelwood (Shackleton et al., 2013), and shifting building styles from traditional dwellings to more modern houses, resulting in declining reliance on forest-based building materials (Cawe and Geldenhuys, 2007; Geldenhuys et al., 2013; 2016); and access to cash incomes from government grants (Chalmers and Fabricius, 2007; Shackleton et al., 2013), and locally created wage work (Hajdu, 2005).

The indigenous forests of the Eastern Cape require urgent management for three reasons. First, harvesting is having negative effects on functional biodiversity, as measured in birds (Leaver et al., 2019b). Second, these forests provide an important source of both subsistence and income for people in the region which must be sustained, particularly in the context of the decline in formal agriculture as a livelihood (Blair et al., 2018; de la Hey and Beinart, 2017; Shackleton et al., 2019). Third, the reforestation associated with this decline in agricultural activity provides an important source of increased carbon sequestration (Lewis et al., 2019), which will endure only in the context of proper management. In the context of increasing forest cover and changing socio-economic conditions, this study aimed to assess resource use patterns across five forest types across the Eastern Cape, focusing on extraction of live plant biomass in three key use categories: understory trees for poles; canopy trees for timber and crafts; and bark for medicinal purposes. We determine the nature of resource use for each use type in terms of harvest intensity (based on percent of available resource harvested) and target species; and assess how harvest patterns vary across forest types. This study thus provides an updated assessment of forest resource use from state forests across the Eastern Cape region since the promulgation of harvesting regulations over a decade ago. We discuss options for sustainable management in the light of these findings.

2.3 Material and methods

2.3.1   Study area

Indigenous forests in the study region of the Eastern Cape, South Africa are naturally fragmented (von Maltitz et al., 2003; Fig. 1), a state which has varied in intensity corresponding to different glacial maxima/minima during the Pliocene and Pleistocene epochs. Forest age and persistence are consequently variable. Mistbelt and scarp forests predate the last glacial maximum ~18 000 yrs ago, likely dating back millions of years, whereas coastal forests emerged only 8 000 yrs ago. Climatic fluctuations resulted in natural afforestation/deforestation events wherein certain forests perished while others were able to persist as refugia for forest-dependent species. These refugia later acted as source populations from which forest faunal species would colonise newer forests (Lawes et al.,

2007a). Consequently, variation in palaeoclimatic history, and current climate, altitude, latitude and topography across the distribution of forest cover in South Africa has resulted in a diversity of forest types, with a formalised biogeographic-floristic assessment classifying 25 distinct forest types in South Africa, seven of which occur in the Eastern Cape (von Maltitz et al., 2003).
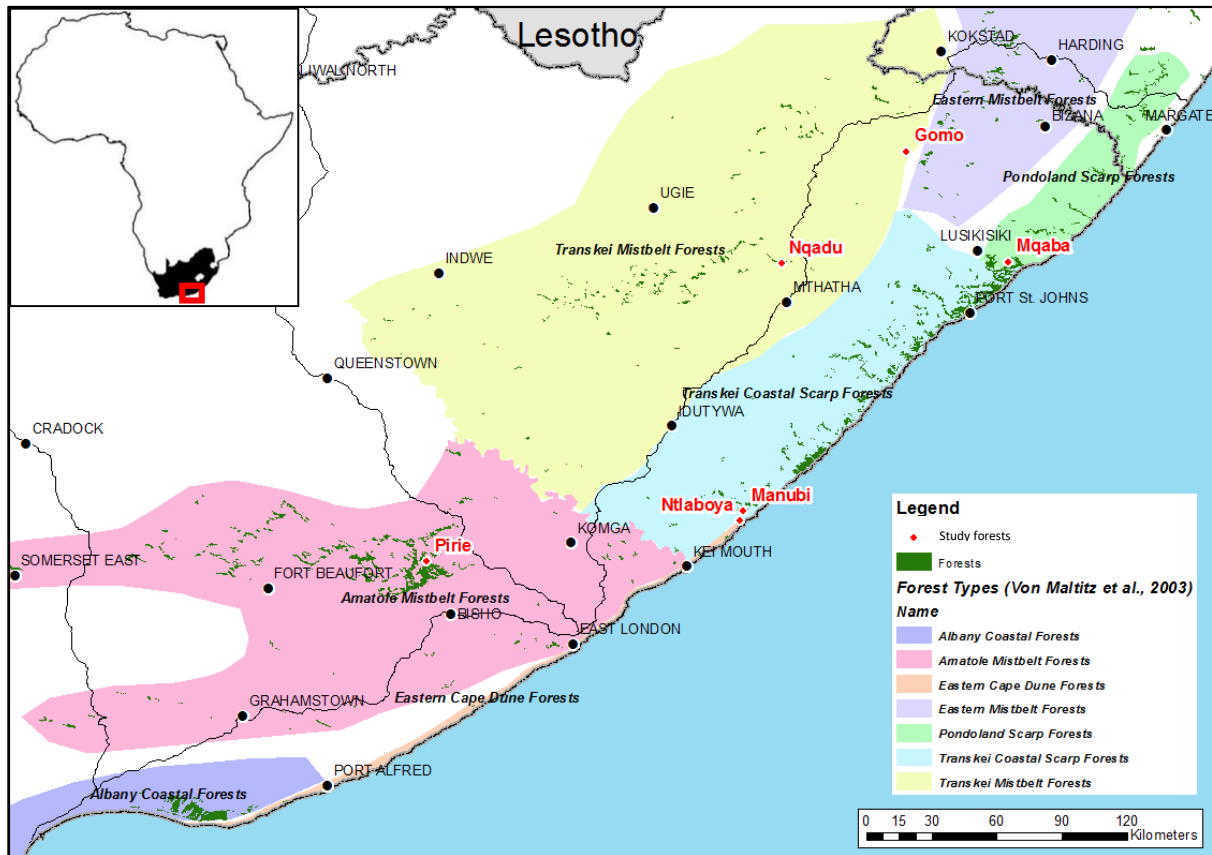
Figure 2.1 Location of the six study forests in the Eastern Cape Province, South Africa (Map drawn by A. Wannenburgh).

The study was conducted between April and July 2016 and included five of the seven forest types in the Eastern Cape Province (Table 1). Two forest types not sampled were Albany dune forest, most of which falls within the jurisdiction of South African National Parks (the national parks board) and is thus a protected forest reserve; and the Eastern mistbelt forests, most of which falls within the province of KwaZulu-Natal (Fig. 1). For each forest type, a representative study forest was selected (Fig. 1, Table 1) based on its size, protected status, and the proximity of surrounding human settlements. Specifically, all selected forests were greater than 150 ha, and unfenced; managed by DEFF; and had

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rural settlements within 4 km of the forest boundary. While most forest patches in the Eastern Cape are smaller than 150 ha, and prone to negative effects of fragmentation (Berliner, 2009), study forests were selected to represent larger, more 'intact' forest patches given their critical biodiversity value. Within the Transkei mistbelt region, forests located within matrixes of timber plantations leased by the state to private companies are often deemed to be better protected than those which are not , so a forest in each category was sampled, i.e. Nqadu, associated with surrounding private forestry activities; and Gomo managed entirely by DEFF (Fig. 1). Mistbelt forests sampled occur on south to south-eastern mountain slopes, between 550 – 1550 meters above sea level (m.a.s.l), and experience colder winter temperatures, with occasional snow, while coastal and scarp forests sampled occur between 20 – 400 m.a.s.l., and experience milder minimum temperatures.

Table 2.1 Study forest characteristics.

Forest	Type	Co-ordinates	Size (ha)	Elevation (m)	Min. temp. (°C)	Mean (± SD) plot distance to nearest community (m)	Mean (± SD) plot distance to nearest road (m)
Montane							
Gomo (n = 14)	Transkei Mistbelt	31°0'39.34"S 29°20'44.25"E	500	920 – 1550	2 – 6	2048 ± 133	105 ± 62
Nqadu (n = 15)	Transkei Mistbelt	31°25'51.12"S 28°45'56.56"E	760	980 – 1240	2 – 6	1467 ± 462	691 ± 569
Pirie (n = 16)	Amathole Mistbelt	32°45'57.88"S 27°15'24.19"E	3170	550 - 1200	1 – 10	3797 ± 377	1278 ± 364
Lowland							
Mqaba (n = 16)	Pondoland Scarp	31°26'8.36"S 29°44'9.36"E	1600	60 - 400	8 – 12	2207 ± 312	125 ± 89
Manubi (n = 18)	Transkei Coastal	32°27'7.30"S 28°35'52.94"E	900	80 - 220	7 – 11	862 ± 467	566 ± 340
Ntlaboya (n = 10)	Eastern Cape Dune	32°30'45.99"S 28°35'28.78"E	160	20 - 60	7 – 11	862 ± 158	219 ± 138

Population densities associated with sampled forests were largely comparable, except for Mqaba, where the population density was notably lower (Table 2). Across the study region, employment rates and education levels are low, with the ward associated with Pirie forest showing the highest rate of employment (23%) and high school level education (31%), and lowest percentage of traditionally built

households (13%) relative to other study sites (Table 2). Study forests sampled thus represent distinct forest types, in terms of natural history, species composition and biogeography, and variable socio-economic conditions, such that data collected from representative forests present case studies of forest resource use from across ecological and socio-economic variation associated with indigenous forests in the study region.

Table 2.2 Demographic and socio-economic variables within municipal wards of sample forests. Annual median income per household across all wards is estimated to be R 14 600 (~US$ 980).

Forest	District; Local Municipality (Ward)	Popln. density (people per km²)	% households traditionally built (2016)	% employed (2011)	% high school or higher (2016)
Montane					
Gomo	Alfred Nzo; Ntabankulu (Ward 7)	69.3	76	7	8
Nqadu	O.R. Tambo; King Sabata Dalinyebo (Mhlontlo Ward 4)	57.5	45	16	17
Pirie	Amathole; Amahlathi (Ward 36)	54.8	13	23	31
Lowland					
Mqaba	O.R. Tambo; Ngquza Hill (Ward 23)	18.4	80	14	10
Manubi Ntlaboya	Amathole; Mnquma (Ward 27)	53.8	67	6.5	10

2.3.2 Study design

A total of 89 plots were sampled, with an average of 15 plots sampled per forest. Sampling plots in each forest were selected to represent varying harvest intensities, based on discussion and guided walks in each forest with DEFF staff (forest managers and/or forest guards), and local community members, in addition to visual assessment by JL of human use in each forest, conducted over two reconnaissance trips prior to sampling. Discussions and guided walks identified areas prone to harvest activities, i.e. those close to roads, major forest trails, or communities, and areas less prone to harvesting, i.e. those further from roads, major trails and communities. However, while accessibility is an important factor affecting levels of resource use (Furukawa et al., 2011a; Sassen and Shiel, 2013),

it was found that watertight classification of "harvested" and "unharvested" areas was difficult given that the spatial distribution of harvesting within a forest was also largely influenced by the type of resource use, as determined by the distribution of target species. Consequently, sample plots were established to represent the different harvest types and intensities present in each forest based on visual assessment of the extent of harvest activities, namely the number of tree stumps, and bark-harvested trees present within a fine spatial-scale, i.e. tens of metres. Non-random selection of plots thus represented the continuum of harvesting disturbances present at each forest, from heavily harvested sites to those with little or no harvesting present, after Kumar and Shahabuddin (2005). Consequently, sample plots presented different intensities of biomass extraction, based on the percentage of trees harvested at the plot-level, rather than categorical classes of resource use disturbance. This approach aimed to provide sample plots representative of the different nature and intensity of harvesting occurring within each forest to allow for the comparison of harvest activities across forests; as well as samples from the full range of harvest activities and intensities, against which to investigate habitat and avifaunal responses to resource use measured on a continuous scale, in linked studies. A minimum distance of 150 m was maintained between plots, and 50 m between plots and the forest edge (i.e. all were within the forest interior).

2.3.3   Data collection

Circular plots of 11.3 m radius (0.04 ha) were used to quantitatively record all harvesting activities and stem diameter 1.3 m above the ground (DBH) of all standing trees ≥5 cm DBH (living and dead). Trees harvested for poles or timber were recorded by: stump diameter; species (where possible); response to harvesting (recorded as a stump being dead or alive); and stump age (based on a scale of 1 - 4 according to the degree of stump decay, from Boudreau et al., 2005, pg. 151). Based on diameter, stumps were categorized as pole (5 – 19.9 cm diameter) or timber (>20 cm diameter) harvesting, after Obiri et al., 2002.

Trees harvested for medicinal bark were recorded using: DBH; extent of bark removal on individual trees up to 3 m on the tree stem (scored 1 – 6 based on percentage of bark removed, where 1 = 1-

10%; 2 = 11-25%; 3 = 26-50%; 4 = 51-75%; 5 = ring-barked to any extent %; 6 = total ring-bark i.e. up to 3m, where ring-barked stems are those where bark has been removed from around the full circumference of the stem, after Cunningham, 1993); species (where possible); and response to harvesting (dead or alive). In the majority of cases, bark was harvested from standing trees, with only two cases (in Manubi and Ntlaboya) observed where trees were felled to strip bark.

2.3.4   Data analyses

Stem density and basal area were calculated from standing tree diameters of living trees recorded at each survey site (all stems with DBH ≥5 cm).

Pole and timber harvest intensity were assessed for each size class respectively based on the accumulated harvestable stems (stumps plus standing stems) as follows:

Tree Harvest Index$_j$ = number stumps$_j$ / (number stumps$_j$ + number stems$_j$),

   where *j* represents the size class being assessed

Bark harvest intensity was assessed based on the proportion of trees harvested for bark to any extent, based on accumulated harvestable stems (standing trees alive and dead); and on a bark harvest index derived from summed bark removal scores assigned to individual bark-harvested trees, calculated at each plot, as follows:

Bark Harvest Index = summed bark removal score/no. individuals bark-harvested

The proportion of trees harvested was based on trees with stem diameter ≥10 cm, as no trees <10 cm DBH were observed to have been harvested for bark.

Non-parametric tests (Kendall's tau-b rank correlation) were used to assess the relationship between harvest intensities and distance to the nearest community and road, respectively. Harvest intensities recorded in each forest were compared across forests using Kruskal-Wallis Tests, followed by Dunn's post-hoc test, for each resource use respectively.

2.4   Results

2.4.1   Bark harvesting

Bark harvesting was recorded in all six forests, and in 57% of plots overall: an average of 4.6 ± 0.7% of trees ≥10 cm DBH were harvested, with an average of 1 ± 0.2% of recorded stems ≥10 cm DBH dead

due to bark harvesting. Of the 147 trees recorded as harvested for bark, 29% were dead. The proportion of trees dead due to harvesting was negatively correlated to distance from the nearest community ($z = -2.13$, $p = 0.03$), while the negative relationship with distance to the nearest road was marginally significant ($z = -1.70$, $p = 0.09$). Most (73%) bark-harvested trees were identified, yielding a list of 15 bark-harvested species: eight of these were recorded three times or more (Fig. 2.2a), while seven were recorded only occasionally (Table S2.1). *Ocotea bullata, Protorhus longifolia* and *Rapanea melanophloeos* were harvested most and were recorded in both montane and lowland forests. *Cassipourea gummiflua, Calodendrum capense* and *Curtisia dentata* each represented < 10% of harvested trees. Cumulatively, these six species represent 82% of all bark-harvested species recorded, with all except *C. capense* frequently ring-barked. Bark harvest intensities differed among forests, with Gomo and Manubi most heavily harvested, and Pirie least harvested (Fig. 2.3a; Table S2.2). Bark harvesting was most extensive at Gomo, where an average of 7 ± 1.0% of trees were harvested for bark to some extent, with mean tree mortality due to extensive bark removal at 2.5 ± 0.6% of trees (Table S2.2). Notably, harvest intensities at Manubi, Nqadu and Ntlaboya were not significantly lower than those recorded at Gomo, indicating comparatively high levels of bark harvesting at four of the six forests sampled (Fig. 2.3a; Table S2.2).
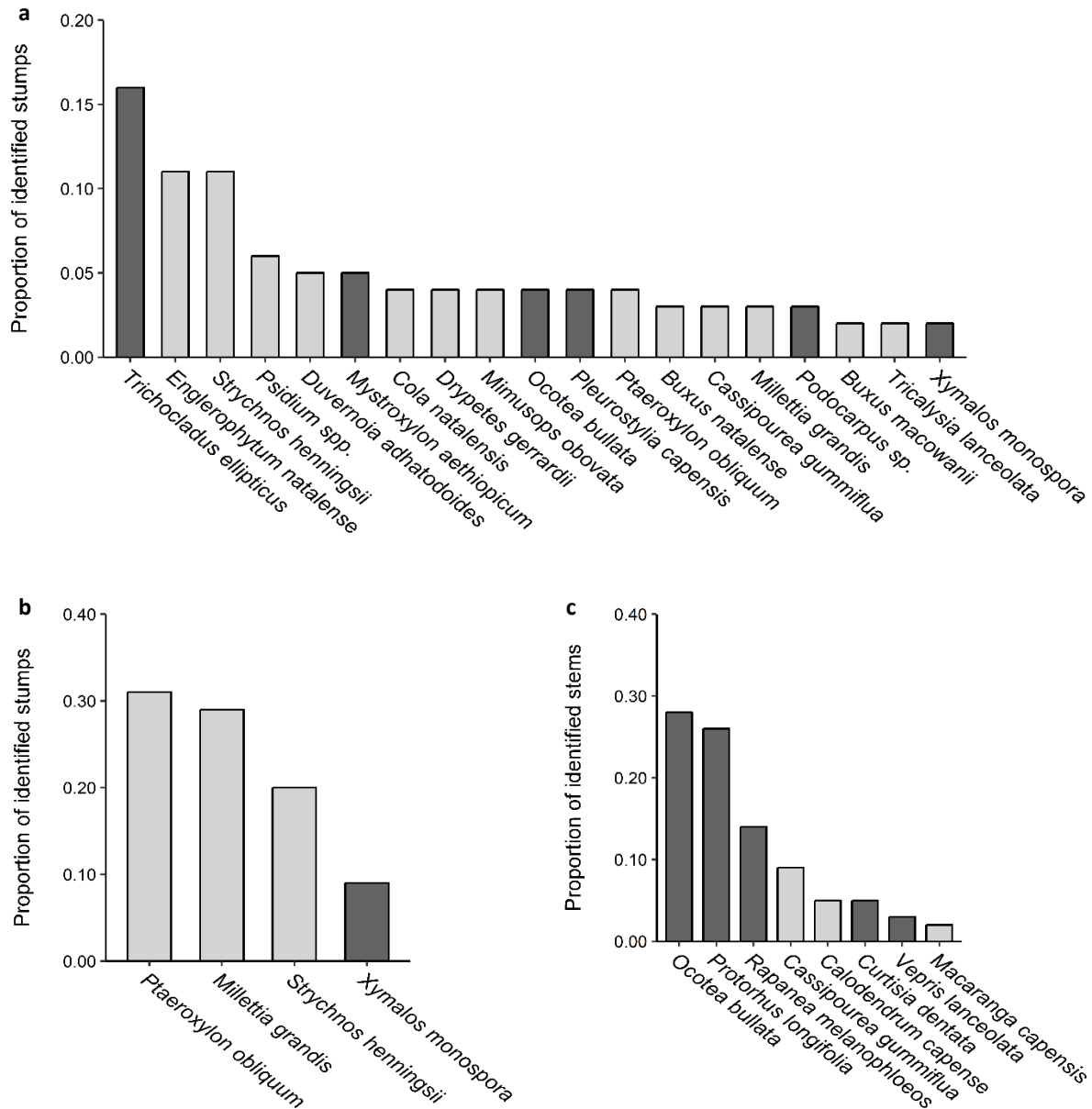
Figure 2.2 Frequency of commonly encountered species harvested for **a)** pole, **b)** timber and **c)** bark, represented as proportion of identified species. Species recorded more than three times are depicted. In **a)** light grey bars represent species harvested in lowland forests, while dark grey bars represent harvested species recorded in montane forests. In **b)** and **c)** light grey bars represent lowland species and dark grey bars represent species harvested in both lowland and montane forests.

2.4.2 Pole harvesting

Pole harvesting was observed in all forests except Pirie and recorded in 60% of plots overall, with an average of 7.3 ± 1.0% of available trees harvested. The extent of pole harvesting was negatively correlated to distance to the nearest community (z = -2.97, p = 0.003), and distance to the nearest

road (z = -4.75, p < 0.001). Thirty-nine percent of pole-sized stumps had a decay score of 1 or 2, indicating that they were harvested fairly recently i.e within the last five years, while the majority of stumps (61%) exhibited more advanced decay (score 3 or 4). Two-thirds of pole-sized stems died from harvesting (i.e. no coppice regrowth occurred, or coppice regrowth was dead). Fifty-five percent of pole-sized stumps were identified, revealing 28 species: 19 were observed three times or more (Fig. 2.2c), while nine were recorded occasionally (Table S2.1). The most frequently encountered species was *Trichocladus ellipticus*, which occurs in the montane forests sampled, and represented 16% of identified stumps. *Englerophytum natalense* and *Strychnos henningsii* occur in lowland forests and each represented 11% of identified stumps, with *E. natalense* the most commonly harvested pole species at Manubi, whereas *Strychnos henningsii* was the most commonly harvested species at Mqaba. An exotic *Psidium* species was harvested only in Manubi. At Pirie, no pole harvesting was recorded, while the highest intensity of harvesting was at Gomo (Fig. 2.3b; Table S2.2), where a mean of 14 ± 4.0% of available stems where harvested. However, pole harvesting intensities recorded at Gomo did not differ from those recorded at Nqadu, Mqaba, Manubi and Ntlaboya, indicating comparative levels of pole harvesting across all forests, with the exception of Pirie (Table S2.2).
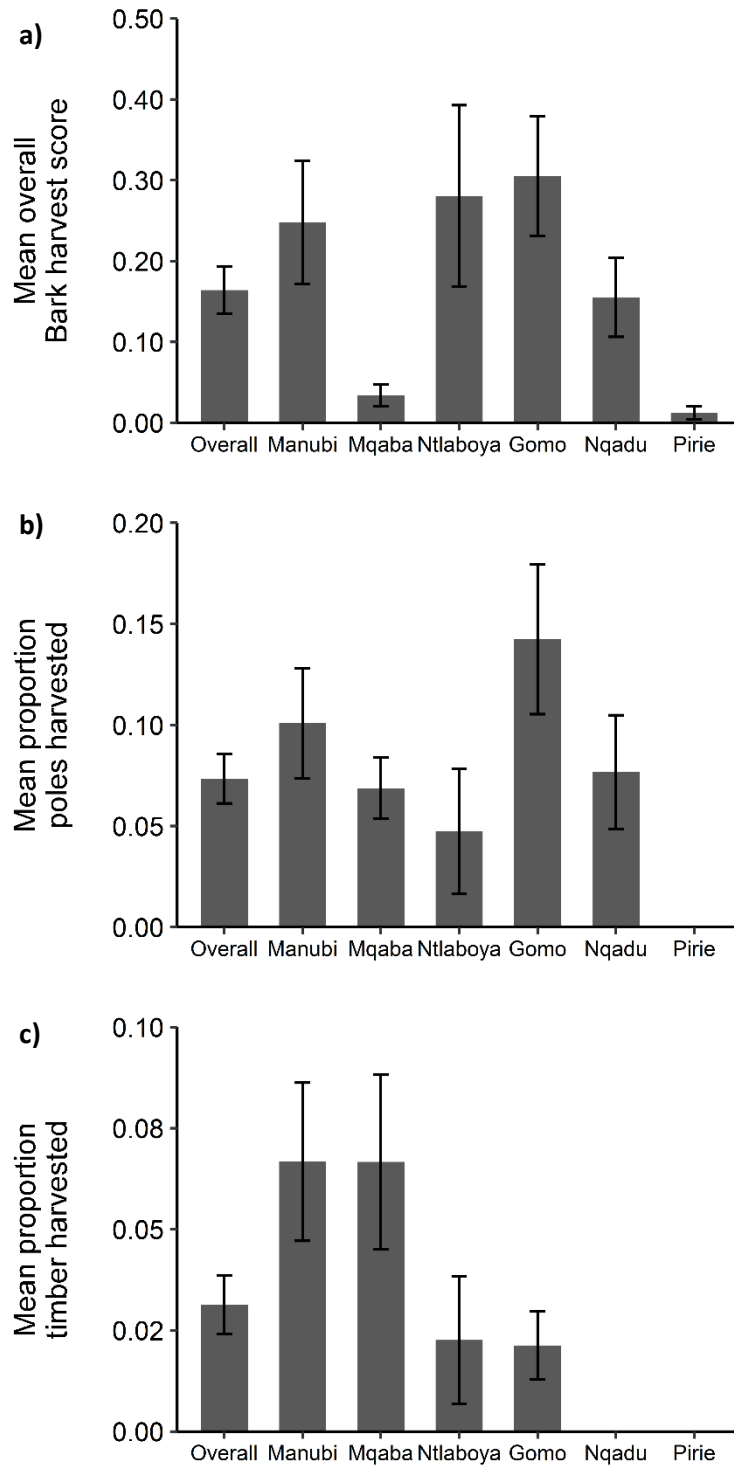
Figure 2.3 Mean harvest intensities based on **a)** bark harvest index derived from extent of bark removal on individual trees summed within plots, **b)** proportion of pole-sized stems harvested, and **c)** proportion of timber-sized trees harvested, compared between forests and relative to the overall mean across forests.

2.4.3 Timber harvesting

Timber harvesting was the least common harvest activity, observed in four of the six forests (Gomo, Mqaba, Manubi and Ntlaboya) and recorded in 27% of plots overall. A mean of 3.1 ± 0.7% of available timber-sized trees was harvested across all forests: 24% of stumps showed signs of having been harvested recently i.e within the last five years, with a decay score of 1 or 2, while the majority of stumps (76%) exhibited more advanced decay (score 3 or 4), and 78% of stumps were dead. Timber harvest intensities recorded per plot were negatively correlated with distance from the nearest community ($z = -2.41$, $p = 0.02$), and distance to the nearest road ($z = -2.51$, $p = 0.01$). Seventy-one percent of stumps were identified: four species were encountered three times or more (Fig. 2b), while three were observed only occasionally (Table S2.1). *Ptaeroxylon obliquum, Millettia grandis* and *Strychnos henningsii*, together represented 78% of trees, and were recorded only in two lowland forests: Mqaba and Manubi. *Xymalos monospora* represented 8% of harvested species, and was recorded in both lowland (Mqaba) and montane (Gomo) forests. The highest levels of timber harvesting were recorded at Manubi and Mqaba, where 7.0 ± 2.0% of available stems were harvest, whereas no harvesting was recorded at Nqadu and Pirie (Fig. 2.3c; Table S2.2).

2.5 Discussion

This study demonstrates that valuable information regarding patterns of resource use can be derived from assessing evidence of harvesting in forests, such as stumps and bark-harvest scars. Our findings indicate that state forests were widely used by people, but that patterns of resource use were largely site-specific. Thus, while harvest intensities measured at the regional scale were relatively low, patterns of resource use, in terms of resource type and harvest intensities, varied widely across forests.

Overall, very low levels of harvesting were recorded at Pirie compared to other forests. This may be attributed to the fact that Pirie was less accessible than other sampled forests, with the closest community and road more than 3 km, and 1 km away, respectively, supported by the positive associations found between harvest rates and accessibility i.e. distance from roads and communities.

Thus, in agreement with previous studies, results indicate that harvest levels at the forest-scale are influenced by accessibility (Boudreau et al. 2005; Olupot et al. 2009; Thapa and Chapman 2010). Forests close to raods and communities are thus likely to be prone to higher levels of harvesting and should receive management priority. Furthermore, interviews of nearby village residents suggest that forest officials actively monitor harvesting at Pirie (Opperman et al., 2018). Additionally, slightly better socio-economic conditions in the region, such as higher employment rates, education levels and more modern building styles relative to other study forest regions (Table 2.2), may result in lower reliance on forest products by surrounding communities. With the exception of Pirie, pole harvest intensities were comparable across forests sampled, while timber harvesting was largely limited to lowland forests, namely Manubi and Mqaba. While bark harvesting was recorded to some extent in all forests, extensive harvesting, indicative of commercial-scale demand, was evident in four forests; two montane (Gomo and Nqadu) and two lowland (Manubi and Ntlaboya).

Resource use was also shown to be species-specific, with different species used for poles, timber and bark respectively. Consequently, harvest intensities vary at the species-level such that sustainable resource use is highly dependent on the ecology of target species. Furthermore, given the variable species composition at the different forest types sampled, species use varied across forests, with a clear distinction in species used from montane and lowland forest types. Lastly, findings of this study reveal that much of the harvesting occurring in state forests in the Eastern Cape, particularly of bark and timber, is occurring at a commercial-scale, and thus driven by demand beyond that of surrounding communities. This has important implications for management as harvesting of this nature has greater ecological implications, and involves a wider range of role players.

Consequently, three key resource use issues require urgent management attention: i) exploitation of certain tree species under high commercial-scale demand for timber and medicinal bark; ii) depletion of certain preferred species harvested for poles, and iii) forest degradation as a result of past and current harvest activities. Harvesting is having measurable effects on avian functional diversity and forest-specialist species richness (Leaver et al., 2019a; 2019b) suggesting that other faunal groups are

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likely being similarly affected, despite there having been an increase in forest cover across the province over the past 30 years (Chalmers and Fabricius, 2007; de Klerk, 2007; Shackleton et al., 2013; Cooper et al., 2017). Consequently, management action is needed to better regulate current commercial-scale harvesting activities, and to address issues of habitat degradation arising from previous unsustainable harvesting. These issues are discussed in further detail for each resource use type separately in the following sections.

2.5.1 Bark harvesting

Bark was the most widespread harvested resource, recorded in all six forests. The extent of bark removal on individual trees distinguishes between commercial and subsistence bark harvesting: commercial practices often result in ring-barking of tree stems up to a height of 3 m, and subsequent tree death, whereas subsistence use is indicated by more moderate bark removal with negligible impact (Cunningham, 1993; Geldenhuys, 2004; Tshisikhawe et al., 2012). Regionally, a third of recorded bark-harvested trees were ring-barked, closely matching the 29% mortality rate recorded, and indicating wide-spread commercial-scale bark harvesting from state forests in the Eastern Cape. Commercial-scale harvesting, as indicated by a high incidence of ring-barking, was highly species-specific, with five focal target species identified: *O. bullata, Protorhus longifolia, R. melanophloeos, C. gummiflua* and *C. dentata*. Thus, although only 5% of all trees were harvested for bark, harvest intensities for these five species would reveal much higher levels of use. Findings of this study thus reflect the declining population status of *O. bullata, R. melanophloeos, C. gummiflua* and *C. dentata*, which has been largely attributed to unsustainable bark harvesting for the medicinal plant trade (Williams et al., 2010; SANBI, 2017). Beyond species-level resource depletion, increased canopy tree mortality rates due to ring-barking has significant impacts on forest structure (Leaver et al., 2019b).

Current control of bark harvesting from state forests is thus not effective, leading to habitat degradation and resource depletion. Better management is urgently required, both in terms of ensuring that current demand is supplied sustainably, and that habitat degradation from past harvest activities is addressed. Given the commercialised context within which bark harvesting occurs (Dold

and Cocks, 2002; Williams et al., 2010), sustainable management requires the integration of ecological, socio-economic and policy components (Geldenhuys, 2004a). In this regard, an integrated action plan has been implemented, and well-documented, in the Umzimkulu region of the Eastern Cape (Geldenhuys, 2002; 2004a; 2004b), and provides a model upon which future sustainable bark harvesting management could be based. Specifically, this approach aims to bring resource users and the Department of Environment, Forestry and Fisheries (DEFF) together in the process of acquiring a licence for user associations to conduct legal commercial harvesting, with the license subject to a management plan for sustainable use which includes: guidelines for sustainable harvest practices; planting for alternative resources; and monitoring of resource use impacts. This approach thus draws on the legislative framework provided by the National Forest Act (1998), which makes provision for licencing resource harvesting for commercial purposes; aims to promote Participatory Forest Management, where there is shared responsibility of forest management between key stakeholders and the state; and aims to develop indigenous forests for sustainable use.

A vital component of licencing commercial harvesting is ensuring that wild populations are sustainably harvested, and in developing different sources of bark, thereby alleviating pressure on mature trees in indigenous forests. In the case of the former, studies have shown that the extent to which a tree has been ring-barked has a greater impact on tree canopy health than the overall percent of bark removed from the stem (Geldenhuys, 2002). Consequently, the likelihood of post-harvest tree survival is much greater if bark is harvested in narrow, vertical strips rather than from horizontal strips around the tree stem. It has thus been proposed that controlled bark harvesting of individual trees, wherein bark is harvested from 1 m long vertical strips that are 5 cm wide in 5-year cycles, would ensure the survival of debarked trees. While this strip harvesting approach represents a simple shift in harvest practice, implementation requires the development of effective regulating mechanisms, as should arise from any licensing agreement entered between harvesters and DEFF.

However, the variable response of target species to strip harvesting suggests that best practice for sustainable harvesting needs to be species-specific (Vermeulen et al., 2012). For example, while strip

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harvesting of *O. bullata* presents a sustainable management option, given good bark regrowth and limited susceptibility to insect and fungal attack, the comparatively poor response of *C. dentata* and *R. melanophloeos*, due to poor bark regrowth and susceptibility to fungal and insect attack, especially in the case of *R. melanophloeos*, indicate that these species require alternative harvesting methods. Specifically, full-tree harvesting has been proposed as a possible option for high-demand tree species that do not recover from bark stripping, such as *R. melanophloeos,* with cutting rates dependent on the species population dynamic (Geldenhuys, 2004; Vermeulen et al., 2012). This option presents the opportunity to harvest all bark from a felled tree, as well as the timber. Furthermore, the creation of canopy gaps through full-tree harvesting, may facilitate the regeneration of target species such as *O. bullata* and *R. melanophloeos* (Geldenhuys, 2004).

Findings of this study show that urgent management action is needed to address the issue of trees that have been ring-barked, and are dying as a result. In this regard, studies have shown that dying trees may be salvaged by cutting, if they produce coppice shoots in response, as in the case of *O. bullata* (Geldenhuys, 2002; 2004). Cutting of dying, ring-barked trees would thus allow for tree survival through coppice development, and for all remaining bark on the cut tree to be harvested, as well as the bole and braches to be harvested for timber and crafts, respectively. Fewer trees would thus need to be harvested to supply bark demand, and timber could be supplied as a by-product, thereby reducing the impact on the forest. Furthermore, coppice shoots, if adequately protected from browsers, would provide stems from which young bark could be strip harvested in the future (Geldenhuys, 2002; 2004). Additionally, the leaves of many high demand species have been shown to contain medicinal compounds present in the bark, such that plant-part substitution has been suggested as an important mechanism to reduce bark harvesting pressure (Drewes and Horn 2000; Zschocke et al., 2000; Shai et al., 2009). Coppicing shoots of cut trees could thus also provide leaves which could be easily harvested.

Lastly, the propensity of certain high-demand species, such as *O. bullata* and *R. melanophloeos,* to regenerate naturally under pioneer stands on forest margins, including plantations and stands of

exotics, presents the opportunity to collect and re-plant seedlings to develop cost-effective alternative sources of bark and leaves. Specifically, seedlings from outside the forest could be used to rehabilitate forest gaps created by cut ring-barked trees or full-tree harvesting inside the forest (Geldenhuys and Delvaux, 2002), or abandoned cultivated fields on forest margins. Furthermore, seedlings could be planted and cultivated as low, multi-stemmed coppice systems near communities, from which young bark and leaves could be harvested sustainably. Consequently, several important management options exist, and have been proposed for the development of sustainable harvest practices; alternative sources of high-demand bark species; and rehabilitation of degraded forests. However, effective implementation ultimately requires effective communication and collaboration between resources users and DEFF.

2.5.2   Pole harvesting

Pole harvesting was recorded in all forests except Pirie, with the highest frequency of occurrence at the plot-level (60%), indicating that it was the most prolific resource use encountered, with harvest intensities ranging from 5% (Ntlaboya) to 14% (Gomo) of available stems. The regional harvest intensity of 7.3% of available pole-sized stems is relatively low compared to those recorded in east and southern Africa, where harvest intensities ranged from 7 to 72% (Boudreau et al., 2005). Within South Africa, Obiri et al. (2002) recorded 10% of pole-sized stems harvested in the community forests of coastal Pondoland in the Eastern Cape, whereas Boudreau et al. (2005) reported a harvest intensity of 11.6% at Ongoye, while Lawes et al. (2007b) recorded harvest levels of 36% at iGxalingenwa, lowland and montane forests respectively, located in the neighbouring province of KwaZulu-Natal. Low pole harvesting may reflect declining demand for poles in the Eastern Cape, where houses are increasingly being built with bricks and corrugated iron instead of traditional materials (Cawe and Geldenhuys, 2007; Chalmers and Fabricius, 2007; Geldenhuys et al., 2013; Shackleton et al., 2013; Geldenhuys et al., 2016). This is supported by the observation that most recorded stumps were estimated to be more than ten years old based on stump decay, suggesting that extraction levels may have declined over time.

Susceptibility to overexploitation is largely dependent on the life-history traits of harvested species, such as the spatial scale at which regeneration takes place; availability; and the size of the forest harvested (Obiri et al., 2002; Boudreau et al., 2005). In montane forests (Gomo and Nqadu), *Trichocladus ellipticus,* a dominant understory species, represented the largest proportion (45%) of trees harvested. Similarly, *Englerophytum natalense,* an abundant understory tree occurring in the lowland forests sampled (Manubi, Mqaba and Ntlaboya), was one of the most commonly harvested pole species. Given the high availability of these species, their fine-grained spatial scale of regeneration, and the size of the forests sampled, current harvest intensities of less than 10% in each case, are likely to be sustainable (Obiri et al., 2002; Boudreau et al., 2005; Boudreau and Lawes, 2005). Understory species may at high densities even exclude or inhibit the regeneration of canopy tree species, so thinning of these species through harvesting may be beneficial for forest regeneration (Geldenhuys et al., 2013), particularly in forests with an historical legacy of intensive logging (King 1941), where a dense understory can suppresses canopy-tree recruitment (Lawes et al., 2007b). However, potential benefits of harvesting are highly dependent on the ecology of the species harvested. For example, Lawes et al. (2007b) showed that the preference for young canopy trees species (as opposed to understory species) by pole-harvesters in iGxalingenwa forest, due to their straight-stems, suppressed the regeneration of these canopy species. This, compounded by the dense understory resulting from logging disturbance of the past, has negative long-term ecological implications. This raises concern over the high harvest levels of *Strychnos henningsii*, a canopy species which was the most commonly harvested pole species in Mqaba. Furthermore, unlike *T. ellipticus* and *E. natalense,* which were harvested exclusively for poles, *S. henningsii* was harvested for poles, timber and medicinal bark in Mqaba. Anecdotal observations of local harvesters indicate that the abundance of this species has declined severely in Mqaba, with only individuals without straight stems persisting. Similarly, this species was found to be absent in several coastal forests of the Nqabara region of the Eastern Cape, possibility due to over-exploitation (Geldenhuys et al., 2013). Sustainable management

of pole harvesting thus necessitates that species-specific management practices be developed, as the different ecology of targeted species determines their susceptibility to over-exploitation.

2.5.3   Timber harvesting

Timber harvesting was the least encountered harvest activity, with current timber felling activities restricted to lowland forests, namely Manubi and Mqaba. At Gomo and Ntlaboya, recorded stumps were in advanced stages of decay, indicating that these harvest activities occurred more than ten years ago, while no timber harvesting was recorded at two of the three inland forests sampled, namely Pirie and Nqadu. While harvesting of canopy trees for timber was most common at Mqaba and Manubi, where 7 ± 0.2 % of canopy trees had been harvested, the vast majority (85%) of timber-sized stumps recorded at Manubi were old, indicating that timber harvesting has largely declined over time in this forest. Conversely, close to half (43%) recorded at Mqaba were recent, indicating that informal selective harvesting of canopy trees is still an important form of resource use in this forest.

Timber harvesting was highly species-specific, with four focal species identified: *Ptaeroxylon obliquum, Millettia grandis, Strychnos henningsii* and *Xymalos monospora. Ptaeroxylon obliquum* and *M. grandis* were the most commonly harvested timber species, comprising 60% of timber-sized trees harvested. Previous studies in coastal regions of the Eastern Cape have reported similarly high use of these species (Obiri, 1997; Ham and Theron, 2001; Obiri et al., 2002; Cawe and Geldenhuys, 2007; Fearon, 2010). Specifically, the high desirability of *P. obliquum* for fence posts*;* and *M. grandis* for crafts, has resulted in past unsustainable harvest rates of these two species in the Pondoland region (Obiri, 1997; Obiri et al., 2002). However, the ability of both species to coppice in response to harvesting, and their abundant regeneration observed in harvested forests, indicates that these high-demand species have the potential to be harvested sustainably (Obiri et al. 2002; Cawe and Geldenhuys, 2007; Geldenhuys et al., 2013). However, this would require the implementation of effective management practices, particularly in forests such as Mqaba, where current informal timber harvesting practices select for large, straight-stemmed individuals, which are consequently becoming less abundant in the forest (personal comm, S.Tsini, May 2017).

The degree to which current illegal timber harvest activities threatens forest biodiversity, beyond direct population-level impacts on target species, is dependent on the frequency of disturbance, and the extent of incidental habitat damage associated with harvest activities. For example, mechanised selective logging operations cause considerable damage to the broader forest environment through indirect damage due to clearing for roads and log storage sites (Johns, 1988). Conversely, informal timber harvesting in Mqaba was largely un-mechanised, beyond the use of chain-saws, with felled timber split in the forest, and carried out on foot along narrow footpaths (personal observations). The frequency of disturbance is thus of greater concern, particularly in the case of Mqaba, which had the highest current level of timber harvesting in the region. Mqaba is one of the largest remaining patches of the nationally threatened Pondoland scarp forest, and the presence of an informal trade network transporting locally harvested timber to Lesotho appears to be driving timber harvest activities in this forest, and requires urgent management (personal comm., Monica Mvakade, October 2016). Given the commercial nature of this harvesting, it is suggested that an approach similar to that described above for sustainable commercial bark harvesting be implemented. Specifically, through the formation of harvesters associations, agreements between harvesters and DEFF could be negotiated, and a commercial harvesting licence issued subject to the development of an ecologically-informed management plan and guidelines for sustainable timber harvesting from Mqaba forest. This should include the development of alternative resources of target species, such as the planting of *P. obliquum* and *M. grandis* in previously degraded areas of the forest, forest margins and abandoned cultivated fields, where these light-demanding species will do well (Obiri et al., 2002; Njwaxu and Shackleton, 2019). Furthermore, planting of preferred species in abandoned cultivated fields along forest edges would increase resource availability.

2.5.4 Management recommendations

To our knowledge, this is the first regional-scale study of forest resource use in the Eastern Cape subsequent to the promulgation of regulations regarding resource use issued in 2008 and 2009. Although these provide for permits to be issued for commercial-scale harvesting of poles, timber and

bark, none have been issued by the Eastern Cape regional office, so all harvesting of this nature reported here is illegal. This study is limited by a relatively small sample size, given that the approach aimed to cover a broader range of forest types, at the cost of more intensive sampling in fewer forest types, such that data presented here may not be regionally representative. Nonetheless, we provide a recent assessment of resource use patterns across a representative range of forest types, which sheds light on critical resource use issues in the region. In our view, DEFF should consider issuing licences for commercial-timber harvesting of *P. obliquum* and *M. grandis,* in an effort to regulate illegal timber harvesting in lowland forests such as Mqaba. Specifically, the licencing process should be subject to assessments to determine current stocks; development of sustainable harvest quotas and ensuring that these are regulated. Pole harvesting is of less concern as it appears to be on the decline owing to reduced demand; is occurring at sustainable levels in any event; and is likely to be mostly for household use, although the regulations do not provide for it. With regard to bark, harvesting for household use is legal, but it is suggested that foresters oversee harvesting in terms of the exemption regulations; and record quantities of each species harvested so that sustainable levels can be ascertained. In addition, keeping records of the products collected by individual harvesters should at least limit the extent of sale of forest products. However, a large portion of bark harvesting is driven by commercial demand, and is thus illegal. As in the case of timber, legalization of bark harvesting for commercial purposes may provide for better regulation; and ensure that local forest communities benefit from forest products. Regulations pertaining to both household and commercial harvesting can be properly implemented only in the event of the development of appropriate capacity within the DEFF, where the Forestry and Fisheries divisions of the former Department of Agriculture, Forestry and Fisheries are currently being amalgamated with the former Department of Environmental Affairs.

The management of indigenous forests in South Africa dates back to the colonial period, historically characterised by policing, exclusion and enforcement of laws (Brown, 2003). However, as seen in other developing African nations (Wily, 2000a), forest policies in South Africa have been reformed under the NFA (1998), which aims for joint forest management between the state and local communities. This

global trend of delegation of rights and responsibilities at the local-level has been motivated by acceptance that state-level management is often inadequate to protect forests (Wily, 2000a; Obiri and Lawes, 2002), particularly where they are widely dispersed and fragmented, as in South Africa. Furthermore, public participation is considered a vital component of developing effective sustainable use policies. Consequently, Participatory Forest Management (PFM), which aims for the shared responsibility of forest management between resources users and the state, has been legislatively adopted as the key process to drive forest management in South Africa (NFA, 1998). Legalization of commercial-scale timber and bark harvesting, as proposed by this study as a means to improve regulation of these practices, thus necessitates that resource users be involved in this process. While similar policies of joint, or collaborative forest management have been successfully implemented in several developing nations, such as India (Prasad and Kant, 2002), Nepal (Gautam et al., 2004) and Tanzania (Wily, 2000b; Blomely et al., 2008), this has remained elusive in South Africa (Horn, 2000). Capacity-development within DEFF should thus focus on issues relating to implementing PFM policies, such as the establishment of community-based harvester associations, through which negotiation and collaboration with state forest bodies may occur (Geldenhuys, 2004). While forest-user communities in South Africa support the notion of PFM (Obiri and Lawes, 2002; Robertson and Lawes, 2005), this process must be driven by DEFF, and cannot take place in the current context of a void in personnel, both on the ground and at management level. No new forest guards have been appointed since 2013 to replace those who have left the department, where the post of Deputy-Director General (Forestry) has been vacant for some years.

2.6 Appendices

Table S2.1 List of all harvested species identified in order of frequency of harvesting encountered, and forest where harvesting was recorded. (Freq. = Frequency of recording; Prop. = Proportion of overall recorded stumps; Cum. prob = cumulative proportion).

Product	Species name	Xhosa name	Freq.	Prop.	Cum. prop.	Gomo	Manubi	Mqaba	Nqadu	Ntlaboya	Pirie
Pole	*Trichocladus ellipticus*	Umqongci	30	0.16	0.16	X			X		
Pole	*Strychnos henningsii*	Omnonono	20	0.11	0.27		X	X			
Pole	*Englerophytum natalense*	Umtongwane	20	0.11	0.37		X	X		X	
Pole	*Psidium spp.*	Cherry gauva	11	0.06	0.43		X				
Pole	*Mystroxylon aethiopicum*	umnqayi	10	0.05	0.48	X					
Pole	*Duvernoia adhatodoides*	isiPheka	9	0.05	0.53			X			
Pole	*Buxus natalense*	isiXeza	6	0.03	0.56		X				
Pole	*Ocotea bullata*	Nukane	8	0.04	0.61	X					
Pole	*Ptaeroxylon obliquum*	Mthathi	8	0.04	0.65		X	X			
Pole	*Pleurostylia capensis*	Umbomvana	8	0.04	0.69	X					
Pole	*Cola natalensis*	Intenendende	7	0.04	0.73			X			
Pole	*Mimusops obovata*	Mnthunzi	7	0.04	0.77		X				
Pole	*Drypetes gerrardii*	Umhlakela	7	0.04	0.80			X			
Pole	*Cassipourea gummiflua*	Umemezi	5	0.03	0.83		X				
Pole	*Millettia grandis*	Umzimbeeti	5	0.03	0.86		X	X			
Pole	*Podocarpus sp.*	Umkhoba	5	0.03	0.88	X			X		
Pole	*Xymalos monospora*	Uvethe	3	0.02	0.90	X					
Pole	*Tricalysia lanceolata*	isiXeza	3	0.02	0.91		X				
Pole	*Buxus macowanii*	Galagala	3	0.02	0.93		X				
Pole	*Curtisia dentata*	Umlahleni	2	0.01	0.94	X					
Pole	*Hlolo*	Hlolo	2	0.01	0.95	X					
Pole	*Trichocladus crinitus*	Ithambo	2	0.01	0.96		X				
Pole	*Cussonia spp.*	Umsenge	1	0.01	0.97					X	
Pole	*isiTheba*	isiTheba	1	0.01	0.97		X				
Pole	*Chaetacme aristata*	umKhovoti	1	0.01	0.98					X	
Pole	*Searsia chirindensis*	Mhlolotshane	1	0.01	0.98		X				

Table S2.1 (continued) List of all harvested species identified in order of frequency harvesting encountered, and forest where harvesting was recorded. (Freq. = Frequency of recording; Prop. = Proportion of overall recorded stumps; Cum. prob = cumulative proportion).

Product	Species name	Xhosa name	Freq.	Prop.	Cum. prop.	Gomo	Manubi	Mqaba	Nqadu	Ntlaboya	Pirie
Pole	*Sibindi*	Sibindi	1	0.01	0.99		X				
Pole	*Vepris lanceolata*	Umzane	1	0.01	0.99					X	
Pole	*Unqande*	Unqande	1	0.01	1.00					X	
Timber	*Ptaeroxylon obliquum*	Mthathi	11	0.31	0.31		X	X			
Timber	*Millettia grandis*	Umzimbeeti	10	0.29	0.60		X	X			
Timber	*Strychnos henningsii*	Omnonono	7	0.20	0.80			X			
Timber	*Xymalos monospora*	Uvethe	3	0.09	0.89	X		X			
Timber	*Mimusops obovata*	Mnthunzi	2	0.06	0.94		X				
Timber	*Cussonia spp.*	Umsenge	1	0.03	0.97					X	
Timber	*Duvernoia adhatodoides*	isipheka	1	0.03	1.00			X			
Bark	*Ocotea bullata*	nukane	35	0.28	0.28	X	X		X		
Bark	*Protorhus longifolia*	izintlwa	33	0.26	0.54		X			X	X
Bark	*Rapanea melanophloeos*	umaphipha	18	0.14	0.68	X	X		X	X	
Bark	*Cassipourea gummiflua*	umemezi	11	0.09	0.77		X				
Bark	*Curtisia dentata*	umlahleni	6	0.05	0.82	X	X				
Bark	*Calodendrum capense*	umemezi	6	0.05	0.87			X		X	
Bark	*Vepris lanceolata*	umzane	4	0.03	0.90				X		X
Bark	*Macaranga capensis*	imphumeleli	3	0.02	0.92			X			
Bark	*Harpephyllum caffrum*	umgwenya	2	0.02	0.94			X			
Bark	*Strychnos spp.*	Omnonono	2	0.02	0.95			X			
Bark	*Ptaeroxylon obliquum*	Mthathi	2	0.02	0.97				X		
Bark	*Albizia adianthifolia*	Umnebelele	1	0.01	0.98			X			
Bark	*Cussonia spp.*	umsenge	1	0.01	0.98				X		
Bark	*Rauvolfia caffra*	umjelo	1	0.01	0.99			X			
Bark	*Trichilia dregeana*	umkhuhlu	1	0.01	1.00			X			

Table S2.2 Extent of harvesting activities recorded at each study forest, showing means ± SE within each forest, with different letters indicating significant differences across forests.

Variable	Lowland forests			Montane forests			Test statistic and p-value
	Manubi	**Mqaba**	**Ntlaboya**	**Gomo**	**Nqadu**	**Pirie**	
Bark harvesting							
Proportion of trees bark harvested	0.06 ± 0.02 (ab)	0.02 ± 0.01 (bc)	0.09 ± 0.04 (abc)	0.07 ± 0.01 (a)	0.04 ± 0.01 (abc)	0.01 ± 0.01 (c)	$\chi2 = 24.31$, df $= 5$, $p < 0.01$
Proportion of trees dead from bark harvesting	0.015 ± 0.005 (ab)	0.0003 ± 0.0003 (b)	0.016 ± 0.008 (ab)	0.025 ± 0.006 (a)	0.011 ± 0.003 (ab)	0.0003 ± 0.0003 (b)	$\chi2 = 34.33$, df $= 5$, $p < 0.01$
Bark harvest index	0.25 ± 0.08 (ab)	0.03 ± 0.01 (bc)	0.28 ± 0.11 (abc)	0.31 ± 0.07 (a)	0.16 ± 0.05 (abc)	0.01 ± 0.01 (c)	$\chi2 = 27.02$, df $= 5$, $p < 0.01$
Pole harvesting							
Proportion of pole-sized trees harvested per plot	0.10 ± 0.03 (a)	0.07 ± 0.02 (a)	0.05 ± 0.03 (ab)	0.14 ± 0.04 (a)	0.08 ± 0.03 (ab)	0.00 ± 0.00 (b)	$\chi2 = 28.45$, df $= 5$, $p < 0.01$
Diameter of pole-sized stumps (cm)	7.56 ± 0.36 (b)	9.40 ± 0.41 (ac)	8.00 ± 0.88 (bc)	10.21 ± 0.26 (a)	10.38 ± 0.40 (a)	0.00 ± 0.00	$\chi2 = 56.98$, df $= 4$, $p < 0.01$
Timber harvesting							
Proportion of timber-sized trees harvested	0.07 ± 0.02 (a)	0.07 ± 0.02 (a)	0.02 ± 0.02 (ab)	0.02 ± 0.01 (ab)	0.00 ± 0.00 (b)	0.00 ± 0.00 (b)	$\chi2 = 21.72$, df $= 5$, $p < 0.01$
Diameter of timber-sized stumps (cm)	34.70	39.67	27.00	23.17	NA	NA	$\chi2 = 6.83$, df $= 3$, $p = 0.08$

CHAPTER III: FOREST PRODUCT HARVESTING IN THE EASTERN CAPE, SOUTH AFRICA: IMPACTS ON HABITAT STRUCTURE

Jessica Leaver and Michael I. Cherry

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3.1 Abstract

The Eastern Cape harbours 46% of South Africa's remaining indigenous forest cover, and is one of the country's poorest and least developed provinces. Forest resources thus represent a vital component of rural livelihoods in this region. Consequently, forest management policies aim to balance the needs of resource users with the ecological integrity of forest ecosystems. In a recent study, forest bird ranges were shown to have declined in the Eastern Cape over the past 20 years, despite increases in forest cover over the same time period, suggesting that habitat degradation may be driving forest bird losses. Given that harvesting of forest products represent a primary human disturbance in forests in the Eastern Cape today, insight is needed regarding the link between resource use and habitat modification. This study reports on effects of harvesting of three key forest products, namely poles, timber and medicinal bark, on habitat structure at the ground, understory and canopy layers in indigenous forests in the province. Harvest activities had considerable impacts on habitat structure, dependent on the nature and extent of harvesting. Bark and timber harvesting resulted in canopy gaps, whereas pole harvesting reduced tree density, resulting in understory gaps. Overall, harvest activities increased the frequency of canopy disturbance, and density of understory layer foliage. Unsustainable bark harvesting practices increased the mortality rate of canopy trees, thereby increasing dead wood availability. By providing insight into human-mediated habitat modification in forests of the Eastern Cape, this study contributes to the development of ecologically-informed sustainable resource management policies.

Keywords: medical bark harvesting; timber harvesting; pole harvesting; resource use; habitat degradation; habitat modification

3.2 Introduction

Habitat loss and modification are currently the primary drivers of forest biodiversity loss globally (Arroyo-Rodríguez et al., 2017). Unlike many parts of Africa, forest cover in the Eastern Cape, which harbours close to half (46%) of the South Africa's remaining indigenous forest cover, has increased

over the past 30 years (Chalmers and Fabricius, 2007; de Klerk, 2007; Shackleton et al., 2013; Cooper et al., 2017), attributed to the revegetation of previously cultivated fields in response to increasing trends of de-agrarianisation in rural areas (Shackleton et al., 2019), together with carbon fertilization (Bond and Midgley, 2000). Thus, while habitat loss appears not to be a major threat to forest biodiversity in the region, habitat degradation has been identified as a major concern (Castely and Kerly, 1996; Obiri et al., 2002; von Maltitz et al., 2003; Berliner, 2009; Hoppe-Speer et al., 2015). While much forest degradation in South Africa is attributed to extensive historical logging (King, 1941), commercial-scale logging has not occurred in indigenous forests of the Eastern Cape for the past 80 years, having been outlawed in 1939 in all except one forest complex, where limited commercial harvesting was re-introduced in 1975 (von Maltitz et al., 2003). Consequently, informal harvesting of forest products now comprises a major anthropogenic disturbance in forest habitats in the region (Castley and Kerley, 1996; Obiri et al., 2002; von Maltitz et al., 2003; Berliner, 2009; Hoppe-Speer et al., 2015).

Forest product harvesting in the Eastern Cape is largely driven by poor socio-economic conditions in the province, which has a weak infrastructure, limited economic opportunities and high rates of unemployment (Statistics South Africa, 2018). Thus, although forests comprise a mere 2.2 percent of provincial land cover (Dold and Cocks, 2002), their socioeconomic value is significant, with thousands of rural households dependent on forest resources for subsistence and commercial use (Shackleton and Shackleton, 2004). While forest policies in South Africa aim to develop forests for sustainable use, several studies have reported unsustainable harvest rates occurring across the region (Dold and Cocks, 2002; Obiri et al., 2002; Geldenhuys, 2004; Hoppe-Speer et al., 2015), largely attributed to a decline in the capacity of institutional and traditional structures to regulate forest resource use (Obiri and Lawes, 2002; von Maltitz and Shackleton 2004). A *de facto* open-access system thus governs forest

resource use in South Africa today, leading to increasing concern that unregulated resource use is degrading forest habitats and compromising the conservation of forest biodiversity.

Long-term harvesting of forest products has significant effects on temperate forest habitats, driving changes in habitat structure and tree species composition, even when occurring at relatively low levels (Boudreau and Lawes 2005; Obiri et al., 2002). Human activities that modify habitat structure, in turn, may influence faunal community assemblage in forests. For example, habitat features at the local-scale relate to the occurrence of specific functional traits and community structure in avifaunal populations (Leaver et al., 2019). Consequently, studies have shown forest faunal populations, including amphibians, bats, birds and reptiles, to be sensitive to human-mediated changes in habitat structure, with species specialised in their foraging or micro-habitat requirement particularly sensitive (Bawa and Seidler, 1998; Sekercioglu, 2002; Cleary et al., 2007; Presley et al., 2007; Gardner et al., 2016; Asefa et al., 2017). Given the critical ecosystem functions provided by forest fauna, including seed dispersal, pest control and pollination (Sekercioglu, 2006), human activities that modify habitat structure may affect forest ecosystem functioning.

Within a forest, different types of resource use have different ecological impacts, and are likely to variably modify habitat structure, as the ecological impact of resource use dependents on the plant part harvested and intensity of use (Ticktin, 2004). For example, while grazing of livestock in forests may affect soil quality (Belsky and Blumenthal, 1997) and increase exotic cover (Yates et al., 2000), timber harvesting affects canopy closure, mean tree size and understory density (Sekercioglu, 2002; Wunderle et al., 2006). The extent to which a resource has been commercialised is also of consequence, as resources used to generate or supplement income in *de facto* open access systems are often harvested more intensely, and frequently unsustainability, thereby having more profound ecological impacts (Dold and Cocks, 2002; Fashing, 2004; Geldenhuys, 2004).

In a recent study, half of South Africa's forest-dependent bird species were shown to have experienced range declines in the past 20 years, with declines most notable in the Eastern Cape, despite no nett losses of forest cover in the region over the same time period (Cooper et al., 2017). This suggests that habitat-scale disturbances rather than landscape-scale habitat loss may be driving bird declines in the region. The current study thus aimed to assess the effects of harvest activities on habitat structure, defined as the composition and arrangement of physical matter at a location (Byrne, 2007), at the forest-scale. Specifically, this study examines how different harvest activities modify habitat structure at the canopy, understory and ground level in five forests, representative of five national forest types, across the Eastern Cape region. Structural habitat variables assessed represent those shown to be important drivers of forest avifaunal (Ehlers Smith et al., 2015; 2017a; 2018; Leaver et al., 2019a) and mammalian communities (Ehlers Smith et al., 2017b) at the forest-scale. Insight into the ways in which harvest regimes affect these structural variables thus sheds light on the potential broader-scale ecological implications of unregulated harvesting. Resource use focused on extraction of live plant biomass, namely, understory trees for poles, canopy trees for timber and crafts, and bark for medicinal purposes, as these represent key resource use types in the region (Obiri et al., 2002). Given the different nature of the extraction of these resources, it was hypothesised that habitat impacts would be dependent on resource use. Furthermore, given that different harvest activities often occur together at a fine-spatial scale, it was hypothesised that resource use types may interactively affect habitat structure.

3.3 Methods

3.3.1 Study site

The study was conducted in the Eastern Cape Province of South Africa between April and July 2016. The study area included five of the national forest types in the two main zones of forest, i.e. the lowland coastal and scarp forests of the subtropical coastal zone, and the warm-temperate mistbelt forests found on the south to south-eastern aspect of inland mountain ranges, and falls within the

Maputaland-Pondoland-Albany biodiversity hotspot (Fig. 3.1). Forest cover in this region is discontinuous and highly fragmented (Fig. 3.1). Six study forests were selected to represent the lowland coastal and scarp forests, and the Afromontane mistbelt forests. In each area, study forests were selected based on their size, protected status, and the proximity of surrounding human settlements. While most forest patches in the Eastern Cape are smaller than 150 ha, and prone to negative effects of fragmentation, study forests were selected to represent the cohort of larger, more 'intact' forest patches within the region. This is because these forests have larger core areas (i.e. portion of forests unaffected by edge effects) and are thus of high biodiversity value, such that insight into anthropogenic pressures within these more limited 'intact' forests is of conservation priority. All selected forests were thus greater than 150 ha, and unfenced; managed by the Department of Environment, Forestry and Fisheries (DEFF); and had rural settlements within 4 km of the forest boundary. Given that 70% of forests in the Eastern Cape region are managed by DEFF, and forests in the region are associated with communities in close proximity, study forests are representative of the current socio-political context within which larger, 'intact' forests in the region occur. Furthermore, study forests have endured colonial logging, followed by subsistence harvesting in recent times, such that they are representative of the history of human impacts. Within this context, forests representative of different national forest types were selected for sampling: Mqaba (Pondoland Scarp Forest), Manubi (Transkei Coastal Forest) and Ntlaboya (Eastern Cape Dune Forest) of the lowland zone, and Gomo, Nqadu (Transkei Mistbelt Forest) and Pirie (Amathole Mistbelt Forest) of the montane zone (Fig. 3.1). Within the Transkei mistbelt region, forests located within matrixes of timber plantations leased by the state to private companies are often deemed to be better protected than those which are not, so a forest in each category was sampled, with Nqadu associated with privately managed plantations while Gomo was associated with plantations managed by DEFF.
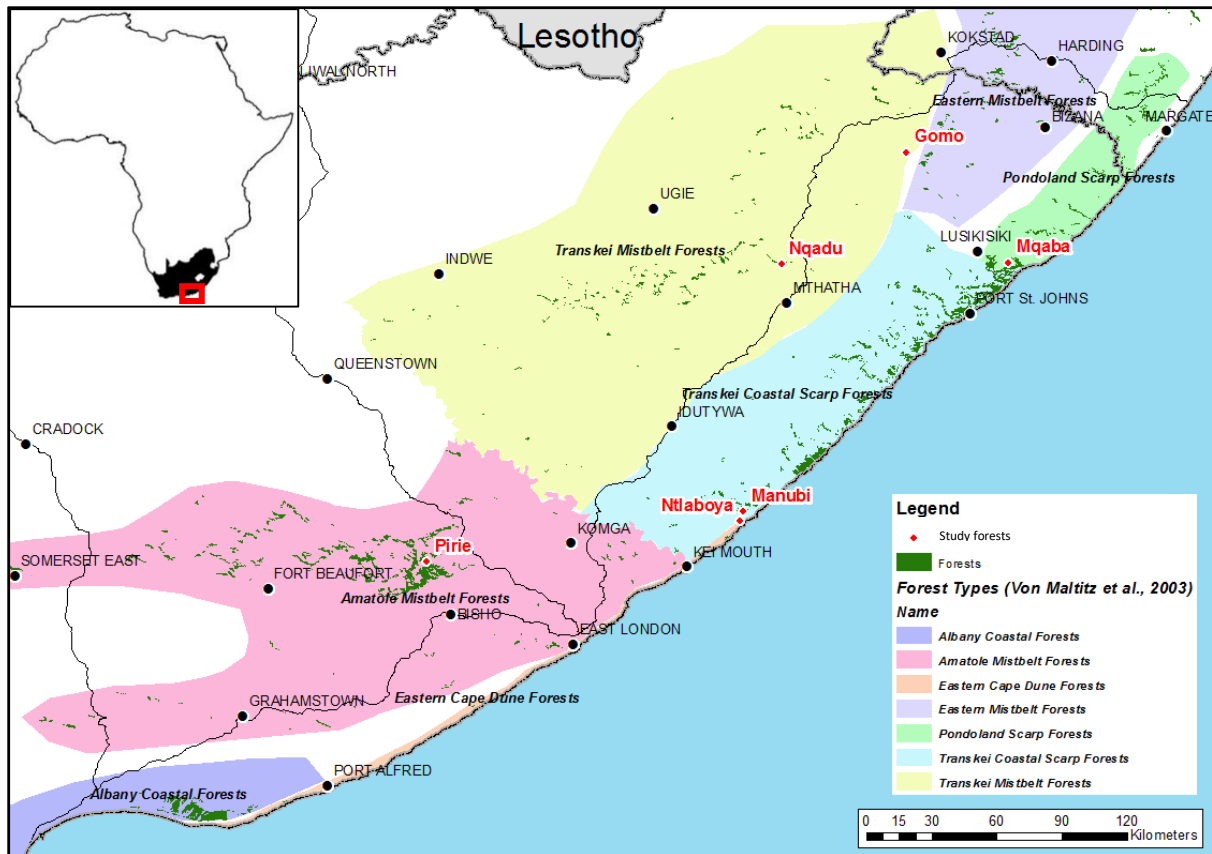
Figure 3.1 Location of the six study forests in the Eastern Cape Province, South Africa. (Map drawn by A. Wannenburgh)

3.3.2 Study design

A total of 89 plots were sampled, with an average of 15 plots sampled per forest. Points for sampling plots in each forest were selected to represent varying levels of disturbance from resource use, based on detailed discussion and guided walks in each forest with DEFF staff (forest managers and/or forest guards), and local community members, in addition to visual assessment by JL of human use in each forest, conducted over two reconnaissance trips prior to sampling. Plot locations were selected to represent the continuum of harvesting disturbances present at each forest, from heavily harvested sites to those with little or no harvesting present. This non-random sampling approach aimed to provide an objective overview of resource use within each forest, as well as samples from the full range of harvest activities and intensities, against which to investigate habitat changes and, in a linked

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study, avifaunal responses to resource use. A minimum distance of 150 m was maintained between selected plots, and 50 m between plots and the forest edge (i.e. all survey sites were within the forest interior).

3.3.3 Data collection

3.3.3.1 Habitat structure data

At each plot, the microhabitat structure and foliage profile were recorded within three nested circular plots: the largest plot was 0.2 ha (radius of 25.2 m), within which two smaller plots of 0.04 ha (radius of 11.3 m), and 0.01 ha (radius of 5.6 m) were nested. In the 0.2 ha plot, all standing dead trees (henceforth, snags) were recorded by diameter (cm) at 1.3 m above the ground, i.e. diameter at breast height (DBH), and cause of death, i.e. natural or due to bark harvesting. Natural snags include standing trees that have died due to factors other than harvesting, such as wind effects, senescence or disease. In the 0.04 ha plot the following variables were recorded: DBH of all living stems (> 5 cm DBH), percentage canopy cover, mean canopy height, percentage coverage of bare ground; leaf litter; grass cover; and herbaceous cover, and foliage density at 0 - 0.5 m; 0.5 – 1 m; 1 – 2 m; 2 – 5 m; 5 – 10 m and 10 – 20 m. Foliage density at each height class was estimated using a telescoping pole eight meters long and marked at each height interval. The pole was sequentially set-up at eight evenly spaced points 11.3 m from the plot centre (i.e. along the 0.04 ha circular plot boundary) and visual estimates of foliage density (as a percentage) at each height class were made from the plot centre. A rangefinder was used to assist with estimates of foliage density beyond the length of the telescoping pole, as well as to estimate mean canopy height at each plot. The amount of course woody debris (CWD) was measured based on the number of grounded dead logs (diameter > 10 cm; length > 1.5 m) in the 0.04 ha plot. In the inner-most plot of 0.01 ha, sapling abundance was recorded by counting all stems with diameter 1 - 5 cm.

3.3.3.2 Harvest data

Within 0.04 ha plots, stumps i.e. trees harvested for poles or timber, were counted and stump diameter measured. Based on diameter, stumps were categorized as pole (5 – 19.9 cm diameter) or timber (>20 cm diameter) harvesting, after Obiri et al., 2002. Trees harvested for medicinal bark were recorded using: DBH, and extent of bark removal on individual trees up to 3 m on the tree stem (scored 1 – 6 based on percentage of bark removed, where 1 = 1-10%; 2 = 11-25%; 3 = 26-50%; 4 = 51-75%; 5 = ring-barked to any extent %; 6 = total ring-bark, where ring-barked stems are those where bark has been removed from around the full circumference of the stem, after Cunningham, 1993).

3.3.4 Data analyses

3.3.4.1 Harvest indices

Pole and timber harvest intensity were calcuatled for each size class respectively based on the accumulated harvestable stems (stumps plus standing stems) as follows:

Tree Harvest Index$_j$ = number stumps$_j$ / (number stumps$_j$ + number stems$_j$),

where *j* represents the size class being assessed

Bark harvest intensity was assessed based on a bark harvest index derived from summed bark removal scores assigned to individual bark-harvested trees, calculated at each plot, as follows:

Bark Harvest Index = summed bark removal score/no. individuals bark-harvested

3.3.4.2 Habitat response to harvesting

Harvest effects on forest structure were investigated using: linear mixed models (LMMs) for habitat variables measured on a continuous scale; and generalized linear mixed models (GLMMs) for habitat variables measured as proportion cover or counts. The mixed-modelling approach accounted for the nested study design, with sample forests included as a random effect throughout the analysis to account for plots being nested within distinct study forests. Separate models were used to assess the response of each measured habitat feature to harvesting, with pole, timber and bark harvest indices included as the explanatory variables in addition to, and in all possible combinations of two-way interactions with one another. The three-way interaction between harvest variables, as well as the

two-way interaction between timber and bark were not included, as bark and timber harvesting, and all three harvest activities were seldom recorded within a single plot. Spearman's rank correlation test was used to test for significant correlations between harvest variables, to avoid issues related to multi-collinearity. The test showed the harvesting variables to be uncorrelated (-0.4 < r > 0.4). Variance inflation factors (VIFs) were examined to assess the extent of any remaining co-linearity between the explanatory variables using the 'vif' function of the car package (Fox and Weisberg, 2011). All variables had VIFs less than 3 and were thus retained (Zuur et al., 2010). Habitat variables measured on a continuous scale (i.e. mean canopy height, mean DBH, basal area per hectare, and foliage height diversity) were modelled using LMMs with Gaussian errors, using the 'lme' function of the nlme package (Pinheiro et al., 2013). Habitat variables measured as counts (tree, snag, sapling and grounded leg abundance) were modelled using GLMMs with the function 'glmer' of the lme4 package (Bates et al., 2015), with a Poisson distribution and log-link. Response variables measured as percent cover were converted to proportions and modelled using a beta regression with the function 'glmmTMB' of the glmmTMB package (Brooks et al., 2017). Model assumptions were verified by plotting residuals versus fitted values, and versus each covariate in the model (Zuur et al 2010; Zuur and Ieno 2016). The residuals were also assessed for spatial dependency using the 'spline.correlog' function of the ncf package (Bjornstad, 2016). Where interaction terms did not improve model strength based on AIC values, they were removed from the final model. Data from Pirie were not included in these analyses as minimal harvesting was recorded in this forest, and this analyses aimed to assess effects in disturbed forests. All analyses were carried out in R version 3.4.3 (R Core Team, 2017).

3.3 Results

Twelve of the 18 measured structural variables were significantly impacted by harvesting activities, with responses dependent on the type and intensity of resource use (Fig. 3.2 – 3.5; Table S3.1). Furthermore, the two-way interaction between pole and timber harvesting was shown to affect structural habitat heterogeneity (Fig. 3.5; Table S3.1). Five habitat features were unaffected by harvest

activities: canopy height; mean diameter at breast height (DBH); lower-understory foliage density (0.5 – 1 m); mid-story foliage density (2 – 5 m); and canopy layer foliage density (5 – 10 m; Table S3.1).

3.4.1 Bark harvesting

Bark harvesting intensity negatively affected canopy cover and sapling abundance (<5 cm DBH), while herb layer (0 – 0.5 m) foliage density, overall understory (0 – 2 m) foliage density, number of grounded logs and snag abundance (i.e. standing dead trees; >10 cm DBH) increased with bark harvesting intensity (Fig. 3.2; Table S3.1).
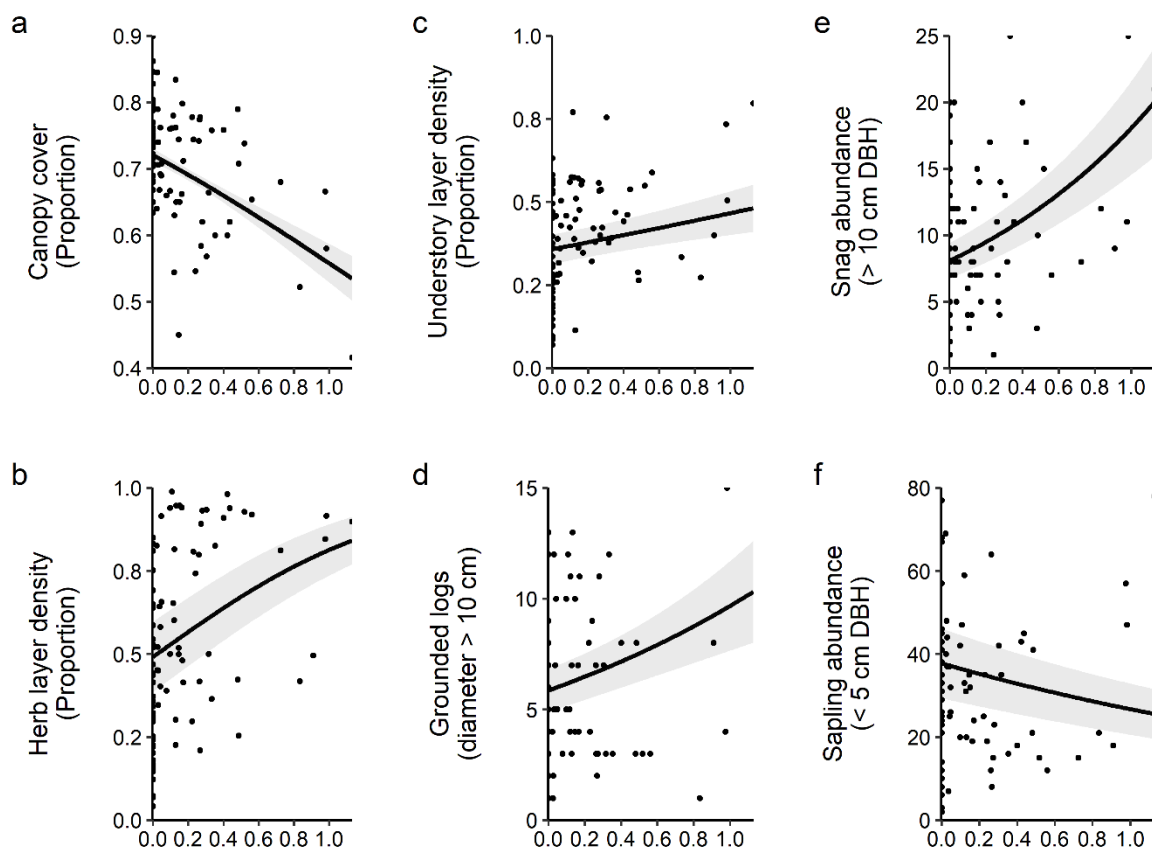
Figure 3.2 Effect of bark harvesting intensity, measured as the summed score of bark removal from individual bark-harvested trees per plot, based on Cunningham (1993) on **a)** canopy cover, **b)** herb layer (0 – 0.5 m) foliage density, **c)** understory (0 – 2 m) foliage density, **d)** number of ground logs, **e)** snag abundance, and **f)** sapling abundance (<5 cm DBH). Relationships shown are derived from mixed

models with forest included as a random effect (Table S3.1), however graphic representations depict population-level predictions (i.e. excluding random effects).

3.4.2 Pole harvesting

Increases in pole harvesting intensity resulted in declines in tree abundance, sapling abundance, basal area per hectare and leaf litter cover. Conversely, herb layer (0 – 0.5 m) foliage density and herb cover increased with pole harvesting intensity (Fig. 3.3; Table S3.1).
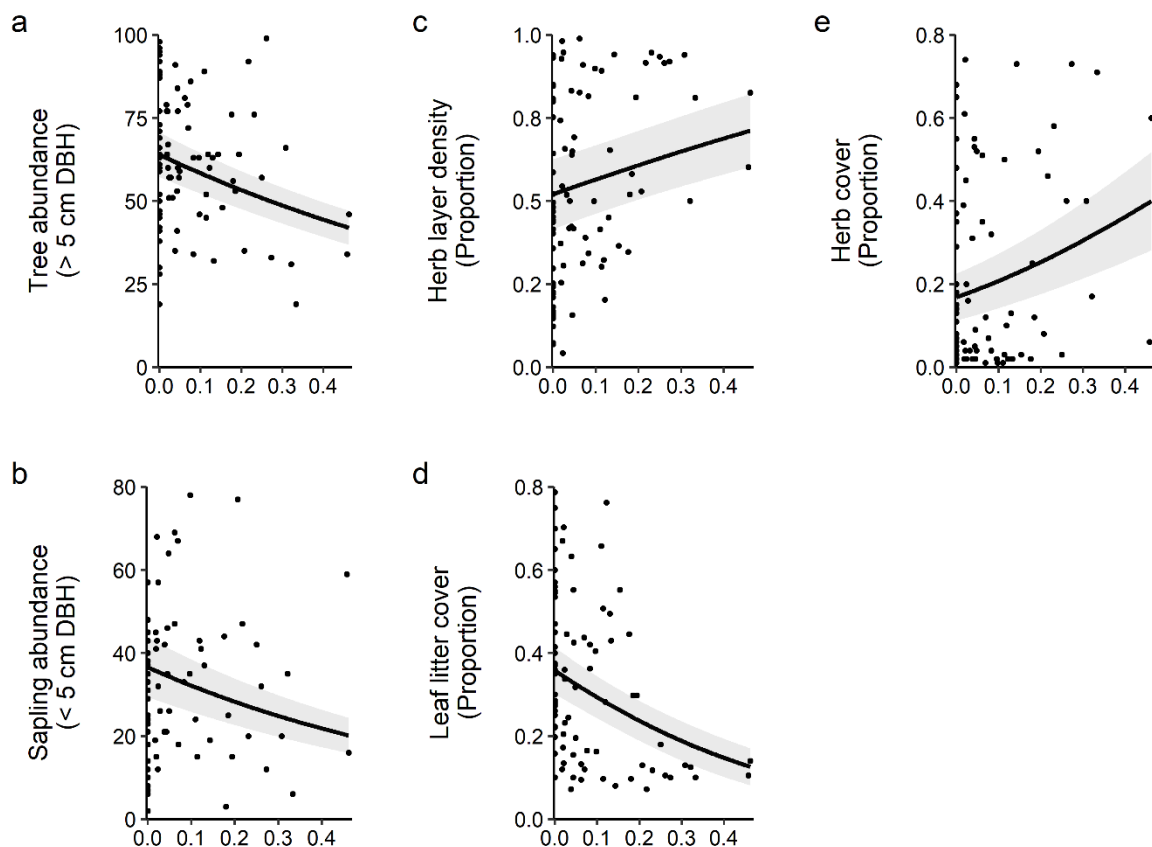
Figure 3.3 Effect of pole harvesting intensity, measured as the proportion of available stems (5 - 19.9 cm DBH) harvested, on **a)** tree abundance (>5 cm DBH), **b)** sapling abundance (<5 cm DBH), **c)** herb layer (0 – 0.5 m) foliage density, **d)** leaf litter cover, and **e)** herb cover. Relationships shown are derived from mixed models with forest included as a random effect (Table S3.1), however graphic representations depict population-level predictions (i.e. excluding random effects).

3.4.3 Timber harvesting

Increasing timber harvesting intensity resulted in a decline in canopy cover, while a positive relationship was found between the extent of timber harvesting and upper-understory layer (1 – 2 m) foliage density, number of grounded logs, bare ground cover, and sapling abundance (Fig. 3.4; Table S3.1).
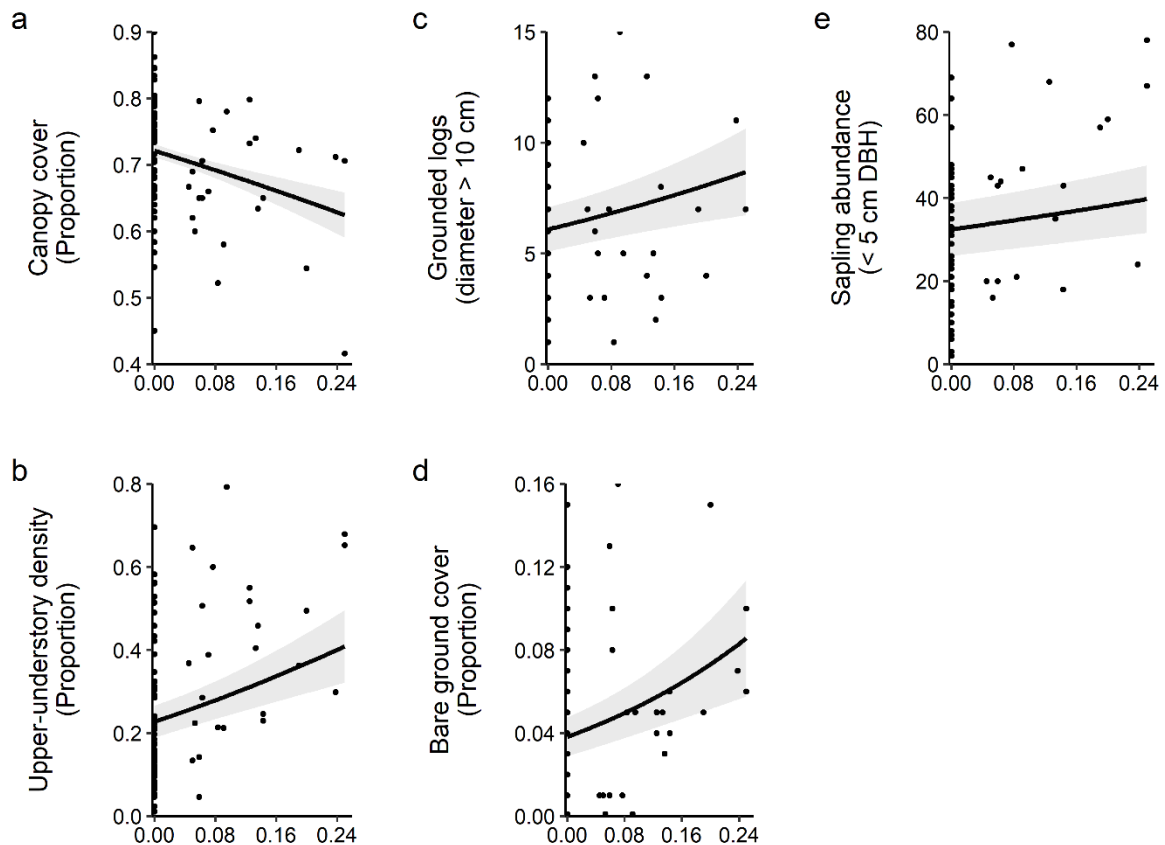
Figure 3.4 Effect of timber harvesting intensity, measured as the proportion of available stems (> 20 cm DBH) harvested, on **a)** canopy cover, **b)** upper-understory layer (1 – 2 m) foliage density, **c)** number of grounded logs, **d)** bare ground cover, and **e)** sapling abundance. Relationships shown are derived from mixed models with forest included as a random effect (Table S3.1), however graphic representations depict population-level predictions (i.e. excluding random effects).

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3.4.4 Interacting harvest effects

Foliage height diversity index (FHDI) was negatively affected by the interaction between timber and pole harvesting. Specifically, FHDI increased in response to increasing timber harvest intensities where pole harvest levels were low (i.e. 5% of available stems), but declined in response to increasing timber harvest levels where pole harvest intensities were high (i.e. 20% of available stems; Fig. 3.5; Table S3.1).
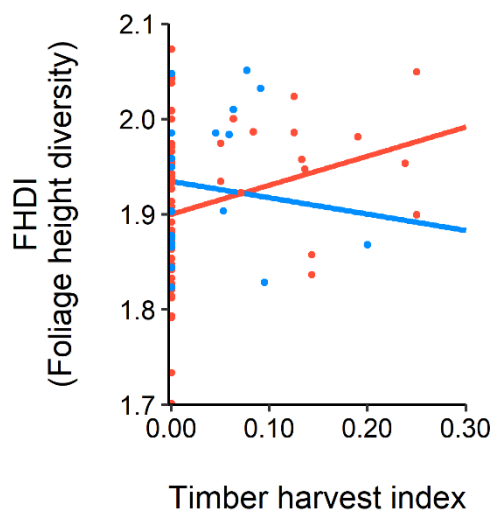
Figure 3.5 Effect of the two-way interaction between pole and timber harvesting on the foliage height diversity index (FHDI). The two lines represent variation in FHDI response to timber harvest intensity in the presence of low (i.e. 5%: red) and high (i.e. 20%: blue) intensities of pole harvesting, respectively. Relationships shown are derived from mixed models with forest included as a random effect (Table S3.1), however graphic representations depict population-level predictions (i.e. excluding random effects).

3.5 Discussion

Findings of this study show that unregulated harvesting of medicinal bark, poles and timber results in multiple structural modifications to forest habitats in state forests of the Eastern Cape. Specifically, bark and timber harvesting created canopy gaps, while pole harvesting created understory gaps, with variable implications for ground and understory layer microhabitat structure respectively. Findings of this study are thus in agreement with previous studies which have shown significant impacts of

resource use on forest habitat structure in temperate forests (Boudreau and Lawes, 2005; Lawes et al., 2007a; Hoppe-Speer et al., 2015). While the long-term ecological effects of harvest-mediated habitat modification are largely unknown (Lawes et al., 2007a), they represent changes to the natural disturbance regime, and are thus likely to have ramifications on forest patterns and processes (Royo and Carson, 2006), and faunal populations (Bawa and Seidler, 1998). However, results of this study show that the extent of habitat modification is dependent on the nature and intensity of harvesting, and that different harvest activities, where occurring together at a fine-spatial scale, may have interactive effects on habitat structure. While this study focussed on the impact of pole, timber and bark harvesting on habitat structure, it is important to consider how impacts of these extractive activities may be further affected by the presence of other disturbance regimes unaccounted for in the current study. Specifically, the presence of cattle in indigenous forests, and concomitant impacts of grazing has been cited by several authors as a threat to forest habitats in South Africa (Castley 1997; Krüger and Lawes, 1997; Castley and Kerley 1996; Hoppe-Speer et al. 2015).

3.5.1   Bark harvesting

While several studies have examined the ecological implications of bark harvesting at the individual- and population-level (Chungu et al., 2007; Gaoue and Ticktin, 2007; Guedje et al., 2007; Vermeulen et al., 2012), concurrent impacts on habitat structure have been relatively under-studied. Increasing bark harvesting intensities resulted in a decline in canopy cover and sapling abundance, and an increase in herb layer (0 – 0.5 m) and understory layer (0 – 2 m) foliage density, grounded logs, and snag density (i.e. standing dead trees). These habitat modifications are the result of excessive bark removal from tree stem circumferences, preventing the transport of photosynthetic products to tree roots, leading to root loss or death, thereby driving declines in canopy health and potential tree mortality (Cunningham, 2001). This creates gaps in the forest canopy thereby increasing light availability on the forest floor such that ground layer foliage density increased. Finally, as bark-harvested snags decay, dead branches drop to the ground, increasing the amount of grounded dead wood.

The substantial habitat-scale impacts of bark harvesting are perhaps best demonstrated by the close to 50% mean increase in snag abundance recorded across the four forests which experienced the highest levels of bark harvesting (Gomo, Manubi, Nqadu and Ntlaboya; Table S3.2), and associated increases in the number of grounded logs. While the ecological implications of the collection of dead wood for fuelwood from indigenous forests in South Africa has been cause for concern (Castley and Kerley, 1996; Berry et al. 2005), and shown to negatively affect cavity-nesting mammals and birds (Du Plessis, 1995), few studies have highlighted the creation of dead wood in forests due to bark harvesting. The important ecological role of dead wood has long been recognised by ecologists (Zhou et al., 2007). However, the value to forest taxa of harvested-mediated dead wood creation, at the cost of living canopy trees of a select few species and canopy cover, is unknown.

3.5.2   Pole harvesting

Unlike bark and timber harvesting, pole harvesting did not affect the forest canopy, but resulted in a decline in basal area, and trees and sapling abundance. This reflects the nature of pole-harvesting wherein multiple understory trees are harvested at a fine spatial-scale, thereby creating gaps in the understory, as shown by Boudreau and Lawes (2005). Despite the lack of any major canopy disturbances, as pole harvesting intensity increased, multiple understory layer features were affected: foliage density at the herb layer (0 – 0.5 m), and herb cover increased, while leaf litter cover declined. Thus, while declines in basal area, tree and sapling density were a direct effect of harvesting, altered understory and ground layer conditions represent an indirect response driven by increases in light availability and soil moisture content due to a reduction in tree density (Boudreau and Lawes, 2005; Louw, 2010).

While beyond the scope of this study, increased herb cover in understory gaps caused by pole harvesting may supress seedling establishment (Louw, 2010). Thus pole harvesting has the potential to alter not only structural habitat features, but also seedling recruitment, and therefore the

maintenance of forest tree diversity. As indicated by this study, changes in understory conditions are dependent on the harvest intensity. Similarly, changes in seedling recruitment caused by pole harvesting are determined by understory gap size (Louw, 2010), with larger gaps causing a potential successional shift in seedling recruitment. However, Boudreau and Lawes (2005) showed that under low harvesting intensity (11.6% of available pole-sized stems), pole harvesting did not negatively affect the long-term maintenance of tree diversity, suggesting that pole harvest intensities measured in the current study (regional average of 7% of available pole-sized stems; Table S3.2) may not adversely affect tree species composition. However, modifications to understory layer conditions may affect forest fauna. For example, leaf litter cover is a critical habitat for many forest invertebrates (Banks et al., 2010).

3.5.3 Timber harvesting

At the habitat scale, timber harvesting resulted in the creation of canopy gaps through the selective extraction of canopy trees, resulting in an increase in upper-understory (1 – 2 m) foliage density, sapling abundance, and bare ground cover. Furthermore, timber harvesting increased the number of grounded logs at the plot-level. This is due to the large portions of harvested trees that are left in the forest given that only the main stem of the harvested tree is removed, with the rest of the harvested tree left in the forests. Furthermore, increases in dead wood may be associated with incidental tree damage associated with canopy-tree felling. Similar structural responses to selective timber harvesting have been shown by studies in tropical forests (Thiollay, 1992; Sekercioglu, 2002; Wunderle et al., 2006). The creation of canopy gaps in forest systems represents a vital component of natural forest disturbance regimes, given their important role in promoting regeneration, tree diversity and habitat heterogeneity (Brokaw, 1985; Levey, 1988; Kneeshaw and Bergeron, 1998; Obiri and Lawes, 2004; Wunderle et al., 2006). Specifically, the gap phase represents a time of rapid plant growth (Brokaw, 1985) attributed to increased resource availability and/or decreased resource competition (Canham, 1988), demonstrated in the current study by the increased foliage density in the understory.

Furthermore, habitat conditions in canopy gaps compared to intact forest have been shown to differ significantly with respect to microclimate (Canham, 1988; Gray et al., 2002), detritus (Cleary et al., 2007), productivity (Prescott, 2002) and plant species composition (Brokaw, 1985; Kneeshaw and Bergeron, 1998). Consequently multiple forest taxa, including birds, reptiles and invertebrates have been shown to distinguish between canopy gap and intact habitats (Levey, 1988; Thiollay, 1992; Vitt et al., 1998; Wunderle et al., 2006; Richards and Windsor, 2007). This suggests that timber harvest activities, and concomitant habitat modifications as shown by this study, are likely to have ramifications on forest biodiversity.

The degree to which timber harvest activities affect forest biodiversity, beyond direct population-level impacts on target species, is likely to be dependent on the frequency of the disturbance, and the extent of incidental habitat damage. With regards to the former, selective harvesting practices in the Eastern Cape region are likely to be less destructive than mechanised selective logging operations, which cause considerable damage through clearing for roads and log storage sites (Thiollay, 1992). Informal timber harvesting in the Eastern Cape is generally un-mechanised, with felled timber split in the forest, and carried out on foot along narrow footpaths (personal observation). The frequency of disturbance is thus likely to be more cause for concern, as the harvest-driven increase in the proportion of forest under gap conditions is likely to have implications on ecosystem functioning (Royo and Carson, 2006).

3.5.4   Interacting harvest effects

The positive relationship between foliage height diversity and biodiversity has been well-established, and is based on niche-theory which predicts that greater diversity of habitats supports a greater diversity of species (MacArthur and MacArthur, 1961). The decline in foliage height diversity in response to the interaction between pole and timber harvesting activities shown in this study indicates that, where these harvest types occur together at high intensities, structural habitat

complexity is reduced, likely to negatively affect biodiversity at the habitat-scale. This finding suggests that management strategies should limit the extent to which pole and timber harvesting activities occur together, and reduce the damage/lopping of smaller, non-target trees often associated with timber harvesting activities (personal observation) so as to maintain habitat heterogeneity in harvested areas.

3.5.5   Conclusion

Findings of this study indicate that resource use from state forests in the Eastern Cape has a significant impact on forest structure, though the nature and extent of the impact is dependent on the type and intensity of resource use. These results should be viewed within the context of forests that have a long history of human exploitation, from extensive colonial era logging to current subsistence and informal commercial harvesting of multiple forest products. However, the effects of long-term human exploitation are likely to have affected the current condition of all sampled forests, such that findings of this study are indicative of habitat responses to more recent resource use disturbances. Similarly, while habitat structure is modified by random natural disturbances, such as wind-falls, lightening or fire-spotting, which are a vital component of natural disturbance-recovery regimes that maintain forest dynamics, resource use represents disturbances that occur in addition to these natural disturbances under which forest species have adapted, and thus may affect ecosystem persistence and resilience. Further research is needed to determine specific levels of resource use that can be sustained without negatively affecting forest biodiversity. Specifically, research regarding the impact of resource use on forest taxa at multiple trophic levels is needed to provide insight into ecosystem-wide implications of harvest-mediated habitat modification, and contribute to the development of ecologically-informed forest management policies.

3.6 Appendices

Table S3.1 Response of structural habitat variables to pole harvesting intensity (Pole), timber harvesting intensity (Timber) and bark harvesting itensity (Bark) derived from linear mixed models (LMMs).

Response	Fixed effect	Estimate	SE	T value	P value
Foliage height diversity index	Intercept	1.87	0.04	45.87	0.00
	Pole	0.24	0.13	1.85	0.07
	Timber	0.47	0.24	1.97	0.05
	Bark	-0.01	0.04	-0.32	0.75
	Pole*Timber	-3.20	1.41	-2.26	**0.03**
Canopy height (m)	Intercept	12.56	0.91	13.87	0.00
	Pole	-0.14	1.85	-0.08	0.93
	Timber	0.25	3.27	0.08	0.94
	Bark	0.27	0.79	0.33	0.74
Mean DBH (log-transformed)	Intercept	1.25	0.04	31.13	0.00
	Pole	0.06	0.10	0.64	0.52
	Timber	-0.20	0.18	-1.13	0.26
	Bark	-0.02	0.04	-0.51	0.61
Mean basal area per ha (log)	Intercept	1.79	0.06	28.99	0.00
	Pole	-0.42	0.13	-3.22	**< 0.01**
	Timber	-0.02	0.23	-0.09	0.93
	Bark	-0.02	0.06	-0.43	0.67
Coarse woody debris (CWD)	Intercept	1.78	1.17	10.68	0.00
	Pole	-0.82	0.43	-1.88	0.06
	Timber	1.42	0.73	1.94	**0.05**
	Bark	0.50	0.17	3.02	**< 0.01**
Tree abundance (>5 cm DBH)	Intercept	4.16	0.11	39.32	0.00
	Pole	-0.91	0.16	-5.83	**< 0.01**
	Timber	0.18	0.26	0.68	0.50
	Bark	-0.03	0.07	-0.43	0.68
Sapling abundance (<5 cm DBH)	Intercept	3.63	0.20	18.46	0.00
	Pole	-1.29	0.19	-6.73	**< 0.01**
	Timber	0.81	0.27	3.06	**< 0.01**
	Bark	-0.34	0.07	-4.49	**< 0.01**
Snag abundance (DBH > 10 cm)	Intercept	2.16	0.17	12.93	0.00
	Pole	-0.65	0.38	-1.70	0.09
	Timber	-0.62	0.65	-0.95	0.34
	Bark	0.08	0.14	5.87	**< 0.01**
Canopy cover (%)	Intercept	1.06	0.06	17.55	0.00
	Pole	-0.64	0.36	-1.81	0.07
	Timber	-1.41	0.57	-2.45	**< 0.05**
	Bark	-0.72	0.14	-5.10	**< 0.01**
Herb cover (%)	Intercept	-1.41	0.46	-3.05	0.00
	Pole	2.49	0.81	3.08	**< 0.01**
	Timber	-2.22	1.72	-1.30	0.20
	Bark	0.13	0.36	0.35	0.73

Table S3.1 (continued) Response of structural habitat variables to pole harvesting intensity (Pole), timber harvesting intensity (Timber) and bark harvesting itensity (Bark) derived from linear mixed models (LMMs).

Response	Fixed effect	Estimate	SE	T value	P value
Leaf litter cover (%)	Intercept	-0.52	0.30	-1.75	0.00
	Pole	-2.95	0.77	-3.79	**< 0.01**
	Timber	-1.45	1.13	-1.28	0.20
	Bark	-0.46	0.30	-1.55	0.12
Bare ground cover (%)	Intercept	-3.17	0.27	-11.87	0.00
	Pole	0.22	0.86	0.26	0.80
	Timber	3.43	1.21	2.84	**< 0.01**
	Bark	-0.44	0.33	-1.32	0.19
Herb layer foliage density (0 – 0.5 m)	Intercept	-0.003	0.48	-0.007	0.99
	Pole	1.72	0.85	2.02	**< 0.05**
	Timber	0.36	1.27	0.28	0.77
	Bark	1.48	0.35	4.26	**< 0.01**
Lower-understory foliage density (0.5 – 1 m)	Intercept	-0.61	0.22	-2.76	0.00
	Pole	0.99	0.78	1.27	0.21
	Timber	1.73	1.37	1.26	0.21
	Bark	0.36	0.32	1.14	0.26
Upper-understory foliage density (1 – 2 m)	Intercept	-1.10	0.23	-4.76	0.00
	Pole	0.81	0.82	0.99	0.32
	Timber	3.41	1.37	2.48	**< 0.05**
	Bark	-0.20	0.34	-0.59	0.56
Understory foliage density (0 – 2 m)	Intercept	-0.53	0.14	-3.68	0.00
	Pole	0.96	0.54	1.76	<u>0.08</u>
	Timber	1.65	0.94	1.75	<u>0.08</u>
	Bark	0.43	0.23	1.93	**0.05**
Mid-story foliage density (2 – 5 m)	Intercept	-0.90	0.22	-4.17	0.00
	Pole	-0.22	0.65	-0.34	0.74
	Timber	0.10	1.12	0.09	0.93
	Bark	0.001	0.30	0.00	1.00
Canopy layer foliage density (5 – 10 m)	Intercept	-0.12	0.18	-0.66	0.51
	Pole	0.78	0.47	1.66	0.10
	Timber	-0.92	0.84	-1.10	0.27
	Bark	-0.24	0.20	-1.19	0.23

Table S3.2 Extent of harvesting activities recorded at each study forest, showing means (± SE) within each forest, with letters indicating significant differences between forests. While data from Pirie was exluded from analyses of habitat response to harvesting, harvest intensity data is presented here, showing the low levels of harvesting recorded in this forest.

Harvest type	Lowland forests			Montane forests			Test statistic and p-value
	Manubi	Mqaba	Ntlaboya	Gomo	Nqadu	Pirie	
Bark harvest index	0.25 ± 0.08 (ab)	0.03 ± 0.01 (bc)	0.28 ± 0.11 (abc)	0.31 ± 0.07 (a)	0.16 ± 0.05 (abc)	0.01 ± 0.01 (c)	χ^2 = 27.02, df = 5, p < 0.01
Proportion of pole-sized trees harvested per plot	0.10 ± 0.03 (a)	0.07 ± 0.02 (a)	0.05 ± 0.03 (ab)	0.14 ± 0.04 (a)	0.08 ± 0.03 (ab)	0.00 ± 0.00 (b)	χ^2 = 28.45, df = 5, p < 0.01
Proportion of timber-sized trees harvested	0.07 ± 0.02 (a)	0.07 ± 0.02 (a)	0.02 ± 0.02 (ab)	0.02 ± 0.01 (ab)	0.00 ± 0.00 (b)	0.00 ± 0.00 (b)	χ^2 = 21.72, df = 5, p < 0.01

CHAPTER IV: RESPONSE OF BIRD FUNCTIONAL DIVERSITY TO FOREST PRODUCT HARVESTING IN THE EASTERN CAPE, SOUTH AFRICA

Jessica Leaver, Jake Mulvaney, David A. Ehlers Smith, Yvette C. Ehlers Smith, Michael I. Cherry

4.1 Abstract

The ecological impact of forest product harvesting is poorly understood despite the reliance of millions of impoverished households on forest resources. As birds are indicators of environmental change and essential for the function and regeneration of forest ecosystems, this study aimed to assess the response of bird species richness and functional diversity to unregulated forest product harvesting, to illuminate the impact of harvest disturbances on forest biodiversity. Five forest types in the Eastern Cape Province, South Africa were sampled by means of circular plots in which bird communities, habitat structure and harvest intensities of sub-canopy trees harvested for poles, canopy trees harvested for timber, and bark harvested for medicinal use, were recorded. Generalized linear models (GLMs) were used to assess the response of bird diversity to harvesting activities measured on a continuous scale, and forest type. Correlations between feeding traits and environmental variables relating to habitat structure and harvest disturbances were investigated using RLQ and fourth-corner analysis to better understand which traits were sensitive to harvest disturbances. Results indicated that forest type was an important driver of variation in species richness and functional diversity. Additionally, harvesting disturbances negatively affected two measures of functional diversity, while species richness and functional richness were unaffected by harvesting. Specifically, functional evenness was negatively affected by timber harvesting, while functional dispersion declined in response to pole and bark harvesting. Bird traits relating to feeding ecology (i.e. primary diet and foraging strategy) were associated with habitat structure and harvest disturbances, indicating that harvest activities affected community structure. Specifically, frugivores and granivores were negatively affected by pole and bark harvesting respectively, while omnivorous species were positively affected by these harvest activities. Conversely, timber harvesting negatively affected omnivores, and positively affected nectarivores. Bark and timber harvesting, which resulted in canopy gaps, negatively affected species which forage in the understory or on the forest floor, while pole harvesting, which reduced tree abundance but not canopy cover, negatively affected canopy-foraging species. These

results suggest that current unregulated forest product harvesting in the Eastern Cape may negatively affect forest productivity and ecosystem functioning. Specifically, this is the first study to measure the effects of harvesting of poles and medicinal bark on the functional diversity of avian forest communities.

Keywords: extractive disturbance; ecosystem function; avian community structure; RLQ; medicinal bark harvesting; timber harvesting

4.2 Introduction

Across developing nations, there is a geographical convergence of remaining natural forests with regions characterised by severe rural poverty (Sunderlin et al., 2005). Forests in these regions face high levels of biomass extraction, given that forest products, ranging from fuelwood to medicine, comprise a critical component of rural livelihood strategies (Hegde et al., 1996; Hegde and Enters 2000; Ambrose-Oji, 2003; Shackleton and Shackleton, 2004). While the significant role of forest products in rural livelihoods is well-documented and globally recognised (Kaimowitz, 2003; Lawes et al., 2004), the implications of this anthropogenic disturbance on ecosystem health are poorly understood. Specifically, existing research is largely focused on population-level effects with fewer studies investigating community- or ecosystem-level responses (Ticktin, 2004; Brites and Morsello, 2012). Research aimed at understanding the effects of forest product harvesting on biodiversity is thus urgently needed to inform management strategies aimed at balancing the socio-economic needs of people with the long-term resilience of forest ecosystems.

Measuring change in ecosystem health directly is complex given the multifaceted nature of biodiversity loss. Indicators which act as surrogate measures of biodiversity thus provide vital diagnostic tools to monitor and assess the response of biodiversity to disturbance. In this regard, birds are considered effective biodiversity indicators: they occupy various trophic levels and are sensitive to environmental change (both anthropogenic and natural), are widespread, diverse and mobile,

relatively easy to identify and survey, and their phylogenetic status is well-defined (Gregory and van Strien, 2010). Furthermore, birds provide many ecosystem functions through their divergent use of forest resources, such as seed dispersal, pollination and pest control, such that the persistence of bird diversity is critical for the functioning and regeneration of forest ecosystems (Pimm, 1986; Sekercioğlu, 2006). The use of birds as indicators of biodiversity response to forest product harvesting thus provides the opportunity to investigate ecosystem-level implications of this widespread human disturbance. Despite this, few studies have examined the impact of local-scale biomass extraction on bird diversity (Du Plessis 1995; Laiolo, 2003; Shahabuddin and Kumar, 2006; 2007; Gardner et al., 2016; Asefa et al., 2017). Moreover, studies which have used birds as indicators of biodiversity loss in response to forest product harvesting have focussed largely on taxonomic measures of species diversity, such as species richness and Shannon Diversity, or on responses by coarse functional categories or guilds (e.g. 'insectivores'). Given that niche complementarity links diversity to ecosystem processes (Tilman, 2001a), indicators of biodiversity based on species richness or coarse functional groups, may not adequately depict changes in community structure or ecosystem functioning in response to disturbance (Nummelin and Kaitala, 2004; Ernst et al., 2006; Lamb et al., 2009). This is because these measures do not take into account the degree of functional redundancy or complementarity that may exist in an assemblage.

Consequently, functional diversity (FD) has been shown to provide a stronger link between diversity and ecosystem functioning (Díaz and Cabido, 2001; ; Petchey and Gaston, 2002; Mason et al., 2005; Mouillot et al., 2013). This is because FD measures the range, abundance and distribution of functional trait values in a community (Tilman, 2001b), typically focussing on morphometrics, physiological and behavioural traits that define a species' ecological role in a community, thereby providing a more robust approach to evaluate the effects of disturbance on the functional roles performed by species (Petchey and Gaston, 2002; Villéger et al., 2008). This is important given that specialist species, which

have more specific niche and resource requirements, and therefore more diverse and specialised functional roles, are more sensitive to disturbance than generalist species, which are better adapted to take advantage of environmental change, but have similar functional roles (Kassen, 2002; Marvier et al., 2004). Thus, while species richness may increase or remain unchanged in reponse to disturbance due to an increase in generalist species, functional diversity is sensitive to the replacement of specialist by generalist species, and is therefore a more appropriate indicator of disturbance. Consequently, functional homogenization, which refers to a decrease in functional diversity among species in local assemblages, is ecologically of far more concern than changes in species richness (Devictor et al., 2008a). Indicators based on functional, rather than taxonomic measures of diversity are thus needed to gain insight into the ecosystem-level effects of disturbance (Villéger et al., 2008; Laliberté and Legendre, 2010) and inform sustainable forest management (Vandewalle et al., 2010).

Growing recognition of the importance of functional measures of diversity has resulted in an increasing number of studies using trait-based measures of diversity to understand the effects of disturbance on ecosystem function. Several such studies have shown that functional diversity declines in response to anthropogenic disturbance (Flynn et al., 2009; Villéger et al., 2010; Luck et al., 2013; Ibarra and Martin, 2015; Coetzee and Chown, 2016; Ehlers Smith et al., 2018;). These studies have, however, largely used categorical measures of disturbance and have been conducted at the landscape scale. From an ecological perspective, the relationships between continuous measures of disturbance and functional diversity are likely to provide more insight than broad categorical groups given that variation in functional traits is prone to change continuously across a disturbance gradient (McGill et al., 2006; Cadotte et al., 2011). Second, from a management perspective, although large-scale studies help inform conservation policy at the global and national scale, conservation action, specifically regarding natural resource management, is generally conducted at the local scale. Moreover, few studies consider the varying nature of local-scale anthropogenic disturbances and thus, potential

variation in responses by biodiversity. This is particularly pertinent in the case of forest product harvesting, which incorporates a range of harvest activities, with variable impacts on forest structure.

Habitat structure has been associated with changes in bird species communities (Sekercioğlu, 2002; ; Watson et al., 2004; Shahabuddin and Kumar, 2006; Rocha et al., 2015) and functional trait distribution, with habitat structures shown to benefit certain avian traits whilst reducing others (Cleary et al., 2007; Seymour and Dean, 2009; Ehlers Smith et al., 2015; 2017). The harvesting of forest products, through its impact on habitat structure, may thus affect ecosystem functioning by promoting conditions that selectively hinder or help particular species based on their functional traits. However, the impacts of human-mediated disturbances on functional components of biodiversity, and how this may vary across disturbance regimes given their variable impacts on habitat structure, is poorly understood (Villéger et al., 2010; Lee and Martin, 2017).

In South Africa, the number of threatened forest bird species increased from 10 % in 2009 to 19 % in 2014 (Berliner, 2009; BirdLife South Africa, 2014). Furthermore, a recent study found that half of South Africa's forest-dependent bird species have experienced range declines since 1992, with declines most prominent in the Eastern Cape Province, despite an increase in forest cover in this region over the same period (Cooper et al., 2017). This indicates that habitat degradation, rather than habitat loss, may be driving local extinctions of forest birds in the region. The harvesting of forest products is considered the most widespread disturbance in forests in South Africa (von Maltitz et al., 2003). Of particular concern is the increasing commercialization of forest products (Shackleton and Shackleton, 2004; Shackleton et al., 2005; Paumgarten and Shackleton, 2009) which has resulted in destructive and unsustainable harvest rates (Dold and Cocks, 2002; Williams et al., 2013), raising concern over harvest-driven habitat degradation. However, the impact of forest product harvesting on biodiversity in South Africa is poorly understood and scarcely studied (Du Plessis, 1995; Krüger and Lawes, 1997). More specifically, to the authors' knowledge, no previous studies have employed measures of

functional diversity to investigate the link between forest product harvesting and biodiversity loss in indigenous forests in South Africa, and the mechanisms that may drive this. In light of this knowledge gap, the current study aimed to: 1) assess the response of bird species richness and functional diversity to three prevalent harvest activities, namely sub-canopy tree harvesting, canopy tree felling and bark harvesting, and 2) determine associations between bird functional traits and harvest activities. This study was conducted in the drier, colder winter period in the study region, a time of food scarcity in forest habitats. Food availability and accessibility were thus considered important factors affecting birds at the time of sampling. The response of primary diet and foraging strategy to harvesting activities were thus investigated specifically, as these traits have been shown to influence bird species' response to disturbance (Cleary et al., 2007; Seymour and Dean, 2009; Edwards et al., 2013; Ehlers Smith et al., 2015).

4.3 Materials and methods

4.3.1   Study area

The study was conducted in the Eastern Cape Province of South Africa between April and September 2016. The Eastern Cape harbours 46 % of South Africa's limited remaining forest cover, including many of the country's most threatened forest types, and forms part of the Maputaland-Pondoland-Albany Hotspot for biodiversity (Berliner, 2009). Beyond this ecological distinction, the Eastern Cape is characterised as being one of South Africa's poorest and least developed provinces, incorporating two of the former 'homelands' of the Apartheid era (Cocks and Møller, 2002). Although these areas were amalgamated into the Eastern Cape Province following the advent of democracy in 1994, they are still characterised by a weak economy, poor infrastructure, and high levels of unemployment and rural poverty. Forests sampled in the current study were located in these former 'homelands', namely the Ciskei and Transkei. These forests are relics of a forest belt which, during the Miocene stretched all the way along the south-east coast of Africa, but is now highly fragmented due largely to

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palaeoclimatic change, and augmented more recently by anthropogenic disturbances (von Maltitz et al., 2003). The study area included five of the national forest types in the two main zones of forest in the Eastern Cape, i.e. the lowland coastal and scarp forests of the subtropical coastal zone, and the warm-temperate mistbelt forests found on the south to south-eastern aspect of inland mountain ranges (von Maltitz et al., 2003). Forest cover in this area is discontinuous and highly fragmented (von Maltitz 2003; Fig. 4.1), with the forest matrix dominated by grassland vegetation, largely under communal land-tenure systems (Kepe, 1997). Agriculture, predominantly subsistence crop and livestock farming, constitutes the major land-use in the region, while rural settlements, plantation forestry and protected areas represent other important, although smaller, land-use types.

Table 4.1 Study forest characteristics.

Study forest	Forest type	Co-ordinates	Size (ha)	Elevation (m)	Mean annual rainfall (mm)
Gomo	Transkei Mistbelt	31°0'39.34"S 29°20'44.25"E	500	820 – 1550	600 - 1200
Pirie	Amathole Mistbelt	32°45'57.88"S 27°15'24.19"E	3170	550 – 1200	800 – 1800
Manubi	Transkei Coastal	32°27'7.30"S 28°35'52.94"E	900	80 - 220	630 - 1200
Mqaba	Pondoland Scarp	31°26'8.36"S 29°44'9.36"E	1600	60 - 400	660 - 1200
Ntlaboya	Eastern Cape Dune	32°30'45.99"S 28°35'28.78"E	160	20 - 60	630 - 1200

The montane forests sampled occur at altitudes of between 550 m and 1550 m while the lowland forests are found below 400 m, and down to less than 20 m at the coast. Rainfall occurs predominantly during the summer months in the region (October – April), with mean annual rainfall ranging from 600 – 1200 mm (von Maltitz et al., 2003, Table 4.1). Temperatures across the region are mild (mean temperature range: 14 - 20°C). Conditions at lowland forests are moderated by proximity to the coast, with minimum winter temperatures ranging from 7 - 11°C. Minimum winter temperatures at the higher-elevation montane forests are lower, ranging from 1 - 10°C.
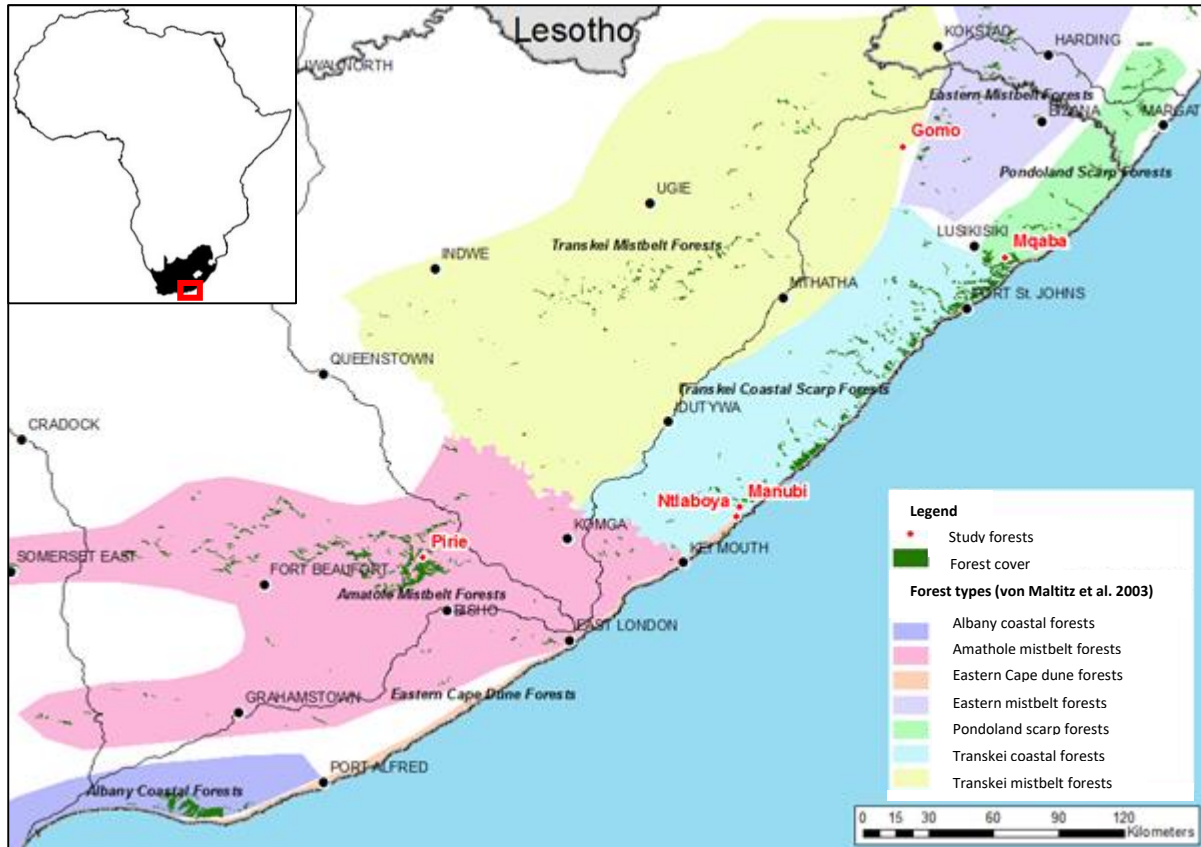
Figure 4.1 Location of the five study forests in the Eastern Cape Province, South Africa (Map drawn by: A. Wannenburgh).

4.3.2 Study design

Five study forests were selected to represent the lowland coastal and scarp forests of the subtropical coastal zone, and the Afromontane mistbelt forests (von Maltitz et al., 2003). In each forest zone, study forests were selected based on their size, protected status, and the proximity of surrounding human settlements. While most forest patches in the Eastern Cape are smaller than 150 ha, and prone to negative effects of fragmentation (Berliner, 2009; von Maltitz, 2003), study forests were selected to represent the cohort of larger, 'intact' forest patches within the region. This is because these forests have larger core areas (i.e. portion of forests unaffected by edge effects) and are thus of high biodiversity value, such that insight into anthropogenic pressures within these more limited 'intact' forests is a conservation priority (Berliner, 2009). All selected forests were thus greater than 150 ha,

and unfenced; managed by the state under the Department of Agriculture, Forestry and Fisheries (DAFF); and had rural settlements within 4 km of the forest boundary. Given that 70 % of forests in the Eastern Cape region are managed by DAFF, and forests in the region are associated with rural communities in close proximity (Berliner, 2009), study forests were representative of the current socio-economic and -political context within which larger, 'intact' forest in the region occur. Furthermore, study forests have endured colonial logging (King, 1941), followed by subsistence harvesting in recent times, such that they are representative of the history of human impacts in the region. Within this context, forests representative of different national forest types were selected for sample as follows (national forest type stated between brackets): Mqaba (Pondoland Scarp Forest), Manubi (Transkei Coastal Forest) and Ntlaboya (Eastern Cape Dune Forest) of the lowland zone, and Gomo (Transkei Mistbelt Forest) and Pirie (Amathole Mistbelt Forest) of the montane zone (Fig. 4.1, Table 4.1).

In each study forest, an average of 15 circular 0.04 ha (11.3 m radius) plots were sampled, in which all harvesting activities were quantified, microhabitat structure and foliage profiles measured, and the bird community recorded (n = 74). Points for sampling plots in each forest were selected to represent the varying levels of harvesting disturbance present in each forest, based on detailed discussion and guided walks with DAFF staff (forest managers and/or forest guards), and local community members, in addition to visual assessment by JL of human use in each forest, conducted over two reconnaissance trips to each forest prior to sampling. Plot locations were subsequently selected to represent a continuum of harvesting disturbances present at each forest, from heavily harvested sites to those with little or no harvesting present. This non-random sampling approach aimed to provide an objective overview of resource use within each forest, and samples from the full range of harvest activities and intensities against which to investigate avifaunal responses to resource use (after Kumar and

Shahabbudin, 2005). A minimum distance of 150 m was maintained between selected plots, and 50 m between plots and the forest edge (i.e. all survey sites were within the forest interior).

4.3.3 Habitat structure

At each plot, the microhabitat structure and foliage profile were recorded within three nested circular plots: the largest plot was 0.2 ha (radius of 25.2 m), within which two smaller plots of 0.04 ha (radius of 11.3 m), and 0.01 ha (radius of 5.6 m) were nested. In the 0.2 ha plot, all standing dead trees (henceforth, snags) were recorded by diameter (cm) at 1.3 m above the ground, i.e. diameter at breast height (DBH), and cause of death, i.e. natural or due to bark harvesting. Natural snags include standing trees that have died due to factors other than harvesting, such as wind effects, senescence or disease. In the 0.04 ha plot the following variables were recorded: DBH of all living stems (> 5 cm DBH), diameter of all trees harvested for poles or timber (i.e. cut tree stumps), percentage canopy cover, mean canopy height, percentage coverage of bare ground; leaf litter; grass cover; and herbaceous cover, and foliage density at 0 - 0.5 m; 0.5 – 1 m; 1 – 2 m; 2 – 5 m; 5 – 10 m and 10 – 20 m. Foliage density at each height class was estimated using a telescoping pole eight meters long and marked at each height interval. The pole was sequentially set-up at eight evenly spaced points 11.3 m from the plot centre (i.e. along the 0.04 ha circular plot boundary) and visual estimates of foliage density (as a percentage) at each height class were made from the plot centre. A rangefinder was used to assist with estimates of foliage density beyond the length of the telescoping pole, as well as to estimate mean canopy height at each plot. In the inner-most plot of 0.01 ha, sapling abundance was recorded by counting all stems with diameter 1 - 5 cm.

4.3.4 Harvest activities

Based on the diameter of cut tree stumps recorded in 0.04 ha circular plots, harvested trees were classified as pole harvesting (stump diameter 5 – 19.9 cm) or timber harvesting (stump diameter > 20 cm), based on Obiri et al. (2002). Separate pole and timber harvest indices were thus calculated per plot as the proportion of pole-sized and timber-sized trees harvested in each plot, based on the

accumulated harvestable stems (stumps plus standing stems) in each size class respectively, as follows:

Tree Harvest Index$_j$ = number stumps$_j$ / (number stumps$_j$ + number stems$_j$),

> where *j* represents the size class being assessed, namely pole- or timber-sized trees

A bark harvesting index was assigned to each plot based on the proportion of trees that were dead due to bark harvesting (i.e. bark harvested snags). This was calculated by dividing the number of bark-harvested snags (standing dead bark-harvested trees > 10 cm DBH) by the total number of stems (living and dead > 10 cm DBH) in each plot. Trees > 10 cm were considered as no trees smaller than this were observed as being bark-harvested. Given that snags were measured in 0.2 ha plots, and living stems in 0.04 ha plots, snag and tree abundances were standardized to abundances per hectare, and the intensity of bark harvesting per plot calculated as the overall proportion of bark-harvested snags per hectare:

Bark Harvest Index = number of bark-harvested snags ha^{-1}/ (total number of living + dead stems ha^{-1})

Bark stripping in the study region is done almost exclusively for medicinal purposes due to the high, species-specific market demand for medicinal bark (Williams et al., 2013). Based on the harvested species recorded in the current study, and their previously documented high demand for medicinal use, all bark-harvested trees were assumed to be harvested for medicinal purposes.

4.3.5   Bird surveys

Bird surveys were conducted at each plot during the non-breeding season of 2017, i.e. winter in the study region. Fixed-radius point-count surveys were conducted to record all bird species seen or heard in a 30 m radius of each plot centre. Each plot was surveyed twice during the morning period (sunrise +3 hours), with repeat surveys conducted on different days and each count done over a 10-minute period (Bibby et al., 2000). Surveys were conducted in alternating sequence so as to ensure that repeat surveys at each plot were done at different times within the three-hour morning period. Bird surveys were consistently conducted by JM on dry, still days. Observations at each plot were pooled, thereby

determining species richness as the cumulative number of species recorded per plot, based on presence/absence data recorded. Thus, bird count data recorded were transformed to species incidence per plot to minimize detection bias among species (Murray et al., 2017). Any birds seen or heard which could not be confidently identified were unrecorded. Given that the focus of the study was on habitat-scale use by the forest bird assembly, birds observed flying above the forest canopy were not included in analyses. Furthermore, point counts are limited in their accuracy for surveying aerial feeders and raptors (Bibby et al., 2000), which were consequently excluded from analyses. Thus, although the point-count method used does not provide a comprehensive assessment of the bird community present at each survey site, it does allow for a standardized method to compare diversity of the bird assemblage at the habitat-scale (Neuschulz et al., 2011), appropriate for the objectives of this study.

4.3.6   Bird diversity indices

Bird species diversity was measured using species richness (SRic: the number of species, excluding aerial feeders and raptors), while functional diversity was measured using three indices: functional richness (FRic), functional evenness (FEve, Villéger et al., 2008) and functional dispersion (FDis, Laliberté and Legendre, 2010). To calculate these indices, first species-species Gower dissimilarity matrices, calculated from a combination of continuous, ordinal and categorical traits (Gower, 1971), were developed for each forest. Traits selected were those associated with resource acquisition and use, which are expected to affect the relationship between species diversity and ecosystem functioning (Spehn et al., 2005), namely: body mass, wing length, clutch size, primary diet, foraging strategy, foraging location, nest type and migratory status (Table 4.2). Species traits were obtained from existing literature (Hockey et al., 2005). Principal coordinates analysis of the Gower matrices provided a reduced set of axes to develop a functional space for each forest from which functional diversity metrics were calculated (Mason et al., 2005; Villéger et al., 2008). FRic is the proportion of the total niche space occupied by the species in one assemblage. Its value is derived by dividing the

convex hull volume of an assemblage by the convex hull volume of the forest-wide species pool (Villéger et al., 2008). FEve quantifies the regularity of the species distribution in the convex hull volume. FRic and FEve are analogous with species richness and evenness, and are independent of one another. FDis is a measure of the dispersion of species in functional trait space, based on the average distance of individual species to the centroid of all species. FRic and FDis have no upper limits while FEve ranges from zero to one. Species and their functional traits used to calculate function diversity metrics are listed in Table S4.1. Functional diversity indices were calculated using the R package FD (Laliberté and Legendre, 2010; Laliberté et al., 2014).

Table 4.2 Traits used to calculate functional diversity indices.

Trait	Description	Range or levels
Body mass	Continuous	6.5 - 644
Wing length	Continuous	47.75 - 275.5
Clutch size	Ordinal	1 - 5
Primary diet	Categorical	Insectivore, omnivore, granivore, frugivore, nectarivore
Foraging strategy	Categorical	Arboreal probe, terrestrial probe, hawk, perch-and-swoop, glean, harvest, various
Foraging location	Categorical	Canopy, understory, ground, ground and canopy, throughout
Nest type	Categorical	Platform, built, ground, cavity
Migratory status	Categorical	Migrant, resident

4.3.7 Statistical analyses

To ensure that bird surveys had sufficiently sampled the bird community in each forest, Choa2 non-parametric species richness estimator, to compare observed species richness with expected richness values, and species accumulation curves based on Coleman's method, were use. These analyses were carried out in the R statistical environment (R Core Team, 2017) using the fossil (Vavrek, 2011) and vegan package (Oksanen et al., 2018). Further data analysis involved two steps. First, the response of bird diversity to different forest type and harvest activities was assessed. Second, the relationship between bird traits and environmental covariates (i.e. structural habitat features and harvest activities) was explored. Four bird response variables (species richness, functional richness, functional

evenness and functional dispersion) were modelled separately using generalized linear models (GLMs), with forest type and harvest covariates (pole, timber and bark harvest indices) set as explanatory variables. Additionally, the interactive effect of harvest activities was tested by including all possible combinations of two-way harvest interactions, as well as the interaction between forest type and each harvest covariate to test whether responses to main harvest effects differed across forests. Forest type was a categorical variable, with Gomo set as the reference forest based on alphabetical order. The three-way interaction between all harvest variables, as well as the two-way interaction between timber and bark were not included, as bark and timber harvesting, and all three harvest activities were seldom recorded occurring within a single plot. To avoid issues of co-linearity between explanatory harvest variables, correlations between covariates were tested pairwise (Pearson's product moment test, $p < 0.05$ significance threshold). No significant correlations were found, indicating that explanatory variables were independent. Variance inflation factors (VIFs) were examined to assess the extent of any remaining co-linearity between the explanatory variables included in the optimal model. All variables had VIFs less than the threshold value of 5 and were thus retained (Zuur et al., 2010). Spatial autocorrelation of bird diversity metrics was also tested using Global Moran's I test in ArcGIS (ESRI v10.3, 2011), which tests for auto-correlation of the Euclidean distance of all bird diversity measures for each survey site. This revealed that bird diversity metrics were not spatially auto-correlated at the forest-scale, i.e. the response data points were independent in each forest. All models were run using the 'glm' function of the stats package in R version 3.4.3 (Pinheiro et al., 2013; R Core Development Team, 2017). AIC-based backward selection of global models containing all explanatory variables was used to determine which variables best explained variation in bird indices, using the 'stepAIC' function in the MASS package (Venables and Ripley, 2002). A Gaussian distribution was used in the case of the three functional diversity measures while a Poisson distribution was applied to model species richness. Functional diversity measures were natural log-transformed, and functional richness was modelled with a log-link function to improve model fit, as

shown by visual assessments of residual distributions (by plotting residuals versus fitted values, and versus each covariate in the model), which confirmed that model assumptions of normality and homogeneity were met in all cases (Zuur et al., 2010). Goodness-of-fit for each model was assessed using the coefficient of determination (R^2) using the rsq package (Zhang, 2018).

Changes in functional diversity can be due to shifts in species composition, and the concomitant loss or gain of functional traits (Edwards et al., 2013). RLQ analysis was thus performed to assess the relationship between environmental variables relating to structural habitat features and harvest regimes across forests, and functional traits relating to feeding ecology. The RLQ analysis uses three data matrices: a matrix with environmental variables and sampling sites (R), a matrix of presence/absence of species at each site (L), and a matrix with qualitative life history traits (Q) (Doledec et al., 1996). Traits included in the RLQ analysis were primary diet and foraging strategy as food acquisition was assumed to be one the most important factors affecting forest birds at the time of the study i.e. the non-breeding, winter period. Only bird species recorded in more than 5% of the survey sites overall were included in the RLQ analysis. Environmental covariates used in the RLQ analysis, and information regarding their values across sample forests are listed in Table S4.2, while bird species included in the RLQ and the qualitative traits assigned to them are listed in Table S4.3. Three separate ordinations of the R (harvest variables), L (species composition) and Q (species trait) tables were performed before conducting the RLQ. Principal component analysis (PCA) was used to calculate the variance in the R matrix, correspondence analysis for L, and a Hill-Smith PCA for Q. The joint structure of the three ordinations was then explored via RLQ analysis, including the calculation of the total inertia values for the R and Q data matrices. Inertia values provide an index that indicates the independence between two datasets, with high inertia indicating strong links between R and Q datasets through the L matrix. The significance of the relationship between species traits and environmental variables was tested using a permutation test with 1000 permutations (Doledec et al.,

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1996), with all analyses conducted in the R statistical environment, using the ade4 package (Dray and Dufour, 2007).

While the RLQ analysis provides a broad qualitative overview of how traits and environmental variables are associated across the forests, it does not provide specific detail on these associations. A fourth corner model was thus used to further assess how variation in environmental responses across species was mediated by their functional feeding traits. Using the 'trait.glm' function in the mvabund package (Wang et al., 2018), a single generalized linear model (GLM) with a binomial distribution and LASSO (least absolute shrinkage and selection operator) penalty was fit in which the presence/absence of all species (L) at all sites simultaneously (as the response variable) was assessed in relation to three types of explanatory variable: the environmental variables measured at each site (R), species traits (Q), and the interaction between environmental variables and functional traits (R:Q). The LASSO approach simplifies interpretation by setting model terms that do not explain any variance to zero. This method complements the exploratory ordination approach of the RLQ analysis by quantifying the nature and strength of environment-trait associations, thereby increasing interpretability, and identifying specific environmental and trait variables that are important drivers of species occurrence (Brown et al., 2014).

4.4 Results

4.4.1 Response of avian functional diversity and species richness to harvesting

Overall, 64 species were recorded across the five study forests, excluding raptors and aerial feeders (Table S4.1). At the forest-scale, 23 species were recorded at Gomo, 42 species at Mqaba, 51 species at Manubi, 44 at Ntlaboya, and 38 at Pirie. Chao2 estimator of species richness (based on incidence data) revealed that sampling accounted for an average of 90% of true species presence at sampled forests. Sample-based species richness accumulation curves, based on Coleman's method, were

asymptotic at each forest, further indicating that bird surveys conducted were sufficient to represent

the true species richness present at the forest scale (Fig. S4.1).

Table 4.3 Response of bird diversity indices to forest type and harvest intensities derived from AIC-based backward selection of generalised linear models (GLMs).

Response	Fixed effect	Estimate	SE	T value	P value	R²
Species richness						0.49
	Intercept	2.38	0.08	29.40		
	Forest: Manubi	0.63	0.10	6.53	**< 0.001**	
	Forest: Mqaba	0.46	0.10	4.58	**< 0.001**	
	Forest: Ntlaboya	0.43	0.11	3.84	**< 0.001**	
	Forest: Pirie	0.37	0.10	3.58	**< 0.001**	
Functional richness						0.32
	Intercept	0.46	0.09	5.23		
	Forest: Manubi	0.39	0.09	4.30	< 0.001	
	Forest: Mqaba	0.26	0.10	2.67	**< 0.01**	
	Forest: Ntlaboya	0.23	0.11	2.10	**< 0.05**	
	Forest: Pirie	0.36	0.10	3.61	**< 0.001**	
	Pole	-0.46	0.31	-1.50	0.14	
Functional evenness						0.36
	Intercept	-0.31	0.02	-12.56		
	Forest: Manubi	-0.08	0.03	-2.62	**< 0.01**	
	Forest: Mqaba	-0.09	0.03	-2.83	**< 0.01**	
	Forest: Ntlaboya	-0.06	0.03	-1.93	0.06	
	Forest: Pirie	-0.11	0.03	-3.54	**< 0.001**	
	Bark	1.05	0.55	-2.43	0.06	
	Timber	-0.37	0.15	1.90	**< 0.05**	
Functional dispersion						0.14
	Intercept	0.42	0.01	28.51		
	Pole	-0.35	0.14	-2.51	**< 0.05**	
	Bark	-1.80	0.77	-2.34	**< 0.05**	
	Pole*Bark	9.36	6.03	1.55	0.13	

Following AIC-based backward selection, species richness (SRic) was found to be best predicted by

forest type, while none of the harvest variables were retained in the top model (Table 4.3). Model

parameter estimates showed that SRic was significantly higher at Manubi (ß = 0.63 ± 0.10, $p < 0.01$),

Mqaba (ß = 0.46 ± 0.11, $p < 0.01$), Ntlaboya (ß = 0.43 ± 0.11, $p < 0.01$) and Pirie (ß = 0.37 ± 0.11, $p <$

0.01) compared to Gomo, as the reference forest (Fig. 4.2a).

Forest type and pole harvesting were retained in the top model predicting functional richness (FRic;

Table 4.3). FRic differed across forests, with FRic values at Manubi (ß = 0.39 ± 0.09, $p < 0.001$), Mqaba

(ß = 0.26 ± 0.10, *p* < 0.01), Ntlaboya (ß = 0.23 ± 0.11, *p* < 0.05), and Pirie (ß = 0.36 ± 0.10, *p* < 0.001) significantly higher than those in Gomo (Fig. 4.2b). FRic was negatively associated with pole harvesting, but this relationship was not significant (ß = -0.47 ± 0.31, *p* > 0.05).

Forest type, bark harvesting and timber harvesting were retained in the top model predicting functional evenness (FEve; Table 4.3). Forest type significantly affected FEve, with Manubi (ß = -0.08 ± 0.03, *p* > 0.001), Mqaba (ß = -0.09 ± 0.03, *p* > 0.001) and Pirie (ß = -0.11 ± 0.03, *p* > 0.001) having FEve values significantly lower than those recorded at Gomo, as the reference group (Fig. 4.2c). FEve was negatively associated with timber harvesting (ß = -0.37 ± 0.15, *p* < 0.05; Fig. 4.3a), while the positive relationship with bark harvesting approached significance (ß = 1.05 ± 0.55, *p* = 0.06).

Functional dispersion (FDis) was best predicted by the model retaining bark and pole harvesting, and the interaction between these variables (Table 4.3). Forest type was thus not shown to be an important driver of variation in FDis. Model results revealed a significant negative association between FDis and pole harvesting (ß = -0.35 ± 0.15, *p* < 0.05; Fig. 4.3b), and FDis and bark harvesting (ß = -1.80 ± 0.77, *p* < 0.05; Fig. 4.3c, while the interaction between pole and bark harvesting was not significant (ß = 9.36 ± 6.03, *p* > 0.05).
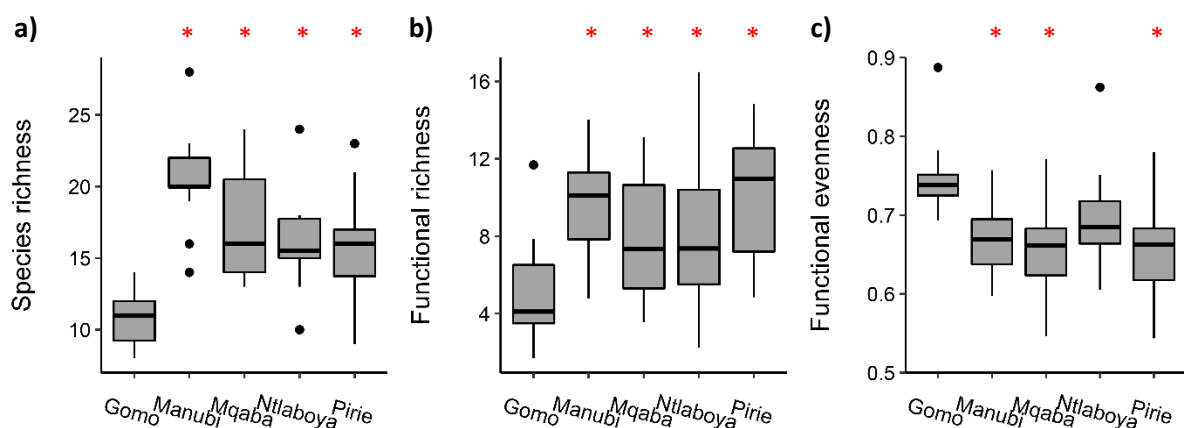
Figure 4.2 Variation in **a)** species richness, **b)** functional richness, and **c)** functional evenness across study forests. Forests with diversity measures significantly different from Gomo, as the reference category, are indicated with asterisks, as derived from generalized linear models (GLMs). Functional dispersion values did not differ significantly across forests.
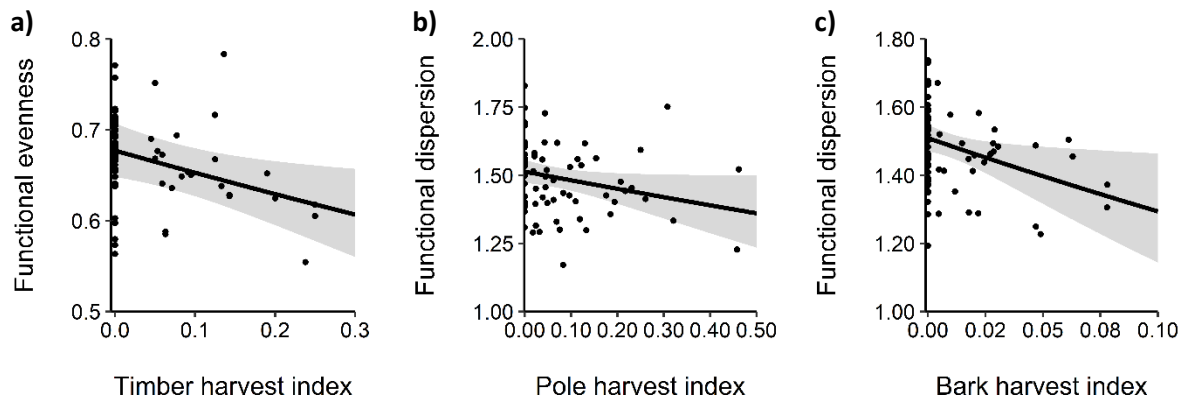
Figure 4.3 Response of **a)** functional evenness to timber harvesting, **b)** functional dispersion to pole harvesting, and **c)** functional dispersion to bark harvesting. Note that intercepts for functional evenness vary across forests, with the intercept shown being that of Manubi, as the study forest with the largest number of plots (n = 18).

4.4.2   Relating species traits to harvest disturbances

Of the 64 species recorded across the study forests, 46 were recorded in more than 5% of the survey sites and were thus included in the RLQ analysis (Table S4.3). Changes in species composition across forests with different habitat structures and harvest regimes altered the functional traits exhibited by the community, with the RLQ analysis revealing a significant association (Monte-Carlo; P = 0.002, 999 permutation) between environmental covariates and functional traits. Variation in environmental responses across bird species was thus mediated by traits relating to their feeding ecology (i.e. primary diet and foraging strategy). The first two RLQ axes were considered, and together explained 71.54 % of the variance in the analysis. This represented 83.45% and 84.81% of the correlation expressed along the first two axes of the principal component analysis of the environmental disturbances (R), 53.87% and 55.74% of the correlation expressed in the Hill-Smith component analysis of species traits (Q), and 32.10% and 27.19% of the correlation expressed in the correspondence analysis of species presence (L; Table 4.4). Given that RLQ analysis rearranges species and site scores to maximize the covariance between environmental variables (R) and species traits (Q), the L table usually accounts for less variance than the R or Q tables (Cleary et al., 2007).

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Table 4.4 Results of the RLQ analysis of correspondence and correlations between survey sites and bird species richness (L), environmental covariates (R) and the qualitative functional traits (Q) of the bird community.

	Axis 1: Eigenvalue	Axis 1: Variance explained (%)	Axis 2: Eigenvalue	Axis 2: Variance explained (%)
Individual ordination				
R (PCA)	2.49	24.92	1.85	18.54
L (CA)	0.22	11.33	0.19	10.06
Q (Hill-Smith)	1.92	17.47	1.71	15.57
RLQ combined				
RLQ	0.05	47.59	0.02	23.95
Covariance	0.22		0.15	
Projected variance: R	2.49	83.45	4.35	84.81
Projected variance: Q	1.92	53.87	3.63	55.74
Correlation: L	0.47	32.10	0.44	27.19

The RLQ analysis revealed a high degree of clustering among survey sites sampled within the same forest (Fig. 4.4a), indicating that different forests contained species with different functional feeding traits driven by variation in habitat structures and harvest regimes (Fig. 4.4). Along Axis 1, the two mistbelt forests sampled occupied non-overlapping ordination space, with Pirie occupying the left, while Gomo sites clustered towards the right of Axis 1 (Fig. 4.4a). This separation of the two mistbelt forests was driven by environmental conditions represented by Axis 1, namely, ground cover conditions and harvest disturbances (Fig. 4.4a and 4.4b). Thus, while Pirie was characterised by high bare ground cover (positively associated with canopy cover) and low harvest disturbance, Gomo was defined by dense ground layer foliage (negatively associated with canopy cover), and high levels of pole and bark harvesting. Consequently, despite both being mistbelt forest types, Gomo and Pirie contained species with a different set of functional feeding traits: understory hawkers, granivores and canopy gleaners showed a preference for undisturbed, open ground, and high canopy closure conditions present at Pirie, while omnivores and understory gleaners were more associated with densely vegetated forest floor conditions, more open canopy cover, and sites disturbed by pole and bark harvesting, representative of Gomo (Fig. 4.4). To a lesser extent, Manbui and Mqaba sites were also delineated from one another by their separate clustering along Axis 1. However, there was a small

degree of overlap between these two coastal forests (Fig. 4.4a). The clustering of Mqaba and Manubi along Axis 1 indicated that Mqaba had more open ground cover conditions, and lower levels of pole and bark harvesting relative to Manubi. Understory hawkers showed a preference for habitat conditions at Mqaba, while terrestrial probers were more strongly associated with habitat conditions present at Manubi (Fig. 4.4).

Axis 2 represented an environmental gradient delineating mistbelt forest conditions from coastal forest habitats (Fig. 4.4a). Thus, while Gomo and Pirie sites largely clustering below Axis 2, Manubi and Mqaba were largely clustered above this axis. Accordingly, mistbelt and coastal forests were largely distinct from one another based on habitat variables represented along Axis 2, i.e. tree abundance, sapling abundance, foliage density at 2 – 5 meters, leaf litter and timber harvesting. Pirie and Gomo were associated with high tree abundance (negatively correlated to mean tree diameter) and low timber harvest disturbance, conditions which were preferred by arboreal probing insectivores (Fig. 4.4). Conversely, Manubi and Mqaba had fewer, bigger trees, and high sapling abundance, mid-story foliage density (2 – 5 m), leaf litter cover and timber harvest rates, conditions associated with nectarivores and canopy hawking insectivores. Environmental conditions and the bird community at Ntlaboya represented that of an intermediate forest, positioned between the two mistbelt forests along Axis 1, and the mistbelt and coastal forests, along Axis 2. The clustering of Ntlaboya plots towards the right of Axis 1, and below Axis 2 reflects the relatively high levels of bark harvesting and low levels of timber harvesting recorded in this forest (Fig. 4.4a and 4.4b).
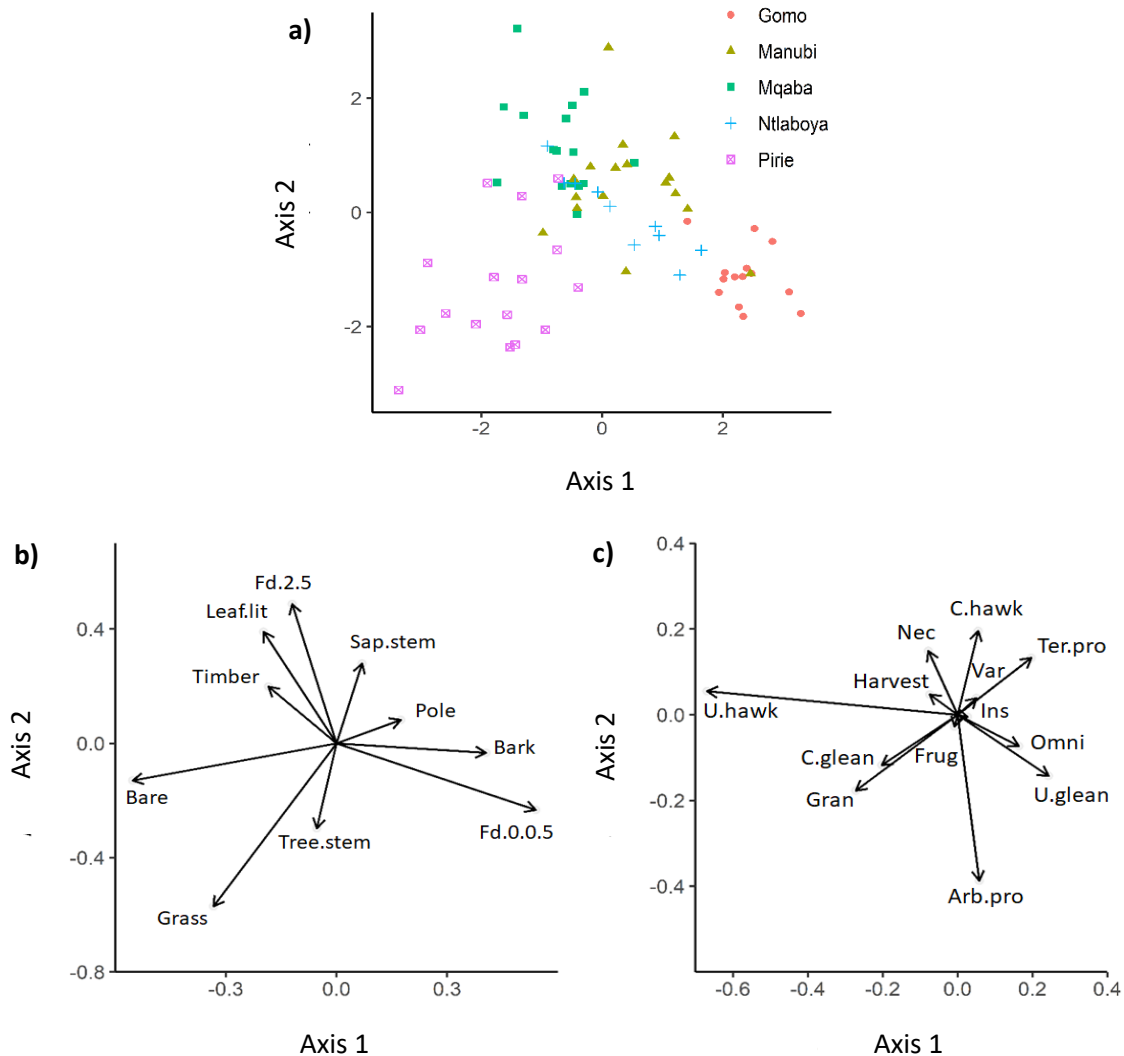
Figure 4.4 a) Row scores of sites for the first two RLQ axes. Symbols indicate sites from the different forest sampled. RLQ scores of **b)** environmental characteristics and, **c)** species feeding traits driving the clustering shown in **a)**. Abbreviations for environmental variables are: Timber = timber harvest index; Pole = pole harvest index; Bark = bark harvest index; Bare = % bare ground cover; Grass = % grass cover; Leaf.lit = % leaf litter cover; Tree.stem = no. stems > 5 cm dbh; Sap.stem = no. stems < 5 cm dbh; Fd.0.05 = foliage density at $0 - 0.5$ m; Fd.2.5 = foliage density at $2 - 5$ m. Abbreviations for species traits are: Nec = nectarivore; Frug = frugivore; Gran = granivore; Ins = insectivore; Omni = omnivore; Arb.Pro = aboreal probing; Ter.Pro = terrestrial probing; C.hawk = canopy hawking; Un.hawk = understory hawking; C.glean = canopy gleaning; Un.glean = understory gleaning; Var = various foraging strategies.

The fourth-corner analysis highlighted strong associations between traits and environmental variables, while weak associations were ignored. Findings of this analysis thus supported those of the RLQ by offering a regression-based method of assessing the strength of observed associations, aiding

in separating associations related to natural variation in habitat structure from those that were driven by harvest disturbances. With regards to direct associations between harvest covariates and functional feeding traits, the fourth corner analysis indicated that canopy gleaners and frugivores were negatively associated with pole harvesting, while a weak positive association was found with omnivores (Fig. 4.5). Nectarivores, and to a lesser extent canopy gleaners were positively associated with timber harvesting, while understory gleaners, terrestrial probers and omnivores were negatively affected by timber harvesting. A weak positive association was found between bark harvesting and omnivores, while understory hawkers and granivores were negatively associated with bark harvesting.
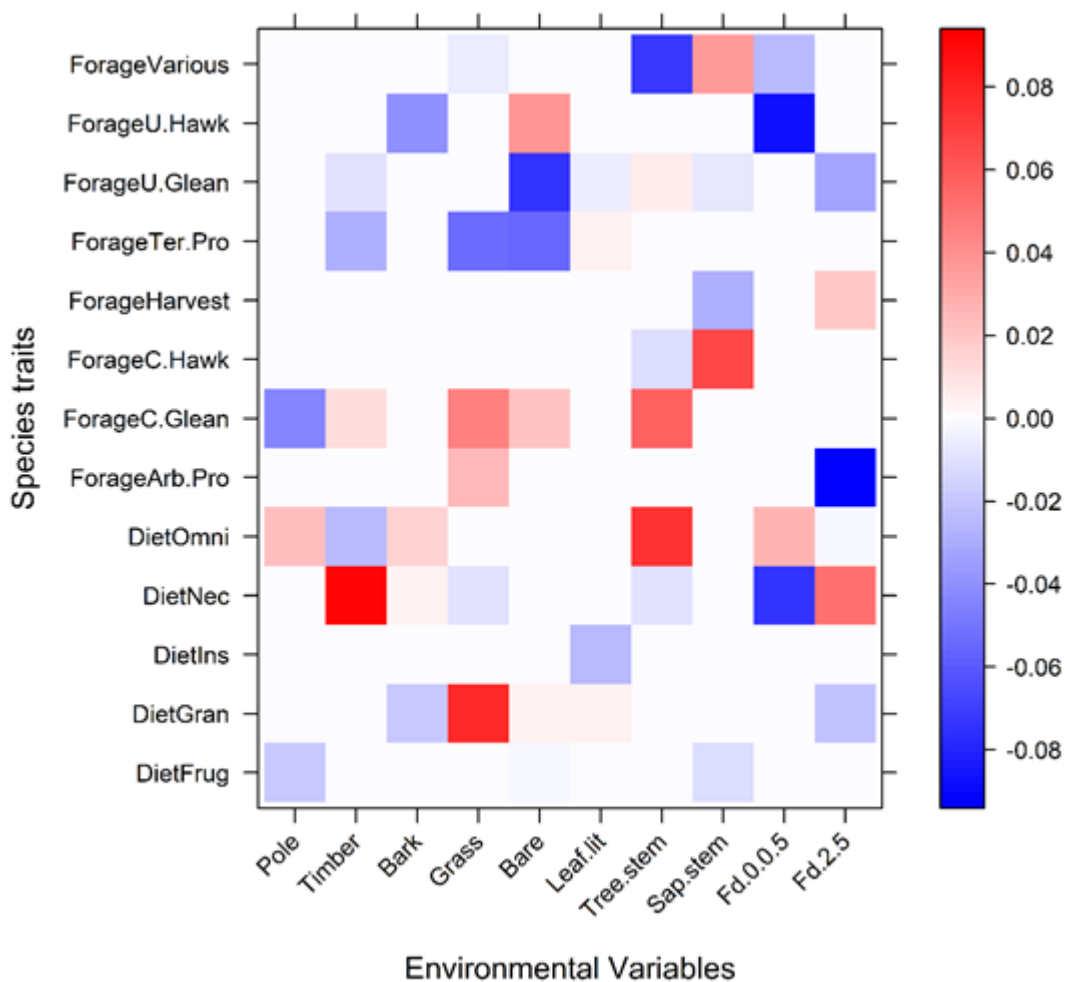
Figure 4.5 Standardized interaction coefficient estimates for interaction term from fourth corner analysis testing the relationship between bird functional feeding traits and habitat characteristics, based on species

presence/absence. Coefficients shown in red (positive) and blue (negative) improved the strength of the top model, with darker shades indicating stronger associations than lighter shades. Abbreviations for environmental variables are: Pole = pole harvest index; Timber = timber harvest index; Bark = bark harvest index; Grass = % grass cover; Bare = % bare ground cover; Leaf.lit = % leaf litter cover; Tree.stem = no. stems > 5 cm dbh; Sap.stem = no. stems < 5 cm dbh; Fd.0.05 = foliage density at $0 – 0.5$ m; Fd.2.5 = foliage density at $2 – 5$ m. Abbreviations for species traits are: DietNec = nectarivore; DietFrug = frugivore; DietGran = granivore; DietIns = insectivore; DietOmni = omnivore; ForageArb.Pro = aboreal probing; ForageTer.Pro = terrestrial probing; ForageC.hawk = canopy hawking; ForageUn.hawk = understory hawking; FprageC.glean = canopy gleaning; ForageUn.glean = understory gleaning; ForageVar = various foraging strategies.

4.5 Discussion

Results of this study show that unregulated harvesting of forest products may have a negative effect on ecosystem functioning in indigenous forests of the Eastern Cape by reducing functional diversity of avifaunal communities. Thus, in addition to the expectation that forest bird diversity would differ at the regional scale due to inherent differences in forest types sampled, this study found evidence for significant harvest disturbance effects on bird community structure. Specifically, while species richness (SRic) and functional richness (FRic) were unaffected by harvesting disturbances, different harvest activities were shown to affect aspects of functional community structure dynamically: harvesting of sub-canopy trees and medicinal bark negatively affected functional dispersion (FDis), while canopy tree removal drove a decline in functional evenness (FEve). The lack of a significant decline in FRic in response to harvest disturbances indicates that bird communities exposed to harvesting maintain a diversity of functional traits similar to that of communities in undisturbed habitats. While this is an important finding supporting the notion that resource use may be sustainably managed, observed declines in FEve and FDis indicate that harvesting disturbances affect functional processes, and thus require better management. Consistent with findings of previous studies, these results indicate that biodiversity responses to disturbance vary depending on the aspect of biodiversity considered (Ernst et al., 2006; Villéger et al., 2010; Asefa et al., 2017; Lee and Martin, 2017) and the nature and extent of disturbance (Murray et al., 2017). Specifically, results showed that

avian species' responses to disturbance were dependent on their functional traits, with different harvest activities shown to variably affect traits relating to bird feeding ecology. More feeding traits were hindered than helped by harvest disturbances, most likely mediated by associated changes in habitat structure and resource availability. These findings have important management implications as they show that different harvesting activities have variable ecological consequences and require harvest-specific management approaches.

While the focus of this study was to investigate the effect of harvesting disturbances on avifaunal community structure, findings relating to local-scale responses to disturbance should be viewed within the context of large-scale processes, as these determine the regional pool of species from which local communities are assembled (Ricklefs, 1987; Ricklefs and Schluter, 1993). At the regional scale, taxonomic and functional measures of bird diversity varied across study forests. Specifically, Gomo exhibited significantly lower species richness and FRic, and higher FEve, compared to other study forests. This finding is unsurprising when considered within the context of the large-scale historic patterns that have shaped the contemporary composition of avifaunal assemblages in South Africa (Lawes et al., 2007b). Afrotemperate forests (i.e. Gomo and Pirie) have persisted in the region since the Miocene, while Indian Ocean Coastal Belt Forests (i.e. Ntlaboya) are much younger, having become established with modern sea levels since 8000 year BP (Lawes et al., 2007b). Scarp Forests, (i.e. Mqaba and Manubi), occur between Afrotemperate and Indian Ocean Coastal Belt forests. Although of Afrotemporate origin, scarp forests were relatively unaffected by Quaternary climate changes due to their position along coastal escarpments close to the sea, which offered some protection from the repeated palaeoclimatic changes and associated multiple extinction filtration events, ending with the Last Glacial Maximum (LGM) 18000 years ago, experienced by mistbelt Afrotemperate forests. Subsequently, scarp forests, acted as refugia for forest species, from which much faunal recolonization occurred (Eeley et al., 1999; Lawes et al., 2007b). As a result,

Afrotemperate forests, despite their age, are characterised by lower species richness relative to Indian Ocean Coastal Belt and scarp forests. Furthermore, these extinction filtration events resulted in the removal of ecologically sensitive species in Afrotemperate forests, resulting in bird communities that, although comparatively species poor, are relatively robust and persistent (*sensu* Balmford, 1996). Thus, while the low taxonomic and functional richness at Gomo reflects the lower number of relatively unspecialised species supported by this forest type, the high level of functional evenness indicates that, although few in number relative to coastal forests, functional traits are relatively evenly distributed within trait space, indicative of a robust community (Mason et al., 2005). Conversely, coastal and scarp forests, which have experienced fewer extinction filtration events, are expected to have higher species richness, including species that are more ecologically specialised. This is reflected in the current study by the higher species richness and functional richness recorded at Manubi, Mqaba and Ntlaboya. Similarly, the difference in species richness recorded at Pirie and Gomo (both mistbelt forests), can be attributed to the Eastern Amathole complex, of which Pirie forms a part, serving as a persistent forest refuge (Hughes et al., 2005). The bird community at Gomo, by contrast, appears to have been predominantly shaped by extinction filtering and subsequent recolonization from scarp forest refugia.

In addition to the effect that broad-scale historic patterns have had on baseline levels of species richness and functional diversity supported by different forest types at a regional scale, we found that more recent disturbances derived from the harvesting of forest products also play a role in shaping bird communities. Specifically, findings of this study showed that local-scale environmental variables relating to habitat structure and harvest regimes resulted in different forests providing more or less favourable habitat conditions for different species dependent on functional traits relating to their feeding ecology, thereby shaping bird communities at the regional scale. These findings suggest that, while broad-scale historic patterns have largely determined the regional pool of species from which

local communities are assembled, variation in local-scale habitat conditions, including human disturbance, further shape bird species communities present within forests. Importantly, this study provides evidence that both inherent natural variation in forest structure, and variation in anthropogenic disturbances jointly affect functional traits, and thus shape bird communities at the regional scale. While previous studies have shown that variation in habitat structure is associated with changes in bird species assemblages (Sekercioglu, 2002; Watson et al., 2004; Shahabuddin and Kumar, 2006; Rocha et al., 2015) and functional trait distribution (Cleary et al., 2007; Seymour and Dean, 2009; Ehlers Smith et al., 2015; 2017), the role of forest product harvesting in shaping bird communities is largely understudied. Here, we show that different harvest activities variably affected aspects of functional community structure and functional feeding traits, respectively. These findings indicated the nuanced effect of anthropogenic disturbances on forest biodiversity, and the importance of considering disturbance-specific responses. To our knowledge, no previous studies have investigated the effects of the harvesting of sub-canopy trees and medicinal bark on bird functional diversity. While previous studies have investigated the effects of logging on functional diversity, most have focussed on the effects of large-scale logging operations (Murray et al., 2017), or have been conducted in the tropics (Cleary et al., 2007; Edwards et al., 2013), with few studies investigating the effect of unregulated, selective harvesting of canopy trees on functional diversity in temperate forests. Findings of this study thus present novel insights into the role of different harvesting activities in shaping bird communities in a temperate biodiversity hotspot, and the mechanisms that may drive this.

4.5.1 Bark harvesting

The harvesting of medicinal bark from canopy trees in indigenous forests of South Africa has received relatively wide-spread attention given its increasingly unsustainable nature which has resulted in population declines in several forest tree species (Williams et al., 2013). Despite this, no previous studies have assessed how harvest-mediated increases in tree mortality, and thus snag abundance (i.e. standing dead trees), affect bird community structure. We showed that as the number bark-

harvested snags increased, the dispersion of functional traits within the bird community declined, i.e. the average distance of species from the centroid of all species decreased, such that less niche space was occupied by the species in the local community, and functional dissimilarity was reduced. Consequently, bark harvesting resulted in higher resource competition and a lower degree of niche differentiation within the local bird community. Specifically, high tree mortality due to bark harvesting was shown to negatively affect understory hawking insectivores and granivores, while omnivores were positively affected. The understory hawking guild consisted of three species of flycatcher: *Melaenornis pammelaina* (Southern Black Flycatcher), *Trochocercus cyanomelas* (Blue-mantled Crested Flycatcher) and *Muscicapa adusta* (African Dusky Flycatcher). The loss of canopy cover due to bark harvesting, and resultant changes to microhabitat conditions such as increased light availability, heat and water stress on the forest floor, may result in reduced invertebrate prey availability (Sodhi et al., 2011). Furthermore, given that the study was conducted in winter, a drier period in the study region associated with lower invertebrate abundance, the loss of canopy cover may have compounded this resource scarcity by reducing moisture retention capacity.

The mechanism driving the negative effect of bark harvesting on granivores - three species of seed-eaters; *Crithagra scotops* (Forest Canary), *Mandingoa nitidula* (Green Twinspot) and *Aplopelia larvata* (Lemon Dove) - is unclear but may be linked to the positive association shown between these species and grass cover. A decline in seed-eating species in habitats with a high number of dead canopy trees may be related to the increased density of ground layer foliage associated with a reduction in canopy cover, thereby limiting the amount of grass able to colonize following disturbance, reducing seed availability. Alternatively, the dense ground layer itself may present unfavourable conditions for granivores, limiting their ability to access seeds available on the forest floor.

While it may be expected that the increased dead wood availability due to bark harvesting would positively affect avian communities by providing additional habitat for saprophytic invertebrates

(MacNally et al., 2001; Lohr et al., 2002; Rosenvald et al., 2011), and nest sites for cavity-nesting species (Du Plessis, 1995; Kilgo and Vukovich, 2014), the nature of the dead wood needs to be considered. Specifically, snags and woody debris created by bark harvesting are relatively young, potentially limiting their ability to support significant increases in invertebrate abundance. Over time as the wood softens and decays, habitats disturbed by bark harvesting may support abundant invertebrate populations, demonstrating the strong temporal affects that are likely to mediate the effects of bark harvesting on forest biodiversity. Furthermore, bark-harvested snags comprise a subset of high-demand medicinal species, such that the potential benefit of harvest-mediated snag creation to forest fauna is likely to be constrained by the susceptibility of these target tree species to provide cavities favourable to cavity-nesting species (Martin et al., 2004). However, ecological processes affecting cavity-nesting communities in indigenous forests in South Africa remain unstudied.

4.5.2 Pole harvesting

Pole harvesting, i.e. the selective removal of sub-canopy trees, also resulted in a decline in the dispersion of functional traits in a community (i.e. FDis). Based on a subset of functional traits relating to feeding ecology, forest habitats disturbed by high rates of pole harvesting were shown to negatively affect canopy gleaners and frugivorous species, while omnivorous species were positively affected by disturbance. Thus, species with specialist feeding traits and diets were negatively affected by disturbance while a more generalist, omnivorous diet was positively affected. Specifically, the canopy gleaning guild consisted of seven species, five of which were forest specialists, namely *Ploceus bicolor* (Dark-backed Weaver), *Coracina caesia* (Grey Cuckooshrike), *Chlorophoneus olivaceus* (Olive Bushshrike), *Phyllastrephus flavostriatus* (Yellow-streaked Greenbul) and *Phylloscopus ruficapilla* (Yellow-throated Woodland Warbler). Conversely, the omnivore guild consists of two generalist species i.e. *Zosterops capensis* (Cape White-eye) and *Oriolus larvatus* (Black-headed Oriole), which were shown to be positively affected by pole harvesting.

Structurally, pole harvesting resulted in the removal of multiple sub-canopy trees within a fine spatial scale, thereby reducing tree abundance. The decline in canopy-gleaning insectivores and frugivores in response to pole harvesting was thus most likely mediated by the local-scale reduction in tree abundance associated with this disturbance. This notion was supported by the strong positive association found between tree abundance and canopy gleaners in the current study. Similarly, Laiolo (2003) found that insectivorous gleaners were negatively affected by harvesting disturbance in the subalpine mixed forests of Nepal during the winter period, attributed to a decline in tree abundance. Similarly, in Afromontane forests in Ethiopia, Asefa et al. (2017) showed that abundance of canopy foraging species was negatively affected by changes to forest structure associated with harvesting disturbances. Beyond a structural reduction in tree abundance, the highly species-specific nature of harvesting has been shown to result in changes in species composition and declines in overall tree species diversity (Murali et al., 1996; Obiri et al., 2002; Kumar and Shahabuddin, 2005; Ndangalasi et al., 2007; Thapa and Chapman, 2010; Sassen and Sheil, 2013). It is thus possible that selective harvesting of sub-canopy trees, and resultant changes to species composition, leads to reduced fruit availability and canopy-dwelling invertebrates. For example, *Englerophytum natalense*, a fairly abundant, sub-canopy tree harvested for poles in the coastal forests of the Eastern Cape, produces medium-sized red fruit favoured by frugivorous birds, and is also an important larval plant for butterflies in the *Pseudacraea* family (van Wyk and van Wyk, 2010). A reduction in the abundance of species such as *E. natalense* may thus result in harvest-induced impoverishment of fruit availability and invertebrate prey base for frugivores and canopy gleaning insectivores respectively. However, it is unclear whether the decline in FDis, and particularly, canopy gleaners and frugivores in response to pole harvesting was due to a decline in resource availability, or whether this functional response resulted in under-utilisation of available resources. Further research is thus required in this regard.

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4.5.3   Timber harvesting

Timber harvesting was shown to result in a decline in functional evenness (FEve). Thus, as timber harvesting intensity increased, while the number of functional traits was unaffected (FRic), the relative abundance of species with different functional traits became less even. The decline in FEve in response to timber harvesting observed by the current study is similar to the finding of Edwards et al. (2013), who showed that FEve was significantly lower in the bird community present in logged forests relative to primary tropical forest of Borneo. This decline in FEve suggests that timber harvesting affects functional processes given that certain areas of niche space are either over- or under-utilized, thereby reducing ecosystem productivity and resilience (Mason et al., 2005), and affecting the strength of species interactions (Hillebrand et al., 2008).

Based on a subset of functional traits relating to feeding ecology, the current study found that timber harvesting disturbance positively affected nectarivores and canopy gleaners, while terrestrial probers and understory gleaning insectivores were negatively affected. Habitats disturbed by timber harvesting were thus favourable for species that feed on nectar, or forage by gleaning in the canopy, but were unfavourable for species that forage on the forest floor or understory, thereby reducing the regularity of trait abundance within the bird community. This decrease in the evenness of functional trait distribution reflects the findings of previous studies based on taxonomic bird responses to timber harvesting, which have reported increased levels of species dominance following logging (Thiollay, 1992; Wunderle et al., 2006). Previous studies have reported a similar change in species assemblage in response to small-scale canopy gaps and selective timber harvesting, characterised by increases in nectarivores (Levey, 1988; Wunderle et al., 2006; Cleary et al., 2007), and declines in ground-feeders and understory insectivores (Thiollay, 1992; 1997; Cleary et al., 2007; Gray et al., 2007; Arcilla et al., 2015; Hamer et al., 2015). Given that timber harvesting results in opening of the forest canopy, observed changes in bird community structure are likely attributed to habitat modifications associated with canopy-gap conditions. Specifically, the increase in nectarivores is attributed to post-harvest

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resource blooms of flowers of canopy trees and pioneer colonizers that exploit disturbed habitats, commonly associated with canopy gaps (Levey, 1988; Wunderle et al., 2006; Cleary et al., 2007). On the other hand, changes in microhabitat conditions following the removal of canopy cover, such as increased light levels, understory foliage density, heat and water stress may hinder species that forage on the forest floor or understory (Thiollay, 1992; 1997; Arcilla et al., 2015), due to associated declines in invertebrate food availability in the understory (Sodhi et al., 2011). Moreover, the majority of the terrestrial probing species recorded by the current study were forest specialists, i.e. *Cercotrichas signata* (Brown Scrub-robin), *Cossypha dichroa* (Chorister Robin-chat), *Aplopelia larvata* (Lemon Dove), *Zoothera guttata* (Spotted Ground Thrush), and *Zoothera gurneyi* (Orange Ground Thrush), and thus adapted to forage in closed-canopy conditions. Conversely, the positive association between canopy gleaners and timber harvesting may be attributed to increased accessibility and/or visibility in the canopy under gap conditions, thereby allowing canopy gleaners to detect prey more easily in areas affected by timber harvesting (Barbaro et al., 2014).

Interestingly, Barbaro et al. (2014) found that FEve was positively associated with the rate of avian insectivory in temperate forests of New Zealand and France, regardless of other measures of functional diversity. Observed declines in understory and terrestrial probing insectivores, comprising 11 species, may not be compensated for by the increase in canopy gleaning insectivores, comprising seven species, suggesting that timber harvesting may negatively affect the rate of avian insectivory. Ecologically, the loss of FEVe in response to timber harvesting is of great significance as it has been suggested that FEve is a more meaningful measure of ecosystem functioning than other functional diversity metrics (Gagic et al., 2015). This corroborates the predictions that ecosystem processes are above all predicted to be influenced by the evenness of abundance in species or trait distribution, independent of species richness or functional richness (Petchey and Gaston, 2002). Moreover, several studies have shown FEve to be the key mechanism driving efficient resource use by predatory birds

(Hillebrand et al., 2008; Crowder et al., 2010; Barbaro et al., 2014). Thus, declining FEve in the bird community in response to timber harvesting indicates that overall resource use efficiency may be reduced, and ecosystem functioning impaired by this harvest disturbance.

4.5.4 Conclusion

Understanding the response of biodiversity to human-mediated disturbance is a key theme in ecological studies given the increasing prevalence and magnitude of anthropogenic activities globally. Such studies have been guided by the recognition that effective conservation measures rely on understanding the mechanisms driving human-mediated impacts on biodiversity. Our study aimed to assess the response of bird species richness and functional diversity to forest product harvesting, thereby contributing to our understanding of one of the most prevalent human disturbances in indigenous forests in South Africa today. While several studies have assessed the response of bird diversity to categorical levels of disturbance, this study is the first to assess the impact of forest product harvesting on indigenous forest ecosystems by investigating the response of bird functional diversity to specific harvest activities measured on a continuous scale. Findings of this study support the notion that use of species richness alone, as a measure of diversity, provides an incomplete signal of ecosystem response to disturbance (Mouillot et al., 2013; Gagic et al., 2015) given that species responses to disturbance are mediated by their functional traits (Cleary et al., 2007; Clavel et al., 2011; Newbold et al., 2013). Understanding the response of functional diversity to forest product harvesting is thus required to guide management practises aimed at balancing ecosystem functioning with the needs of people. Furthermore, the variable response of bird diversity to the three primary harvest activities recorded in the study region indicated that harvest disturbances were not equal in their impact on diversity, demonstrating the importance of considering disturbance-specific effects and management strategies. These results emphasise the importance of a multifaceted framework, which includes functional traits, when assessing the impact of disturbance on biodiversity (Bellwood et al., 2006; Villéger et al., 2010).

4.6 Appendices

Table S4.1 Bird species and functional traits used to calculate functional diversity measures at each forest. Raptors and birds recorded above the canopy were excluded. Crosses in columns indicate the species included in analyses of functional diversity response to harvesting at each forest: Gom = Gomo; Man = Manubi; Mqa = Mqaba; Ntl = Ntlaboya; Pir. = Pirie.

Common name	Latin name	Mass	Wing	Clutch	Diet	Foraging strategy	Nesting strategy	Foraging strata	Migratory status	Gom.	Man.	Mqa.	Ntl.	Pir.
Thick-billed weaver	*Amblyospiza albifrons*	56	92.3	3	Frugivore	Harvest	Ball/cup	Canopy	Migrant				x	
Sombre greenbul	*Andropadus importunus*	31	90.4	2	Frugivore	Harvest	Ball/cup	Canopy	Resident	x	x	x	x	x
Yellow-breasted apalis	*Apalis flavida*	8	49.9	3	Insectivore	Glean	Ball/cup	Canopy	Resident		x	x	x	x
Bar-throated apalis	*Apalis thoracica*	10.5	54.1	3	Insectivore	Glean	Ball/cup	Understory	Resident	x	x	x	x	x
Narina trogon	*Apaloderma narina*	67	132	3	Insectivore	Perch and swoop	Cavity	Canopy	Resident		x		x	x
Lemon dove	*Aplopelia larvata*	150.1	150.6	2	Granivore	Terrestrial probe	Platform	Ground	Resident	x	x	x		x
Cape batis	*Batis capensis*	12	61.1	2	Insectivore	Glean	Ball/cup	Understory	Resident	x	x	x	x	x
Trumpeter hornbill	*Bycanistes bucanitor*	644	275.5	3	Frugivore	Harvest	Cavity	Canopy	Resident		x	x	x	
Green-backed camaroptera	*Camaroptera brachyura*	11	52.8	3	Insectivore	Glean	Ball/cup	Understory	Resident	x	x	x	x	x
Black cuckooshrike	*Campephaga flava*	32	104	2	Insectivore	Glean	Ball/cup	Canopy	Migrant				X	X
Golden-tailed woodpecker	*Campethera abingoni*	70	118	3	Insectivore	Arboreal probe	Cavity	Canopy	Resident	x		x		
Knysna woodpecker	*Campethera notata*	62	106	3	Insectivore	Arboreal probe	Cavity	Canopy	Resident		x		x	x

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Table S4.1 (Cont.) Bird species and functional traits used to calculate functional diversity measures at each forest. Raptors and birds recorded above the canopy were excluded. Crosses in columns indicate the species included in analyses of functional diversity response to harvesting at each forest: Gom = Gomo; Man = Manubi; Mqa = Mqaba; Ntl = Ntlaboya; Pir. = Pirie.

Common name	Latin name	Mass	Wing	Clutch	Diet	Foraging strategy	Nesting strategy	Foraging strata	Migratory status	Gom.	Man.	Mqa.	Ntl.	Pir.
Brown scrub robin	*Cercotrichas signata*	38	83.9	3	Insectivore	Terrestrial probe	Cavity	Ground	Resident		x	x	x	x
Olive bushshrike	*Chlorophoneus olivaceus*	33	83.1	2	Insectivore	Glean	Ball/cup	Canopy	Resident				x	x
African emerald cuckoo	*Chrysococcyx cupreus*	35	110.3	3	Insectivore	Perch and swoop	Ball/cup	Canopy	Migrant				X	
Southern-double collared sunbird	*Cinnyris chalybeus*	8	52.4	2	Nectarivore	Harvest	Ball/cup	Throughout	Resident	x	x	x	x	x
Swee waxbill	*Coccopygia melanotis*	6.5	47.75	5	Granivore	Harvest	Ball/cup	Ground	Resident					x
Speckled mousebird	*Colius striatus*	55	92.7	3	Frugivore	Harvest	Ball/cup	Canopy	Resident				x	
Olive pigeon	*Columba arquatrix*	407	223.2	1	Frugivore	Harvest	Platform	Canopy	Resident				x	
Grey cuckooshrike	*Coracina caesia*	60	129.3	2	Insectivore	Glean	Ball/cup	Canopy	Resident	x	x	x	x	x
Chorister robin-chat	*Cossypha dichroa*	46	98	3	Insectivore	Terrestrial probe	Cavity	Ground	Migrant		x		x	x
Red-capped robin-chat	*Cossypha natalensis*	32	89.4	3	Insectivore	Terrestrial probe	Ball/cup	Ground	Migrant				x	
Yellow-fronted canary	*Crithagra mozambica*	11.7	68.7	3	Granivore	Harvest	Ball/cup	Ground	Resident		x			
Forest canary	*Crithagra scotops*	15	67.4	3	Granivore	Harvest	Ball/cup	Canopy/ Ground	Resident	x				x

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Table S4.1 (Cont.) Bird species and functional traits used to calculate functional diversity measures at each forest. Raptors and birds recorded above the canopy were excluded. Crosses in columns indicate the species included in analyses of functional diversity response to harvesting at each forest: Gom = Gomo; Man = Manubi; Mqa = Mqaba; Ntl = Ntlaboya; Pir. = Pirie.

Common name	Latin name	Mass	Wing	Clutch	Diet	Foraging strategy	Nesting strategy	Foraging strata	Migratory status	Gom.	Man.	Mqa.	Ntl.	Pir.
Olive sunbird	*Cyanomitra olivacea*	11.5	63.5	2	Nectarivore	Harvest	Ball/cup	Throughout	Resident		x	x	x	x
Grey sunbird	*Cyanomitra veroxii*	13	63.6	2	Nectarivore	Harvest	Ball/cup	Throughout	Resident		x	x	x	
Olive woodpecker	*Dendropicus griseocephalus*	45	108	4	Insectivore	Arboreal probe	Cavity	Canopy	Resident	x	x	x	x	x
Fork-tailed drongo	*Dicrurus adsimilis*	43.75	137	3	Insectivore	Hawk	Ball/cup	Canopy	Resident		x	x	x	x
Square-tailed drongo	*Dicrurus ludwigii*	30	101.1	3	Insectivore	Hawk	Ball/cup	Canopy	Resident	x	x	x	x	
Black-backed puffback	*Dryoscopus cubla*	26	80.3	3	Insectivore	Glean	Ball/cup	Canopy	Resident	x	x	x	x	x
Collared sunbird	*Hedydipna collaris*	8	50.8	2	Omnivore	Various	Ball/cup	Throughout	Resident	x	x	x	x	x
Scaly-throated honeyguide	*Indicator variegatus*	48	107.5	1	Insectivore	Hawk	Cavity	Canopy	Resident		x			x
Red-throated wryneck	*Jynx ruficollis*	52	92.5	3	Insectivore	Terrestrial probe	Cavity	Ground	Resident		x			
Southern boubou	*Laniarius ferrugineus*	59	96	3	Insectivore	Various	Ball/cup	Ground	Resident		x	x	x	x
Black-collared barbet	*Lybius torquatus*	54.1	93.3	3	Frugivore	Harvest	Cavity	Canopy	Resident		x			
Grey-headed bushshrike	*Malaconotus blanchoti*	76.9	114	3	Insectivore	Perch and swoop	Ball/cup	Throughout	Resident		X			
Green twinspot	*Mandingoa nitidula*	9.5	50	5	Granivore	Harvest	Ball/cup	Canopy/ Ground	Resident		x	x	x	

Table S4.1 (Cont.) Bird species and functional traits used to calculate functional diversity measures at each forest. Raptors and birds recorded above the canopy were excluded. Crosses in columns indicate the species included in analyses of functional diversity response to harvesting at each forest: Gom = Gomo; Man = Manubi; Mqa = Mqaba; Ntl = Ntlaboya; Pir. = Pirie.

Common name	Latin name	Mass	Wing	Clutch	Diet	Foraging strategy	Nesting strategy	Foraging strata	Migratory status	Gom.	Man.	Mqa.	Ntl.	Pir.
Southern black flycatcher	*Melaenornis pammelaina*	30	107.5	3	Insectivore	Perch and swoop	Ball/cup	Understory	Resident		x		x	
Mountain wagtail	*Motacilla clara*	20	79	2	Insectivore	Terrestrial probe	Ball/cup	Ground	Resident					x
Dusky flycatcher	*Muscicapa adusta*	11	67.7	3	Insectivore	Hawk	Ball/cup	Understory	Resident		x	x	x	x
Ashy flycatcher	*Muscicapa caerulescens*	16.5	74.8	3	Insectivore	Hawk	Ball/cup	Canopy	Resident		x	x	x	x
Black-bellied starling	*Notopholia corruscus*	50	108	3	Frugivore	Harvest	Cavity	Canopy	Migrant				x	
Black-headed oriole	*Oriolus larvatus*	65	138.2	2	Omnivore	Various	Ball/cup	Canopy	Resident	x	x	x	x	x
Southern black tit	*Parus niger*	21	82.8	4	Insectivore	Glean	Cavity	Canopy	Resident				x	
Green wood hoopoe	*Phoeniculus purpureus*	76	136.4	4	Insectivore	Arboreal probe	Cavity	Canopy	Resident		x		x	x
Yellow-streaked greenbul	*Phyllastrephus flavostriatus*	31.01	92.1	2	Insectivore	Glean	Ball/cup	Canopy	Resident				x	
Terrestrial brownbul	*Phyllastrephus terrestris*	36	82.7	2	Insectivore	Terrestrial probe	Ball/cup	Ground	Resident		x	x	x	x
Yellow-throated woodland warbler	*Phylloscopus ruficapilla*	8	53.3	3	Insectivore	Glean	Ground	Canopy	Resident	x	x	x	x	x
Dark-backed weaver	*Ploceus bicolor*	35	86.5	3	Insectivore	Glean	Ball/cup	Canopy	Resident		x	x	x	x

Table S4.1 (Cont.) Bird species and functional traits used to calculate functional diversity measures at each forest. Raptors and birds recorded above the canopy were excluded. Crosses in columns indicate the species included in analyses of functional diversity response to harvesting at each forest: Gom = Gomo; Man = Manubi; Mqa = Mqaba; Ntl = Ntlaboya; Pir. = Pirie.

Common name	Latin name	Mass	Wing	Clutch	Diet	Foraging strategy	Nesting strategy	Foraging strata	Migratory status	Gom.	Man.	Mqa.	Ntl.	Pir.
Yellow-rumped tinkerbird	*Pogoniulus bilineatus*	15	56.8	3	Frugivore	Harvest	Cavity	Canopy	Resident				x	x
Red-fronted tinkerbird	*Pogoniulus pusillus*	17	60.1	3	Frugivore	Harvest	Cavity	Canopy	Resident		x	x	x	x
White-starred robin	*Pogonocichla stellata*	21	81.9	3	Insectivore	Glean	Ground	Throughout	Migrant	x	x	x		x
Dark-capped bulbul	*Pycnonotus tricolor*	37.3	95.4	3	Frugivore	Harvest	Ball/cup	Canopy	Resident	x	x	x	x	x
Brimstone canary	*Serinus sulphuratus*	25	74	3	Granivore	Harvest	Ball/cup	Canopy/ Ground	Resident				x	
Bronze mannikin	*Spermestes cucullatus*	10	48.8	5	Granivore	Harvest	Ball/cup	Canopy/ Ground	Resident		X			
Ring-necked dove	*Streptopelia capicola*	150	161.8	2	Granivore	Terrestrial probe	Platform	Ground	Resident		x			
Red-eyed dove	*Streptopelia semitorquata*	235	189	2	Granivore	Terrestrial probe	Platform	Ground	Resident			x		x
Knysna turaco	*Tauraco corythaix*	310	185	2	Frugivore	Harvest	Platform	Canopy	Resident	x	x	x	x	x
Crowned hornbill	*Tockus alboterminatus*	225	244.5	4	Omnivore	Various	Cavity	Canopy	Resident		x			
Blue-mantled crested flycatcher	*Trochocercus cyanomelas*	10	68	2	Insectivore	Hawk	Ball/cup	Understory	Migrant		x	x	x	x
Olive thrush	*Turdus olivaceus*	79	113.7	3	Insectivore	Terrestrial probe	Ball/cup	Ground	Resident	x	x	x		
Tambourine dove	*Turtur tympanistra*	71	114.9	2	Granivore	Terrestrial probe	Platform	Ground	Resident		x			

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Table S4.1 (Cont.) Bird species and functional traits used to calculate functional diversity measures at each forest. Raptors and birds recorded above the canopy were excluded. Crosses in columns indicate the species included in analyses of functional diversity response to harvesting at each forest: Gom = Gomo; Man = Manubi; Mqa = Mqaba; Ntl = Ntlaboya; Pir. = Pirie.

Common name	Latin name	Mass	Wing	Clutch	Diet	Foraging strategy	Nesting strategy	Foraging strata	Migratory status	Gom.	Man.	Mqa.	Ntl.	Pir.
Orange ground-thrush	*Zoothera gurneyi*	68	111.5	2	Insectivore	Terrestrial probe	Ball/cup	Ground	Migrant	x				
Spotted ground thrush	*Zoothera guttata*	68	117.9	2	Insectivore	Terrestrial probe	Ball/cup	Ground	Migrant		x		x	
Cape white-eye	*Zosterops capensis*	11	62.6	3	Omnivore	Various	Ball/cup	Canopy	Resident	x	x	x	x	x

Table S4.2 Environmental variables, i.e. harvest intensities and structural habitat variables, included in the RLQ and fourth corner analysis. Mean (± SD), maximum and minimum measured at each forest are shown.

Environmental variable	Gomo	Manubi	Mqaba	Ntlaboya	Pirie
Bark harvest (% tree mortality)					
Mean (± SD)	0.02 (0.02)	0.01 (0.02)	0.00 (0.00)	0.02 (0.03)	0.00 (0.00)
Max	0.08	0.08	0.00	0.06	0.00
Min	0.00	0.00	0.00	0.00	0.00
Pole harvest (% harvested)					
Mean (± SD)	0.14 (0.14)	0.10 (0.12)	0.07 (0.06)	0.05 (0.10)	0.00 (0.00)
Max	0.46	0.46	0.19	0.32	0.00
Min	0.00	0.00	0.00	0.00	0.00
Timber harvest (% harvested)					
Mean (± SD)	0.02 (0.03)	0.07 (0.08)	0.07 (0.09)	0.02 (0.05)	0.00 (0.00)
Max	0.09	0.25	0.25	0.14	0.00
Min	0.00	0.00	0.00	0.00	0.00
Grass cover (%)					
Mean (± SD)	5.21 (3.17)	5.50 (6.94)	5.56 (5.99)	4.90 (5.49)	21.75 (12.50)
Max	14.00	23.00	21.00	19.00	50.00
Min	1.00	0.00	0.00	0.00	6.00
Bare ground cover (%)					
Mean (± SD)	0.71 (0.83)	5.06 (0.44)	6.25 (3.55)	4.30 (1.77)	10.25 (5.26)
Max	3.00	16.00	13.00	8.00	22.00
Min	0.00	1.00	0.00	2.00	1.00
Leaf litter cover (%)					
Mean (± SD)	18.68 (10.45)	32.72 (16.07)	56.88 (15.71)	19.80 (10.33)	43.88 (16.93)
Max	37.50	60.00	81.50	36.00	75.00
Min	7.25	10.50	29.75	7.25	25.00
Foliage density 0 – 0.5 m (%)					
Mean (± SD)	90.68 (6.13)	49.46 (21.39)	41.98 (15.39)	32.48 (21.28)	27.09 (13.10)
Max	98.88	93.44	64.94	69.19	46.88
Min	81.19	25.38	15.63	4.19	6.94
Foliage density 2 – 5 m (%)					
Mean (± SD)	21.31 (9.27)	26.06 (13.52)	48.03 (9.82)	27.78 (12.84)	23.99 (7.78)
Max	39.75	60.13	72.25	50.88	40.13
Min	7.50	10.25	31.25	12.13	12.13
Tree abundance (0.04 ha)					
Mean (± SD)	78.64 (18.13)	50.72 (13.68)	72.94 (12.04)	41.20 (12.58)	77.94 (15.15)
Max	108.00	86.00	91.00	59.00	98.00
Min	46.00	32.00	53.00	19.00	47.00
Sapling abundance (0.01 ha)					
Mean (± SD)	32.86 (15.71)	74.89 (27.54)	49.44 (21.79)	18.90 (8.27)	26.56 (10.51)
Max	69.00	120.00	105.00	35.00	40.00
Min	15.00	25.00	24.00	8.00	6.00

Table S4.3 Bird species and their feeding traits included in the RLQ and fourth corner analysis, with species occurrence at each forest indicated. Gom = Gomo; Man = Manubi; Mqa = Mqaba, and Ntl = Ntlaboya.

Latin name	Common name	Diet	Forage	Gom	Man	Mqa	Ntl	Pirie
Andropadus importunus	Sombre greenbul	Frugivore	Harvest	x	x	x	x	x
Apalis flavida	Yellow-breasted apalis	Insectivore	Canopy glean		x	x	x	x
Apalis thoracica	Bar-throated apalis	Insectivore	Understory glean	x	x	x	x	x
Apaloderma narina	Narina trogon	Insectivore	Canopy hawk		x		x	x
Aplopelia larvata	Lemon dove	Granivore	Terrestrial probe	x	x	x		x
Batis capensis	Cape batis	Insectivore	Understory glean	x	x	x	x	x
Bycanistes bucanitor	Trumpeter hornbill	Frugivore	Harvest		x	x	x	
Camaroptera brachyura	Green-backed camaroptera	Insectivore	Arboreal prober	x	x	x	x	x
Campethera abingoni	Golden-tailed woodpecker	Insectivore	Arboreal prober	x		x		
Campethera notata	Knysna woodpecker	Insectivore	Arboreal prober		x		x	x
Cercotrichas signata	Brown scrub robin	Insectivore	Terrestrial probe		x	x	x	x
Chlorophoneus olivaceus	Olive bushshrike	Insectivore	Canopy glean			x	x	
Cinnyris chalybeus	Southern-double collared sunbird	Nectarivore	Harvest	x	x	x	x	x
Coracina caesia	Grey cuckooshrike	Insectivore	Canopy glean	x	x	x	x	x
Cossypha dichroa	Chorister robin-chat	Insectivore	Terrestrial probe		x		x	x
Cossypha natalensis	Red-capped robin-chat	Insectivore	Terrestrial probe				x	
Crithagra scotops	Forest canary	Granivore	Harvest	x				x
Cyanomitra olivacea	Olive sunbird	Nectarivore	Harvest		x	x	x	x
Cyanomitra veroxii	Grey sunbird	Nectarivore	Harvest		x	x	x	
Dendropicus griseocephalus	Olive woodpecker	Insectivore	Arboreal prober	x	x	x	x	x
Dicrurus adsimilis	Fork-tailed drongo	Insectivore	Canopy hawk		x	x	x	x
Dicrurus ludwigii	Square-tailed drongo	Insectivore	Canopy hawk	x	x	x	x	
Dryoscopus cubla	Black-backed puffback	Insectivore	Canopy glean	x	x	x	x	x
Hedydipna collaris	Collared sunbird	Nectarivore	Various	x	x	x	x	x
Indicator variegatus	Scaly-throated honeyguide	Insectivore	Canopy hawk		x			x

Table S4.3 (Cont.) Bird species and their feeding traits included in the RLQ and fourth corner analysis, with species occurrence at each forest indicated. Gom = Gomo; Man = Manubi; Mqa = Mqaba, and Ntl = Ntlaboya.

Latin name	Common name	Diet	Forage	Gom	Man	Mqa	Ntl	Pirie
Laniarius ferrugineus	Southern boubou	Insectivore	Various		x	x	x	x
Mandingoa nitidula	Green twinspot	Granivore	Harvest		x	x	x	
Melaenornis pammelaina	Southern black flycatcher	Insectivore	Understory hawk		x		x	
Muscicapa adusta	Dusky flycatcher	Insectivore	Understory hawk		x	x	x	x
Muscicapa caerulescens	Ashy flycatcher	Insectivore	Understory hawk		x	x	x	x
Oriolus larvatus	Black-headed oriole	Omnivore	Various	x	x	x	x	x
Phoeniculus purpureus	Green wood hoopoe	Insectivore	Arboreal probe		x		x	x
Phyllastrephus flavostriatus	Yellow-streaked greenbul	Insectivore	Canopy glean			x		
Phyllastrephus terrestris	Terrestrial brownbul	Insectivore	Terrestrial probe		x	x	x	x
Phylloscopus ruficapilla	Yellow-throated woodland warbler	Insectivore	Canopy glean	x	x	x	x	x
Ploceus bicolor	Dark-backed weaver	Insectivore	Canopy glean		x	x	x	x
Pogoniulus bilineatus	Yellow-rumped tinkerbird	Frugivore	Harvest			x	x	
Pogoniulus pusillus	Red-fronted tinkerbird	Frugivore	Harvest		x	x	x	x
Pogonocichla stellata	White-starred robin	Insectivore	Understory glean	x	x	x		x
Pycnonotus tricolor	Dark-capped bulbul	Frugivore	Harvest	x	x	x	x	x
Tauraco corythaix	Knysna turaco	Frugivore	Harvest	x	x	x	x	x
Trochocercus cyanomelas	Blue-mantled crested flycatcher	Insectivore	Canopy hawk		x	x	x	x
Turdus olivaceus	Olive thrush	Insectivore	Terrestrial probe	x	x	x		
Zoothera gurneyi	Orange ground-thrush	Insectivore	Terrestrial probe	x				
Zoothera guttata	Spotted ground thrush	Insectivore	Terrestrial probe		x		x	
Zosterops capensis	Cape white-eye	Omnivore	Various	x	x	x	x	x
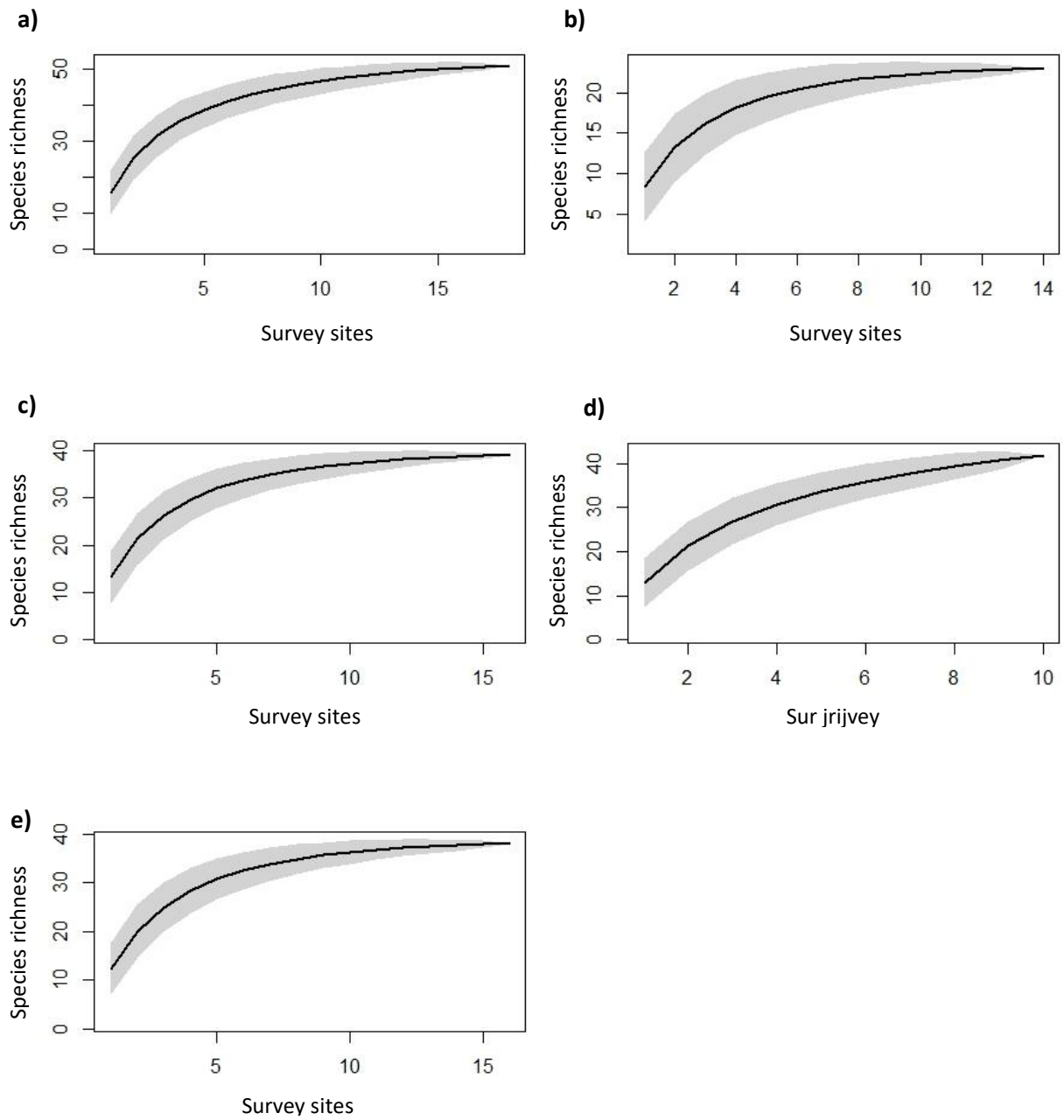
Figure S4.1 Sample-based species accumulation curves based on Coleman's method from **a)** Gomo, **b)** Manubi, **c)** Mqaba, **d)** Ntlaboya and, **e)** Pirie,. Values shown are based on accumulating species across plots sampled, with 95 % confidence intervals shown in grey.

CHAPTER V: HARVESTING OF FOREST PRODUCTS AND IMPLICATIONS FOR AFROTEMPERATE BIRD COMMUNITIES IN A MONTANE FOREST OF THE EASTERN CAPE, SOUTH AFRICA

Jessica Leaver, Johann C. Carstens and Michael I. Cherry

5.1 Abstract

Harvesting of forest products is a widespread driver of disturbance in developing nations, where policies are increasingly aimed at managing natural forests for sustainable use. There is thus need for research aimed at understanding the impact of resource use on forest habitats and concomitant effects on biodiversity. Afromontane forests in the Eastern Cape, South Africa are harvested informally for poles and medicinal bark and occur along elevational gradients of 800 – 1600 m above sea level. Patterns of spatial diversity and human disturbance are expected to be affected by elevation. Furthermore, species' responses to disturbance are expected to vary depending on their level of habitat specialisation. Understanding harvest impacts on forest biodiversity thus requires disentangling the separate effects of elevation and disturbance, and considering forest-specialist and forest-generalist species separately. This study comprises two components. First, harvest activities, resultant harvest-mediated habitat heterogeneity, and avifaunal species richness, composition and beta-diversity were compared across two elevational zones in a harvested forest. Second, the role of harvest-mediated habitat heterogeneity in driving patterns of avifaunal diversity were assessed, while controlling for elevation, and considering forest-specialist and forest-generalist species separately. Harvest intensities were higher, and activities more varied in the lower elevation zone, with significant impacts of harvesting on habitat features resulting in higher harvest-mediated habitat heterogeneity at lower elevations. Harvest-mediated increases in habitat heterogeneity positively affected forest-generalist species richness, while forest-specialist richness was negatively affected. While species composition of both groups differed across elevational zones, variation in harvest-mediated habitat heterogeneity did not fully account for this, suggesting that factors other than disturbance shape avifaunal communities along the elevation gradient. However, variation in harvest-mediated habitat heterogeneity accounted for the amount of beta-diversity attributed to species turnover in the forest-specialist assemblage, indicating that harvest disturbances affect the mechanisms driving beta-diversity of this group. Spatial patterns of avifaunal diversity are affected by elevation over a 300

metre gradient. Harvesting results in increased habitat heterogeneity, which variably affects avifaunal communities at the forest-scale, with positive effects for forest generalists and negative effects for forest-specialists.

Keywords: human disturbance; habitat heterogeneity; habitat modification; beta-diversity; elevation; generalist species; forest-specialist species

5.2 Introduction

Human disturbances and their impact on forest habitats are threatening biodiversity (Bradshaw et al., 2009; Newbold et al., 2014). In developing regions, harvesting of forest products represents the most widespread human disturbance in natural forests (Vermeulen, 1996; Luoga et al., 2000a; von Maltitz et al., 2003; Kumar and Shahabuddin, 2005; Lawes et al., 2007a). While forest management policies in many developing nations aim to balance the socio-economic benefits of resource use with the conservation of forest biodiversity (Shackleton et al,. 2002; Robertson and Lawes, 2005), regulation of resource use is often limited, such that *de facto* open-access systems prevail (Thapa and Weber, 1995; Pandit and Thapa, 2004; Robertson and Lawes, 2005; Sunderlin et al., 2005). Several studies have investigated the ecological implications of unregulated forest resource use, revealing significant impacts on forest habitats, from population-level declines of target species (Guedje et al., 2007; Williams et al., 2013) to community-level changes in floristics and structure (Kumar and Shahabuddin, 2005; Sassen and Sheil, 2013). While these studies show that resource use is a major driver of habitat modification, our understanding of concomitant effects on faunal biodiversity is limited (Laiolo, 2003; Shahabuddin and Kumar, 2006; 2007; Gardner et al., 2016; Asefa et al., 2017). Birds are particularly good indicators of environmental change (Gregory and Strien, 2010), as well as being essential for the function and regeneration of forest ecosystems (Pimm, 1986; Sekercioglu, 2006).

Understanding the impact of habitat modification on forest avifaunal communities is challenging given its dynamic nature, and thus requires the consideration of multiple factors. First, avifaunal responses

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depend on the nature and intensity of habitat change, specifically regarding implications for habitat heterogeneity (Stirnemann et al., 2014; Murray et al., 2017; Schulze et al., 2019). For example, disturbances that maintain or enhance habitat heterogeneity may maintain or increase avifaunal abundance and diversity by providing a diversity of resources and niches (Seymour and Dean, 2010; Murray et al., 2017; Schulze et al., 2019), while disturbances that reduce habitat complexity are more likely to promote biotic homogenization (Arroyo-Rodríguez et al., 2013; Morante-Filho et al., 2016). Second, responses to habitat change may differ across species based largely on their level of habitat specialisation, with habitat specialists thought to be more sensitive to disturbance than generalists (Devictor et al., 2008b; Clavel et al., 2011). The loss of disturbance-sensitive specialist species in response to habitat change may be compensated for by an increase in disturbance-adapted generalist species, thereby masking community-level responses to disturbance (Supp and Ernst, 2014). Furthermore, given that habitat specialists are generally less wide-spread than other species, they are of greater conservation concern. Third, levels of human-mediated habitat disturbance are often correlated with environmental gradients along which forest environments occur, such as elevation, given that more accessible areas, i.e. at lower elevations, are more likely to be disturbed (Montaño-Centellas and Garitano-Zavala, 2015). Avifaunal responses to human disturbances may thus be confounded by correlated changes in elevation, given that avian species richness and composition change along elevational gradients due to associated natural changes in habitat conditions (Jankowski et al., 2009; 2013; Montaño-Centellas and Garitano-Zavala, 2015). Despite the prevalent interaction of elevation and disturbance gradients in forests, few studies have aimed to separate their respective effects on bird communities (Montaño-Centellas and Garitano-Zavala, 2015). Last, variation in species composition across locations (i.e. beta-diversity) is an important determinant of the number of species that can accumulate at greater scales, and thus a vital component of understanding biodiversity responses to disturbance (Arroyo-Rodríguez et al., 2013). However studies assessing human impacts on avifaunal diversity often overlook the impact that habitat disturbances may have on beta-diversity

(Morante-Filho et al., 2015). Understanding the impact that habitat disturbances may have on the mechanisms that drive variation in species composition, namely species loss and species turnover is important because this informs what conservation actions are necessary (Baselga, 2010; 2012).

The Eastern Cape, South Africa harbours 46% of the country's remaining natural forest cover, and falls within the Maputaland-Pondoland-Albany biodiversity hotspot (Berliner, 2009). Thus, while rich in biodiversity, the region is economically one of South Africa's poorest and least developed provinces, with high levels of unemployment and rural poverty (Statistics South Africa, 2018). In this economically impoverished context, forest resources comprise a critical contribution to livelihood strategies for communities close to forests (Shackleton and Shackleton, 2004; Stadler, 2012). Poorer households in particular may have a high dependence on forest resources for fuelwood, building and fencing material, medicine, food, and increasingly, income earning opportunities through the commercialisation of certain forest products (Paumgarten and Shackleton, 2009; 2011; Stadler, 2012), particularly medicinal plants (Dold and Cocks, 2002; Williams et al., 2013). While the National Forest Act (1998) recognises the socio-economic importance of forest resources, and aims to manage natural forests sustainably, the Department of Environment, Forestry, and Fisheries , which manages 70% of South Africa's natural forests, exercises little regulation of resource use (Obiri and Lawes, 2002). In the context of increasing commercialisation of medicinal plants, there is increasing concern that unregulated resource use in South Africa's natural forests is degrading forest habitats (Hoppe-Speer et al., 2015) and compromising forest biodiversity (Castley and Kerley, 1996; Krüger and Lawes, 1997; Leaver et al., 2019).

In this study, we examine forest disturbance due to resource use, impacts on habitat structure, and concomitant effects on avifaunal communities in Gomo, a representative Afromontane forest occurring along an elevational gradient in the Eastern Cape, South Africa. Specifically, this study comprises of two major components: first, we compare harvest disturbances, resultant harvest-

mediated habitat heterogeneity, and avifaunal species richness, composition and beta-diversity across two elevational zones within the forest. Second, we test for associations between harvest-mediated habitat heterogeneity and avifaunal species richness and beta-diversity (and the mechanisms driving this i.e. species turnover and species loss), while controlling for elevation, to assess whether human-mediated habitat modification influence observed patterns of spatial diversity at the forest-scale; and the mechanisms driving this.

5.3 Materials and methods

5.3.1 Study site

This study was conducted at Gomo forest (31°0'39.34"S, 29°20'44.25"E) within the Alfred Nzo district, in the northern, inland zone of the Eastern Cape Province, South Africa (Fig. 5.1). The topography of this region is mountainous, with fragmented forest patches within a grassland matrix, together with smaller stands of commercial pine plantations; and scattered rural settlements (von Maltitz et al., 2003). Indigenous forests in this region are classified as Transkei mistbelt forests, and occur along a fragmented band at mid-elevations (850 – 1 600 m above sea level), confined to fire refugia on south, south-eastern and south-western mountain slopes. Mean annual rainfall in the region varies between 600 and 1200 mm, with rainfall occurring predominantly in the summer, between October and March. Heavy mists also occur during these months, contributing to the moist summer conditions in the region. Temperatures are mild, with mean annual temperatures ranging from 14 to 18°C, although temperatures during the winter months can drop to 2°C, and occasional winter snowfall occurs.

Socio-economically, this district falls entirely within the former homeland of the Transkei, and remains characterised by a weak infrastructure and limited economic opportunities. Consequently, this district has some of the highest unemployment rates in the province (43.5%), with close to 40% of households having monthly incomes below the poverty line, i.e. less than R800 (~$56.00) per month (Statistics South Africa, 2018). Subsequently, Transkei mistbelt forests represent the inland forest type under the highest resource use pressure in the Eastern Cape (Berliner, 2009).

Gomo encompasses a ~500 ha patch of indigenous Transkei mistbelt forest, and represents one of the more limited, larger remnant patches of Transkei mistbelt forest with a larger core area and higher biodiversity value on account of being less affected by edge effects. Environmentally, Gomo is located on a south-easterly slope, with an elevation gradient ranging from 850 m – 1 500 m above sea level, typical of Transkei mistbelt forests. Furthermore, pockets of commercially managed pine plantation occur along the forest boundary or nested within the forest itself, and a gravel road intersects the length of the forest, features commonly associated with Transkei mistbelt forests (Berliner, 2009). Historically, Gomo has endured logging pre-1940, followed by subsistence harvesting in recent times, and is thus representative of the disturbance history of forests in the region. Socio-economically, a number of rural communities occur less than 3 km from its boundary, characteristic of forests in the region, and is managed by the Department of and Environmental Affairs, Forestry, Fisheries (DEFF).
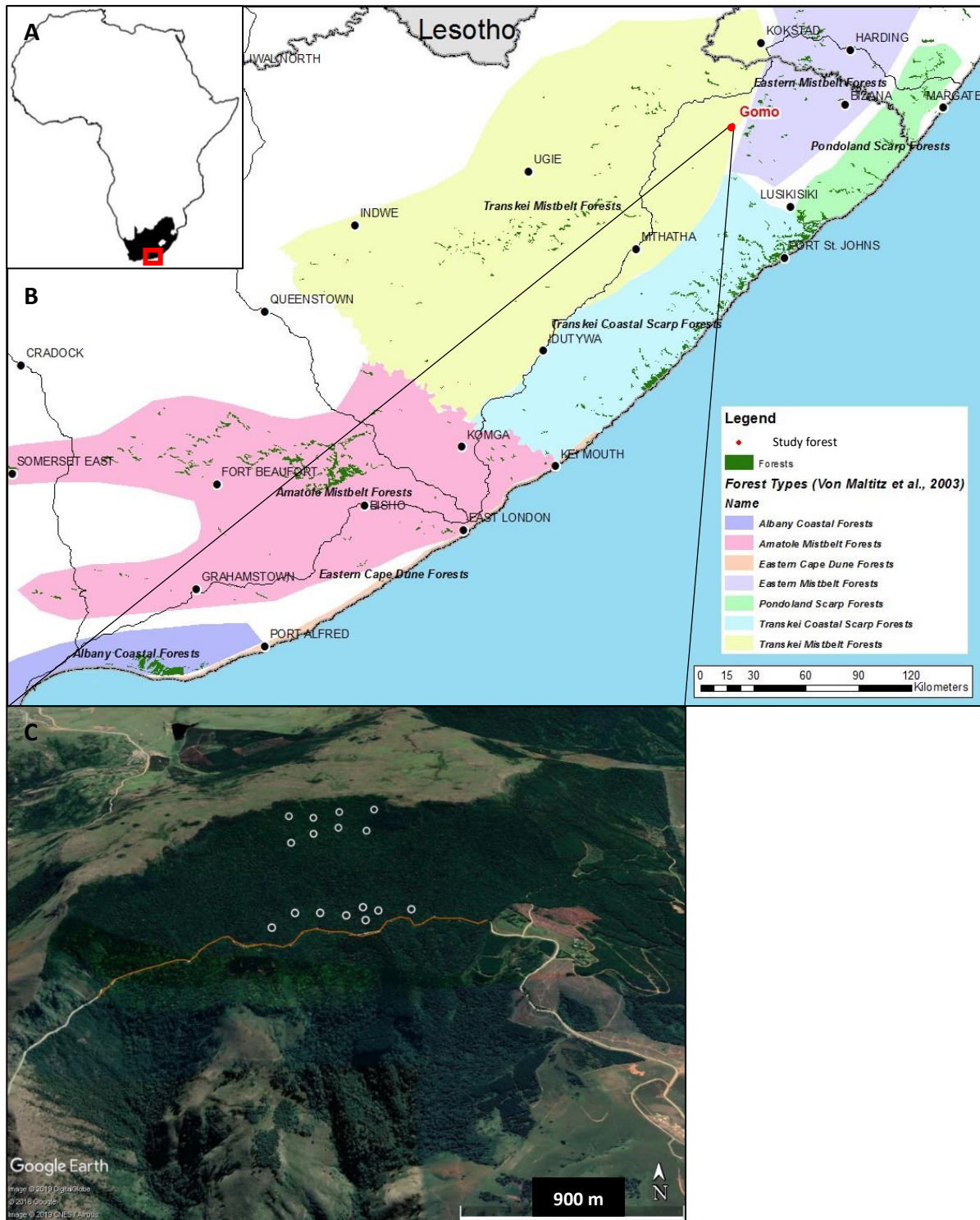
Figure 5.1 Location of **A)** the Eastern Cape Province within Africa, **B)** Gomo forest within the Eastern Cape (Map drawn by: A. Wannenburgh), and **C)** plot location (white circles) within Gomo forest, with the intersecting road shown in brown. (Map data: Google Earth).

5.3.2 Study design

To investigate the effect of forest product harvesting on the bird community at the forest-scale, 16 circular plots (0.04 ha) were sampled within two distinct elevational zones (Fig. 5.1C): eight plots were located within the mid-elevational zone of the forest, close to the road (hereafter mid-zone), and eight plots were located towards the upper forest boundary within the high-elevational zone of the forest, further from the road (hereafter high- zone). Mid-zone plots occurred at a mean elevation of 1 225 m above sea level, and were, on average 82 m away from the road, while high-zone plots had a mean elevation of 1 473 m above sea level, and were on average 770 m away from the road. A mean elevational gradient of 250 m existed between mid- and high-zone plots. Within each elevational zone, a transect perpendicular to the forest slope, and representing similar slope conditions within each zone was identified, i.e. respective transects differed in elevation, but were similar with regards to variation in slope. Plots within each elevational zone were then randomly selected within a maximum distance of 50 m either side of each transect, and a minimum distance of 100 m away from the nearest plots. Plots within the mid-zone were more widely spread along the length of the transect given the more consistent slope conditions in this zone. Within the high-zone, a shorter transect of comparable slope conditions was identified, such that plots were located within a narrower band, and placed either side of the transect (Fig. 5.1C). Within each plot, harvest disturbances, habitat structure and the bird community were recorded.

5.3.3 Data collection

5.3.3.1 Habitat variables

At each plot, habitat variables were recorded within three nested circular plots: the largest plot was 0.2 ha (radius of 25 m), within which two smaller plots of 0.04 ha (radius of 11.3 m), and 0.01 ha (radius of 5.6 m) were nested. In the 0.2 ha plot, all standing dead trees (henceforth, snags) were recorded by diameter at 1.3 m above the ground (DBH), and cause of death (i.e. natural or due to bark harvesting). In the 0.04 ha plot, the following variables were recorded: DBH of all living stems (> 5 cm

DBH), diameter of all harvested trees (henceforth stumps), percentage canopy cover, mean canopy height, percentage coverage of bare ground; leaf litter; grass cover; and herbaceous cover, and foliage density at 0 - 0.5 m; 0.5 – 1 m; 1 – 2 m; 2 – 5 m; 5 – 10 m and 10 – 20 m. Foliage density at each height class was estimated using a telescoping pole eight meters long and marked at each height interval. The pole was sequentially set-up at eight evenly spaced points 11.3 m from the plot centre (i.e. along the 0.04 ha circular plot boundary) and visual estimates of foliage density (as a percentage) at each height class were made from the plot centre. A rangefinder was used to assist with estimates of foliage density beyond the length of the telescoping pole, as well as to estimate mean canopy height at each plot. Lastly, the number of *Ocotea bullata* stems (> 5 cm DBH) was recorded in each plot as this nationally endangered tree species was shown to be under heavy resource use pressure in Gomo in a previous linked study due to its durable wood harvested for poles, and its medicinal bark which is in high market demand. In the inner-most plot of 0.01 ha (radius of 5.6 m) stem density of saplings was recorded by counting all stems with diameter 1 - 5 cm.

5.3.3.2 Bird surveys

Bird surveys were conducted at plots (n = 16) during the summer breeding season in the study region (November – December 2017). Non-fixed-radius point-counts (Blondel et al., 1981) were conducted to sample birds only within the confines of the plot. All birds calling over a 10 minute period were recorded using a Song Meter SM4 acoustic recorder attached to a tree at a height of 1.5 m near the centre of each plot. Birds seen during the 10 min period were visually identified by JL in the field, and birds recorded on the Song Meter were audibly identified thereafter through playback of recordings by JCC. Each site was surveyed three times during the morning period (sunrise +3 hours), with repeated surveys conducted on different days. Surveys were conducted in alternating sequence so as to ensure that repeat surveys at each survey site were done at different times within the three-hour morning period. Bird surveys were consistently conducted on dry, still days. Any birds which could not be confidently identified from audio recordings were not included in analyses (five percent of recorded

bird calls). Presence/absence data at each plot were pooled, thereby determining species richness as the cumulative number of species recorded within a plot. The use of presence/absence data as opposed to abundance data was used to avoid potential inaccuracies in estimating abundance from bird survey recordings. Following identification, recorded bird species were classified into two groups based on their level of forest dependency, namely, forest-specialist or forest-generalists, based on Oatley (1989) and Hockey et al. (2005) (Table S5.1). Forest-specialist species were defined as those that rely on forest resources to survive and reproduce (Oately, 1989). Conversely, the forest generalist guild included species that are not, or only partly, dependent on forest resources and thus occur in forests as well as other habitats (Oatley, 1989; Neuschulz et al., 2011).

5.3.4 Data analyses

5.3.4.1 Habitat data

Mean DBH (all stems > 5 cm DBH), stem density and basal area were calculated from tree diameters recorded within plots. Foliage density at each height class interval was calculated as the mean percent density from the eight separate estimates taken.

5.3.4.2 Comparing harvest intensities across elevational zones

A bark harvesting index was assigned to each plot based on the proportion of trees dead due to bark harvesting (i.e. bark harvested snags). This was calculated by dividing the number of bark-harvested snags (standing dead trees > 10 cm DBH) in a plot by the total number of stems (living and dead > 10 cm DBH). Given that snags were measured within the 0.2 ha plot, and trees within the 0.04 ha plot, snag and tree abundances were standardized to abundance per hectare, and the intensity of bark harvesting per plot calculated as the overall proportion of bark-harvested snags per hectare:

number of bark-harvested snags ha^{-1}/ (total number of living + dead stems ha^{-1})

A pole harvesting index was assigned to each plot based on the proportion of trees (diameter > 5 cm) harvested per plot. This was calculated based on the accumulated harvestable stems (stumps plus standing stems > 5 cm diameter) and used as an index of tree harvesting at each plot as follows:

number stumps per plot / (number stumps + number stems) per plot

Lastly, a composite harvest disturbance index (HDI) was developed to score each plot according to its overall level of harvest disturbance at the forest-scale. The two measured harvest indices (bark harvest index and pole harvest index) were relativized by their respective maximum values recorded within the forest. Relativized scores were then summed at each plot such that an overall HDI score, ranging from 0 (indicating no harvest disturbance) to a maximum potential score of 2 (indicating the most harvest disturbance), was assigned to each plot. Calculated HDI scores and harvest intensities of each forest product were not normally distributed (Shapiro-Wilks test, $p < 0.05$ significance threshold). Therefore, Wilcoxon tests were used to compare HDI scores and harvest intensities across sample forests.

5.3.4.3 Effects of harvesting on habitat structure

Harvest disturbance effects on measured structural variables were investigated using linear mixed models (LMMs). The mixed-modelling approach accounted for the nested study design, with elevational zone set as a random effect to account for plots being nested within two distinct, spatially clustered groups. Separate LMMs were used to assess the response of each measured habitat feature to harvesting, with the Harvest Disturbance Index score per plot set as the explanatory variable, with Gaussian errors, using the 'lme' function of the nlme package in R version 3.4.3 (Pinheiro et al., 2013; R Core Development Team 2017). Assumptions of normality and homogeneity were assessed using graphical outputs of models. Response variables that were measured as percentages were logit-transformed to improve the model assumption of normality. Where variance heterogeneity affected the estimation of harvesting effects, models were run with a constant variance function structure using the 'varIdent' function in the nlme package. To quantify the goodness-of-fit for each model, the MuMin package was used to evaluate marginal R^2 and conditional $R,^2$ which can be respectively interpreted as the variance explained by the fixed effects only; and by both fixed and random effects (Nakagawa and Schielzeth, 2013).

5.3.4.4 Comparing harvest-mediated habitat dissimilarity across elevational zones

Given that the range of harvest activities, in terms of both nature and extent, was expected to differ across zones due to their varying proximity to the road, it was expected that harvest activities would result in different levels of habitat dissimilarity, i.e. heterogeneity, across elevational zones. This was tested by creating a distance matrix based on scaled Euclidean distances of all habitat variables shown to be significantly affected by harvest activities (derived from the outcome of LMM analyses described above), and calculating the mean pairwise distance of plots within each elevational zone respectively. Each plot was thus assigned a habitat heterogeneity score based on its mean pairwise dissimilarity from other plots within the same zone. Mean harvest-mediated habitat heterogeneity was then compared between mid- and high-zone plots using a non-parametric Wilcoxon test.

5.3.4.5 Comparing bird species richness and beta-diversity across elevational zones

Bird analyses were conducted from a total of 15 plots. A single high-zone plot was removed from analyses as it had a very small number of observations relative to other plots, on account of the presence of loud calling insects during one of the surveys compromising the quality of the recording. Mean species richness was compared across elevational zones for the forest-specialist and forest-generalist group using t-tests and non-parametric Wilcoxon tests, based on the distribution of the data. To assess variation in taxonomic composition between elevational zones, analysis of similarity (ANOSIM) and non-metric multi-dimensional scaling (nMDS) were used, with each bird group analysed respectively. ANOSIM tested for statistically significant differences in species composition between mid-zone and high-zone plots (Sørensen's presence/absence index), while nMDS was applied as a visual aid to interpretation of how plots differed between elevational zones. These analyses were conducted using the 'vegan' package in R (Oksanen et al. 2012; R Development Core Team 2011). Measurements of change in species composition across sites (i.e. beta-diversity) were quantified by the dissimilarity in species composition using presence/absence species data, and was assessed within each elevational zone. Comparison of within-zone beta-diversity was based on the quantitative

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Sørensen's index of pairwise dissimilarity: $\beta_{Sor} = (b + c)/(2a + b + c)$, where a is the number of species common to both sites, b is the number of species that occur in the first site but not the second site, and c is the number of species that occur in the second site but not the first site. This measure incorporates change due to species loss, including nestedness of sites where one set of species is a subset of another set, and change due to replacement of one set of species by another, i.e. species turnover (Koleff et al. 2003; Baselga 2010) These processes were distinguished in this study by partitioning total beta-diversity (β_{Sor}) into contributions by turnover (Simpson's dissimilarity: β_{Sim}), and nestedness-resultant dissimilarity (β_{nes}), following Baselga (2010). β_{Sim} describes turnover without the influence of richness gradients, and β_{nes} is derived from the difference between β_{Sor} and β_{Sim}, accounting for the nestedness component of beta-diversity. Each index varies between 0 and 1, with lower values indicating a greater proportion of shared species richness, and larger values indicating greater dissimilarity between locations. Overall dissimilarity (based on Sørensen's index), and the proportion of dissimilarity attributed to turnover (based on Simpson's dissimilarity) and species loss (based on nestedness-resultant dissimilarity), were calculated between every pair of plots within each zone respectively to compare within-zone variability in species composition, and the processes driving this for each bird group separately. Beta-divesrity values were calculated based on the 'betapart' package in R (Baselga et al. 2018). Levels of species turnover and species loss were compared across elevation zones for each bird group using t-tests or a Wilcoxon rank sum test, depending on the distribution of the data.

5.3.4.6 Assessing the effect of habitat modification on bird species richness

Linear mixed models (LMMs) were used to assess the effect of harvest-mediated habitat heterogeneity on bird species richness, with elevational zone again included as a random effect to account for plots being nested within two distinct, spatially clustered groups. Species richness values for each group were included as the response variable in separate models, and harvest-mediated habitat heterogeneity scores per plot were included as the explanatory variable. Response variables

were modelled using LMMs with Gaussian errors, using the 'lme' function of the nlme package in R version 3.4.3 (Pinheiro et al., 2013; R Core Development Team, 2017). Species richness values were log-transformed to improve the model assumption of normality, and model assumptions were assessed using graphical outputs of models (Zuur et al., 2010).

### 5.3.4.7 Assessing associations between elevation and habitat modification on beta-diversity

Beta-diversity was examined with respect to difference in elevational zone and harvest-mediated habitat heterogeneity. As the distance matrices of elevational zone and harvest-mediated habitat heterogeneity were inter-correlated, two partial Mantel tests were used to test: i) whether beta-diversity was related to differences in elevational zone (i.e. mid-zone vs. high-zone), controlling for differences in harvest-mediated habitat heterogeneity; and ii) whether beta-diversity was related to differences in harvest-mediated habitat heterogeneity, controlling for elevational zone. Beta-diversity was based on i) overall Sørensen's dissimilarity values, ii) Simpson's dissimilarity (i.e. dissimilarity attributed to turnover), and iii) nestedness-resultant dissimilarity values (i.e. dissimilarity attributed to species loss or gain), whereas distance matrices for elevational zone and harvest-modified habitat structure where based on Euclidean distances, scaled in the case of the habitat variables. Separate partial Mantel Tests were run to examine correlations between environmental variation and beta-diversity in the forest-specialist guild and forest-generalist guild respectively.

5.4   Results

5.4.1 Harvest intensities across elevation zones

Harvest intensity of medicinal bark, although higher in the mid-zone, did not differ between elevational zones (mid-zone: 0.06 ± 0.04 vs. high-zone 0.03 ± 0.04, W = 18.5, p = 0.17; Fig. 5.2a). Conversely, pole harvest intensity was higher in the mid-zone, where pole harvesting was recorded in all but one plot, compared to the high-zone, where pole harvesting was recorded only in a single plot (mid-zone: 0.16 ± 0.13 vs. high-zone 0.006 ± 0.02, W = 6, p < 0.005; Fig. 5.2b). Consequently, overall
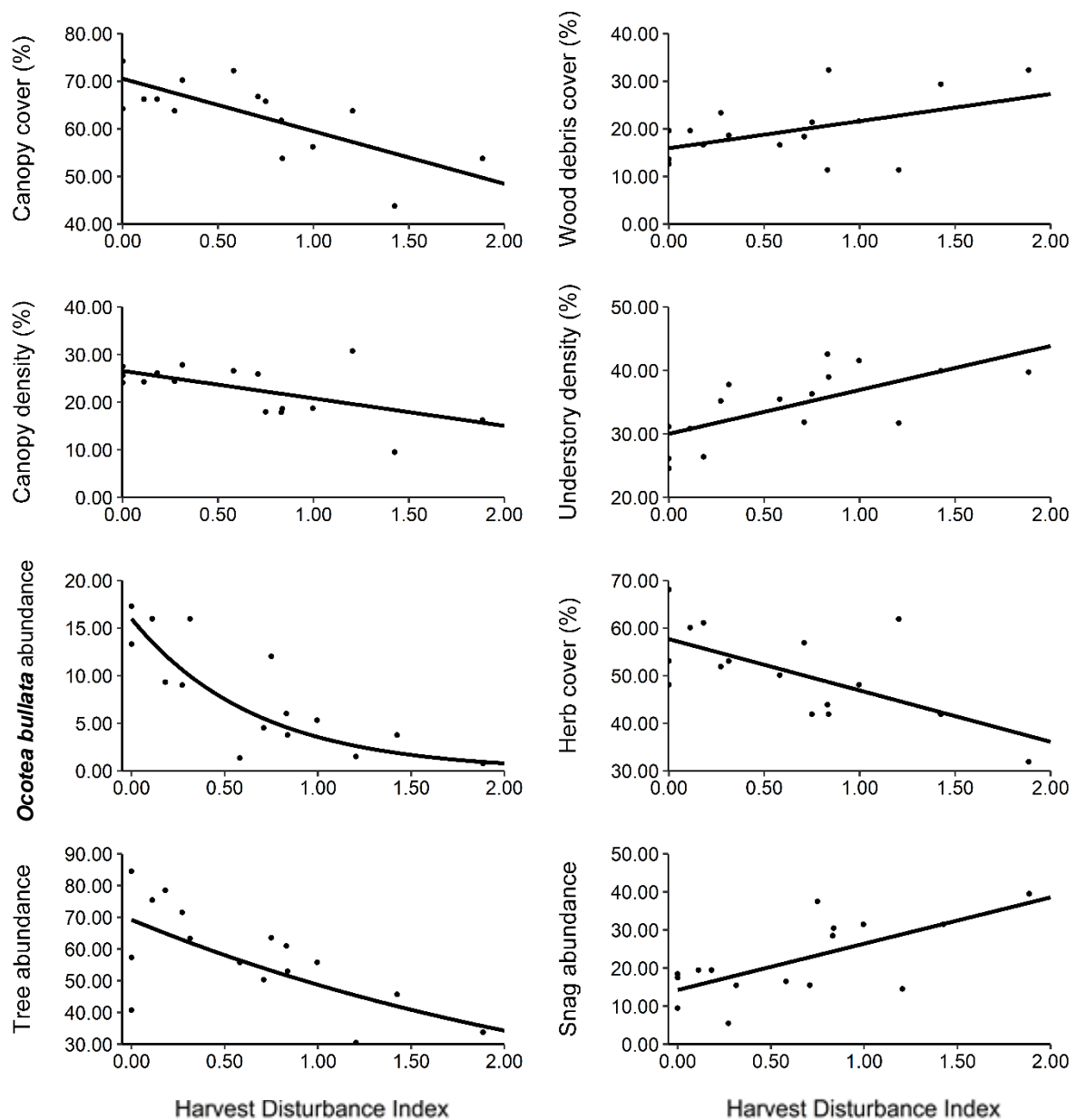
harvest disturbance index (HDI) was higher in the mid-zone compared to the high-zone (mid-zone: 0.98 ± 0.51 vs. high-zone 0.27 ± 0.35, W = 3, p < 0.005; Fig. 5.2c).
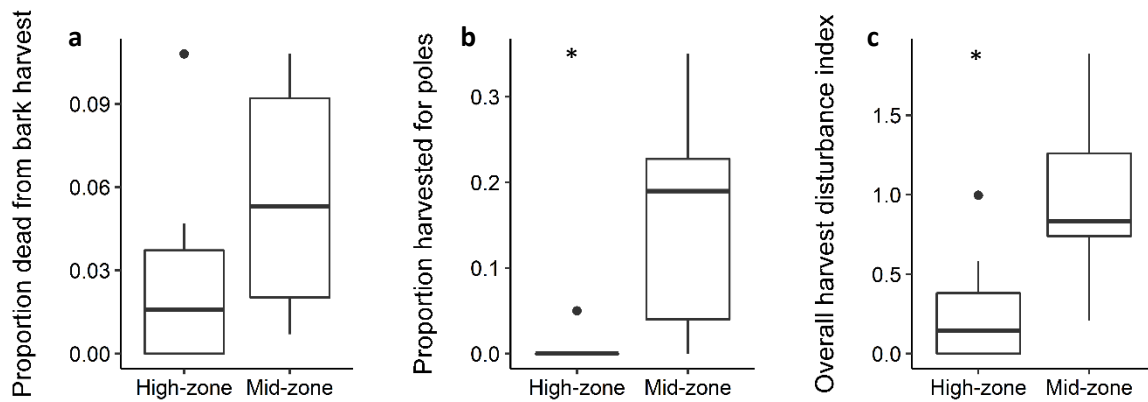
Figure 5.2 Harvest intensities compared across two elevation zones in Gomo forest indicating **a)** proportion of standing stems (dbh > 10 cm) dead due to medicinal bark harvesting, **b)** proportion of stems (dbh > 5 cm) harvested for poles, and **c)** overall harvest disturbance index, based on the combined intensity of pole and bark harvesting recorded in a plot. Asterisks indicates significant differences across zones.

5.4.2 Effects of harvesting on habitat structure

At the forest-scale, harvest disturbances based on overall harvest disturbance index scores (HDI) negatively affected canopy cover, canopy foliage density (5 – 10 m), abundance of *Ocotea bullata* stems (> 5 cm DBH), overall abundance of trees (> 5 cm DBH) and herb cover. Conversely, woody debris cover, understory foliage density (0 - 2 m) and snag abundance were positively associated with HDI (Fig. 5.3; Table S5.2).

Figure 5.3 Response of habitat variables to overall harvest disturbance index scores (i.e. combined bark and pole harvest intensity per plot). Relationships shown are significant ($p < 0.05$), derived from linear mixed models with elevation zone included as a random effect (Table S5.2).

Based on this subset of eight habitat variables significantly affected by harvest disturbances, calculated habitat dissimilarity scores per plot, i.e. harvest-mediated habitat heterogeneity, was higher in the mid-zone compared to the high-zone (mid-zone: 3.38 ± 0.41 vs. high-zone 2.25 ± 0.51, t = -4.91, p = 0.0003; Fig. 5.4).

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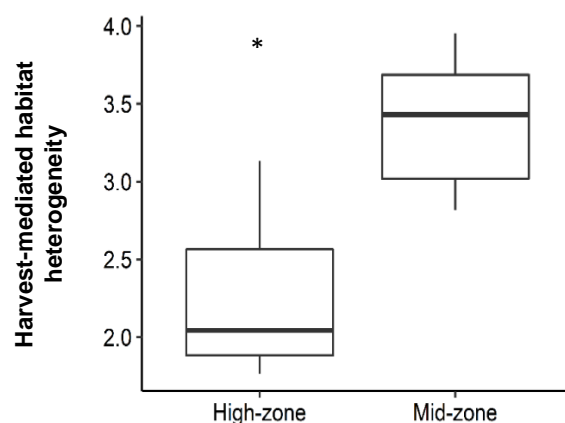
Figure 5.4 Harvest-mediated habitat heterogeneity compared across elevation zones based on dissimilarity of habitat variables affected by harvesting between plots within high- and mid- elevation zones respectively.

5.4.3 Bird species richness, occurrence and beta-diversity

Overall, 34 species were recorded during bird surveys conducted at mid- and high-zone plots (18 ± 3 species per survey site; mean ± SD, range 13 – 22; Table S5.1). Thirty-three species were recorded in the mid-zone (20 ± 2 species per survey site; mean ± SD, range 17 – 22), whereas 26 species were recorded in the high-zone (16 ± 2) species per survey site; mean ± SD, range 13– 18). Based on Chao2 estimator of true species richness, the sampling effort yielded 98% and 95% of the "true" species present in the mid- and high-zones respectively. Sample-based species accumulation curves based on Coleman's method were asymptotic for both zones, further indicating that the sampling effort was sufficient to represent true species richness present in each zone (Fig. S5.1). Mean species richness of the forest-generalist group was higher in the mid- zone, whereas forest-specialist species richness did not differ significantly across elevational zones (Table 5.1).

Table 5.1 Comparison of species richness across two elevational zones in Gomo forest. Mean ± SD species richness is shown for the forest-specialist and forest generalist assemblage in each zone.

| Bird diversity indices	Mid-zone (Mean ± SD)	High-zone (Mean ± SD)	Test statistic
Forest-specialist richness (n = 18)	9 ± 2	7 ± 2	W = 15.5 p = 0.15
Forest generalist richness (n = 16)	11 ± 1	8 ± 1	t = -4.55, df = 10.02, **p < 0.05**

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Three-quarters of the 34 recorded species were observed in both mid- and high-zones (Table S5.2), indicating forest-wide distributions of most species. Nonetheless, bird communities of both groups differed significantly across elevational zones in taxonomic composition (ANOSIM, Jaccard's presence/absence index, 9999 permutations, Forest-specialist group: Global R = 0.34, p < 0.01; Forest-generalist group: Global R = 0.57, p < 0.01). In support of this, nMDS analyses showed clustering of survey sites according to elevation, based on species presence/absence (Fig. 5.5; Fig. S5.2 and Fig. S5.3). Of the 34 species recorded, only one species, *Apalis thoracica* (Bar-throated apalis), was absent from the mid-zone, while eight species present in the mid-zone were not recorded at the high-zone, comprising four forest-specialist species: *Chrysococcyx cupreus* (African Emerald cuckoo), *Poicephalus robustus* (Cape parrot), *Apaloderma narina* (Narina trogon) and *Bycanistes bucinator* (Trumpeter hornbill); and four forest-generalist species: *Dicrurus adsimilis* (Fork-tailed drongo), *Campethera notata* (Knysna woodpecker), *Pogoniulus pusillus* (Red-fronted tinkerbird) and *Apalis flavida* (Yellow-breasted apalis) (Table S5.1). Interestingly, five of the eight species not recorded in the high-zone were cavity-nesting species (*Poicephalus robustus, Campethera notate*, *Apaloderma narina, Pogoniulus pusillus* and *Bycanistes bucinator*).

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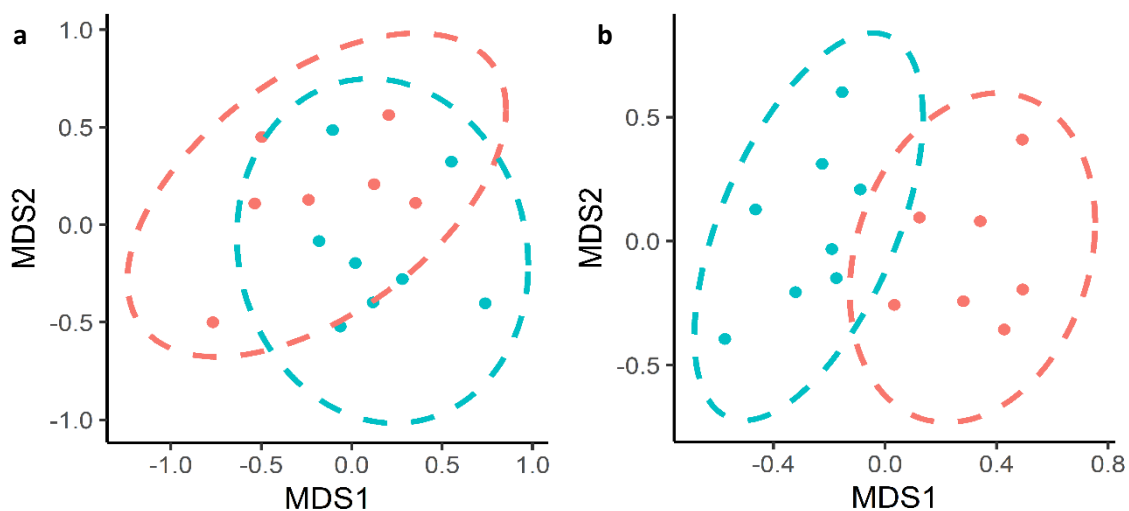
Figure 5.5 Non-metric multidimensional scaling (nMDS) representing clustering of high-zone (red) and mid-zone (blue) plots by **a)** forest-specialist species, and **b)** forest-generalist species, based on species presence/absence (Sørensen's dissimilarity, 95% ellipses) in Gomo forest.

Pairwise beta-diversity and the relative contribution of the two mechanisms driving this (i.e. species turnover and species loss) differed across groups and elevational zones (Fig. 5.6). Across both zones, beta-diversity was greater in the forest-specialist community compared to the forest-generalist community. Within the mid-zone, species turnover was the dominant driver of beta-diversity, close to four times that attributed to species loss for both forest-specialist and forest-generalist communities. In the high-zone, the relative contribution of species loss to beta-diversity increased for both groups. However, species turnover remained the dominant driver of beta-diversity in the forest-specialist community in the high-zone, while species loss became the dominant driver of beta-diversity in the forest-generalist community. Consequently, for the forest-generalist community, the amount of beta-diversity attributed to species turnover was higher in the mid-zone compared to the high-zone (W = 402.5; p = 0.03), while the relative contribution of species loss was greater in the high-zone compared to the mid-zone (W = 144; p = 0.002). Conversely, the relative contribution of species turnover (t = 1.21; df = 44.07; p = 0.23) and species loss (W= 218.5; p = 0.13) did not differ across zones for the forest-specialist group.
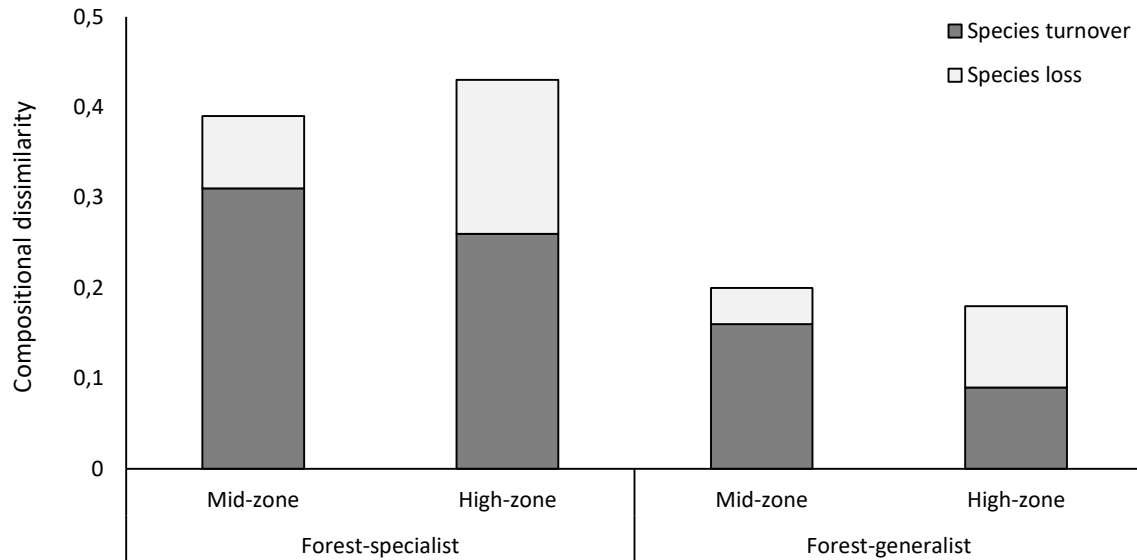
Figure 5.6 Overall pairwise beta-diversity represented as that contributed by species turnover (ß$_{sim}$: dark grey) and species loss (ß$_{nes}$: light grey) within elevational zones in Gomo across the two bird groups: forest-specialist species, and forest-generalist species. Mean dissimilarity values are shown, with higher values indicating greater dissimilarity.

5.4.4   Effect of harvest-mediated habitat heterogeneity on bird species richness

Forest-specialist species richness declined in response to harvest-mediated habitat heterogeneity (ß = -0.39 ± 0.15; p = 0.04), while forest-generalist species richness was positively associated with harvest-mediated habitat heterogeneity (ß = 0.15 ± 0.06; p = 0.03; Fig. 5.7; Table S5.3). Harvest-mediated habitat heterogeneity explained 20% and 32% of the variation in forest-specialist and generalist species richness respectively (Table S5.3).
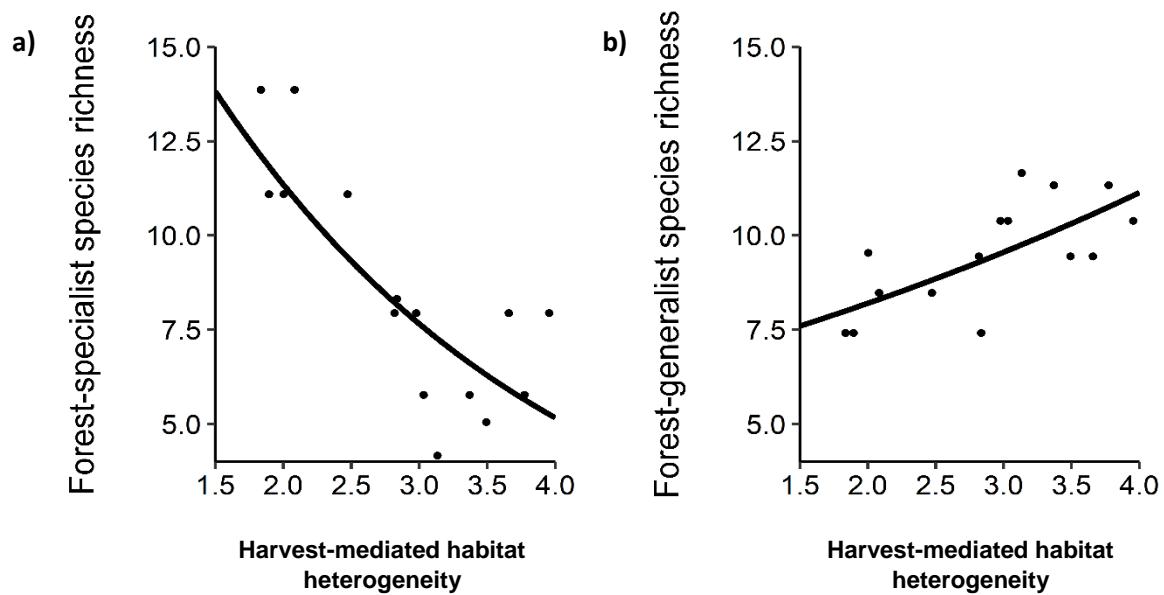
Figure 5.7 Response of **a)** forest-specialist species richness and **b)** forest-generalist species richness to harvest-mediated habitat heterogeneity, based on linear mixed models (LMMs), controlling for variation in elevation zone.

5.4.5 Role of elevational zone and harvest-mediated habitat modification in explaining differences in bird composition

Beta-diversity based on Sørensen's index was positively correlated with difference in elevational zone when controlling for harvest-mediated habitat heterogeneity in the case of both groups (Table 5.2). This indicates that there were effects of elevation on avifaunal composition in addition to those caused by variation in harvest disturbances, reflecting results of the ANOSIM and nMDS plots (Figure 5). Beta-diversity attributed to species turnover (Simpson's dissimilarity index) was not correlated with difference in elevational zone for both groups, while beta-diversity attributed to species loss (i.e. nestedness-resultant index) was positively correlated with elevational zone in the forest-generalist group when controlling for harvest-mediated habitat heterogeneity, i.e. there were effects of elevation on patterns of generalist species loss in addition to those caused by harvest disturbances. There was a postive correlation between Sørensen's dissimilarity and harvest-mediated habitat heterogeneity when controlling for elevational zone in the forest-generalist group, indicating that variation in harvest disturbances accounted for compositional variation in this group, but not in the

forest-specialist group. However, there was a positive correlation between beta-diversity attributed to species turnover and harvest-mediated habitat heterogeneity in the forest-specialist group when controlling for elevation, indicating that variation in harvest disturbances accounted for the amount of beta-diversity attributed to species turnover in this group (Table 5.2).

Table 5.2 Partial mantel correlations testing i) the association between avifaunal beta-diversity and difference in elevational zone, while controlling for harvest-mediated habitat heterogeneity, and ii) the association between avifaunal beta-diversity and harvest-mediated habitat heterogeneity, while controlling for difference in elevation for plots sampled in Gomo forest, using presence/absence bird data to derive indices of dissimilarity: Sørensen's index, Simpson's index and Nestedness-resultant index. Values in bold, with asterisks indicate significant correlations.

	i) Does dissimilarity in avifaunal composition correspond to dissimilarity in elevation zone, controlling for difference in habitat heterogeneity?			ii) Does dissimilarity in avifaunal composition correspond to dissimilarity in habitat heterogeneity, controlling for difference in elevational zone?		
	Sørensen's index ($ß_{sor}$)	Simpson's index ($ß_{sim}$)	Nestedness -resultant index ($ß_{nes}$)	Sørensen's index ($ß_{sor}$)	Simpson's index ($ß_{sim}$)	Nestedness -resultant index ($ß_{nes}$)
Forest-specialist guild	**0.19***	0.07	0.10	0.13	**0.23***	-0.15
Forest-generalist guild	**0.30****	-0.002	**0.37****	**0.27***	0.16	0.09

* $P < 0.05$; ** $P < 0.01$

5.5 Discussion

Habitat modification caused by the harvesting of poles and medicinal bark variably affected forest-generalist and -specialist avifaunal communities in Gomo. Specifically, the variable nature, extent and spatial distribution of harvest activities increased habitat heterogeneity, positively affecting forest-generalist species richness, but negatively affecting forest-specialist richness (Fig. 5.7). Elevation affected spatial patterns of harvest disturbances and avifaunal diversity in Gomo, despite the relatively small gradient (< 300 m) investigated: harvest intensities were higher, and harvest activities more varied at lower elevations, associated with proximity to the intersecting forest road resulting in greater harvest-mediated habitat heterogeneity; and avifaunal species richness, community composition and the mechanisms driving beta-diversity differed across elevational zones. By

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controlling for elevation, we show that harvest-mediated habitat heterogeneity was positively associated with overall beta-diversity of the forest-generalist community, and the amount of beta-diversity attributed to species turnover in the forest-specialist community (Table 5.2). By controlling for variation in harvest-mediated habitat heterogeneity, we show that natural variation associated with changes in elevation also affected patterns of overall beta-diversity in forest-generalist and – specialist communities. Similarly, beta-diversity attributed to species loss in the forest-generalist community was positively correlated with changes in elevation. Thus, while overall beta-diversity of the forest-generalist group was affected by elevation and habitat modification, mechanisms driving generalist beta-diversity (i.e. species loss) were affected by elevation. On the other hand, overall beta-diversity of the forest-specialist group was affected by elevation only, while the mechanisms driving specialist beta-diversity (i.e. species turnover) were affected by harvest disturbances. Importantly, these findings show that avifaunal communities in Gomo are shaped by natural environmental gradients associated with changes in elevation and human-mediated disturbance gradients associated with harvesting activities, with responses dependent on species' level of habitat specialisation.

5.5.1 Species richness

This study demonstrates that forest-scale habitat heterogeneity is an important predictor of avian species richness, but that the direction of response is dependent on species' level of habitat specialisation. Specifically, the positive response of forest-generalist species to human-meditated habitat heterogeneity reflects the well-established finding that ecological generalists are more likely to benefit from unstable, heterogeneous environments, and thus habitat modification, given their ability to exploit a wide range of habitat conditions (McKinney and Lockwood, 1999). Similarly, the decline in forest-specialist species richness in response to harvest-mediated habitat heterogeneity shown in this study can be explained by niche theory which predicts that habitat specialists should benefit from more stable, homogenous environments, and thus be negatively affected by human-mediated habitat modification (Soh et al., 2006; Devictor et al., 2008a; Clavel et al., 2011). The habitat

heterogeneity hypothesis (MacArthur and MacArthur, 1961) stipulates that resources and niches increase with spatial heterogeneity (Pianka, 1972; Bazzaz, 1975), which should in turn facilitate the co-occurrence of species (Jeltsch et al., 1999; Palmer, 2003) and provide habitat for species with multiple resource requirements (Perkins et al., 2000), thereby increasing species richness (Terborgh, 1977). In the current study, this applies to forest-generalists but not to specialist species. Similarly, Stirnemann et al. (2014), showed that increases in habitat heterogeneity did not always result in increased avifaunal species richness in a temperate forest in Australia, and that species' responses to habitat heterogeneity depended on their ecology. Stirnemann et al. (2014) explains this in terms of increases in niches or resources through increased heterogeneity leading to increased competition for resources among species, resulting in species turnover rather than opportunities for additional species to establish. This may explain our finding that harvest-mediated habitat heterogeneity was positively correlated with species turnover in the forest-specialist group, but not the forest-generalist group: it may provide increased opportunities for forest-generalist species, thereby increasing species richness, but result in increased competition between forest-specialist species, driving increased species turnover, and an overall loss of species richness.

It is also important to consider that increased heterogeneity does not always result in increased niches or resources becoming available (Stirnemann et al., 2014). In the current study, we measured how variable plots within elevation zones were from one another based on a number of harvest-modified variables relating to the amount of cover of different habitat features; and the number of living trees; dead trees; and *Ocotea bullata* stems. This measure thus combined aspects of spatial habitat heterogeneity and cover, which reflect different needs for birds: cover may relate to amounts of resources while heterogeneity relates to the spatial arrangement of those resources. The combination of these factors may influence whether heterogeneity results in increased species richness: Stirnemann et al. (2014) showed that species richness increased where both cover and spatial

heterogeneity were high, but declined where heterogeneity was high but cover was low. Given that the measure of habitat heterogeneity used in the current study combined spatial heterogeneity and cover, it was not possible to investigate how these factors separately affected patterns of species richness. However, while harvest activities did increase spatial habitat heterogeneity across plots, they were also shown to decrease canopy cover, canopy foliage density and herb cover. This may offer an alternative explanation for the respective responses to harvest-mediated habitat heterogeneity by forest-generalist and –specialist species, in that forest-specialists may be unable to benefit from increases in spatial heterogeneity when cover of certain habitat features, such as the canopy and herb layer, have been reduced in the process; while habitat-generalists may be more resilient to open-canopy conditions and thus better able to take advantage of spatial habitat heterogeneity.

5.5.2 Species composition and beta-diversity

While species richness is an important measure to assess community-level responses to disturbance, it provides little information on concomitant changes in species composition. Thus, in addition to species richness, this study assessed beta-diversity and the mechanisms driving this across elevational zones for each avifaunal group separately. Specifically, findings of this study provide insight into the separate effects of harvest-mediated habitat heterogeneity and elevation on patterns of avifaunal community composition at the forest-scale respectively, and how this varied across forest-generalist and forest-specialist species.

Species composition of the forest-generalist and forest-specialist group differed across elevational zones (Fig. 5.5; Fig. S5.2 and S5.3). However, the effect of elevation on bird species composition was not fully accounted for by accompanying variation in harvest-mediated habitat heterogeneity (Table 5.2). Thus, despite the relatively small elevational gradient assessed (< 300 m), variation in environmental conditions other than disturbance, such as moisture availability, soil characteristics and floristic composition, likely affected patterns of beta-diversity across the elevational gradient in Gomo.

For example, tree species richness and composition were observed to change across elevational zones, with tree species richness declining with increasing elevation (personal observation). Changes in avifaunal composition across elevational zones may thus be associated with changes in tree species richness, as shown by Jankowski et al. (2013) along an Andean elevational gradient.

While elevation was an important driver of overall forest-scale beta-diversity of forest-specialist and –generalist species, evidence of a particular mechanism driving this was only shown in the case of the forest-generalist community (Table 5.2). Specifically, the amount of beta-diversity attributed to species loss increased with elevation for forest-generalists in Gomo (Table 5.2). Jankowski et al. (2013) found a similar trend in the avifaunal community along an elevation gradient in the Andes. Our finding indicates that the generalist community in the high-zone was largely a subset of the species occurring in the mid-zone, supported by the lower species richness of forest-generalists recorded in the high-zone (Table 5.1). Thus, natural environmental gradients associated with elevation affected forest-scale beta-diversity of the forest-generalist through a process of species loss, with the high-zone representing an impoverished zone. Conversely, the role of elevation in driving forest-scale beta-diversity of the forest-specialist community was not clearly attributed to either species turnover or species loss when controlling for variation in harvest-mediated habitat heterogeneity. Furthermore, there was considerably higher overlap in taxonomic species composition across zones in the forest-specialist community compared to the forest-generalist community (Fig. 5.5), reflecting the stronger correlation between elevation and forest-generalist beta-diversity (0.30) compared to that observed between elevation forest-specialist beta-diversity (0.19; Table 5.2). This suggests that the forest-specialist community was less strongly influenced by natural changes along the elevation gradient at Gomo compared to the forest-generalist community. On the other hand, human-mediated disturbance gradients, namely variation in harvest-mediated habitat heterogeneity, affected the mechanisms driving beta-diversity of the forest-specialist community. Specifically, forest-specialist

species turnover was positively correlated with harvest-mediated habitat heterogeneity when controlling for elevation (Table 5.2). Similarly, Palmeirim et al. (2017) showed that the contribution of species turnover to beta-diversity of lizard and amphibian communities increased with human disturbance in the Neotropics. Thus, human-mediated habitat heterogeneity in Gomo was an important driver of forest-specialist species turnover, indicating that harvest disturbances operate as environmental filters for specialist species, but not generalists (Baselga, 2009).

Results of this study thus show that avifaunal communities in Gomo are structured by harvest disturbances and elevation, despite the relatively small gradient assessed (< 300 m). Similarly, a study conducted in the Andes showed that bird communities along far greater elevation gradients were shaped by both changes in elevation and disturbance (Montaño-Centellas and Garitano-Zavala, 2015). Furthermore, Peters et al. (2019) recently showed that variation in species richness and composition of multiple taxa along an elevational gradient of Mount Kilimanjaro was explained by the interaction of land-use intensity and climate, rather than by single drivers. Patterns of Afrotemperate biodiversity along elevational gradients in the Eastern Cape are similarly likely affected by the interaction of multiple factors. Further research is thus needed to assess the drivers of Afromontane bird communities along elevational gradients, in particular, the interactive effect of harvest disturbances and varying environmental conditions along elevational gradients.

### 5.5.3 Conclusion and conservation implications

The combined effect of harvesting medicinal bark and poles in Gomo affected avifaunal communities at the forest-scale, mediated by harvest-mediated increases in habitat heterogeneity. Specifically, while forest-generalist species richness and overall beta-diversity were positively affected by harvest-mediated increases in habitat heterogeneity, forest-specialist species richness was negatively affected, but species turnover positively affected by harvest-mediated habitat heterogeneity. These results suggest that harvest disturbances and concomitant habitat modifications provided more

niches and resources, allowing more opportunities for habitat generalist species, but not for forest-specialist species. Furthermore, harvest-mediated habitat modifications acted as environmental filters for specialist species but not generalists. Findings of this study thus indicate the importance of using different biodiversity metrics when assessing forest biodiversity responses to habitat disturbance. Specifically, the use of a single measure of species richness is cautioned against, as an increase in forest-generalist species in response to disturbance may mask the loss of forest-specialists. However, conclusions drawn from this study are to be considered with caution given that a single spatial scale was considered, thereby limiting insight into disparate patterns that may be revealed at larger scales (Hill and Hamer, 2004; Morante-Filho et al., 2016; Rocha et al., 2015). Thus, while findings show that current unregulated levels of harvesting increase habitat heterogeneity at the forest-scale, particularly in accessible areas at lower elevations and/or close to forest roads, with concomitant positive impacts on forest generalist bird communities and negative impacts on forest-specialist species, further research is needed to assess harvest impacts on forest habitats and biodiversity at broader spatial scales. Nonetheless, this study provides previously unexplored, yet important insights into the role of elevation and harvest disturbance in driving spatial patterns of avifaunal diversity in temperate forests of South Africa, specifically the different mechanisms driving beta-diversity at the forest-scale, and how these vary across the relatively small elevation gradient of this Afromontane forest. Results show that elevation has a strong effect on spatial patterns of harvesting patterns, habitat structure and avifaunal communities, despite the small elevational gradient examined.

5.6   Appendices

a)

b)
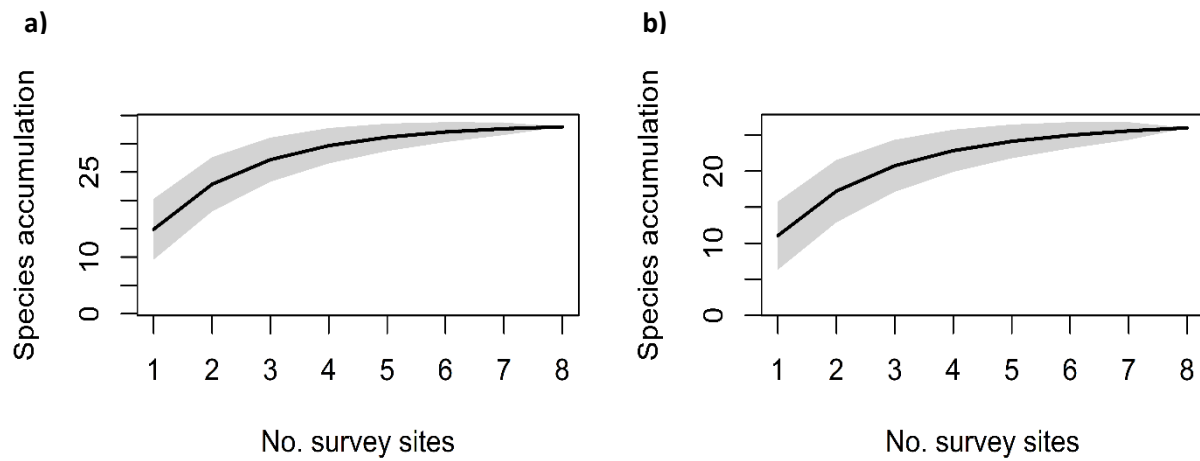
Figure S5.1 Sample-based species accumulation curves based on Coleman's method from the **a)** mid-zone, and **b)** high-zone, sampled in Gomo forest. Values shown are based on accumulating species across plots sampled, with 95 % confidence intervals in grey.
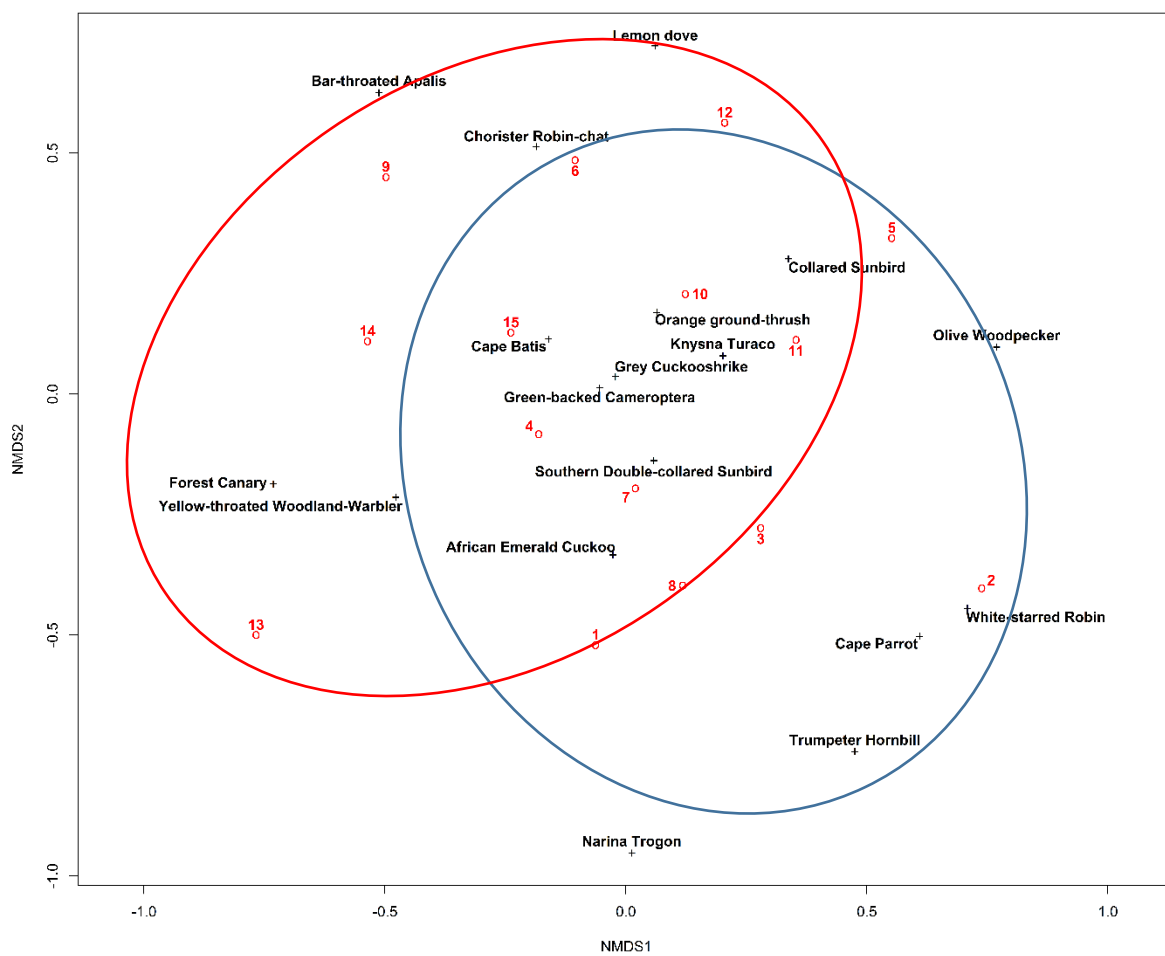
Figure S5.2 nMDS ordination of plots sampled (red) and forest-specialist species recorded (black). Plots 1-7 in the blue circle represent mid-zone plots, and 9-16 in red circle represent high-zone plots.
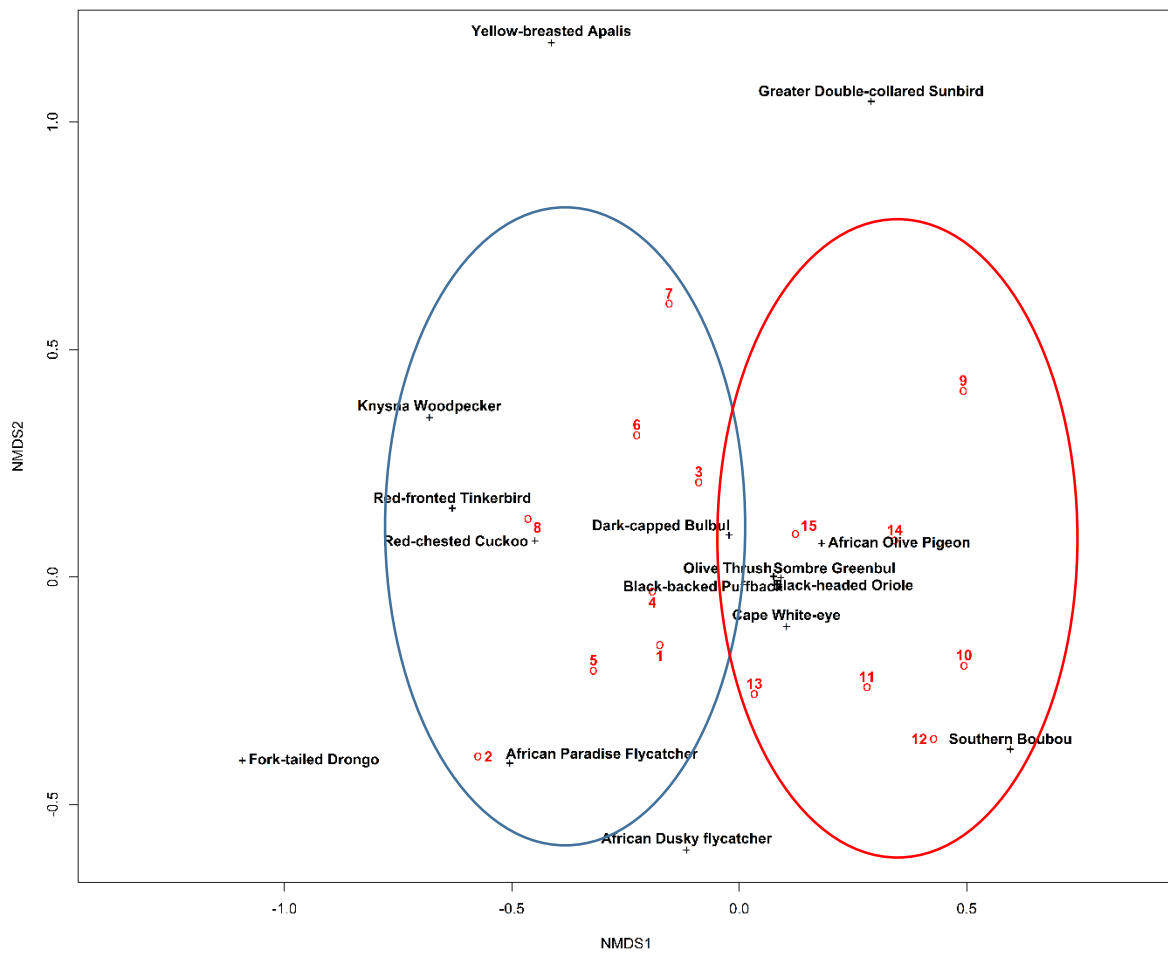
Figure S5.3 nMDS ordination of plots sampled (red) and forest-generalist species recorded (black). Plots 1-7 in the blue circle represent mid-zone plots, and 9-16 in red circle represent high-zone plots.

Table S5.1 List of species recorded at Gomo over the summer sampling period. Their ecological group is shown (FD = forest-dependent; FG = forest generalist), with crosses indicating the elevational zones in which each species was recorded.

Scientific name	Common name	Ecological group	Mid-zone	High-zone
Andropadus importunus	Sombre greenbul	FG	x	x
Apalis flavida	Yellow-breasted apalis	FG	x	
Apalis thoracica	Bar-throated apalis	FD		x
Apaloderma narina	Narina trogon	FD	x	
Aplopelia larvata	Lemon dove	FD	x	x
Batis capensis	Cape batis	FD	x	x
Bycanistes bucanitor	Trumpeter hornbill	FD	x	
Camaroptera brachyura	Green-backed cameroptera	FD	x	x
Campethera notata	Knysna woodpecker	FG	x	
Chrysococcyx cupreus	African emerald cuckoo	FD	x	
Cinnyris afer	Greater double-collared sunbird	FG	x	x
Cinnyris chalybeus	Southern double-collared sunbird	FD	x	x
Columba arquatrix	African olive pigeon	FG	x	x
Coracina caesia	Grey cuckooshrike	FD	x	x
Cossypha dichroa	Chorister robin-chat	FD	x	x
Crithagra scotops	Forest canary	FD	x	x
Cuculus solitarius	Red-chested cuckoo	FG	x	x
Dendropicus griseocephalus	Olive woodpecker	FD	x	x
Dicrurus adsimilis	Fork-tailed drongo	FG	x	
Dryoscopus cubla	Black-backed puffback	FG	x	x
Hedydipna collaris	Collared sunbird	FD	x	x
Laniarius ferrugineus	Southern boubou	FG	x	x
Muscicapa adusta	African dusky flycatcher	FG	x	x
Oriolus larvatus	Black-headed oriole	FG	x	x
Phylloscopus ruficapilla	Yellow-throated woodland-warbler	FD	x	x
Pogoniulus pusillus	Red-fronted tinkerbird	FG	x	
Pogonocichla stellata	White-starred robin	FD	x	x
Poicephalus robustus	Cape parrot	FD	x	
Pycnonotus tricolor	Dark-capped bulbul	FG	x	x
Tauraco corythaix	Knysna turaco	FD	x	x
Terpsiphone viridis	African paradise flycatcher	FG	x	x
Turdus olivaceus	Olive thrush	FG	x	x
Zoothera gurneyi	Orange ground-thrush	FD	x	x
Zosterops capensis	Cape white-eye	FG	x	x

Table S5.2 Response of structural habitat variables to harvest disturbance (HDI – human disturbance index based on relativized levels of pole and bark harvesting recorded in each plot) derived from linear mixed models. R^2m represents the amount of variation explained by the fixed effect only (i.e. DI), and R^2c represents the amount of variation explained by both the fixed effect and random effect (i.e. DI and elevational zone). All variables measured as percentages were logit-transformed.

Response variable	Fixed effect	Estimate	SE	T value	P value	R^2m	R^2c
Canopy cover (%)						0.33	0.68
	Intercept	0.89	0.23	3.92	0.00		
	DI	-0.47	0.15	-3.06	**0.009**		
Canopy density (%)						0.25	0.88
	Intercept	-1.05	0.23	-4.58	0.00		
	DI	-0.33	0.12	-2.68	**0.02**		
Understory (0-2 m) density (%)						0.13	0.83
	Intercept	-0.90	0.34	-2.67	0.00		
	DI	0.34	0.14	2.50	**0.03**		
Herb cover (%)						0.20	0.69
	Intercept	0.34	033	1.04	0.32		
	DI	-0.48	0.20	-2.44	**0.03**		
Woody debris cover (%)						0.27	0.73
	Intercept	-1.76	0.27	-6.58	0.00		
	DI	0.44	0.20	2.19	**0.04**		
O. bullata abundance						0.54	0.71
	Intercept	2.77	0.43	6.40	0.00		
	DI	-1.50	0.36	-4.20	**0.001**		
Overall tree abundance (> 5 cm)						0.11	0.91
	Intercept	75.90	27.16	2.79	0.00		
	DI	-25.48	7.81	-3.26	**0.006**		
Snag abundance (> 5 cm)						0.36	0.53
	Intercept	14.26	4.65	3.07	0.00		
	DI	12.16	4.34	2.80	**0.02**		

Table S5.3 Response of species richness to harvest-mediated habitat heterogeneity derived from linear mixed models (LMMs). R^2m represents the amount of variation explained by the fixed effect only (i.e. habitat heterogeneity), and R^2c represents the amount of variation explained by both the fixed effect and random effect (i.e. habitat heterogeneity and elevational zone). Species richness data were log-transformed.

Response variable	Fixed effect	Estimate	SE	T value	P value	R^2m	R^2c
Forest-generalist richness						0.32	0.60
	Intercept	1.80	0.20	8.96	0.00		
	Habitat heterogeneity	0.15	0.06	2.36	**0.04**		
Forest-dependent richness						0.20	0.82
	Intercept	3.22	0.56	5.74	0.00		
	Habitat heterogeneity	-0.39	0.15	-0.25	**0.03**		

CHAPTER VI: IMPACT OF INFORMAL TIMBER HARVESTING ON HABITAT STRUCTURE AND BIRD ASSEMBLAGES IN A COASTAL FORESTS OF THE EASTERN CAPE, SOUTH AFRICA

Jessica Leaver, Johann C. Carstens and Michael I. Cherry

This chapter is under review for *Bird Conservation International.*

6.1 Abstract

African forests are under increasing pressure to supply local, regional and international demand for timber. Much of this trade is unregulated, such that there is increasing concern regarding the ecological sustainability of this resource use. However, there is a lack of studies investigating the ecological impact of informal timber harvesting in Afrotemperate forests. While forest species have adapted to natural canopy gap dynamics, harvesting may alter natural disturbance regimes with adverse effects on biodiversity. Information regarding harvest gaps, and concomitant impacts on habitat and biodiversity is thus essential to inform sustainable management. This study compared the frequency and nature of harvest gaps and natural gaps in a coastal forest in the Eastern Cape, South Africa, where informal selective timber harvesting occurs. Habitat condition and avifaunal species richness and composition were compared across intact forest, natural gaps and harvest gaps. Harvest-created gaps increased the number of canopy gaps by 30%, but were comparable with natural gaps in area. Habitat conditions in harvest gaps represented an intermediate state between intact forest and natural gaps, thereby increasing forest-scale habitat heterogeneity. While avifaunal species richness was not affected, species composition differed across intact forest, harvest gaps and natural gaps, associated with changes in habitat condition. While there was considerable overlap in species across gap types and intact forest, some species showed habitat preference. Specifically, nectarivores and frugivores were more common in canopy gaps, while species that forage or nest on the ground were more abundant in intact forest. While single-tree selective harvesting currently used in the region largely emulates natural canopy disturbances, the increased frequency of canopy gaps due to harvesting may reduce the abundance of certain avifaunal species sensitive to canopy gap conditions, and reduce forest-scale beta-diversity. Better management of canopy tree extraction from this highly biodiverse forest type is urged.

Keywords: selective timber harvesting; canopy gaps; bird species composition; habitat heterogeneity; forest product harvesting

6.2 Introduction

The need to conserve forest ecosystems has been globally recognised given the high levels of biodiversity they support and the vital ecosystem services they provide (Gardner et al., 2009). In developing nations, the socio-economic value of forests is particularly important as the resources they provide comprise a critical component of livelihood strategies for millions of people (Sunderlin et al., 2005; 2008). While the value of forest resources in these nations has traditionally been realised through their domestic use, trade incomes derived through the informal commercialisation of certain forest products, such as timber, has become increasingly important (Obiri, 1997; Luoga et al., 2000b; Paumgarten and Shackleton, 2011; European Commission, 2013; Weng et al., 2014; Cerutti et al., 2018). Consequently, there is urgent need for forest management strategies in developing nations that integrate sustainable timber harvesting with the conservation of forest biodiversity, necessitating an understanding of the ecological implications of this resource use. However, while several studies have examined the ecological impact of commercial timber harvesting in tropical forests, comparatively few studies have aimed at understanding the effect of informal timber harvesting in temperate forests, particularly in subtropical Africa (LaManna and Martin, 2017).

Disturbance in forests is natural, and one of multiple important factors influencing the distribution and composition of species (von Maltitz et al., 2003; Phillips, 2004; Moore et al., 2009). The creation of small-scale openings in the canopy (i.e. canopy gaps) through windfalls, or natural tree or limb death, is a key natural disturbance in temperate forests, affecting both the dynamics and abundance of tree species (Ott and Juday, 2002; Richards and Hart, 2011; Kern et al., 2014) and forest-scale habitat heterogeneity through the creation of a shifting mosaic of habitat patches following a disturbance (Runkle 1981; Canham and Marks, 1985; Shure et al., 2006). Thus, a direct effect of canopy gap creation is the loss or modification of microhabitat used by forest organisms (Vitt et al., 1998; Fuller, 2000). However, given that canopy gap formation is an integral component of the natural disturbance-recovery regimes that drive forest dynamics, forest species have adapted to such

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disturbances (Pickett, 1980; Pickett and White, 1985; Sprugel, 1991; Laska, 2001). Consequently, a central guiding principle of sustainable forest management is that harvesting practices should aim to mimic natural disturbance processes as it is thought that this will minimise the ecological impact of human-mediated disturbances (Geldenhuys and Maliepaard, 1983; Seymour et al., 2002; Mori, 2011). It is thus important to understand how human-mediated canopy disturbances deviate from the nature and frequency of natural canopy disturbances, and consequent biodiversity responses.

Canopy gaps result in habitat conditions that are in stark contrast to those in the surrounding intact forest, shown to differ in terms of microclimate (Vitt et al., 1998; Champlin et al., 2009), primary productivity (Phillips and Shure, 1990), habitat structure (Fuller, 2000), detritus (Greenberg and Lanham, 2001) and plant species composition (Kern et al., 2014). Given the altered physical and biological characteristics associated with gaps, forest animals, such as birds, have been shown to distinguish between gap and intact habitat conditions (Blake and Hoppes, 1986; Levey, 1988; Greenberg and Lanham, 2001; Moorman and Guynn, 2001; Faccio, 2003; Fuller, 2000; Forsman et al., 2013). Specifically, studies have shown that forest gaps may attract birds in temperate (Forsman et al., 2010) and tropical forests (Blake and Hoppes, 1986; Levey, 1988; Wunderle et al., 2006), as they offer superior foraging habitat compared to intact forest, driven by increased productivity due to higher light levels in forest gaps which create greater vegetation density, structural heterogeneity, and food availability. Bird responses to canopy gaps are however dependent on multiple variables, including the age, size and frequency of canopy gaps (Moorman and Guynn, 2001; Jobes et al., 2004; Forsman et al., 2010), season (Bowen et al., 2007), latitude and forest type (LaManna and Martin, 2017), and the life history and ecological traits of bird species (Levey, 1988; Wunderle et al., 2006; Forsman et al., 2010; LaManna and Martin, 2017). Consequently, the spatial distribution and species composition of avifaunal communities has been shown to be affected by canopy gaps, mediated by species' variable sensitivity to habitat modifications following canopy disturbances (Thiollay, 1997;

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Greenberg and Lanham, 2001; Fuller, 2000; Faccio, 2003). Specifically, habitat specialisation, size and diet have been shown to be important determinants of bird responses to canopy gaps (Thiollay, 1997; LaManna and Martin, 2017). While several studies have compared habitat conditions and avifaunal communities across intact forest and natural canopy gaps (Levey, 1988; Fuller, 2000; Greenberg and Lanham, 2001; Faccio et al., 2003); or intact forest and harvest gaps (Geldenhuys and Maliepaard, 1983; Vitt et al., 1988; Jobes et al., 2004; Wunderle et al., 2006; Cleary et al., 2007; Politi et al., 2012) respectively, to the authors' knowledge, no studies have assessed variation across intact forest, natural gaps and harvest gaps simultaneously. This approach has the advantage of providing insight into the effect of timber harvesting disturbances on forest habitat and bird community relative to intact forests and natural disturbance processes, and could thus be useful in guiding sustainable timber harvesting practices.

In unmanaged indigenous coastal forests of the Eastern Cape, canopy gaps are an important component of the natural disturbance regime, caused by strong coastal winds, natural tree-falls or senescence (Obiri and Lawes, 2004). Currently, informal timber harvesting in these forests is resulting in canopy gaps in addition to those caused by natural disturbances. While Obiri and Lawes (2004) showed that rates of harvest gap creation did not negatively affect tree species richness in this region, the impact of harvest gaps on forest habitat condition, and concomitant responses by forest birds is currently unknown. This represents a critical gap in our knowledge, particularly in light of recent findings by Cooper et al. (2017), which showed that over half of South Africa's forest-dependent birds have suffered range declines in the past 20 years, with declines most prominent in the Eastern Cape, despite increases in forest cover over the same time period, suggesting that habitat degradation may be driving forest bird declines in this region. This study thus aimed to determine the impact of harvest-created canopy gaps on habitat structure, avifaunal species richness and community structure in a threatened lowland forest type in the Eastern Cape. Specifically, this study aimed to: i) compare the

abundance and characteristics of harvest-created gaps and natural gaps; ii) assess habitat structure across intact forest, harvest gaps and natural gaps; and iii) determine the response of breeding forest bird assemblages to harvest gaps at the forest-scale.

6.3 Materials and methods

6.3.1 Study site

This study was conducted at Mqaba forest (31°26'8.36"S, 29°44'9.36"E) within the O.R. Tambo district, in the north-eastern, coastal region of the Eastern Cape Province, South Africa (Fig. 6.1). The topography of this region is mountainous, with fragmented forest patches within a grassland matrix, and scattered rural settlements (von Maltitz et al., 2003). Indigenous forests in this region are classified as Pondoland scarp forests, occurring on south- or east-facing slopes of the coastal scarp ridge (Figure 1B). Mean annual rainfall in the region varies between 660 and 1200 mm, with rainfall occurring predominantly in the summer period, between October and March. Temperatures are mild, with mean annual temperatures ranging from 18 to 20°C.

Socio-economically, this district falls entirely within the former homeland of the Transkei, and remains characterised by a weak infrastructure and limited economic opportunities. Consequently, the region has some of the highest rates of poverty (43.5%) and unemployment (35.5%) in the province (Statistics South Africa, 2018). The district is the most populous in the Eastern Cape (21% of the total provincial population), with a positive growth rate (annual growth rate of 1.5%). Furthermore, it is has the highest youth population (39% between the ages of 15 and 34) and lowest levels of education (17% of people over 20 have no formal education) in the province. The number of households is growing (annual growth rate of 1.8%), and unlike other districts in the Province, the majority (55%) of households reside in traditional dwellings (i.e. dwellings constructed from natural resources). Given these socio-economic conditions, subsistence and commercial use of forest products represent a critical contribution to rural livelihoods in this district (Obiri, 2002).

Mqaba is representative of one of the last remnant patches of Pondoland scarp forest > 1000 ha. This forest thus has high biodiversity value, given its large core area and subsequent reduced edge effects impacts. Furthermore, Pondoland scarp forests are the most plant species diverse forest type in South Africa, with the highest number of unique and endemic plant species, many of which are red listed (Berliner, 2009). Despite their high biodiversity, Pondoland scarp forests have the lowest level of formal protection and are thus highly vulnerable to biodiversity loss. Effective sustainable management within these biodiverse rich, unprotected forests is thus a conservation priority. Mqaba is located on a south-easterly slope, spanning an elevational gradient of 40 - 440 m above sea level, typical of Pondoland scarp forests. Formal logging of high value indigenous trees occurred in Mqaba prior to the ban on indigenous forest logging in 1939, although logging activities of this era were largely focussed on inland forests, such that historical logging levels are likely to have been low in this forest (Obiri, 2002). In more recent times, informal timber harvesting has occurred as an important way for rural households to supplement income (Obiri, 1997; 2002). Although current forest legislation aims for sustainable resource use, and thus allows for the issue of permits for commercial-scale harvesting, no permits have been issues in the region such that all timber harvesting is currently illegal and unregulated. A number of rural communities occur less than 3 km from the forest boundary, and a gravel road intersects the length of the forest. As with 70% of indigenous forests in the Eastern Cape, Mqaba in managed by the state under the Department of Environment, Forestry and Fisheries (DEFF).
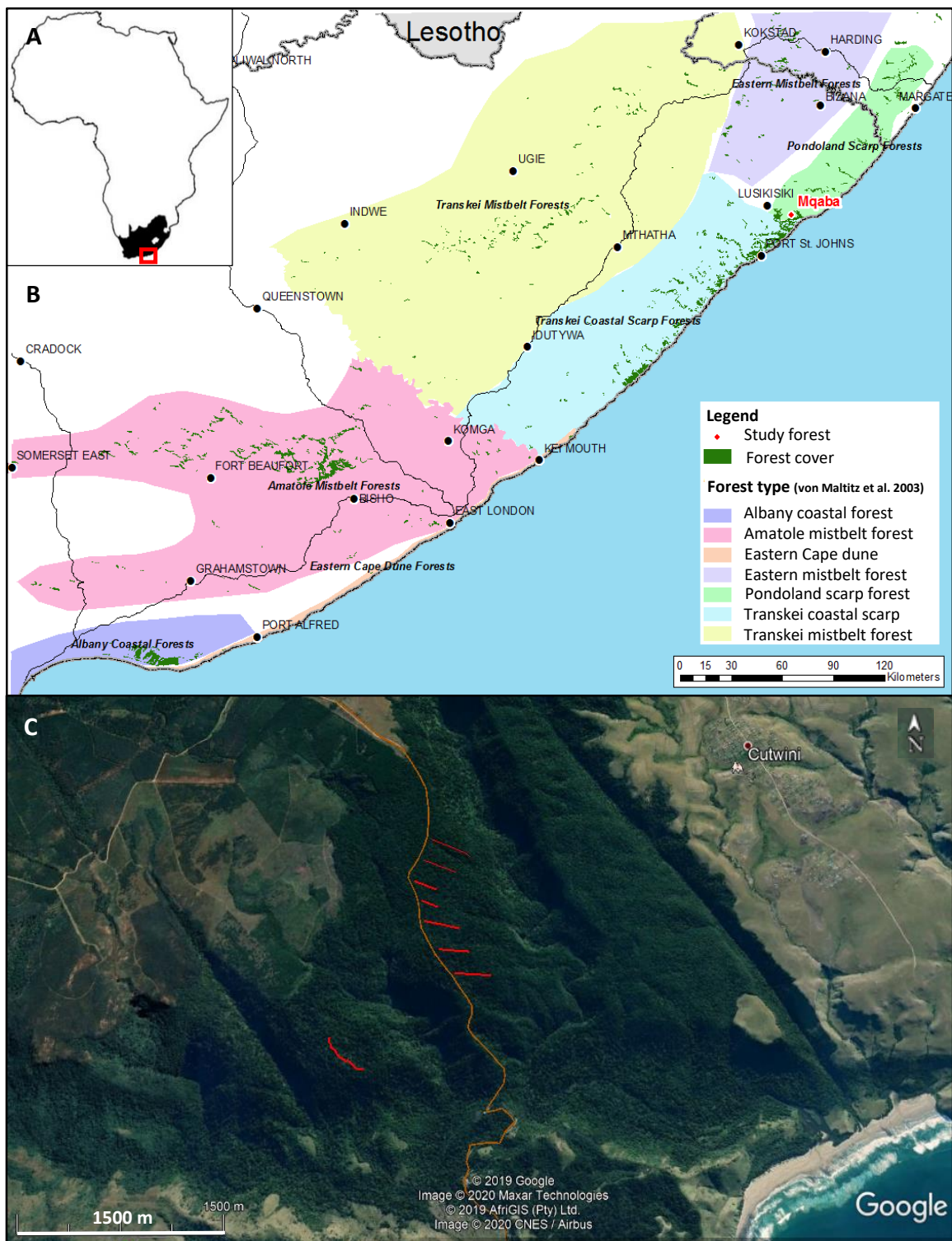
Figure 6.1 Location of **A)** the Eastern Cape within South Africa, **B**) Mqaba forest within the Eastern Cape (Map drawn by: A. Wannenburgh), and **C)** transect locations (red lines) within Mqaba forest, with the road shown in brown. (Map data: Google Earth).

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6.3.2 Study design

The study comprised of two components: first, straight-line transects were walked to quantify and characterise natural- and harvest- canopy gaps across the forest; second, habitat variables and the bird community were sampled at a subset of natural gaps sites, harvest gap sites and intact forest sites (i.e. no major canopy disturbance present) to assess the response of birds to different habitat conditions.

6.3.2.1 Gap occurrence and characteristics

Gaps were sampled along eight belt transects 20 m wide and a mean of 290 m long (range: 150 – 420 m; Table 6.1). Transects were located from 400 meters above sea level (m.a.s.l) to a minimum of 288 m.a.s.l, with individual transects having an average elevational range of 22.88 (range: 5 – 63 m), and running along moderate slopes (Table 6.1). All transects ran along an east-west axis, except for T7, which had a north-south orientation (Fig. 6.1C). All canopy gaps or part of a gap falling within the 20 m wide belt were included in the sample. A gap was defined as an opening in the forest canopy, extending to the bases of canopy trees surrounding the canopy opening, and where regeneration height within the gap was < 50% of the surrounding canopy height (Runkle, 1981; Liu and Hytteborn, 1991). The gap perimeter was identified as the line joining the stems of canopy trees surrounding the canopy gap (after Obiri and Lawes, 2004), and was walked with a handheld Garmin GPS to map their location and extent. This definition of canopy gaps thus includes the forest area directly and indirectly affected by the canopy opening, and can thus be considered the delineation of "expanded gaps" (Runkle, 1981). Sampled gaps were defined as natural gaps (e.g. due to wind-fall, branch- or bole-snapped trees or naturally dead standing trees) or harvest gaps (i.e. due to the selective harvesting of canopy trees). Gap length (defined as the largest distance between gap edges) and width (defined as the largest distance perpendicular to length) were recorded at each gap using a range meter, from which gap area in m^2 (defined as πLength*Width/4), and L:W ratio, as a measure of gap shape, were later calculated. The following gap-maker (i.e. the tree that created the canopy gap) variables were

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also recorded: i) species (where identifiable), ii) diameter at breast height (DBH), iii) estimated height (along the fallen stem), iv) stage of decay (based on a scale of 1 – 5 from fresh to highly decayed, Appendix 1), and v) whether the fallen stem was removed from the gap or not.

6.3.2.2 Habitat structure across natural gaps, harvest gaps and intact forest sites

To assess variation in habitat, six harvest-created gaps, six natural gaps and six intact sites were sampled using circular plots of 0.04 ha (11.3 m radius). Harvest- and natural gap sites sampled represented a subset of those identified during transect walks (section 6.3.2.1), and were selected such that a minimum distance of 150 m was maintained between all sampled gaps. The centre of harvest- and natural gap plots was placed at the base of the gap-maker. Canopy gaps sampled included a range of gap ages, with 30% and 25% of harvest and natural gaps sampled estimated to have occurred within the past 5 years respectively, while the majority of gaps of both types were estimated to be older than 5 years old. Intact sites were identified as sites where the canopy was undisturbed, and where there were no major canopy disturbances within 50 m of the centre of the plot. Intact sites were located in a random outward direction, but within 200 meters from either the start or end point of belt transects sampled, while ensuring that a minimum distance of 150 m was maintained between all selected intact sites, and natural- and harvest gap sites sampled.

Within circular 0.04 ha plots of intact, harvest gaps and natural gaps the following microhabitat variables were measured: i) estimated percentage cover of canopy, shrub, exotic species, herb, grass, leaf litter, woody debris, liana and bare ground. ii) The vertical foliage profile was recorded by estimating foliage density at incremental height classes: 0 - 0.5 m; 0.5 – 1 m; 1 – 2 m; 2 – 5 m; 5 – 10 m and >10 m. Foliage density at each height class was estimated using a 8-m long telescoping pole, marked at each height interval. The pole was sequentially set-up at eight evenly spaced points along the plot boundary. Visual estimates of foliage density (as a percentage) at each height class were made from the plot centre. A rangefinder was used to assist with estimates of foliage density beyond the 8-m length of the telescoping pole. Foliage density at each height class interval was calculated as the

mean percent density from the eight separate estimates. Foliage density scores were later converted into a foliage height diversity index (FHDI) per plot using the Shannon-Wiener Diversity Index (SWDI) formula, as follows:

$$H = -\sum_{i-1}^{s} p_i \ln(p_i)$$

where p_i is the proportion of the total foliage which lies in the ith layer of the chosen horizontal layers (Bibby et al. 2000). This index thus provided a measure of the vertical heterogeneity at each plot. iii) Understory fruit and flower availability were scored respectively on a scale of 0 – 3, where 0 = none; 1 = 1 - 10; 2 = 10 – 20; and 3 = > 20, based on the number of fruit and flowers present.

6.3.2.3 Bird surveys

Bird surveys were conducted at selected intact (n = 6), harvest gap (n = 6) and natural gap (n = 6) sites during the summer breeding season in the study region (December 2017). Non-fixed-radius point-counts were conducted to sample birds (Blondel et al., 1981). All birds calling over a 10 minute period were recorded using a Song Meter SM4 acoustic recorder attached to a tree at a height of 1.5 m near the centre of each plot. Birds seen during the 10 min period were visually identified by JL in the field, and birds recorded on the Song Meter were audibly identified thereafter through playback of recordings by JCC. Each site was surveyed twice during the morning period (sunrise +3 hours), with repeated surveys conducted on different days. Surveys were conducted in alternating sequence so as to ensure that repeat surveys at each survey site were done at different times within the three-hour morning period. Bird surveys were consistently conducted on dry, still days. Any birds seen or heard which could not be confidently identified were not recorded. Presence/absence data at each plot were pooled, thereby determining species richness as the cumulative number of species recorded within a plot. The use of presence/absence data as opposed to abundance data was used to avoid potential inaccuracies in estimating abundance from bird survey recordings. Any birds seen or recorded which

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could not be confidently identified were unrecorded. Given that the focus of the study was on habitat-scale use by the forest bird assemblage, birds observed flying above the forest canopy were not included in analyses.

6.3.3 Data analyses

6.3.3.1 Gap occurrence and characteristics

The percentage of each straight-line transect intersected by gap condition was assessed by overlaying mapped gap shape files onto walked transects using Google Earth. Mean percent of transect length intersected by gaps was calculated, as well as the relative contribution of natural-gaps and harvest-gaps to this overall percentage. Gap and gap-maker characteristics were compared across natural gaps and harvest gaps using Mann-Whitney U Tests where data were non-normally distributed and t-tests for normally distributed data. A chi^2 test was used to compare gap variables measured categorically (i.e. stem decay and stem removal).

6.3.3.2 Habitat across natural gaps, harvest gaps and intact forest sites

To assess local-scale habitat variation across intact sites, natural gaps and harvest gaps, and the variables driving this, a Principal Components Analysis (PCA) was applied to a matrix of 18 rows (all plots sampled) and 16 columns (measured habitat variables). The PCA thereby created different habitat gradients (i.e. principal components or PCs), and visual assessment of the location of sampled sites along these gradients. PCA was run using the 'PCA' function (FactoMineR package) in R (R Core Team, 2017). Difference in vertical profiles across intact sites, natural gaps and harvest gaps was assessed by comparing foliage density at different height classes using analysis of variance (followed by Tukey's test for pairwise comparisons) where data were normally distributed, or Kruskal-Wallis Test (followed by Dunn's post-hoc test) where data were non-normally distributed using R. P-values were adjusted based on Bonferroni's adjustment to account for multiple testing.

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6.3.3.3 Bird species richness and composition across natural gaps, harvest gaps and intact forest sites

To ensure that bird surveys had sufficiently sampled the bird community at each habitat type (harvest gaps, natural gaps and intact forest), Choa2 non-parametric species richness estimator, to compare observed species richness with expected richness values, and species accumulation curves based on Coleman's method, were used. Differences in bird species richness and community dissimilarity based on species presence/absence (Jacccard dissimilarity) were compared directly across groups (natural gaps, harvest gaps and intact sites) using analysis of variance, (followed by Tukey's test for pairwise comparisons). Additionally, differences in assemblage composition across sites were assessed using non-metric multidimenstional scaling (nMDS) ordination based on species presence/absence (Jaccard dissimilarity; vegan package R). This analysis was appropriate as it makes no assumption about the distribution of the data and is thus widely used for analysis of community data. Differences in community species composition across habitat gradients (i.e. PC1, PC2 and PC3 derived from PCA of habitat variables) were tested for significance based on a permutation test with 999 permutations, and habitat gradients (PC1-PC3) were fitted onto the nMDS ordination, using the function 'envfit' (vegan package). Analysis of similarity (ANOSIM) was used to test for significant differences in community structure across harvest gaps, natural gaps and intact sites (Jaccard presence/absence index). SIMPER (similarity percentage analysis) was used to determine the contribution that individual species made towards distinguishing differences in community structure across harvest gaps, natural gaps and intact sites. Analyses were all carried out in the R statistical environment (R Core Team, 2017).

6.4 Results

6.4.1 Gap occurrence and characteristics

A total of 2 327 m were sampled over eight transects, along which a total of 29 gaps were encountered: 20 natural and 9 harvest-created. Overall, an average of 17.97 ± 3.37% of transect length

was under gap conditions, with 14.08 ± 3.49% attributed to natural gaps, and 4.22 ± 1.64% due to harvest-created gaps (Table 6.1). Harvest-created gaps thus resulted in a 30% increase in the amount of forest under canopy gap conditions. On average, 1.24 ± 0.57 gaps were encountered per 100 m, with natural and harvest gaps encountered at a mean rate of 0.72 ± 0.12 gaps/100 m, and 0.41 ± 0.15 gaps/100 m respectively.

Table 6.1 Transects sampled, showing percent intersected by gap conditions, with respective contribution by natural and harvest-created gaps shown per transect and mean ± SE calculated across all transects.

|	Transect variables				Canopy gap conditions		
	Length (m)	Start elevation (m)	Elevation range (m)	Mean slope (%)	% total gap (gaps/100 m)	% natural gap (gaps/100 m)	% harvest gap (gaps/100 m)
T1	204	373	18	-10.4	20.10 (1.47)	8.33 (0.49)	11.76 (0.98)
T2	300	387	23	-7.9	31.50 (1)	31.50 (0.33)	0.00 (0)
T3	400	400	63	-15.8	30.38 (2.25)	22.63 (1.25)	10.38 (1)
T4	300	345	11	-3.8	5.00 (0.67)	2.17 (0.33)	2.83 (0.33)
T5	250	326	13	-5.6	19.60 (0.8)	19.60 (0.80)	0.00 (0)
T6	305	294	5	-2.1	16.60 (0.98)	12.50 (0.66)	4.10 (0.33)
T7	420	288	44	-10.5	11.22 (1.19)	11.22 (1.19)	0.00 (0)
T8	150	357	6	-2.2	9.33 (1.33)	4.67 (0.67)	4.67 (0.67)
Mean ± SD	291.13 ± 32.19	346.25 ± 14.59	22.88 ± 7.22	-7.29 ± 1.69	17.97 ± 3.37 (1.24 ± 0.57)	14.08 ± 3.49 (0.72 ± 0.12)	4.22 ± 1.64 (0.41 ± 0.15)

Gap characteristics were compared across harvest (n = 12) and natural (n=20) gaps. Three harvest-gaps located outside of belt-transects were added to increase the harvest-gap sample. Natural- and harvest-created gaps did not differ in length or mean area, although natural gaps tended to be larger (Table 6.2). Gap width differed across gap types, with harvest gaps narrower than natural gaps. Consequently, width to length ratio differed across gap type, with natural gaps having a larger width: length ratio, indicating they were more circular, relative to harvest-gaps which tended to be more elliptical. Stem diameter and length of the gap-maker tree did not differ across gap types. However there was a difference in the level of stem decay, with gap-maker stems in natural gaps showing a relatively even distribution of decay, while gap-maker stems in harvest-gaps were all classed within the first three stages of decay. Gap-maker stem removal differed across gap types, with no natural

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gap-maker stems being removed from the gap, while only two harvest-gaps had the full gap-maker stem left in the gap. The majority (n = 8) of harvest-gaps had the gap-maker stem removed, while only bark was removed, with the debarked stem left, in two harvest gaps, i.e. trees were felled to be stripped of medicinal bark, and not for use as timber. In cases where stems were recorded as removed from harvest gaps, it is worth noting that these removals were partial, i.e. while a majority of the main stem was removed, the rest of the felled tree biomass was left in the gap.

Table 6.2 Comparison of natural (n = 20) and harvest (n = 12) gap characteristics recorded in Mqaba forest.

Variable	Natural gap	Harvest gap	Test statistic and p-value
Gap size and shape			
Gap area (m^2)	421.79 ± 94.13	209.08 ± 37.37	W = 79; p = 0.11
Gap length (m)	26.10 ± 2.78	22.96 ± 2.05	W = 109; p = 0.68
Gap width (m)	17.31 ± 1.84	10.85 ± 1.37	W = 55; **p = 0.011**
Width : Length ratio	0.68 ± 0.03	0.48 ± 0.05	t = -3.47; df = 19.99; **p = 0.002**
Gap-maker characteristics			
Stem diameter (cm)	57.03 ± 5.10	50.60 ± 4.79	t = - 0.92; df = 28.71; p = 0.37
Stem height (m)	15.60 ± 1.03	14.75 ± 1.52	t = - 0.46; df = 20.84; p = 0.65
Stem decay class (1 – 5 - %)	25; 0; 25; 25; 25	25; 33.3; 41.7; 0; 0	X^2 = 13.33, df = 4, **p = 0.009**
Stem removed (No; Yes; Bark)	100; 0; 0	16.7; 66.7; 16.7	X^2 = 24.24, df = 2, **p = 0.005**

The majority (60%) of natural gap-maker species were identified, while 40% were unidentified due to advanced levels of stem decay, or multiple potential gap-makers being present in the gap. Of stems identified, *Milletia sutherlandii* was the most frequently observed natural gap-maker species (Fig. 6.2). All harvest gap-maker species were identified, representing five species of which *Xymalos monospora, Ptaeroxylon obliquum* and *Strychnos sp.* were the most frequently recorded.
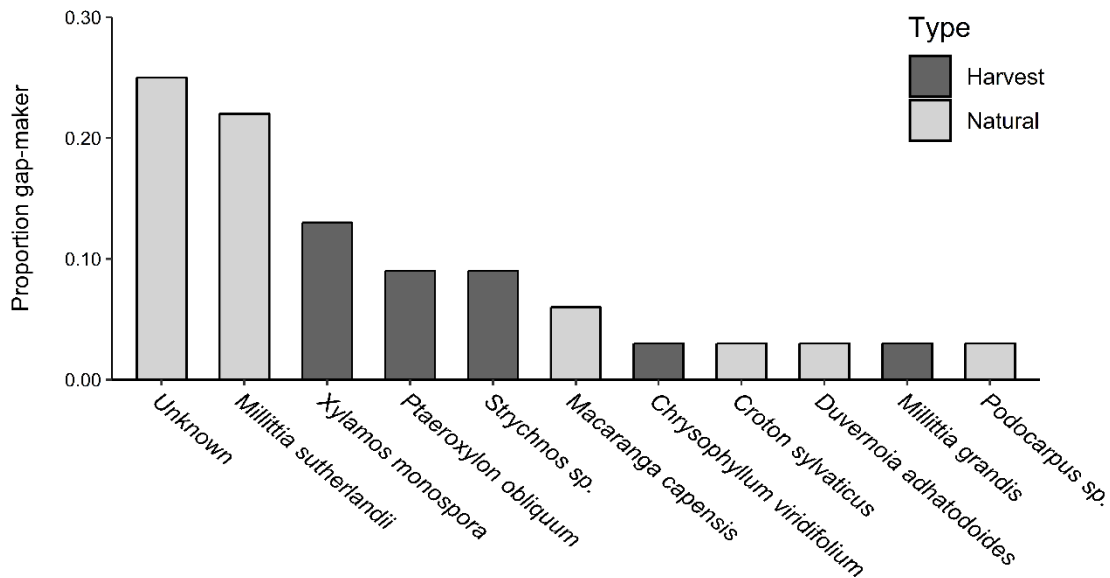
Figure 6.2 Gap-maker species recorded in natural and harvest gaps.

6.4.2 Habitat structure across natural gaps, harvest gaps and intact forest

Together PC1 – PC3 explained 80.7% of variation in habitat across intact, natural gaps and harvest gap

sites. PC1 explained 60.6% of habitat variation and represented a habitat gradient from intact sites,

characterised by high canopy cover, sub-canopy (5 – 10 m) and canopy foliage density (> 10 meters),

leaf litter cover and foliage height diversity (FHD), to natural gap sites with high understory foliage

density (0 – 2 m), understory fruit and flower availability, vine cover, exotic species cover, woody

debris cover, herb cover and shrub cover (Fig. 6.3). PC2 explained 13% of habitat variation and

represented a gradient from sites with abundant shrub and mid-story foliage density (2 – 5 m) to sites

with high bare ground cover and grass cover. Intact and natural gap sites occupied non-overlapping

ordination space separated along axis 1, while harvest gap sites were located between intact and

natural gap sites. This indicated that harvest gaps had a habitat that was intermediate between intact

and natural gaps. Specifically, herb cover, shrub cover, vine cover, bare ground cover and FHDI did not

differ across harvest gaps and intact sites (Fig. S6.2). There was, however, a tendency for harvest gap

sites to occur on the right of axis 1 (Fig. 6.3), suggesting they had a habitat more closely associated

with natural gaps than intact sites. Specifically, harvest gaps, like natural gaps, were characterised by

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greater woody debris cover, understory flower and fruit availability, exotic species cover, and understory foliage density compared to intact sites (Fig. 6.3; Fig. S6.2 and S6.3). Furthermore, the vertical profile of harvest gaps reflected that of natural gaps, differing significantly from the vertical profile of intact sites (Fig. 6.4).
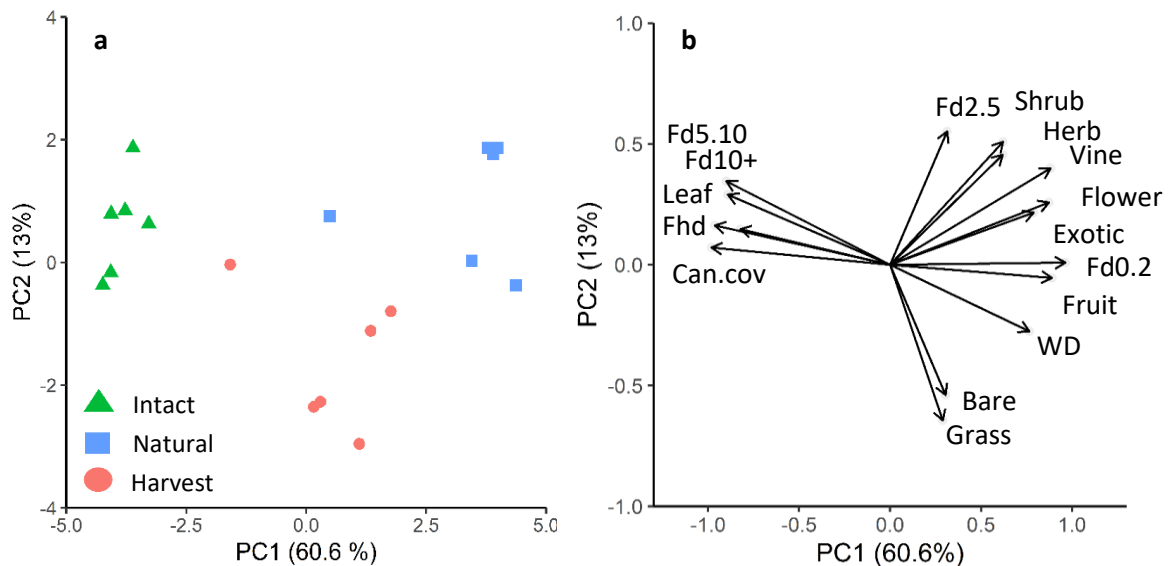
Figure 6.3 Principal components analysis (PCA) showing **a)** clustering of sites and **b)** habitat variables driving this. Habitat abbreviations are: Flower = understory flower availability; Exotic = exotic species cover; Fruit = understory fruit availability; Herb = % herb cover; Vine = % vine cover; Fd0.2 = % foliage density below 2 m; WD = % woody debris cover; Shrub = % shrub cover; Grass = % grass cover; Bare = % bare ground cover; FHD = foliage height diversity index; Can.cov = canopy cover; Leaf = % leaf litter; Fd10+ = % foliage density above 10 m; Fd5.10 = % foliage density 5-10 m; Fd2.5 = % foliage density 2-5 m.
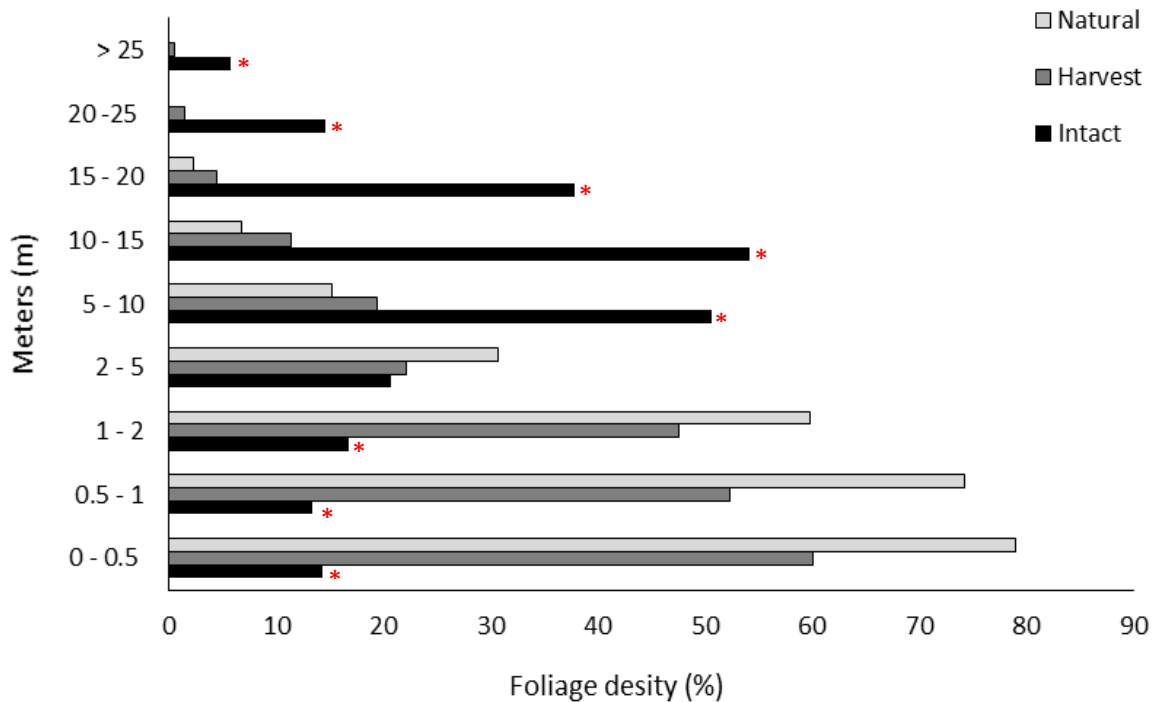
Figure 6.4 Vertical profile of foliage density compared across natural gaps (light grey), harvest gaps (dark grey) and intact forest (black). Bars with red asterisks indicate significant differences (p < 0.006 with Bonferroni adjustment) in foliage density relative to other groups.

6.4.3 Bird assemblages across natural gaps, harvest gaps and intact forest

Overall, 48 species were recorded during bird surveys across all plots (17 ± 3 species per survey site; mean ± SD, range 11 – 23; Table S6.1). Forty species were recorded at harvest gap sites (19 ± 3 species per survey site; mean ± SD, range 15 – 23), 35 species were recorded at natural gap sites (17 ± 3 species per survey site; mean ± SD, range 12 – 18), and 38 species were recorded at intact sites (16 ± 4 species per survey site; mean ± SD, range 11 – 22). Based on Chao2 estimator of true species richness, the sampling effort yielded 87%, 87% and 85% of the "true" species present at harvest gaps, natural gaps and intact sites respectively. Sample-based species accumulation curves based on Coleman's method were largely asymptotic for all habitat groups, further indicating that the sampling effort was sufficient to represent species richness present at each (Fig. S6.1).

Variation in species richness across intact forest, harvest gaps and natural gaps was not significant (F-value = 1.44, df = 2, p-value = 0.27; Fig. 6.5a). Conversely, within-group community dissimilarity

differed across groups (F-value = 7.94, df = 2, p-value = 0.001; Fig. 6.5b), with communities at intact sites showing higher dissimilarity compared to communities occurring at harvest gap sites, while community dissimilarity at natural gap sites did not differ from that observed at intact sites or harvest gap sites.
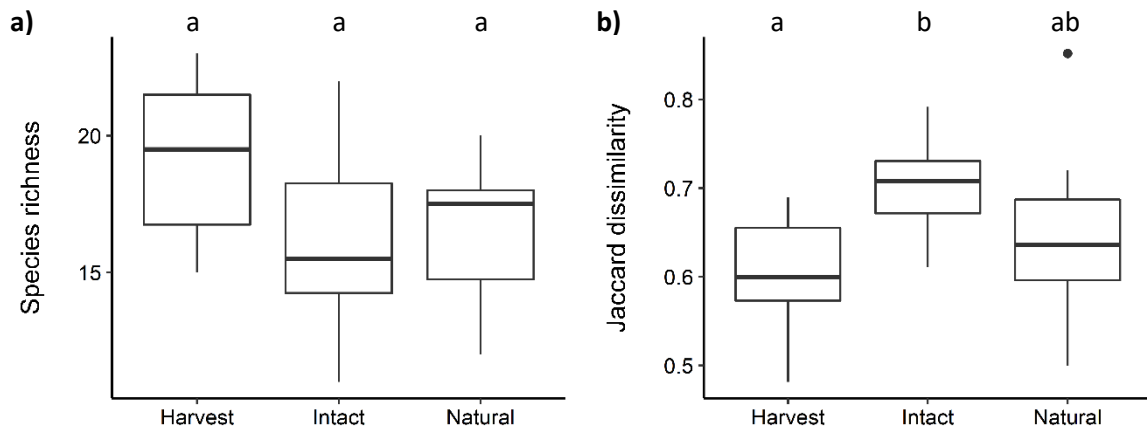
Figure 6.5 Comparison of **a)** species richness and **b)** within-group community dissimilarity based on species presence/absence across harvest gaps, intact sites and natural gaps. Different letters represent significant differences across groups (p < 0.05).

Differences in avian community between harvest gaps, natural gaps and intact sites were significant based on presence/absence data (ANOSIM, R = 0.22, *p* = 0.01). Non-metric multidimensional scaling (nMDS) showed some degree of clustering of sites according to habitat type (i.e. natural gaps, harvest gaps and intact forest) based on presence/absence of birds (Jaccard index, stress value 0.22; Fig. 6.6). As with ordination of habitat variables (Fig. 6.3a), harvest gaps and natural gaps tended to cluster closer together than to intact forest, although clustering of sites based on bird species presence (Fig. 6.6) was much less distinct than clustering of sites based on habitat variables (Fig. 6.3), and there was a large degree of central overlap indicating that many species occurred across habitat types (Table S6.1). Nonetheless, natural gaps and harvest gaps tended to occur on the left side of the plot, whereas bird communities of intact sites were predominantly located on the right side of the plot. According to fitted environmental variables (i.e. PC1, PC2 and PC3 based on PCA of habitat variables), bird

communities were separated along NMDS1 from right to left with decreasing values of PC1 (R^2 = 0.39, p = 0.03) , while PC2 (R^2 = 0.05, p = 0.67) and PC3 (R^2 = 0.07, p = 0.59) did not affect bird community composition (Fig. 6.6). Thus, bird communities responded to changes in habitat condition along a gradient from intact forest sites to natural gap sites defined by PC1, with bird communities of harvest gap sites representing an intermediate between intact forest and natural gap bird communities.
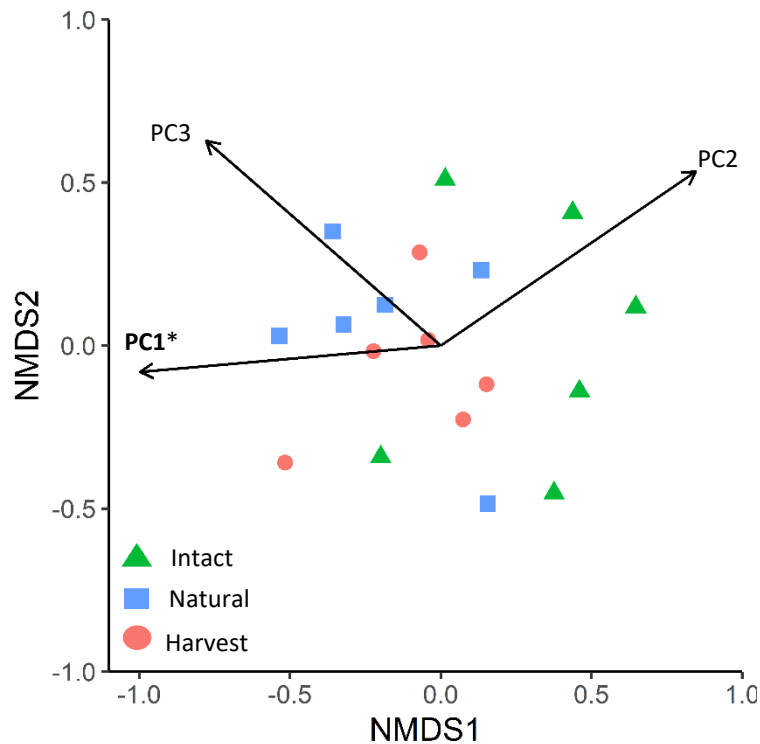
Figure 6.6 Non-metric multi-dimensional scaling (NMDS) based on bird species presence/absence (Jaccard method). Fitted environmental variables were habitat principal components 1 – 3 derived from the principal components analysis (PCA) of measured habitat variables (* p < 0.05).

SIMPER analysis showed that the avifaunal community structure across harvest gaps and intact sites; harvest gaps and natural gaps; and intact forest and natural gaps were differentiated by varying presence of certain species across habitat types (Table 6.3). Across-group species dissimilarity was highest between intact forest sites and natural gaps (0.59) and lowest between harvest gaps and natural gaps (0.46), with species dissimilarity between harvest gaps and intact forest being intermediate (0.53).

Table 6.3 Results from SIMPER analysis showing top ten species contributing to pairwise differences in avian communities across harvest gaps, natural gaps and intact forest.

Comparison (overall dissim.)	Species	Mean presence		Mean dissim.	SD	Cumulative % dissim.
Harvest vs. Intact (0.53)		Harvest	Intact			
	Cape white-eye	**1.00**	0.17	0.02	0.01	0.05
	Square-tailed drongo	0.00	**0.83**	0.02	0.01	0.09
	Collared sunbird	**1.00**	0.33	0.02	0.01	0.13
	Brown scrub-robin	0.33	**0.83**	0.02	0.01	0.16
	Knysna turaco	**0.67**	0.33	0.02	0.02	0.19
	Southern double-collared sunbird	**0.67**	0.33	0.02	0.02	0.22
	Dark-backed weaver	**0.83**	0.50	0.02	0.02	0.25
	White-starred robin	0.50	**0.83**	0.01	0.02	0.28
	Red-fronted tinkerbird	0.33	**0.50**	0.01	0.02	0.31
	African dusky flycatcher	**0.50**	0.17	0.01	0.02	0.34
Harvest vs. Natural (0.46)		Harvest	Natural			
	Dark-backed weaver	**0.83**	0.33	0.02	0.01	0.04
	Greater double-collared sunbird	0.17	**0.67**	0.02	0.01	0.08
	Knysna turaco	**0.67**	0.33	0.02	0.01	0.11
	Bar-throated apalis	0.33	**0.67**	0.02	0.01	0.14
	Southern boubou	**0.67**	0.33	0.02	0.01	0.18
	Black-headed oriole	0.33	**0.67**	0.02	0.01	0.21
	African dusky flycatcher	**0.50**	0.00	0.01	0.02	0.24
	Terrestrial brownbul	0.33	**0.50**	0.01	0.01	0.27
	Sombre greenbul	**0.67**	0.50	0.01	0.01	0.30
	African green pigeon	**0.50**	0.00	0.01	0.01	0.33
Intact vs. Natural (0.59)		Intact	Natural			
	Brown scrub-robin	**0.83**	0.00	0.03	0.01	0.04
	Square-tailed drongo	**0.83**	0.00	0.03	0.01	0.09
	Cape white-eye	0.17	**0.83**	0.02	0.02	0.13
	White-starred robin	**0.83**	0.17	0.02	0.01	0.17
	Greater double collared sunbird	0.00	**0.67**	0.02	0.02	0.20
	Bar-throated apalis	0.00	**0.67**	0.02	0.01	0.23
	Southern double-collared sunbird	0.33	**0.67**	0.02	0.02	0.26
	Southern boubou	**0.67**	0.33	0.02	0.02	0.29
	Collared sunbird	0.33	**0.67**	0.02	0.02	0.32
	Red-fronted tinkerbird	**0.50**	0.33	0.02	0.02	0.35

6.5 Discussion

Findings of this study show that informal timber harvesting increased the proportion of forest under canopy gap conditions considerably, with concomitant impacts on habitat, and avifaunal assemblages at the forest-scale. While avifaunal species richness did not differ across harvest gaps, natural gaps and intact forest (Fig. 6.5a), communities associated with harvest gaps showed lower levels of compositional dissimilarity across sites compared to intact forest sites, while compositional dissimilarity across natural gap sites did not differ from that recorded across intact forest or harvest gap sites (Fig. 6.5b). Furthermore, taxonomic composition differed across harvest gaps, natural gaps and intact forest, associated with changes in habitat conditions (Fig. 6.6). Findings of this study thus support those found in other tropical (Levey, 1988; Vitt et al., 1998; Whitman et al., 1998; Wunderle et al., 2006) and temperate forests (Fuller, 2000; Greenberg and Lanham, 2001), which show that canopy gaps, whether created by selective harvesting or natural treefalls, present distinct habitat patches within a matrix of intact forest, and that some bird species distinguish between these. Importantly, harvest gaps in Mqaba represented an intermediate state between intact forest and natural gaps in terms of habitat and avifaunal composition, suggesting that informal timber harvesting disturbances retained some aspects of intact forest habitat structure and avifaunal communities, while emulating some aspects of natural gap disturbances.

Harvest activities increased the frequency of canopy gaps, and the proportion of forest under gap conditions in Mqaba by close to 30% (Table 6.1). Much of this harvesting is driven by the presence of an informal trade network transporting timber harvesting in Mqaba to Lesotho (personal comm., Monica Mvakade, October 2017). While this increased the frequency of canopy gaps, harvest gaps resembled natural gaps in terms of gap area (Table 6.2). Similarly, Obiri (2002) found no difference in gap size between canopy gaps created my informal timber harvesting and natural gaps in Pondoland scarp forests sampled in the Umzimvubu District of the Eastern Cape. By comparison, harvest gaps formed by legal commercial logging activities in forest of the southern Cape were found to be larger

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than natural gaps (Geldenhuys and Maliepaard, 1983). This inconsistency across forest types is likely due to the variable nature of natural gap formation: in southern Cape forests natural gaps are predominantly the result of standing dead trees (i.e. snags), and are thus relatively small (Midgley et al., 1995), compared to natural gaps in coastal scarp forests, which are caused predominantly by canopy tree windfalls due to strong coastal winds, and thus tend to be larger (Obiri and Lawes, 2004). Consequently, the nature of informal timber harvesting in Mqaba, i.e. single-tree selective harvesting, resembles the primary driver of natural gap creation in these forests, i.e. single-tree windfalls (Obiri, 2002; Obiri and Lawes, 2004). Given that gap area has been shown to be an important determinant of variation in plant (Shure et al., 2006; Kern et al., 2014) and avifaunal responses (Moorman and Gynn, 2001; Jobes et al., 2004; Forsman et al., 2010) to canopy gaps, the lack of a significant difference in gap size across harvest and natural gaps in Mqaba suggests that informal timber harvesting closely emulates the small-scale gap phase disturbances associated with natural gap dynamics in these forests, and likely explains the large degree of overlap between habitat and bird species composition across gap types observed in this study (Fig. 6.3 and 6.6).

Whereas gap area of harvest and natural gaps were comparable, gap shape differed, attributed to the shorter width of harvest gaps compared to natural gaps (Table 6.2). Subsequently, harvest gaps had a smaller width-to-length ratio, i.e. were more strongly elliptical in shape, compared to natural gaps. While the reason for this is unclear, the narrower width of harvest gaps may allow for lateral growth expansion of surrounding canopy trees to close harvest gaps more rapidly than natural gaps, which may be more dependent on subcanopy recruitment to close given their broader width (Richards and Hart, 2011). Furthermore, while harvest gaps and natural gaps were both predominantly created by a single gap-maker tree, gap-maker species differed across gap types (Fig. 6.2). *Millettia sutherlandii* was the most commonly identified gap-maker species in natural gaps in Mqaba, in agreement with Obiri and Lawes (2004), likely due to the high abundance of this species in Pondoland scarp forests

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(Obiri, 2002). The dominance of a single species in driving natural gap formation has been reported by studies examining forest canopy gap dynamics globally (Clinton et al., 1993; Midgely et al., 1995; Kneeshaw and Bergeron, 1998; Ott and Juday, 2002; Obiri and Lawes, 2004). Harvest gaps, in comparison, were associated with a number of gap-maker species compared to natural gaps, with three species being prevalent harvest gap-makers, namely *Xymalos monospora, Ptaeroxylon obliquum* and *Strychnos henningsii*. Unlike *M. sutherlandii*, which is a soft-wooded species, unfavoured by harvesters, the prevalent harvest gap-maker species represent hard-wood species, selected for their high quality, durable timber used for fence posts, building and crafts. This distinction in wood durability across natural- and harvest gap-maker species is reflected by the higher levels of gap-maker stem decay recorded in natural gaps relative to harvest gaps. Unlike Obiri (2002), who found that harvest gap-maker stem diameters were smaller than natural gap-maker stems, the current study showed no difference in gap-maker stem diameter across gap types (Table 6.2). The large mean stem diameter of harvest gap-maker stems (50.6 cm) recorded indicates that timber harvesting in Mqaba was both species- and size-specific, with larger trees (diameter > 40 cm) preferentially selected for harvesting.

The important contribution of natural canopy gap formation to the creation of a habitat mosaic in forests, and thus the maintenance of forest-scale habitat heterogeneity, has been well documented in forests globally (Runkle, 1981; Brokaw, 1985; Greenberg and Lanham, 2001). Findings of this study show that canopy gaps formed by informal selective harvesting further contribute to forest-scale habitat heterogeneity by creating unique habitat conditions representative of an intermediate state between intact forest and natural gaps (Fig. 6.3). Thus, while harvest gaps retained several microhabitat features of intact forest, they resembled natural canopy gap habitat conditions in terms of their vertical forest profile, characterised by dense understory foliage and limited canopy-layer foliage density (Fig. 6.4), lower levels of leaf litter and canopy cover, and higher abundance of vine

cover, coarse woody debris cover, exotic species occurrence, and fruit and flower availability relative to intact forest (Fig. 3.3). Consequently, a habitat gradient was identified in Mqaba, ranging from intact forest characterised by closed-canopy conditions, to natural gaps characterised by open-canopy conditions, with harvest gaps occurring between the two. Thus, consistent with findings from other tropical (Levey, 1988; Wunderle et al., 2006) and temperate forests (Blake and Hoppes, 1986; Martin and Karr, 1986; Wunderle et al., 2006), the abundance and distribution of avain food resources, in the form of understory fruit and flower availability, was shown to be affected by canopy gap formation in Mqaba. Specifically, the higher availability of fruit in canopy gaps in Mqaba was largely driven by the greater abundance of two fruiting exotic species, namely *Solanum mauritianum* and *Rubus flagellaris*, which were frequently observed to colonize canopy gaps. Similarly, greater understory foliage density and coarse woody debris in gaps relative to intact forest in Mqaba is a common feature of canopy gaps in forests globally (Fuller, 2000; Greenberg and Lanham, 2001; Jobes et al., 2004; Wunderle et al., 2006, Cleary et al., 2007), and has been related to increased arthropod abundance in canopy gaps (Blake and Hoppes, 1986; Martin and Karr, 1986; Jokimäki et al., 1998; Richards and Windsor, 2007).

The variable habitat conditions present at intact forest, harvest gaps and natural gaps affected avifaunal community composition in Mqaba, consistent with previous studies showing the significant effect of canopy gaps on avian species composition in tropical (Blake and Hoppes, 1986; Martin and Karr, 1986; Levey, 1988; Sekercioglu, 2002; Wunderle et al., 2006) and temperate (Fuller, 2000; Greenberg and Lanham, 2001; Faccio et al., 2003; Forsman et al., 2013) forests. Specifically, variation in avifaunal community composition was related to changes in habitat condition along a gradient from intact forest sites to natural canopy gaps, with the avian community recorded at harvest gaps representing an intermediate community between that observed at intact forest sites and natural gap sites. However, there was considerable overlap in species composition at natural gaps and harvest

gaps, showing that avian communities in gap habitats, whether natural or harvest caused, were more similar to each other than they were to avian communities of intact forest.

In tropical forests, the influence of forest gaps on avifaunal communities has been largely attributed to increases in fruit, flower and invertebrate food availability in gaps relative to surrounding intact forest (Blake and Hoppes, 1986; Martin and Karr, 1986; Wunderle et al., 2006). Alternatively, it has been proposed that modified vegetation structure in canopy gaps may be a more important determinant of avian use of gaps than food availability in temperate forests (Bowen et al., 2007; Champlin et al., 2009). For example, dense understory foliage in gaps may provide cover from predators, and increased opportunity for understory-nesting species (Fimbrel et al., 2001). In the current study, the habitat gradient shown to affect avifaunal compositions incorporated variables relating to vegetation structure and food availability. Consequently, further research would be required to disentangle the relative importance of these factors in driving variation in avifaunal composition across gap and intact habitats in forests of the Eastern Cape. Nonetheless, findings suggest that variation in fruit and flower abundance affected species composition across gap and intact habitats as several nectarivorous species, e.g. *Cinnyris afer* (Greater double-collared sunbird), *Cinnyris chalybeus* (Southern double-collared sunbird), and *Hedydipna collaris* (Collared sunbird), and frugivorous species, e.g. *Tauraco corythaix* (Knysna turaco), were more frequently recorded in gaps relative to intact forest sites. This is in agreement with several studies which have shown increases in nectarivorous and frugivorous species in response to timber harvesting, attributed to this species' ability to take advantage of post-harvest increases in flower and fruit availability (Mason, 1996; Johns, 1988; Wunderle et al., 2006; Cleary et al., 2007; Leaver et al., 2019). On the other hand, loss or modification of microhabitat structure associated with canopy gaps may affect avian species composition based on their life history traits. For example, ground foraging/nesting species have been shown to be negatively affected by selective timber harvesting, related to unfavourable microclimate

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and foraging conditions associated with reductions in canopy cover (Thiollay, 1992; 1997; Cleary et al., 2007; Arcilla et al., 2015; Leaver et al., 2019). This may explain the higher abundance of *Cercotrichas signata* (Brown scrub-robin) and *Pogonocichla stellata* (White-starred robin) in intact forest compared to gaps, species which forage and nest on the forest floor, respectively (Hockey et al., 2005). Importantly, studies have shown that species' responses to canopy gaps are largely dependent on their dependency on forest habitats, with forest-dependent/interior species tending to avoid gap habitats, while forest-generalist/edge species are able to take advantage of canopy gap conditions (Thiollay, 1997; Greenberg and Lanham, 2001; Sekercioglu, 2002; Faccio et al., 2003).

While avian community composition differed across harvest gaps, natural gaps and intact forest, there were no significant difference in species richness, consistent with previous studies from tropical (Whitman et al., 1998; Wunderle et al., 2006) and temperate forests (Forsman et al., 2013). However, the tendency towards higher species richness in harvest gaps observed in this study is in line with several studies from temperate forests, which have shown species richness to be higher in canopy gaps relative to intact forest (Fuller, 2000; Greenberg and Lanham, 2001; Faccio, 2003; Forsman et al., 2010). This has been attributed to increased breeding and foraging opportunities in gaps, particularly for species preferring early-successional stages when habitat heterogeneity increases (Campbell et al., 2007). While findings of this study show that informal timber harvesting increased forest-scale habitat heterogeneity, further research is needed at a broader spatial-scale to assess whether this results in increased bird species richness at the landscape-scale, and whether there is a threshold level beyond which the potential positive effects of harvest-mediated increases in habitat heterogeneity are over-ridden by the potential negative effects of increased canopy openness. The lack of a decline in species richness in harvest gaps observed in the current study may be attributed to the high levels of natural background disturbance in the study forest, through windfall gaps due to strong coastal winds, and a long history of anthropogenic disturbances, resulting in a forest bird community that is relatively

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resilient to canopy disturbances (Lawes et al., 2007b). While species richness was maintained across habitat types, within-group species dissimilarity was significantly lower across harvest gaps than across intact forest. This may have important implications for forest biodiversity, as it suggests that forest-scale beta-diversity may decline as the proportion of forest under harvest gap conditions increases.

6.5.1 Conclusion and management considerations

Findings of this study showed that informal timber harvesting increased the frequency of canopy gaps by 30%, but that the harvesting method used, i.e. single-tree selection, largely emulated natural disturbance processes. This method of harvesting increased habitat heterogeneity at the forest-scale by creating habitat conditions and associated bird communities representing an intermediate state between intact forest and natural gaps. Findings thus suggest that while canopy gaps formed by informal timber harvesting largely retain the forest bird community, some forest specialist species show a preference for intact forest habitats. Additionally, harvest gaps supported communities with lower levels of species dissimilarity. These findings have important implications for sustainable timber management in these forests: while the single-tree selection method currently used by informal harvesters largely mimics processes of natural canopy gap formation, and is thus likely to be the most sustainable method of harvesting, the increased frequency of canopy gaps due to timber harvesting is of greater concern for two reasons. First, given that timber harvesting was shown to be size- and species-specific, increased demand for certain tree species may result in their over-exploitation, which could have profound ecological and socio-economic ramifications. Second, harvest-mediated increases in the proportion of forest under canopy gap conditions may negatively affect the abundance of avifaunal species that prefer intact forest conditions, likely to be forest specialist species which have limited distributions and are thus of conservation concern.

Although this study lacks adequate replication, plots sampled were representative of the nature of informal timber harvesting currently occurring in the study region, and we thus expect that observed

bird responses are representative of what would occur in other Pondoland scarp forests in the region. Furthermore, although this study examined only avifaunal responses to timber harvesting activities, birds are widely recognised as ecological indicators (Gregory and Strien, 2010), and it is thus likely that a measurable effect on birds, as shown by the current study, suggests that other taxa may be affected. Lastly, the study lacked a temporal aspect with regards to the age of canopy gaps sampled, which has been shown to be an important determinant of bird responses (Jobes et al., 2004). Further research is needed to gain insight into the recovery process, and length of effect time in terms of impacts of harvest gaps on forest habitat and bird communities. Despite these limitations, this study is, to the authors' knowledge, the first to report on the implications of informal timber harvesting on forest habitat and avifaunal communities in a nationally threatened, highly biodiverse forest type. The presence of an informal market transporting locally harvested timber across the country's border is of particular concern and requires the prioritisation of sustainable management plans that will allow local harvesters to benefit from forest resources, without compromising the biodiversity of this ecologically valuable forest.

6.6 Appendices
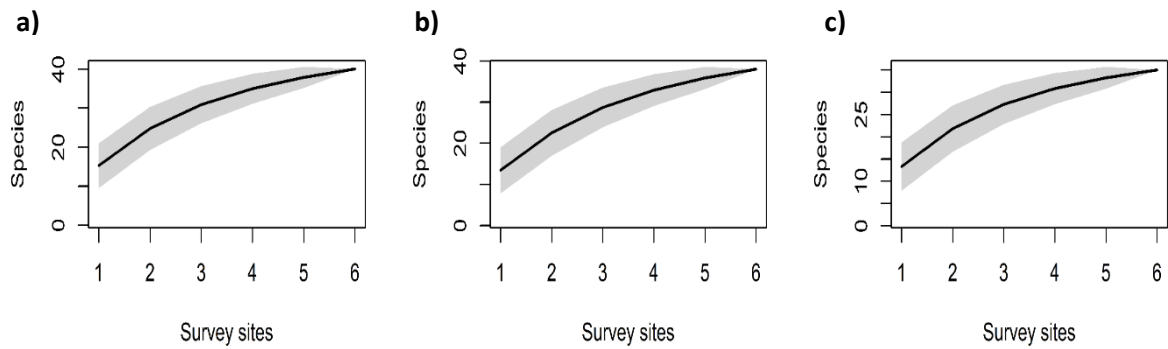
Figure S6.1 Sample-based species accumulation curves based on Coleman's method from the **a)** harvest gaps, **b)** natural gaps and **c)** intact sites sampled in Mqaba forest. Values shown are based on accumulating species across plots sampled, with 95 % confidence intervals in grey.
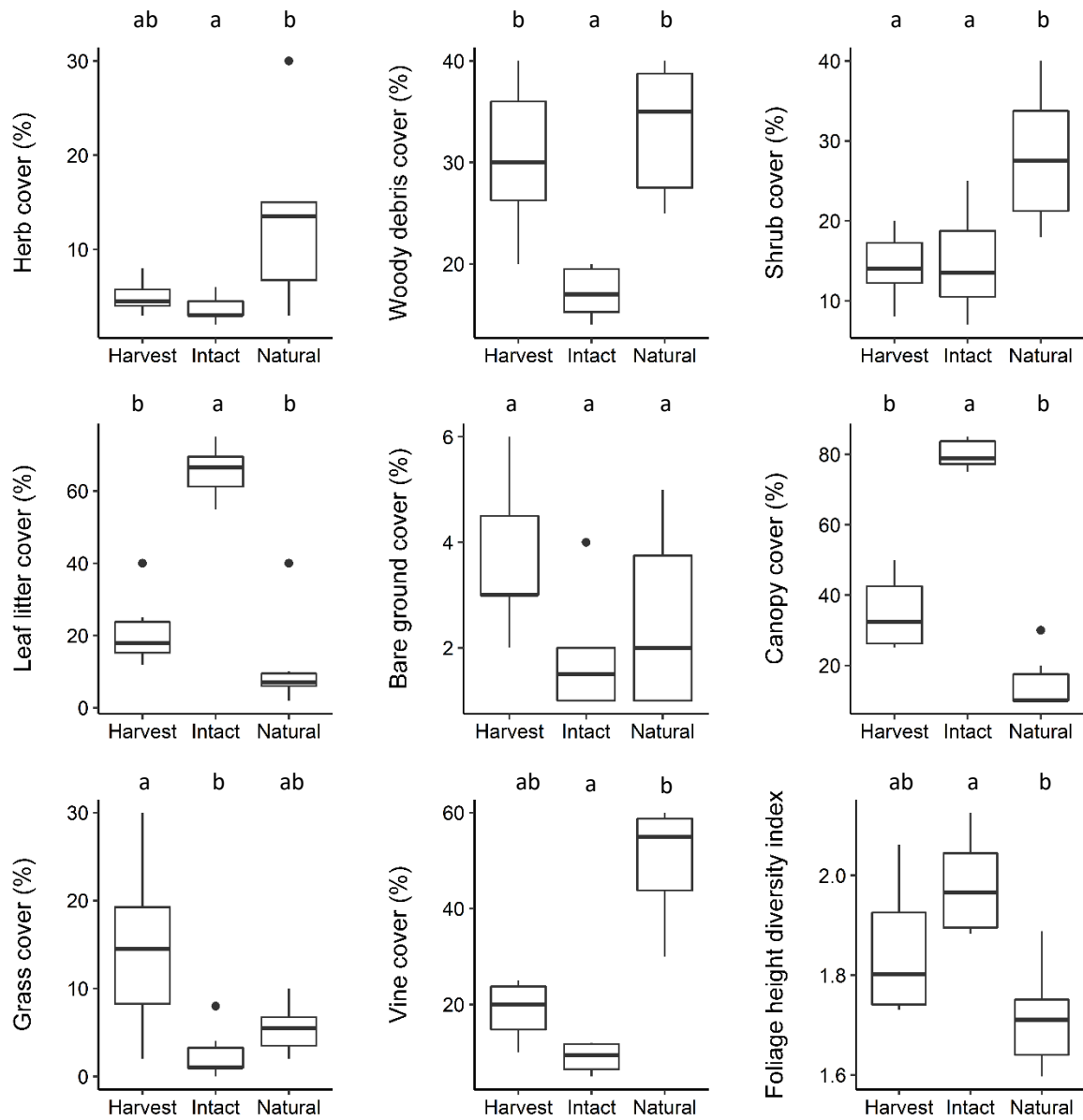
Figure S6.2 Habitat variables compared across harvest gaps (n = 6), intact site (n = 6) and natural gaps (n = 6). Different letters indicate significant difference across groups (p < 0.05).

$\chi^2 = 19.93$, df = 6, **p = 0.003** $\chi^2 = 18.2$, df = 6, **p = 0.006** $\chi^2 = 17.6$, df = 6, **p = 0.007**
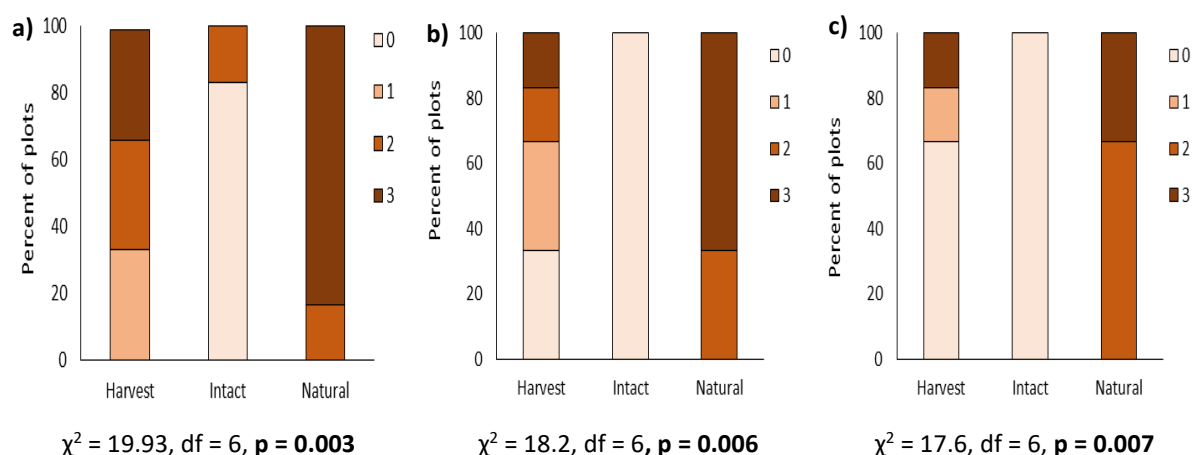
Figure S6.3 Presence of **a)** fruit, **b)** flowers and **c)** exotic species in the understory as percentage in each abundance class (0 = none; 1 = 1 – 10; 2 = 11 - 20; 3 = > 20) across harvest gaps (n = 6), intact sites (n = 6) and natural gaps (n =6) in Mqaba forest. Results of Chi-squared test comparing differences across groups are shown.

Table S6.1 List of bird species recording during bird survey in Mqaba forest, and occurrence at different habitat types sampled: harvest gaps, intact forest and natural gaps.

Common name	Scientific name	Harvest gap	Intact forest	Natural gap
African Dusky Flycatcher	*Muscicapa adusta*	x	x	
African Emerald Cuckoo	*Chrysococcyx cupreus*	x	x	x
African Goshawk	*Accipiter tachiro*	x	x	x
African Green Pigeon	*Treron calvus*	x	x	
African Olive Pigeon	*Columba arquatrix*			x
Bar-throated Apalis	*Apalis thoracica*	x		x
Black Cuckoo	*Cuculus clamosus*	x	x	x
Black-backed Puffback	*Dryoscopus cubla*	x	x	x
Black-bellied starling	*Notopholia corruscus*	x		x
Black-headed Oriole	*Oriolus larvatus*	x	x	x
Blue-mantled Crested Flycatcher	*Trochocercus cyanomelas*	x	x	x
Brown Scrub Robin	*Cercotrichas signata*	x	x	
Cape Batis	*Batis capensis*	x	x	x
Cape White-eye	*Zosterops capensis*	x	x	x
Chorister Robin-chat	*Cossypha dichroa*	x	x	x
Collared Sunbird	*Hedydipna collaris*	x	x	x
Dark-backed Weaver	*Ploceus bicolor*	x	x	x
Dark-capped Bulbul	*Pycnonotus tricolor*			x
Forest Canary	*Crithagra scotops*			x
Fork-tailed Drongo	*Dicrurus adsimilis*	x	x	x
Greater Double-collared Sunbird	*Cinnyris afer*	x		x
Green twinspot	*Mandingoa nitidula*		x	

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Table S6.1 (Cont.) List of bird species recording during bird survey in Mqaba forest, and occurrence at different habitat types sampled: harvest gaps, intact forest and natural gaps.

Common name	Scientific name	Harvest gap	Intact forest	Natural gap
Green Wood-Hoopoe	*Phoeniculus purpureus*	x	x	
Green-backed Camaroptera	*Camaroptera brachyura*	x	x	x
Grey Cuckooshrike	*Coracina caesia*	x	x	x
Grey sunbird	*Cyanomitra veroxii*			x
Knysna Turaco	*Tauraco corythaix*	x	x	x
Knysna Warbler	*Bradypterus sylvaticus*	x	x	
Knysna Woodpecker	*Campethera notata*	x	x	
Little Sparrowhawk	*Accipiter minullus*	x		
Narina Trogon	*Apaloderma narina*	x	x	
Olive Bushshrike	*Chlorophoneus olivaceus*	x		x
Olive sunbird	*Cyanomitra olivacea*	x	x	x
Olive Thrush	*Turdus olivaceus*	x	x	x
Olive Woodpecker	*Dendropicus griseocephalus*	x	x	
Red-chested Cuckoo	*Cuculus solitarius*		x	
Red-fronted Tinkerbird	*Pogoniulus pusillus*	x	x	x
Sombre Greenbul	*Andropadus importunus*	x	x	x
Southern Boubou	*Laniarius ferrugineus*	x	x	x
Southern Double-collared Sunbird	*Cinnyris chalybeus*	x	x	x
Spotted Ground Thrush	*Zoothera guttata*	x	x	x
Square-tailed Drongo	*Dicrurus ludwigii*		x	
Terrestrial Brownbul	*Phyllastrephus terrestris*	x	x	x
Trumpeter Hornbill	*Bycanistes bucanitor*	x		x
White-starred Robin	*Pogonocichla stellata*	x	x	x
Yellow-breasted Apalis	*Apalis flavida*		x	
Yellow-streaked greenbul	*Phyllastrephus flavostriatus*	x	x	x
Yellow-throated Woodland Warbler	*Phylloscopus ruficapilla*	x	x	x

CHAPTER VII: CONCLUSION

7.1 Introduction

This thesis set out to investigate the ecological implications of resource use in state managed indigenous forests of the Eastern Cape, South Africa. Specifically, the effects of harvesting of understory trees for poles, canopy trees for timber and crafts, and bark for medicinal use, on forest habitat structure and bird communities were examined. Based on quantitative assessments, findings showed that state forests in the Eastern Cape are an important source of natural resources for people, used for subsistence and commercial purposes. However, resource use is largely unregulated and results in habitat modification with concomitant impacts on bird communities. However, habitat and bird responses were shown to be dependent on the nature and extent of harvesting. An important conclusion of this thesis is thus that harvesting of forest products has significant impacts on forest ecosystems, mediated by habitat modification and changes to the functional organization, diversity, and composition of forest bird communities, but that these effects are a function of the intensity of resource use, and could thus be sustainably managed. However, a lack of effective management, coupled with the increased commercialisation of certain forest products, has resulted in state forests in the Eastern Cape being prone to unsustainable levels of resource use. Aims outlined by the National Forest Act (1998) of managing indigenous forests so as to balance the needs of resource users with the conservation of forest biodiversity through sustainable use are thus currently not being met. This is of ecological and social concern, given the high levels of biodiversity supported by indigenous forests (Castely and Kerley 1996; Berliner 2009); the importance of natural forests as carbon sinks to mitigate climate change (DEA, 2015); and the significant contribution that forest products make to rural livelihoods in this region (Shackleton and Shackleton 2004; Shackleton et al. 2007c; Dold and Cocks, 2002).

This is the first study to assess resource use and associated ecological impacts in multiple forests across the region since the promulgation of resource use regulations over a decade ago. Furthermore, this study is the first to investigate bird responses to multiple resource use types. Findings of this study

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thus provide insight into current harvest regimes in state forests and associated ecological implications in the context of forest policies that aim for sustainable use, but where, practically, *de facto* open-access systems of forest management prevail. By enhancing our understanding of the ecological implications in this context, the findings of this study should contribute to the development of sustainable management, and thus to overcoming one of the major ecological challenges currently faced by indigenous forests of the Eastern Cape.

7.2 Study approach

The spatial scale of investigation was an important factor underpinning the approach taken, and consequent results derived from this study. Specifically, unlike many studies which have examined forest biodiversity responses to anthropogenic disturbances at large spatial scales, namely forest cover loss (Brooks et al., 1999; Sodhi et al., 2004; Morante-Filho et al., 2015), changing land use patterns (Fairbanks, 2004; Newbold et al., 2013), and associated effects such as habitat fragmentation (Kirika et al., 2008; Farneda et al., 2015; Rocha et al., 2017; Ehlers Smith et al., 2019), this study examined human disturbances and concomitant ecological impacts at the forest-scale. This approach was appropriate given that, while resource demand is driven by various social, economic and cultural factors that operate at multiple spatial scales (Uma Shaanker et al., 2004a; Steele et al., 2015), the ecological implications of harvesting, such as whether a resource is harvested sustainably or not, is largely dependent on factors that operate at the forest-scale, such as resource availability, forest accessibility and size, and the distance and size of the nearest communities (Obiri et al., 2002; Uma Shaanker et al., 2004a; Boudreau et al., 2005). Furthermore, the Eastern Cape, unlike many other parts of Africa, has experienced an increase in forest cover over the past 30 years (Chalmers and Fabricius, 2007; de Klerk, 2007; Shackleton et al., 2013; Cooper et al., 2017). Consequently, human disturbances that operate at finer spatial scales were postulated to be possible drivers of forest biodiversity change. While a number of studies have shown this to be the case for forest tree composition and structure (Obiri et al., 2002; Boudreau et al., 2005; Boudreau and Lawes, 2005; Lawes et al., 2007a; Hoppe-Speer

et al., 2015), comparatively fewer studies have assessed faunal responses to resource use in indigenous forests of the Eastern Cape (Du Plessis 1995; Hayward, 2009).

While many studies which have examined biodiversity responses to categorical classifications of disturbance (Kumar and Shahabuddin, 2005; Thapa and Chapman, 2010; Asefa et al., 2017), this study measured habitat and avifaunal responses to harvest disturbances measured on a continuous scale, based on the proportion of the available resource harvested within sample plots (i.e. at a fine-spatial scale). This approach was appropriate given that there was no clear distinction between harvested and un-harvested areas within sample forests, due to the spatial distribution of harvesting being affected by a number of factors, such as the availability and distribution of target species, and the presence of multiple user communities and access routes. By measuring harvest disturbances on a continuous scale, the varying nature and extent of harvest activities present in each forest was sampled. Furthermore, variation in ecological processes is prone to change continuously across a disturbance gradient (McGill et al., 2006; Cadotte et al., 2011), such that assessing biodiversity responses to disturbance measured on a continous scale is thought to provide more insight compared to those based on responses to broad categorical groups of disturbance.

Six forests, representative of five national forest types, were sampled across the Eastern Cape region. Sampled forests represented some of the largest intact patches within each forest type, as these represent the most valuable refugia for forest biodiversity and important resource bases for people, and are thus of conservation and socio-economic priority (Berliner 2009). Furthermore, all sampled forests were state forests, now managed by the newly formed Department of Environment, Forestry and Fisheries (DEFF). This was appropriate given that the majority (70%) of forests in the Eastern Cape fall under state management (Cooper and Swart, 1997; Berliner, 2009).

Lastly, birds were chosen as the main study taxon for two reasons. First, they have been shown to be effective indicators of environmental change as they are sensitive to human disturbances, and are well

known and thus easy to identify in the field (Gregory and Strien, 2010). Furthermore, there is a connection between birds and people, such that illustrating human impacts through effects on birds is more likely to resonate with people than effects on other, less relatable taxa also known to be good biodiversity indicators, such as insects (Lawes et al., 2005) and amphibians (Ernst and Rödel, 2005). Second, forest birds in South Africa are under threat, with the number of nationally threatened species increasing (BirdLife South Africa 2014), and ranges declining (Cooper et al. 2017). Insight into forest bird responses to resource use, currently considered the primary driver of human disturbance in indigenous forests (von Maltitz et al., 2003; Berliner, 2009), is thus needed. While it is acknowledged that using birds as indicators of environmental change measures only a component of biodiversity, such that the use of results to assist natural resource management must be considered carefully, findings of this study make an important contributution to our currently limited understanding the impacts of resource use on forest fauna in temperate forest ecosystems in South Africa.

The first three chapters of this thesis present findings derived from all sampled forests, providing a regional-scale overview of resource use patterns (Chapter 2); impacts of resource use on habitat structure (Chapter 3); and response of bird functional diversity to resource use (Chapter 4). Based on findings of these broad-scale studies, Chapters 5 and 6 examine critical resource use issues more closely in a representative montane and coastal forest, respectively. Specifically, these single-forest studies assessed harvest-mediated habitat modification and concomitant bird responses to: pole and bark harvesting patterns across an elevation gradient in a montane forest (Chapter 5); and selective timber harvesting in a coastal forest (Chapter 6). Consequently, chapters 3, 4 and 5 cumulatively assessed bird responses to harvest disturbances based on a number of diversity measures, namely: overall species richness; species richness based on habitat specialisation (i.e. forest-specialists vs. forest-generalists); functional diversity (based on three independent metrics); species composition; and beta-diversity. Furthermore, direct and indirect effects of harvesting disturbances were measured

by investigating the response of bird diversity measures to the extent of resource extraction, and harvest-mediated habitat modification, respectively.

7.3 Study limitations

This study reports on the ecological impact of three forest resources types, namely poles, timber and medicinal bark. A focus on these three products was guided by the identification of these as key resource use types in the Eastern Cape region (Obiri et al., 2002). Furthermore, beyond their subsistence use, these products have been shown to be used to supplement cash incomes through their commercialisation, suggesting that they may be prone to increased resource us pressure (Obiri, 1997; Dold and Cocks, 2002; Geldenhuys, 2004). Nonetheless, it is acknowledged that these resources represent a subset of a much wider range of forest products harvested from forests (Shackleton and Shackleton, 2004; Shackleton et al., 2007b). Specifically, it was beyond the scope of this study to investigate the ecological impact of fuelwood collection; hunting of forest fauna; and grazing of livestock in forests, which have been identified by several authors as important anthropogenic pressures on forest ecosystems, requiring further research and management attention (Castley, 1997; Krüger and Lawes, 1997; Obiri, 2002; Berry et al., 2005; Hayward, 2009).

Secondly, this study is limited by the sample size used to assess resource use and concomitant ecological impacts, in terms of the number of forests assessed in each forest type, and plots sampled within each study forest. However, this study approach was chosen as it allowed for a wide range of forest types to be sampled across the Eastern Cape region, thereby providing a regional-scale overview of resource use patterns, while still allowing for variation at the forest-scale to be assessed within the time cont. Furthermore, study forests were selected to be representative of the environmental and socio-economic condtions affecting forests within each study region, such that observed resource use patterns and ecological implications are thought to be representative of those present in other forests within the same forest type. That said, it is acknowledged that forests selected for sampling are

representative of the more limited cohort of forest patches > 100 ha, while the majority of forests in the Eastern Cape are smaller than this (von Maltitz et al. 2003). While sampled forests were larger than average forests in the study region, they were selected as they were likely to be less affected by edge effects, and are thus of high biodiversity value and conservation importance (Berliner 2009; Ehler Smith et al., 2018). Furthermore, given that the study aimed to assess the ecological impacts of resource use specifically, larger forests were selected for sampling so as to reduce confounding factors associated with increased edge effects that affect ecological processes in smaller forest fragments (Kotze and Lawes 2007; Ehler Smith et al., 2018). Thus, while the selection of larger forests was appropriate for the aims of this study, and sheds light on human activities affecting forests of high biodiversity value, it is acknowledged that forest size affects the extent of harvesting and consequent ecological implications, with smaller forests likely to be more prone to over-exploitation (Castley and Kerley 1996; Castely 1997; Berliner 2009). Consequently, results presented by this study should be considered in light of the larger than average forests sampled, and not necessarily representative of the numerous smaller, and more fragemented forests in the study region. However, this is likely to be dependent on the nature of resource use i.e. whether it is for subsistence or commercial use. For example, while subsistence-level impacts may be higher in smaller forests, harvesting operations that aim to supply market-demand may preferably harvest in larger forests, where a higher abundance of target species may be harvested in a single forest.

Lastly, given that this study aimed to asses the ecological implications of resource use, and was thus conducted at the forest-scale, several broader-scale threats to forest biodiversity in the Eastern Cape were not addressed by the study. Specifically, the impact of changing land-use in the forest matrix (particularly conversion of grassland to plantation forestry and concomitant increases in forest fragmentation, isolation, and impacts on hydrological cycles, changing fire regimes, and climate

change are pressing broader-scale threats that require urgent research attention to inform forest conservation.

7.4 Key findings

7.4.1 Resource use

- Regionally, harvest rates were low to moderate, however resource use patterns where site-specific, highlighting the importance of assessing and managing resource use at the forest-scale

- Harvesting of poles, timber and medicinal bark was species-specific, highlighting the need to consider the ecology of target species when developing sustainable use practices

- Destructive and unsustainable bark harvesting was prevalent and widespread indicating the degree to which this product has been commercialised, and the *de facto* open-access system governing resource use in state-managed forests in the Eastern Cape. Regionally, close to a third of bark-harvested trees were dead with *Ocotea bullata, Protorhus longifolia, Rapanea melanophloeos, Cassipourea gummiflua* and *Curtisia dentata* under high resource-use pressure

- Relatively high levels of contemporary timber harvesting were observed in the Pondoland scarp forest assessed, largely driven by an informal trade network transporting locally harvested *Millettia grandis* timber to Lesotho. The presence of unregulated, commercial-scale timber harvesting in this nationally threatened, highly biodiverse forest type is of conservation concern

- The nature and extent of pole harvesting suggests that this resource use is of least concern, and likely to be sustainable because: i) harvest rates were generally low (< 10% of pole-sized stems harvested), ii) the ecology of the two most commonly harvested species recorded in montane and coastal forests, namely *Trichocladus ellipticus* and *Englerophytum natalense* respectively, allow for their sustainable use, and iii) majority of pole-sized stumps recorded were old, indicating that demand for poles is declining. However, high-demand canopy species, especially those that are naturally scarce, are prone to over-exploitation

- The spatial distribution of harvesting was affected by elevation in a montane forest, with more accessible, lower elevation areas prone to multi-use harvesting (i.e. pole and bark harvesting), while less accessible, high elevation areas were harvested for bark only

7.4.2 Effects of resource use on forest habitat structure

- Resource use resulted in significant modifications to ground-, understory- and canopy-layer habitat features within forests, however the severity of habitat change was dependent on the nature and extent of harvesting

- Timber and bark harvesting resulted in canopy gaps, while pole harvesting reduced sapling and tree density, creating understory gaps

- Overall, harvest activities increased the frequency of canopy disturbances, increased ground- and understory-layer foliage density and decreased leaf litter cover

- Bark harvesting resulted in increased dead wood availability in the form of standing dead trees and grounded coarse woody debris

- Where different harvest activities occurred together, they acted synergistically to modify habitat structure. Specifically, co-occurring timber and pole harvesting reduced heterogeneity of the vertical forest profile, while co-occurring high rates of pole and bark harvesting reduced understory foliage density, but increased canopy-layer foliage density

- The variable spatial distribution of different harvest activities along the elevation gradient of a montane forest resulted in increased forest-scale habitat heterogeneity. Specifically, habitat modifications due to spatially overlapping pole and bark harvesting results in greater habitat heterogeneity at lower elevations compared to higher elevations, where only bark harvesting occurred

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- Timber harvesting in a coastal forest increased the proportion of forest under gap conditions, and increased forest-scale habitat heterogeneity by creating habitat conditions distinct from intact forest conditions and natural canopy gaps.

7.4.3 Effects of resource use on forest bird communities

- Variation in resource use patterns, in addition to natural variation in forest structure, affected the structure of forest bird communities at the regional-scale, mediated by species' functional traits

- Resource use did not affect functional richness, i.e. bird communities exposed to harvesting maintained a diversity of functional traits similar to that of communities in undisturbed habitats

- Harvest activities negatively affected two measures of functional diversity (i.e. functional evenness and functional dispersion), indicating that functional processes were negatively affected by resource use

- Species' sensitivity to harvest disturbances was mediated by functional traits relating to their feeding ecology (i.e. primary diet and foraging strategy), with more traits hindered than helped

- Species' level of habitat specialisation affected their response to harvest-mediated habitat modification: forest-generalist species richness and beta-diversity were positively affected, while forest-specialist species richness was negatively affected, and beta-diversity attributed to species turnover positively affected. These findings suggest that habitat modification created increased opportunities for habitat generalist species but increased competition for forest-specialist species

- Species composition was affected by selective timber harvesting, related to changes in habitat structure and food availability associated with canopy-gap formation.

7.5 Discussion of key findings

The extent to which harvest activities affect the ecological integrity of indigenous forests can be assessed based on the ability of harvested habitats to support a community of organisms with a similar functional organisation and species composition to that found in un-harvested habitats (Rempel et al., 2016). Thus, central to understanding whether current resource use is ecologically sustainable is the

question: do areas affected by resource use support similar levels of bird communities and functional diversity as un-harvested areas? The lack of a negative response by overall species richness and functional richness to harvest activities (Chapter 4) indicates that harvested habitats maintain a diversity of species and functional traits similar to that of un-harvested habitats. But the decline in two metrics of functional diversity, and certain feeding traits in response to harvest activities (Chapter 4), declines in forest-specialist species richness, changes in patterns of beta-diversity (Chapter 5), and changes in taxonomic species composition in response to harvest-mediated habitat modification (Chapter 5 and 6), indicate that harvested habitats do not maintain the composition and functional organisation of un-harvested habitats. These findings suggest that resource use negatively affects the ecological integrity of forests in the Eastern Cape. However, these negative responses were shown to be dependent on the extent of resource use, or habitat modification. These findings thus indicate that harvesting of forest products from indigenous forests in the Eastern Cape can be sustainable, but that better resource use management is urgently required to mitigate negative biodiversity effects that arise at high levels of extraction.

The critical question is: how do we ensure that resource use is sustainably managed? Ecologically, to answer this question we need to understand when harvest impacts on biodiversity are acceptable in the context of the overall system, and when they are detrimental to ecosystem resilience and functioning (Geldenhuys, 2011). Essentially, when do harvest regimes compromise the conservation of forest biodiversity, and what management actions would mitigate these adverse ecological effects? Findings of this study show that negative impacts arise as harvest intensities increase, indicating that biodiversity is compromised when harvest levels exceed a certain level of extraction. Following on from this, the severity of harvest impacts on biodiversity at the forest-scale would be determined by the proportion of forest exposed to levels of harvesting beyond this threshold level: if high rates of harvesting are present across the forest, then negative impacts on biodiversity are likely to be severe,

whereas if high levels of harvesting are infrequent and limited to a small portion of the forest, biodiversity impacts are likely to be less severe. Thus, while beyond the scope of this study to determine explicit harvest levels beyond which biodiversity is compromised, findings indicate that:

- High levels of unsustainable bark harvesting practices that result in tree death were widespread at the forest-scale, as observed in four of the six sampled forests, such that negative biodiversity responses to bark harvesting (i.e. declines in functional dispersion, understory hawkers, granivores and forest-specialist species richness) are likely to pose a serious threat to forest ecosystem resilience and functioning. Management is thus urgently needed to limit the number of trees affected by unsustainable bark harvesting methods i.e. ring-barking of canopy trees arising from bark harvesting activities, specifically of *Ocotea bullata, Protorhus longifolia, Rapanea melanophloeos, Cassipourea gummiflua* and *Curtisia dentata*

- While timber harvest rates recorded in the Pondoland scarp and Transkei coastal forests sampled were moderate (a mean of 7% of canopy trees harvested per plot), harvesting was largely driven by market-demand, and is thus unlikely to decline, particularly in the Pondoland scarp forest. Timber harvesting in coastal forests is thus a threat to biodiversity, as increasing species-specific harvesting would mean larger portions of the forest are affected by increasing rates of extraction, such that negative biodiversity responses to timber harvesting (i.e. declines in functional evenness, terrestrial-probing species, understory gleaners, omnivores, and beta-diversity) would pose an increasing threat to ecosystem functioning and resilience in these highly biodiverse forests. Timber harvesting activities, particularly where commercialised, thus requires management attention

- While pole harvesting was shown to negatively affect measures of biodiversity (i.e. functional dispersion, canopy-gleaners and frugivores) at high rates of extraction, this activity was largely limited to the more accessible areas of the forest, and harvest levels were generally low to moderate across sampled forests (mean of 0 – 14%), with rates of harvest beyond 20% of the available pole-sized stems rarely recorded. Consequently, the portion of forest exposed to harvest

rates at a threshold level beyond which biodiversity is negatively affected is likely to be limited, such that pole harvesting impacts on biodiversity are likely to be acceptable, and of least conservation concern

Another fundamental aspect when addressing questions of resource use sustainability is the understanding that disturbance is a natural component of forest ecosystems, under which forest species have adapted, such that the total biodiversity of a forest depends on the maintenance of different natural disturbance-recovery processes (Geldenhuys, 2011). Consequently, the extent to which harvest activities emulate the main natural disturbance regimes in a forest is a vital factor determining the likely ecological implications of this human disturbance (Seymour et al., 2002; Long, 2009; Geldenhuys, 2011). Ecologically-informed resource use guidelines thus need to be based on an understanding of the main natural disturbance-recovery processes that shape each forest, and how different harvest activities relate to these.

Disturbance regimes comprise the frequency of recurrence, area of impact, and intensity of change caused by a disturbance (Geldenhuys, 2011). In temperate forests of the Eastern Cape, canopy gap formation is a key natural disturbance, with forest species representing different adaptations to the frequency, size and seasonality of natural canopy gap disturbances. Findings of this study show that although resource use, specifically selective timber and bark harvesting, result in canopy gaps, thereby simulating this important natural disturbance, it alters the frequency of disturbance, and area of forest affected by canopy gaps. Consequently, while the nature of timber and bark harvesting methods, i.e. single-tree selection that results in canopy gaps, emulates an important natural disturbance process, the increased frequency of disturbance represents a departure from the natural disturbance regime. Importantly, findings of this study show this to have negative impacts on forest ecosystem functioning and bird communities. Specifically, high levels of timber and bark harvesting were associated with declines in functional evenness, functional dispersion, terrestrial probing species, understory gleaners, understory hawkers and granivores (Chapter 4). Furthermore, canopy gaps caused by timber

harvesting had lower beta-diversity compared to intact forest habitats, and lower abundance of ground-dwelling forest-specialist species (Chapter 6), while habitat modification associated with bark harvesting negatively affected forest-specialist species richness (Chapter 5).

The loss of forest specialist bird species in response to harvest-mediated habitat disturbances is particularly concerning. This is because these species have life-history traits that represent an adaptive response to natural forest disturbances, and are thus an important component of maintaining ecological memory, which is central to how ecosystems respond to disturbance (Johnstone et al., 2016). Consequently, disturbances which support or maintain forest specialists enhance ecological resilience and allow for ecosystem recovery, while disturbances that results in a loss of forest specialists, and thus ecological memory, compromise ecosystem resilience, and the system's ability to recover to its natural state following disturbance. Similarly, local extinctions of high-demand tree species for timber and bark as shown by previous studies (Dold and Cocks, 2002; Obiri et al., 2002; Williams et al., 2013), represent a similar loss of ecological memory and potential negative implications for forest ecosystem resilience. These findings emphasis that management actions aimed at regulating the number of trees affected by bark and timber harvesting, and thus the number of canopy gap disturbances, are urgently needed, particularly in the context of these forest products being increasingly commercialised, and thus unlikely to decline in demand.

While this study contributes to our current understanding of the ecological implications of resource use at the forest-scale, it is important to consider how this might translate to impacts at broader scales, given that sampled forests do not exist in isolation from surrounding forests. Specifically, previous studies have detected high bird movement activity across forest fragements in South Africa, with frugivorous and nectivorous birds, forest-specialists, and large-bodied species showing the highest movement abilities (Neushultz et al., 2013). These movement patterns are, in turn, important in maintaining ecological processes within fragemented forest habitats, such as seed dispersal and

pollination. The findings of this study, indicating that frugivorous species (Chapter 4) and forest-specialists (Chapter 5) may be sensitive to harvest-mediated disturbances at the forest-scale, thus suggest that variablility in habitat quality across forests at the landscape-level may give rise to source-sink dynamics (Dias, 1996), wherein less harvested forests (i.e. higher habitat quality) act as source populations from which mobile bird species disperse into more harvested forests (i.e. low habitat quality). This has important implications for forest conservation measures, as it suggests that the persistence of forest bird populations requires strategic identifitication of prioirity forests within each forest type that need effective protection from harvesting activities.

7.6 Towards a future of sustainable forest resource use in the Eastern Cape

A fundamental finding of this study, as shown by previous studies, is that current management of indigenous forests in the Eastern Cape is lacking, and in many cases, absent (Castley and Kerley, 1996; Obiri et al., 2002; Obiri and Lawes, 2002; Hoppe-Speer et al., 2015). Consequently, there are very few data available regarding resource use patterns and forest conditions (e.g. species composition, structure, disturbance regimes etc.) in state forests across the Eastern Cape. There is thus urgent need for better monitoring and evaluation of state forests in the province, particularly where resource use is likely to be high, i.e. in forests closely associated with local communities, or highly accessible by road. Such activities would provide data essential to the development of sustainable management actions, given that these need to be guided by knowledge of: i) resource use patterns (i.e. target species, harvest methods, harvest rates and availability, and spatial distribution of harvesting); and ii) how these relate to the main natural disturbance-recovery processes, at the forest-scale. Forest inventories are thus an important first step in developing sustainable resource use practices (Geldenhuys, 2011) and entail: i) classifying the forest community and calculating importance values of species, ii) calculating the grain of the forest type to understand the spatial scale of forest dynamics i.e. main disturbance-recovery processes, and iii) calculate stem diameter distributions for important target species over different communities to determine their regeneration requirements or

constraints, and resource status. Grain analysis and stem diameter distributions (SDDs) can then be used to guide management actions that are ecologically-informed, i.e. in line with the natural processes that drive the forest dynamics, and resource use demands. For example, fine-grained forests with inverse J-shaped SDDs for dominant canopy species indicate that these species are adapted to small gaps (i.e. shade tolerant), such that regeneration occurs regularly under the forest canopy. Harvest activities should thus create small gaps through single-tree selection system to maintain natural forest regeneration. On the other hand, coarse-grained forests with bell-shaped SDDs for dominant canopy species indicate that the system is adapted to large gaps or disturbed conditions (i.e. light-demanding). In this case, large gaps created by group-felling systems would promote regeneration of canopy species. These assessments need to occur at the forest-scale so that appropriate management action are implemented.

Forest inventories thus provide a wealth of information that allow for the condition of forests to be assessed, and sustainable resource use practices to be developed. Moreover, the methods and equipment required to conduct such inventories are not highly-technical or expensive, respectively, and have been clearly outlined in a sustainable resource use guideline developed for use by the state (DWAF, 2005). Consequently, an important management recommendation is that the newly-formed Department of Environment, Forestry and Fisheries (DEFF) develop and implement a regional-scale strategy to conduct forest inventories in state forests across the province, as an important step towards developing indigenous forests for sustainable management, as outlined by the National Forest Act (1998). Priority forests should be identified as those of high biodiversity value, low protection status and high resource use pressure (i.e. those that are close to communities and access roads).

Beyond providing vital ecological data needed to develop sustainable resource use practices for indigenous forests, a regional-scale strategy of forest inventorying would also provide the opportunity

to develop working relationships, and promote information-sharing between key stakeholder groups, namely departmental forest managers and resources users. This is potentially of huge value given that Participatory Forest Management (PFM) has been adopted by the state as the key process to drive indigenous forest management (National Forest Act, 1998). By definition, PFM aims to integrate planning, research, and decision-making into a comprehensive system with the combined participation of the state and local communities (Slocombe, 1993; Neil, 2000; Wily et al., 2000; Bass, 2001). Thus, while this approach is supported by legal frameworks and, has been positively perceived by resource users (Obiri and Lawes, 2002; Robertson and Lawes, 2005), few examples of successful PFM implementation exist in South Africa given the multiple difficulties involved in reconciling conservation and community needs (Hackel, 1998). By designing inventory operations such that they are conducted by small teams comprised of forest officials and local community members, particularly those involved in resource use, this activity would provide an important first step towards developing functional PFM systems. Specifically, forest inventories could provide a platform for these different stakeholder groups to work together in forest environments towards a common, structured goal, while providing space for different knowledge systems, concerns and attitudes to be discussed. This could offer an important opportunity to lay a foundation of social cohesion upon which future participatory decision-making and policy implementation could be more easily achieved. Furthermore, this opportunity would enable capacity-building for both young foresters and local community members, wherein knowledge and skills required for on-going forest monitoring could be developed.

Given that the state does not have the capacity to ensure the integrity of forest resources into the future without the cooperation of forest users, PFM represents a crucial option in developing forests that are able to supply resource use needs into the future and conserve forest biodiversity. Regional-scale forest inventories, jointly conducted by government personnel and local resource users, would

provide vital data for the development of locally-relevant, ecologically-informed management strategies, and contribute to the development of social cohesion needed between major stakeholder groups for successful PFM implementation.

7.7 Concluding remarks

Findings of this study contribute to the body of knowledge regarding ecological impacts of resource use from indigenous forests. Specifically, results showed that unregulated resource use may negatively affects functional diversity of the bird community, and species richness of forest-specialists birds, as well as change forest bird community composition. These findings are thus in agreement with previous studies which have shown that a lack of effective resource use management current poses a threat to the ecological integrity of indigenous forests in the Eastern Cape (Du Plessis, 1995; Obiri et al., 2002; Geldenhuys, 2004; Berry et al., 2005; Hoppe-Speer et al., 2015).

Over the past 30 years, multiple calls for better forest management have been made by forest ecologists and practitioners in South Africa. From as early as 1992, when Cooper and Swart observed that "there is [also] virtually no professional management of the indigenous forest resource", to Castley and Kerley (1996) who suggested that "a major conservation initiative is needed to maintain South African forest biodiversity", and more recently, with Obiri et al. (2002), stating that "the survival of [coastal Pondoland forests] depends on the establishment of suitable integrated community-based institutions and management practices". Despite a legal framework that recognises the socio-economic and ecological value of forests, and aims to sustain both of these into the future; knowledge gained over the past 30 years regarding resource use patterns and ecological impacts at multiple levels; and the development of guidelines aimed at enhancing sustainable use in the Eastern Cape, *de facto* open-access systems of resource use prevail in the region. Consequently, multiple calls for better management of South Africa's indigenous forests have been largely unheeded, representing a major concern for both the people and biodiversity reliant on forests in the Eastern Cape. This study thus adds impetus to the call for government to acknowledge and address current institutional

inadequacies and lack of capacity regarding indigenous forest management, as a matter of social, economic, ecological and cultural urgency at the national scale. It is hoped that the newly-formed Department of Environment, Forestry and Fisheries (DEFF) will heed this call and end the era of indigenous forest management neglect in South Africa.

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